

# A monographic review of the Thermosbaenacea (Crustacea: Peracarida)

A study on their morphology, taxonomy, phylogeny and biogeography

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Key words: Crustacea; Thermosbaenacea; morphology; chaetotaxy; taxonomy; phylogeny; biogeography.

In addition to a taxonomic review of the whole order Thermosbaenacea, the general morphology and chaetotaxy are discussed in detail. Due to the results of cuticular staining, and through the study of specimens with SEM techniques also, corrections to earlier interpretations could be made. A chaetotaxic classification, modified after the one of Watling (1989), is presented.

In the taxonomic part 34 species are recognized, belonging to seven genera (one new), four families (one new). The examination of adult material of the type species of *Monodella*, i.e., *Monodella stygicola* Ruffo, 1949, warranted the creation of *Tethysbaena* gen. nov., to comprise all other taxa previously included in *Monodella*. Transferred to *Tethysbaena* are: *M. argentarii* Stella, 1951; *M. halophila* S.L. Karaman, 1953; *M. relictata* Pór, 1962; *M. sanctaecrucis* Stock, 1976; *M. somala* Chelazzi & Messana, 1982; *M. atlantomaroccana* Boutin & Cals, 1985; and *M. scabra* Pretus, 1991. Additionally 15 new species of *Tethysbaena* are described: *Tethysbaena juriaani* spec. nov. (type species of the genus); *T. gaweini* spec. nov.; *T. haitiensis* spec. nov.; *T. juglandis* spec. nov.; *T. lazarei* spec. nov.; *T. tinima* spec. nov.; *T. coqui* spec. nov.; *T. colubrae* spec. nov.; *T. scitula* spec. nov.; *T. calsi* spec. nov.; *T. stocki* spec. nov.; *T. tarsiensis* spec. nov.; *T. vinabayesi* spec. nov.; *T. aiakos* spec. nov.; and *T. siracusae* spec. nov. The genus *Tethysbaena* can be divided into six species-groups. One new family, Tulumellidae, was erected for the species of the genus *Tulumella* Bowman & Iliffe, 1988. A second species of *Limnosbaena* Stock, 1976 (Halosbaenidae) is reported, but remains undescribed due to the severe damage of the single specimen available. A lectotype is designated for *Theosbaena cambodjiana* Cals & Boutin, 1985 (Halosbaenidae). All species are discussed with full reference to former publications, distribution, and habitat.

Via a stepwise approach a hypothesized comprehensive phylogenetic tree is constructed with the PAUP computer program.

In the biogeographic part, it is suggested that the actual distributions of the various thermosbaenacean species are the result of vicariance. The distributions are used in reconstructing origins of old tectonic plate fragments of the Tethys Sea belt, in particular those in the northern Caribbean region.

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## 1. Introduction

### 1.1. Historical review

During an inventory and analytical survey of the natural water resources of Tunisia, Prof. L.G. Seurat collected in April 1923 three specimens of a some 2.5-3 mm long isopod-like creature. These animals inhabited a thermal spring (45-48°C) of the ancient Roman *Aquae Tacapitanae* at El Hamma. Monod (1924a) described these animals as *Thermosbaena mirabilis*, being a new type of Malacostraca intermediary between the Isopoda (+ Tanaidacea) and Mysidacea. He did not exclude that the animals represented a new order. The news of this discovery spread quickly over various biological societies and reports of communications held on this subject were published almost instantly (Monod, 1924a, 1924b; Calman, 1924; Anonymous, 1924a). Besides Seurat, who collected 15 additional specimens on 20 October 1925 (Monod, 1927a, 1927b), two other naturalists, Joseph Omer Cooper and Robin Hill, fascinated by this animal, went to El Hamma to collect specimens (Monod, 1927b; Omer Cooper, 1928a, 1928b). Based on the new material collected by Seurat, Monod created the order Thermosbaenacea, belonging to the Peracarida (Monod, 1927a). The same year (1927) Absolon visited El Hamma at April 16, and published his experiences in 1935.

In the meantime some general works on speleological faunas and zoology appeared reproducing Monod's drawings and descriptions (Spandl, 1926; Chappuis, 1927; Zimmer, 1927). Brues (1932) reports the species as one of the rare life forms known to date inhabiting hot springs.

Shortly after Monod created the order Thermosbaenacea, its taxonomic position became a matter of dispute; Sars (1929) united it with the Bathynellacea in a new group that he called the Anomostraca.

In April and May 1938 Anton Bruun of the Zoologisk Museum at Copenhagen, assisted by Miss Lily Due, visited El Hamma. Despite their combined efforts they collected only two specimens at the main spring (Aïn el Bordj), but they found a second locality, called Aïn Baama, where *Thermosbaena mirabilis* lived. In total 156 specimens were collected at this spot (Bruun, 1940). A short while later Monod published an updated paper about the Thermosbaenacea in Bronn's "Klassen und Ordnungen des Tierreichs" (Monod, 1940).

After World War II and the first years of the restoration, time and money became available to resume research. In 1949 Ruffo reported the discovery of a new species of Thermosbaenacea from the cave l'Abisso di Castromarina (Salentinian peninsula, Italy), which he described as *Monodella stygicola* n. g. n. sp. (Ruffo, 1949a, 1949b). His description was based on four (young) specimens of 1.5 mm only.

In the 27 years elapsed since its discovery, the mysterious *Thermosbaena mirabilis* still had not lost its attraction to zoologists, so David Barker organized a six weeks' expedition in order to study the morphology, reproduction and behaviour of the living animals in the field. He also tried to take back live specimens to England, but he did not succeed. The number of specimens was astonishing: 518 at Aïn el Bordj and 196 at Aïn Sidi Abd el Kadar (Barker, 1959). His expedition received a lot of attention in popular magazines (Anonymous, 1950, 1951; Barker, 1952).

In February 1951 F. Baschieri Salvadori and his team, in a lake of the cave «di

Punti degli Stretti» at Monte Argentario (Toscane, Italy), collected small crustaceans that Emilia Stella (1951a) provisionally identified as a new species of the genus *Monodella* viz., *Monodella argentarii* Stella, 1951. Later she carried out some studies on the behaviour, reproduction, and development of the species (Stella, 1951b, 1953, 1955, 1959) and was the first to publish a photograph of a female with dorsal brood-pouch (Stella, 1951b: fig. 3). In 1954 a stygofaunal list of the Monte Argentario was published by Stella & Baschieri Salvadori.

During his paper presented at the Fourteenth Congress of Zoology at Copenhagen in August 1953 Barker showed a slide depicting an ovigerous female of *Thermosbaena mirabilis* with dorsal broodpouch (Barker, MS (1953), 1956, 1959, 1960, 1962). Here-with it was proven beyond doubt that both *Thermosbaena* and *Monodella* belonged to the same order.

Also in 1953, a third species of *Monodella*, viz. *M. halophila* was described by S.L. Karaman, found in the vicinity of Dubrovnik, Yugoslavia.

With so much attention to the Thermosbaenacea in the fifties it is not surprising that various views were postulated on the position of the order within the Crustacea. An anatomical examination of *Monodella argentarii* carried out by Taramelli (1954) showed "... that the Thermosbaenacea should be placed among the most primitive Crustacea Malacostraca, namely between the Syncarida and the Peracarida: since they have some embryological affinities with the Syncarida, and several anatomical characters common with the Peracarida, especially with the Cumacea". Therefore she created the division Pancarida. This point of view is shared by Siewing (1958), who made an anatomical and histological study of *Thermosbaena mirabilis*, basing himself on the preserved materials collected by Bruun in 1938. Almost at the same time Glaessner (1957) suggested a relation between the Thermosbaenacea and the Stomatopoda. Gordon (1958), to the contrary, expressed as her opinion that the Thermosbaenacea clearly belong to the Peracarida. The title of her discussion of Siewing's paper initiated a lot of poetry written about the Thermosbaenacea, and that circulated among various carcinologists at that time (Holthuis & Ingle, 1989; Wagner, 1989). Gordon is supported by Barker (1959), who extensively discusses all points of view and considers a classification of the Thermosbaenacea outside the Peracarida doubtful. However, it should be noted that quite a number of authors maintained the use of the division Pancarida (Monod, 1960; Botosaneanu & Delamare Deboutteville, 1967; Straškraba, 1967; Zilch, 1975a, 1975b; Dumont, 1978; Pinkster, 1978; Newman, 1981; Sieg, 1981, 1983a). Barker (1959, 1960) was the first to suggest that the members of this group are interstitial animals, whose ancestral habitat was the ancient Tethys Sea.

In the first half of the sixties another two new species of Thermosbaenacea were found. *Monodella relicta* was discovered in a spring along the western shore of the Dead Sea at Hamei Zohar (Pór, 1962, 1963). Later it was found also at En-Nur (Tsur-namal & Pór, 1971). In a study on the stygocarid mandible Gordon (1964) compares this mouthpart with various other groups, among them the Thermosbaenacea. Vandel (1964) published his book on biospeology, including a chapter on Thermosbaenacea, which is updated till 1962. In 1964 Maguire reported the capture of six specimens of a *Monodella* in Ezell's Cave at San Marcos, Texas, which was described later by him (Maguire, 1964, 1965) as *M. texana*. This discovery was the first outside the Mediterranean realm.

Research now concentrated on *Monodella argentarii*, which was subject to a more extensive study on the functional morphology and feeding mechanism (Fryer, 1965). This is the first work that deals (to some extent) with the chaetotaxy of the mouthparts. It was a good year for those interested in the Thermosbaenacea as Rouch (1965) also contributed a paper in which he compares specimens from Greece with specimens of *Monodella argentarii* and *M. halophila*. As he found only "minor" differences he considered them to be conspecific.

Except for a popular paper mentioning Thermosbaenacea (Botosaneanu & Delamare Deboutteville, 1967) and general works on Crustacea (Schmitt, 1965, reprinted 1973; Straškraba, 1967; Hessler, 1969) it took until 1969 before another new species, *Monodella finki* was described (Meštrov & Lattinger-Penko, 1969). The fact that the species was quite different in several characters from other *Monodella* species was explained by the authors as result of the different (limnic) biotope.

From 1972-1975 Rudolf Zilch published some excellent studies on the development of *Thermosbaena mirabilis*, which he had collected during August and September 1969 at El Hamma (Zilch, 1972, 1975a, 1975b). In a paper by Noodt (1974) aspects concerning speciation and adaptation of Crustacea to groundwater biota are discussed, and of course attention is given to the Thermosbaenacea. Further the 1970's can be defined best as a period in which many Thermosbaenacea were discovered, but not described. For instance the first southeast Asian Thermosbaenacean (Boutin, 1971) skipped the attention of most scientists, and it lasted until 1985 that a part of the vials was rediscovered and the specimens described (Cals & Boutin, 1985). In the Caribbean a new genus of Thermosbaenacea was collected at Matanzas, Cuba by the first Cuban-Romanian expedition (Botosaneanu, Decou & Negrea, 1973; Orghidan, 1973), but remained undescribed. In 1975 Orghidan and his group discovered again Thermosbaenacea, but this time on Mallorca (Orghidan, Dumitresco & Georgesco, 1975). It was reported several times since, also from Menorca, (Gourbault & Lescher-Moutoué, 1979, as *Monodella* sp.; Pretus, 1982, as *Monodella* sp., 1989, as *Monodella argentarii*; Cals & Monod, 1988, as *Monodella argentarii* ?; Wagner, 1988, 1990, as *Monodella*), but it lasted 16 years until Pretus (1991) described it as *Monodella scabra*. More, as yet undescribed, species were reported later from Isla de Pinos, Cuba (Orghidan & Nuñez Jimenez, 1977; Orghidan, Negrea & Viña Bayés, 1977; Juberthie, Delamare Deboutteville, Viña Bayés & Aminot, 1977; Decou, 1981); Bouches-du-Rhône, France (Bou, 1975); Andalusia, Spain (Bou, 1975); Sicily, Italy (Caruso & Costa, 1979); the Virgin Islands: Anegada, Virgin Gorda, Tortola, Frenchman's Cay, St. John; Culebra; Puerto Rico; and Haiti (Stock, 1979, 1983a, 1983b, 1986a, 1991a, 1991b; Stock & Longley, 1981).

Despite the many new records of thermosbaenaceans found, only Stock (1976) actually described two new species from the Caribbean, viz. *Monodella sanctaerucis* and *Halosbaena acanthura*, the latter being a marine interstitial representative of a new genus. It was also Stock who recognized the importance of some peculiar characters found in *Monodella finki* Meštrov & Lattinger-Penko, 1969, which he placed in a new genus *Limnosbaena*. He also went deeper into the matter of the relict Tethyan distribution of the group as supposed earlier by Barker (1959, 1960).

The Thermosbaenacea are shortly discussed by Ginet & Decou (1977), but they neglected the occurrence of Thermosbaenacea outside the Mediterranean realm.

That pollution endangers the groundwater biotas also was illustrated by Dumont (1978), who visited the thermal springs of El Hamma on 23 March 1967 and 4 June 1976. He did not capture any specimen of *Thermosbaena mirabilis*, and indicated the chlorination of the water and the shampoo used by bathers as one of the most important causes for the extermination of the population in the basins of the Roman bathing house. Monod captured only a few specimens during his visits in 1968 and 1982 in the deeper part of the water supplying tunnel towards the spring, but not in the bath (Monod & Cals, MS).

In 1980 two new records are published. One was by Stock & Botosaneanu who reported finding Thermosbaenacea on Jamaica, but actually it concerned here Mysidacea (Stock, pers. comm.). The other record was from Somalia by Messana, who later described the species with Chelazzi as *Monodella somala* (Chelazzi & Messana, 1982).

At the time Maguire described *Monodella texana* some characters were not in accordance with what was believed to be "typical" *Monodella*. This was reason for Stock & Longley (1981) to re-examine specimens from the type-locality and some nearby places. They proved that these peculiarities were based on wrong observations, and conclude that the species of *Monodella* are remarkably uniform in morphology.

Gasparo collected some Thermosbaenacea at Comarie, Italy, which are reported without specifying the genus (Gasparo, Minelli & Brandmayr, 1984).

Again the position of the Thermosbaenacea became food for thought. Newman (1983) and Sieg (1983a, 1983b) still treat the Thermosbaenacea as a distinct division Pancarida. Schram (1981) and Watling (1981, 1983) create alternative higher classifications wherein divisions like Peracarida do not exist, while Dahl (1981) considers the Thermosbaenacea true Peracarida, an opinion supported by Monod (1984).

In 1985 two new Thermosbaenacea are quickly published one after another. The first is a new species of *Monodella* from Morocco, *Monodella atlantomaroccana*, of which only a few characters are given along with a figure featuring some details (Boutin & Cals, 1985). The other species belongs to a new genus and the characters of the type species (by monotypy) are the same as for the genus (Cals & Boutin, 1985). This species, *Theosbaena cambodjiana*, is the thermosbaenacean Boutin collected and reported in 1971.

A review of all taxa and records of Thermosbaenacea known to date (including new records) appeared in Stygofauna Mundi (Stock, 1986a). Bowman & Iliffe (1986) extended the distribution of *Halosbaena* to that of an amphi-Atlantic genus with their description of *Halosbaena fortunata* from the Jameos del Agua lava tunnel at Lanzarote, Canary Islands.

Cals (in co-operation with others) in the period between 1986 and 1988 presented several papers on setal arrangement and an evolutionary hypothesis based on the ordering of epidermal structures (Cals & Cals-Usciati, 1986; Cals, 1987; Monod & Cals, 1988; Cals & Monod, 1988).

Within a few months period two papers appeared describing three new species, all belonging to a new genus, *Tulumella*, viz., *T. unidens*, *T. grandis*, *T. bahamensis* (Bowman & Iliffe, 1988; Yager, 1988). The distribution tracks of *Tulumella* were discussed by Holsinger (1989) during the International Congress of Speleology at Budapest.

At the symposium on the Evolution of Cave Animals at Hamburg, Wagner pre-

sented a survey at generic level of all Thermosbaenacea found thus far (including new records), with biogeographical comments (Wagner, 1988, 1990).

A re-examination of the type specimen of *Limnosbaena finki* by Meštrov & Cals (1991) solved some problems about its morphology and taxonomic status. In the same year Cals published, in collaboration with Mrs. Cals and Monod, two other papers (Cals & Cals-Usciaty, 1991; Cals & Monod, 1991) that contributed to our knowledge of the metamery of *Thermosbaena mirabilis*, and the anatomy and outer morphology of *Tulumella grandis*.

Recently the known distribution of the Thermosbaenacea was considerably extended with the discovery of a third species of *Halosbaena* on the Australian continent by Poore & Humphreys (1992).

The morphology and protocephalic origin of the carapace of the Thermosbaenacea and some other malacostracans was the subject of Casanova's contribution at the First European Crustacean Conference held in Paris from 31 August to 4 September 1992 (Casanova, 1993).

Also during the 1980's general works on Crustacea repeatedly discussed or mentioned Thermosbaenacea (e.g., McLaughlin, 1980; Schram, 1981, 1986), and stygofaunal lists recorded Thermosbaenacea (Messana, 1982; Pesce, 1985; Messana & Chelazzi, 1986; Sket, 1986, 1988a, 1988b; Sket et al., 1991).

Thus, the substantial (scattered) new information on thermosbaenaceans since 1986 (cf. Stock, 1986a), definitely warrants the presentation of a comprehensive review of the whole order as contained in the present treatise.

## 1.2. Material

The present study is primarily based on the rich collections in the Instituut voor Systematiek en Populatiebiologie (Zoölogisch Museum), Amsterdam University, Amsterdam. Most of the Caribbean material was collected during the Amsterdam Expeditions to the West Indian Islands, which were carried out by various collaborators of the above said institute, in the past 15 years. Additional material has been collected by Prof. Stock and his students in Yugoslavia, southern Spain, the Balearic Islands, and the Canary Islands; or has been obtained through exchange with other institutes and musea. Of those species not represented in the Zoölogisch Museum, Amsterdam, materials were received on loan. Although most of the material remains preserved in the Zoölogisch Museum, Amsterdam, a set of duplicates of well represented species will be kept at the authors disposal, and a part will be deposited in other institutes. Among them are the Centro Oriental de Biodiversidad y Ecosistemas, Santiago de Cuba (Cuba); Institut za Biologijo, Ljubljana (Slovenia); Museo Nacional de Historia Natural, Santo Domingo (Dominican Republic); Museo Zoologico dell'Università di Firenze (Italy); Muséum National d'Histoire Naturelle, Paris (France); Nationaal Natuurhistorisch Museum, Leiden (The Netherlands); National Museum of Natural History, Smithsonian Institution, Washington D.C. (U.S.A.); Natural History Museum, London (U.K.); Western Australian Museum, Perth (Australia); Zoological Museum, Hebrew University, Jerusalem (Israel); Zoologisk Museum, Copenhagen (Denmark).

In the lists of the material examined several abbreviations are used, their explanations are listed below:

AMEWI	Amsterdam Expeditions to the West Indian Islands
BMNH	Natural History Museum, London, U.K.
COBEC	Centro Oriental de Biodiversidad y Ecosistemas, Santiago de Cuba, Cuba
HUJ	Zoological Museum, Hebrew University, Jerusalem, Israel
MCSNV	Museo Civico di Storia Naturale, Verona, Italy
MF	Museo Zoologico dell'Università di Firenze, Florence, Italy
MP	Muséum National d'Histoire Naturelle, Paris, France
MSD	Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic
RMNH	Nationaal Natuurhistorisch Museum, Leiden, The Netherlands
UEKL	University Edvarda Kardelja, Ljubljana, Slovenia
ULA	Università degli Studi di L'Aquila, L'Aquila, Italy
UPMC	Université Pierre & Marie Curie, Paris, France
UR	Università di Roma «La Sapienza», Rome, Italy
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.
UZC	University of Zagreb, Croatia
WAM	Western Australian Museum, Perth, Australia
ZMA	Instituut voor Systematiek en Populatiebiologie (Zoölogisch Museum), Amsterdam University, Amsterdam, The Netherlands.
ZMC	Zoologisk Museum, University of Copenhagen, Copenhagen, Denmark

### 1.3. Methods

The various parts of the animals were examined with the aid of a compound microscope (LM) and scanning electron microscope (SEM). Materials used for the SEM were made suitable for study by the standard procedure of critical point drying. The materials examined by LM were coloured first by a cuticular staining of Black Chlorazol B solved in lactic acid. The advantage of this staining is that internal tissues can be dissolved completely, leaving the cuticula intact, the latter being stained. The setae are also stained by this method, which simplifies chaetotaxic studies by LM. The construction of the mouthparts could be studied excellently as membranes are less intensely stained than the various sclerites. Also the topography of all appendages in the intact animal could be better examined. Below, a modification of the general procedure of the "Black Chlorazol B cuticular staining" is given. The general procedure is made suitable for Thermosbaenacea by Philippe Cals (Université Pierre & Marie Curie, Paris), modified after the one proposed by Humes & Gooding (1964: 240) for Copepoda:

First of all 0.01 mg Black Chlorazol B powder is solved in 10 ml of distilled water, by shaking for 10-15 minutes. This solution is mixed with 200 ml pure lactic acid and again shaken for 10-15 minutes. Then filtration of this mixture is carried out in order to get the undissolved Black Chlorazol B powder out. Subsequently one gets an approximately 0.05% solution of Black Chlorazol B in lactic acid. Now a small incision is made in the dorsal portion between the first two leg-bearing thoracomeres of the animal, which is next put in a small Petri dish filled with the Black Chlorazol B stain. This dish is put in a stove (or placed on a heater) at a temperature of 50-60°C for a couple of days till a week (depending on the dissolution of internal tissues). When the internal tissues form a jelly this can be washed out mostly by rinsing in water.

The lightly stained cuticula and remnants of tissues (generally the intestine and in males the reproductive tract only) is placed back in the Petri dish, but now some drops of a saturated solution of Black Chlorazol B in distilled water (ca. 5% solution) is added, and again heated for a day or a couple of days. Dissection can take place on a slide with a drop of Black Chlorazol B solution in lactic acid, or glycerine, but in the latter case the material must be transferred into ethyleneglycol first, then put into a mixture of ethyleneglycol with glycerin, and finally dissected in pure glycerin before embedding in the medium of the permanent slides; this all in order to avoid collapsing of the cuticula. After staining one can rinse the animal in butanol also, which intensifies the staining and washes out the remnants of almost all dissolved internal tissues (jelly).

It must be remarked that various modifications can be made to this basic procedure. A temperature increase to maximally 100°C can shorten the procedure to a few hours, but is not recommended for the Thermosbaenacea (notably Monodellidae), as their cuticula is too thin to prevent serious damage to the whole animal. Also, the degree of dehydration plays an important role, because specimens that are preserved in alcohol for a long time are often too much dehydrated to get the tissues completely dissolved. It is my experience that specimens killed in saline water and formaldehyde before preservation in alcohol, have the tissues beautifully dissolved during the staining period. When the specimens are dehydrated already there is a method to get a higher degree of dissolved tissue during staining: one can store the animals for a couple of weeks in pure glycerin, or put them for half an hour to an hour in distilled water at a temperature of 60-80°C.

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*baena cambodjiana* Cals & Boutin, 1985, *Tethysbaena atlantomaroccana* (Boutin & Cals, 1985), and *Tethysbaena argentarii* (Stella, 1951). Also our discussions on the chaetotaxy of Thermosbaenacea were illuminating.

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## 2. General morphology

### 2.1. Introduction

With the description of the various species, the terminology of the appendages has automatically been introduced in the literature on Thermosbaenacea. In time some terms were corrected by later authors, but never a discussion on the whole morphology, with an evaluation of all terms, has been given. Only Fryer (1965) devotes separate chapters to the external structures, but his interest focused on mouthpart morphology only. With the treatment herein of the general external morphology some corrections became inevitable, considering the function of the particular body parts named, or simply because the used staining showed me, by the examination of the position of the various sclerites, that observations by earlier authors were incorrect.

### 2.2. Morphology and terminology

This treatment is based on the representatives of all known genera. Some remarks on reproduction and function are given in case of new observations, or to justify corrections of the terminology. All abbreviations given in parentheses in the text allude to figures 1 and 2.

**Habitus.**— The body is small ( $\leq 5.2$  mm), elongate, and somewhat dorsoventrally flattened. *Thermosbaena* is an exception as the body of this species is in comparison to the members of the other genera rather wide, consequently resembling a flabelliferan isopod in its general shape. The body consists of a carapace, a thorax formed by 8 thoracomeres (th.1-8), a pleon (pln. 1-5 (-6)) and the (pleo)telson (T), all carrying various appendages.

**Antenna 1 (A1).**— The antenna 1 is biramous. It fundamentally consists of a 3-segmented peduncle, which has a triangular protrusion distally in between its outer flagellum (exopodite) and inner flagellum (endopodite). The number of segments in both flagella varies among the genera, and to a lesser degree within each genus. For example *Limnosbaena* has a 4-segmented exopodite and a 3-segmented endopodite (fig. 390), whereas in *Theosbaena* these are 29-segmented and 14-segmented (figs. 462-464), respectively. Males have in general more aesthetascs on the exopodite (1 on each segment) than females.

**Antenna 2 (A2).**— The antenna 2 is uniramous, and consists of 8-11 segments which regularly decrease in size from proximal to distal, making a clear distinction between peduncle and flagellum segments impossible. In the literature the peduncle is thus far considered to cover the first 5 segments, in analogy with some peracaridan outgroups (see also figs. 51, 70, 91, 347, 391, 417 and 465).

**Carapace (car).**— The carapace is an expansion consisting of two pallial layers issued from the dorsal part of the cephalic capsule and the two maxillary metameres. The pallial layer is fused to the thoracic tergum by the maxillipedal metamere and partly with the second thoracomere which is carrying the gnathopods (see also Casanova, 1993). In general the carapace overlaps the first four or five thoracomeres, although in *Halosbaena* it can even cover the sixth or seventh (fig. 416). Remarkably these first four or five thoracomeres covered by the carapace have a distinctly thin-

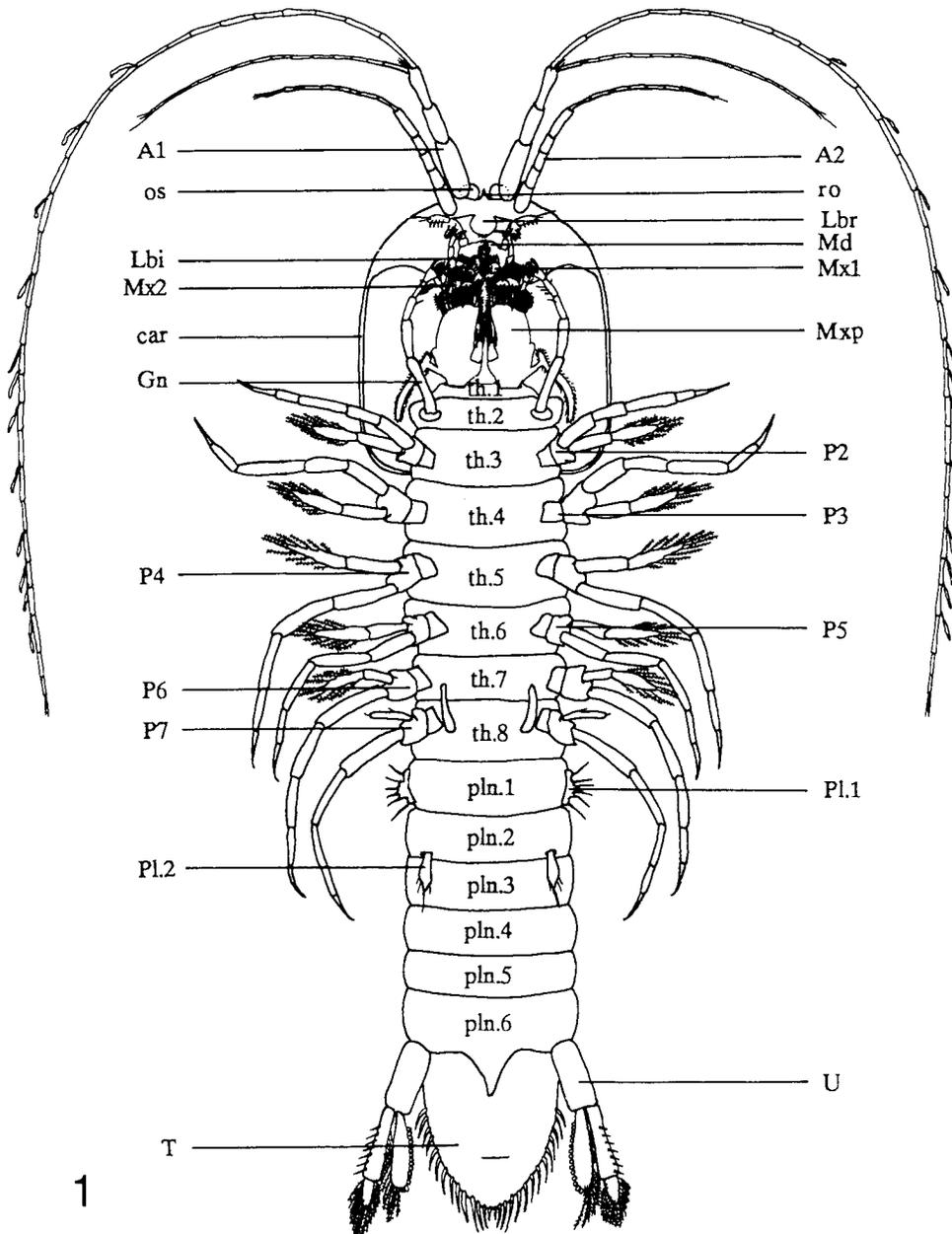


Fig. 1. Ventral view of *Theosbaena cambodjiana* Cals & Boutin, 1985 (modified after Monod & Cals, 1988). For abbreviations see text.

ner cuticula than the other body somites, which may facilitate oxygen uptake through the cuticula. The first thoracomere, carrying the maxillipeds, is ventrally fused with the plastron, thus forming the ventral cephalic skeleton. In front of the carapace a minute rostrum (ro) is visible. In the genera *Halosbaena*, *Limnosbaena*, *Theosbaena*, and *Tulumella* ocular scales (os) are present. In *Thermosbaena* and the Monodellidae, no such structures have been observed, although Siewing (1958: 220, fig. 23) has proven the presence of functional rudimentary eyes in the former. Live specimens of *Tethysbaena juriaani* spec. nov., from the Dominican Republic (Wagner, pers. obs.) showed response to light (escape behaviour), and in the field distinctly more specimens were collected in the dark half of wells than in the other half that was exposed to sunlight. In ovigerous females a dorsal broodpouch (bp) is formed as an extension of the carapace, wherein eggs and juveniles are incubated. There is an infold of the broodpouch laterally, and the arched opening is located at its posterior margin. Internally the broodpouch is connected with the branchial chamber, which gives passage to the respiratory current needed to aerate the eggs.

Mouthparts.— The mouth is surrounded by the labrum, labium, mandibles, maxillae 1 and 2, and the maxillipeds, which are medially connected by the plastron, laterally to the carapace. The general shape of the mouthparts is typically peracaridan, although some reductions and development of parts are unique to the Thermosbaenacea. Fryer's (1965) study describes the morphology and function of the mouthparts very well, and his terminology is generally adopted by me, with the exception of a few corrections as a result of a study on the configuration of the sclerites.

Labrum (Lbr).— The labrum is voluminous and flattened, with on its distal margin many leaf-shaped microsetae (see also figs. 56, 72, 92, 348, 397, 419 and 467). It is a direct extension of the anterior ventral integument of the carapace.

Mandible (Md).— The mandible consists of a corpus mandibulae and a 3-segmented palp. The number and arrangement of setae on the second and third segments of the palp vary among the genera and species. The corpus mandibulae is differentiated into a strong pars incisiva and a pars molaris with a row of setae in between. In the Halosbaenidae and in *Tulumella* the pars molaris is transformed into a more triangular or ensiform way (see for example figs. 350, 393, 423 and 469), unlike in *Thermosbaena* and the Monodellidae, which have robust molars (see for example figs. 52, 75 and 94). The mandibular chaetotaxy varies with the genus. The corpus mandibulae of the left mandible in the Halosbaenidae carries a lacinia mobilis, lacking on the right mandible. *Thermosbaena* has a lacinia mobilis on both mandibles, although the one of the right appendage is distinctly more developed than that on the left. Contrary to what is claimed in the literature, there is only a lacinia mobilis present in the right mandible in the Monodellidae. There is, however, some sort of cleaning seta present on both mandibles, the one of the left mandible being more strongly developed than that on the right mandible.

Labium (Lbi).— The labium is composed of two lobes, which are twice as long as the labrum. The inner margins of the lobes are densely setulose, proximally rounded, followed by a sinus towards the apex, the latter distally with a more or less transverse margin. The outer margins are convex, giving each lobe a rather triangular appearance (see for example fig. 93).

Maxilla 1 (Mx1).— The first maxilla is formed by two endites and a 2- or 3-seg-

mented palp. The most proximal endite has been considered by former authors as a coxopodal endite (Stock, 1976: 50; Chelazzi & Messana, 1982: 166), although Stock (op. cit.) already indicated the possibility of this part being a precoxal endite. The sclerite that forms this endite has one articulation point with the ventral cephalic skeleton, and one with the coxa of the first maxilla, thus representing a precoxal endite rather than a coxal endite. The basipodal endite is somewhat dorsoventrally widened, distally carrying setae (see figs. 49, 77, 101, 346, 395, 424 and 471).

Maxilla 2 (Mx2).— This is the most complex structure of the animal. Formerly the second maxilla was differentiated into a 2-segmented endopodite (palp), a rudimentary exopodite, 2 basipodal endites, and a coxopodal endite. However, after a thorough study of the arrangement of the sclerites this differentiation proved not entirely correct. Actually one can distinguish a large coxal sclerite, followed by a broad but short basal sclerite, both previously believed to form the protopodite and coxopodal endite (Stock, 1976: 60, fig. 45). Stock's (op. cit.), basipodal endites 1 and 2 thereby becoming the second and third basipodal endites, their sclerites arranged in perpendicular position with respect to the first basal sclerite. Also the endopodite occupies a perpendicular position in relation to the latter. Stock's (op. cit.) observation of a lobed exopodite in *Halosbaena* is an artifact, as it is only a part of the (now) third basipodal endite, which has a more or less triangular shape (like a quarter of a circle). When squeezing dissected material under the pressure of a cover glass, Stock's interpretation can be understood. A rudimentary exopodite is only present in *Thermosbaena* and the Monodellidae. A diagrammatic arrangement of the coxal and basal sclerites of this mouthpart is shown in figs. 3-4. For detailed drawings see also figs. 48, 76, 102, 352, 396, 425 and 473.

Maxilliped (Mxp).— The maxilliped of *Thermosbaena* and the Monodellidae is distinctly more complexly built than that of the Halosbaenidae (for example see figs. 54, 68, 96, 399, 426 and 475). In general one can distinguish a 1-segmented coxopodal endite, a basipodal endite, an endopodite, an exopodite, and a very large epipodite. In the Halosbaenidae the endopodite and exopodite (not articulated) are reduced to mere lobes. Meštrov & Lattinger-Penko (1969: 116, fig. 7a) in their description of *Monodella finki* (type species of *Limnosbaena*) mention a 5-segmented endopodite. Basing myself on a re-examination of the type material, and the examination of fresh material from Comaria (northeast Italy) kindly put at my disposal by Prof. B. Sket (Ljubljana, Slovenia), Meštrov & Lattinger-Penko's "endopodite" proved to be the first leg (see also Meštrov & Cals, 1991: 47). The presence of a large 5-segmented endopodite thus is a character restricted to the males of *Tethysbaena* gen. nov. only. In females of the Monodellidae this structure is reduced to a small rounded lobe with a fine seta. I agree with Fryer (1965: 70) that the endopodite presumably functions as a clasper, and that it plays a role in sexual interactions. Contrary to Stock's opinion (1976: 53) the endopodite segments represent the ischium, merus, carpus, propodus and dactylus, respectively.

Gnathopod (Gn).— Though the literature in general does not speak of a gnathopod, this first pair of legs resembles in position and morphology a gnathopod rather than a pereopod. Only Fryer (1965: 73) suggest that it has a gripping function. Living specimens of *Tethysbaena juriaani* spec. nov. (Wagner, pers. obs.), constantly kept their first leg in front of the mouth, only moving them (grasping) when coming

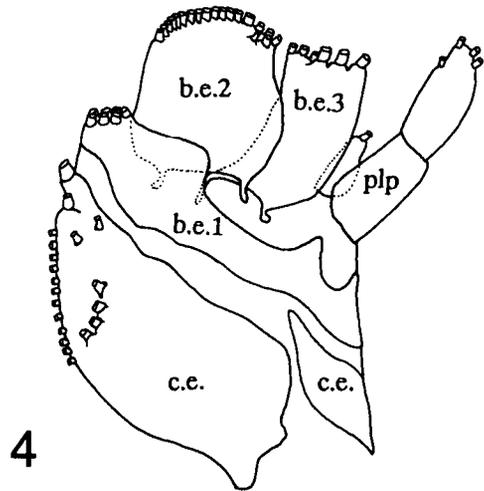
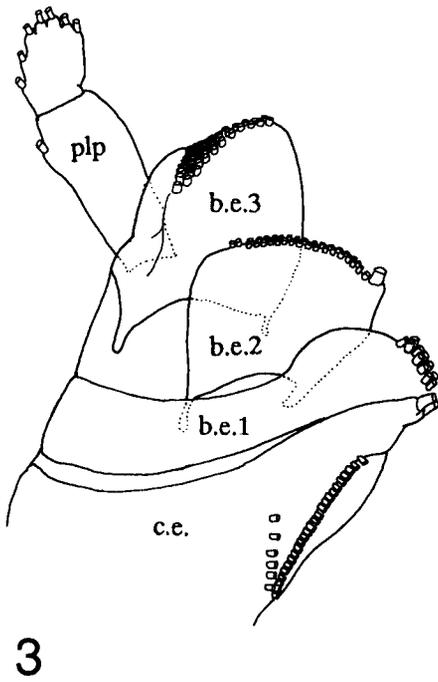
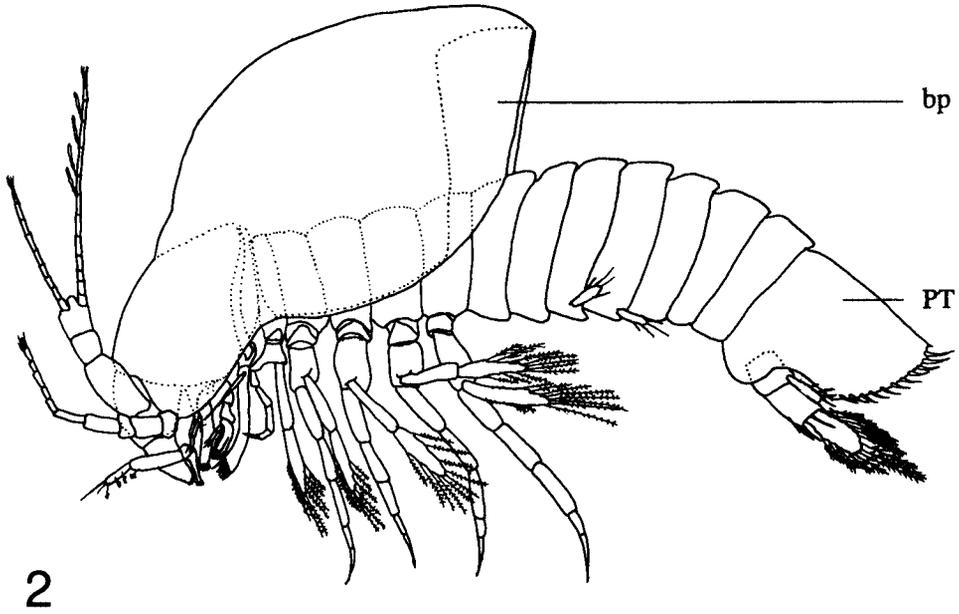
across a piece of vegetable detritus. The "unguis" in the Halosbaenidae (figs. 400, 428 and 472) has a more or less claw-like shape, which also counts in favour of recognizing this pair of legs as true gnathopods. Meštrov & Lattinger-Penko (1969: 118, fig. 11) incorrectly describe the second leg as the gnathopod. The gnathopod was figured by them representing the endopodite of the maxilliped. The segmentation of the gnathopod counts as follows: basis, ischium (or basi-ischium), merus, carpus, propodus, dactylus, and unguis, and thus is different from the pereopods as is shown below. The gnathopods of *Halosbaena*, *Limnosbaena*, and *Theosbaena* are uniramous, characterized by the absence of an exopodite, while those of *Thermosbaena* (fig. 58), *Monodella* (fig. 78) and *Tethysbaena* (fig. 103), new genus, and *Tulumella* (fig. 354) are biramous (exopodite present).

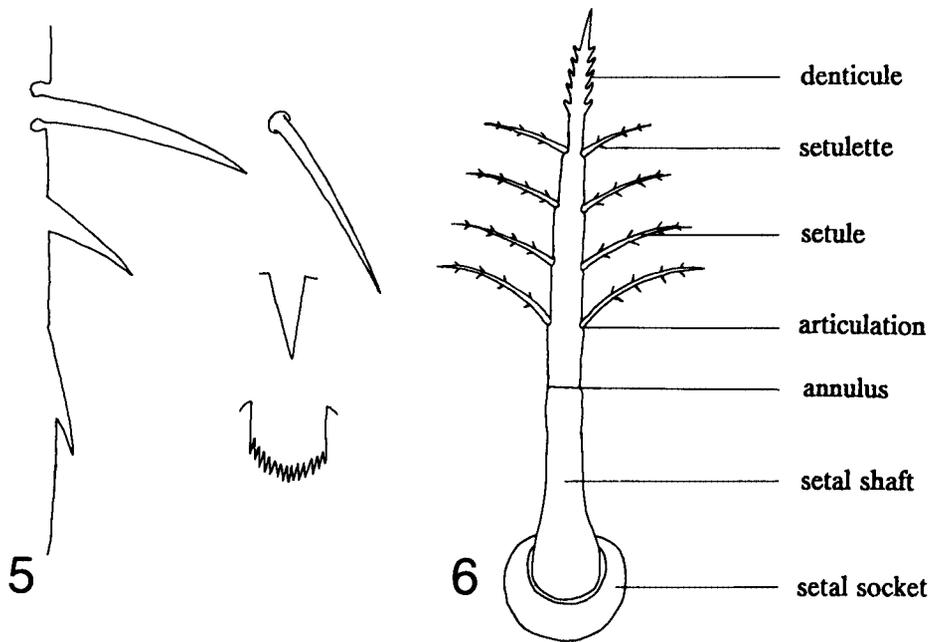
Pereopods 2 to 7 (P2-P7).— Except for *Thermosbaena* (which develops only P2-P5), the other genera have 6 pairs of pereopods (P2-P7). The pereopods are in general biramous, having an endopodite and an exopodite, with the exception of P7 in *Limnosbaena* (fig. 406) where an exopodite is absent. The endopodite consists of a basis, ischio-merus, carpus, propodus, dactylus, and a single "unguis". The exopodite is 2-segmented, with the exception of the 1-segmented exopodite, in P5 of *Thermosbaena* (fig. 64), P6 and P7 of the Monodellidae (figs. 83-84, 108-109), and P7 of *Theosbaena* (fig. 480). *Tethysbaena argentarii* is essentially a benthic organism, although it is a good swimmer (Fryer, 1965: 52). Specimens of a new species collected and observed in the Dominican Republic were frequently swimming (*T. juriaani* spec. nov.) or essentially benthic (*T. gaweini* spec. nov.) (Wagner, pers. obs.). During swimming P2-P7 make an irregular undulating movement. Fryer (1965: 53) mentions one pair always being out of phase with the others. They swim upside down and were often "hanging" in this position to the water surface in the Petri dish or vial. When "hanging", or "standing" as Fryer (op. cit.) calls it, at the water surface the exopodites of P1 and P2 were still beating with short intervals of rest, probably to maintain a current under the carapace lappets into the branchial chamber where gas exchange takes place. In *Tulumella grandis*, a typically nectic species and the largest-sized taxon known of this group, a precoxal expansion is observed on the basis of P2-P4, assumed to function as a "gill" (Cals & Monod, 1991). SEM examination of *Halosbaena* and the *Tethysbaena* revealed the presence of numerous thin microsetae on those parts of the second to fourth thoracomeres that are covered by the branchial chamber (fig. 38).

Pleonites (pln.1-6).— Following the thoracomeres there are 6 separate pleonites, with the sole exception of the sixth pleonite in *Thermosbaena*, which is fused with the telson, forming a pleotelson (fig. 65). Only the first two pleonites bear pleopods, although those setae on pleonites 3-5 in *Halosbaena* that lie in the extension of the second pleopod in my opinion may represent strongly reduced pleopods 3-5, that have lost their original function (see for example fig. 432).

Pleopod 1 (Pl.1).— In the Halosbaenidae the first pleopod consists of a non-articulating lobed protrusion of the pleonite near its lateral margin, that carries setae (see

Figs. 2-4. 2, lateral view of an ovigerous *Thermosbaena mirabilis* Monod, 1924 (modified after Monod & Cals, unpublished MS). For abbreviations see text. 3, sclerite positions in maxilla 2 of *Theosbaena cambodjiana* Cals & Boutin, 1985. 4, sclerite positions in *Thermosbaena mirabilis* Monod, 1924. Abbreviations: c.e. = sclerite of coxopodal endite; b.e.1. = sclerite of basipodal endite 1; b.e.2. = sclerite of basipodal endite 2; b.e.3. = sclerite of basipodal endite 3; ex. = exopodite; plp. = palp.





Figs. 5-6. Chaetotaxic terminology. 5, diagrammatic representation of seta (top), spiniform process (middle) and scale (below), in side view on left and top view on right (after Watling, 1989). 6, diagrammatic view of a plumidenticulate (type IA3) macroseta illustrating associated terminology.

also figs. 407, 430 and 484). The first pleopod of *Thermosbaena* and of the Monodellidae is 1-segmented, articulate, and carries setae also (see also figs. 61, 85 and 110).

Pleopod 2 (Pl.2).— In all taxa concerned pleopod 2 consists of a 1-segmented articulating appendage carrying setae (see for example figs. 62, 86, 111, 370, 408, 430 and 482-483).

Uropod (U).— In all *Thermosbaenacea* the uropod is biramous, the rami being implanted on a protopodite. The endopodite is 1-segmented, the exopodite 2-segmented. In *Thermosbaena* the endopodite is strongly reduced and perpendicularly implanted in comparison with the other genera (see fig. 66). This suggests that species of *Thermosbaena* are walkers rather than swimmers. The shape and chaetotaxy of the uropod is diagnostic at the genus level (see also figs. 87, 112, 363, 410, 427 and 485). In live specimens of *Tethysbaena juriaani* spec. nov. the uropods are used as a rudder during swimming, and in order to slow down speed it spreads the endo- and exopodite to its maximal extent (Wagner, pers. obs.).

Telson (T) or Pleotelson (PT).— The Halosbaenidae, Tulumellidae, and the Monodellidae have a free telson (see for example figs. 88, 113, 364, 411, 434 and 486). Only *Thermosbaena* (Thermosbaenidae) has the 6<sup>th</sup> pleonite fused with the telson, thus forming a pleotelson (fig. 65). The shape and armature of the (pleo)telson are typical for each genus and to a lesser extent for species(groups). In *Thermosbaena* and some species of the Monodellidae the distal portion is incised. The anus is situated subterminally in all taxa.

### 3. Chaetotaxy

#### 3.1. Introduction

In the past twenty years several systems have been proposed in order to classify crustacean setae. Thomas (1970) was the vanguard of the earliest comprehensive setal classificatory system in lobsters, a system later modified by Farmer (1974) and Factor (1978) based on other lobster species. Fish (1972) provided a system based on the chaetotaxy of the isopod *Eurydice pulchra* Leach, 1815, which was previously studied partially by Sars (1889), Nordenstam (1933), and Jones (1969). Till then setal studies on other isopod groups were not comprehensive. The setal studies of decapod crustaceans by Drach & Jacques (1976, 1977, 1978, 1979, 1980) and Jacques (1981) contributed a great deal to the knowledge of the various types of setae encountered in Crustacea. A summary of their system was recently published by Jacques (1989), and is without any doubt the most complex one. The setae of a decapod larva were examined in detail by Pohle & Telford (1981), which resulted in still another system. For amphipods a system was proposed by Steele & Oshel (1987). In the meantime the studies by Cals (1974), Bocquet et al. (1976) and Cals & Brousse-Gaury (1978) concentrated on the development of cuticular and setal extensions. The results and terminology employed therein was used in the first chaetotaxic study of Thermosbaenacea (Cals & Cals-Usciati, 1986). This chaetotaxic study resulted in three alternatives; (1) mapping on presence (+) or absence (-) of setae, without establishing the category the particular seta represents; (2) the distinction of a typical seta for each genus (or species) (S-seta or strigilla); and (3) other (by all taxa shared) types of setae (A-, E-, I- and U-types). This setal arrangement was used in an attempt to resolve the evolutionary scenario in Thermosbaenacea (Cals, 1987; Monod & Cals, 1988; Cals & Monod, 1988).

Although all these classifications have their advantages, they fall short in the use of the homology principle. The use of chaetotaxic characters based on homologies, will enable one to define better the taxonomic status of an organism, and to use these characters for phylogenetic purposes. Watling (1989), being aware of the restrictions of former classifications, proposed a new classificatory model that is based fundamentally on homologies. Therefore I follow the Watling's classification, and propose some modifications on his model.

This part of my study is based on the examination of all setal types encountered in the 7 genera actually known by means of light microscopy (LM) and by scanning electron microscopy (SEM) studies of various representatives of each family.

#### 3.2. Morphology and terminology

A terminology different from previous chaetotaxic studies is employed. Therefore it is necessary to define clearly what is meant by each term.

In recent years the terms macrotrichs and microtrichs were often used for what is defined here as setae. Microtrichs, however, are originally well defined as an expanded part of a cell (Haffer, 1921; Ulrich, 1924; Weber, 1933; Snodgrass, 1935), and not, as advocated by Broodbakker & Danielopol (1982) and Steele & Oshel (1987), as paucicellular complex structures. Thus the microtrichs are in fact subcellular non-articu-

lating expansions of the setae, called denticules by Watling, and partially identical with what is named scutella in Bocquet et al. (1976) and Monod & Cals (1988). The scutella (Bocquet et al., 1976) is defined as a subcellular expansion of both setal and cuticular cells (= scute sensu Cals, 1974). Herein it is suggested to drop the confusing term microtrich, and define the non-articulating subcellular expansions of the setae as denticules, and to restrict the name scutella to the non-articulating subcellular cuticular expansions.

Also a clear distinction must be made between the (multicellular) macrosetae and (unicellular) microsetae (Drach & Jacques, 1979). The term megaseta (Cals & Cals-Usciati 1986) is synonymous with macroseta. The term spine(s) is often employed for the articulating thick-walled seta(e) (sensu Fish, 1972) by most authors in carcinology. In fact, this definition of the term does not distinguish spines from macrosetae, and is in this form considered synonymous with macrosetae. Unicellular "hair-like structures" can be present on the setae as setules (sensu Watling, 1989), but can also arise from the cuticula directly (type IV sensu Watling, 1989). For the former group the name setules is maintained, while latter group will be referred to as microsetae. The confusing term macrotrich (Comstock, 1920) originally is defined as a unicellular seta. In order to avoid future confusion it is suggested to drop this term also in favour of the term microseta. The term setulettes (sensu Pohle & Telford, 1981) is used for the subcellular expansions of the setules and the scutellae.

Next to the macrosetae and microsetae two other cuticular structures can be developed, e.g. spiniform processes and scales. The term spiniform process is proposed here to replace the confusing term spine sensu Comstock (1920) and Watling (1989), which is defined and employed by them in a quite different manner than customary in carcinology. So the definition of spiniform processes as non-articulating cuticular extensions of which the base is generally not as wide as the length of the structure is adopted here from the one defining the spine sensu Comstock (1920) and Watling (1989). The scale is defined as a non-articulate cuticular extension of which the base is generally very wide relative to its length (Watling, 1989). A scale can be either unicellular or multicellular.

The external morphology of the main setal groups, viz. macrosetae, microsetae, spiniform processes and scales is reproduced in figs. 5-6. Definitions of the various external parts of a macroseta are given below:

*Annulus*: a faint ring circumscribing the shaft, which may be located near the base or well along the shaft.

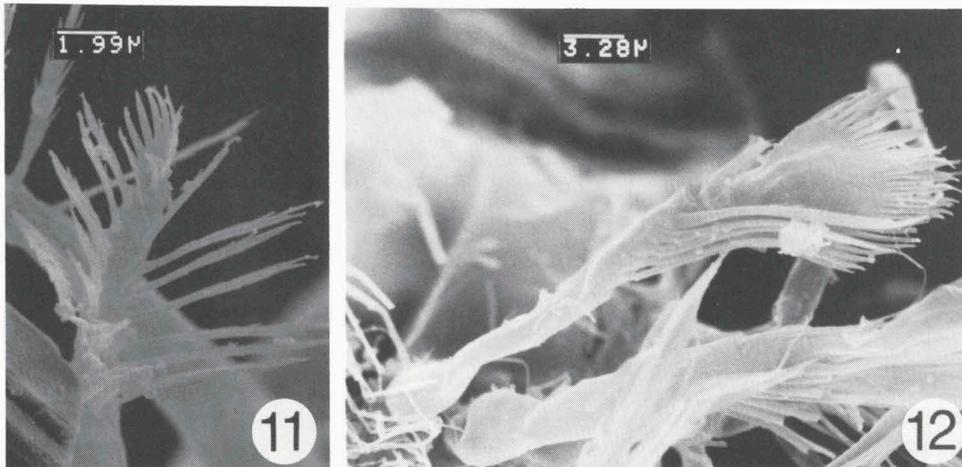
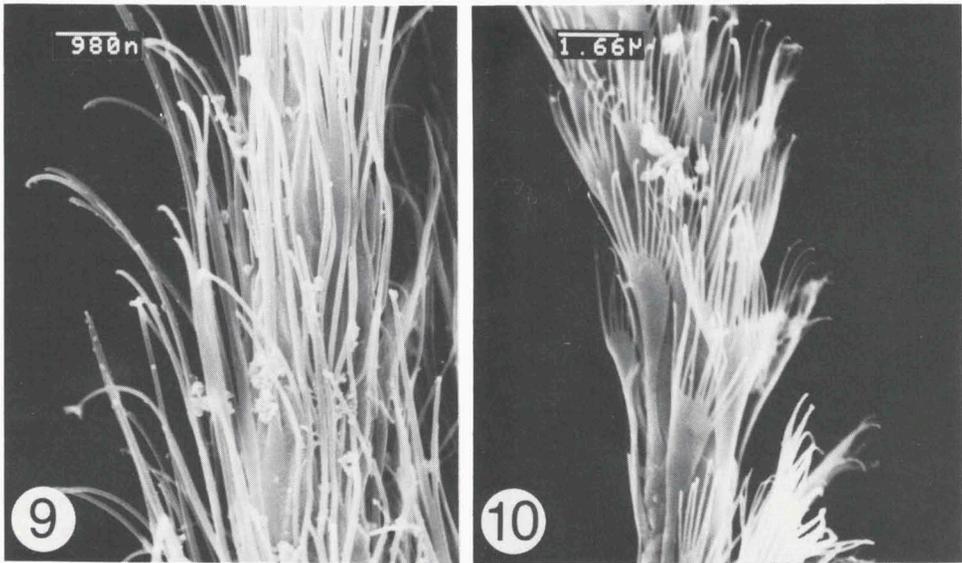
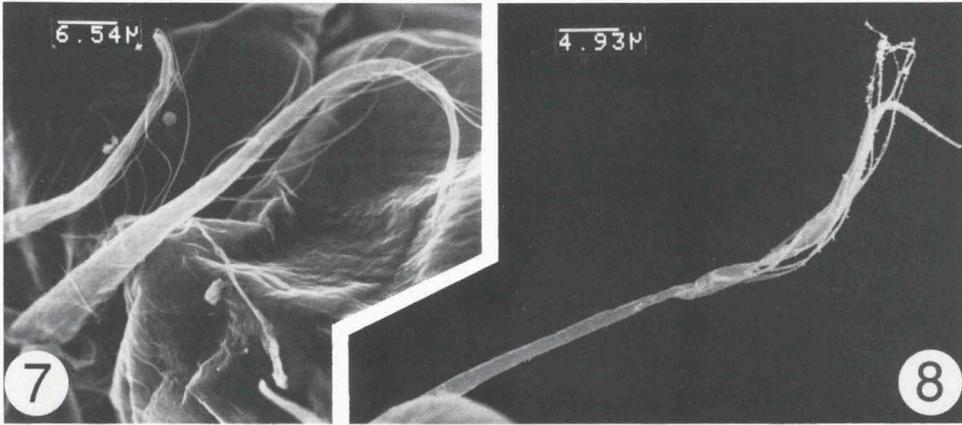
*Denticule*: a non-articulate extension of the shaft of the seta or spiniform process.

*Setule*: an extension of the shaft of a seta, forming an articulate or flexible junction with the shaft.

*Setulette*: a non-articulate extension of the setule.

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Figs. 7-12. Scanning electron micrographs of macrosetae. 7, plumose macroseta (type IA1), peduncle antenna 1 of *Thermosbaena mirabilis*; 8, plumose macroseta (type IA1), distal at dorsal margin propodus of *Tethysbaena juriaani*; 9, detail pappose macroseta (type IA2), coxopodal endite maxilliped of *Thermosbaena mirabilis*; 10, detail pappose macroseta (type IA2), coxopodal endite maxilliped of *Halosbaena acanthura*; 11, plumidenticulate macroseta (type IA3), third segment palp mandibula of *Tethysbaena juriaani*; 12, plumidenticulate macroseta (type IA3), basipodal endite 1 maxilla 2 of *Halosbaena acanthura*. Micrographs by D. Platvoet (figs. 7, 8, 11, 12) and H.P. Wagner (figs. 9, 10).



### 3.3. Chaetotaxic classification

A modified survey of Watling's classification (1989) is presented below, with reference to those setae encountered (or not) in the Thermosbaenacea. The names of setae used in literature on Thermosbaenacea are indicated in parentheses.

#### 3.3.1. Macrosetae

Type I. Annulate, with setules. Mechanoreceptive setae of variable size and shape.

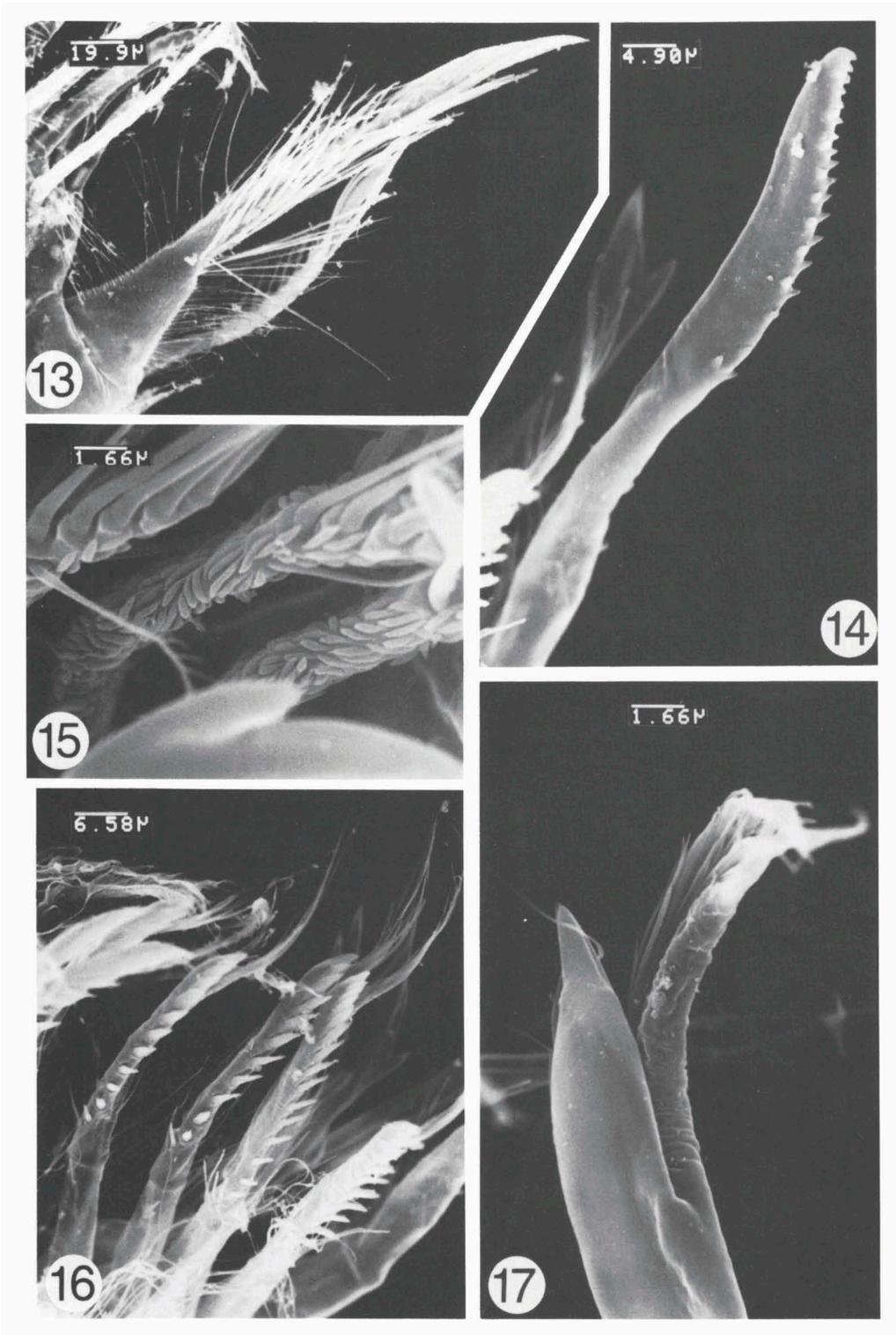
Annules and setules present.

A. Articulation infracuticular. The point of articulation occurs in a sunken socket.

1. Plumose (figs. 7-8). Macrosetae in which the setules rise from the shaft in two opposite rows, thus giving the setae a feather-like shape. A stout form of this type, with the setules arising from the shaft over almost its full length, is present on the inner margin of the antenna 1; slender forms with the setules along the whole shaft are present on the basis of the gnathopod, and with the setules on its distal half only is present on the pereopods in all families. In *Tulumella* this macrosetal type is also present on the exopodite of the maxilla 2 (soie sensorielle, Monod, 1927a; Sinnes Borsten, Monod, 1940; gefiederte Borsten, S.L. Karaman, 1953; gefiederter Stachel, S.L. Karaman, 1953; plumose seta, Stock & Longley, 1981; Chelazzi & Messana, 1982; Yager, 1988).
2. Pappose (figs. 9-10). Macrosetae in which the setules principally rise from the shaft under different angles. This type is only present on the coxopodal endite of the maxilliped in all taxa examined (soie plumeuse, Monod, 1924a; Fiederborsten, Monod, 1940; gefiederte Borsten, S.L. Karaman, 1953; plumose seta, Stock, 1976; Stock & Longley, 1981; Chelazzi & Messana, 1982; Yager, 1988).
3. Plumidenticulate (figs. 11-18). The proximal part of these setae bears setules, while the distal portion is denticulate. This type is well represented on the basal endite of the maxilliped in various forms of all families. It is also present on the basipodal endite 1 of maxilla 2, the precoxal endite of maxilla 1, and on the second and third segment of the mandibular palp (aguillon robuste, Monod, 1924a; épine plumeuse, Monod, 1924a, 1927a; Mestrov & Lattinger-Penko, 1969; Fiederstacheln, Monod, 1940; glatte Stacheln, Monod, 1940; gefiederte Borsten, S.L. Karaman, 1953; spiniform seta, Fryer, 1965; lateral sensory seta, Fryer, 1965; plumose seta, Stock, 1976; Stock & Longley, 1981; Chelazzi & Messana, 1982; Yager, 1988; denticulate spine, Stock, 1976; transformed seta, Stock, 1976; pectinate spine, Stock, 1976; Bowman & Illiffe, 1988; Schram, 1986; ciliated spine, Stock, 1976; Chelazzi & Messana, 1982;

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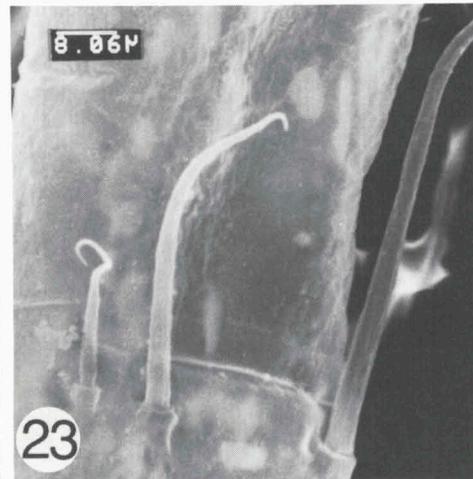
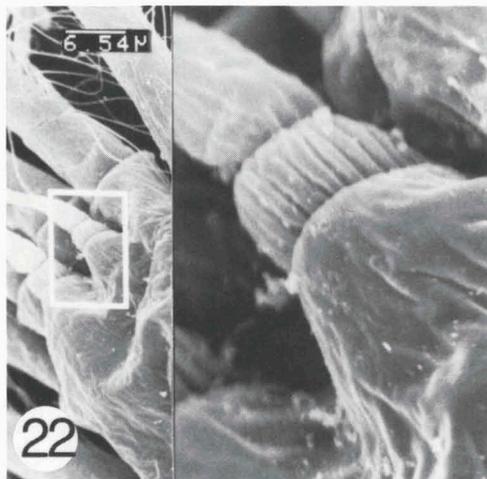
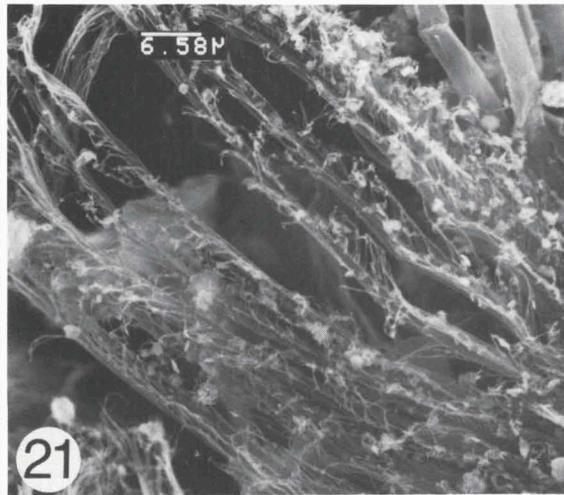
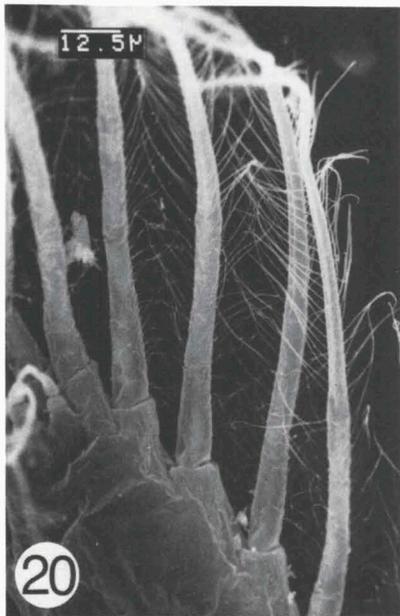
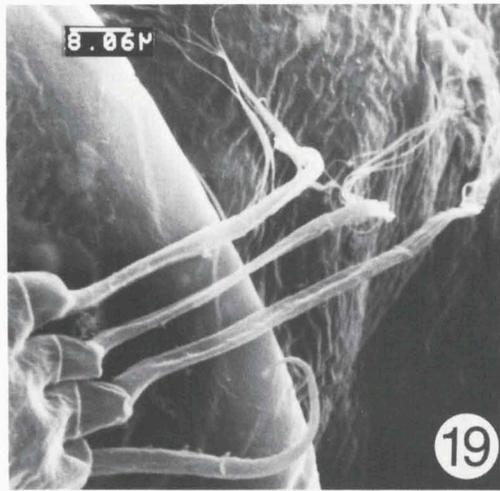
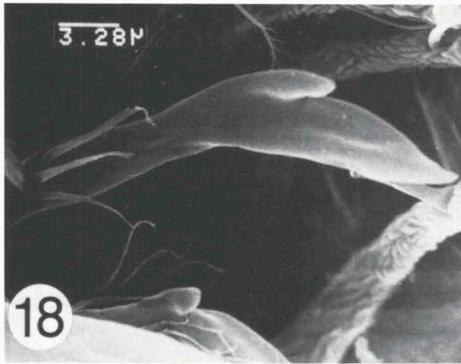
Figs. 13-17. Scanning electron micrographs of macrosetae. 13, plumidenticulate macroseta (type IA3), subapical at inner margin maxilliped of *Tulumella grandis*; 14, plumidenticulate macroseta (type IA3), subapical at inner margin maxilliped of *Halosbaena acanthura*; 15, detail plumidenticulate macroseta (type IA3), central row at distal margin maxilliped of *Halosbaena acanthura*; 16, plumidenticulate macroseta (type IA3), ventral row at distal margin maxilliped of *Halosbaena acanthura*; 17, detail plumidenticulate macroseta (type IA3), tip macroseta of ventral row at distal margin maxilliped of *Halosbaena acanthura*. Micrographs by D. Platvoet (fig. 15) and H.P. Wagner (figs. 13, 14, 16, 17).



- hairy spine, Chelazzi & Messana, 1982; anneaux (A-type), Cals & Cals-Usciatì, 1986; Monod & Cals, 1988; unipennée (U-type), Cals & Cals-Usciatì, 1986; Monod & Cals, 1988; équipennée (E-type), Cals & Cals-Usciatì, 1986; Monod & Cals, 1988; inéquipennée (I-type), Cals & Cals-Usciatì, 1986; Monod & Cals, 1988; soie particulière (S-type), Monod & Cals, 1988).
4. Forked setae. A sharply pointed seta with setules arising opposite of each other just above the annulus. Not observed in Thermosbaenacea.
  5. Acuminate. The seta has a smooth and acuminate outline. Apically fine setules are present, which are only visible under extreme magnification. This seta has been classified by Watling belonging to type IIA1. However, the presence of distal setules, in my opinion justifies classification herein as type IA5. This type has not been observed in Thermosbaenacea.
- B. Articulation supracuticular. The cuticle is flexed outward to form the point of articulation.
1. Plumose (figs. 20-21). The setules rise from the shaft in two opposite rows over almost the whole length of the macroseta, giving the seta its feather-like look. These macrosetae are in general rather stout. Located on the peduncular scale of the antenna 2 in *Tulumella*, and further in Thermosbaenacea in general on the precoxal endopodite of maxilla 1, the coxopodal endite of maxilla 2, exopodites of the maxilliped (when not reduced), exopodites of the gnathopod and pereopods (when present), and on the uropods (soie plumeuse, Monod, 1924a, 1927a; Meštrović Lattinger-Penko, 1969; épine plumeuse, Monod, 1927a; Fiederborsten, Monod, 1940; setole ciliate, Stella, 1951a; setole pennate, Stella, 1951a; gefiederte Borsten, S.L. Karaman, 1953; pushing seta, Fryer, 1965; plumose seta, Stock, 1976; Stock & Longley, 1981; Chelazzi & Messana, 1982; Yager, 1988; feathered seta, Stock, 1976; nearly naked seta, Stock, 1976).
  2. Subplumose (figs. 19, 22). A plumose macroseta that has its basal part proximal of the annulus transformed into a condylar joint, and its distal portion setulose. Located on the peduncular segments of the antenna 1, the first segment of the exopodites of the pereopods 3 to 5, the pleopods, and submarginally on the uropods (tige sensorielle, Monod, 1927a; soie sensitive, Rouch, 1965; plumose seta, Stock, 1976; Chelazzi & Messana, 1982; Yager, 1988).
  3. Setulate (fig. 24). The seta has distally of its obscure annulus one (unisetulate) or two (bisetulate) rows of leaf-shaped setules. The unisetulate form (a) is present on the palp of maxilla 1 in the Thermosbaenidae and the Monodellidae; the bisetulate form (b) is present in the Halosbaenidae. (Aiguillon, Monod, 1927a; unilaterally toothed spine, Stock, 1976; toothed spine, Stock,

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Figs. 18-23. Scanning electron micrographs of macrosetae. 18, plumidenticulate macroseta (type IA3), dorsal row at distal margin maxilliped of *Halosbaena acanthura*; 19, subplumose macroseta (type IB2), peduncle antenna 1 of *Tulumella grandis*; 20, plumose macroseta (type IB1), second segment endopodite uropod of *Thermosbaena mirabilis*; 21, plumose macroseta (type IB1), coxopodal endite maxilliped of *Halosbaena acanthura*; 22, subplumose macroseta (type IB2), second segment endopodite uropod of *Thermosbaena mirabilis*; 23, simple macroseta (type IIA1), exopodite antenna 1 of *Tulumella grandis*. Micrographs by D. Platvoet (figs. 18, 20, 22) and H.P. Wagner (figs. 19, 21, 23).



1976; thorny spine, Chelazzi & Messana, 1982).

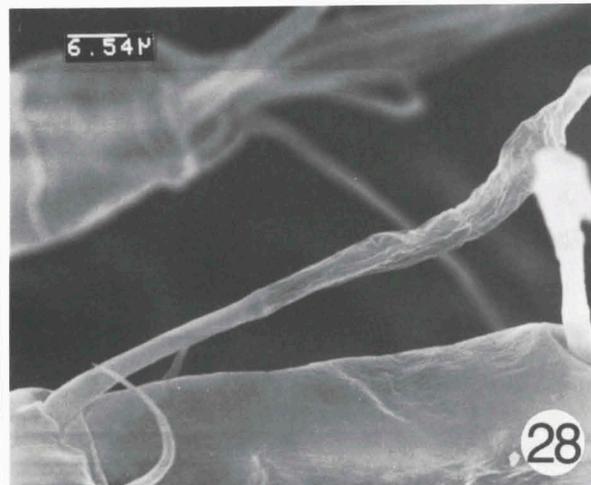
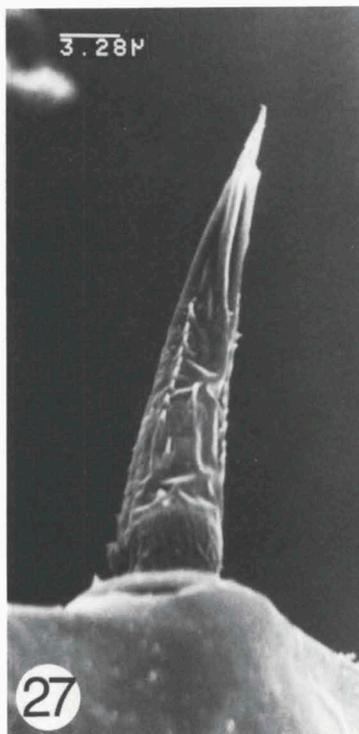
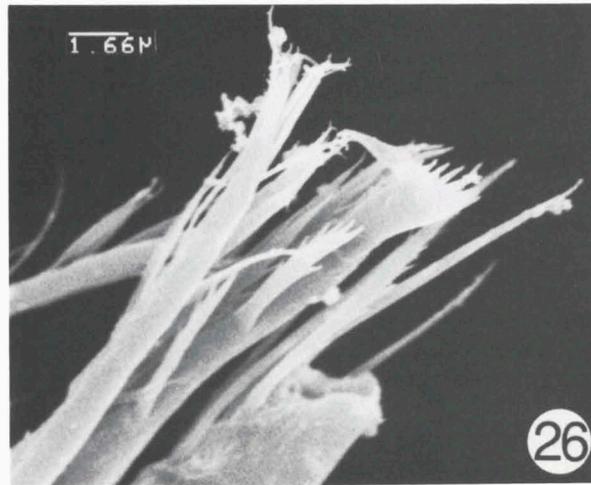
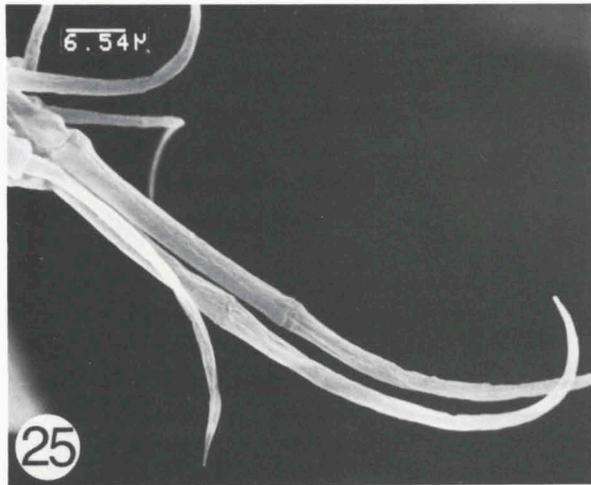
Type II. Annulate, without setules. Chemoreceptive or mechanoreceptive setae of variable length (elongate and stiff, or short and robust). The shaft either smooth or denticulate. Annulus distinctly present.

A. Shaft appearing smooth (obscurely denticulate).

1. Simple (figs. 23, 25). This seta has a smooth and acuminate outline; its apex is pointed and naked. This setal type was classified as type IIA6 by Watling (1989: 25), but it must be remarked that his type IIA1 actually should be type IA5 (see above), and that this basal form of type IIA (type IIA6 sensu Watling, 1989) is re-coded here as type IIA1. This type is found in all Thermosbaenacea on the antennae 1 and 2, the tip of the endopodal palps of maxilla 1, maxilla 2 and the maxilliped, the exopodite of maxilla 2, and the pleonites. Despite Karaman's observation of a "gefiederter Stachel" in both Thermosbaenidae and Monodellidae the distally implanted macroseta of the exopodite of maxilla 2 appears simple (gefiederter Stachel, S.L. Karaman, 1953; naked seta, Stock, 1976; setule, Stock, 1976).
2. Rod (fig. 26). Resembling the simple seta, but its tip is cleft in finger-like lobes. At low magnifications it appears naked and blunt. This type is observed in *Halosbaena*, *Tethysbaena*, and *Monodella* near the medial margin of the coxal endite of maxilla 2, where it also has some scale-like denticules with finger-like lobes at its distal portion (submarginal seta, Fryer, 1965).
3. Cuspidate (fig. 27). Stout, heavily cuticularized, fang-like seta, which has two rows of denticules. The last-named structures are only visible by extreme magnifications. The basal portion is distinctly broader than the distal portion. In the Thermosbaenacea cuspidate macrosetae are only present at the subterminal margin of the first segment of the uropodal exopodite, and the subterminal and lateral margins of the telson (fein beborsteter Stachel, S.L. Karaman, 1953; smooth spine, Stock, 1976).
4. Conate. Shorter in length and more regularly tapering than the cuspidate seta. In contrast to the cuspidate seta the apex is more pointed, the surface smooth. Not observed in Thermosbaenacea.
5. Papillate. Resembling the simple and rod setae, but, contrary to these types, the apex appears to be simple and blunt. This type has only been observed at the tips of the antenna 2.
6. Aesthetasc (fig. 28). Seta composed of stiff basal part ("grip"), an annulus, and a lanceolate distal portion ("whip"). All previous authors leave this highly specialized seta out of their classifications, but in my opinion it best fits here in the classification as it is a multicellular, modified smooth annulate seta. As Watling's type IIA6 seta is here re-coded as type IIA1 seta, the cod-

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Figs. 24-28. Scanning electron micrographs of macrosetae. 24, (uni)setulate macroseta (type IB3(a)), second segment palp maxilla 1 of *Tethysbaena juriaani*; 25, simple macroseta (type IIA1), tip exopodite antenna 1 of *Thermosbaena mirabilis*; 26, rod macroseta (type IIA2), precoxal endite maxilla 1 of *Tethysbaena juriaani*; 27, cuspidate macroseta (type IIA3), telson of *Monodella stygicola*; 28, aesthetasc (type IIA6), exopodite antenna 1 of *Thermosbaena mirabilis*. Micrographs by D. Platvoet (figs. 24-26, 28) and H.P. Wagner (fig. 27).



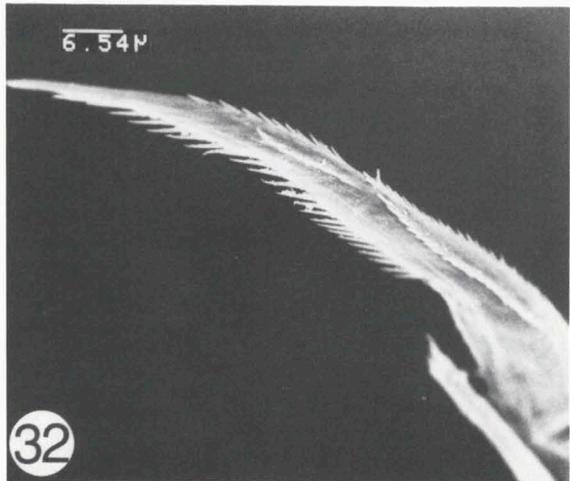
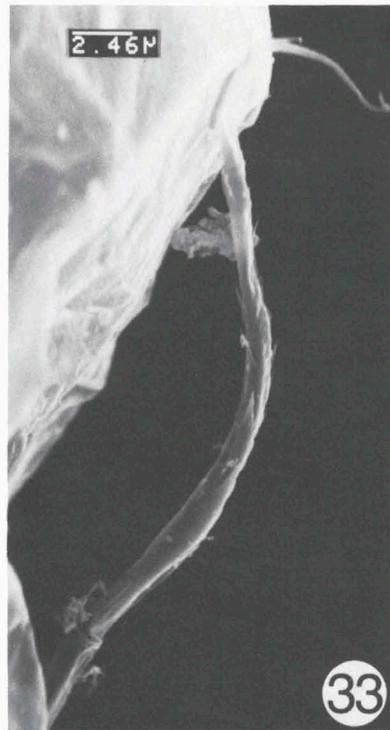
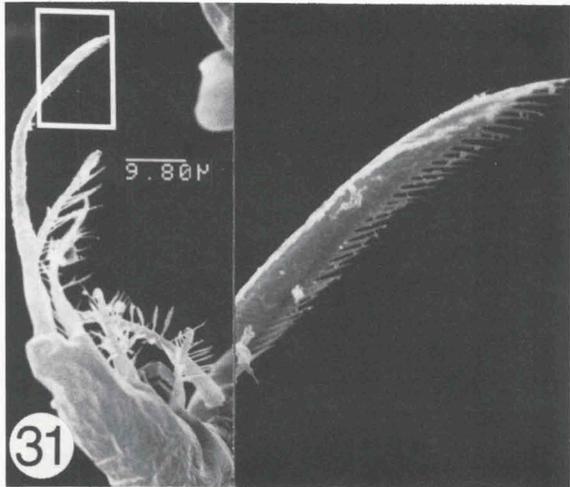
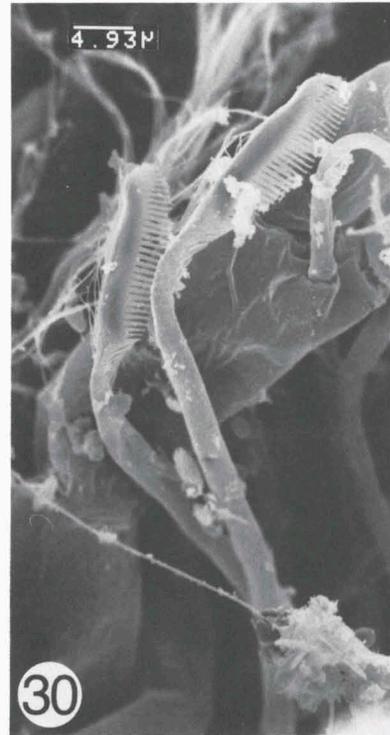
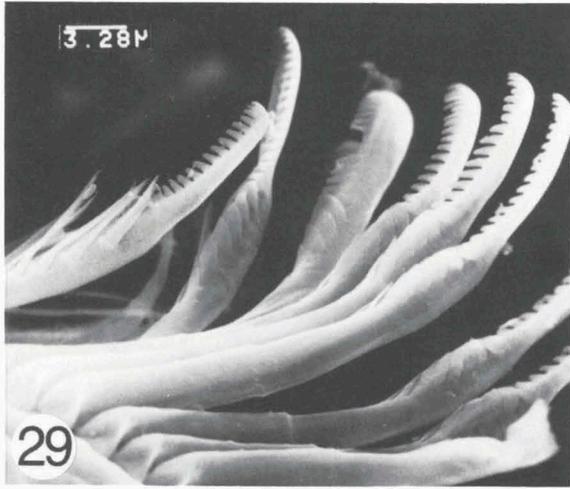
ing Type IIA6 is vacant. This code is now connected with the aesthetasc. Aesthetascs are only present on the exopodite of the antenna 1 (filament sensoriel, Monod, 1924a; Asthetask, Monod, 1940; setole sensoriali, Stella, 1951a; hyaline Stäbchen, S.L. Karaman, 1953; aesthetasc, Meštrov & Lattinger-Penko, 1969; Schram, 1986; aesthete, Stock, 1976; Stock & Longley, 1981; Chelazzi & Messana, 1982; Bowman & Iliffe, 1985, 1988; Yager, 1988).

#### B. Shaft with denticules.

1. Serrate (figs. 29-32). Setae with one (or more) rows of serrations (denticules implanted at one half of the shaft. Various forms can be distinguished; (a) serrate (two rows of denticules at one side of the shaft), (b) serrulate (denticules arranged in two opposite rows), (c) multidenticate (denticules arranged in a multiplicity of rows), and (d) rakes (one row of denticules). The gnathopodal "unguis" of *Tulumella* is the rake-form, while in *Thermosbaena* and the Monodellidae the serrulate type is represented. The "unguis" of pereopod 2 is of a more multidenticate type (2 rows dorsally, 1 row ventrally). Various forms of this type of macroseta can be located in all Thermosbaenacea at the tip of the mandibular palp (these setae are homologous with the pereopodal "unguis"), between the lacinia(e) and the pars molaris of the mandible, basipodal endites 2 and 3 of maxilla 2, the gnathopod, and the pereopods (aiguillon courbe, Monod, 1927a; gekammte Stacheln, Monod, 1940; gezähnte Stacheln, S.L. Karaman, 1953; combing seta, Fryer, 1965; lifting spine, Fryer, 1965; bâtonnets, Meštrov & Lattinger-Penko, 1969; soie courbe, Meštrov & Lattinger-Penko, 1969; ciliated spine, Stock, 1976; Chelazzi & Messana, 1982; hooked spines, Stock, 1976; S-shaped spine, Stock, 1976; rake-like spine, Stock, 1976; transformed S-shaped spine, Stock, 1976; pectinate claw, Stock, 1976; naked seta, Stock, 1976; Stock & Longley, 1981; spoon-shaped seta, Yager, 1988; Bowman & Iliffe, 1988; spoon-shaped spine, Yager, 1988; serrate spine, Yager, 1988; cuspidate crescent, Yager, 1988; peg-shaped spine, Yager, 1988; tricuspid spine, Bowman & Iliffe, 1988; spatulate-ciliate spine, Bowman & Iliffe, 1988; naked spine, Bowman & Iliffe, 1988).
2. Setobranch. A long, thin and pointed seta, which bears leaf-like denticules on the distal portion. Not observed in the Thermosbaenacea.
3. Teazel (fig. 33). Seta with elongate and almost needle-like denticules, but without the slenderness of setules. The denticules are generally arranged in pappose fashion. The peduncles of both antenna 1 and antenna 2 of all Thermosbaenacea are armed with this macrosetal type. At high magnifications one can see that the macrosetae at the margins of the pereopods (one simple and plumose seta on the dorsal margin of the propodus excepted) are of this type also (épine, Monod, 1927a; naked seta, Stock, 1976).

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Figs. 29-33. Scanning electron micrographs of macrosetae. 29, serrate macroseta (type IIB1(d)), basipodal endite 2 maxilla 2 of *Tethysbaena juriaani*; 30, serrate macroseta (type IIB1(d)), basipodal endite 3 maxilla 2 of *Tethysbaena juriaani*; 31, serrate macroseta (type IIB1(b)), tip palp mandibula of *Tethysbaena juriaani*; 32, serrate macroseta (type IIB1(b)), "unguis" pereopod 2 of *Thermosbaena mirabilis*; 33, teazel macroseta (type IIB3), peduncle antenna 1 of *Halosbaena acanthura*. Micrographs by D. Platvoet (figs. 29-32) and H.P. Wagner (fig. 33).



4. Cincinnuli. Setae with basally a short rounded shaft, distally extending into a flattened hood with a digitate margin. Not observed in Thermosbaenacea.

Type III. Non-annulate, robust. Often both chemoreceptive and mechanoreceptive setae. Generally rather large setae, which have a robust habitus as they are present in those places on the appendages where the mechanical stress is high.

1. Toothed (figs. 34-36). Stout, relatively short seta, obliquely implanted in a well-developed socket. Its distal portion is crenulate or truncate, and generally has an apical pore. Toothed macrosetae are present on the distal margin of the basipodal endite of the maxilla 1 (forte épine, Monod, 1924a, 1927a; denticulate spine, Fryer, 1965; Stock, 1976; Yager, 1988; scraper, Fryer, 1965; saw-like tooth, Stock, 1976; tricuspidate spine, Stock, 1976; saw-like spine, Stock & Longley, 1981; toothed spine, Chelazzi & Messana, 1982)

### 3.3.2. Microsetae

Watling (1989: 24) defines his type IV setae as "a heterogeneous assemblage represented by several basic homologies". He states that this group of usually very small setae found on numerous sites on the body surface, are non-annulate and non-robust. Only a subgroup of plumose setae are distinguished, which is divided into two forms: brush (type IVA1) and scaled microsetae (type IVA2). It must be remarked that Fish (1972) distinguishes a brush seta and a brush spine. I presume Watling refers to the former as his type IVA1 seta. This setule, contrary to Fish's statement is non-annulate. Drach & Jacques (1979: fig. 2) figure this setule as their "microsete à barbules", and suppose it to be a transitional stage between "microsetae" and "macrosetae". The "scaled microsetae" of Drach & Jacques (1979: fig. 1) resemble a non-annulate teazel (type IIB3).

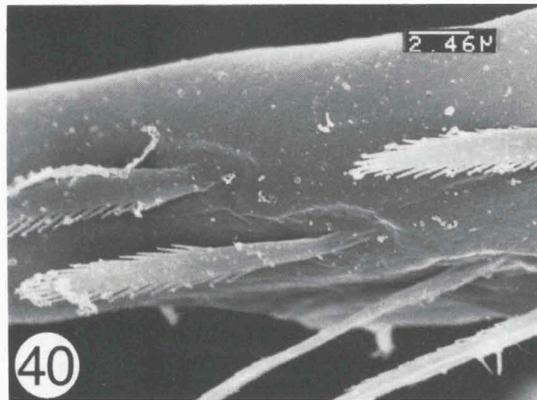
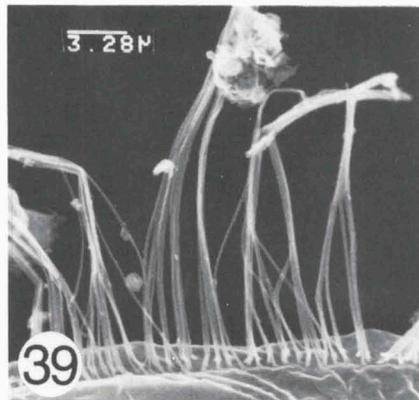
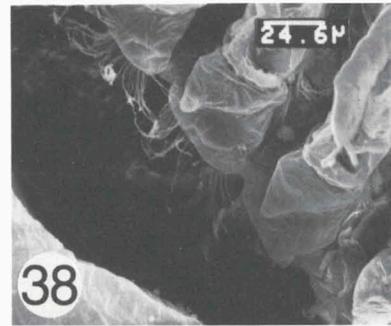
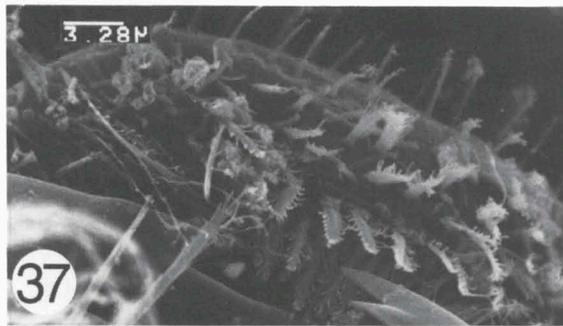
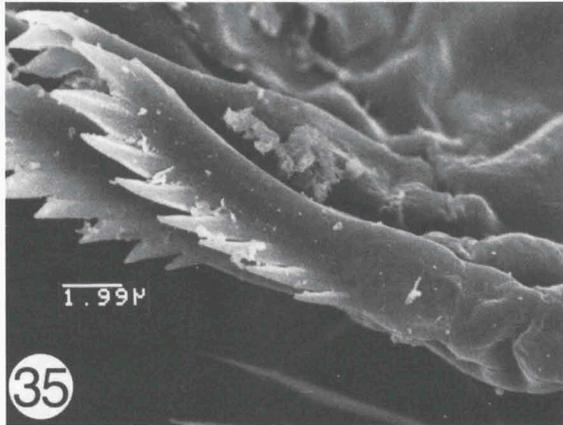
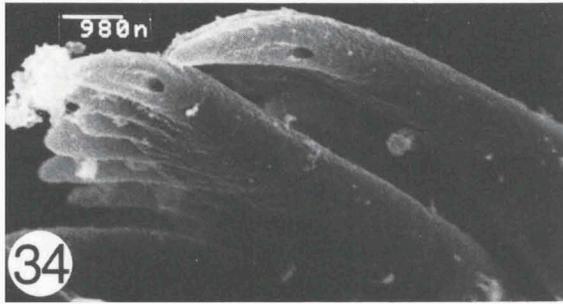
The fine setules observed by me on the second to fourth thoracomeres (fig. 38) appear smooth, but very well might be the same as the "scaled microsetae" of Drach & Jacques, as no larger magnifications of these microsetae have been made by SEM. In Thermosbaenacea I also observed a new type of microseta, which is foliaceous in shape.

Thus far the following microsetae can be classified:

- Type 1. Acuminate. The habitus of these microsetae is acuminate, (sub)circular in cross section, and is either smooth or armed with setulettes
- a. Simple (figs. 38-39). Setule without any outgrowth. This type of microseta is observed on the second to fourth thoracomeres in all thermosbaenacean families, as well on the inner margin of the maxilla 2 and the maxilliped. In the

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Figs. 34-40. Scanning electron micrographs of macrosetae and microsetae. 34, toothed macroseta (type III1), dorsal row at distal margin basipodal endite maxilla 1 of *Tethysbaena juriaani*; 35, toothed macroseta (type III1), ventral row at distal margin basipodal endite maxilla 1 of *Tethysbaena juriaani*; 36, toothed macroseta (type III1), distal margin basipodal endite maxilla 1 of *Tulumella grandis*; 37, ovate microseta (type 2a), labrum of *Halosbaena acanthura*; 38, simple microseta (type 1a), coxae of pereopods 2-5 of *Halosbaena acanthura*; 39, simple microseta (type 1a), epipodite maxilliped of *Tethysbaena juriaani*; 40, ovate microseta (type 2a), dactylus pereopod 4 of *Tethysbaena juriaani*. Micrographs by D. Platvoet (figs. 34, 35, 39, 40) and H.P. Wagner (figs. 36-38).



Halosbaenidae it is present on the coxa and basis of the gnathopods, the rudimentary exopodite and endopodite of maxilla 2, and near the distal margin of the maxilliped.

- b. Scaled. Setule with short broad setulettes, which are obscure. The shape of this microseta is reminiscent of the teazel macroseta. Not observed in the Thermosbaenacea.
- c. Brush. Setule with fine rows of long setulettes distally of a non-annular constriction. In shape closely resembling a plumose macroseta of type IA1, but then without annulus. Not observed in the Thermosbaenacea.
- d. Club. Minute stout microseta that appears to be smooth. Generally regularly tapering, but in *Tethysbaena texana*, more or less rectangular with the tip abruptly pointed. It is reminiscent of a cuspidate macroseta (type IIB3), but then without annulus. This type can be present on the merus, carpus and propodus of the male endopodite of the maxilliped of *Tethysbaena* only.

Type 2. Foliate. Microseta flattened, with setulettes along its margins.

- a. Ovate (figs. 37, 40). A flattened leaf-shaped microseta with fine setulettes on its opposite margins. These microsetae are observed on the labrum of all species of the thermosbaenacean families. On the palp of the maxilla 1 and at the basis of the basipodal endite of the maxilliped of the species of the Monodellidae this type of microseta is present also. A slightly more elongated form of this type is present on the first segment of the exopodite, and on the ischio-merus, propodus and dactylus of the endopodite of the pereipods (P2-P7).
- b. Ciliate (figs. 41-42). This microseta is elongate foliate to very long and ciliate, the setulettes are short, and generally better developed on one of the margins. This type can be found in all families on the epipodite of the maxilliped, on the margin of the labium, on the lateral margins of the basal endite of the maxilla 1, and on the pars molaris of the mandible.

### 3.3.3. Spiniform processes

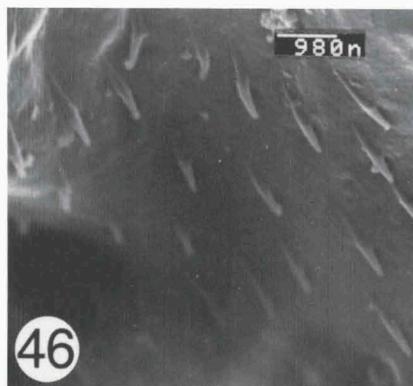
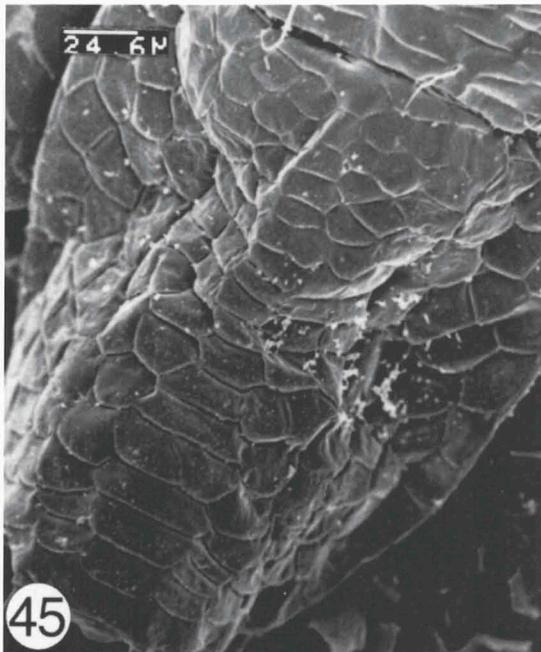
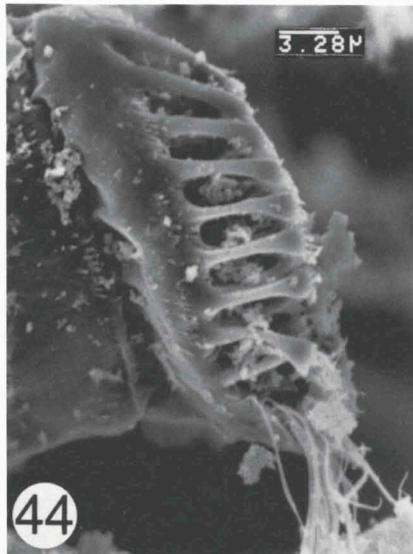
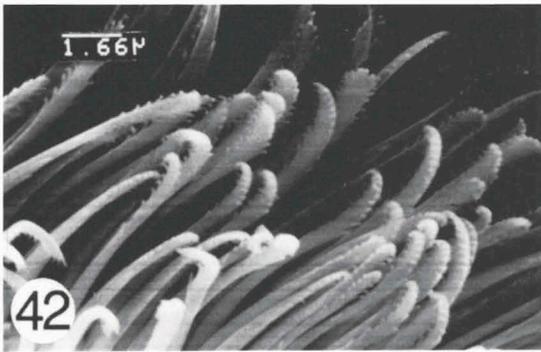
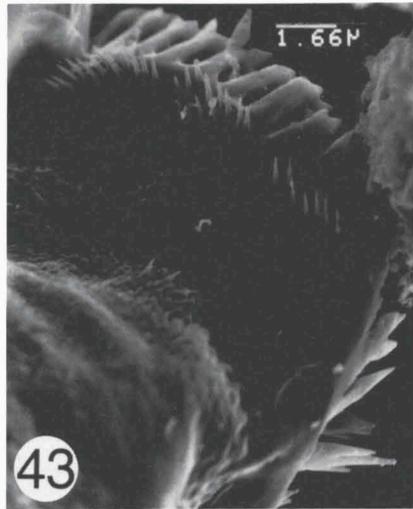
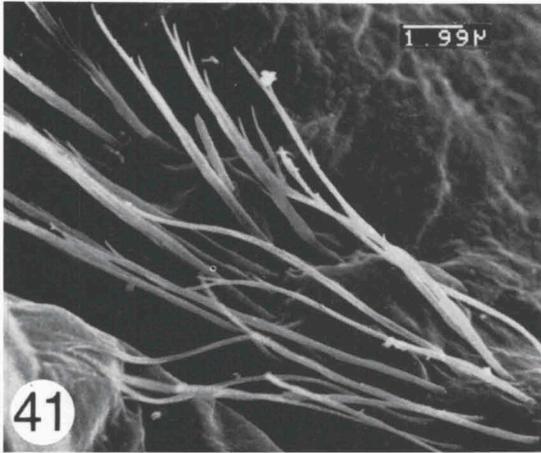
In Thermosbaenacea spiniform processes are rare cuticular structures. They are present on the mandible as the complexly built laciniae, and on the pars molaris of the mandibles in *Tulumella* (serrate), *Tethysbaena* (tripartite tips), and *Monodella* (hexapartite tips) (figs. 43-44).

### 3.3.4. Scales

Scales (fig. 45) are only observed in *Tethysbaena scabra* and *T. siracusae*. These scales cover the whole body. At their margins tiny scutellae are present. In other Thermosbaenacea scutellae are present on various parts of the body (fig. 46).

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Figs. 41-46. Scanning electron micrographs of microsetae, spiniform processes, scales and scutellae. 41, ciliate microseta (type 2b), inner margin basal endite maxilla 1 of *Tethysbaena juriaani*, 42, ciliate microseta (type 2b), inner margin labium of *Thermosbaena mirabilis*; 43, tripartite tipped spiniform processes on pars molaris of *Tethysbaena juriaani*; 44, hexapartite tipped spiniform processes on pars molaris of *Monodella stygicola*; 45, scales on telson of *Tethysbaena scabra*; 46, scutellae on coxal plate maxilla 2 of *Tethysbaena juriaani*. Micrographs by D. Platvoet (figs. 41-44, 46) and H.P. Wagner (fig. 45).



## 4. Systematics

### 4.1. Introduction

In the first fifty years since the discovery and description of the first thermosbaenacean, *Thermosbaena mirabilis* Monod, 1924, only seven named species were described. Except for *Thermosbaena mirabilis*, all other species were classified in the genus *Monodella* Ruffo, 1949. The type species of *Monodella* is *M. stygicola* Ruffo, 1949, the description of which was based on four immature females collected in 1948. A third species, *M. argentarii* Stella, 1951, was described from Monte Argentario in the Toscana Province, Italy, and provisionally placed in *Monodella*, although the author was aware that particular differences with *M. stygicola* existed. Later authors (S.L. Karaman, 1953; Pó, 1962; Maguire, 1964, 1965) noticed the morphology of their species to be similar to *M. argentarii*, but neglected the quite distinct mouthpart morphology of *M. stygicola*, judging the differences a result of the young age of Ruffo's material. The differences between all species were so subtle that Rouch (1965) decided to synonymize *M. halophila* S.L. Karaman, 1953 with *M. argentarii* Stella, 1951. Most probably this was also the reason that the extreme morphological differences between the "*Monodella*" species and a limnic species from Bosnia was overlooked by Meštrov & Lattinger-Penko, who even interpreted the gnathopod as the male endopodite of the maxilliped. The presence of a "bilobed rostrum" (actually the ocular scales) in *M. finki* Meštrov & Lattinger-Penko, 1969, a character that Stock (1976) also discovered in *Halosbaena*, a new genus of thermosbaenacean from Curaçao, led to the creation of the fourth genus known, *Limnosbaena*. Another four species have been added since to *Monodella*, as well as the description of two new genera, viz., *Theosbaena* Cals & Boutin, 1985 (monotypic), and *Tulumella* Bowman & Iliffe, 1988 (three species). With the recently described *Halosbaena tulki* Poore & Humphreys, 1992, the total number of taxa in the order comprises 6 genera, and 18 named species.

In this chapter all material that was available for study is discussed, including a topotypic sample of *Monodella stygicola*, which has resulted in a drastic change of the current view on the classification of the group. Together with the revised terminology and the introduction of a chaetotaxic classification, I have chosen for extensive, detailed descriptions to incorporate the new information in the descriptions of all taxa, this in order to facilitate more extensive comparative studies in the future. Herein solely a taxonomic review of the order is presented. Descriptions of new species of *Tethysbaena* are generally based on a representative set of adult specimens, from which (if available) a male is selected as holotype. Contrary to earlier authors, which gave preference to select a female specimen as a holotype, I have chosen so since the male endopodite of the maxilliped provides extra information of substantial taxonomic value. Although Pretus (1991) observed metrical differences between species, I concentrated my study primarily on non-metrical data, as variable pressure on mounted appendages easily disturbs the natural proportions and thus can provide false information. The sole exception is made for the width/length ratio of the telson, as the margin is distinctly keeled laterally and terminally, which enables one to measure the natural proportions.

## 4.2. General classification

## Order Thermosbaenacea Monod, 1927

Thermosbaenacea Monod, 1927a: 48; Glaessner, 1957: 179; Monod, 1960: 528; Gordon, 1964: 150, 152; Vandell, 1964: 142; Schmitt, 1965 (reprinted 1973): 87; Green, 1967: 168; Hessler, 1969: R366; Kaestner, 1970: 367; Bowman, 1971: 171; Noodt, 1974: 447; Monod, 1975: 102; Stock, 1980b: 107; McLaughlin, 1980: 84; Stock, 1981a: 225; Schram, 1981: 2; Watling, 1981: 203; Bowman & Abele, 1982: 15; Abele, 1982: 276; Stock, 1982: 195; Newman, 1983: 113; Dahl, 1983: 196, 198; Watling, 1983: 214, 217, 219, 221, 223; Sieg, 1983a: 36; Sieg, 1983b: 230; Monod, 1984: 204; Sieg, 1984: 27; Schram, 1984: 305; Bowman et al., 1985: 75, 77; Stock, 1986a: 587; Schram, 1986: 216; Pires, 1987: 233, 235; Bowman & Iliffe, 1988: 221; Stock, 1990: 697; Pretus, 1991: 235; Casanova, 1993: 144.

Thermosbaenacea (sic); G. O. Sars, 1929: 349.

Thermosbaenacés; Delamare Deboutteville, 1957: 61, 66; Rouch & Danielopol, 1987: 350.

Thermosbaenida; Russell-Hunter, 1979: 242, 243.

Diagnosis.— Small ( $\leq 5.2$  mm), strictly stygobiont crustaceans, mainly characterized by the fusion of the carapace to the thoracic tergum by the maxillipedal meta-mere, and by the formation of a dorsal broodpouch in the female incubating two to ten eggs, which is internally connected to the branchial chamber. Oostegites absent. Free larval stages lacking, but postmarsupial juveniles develop seventh (*Halosbaena*), or sixth and seventh pereopods (Monodellidae) by successive moulting. Postmarsupial juveniles of *Thermosbaena* resemble adults, but lack the fully developed genitalia, so they have to moult, too. It is quite possible that adults moult also, since individuals with regenerated pereopods were represented among preserved material. Number of pereopods 5 (*Thermosbaena*) or 7 (other taxa); female genital opening on sixth thoracomere; penes on eighth thoracomere. Body consisting of a carapace, eighth thoracomeres, six pleonites, and a telson. Other appendages are: biramous antennae 1; antennae 2; ocular scales (not in all taxa); labrum; mandibles; labium; maxillae 1; maxillae 2; maxillipeds; pereopods; two pairs of pleopods (articulate or non-articulate basally); one pair of uropods; anus located subterminally.

Key to the families of Thermosbaenacea  
based on characters visible without dissection

1. Body distinctly wider than high; 5 pairs of pereopods; telson fused with pleonite 6 ..... **Thermosbaenidae** Monod, 1927 (p. 38)
- Body elongate; 7 pairs of pereopods; telson separate from pleonite 6 ..... 2
2. Ocular scales absent; gnathopod with one serrate macroseta forming the "unguis"; propodus of gnathopod with "spur"; pleopod 1 with basal articulation ..... **Monodellidae** Taramelli, 1954 (p. 50)
- Ocular scales present; gnathopod with two or three (more or less modified) serrate macrosetae forming a "claw"; propodus of gnathopod lacking "spur"; pleopod 1 a small unarticulated lobe ..... 3
3. Main flagellum of antenna 1 with up to two aesthetascs on second and more distal segments; third peduncular segment of antenna 2 with a scale; gnathopod biramous; pereopods 2 to 7 with ovate microsetae on dactylus ..... **Tulumellidae** fam. nov. (p. 203)
- Main flagellum of antenna 1 with one aesthetasc on second and more distal seg-

ments; third peduncular segment of antenna 2 without scale; gnathopod uniramous (lacking exopodite); pereopods 2 to 7 without ovate microsetae .....  
 ..... **Halosbaenidae** Monod & Cals, 1988 (p. 229)

#### 4.3. Thermosbaenidae Monod, 1927

Thermosbaenidae Monod, 1927a: 48; Monod, 1960: 528; Hessler, 1969: R367; Kaestner, 1970: 369; Bowman & Abele, 1982: 15; Russell-Hunter, 1979: 274; Bousfield, 1982: 241; Stock, 1986a: 587; Schram, 1986: 222; Monod & Cals, 1988: 101; Wagner, 1988: 1st page; Cals & Monod, 1988: 342; Wagner, 1990: 123; Cals & Monod, 1991: 177.

Thermosbanidae (sic); G. O. Sars, 1929: 349.

Thermosbaenidea (sic); Bowman & Iliffe, 1988: 226.

**Diagnosis.**— Thermosbaenaceans in which the body is distinctly wider than high. A transverse groove separates circa one-fourth of the carapace from its posterior part. Rostrum indistinct. Small eye-stalks (ocular scales) absent. Main flagellum of antenna 1 10- to 12-segmented; accessory flagellum 8-segmented. Flagellum of antenna 2 6-segmented. Mandible with one plumidenticulate macroseta on second segment of palp; left pars incisiva 3-dentate, right pars incisiva with 6-dentate; lacinia mobilis absent; pars molaris blunt, robust and rounded, molar surface without spiniform processes. Maxilla 1 with 2-segmented palp, by fusion of segments 1 and 2; basipodal endite with six toothed macrosetae. Basipodal endite 1 of maxilla 2 with simply built plumidenticulate macrosetae; basipodal endites 2 and 3 with two rows of rake-like serrate macrosetae; endopodite 2-segmented; exopodite reduced to a triangular lobe with one simple macroseta, situated between basipodal endite 3 and endopodite. Maxilliped with three simple setulated pappose macrosetae on coxopodite; (sub)terminal margin of basipodite with two rows of plumidenticulate macrosetae; endopodite absent; epipodite well-developed. Five pairs of legs; gnathopod biramous, basis and ischium fully coalesced, propodus without bicuspidate "spur", one serrulate macroseta forming "unguis"; pereopods 2 to 5 biramous, exopodite 2-segmented in pereopods 2 to 4, 1-segmented in pereopod 5, ovate microsetae absent; penis short and blunt. First pleopod basally articulate, with four subplumose macrosetae; second pleopod articulate, somewhat longer than first, with four subplumose macrosetae; pleopods 3 to 5 absent. First segment of uropodal exopodite distinctly larger than endopodite, distomedially with six to seven cuspidate macrosetae, distolaterally with one cuspidate and two subplumose macrosetae. Telson fused with pleonite 6, forming a pleotelson, 11 to 13 pairs of cuspidate macrosetae along its lateral to posterior margin.

**Discussion.**— In mouthpart morphology the Thermosbaenidae are more closely related to the Monodellidae than to other families. The chaetotaxy of both groups expresses a close similarity as well. For instance, the pappose macrosetae of the coxopodal endite of maxilla 2, and the submedial, for each genus typical, very stout plumidenticulate macroseta of the basipodite of the maxilliped, in *Thermosbaena* and the Monodellidae count in favour of regarding both as primitive groups. I am inclined, however, to treat both groups as separate families, because the total number of external morphological differences separating the Monodellidae from the Thermosbaenidae, are just as numerous as the differences between the other families. However, a

common ancestry on the basis of mouthpart morphology and chaetotaxy will not be argued against.

#### 4.3.1. *Thermosbaena* Monod, 1924

*Thermosbaena* Monod, 1924a: 58; Barker, 1952: 27; S.L. Karaman, 1953: 56; Glaessner, 1957: 179; Delamare Deboutteville, 1957: 66; Monod, 1960: 528; Delamare Deboutteville, 1960: 244; Gordon, 1964: 154; Vandel, 1964: 142; Maguire, 1964: 932; Schmitt, 1965 (reprinted 1973): 87; Fryer, 1965: 49; Botosaneanu & Delamare Deboutteville, 1967: 21; Green, 1967: 168; Hessler, 1969: R367; Kaestner, 1970: 367; Bowman, 1971: 171; Noodt, 1974: 447; Schminke, 1976: 295; Stock, 1976: 65; Russell-Hunter, 1979: 274; McLaughlin, 1980: 84, fig. 30B; Bousfield, 1982: 241; Chelazzi & Messana, 1982: 161; Newman, 1983: 113; Sieg, 1983a: 38; Sieg, 1984: 28; Schram, 1984: 308; Boutin & Cals, 1985: 267; Cals & Boutin, 1985: 337; Bowman & Iliffe, 1986: 88; Stock, 1986a: 587; Cals & Cals-Usciati, 1986: 464; Schram, 1986: 216; Cals, 1987: 661, fig. 1; Monod & Cals, 1988: 101, pl. 2; Bowman & Iliffe, 1988: 224; Wagner, 1988: 1st page; Cals & Monod, 1988: 342; Wagner, 1989: 8; Wagner, 1990: fig. 1; Mestrov & Cals, 1991: 42; Cals & Cals-Usciati, 1991: 166; Cals & Monod, 1991: 176; Casanova, 1993: 145.

*Thermosbana* (sic); G. O. Sars, 1929: 349.

Type species.— *Thermosbaena mirabilis* Monod, 1924, by monotypy.

Diagnosis.— Body length (antennae 1 and 2 excluded) up to ca. 3.2 mm. Carapace reaching to the second pedigerous somite. Third peduncular segment of antenna 1 with three subplumose macrosetae on terminal prominence. Basipodal endite of maxilla 1 with spatulate digitate toothed macrosetae. Coxopodal endite of maxilla 2 with two stout plumose macrosetae; basipodal endite 1 with seven simply built plumidenticulate macrosetae, whose tips are finely pointed with subterminally its serrations, and setules at the central portion of the setal body. Pappose macrosetae of coxopodite of maxilliped with long, almost simple setules with a few distal setulettes (as in fig. 9); basipodal, submedially implanted, plumidenticulate macrosetae of maxilliped tall, stout and pointed, its ventro-basal portion with fine setules, setules distad of the annulus distinctly larger in size and arranged in two opposite rows slightly turning around the macrosetal axis. Gnathopod with naked first exopodite segment, endopodite with entirely fused baso-ischium, carpus with two long fine teazel macrosetae, propodus with four teazel macrosetae, "spur" absent. Uropod: first article exopodite with six to seven (terminal one being smaller) cuspidate macrosetae medially and (sub)terminally on the median margin.

Description.— As for the type species.

##### 4.3.1.1. *Thermosbaena mirabilis* Monod, 1924 (figs. 47-66)

*Thermosbaena mirabilis* Monod, 1924a: 58, figs. 1-2; Monod, 1924b: 64; Monod, 1924c: 16; Anonymous, 1924a: 324; Calman, 1924: 171; Spandl, 1926: 87, 183, figs. 58a-b; Monod, 1927a: 29, figs. 1-7; Monod, 1927b: 196, figs. 1-3; Chappuis, 1927: 55, 137, fig. 25; Zimmer, 1927: 809, figs. 861-862; Omer Cooper, 1928a: 48; Omer Cooper, 1928b: 254; Brues, 1932: 223; Absolon, 1935: 4, figs. 5-7; Monod, 1940: 2, figs. 3-28; Bruun, 1940: 494, fig. 3; Ruffo, 1949a: 32; Ruffo, 1949b: 56; Anonymous, 1950: 917; Anonymous, 1951: 9; Stella, 1951a: 1; Stella, 1951b: 227; Barker, 1952: 27; Stella, 1953: 226; Stella & Baschieri Salvadori, 1954: 468; Taramelli, 1954: 10; Stella, 1955: 464; Barker, 1956: 503; Delamare Deboutteville, 1957: 66; Siewing, 1958: 4, figs. 1-39, 40A-C, 41; Gordon, 1958: 1186; Stella, 1959: 121; Barker,

1959: 209; Monod, 1960: 528, figs. 1, 2, 4; Delamare Deboutteville, 1960: 244, 627, figs. 90, 91a, 92c; Barker, 1960: 253; Barker, 1962: 262, figs. 1-8; Pór, 1962: 305; Pór, 1963: 49; Vandel, 1964: 142, fig. 19; Schmitt, 1965 (reprinted 1973): 87, fig. 34; Maguire, 1965: 149; Fryer, 1965: 49; Rouch, 1965: 722; Botosaneanu & Delamare Deboutteville, 1967: 21, fig.; Green, 1967: 168; Hessler, 1969: R367, figs. 181-182; Meštrov & Lattinger-Penko, 1969: 111; Kaestner, 1970: 368 fig. 14-1, 369; Zilch, 1972: 75, figs. 1a, 2-4, 7-14; Zilch, 1975a: 462, figs. 1-81; Zilch, 1975b: 121, figs. 1-6; Stock, 1976: 65; Dumont, 1978: 43; Pinkster, 1978: 234; Russell-Hunter, 1979: 274; Abele, 1982: 276; Bousfield, 1982: 241; Sieg, 1983a: 39; Watling, 1983: 221; Sieg, 1984: 29; Stock, 1986a: 587, fig. 4; Cals & Cals-Usciati, 1986: 459, pl. 2; Schram, 1986: 220; Cals & Monod, 1988: 342; Wagner, 1990: 123; Pretus, 1991: 235.

*Thermosbana* (sic) *mirabilis*; G. O. Sars, 1929: 349.

Material.— **Tunesia:** 4 ♂♂, 3 juveniles; El Hamma, Ain Baama; collected by Miss L. Due; 6.v.1938; ZMA coll. no. C.A. 8099.

- 5 ♀♀; El Hamma, Ain Baama; collected by A. F. Bruun; 18.v.1938; ZMA coll. no. C.A. 8100; RMNH G 42.

- 2 ♂♂, 1 juvenile; El Hamma, Ain Bordj; 24.viii.1960; UEKL [topotypes].

Description.— Body length (antennae 1 and 2 excluded) of male up to 3071 µm, of female up to 3029 µm in the material studied.

Antenna 1 with 3-segmented peduncle and two flagella; peduncular segments 1 to 3 with four, two, and one long plumose macrosetae (type IA1) on median margin; peduncular segment 1 dorsolaterally with two teazel macrosetae (type IIB3), segment 3 with one subterminal and two terminal subplumose macrosetae (type IB2) on terminal prominence; main flagellum 10- to 12-segmented, in male one aesthetasc (type IIA6) on segments 1 to 9 (-11), in female one aesthetasc on segments 7 to 9 (-11), each segment with one mediodistal simple macroseta (type IIA1), except last segment which has subterminally five simple macrosetae (type IIA1) of unequal length; accessory flagellum 8-segmented, segment 5 with one, and segment 6 with two mediodistal simple macrosetae (type IIA1), last segment has five simple macrosetae (type IIA1) of unequal length terminally implanted.

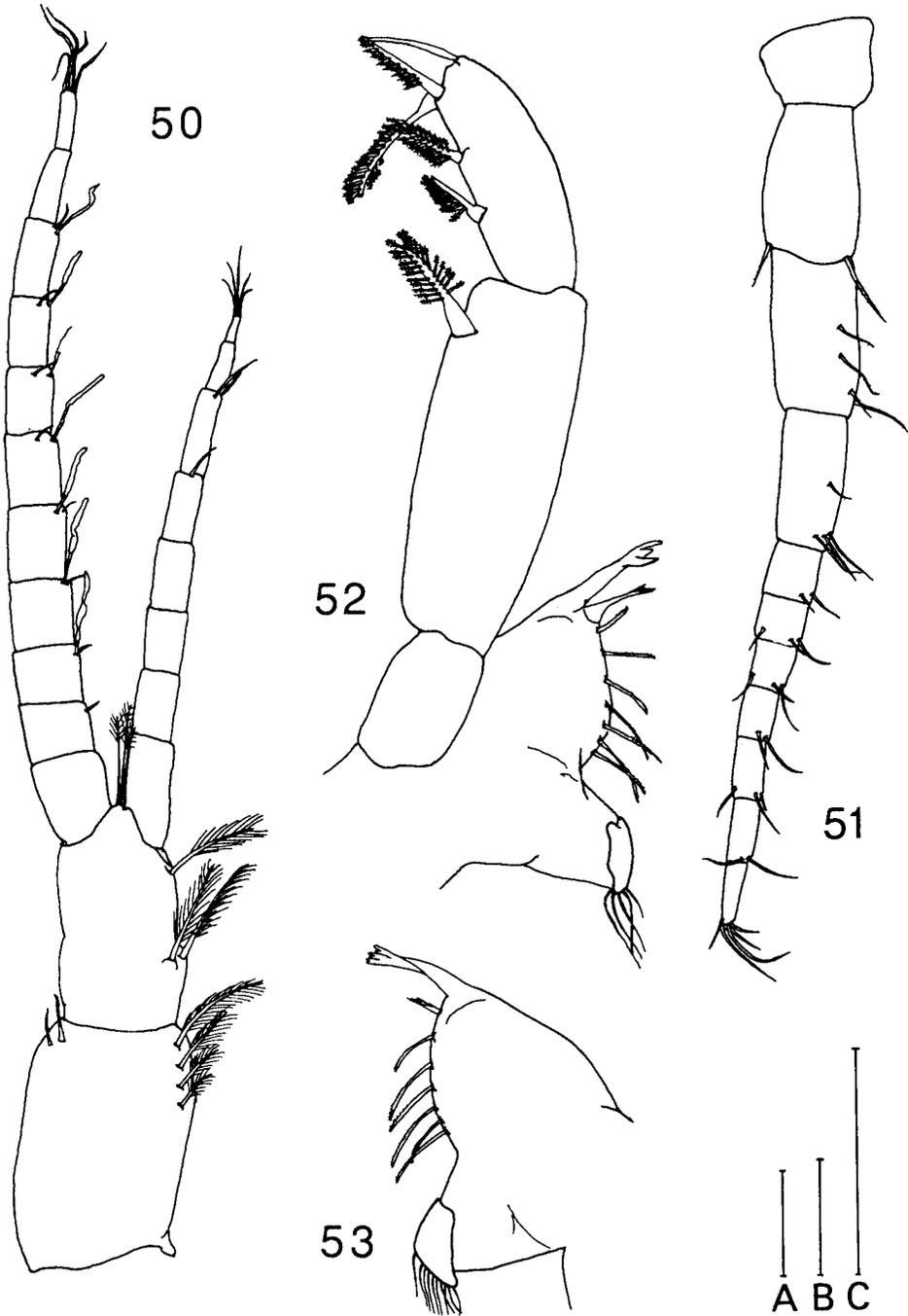
Antenna 2 uniramous, peduncle 5-segmented, segment 1 naked, segment 2 with one teazel macroseta (type IIB3) on both dorsolateral and mediodistal margin, segment 3 with two teazel medial macrosetae (type IIB3) and two on mediodistal margin, segment 4 with one teazel medial macroseta (type IIB3) and three on mediodistal margin, segment 5 with two teazel macrosetae (type IIB3) on mediodistal margin; flagellum 5-segmented, segments 1 to 5 each with two simple macrosetae (type IIA1) mediodistally, segments 1, 2 and 4 with one additional simple macroseta (type IIA1) on the distolateral margin, segment 6 terminally with five simple macrosetae (type IIA1) of unequal length.

Labrum somewhat longer than wide; its proximal portion with ciliate microsetae (type 2b); apically with ovate microsetae (type 2a).

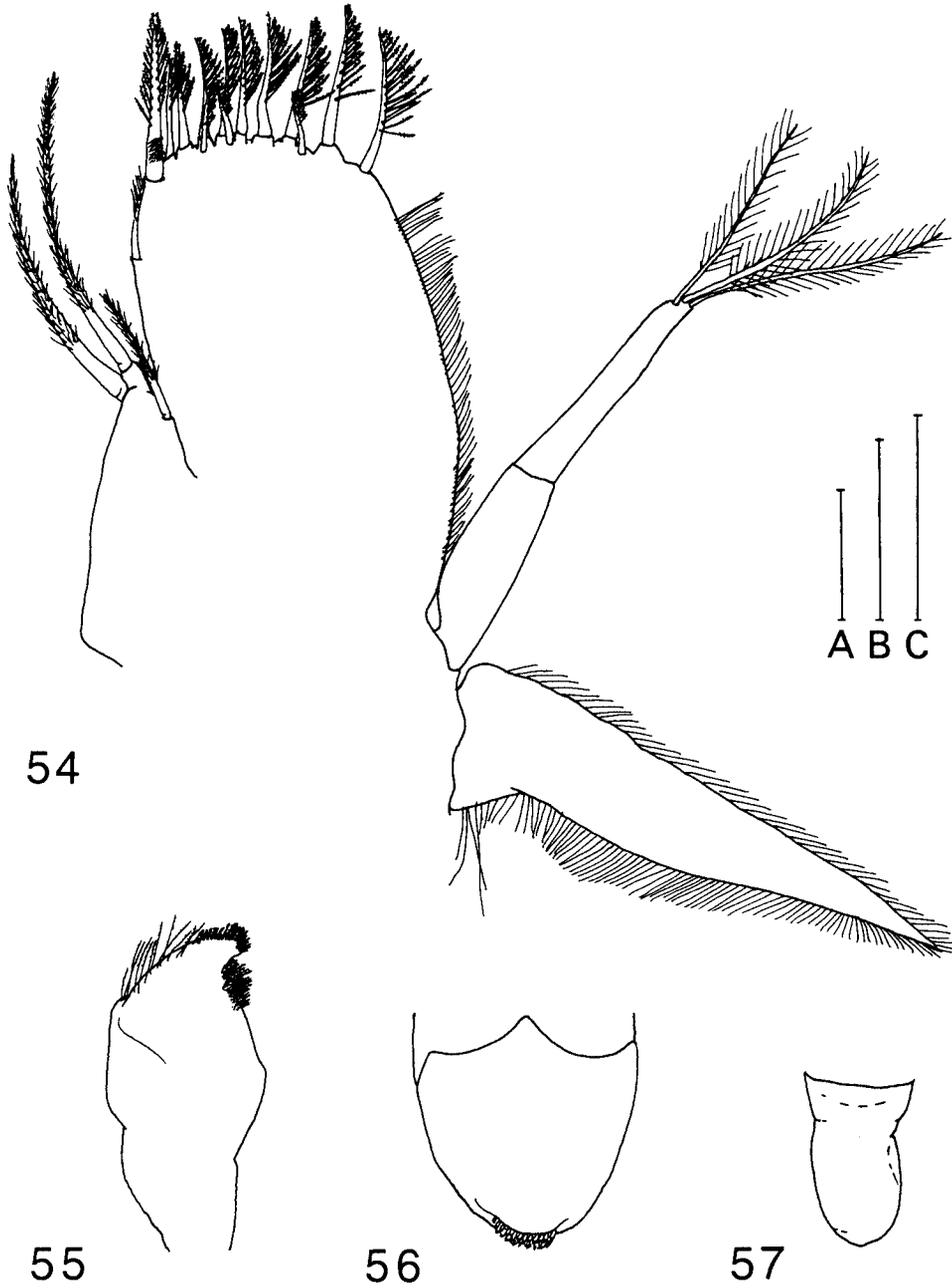
Mandible with 3-segmented palp, basal palp segment short and unarmed, second segment largest with one plumidenticulate macroseta (type IA3), third segment with four plumidenticulate macrosetae (type IA3), apically one serrulate macroseta (type IIB1(b)); corpus mandibulae differentiated into pars incisiva, cleaning seta (modified type IIB1) (in the left mandible more strongly developed than in the right mandible), row of seven (left mandible) or six (right mandible) slender serrate macrosetae (type IIB1(a)), and robust pars molaris having naked molar surface, except for some ciliate



Figs. 47-49. *Thermosbaena mirabilis* (Monod, 1924). 47, lateral view of habitus ♂ (2886  $\mu\text{m}$ ). 48, maxilla 2, ♀. 49, maxilla 1, ♂. Scale indicated 0.1 mm (figs. 48-49).



Figs. 50-53. *Thermosbaena mirabilis* (Monod, 1924), ♂. 50, antenna 1 (scale A). 51, antenna 2 (scale B). 52, left mandible. 53, corpus mandibula of right mandible. (figs. 52-53 scale C). Scales indicated 0.1 mm.



Figs. 54-57. *Thermosbaena mirabilis* (Monod, 1924), ♂. 54, maxilliped (scale C). 55, lobe of labium. 56, labrum (figs. 55-56 scale B). 57, penial lobe (scale A). Scales indicated 0.1 mm.

microsetae (type 2b) distally.

Labium deeply cleft, its two lobes with converging tips, internal distal margin with ciliate microsetae (type 2b), outer distal margin less densely covered by taller ciliate microsetae (type 2b).

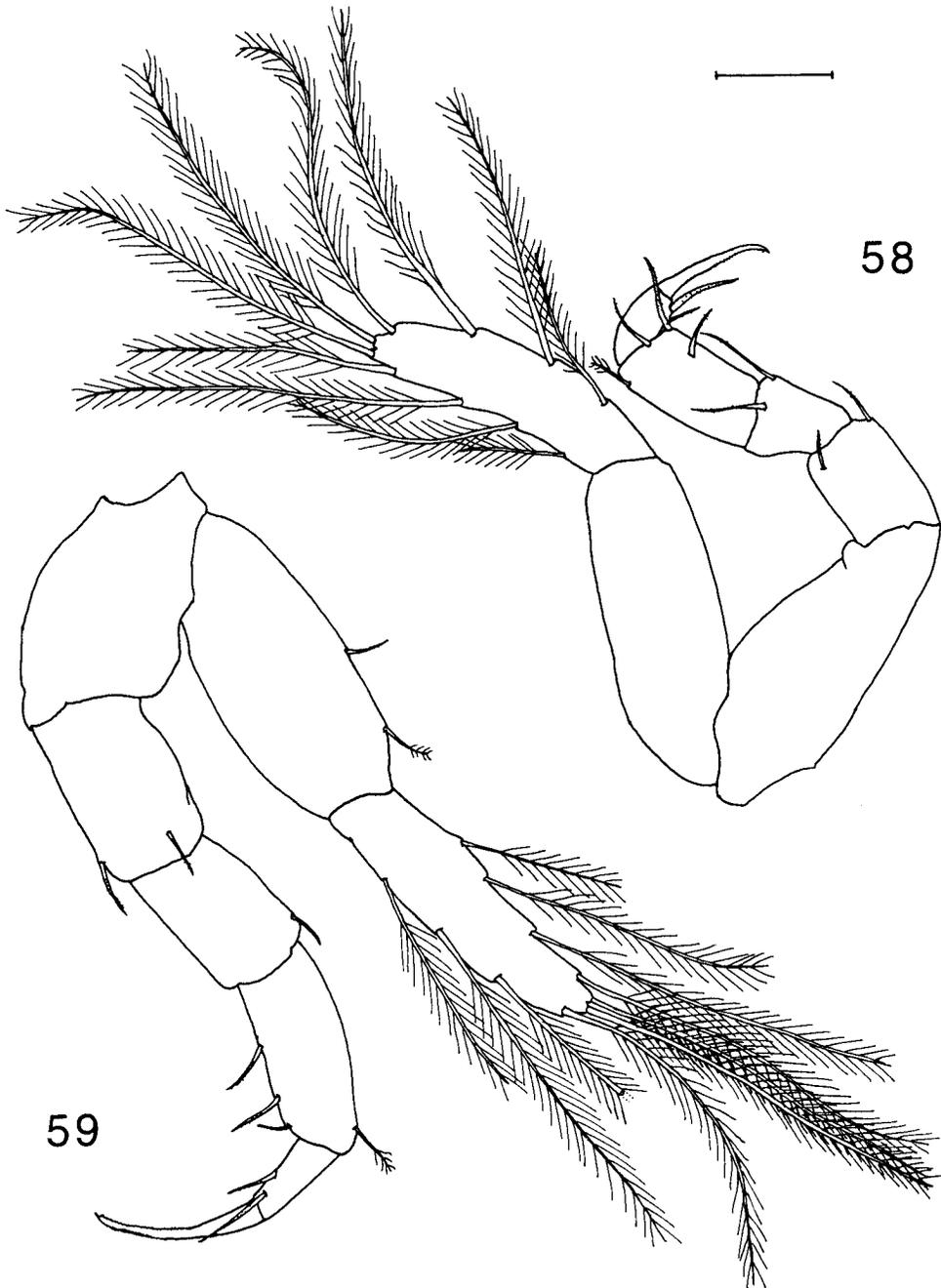
Maxilla 1 differentiated into precoxal endite with medial armature of ten plumidenticulate macrosetae (type IA3), six strong medially and four less developed ones terminally implanted; basipodal endite with distal armature of six toothed macrosetae (type III1), spatulate with blunt serrations along medial margin; endopodite forming a 2-segmented palp, basal segment fused with second segment, which carries one long simple macroseta (type IIA1) and one comparatively large unisetulate macroseta (type IB3(a)) with ten setules, distal segment smaller with one distally implanted simple macroseta (type IIA1) and one well-developed unisetulate macroseta (type IB3(a)) with six prominent setules; subterminal margin finely serrulate.

Maxilla 2: complexly built, a coxopodal endite medially with 12 fine plumose macrosetae (type IB1), six rod macrosetae (type IIA2) mediodorsally, and two stout plumose macrosetae (type IB1); three basipodal endites: basipodal endite 1 with seven rather simply built plumodenticulate macrosetae (type IA3), tips finely pointed with subterminal serrations, setules at central portion of setal body; basipodal endite 2 with 17 rake-like serrate macrosetae (type IIB1(d)) at terminal margin, and two modified longer serrate macrosetae implanted subterminally, of which one has a more developed rake, while the other has its rake strongly reduced to a narrow pointed tip; basipodal endite 3 with six more strongly barbed rake-like macrosetae (type IIB1(d)), increasing laterally and arranged in two rows of three macrosetae; exopodite reduced to triangular lobe with one simple macroseta (type IIA1); endopodite 2-segmented with four simple macrosetae (type IIA1).

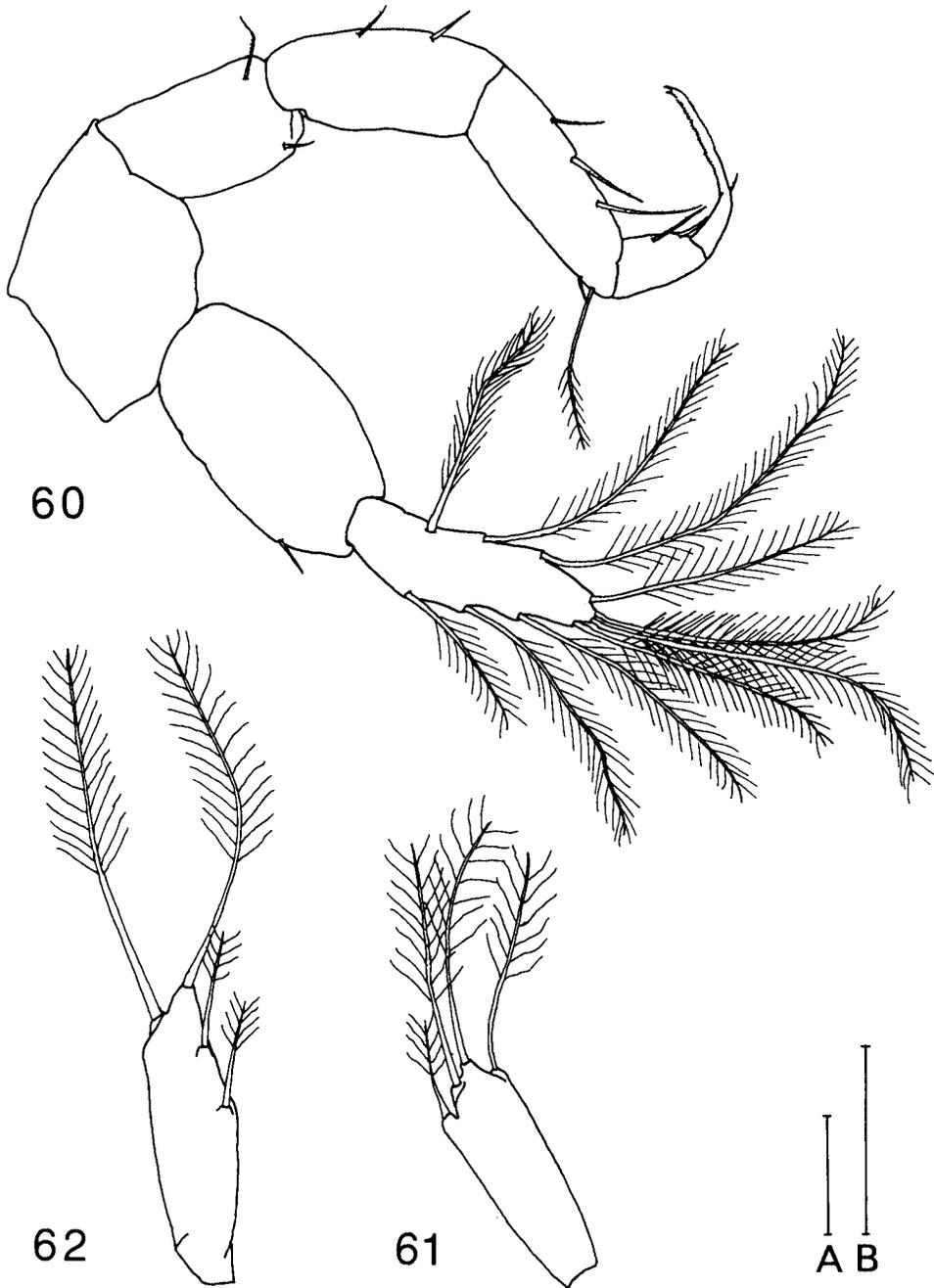
Maxilliped without endopodite; coxopodal endite a tapering lobe with one short and two long pappose macrosetae (type IA2) having long almost simple setules with a few setulettes distally (as in fig. 9); basipodal endite with several plumidenticulate macrosetae (type IA3), 13 of them with long setules, a small one medially, nine long ones terminally, and three shorter ones subterminally, submedially an additional much stouter plumidenticulate macroseta (type IA3) is implanted, its basal portion ventrally with fine setules, setules distally of the annulus distinctly larger in size and arranged in two opposite rows slightly turning around the macrosetal axis; exopodite 2-segmented, distal segment with two terminal and one subterminal plumose macrosetae (type IB1); epipodite a pointedly tapering lobe with simple microsetae (type 1a) along its margin.

Gnathopod with naked basal segment; exopodite 2-segmented, proximal segment unarmed, distal segment with three medial, two subterminal, two terminal and three lateral plumose macrosetae (type IB1); endopodite with entirely fused baso-ischium, merus with subterminally implanted teazel macrosetae (type IIB3) one on dorsal and one on ventral margin; carpus short, with two long fine teazel macrosetae (type IIB3); propodus longer, with four fine teazel macrosetae (type IIB3) in distal half; dactylus with two unequal fine teazel macrosetae (type IIB3) on ventral margin, terminally implanted "unguis" is formed by stout serrulate macroseta (type IIB1(b)).

Pereiopod 2: endopodite having ischiomerus distally with teazel macrosetae (type IIB3), one on ventral and one on dorsal margin; carpus with two teazel macrosetae



Figs. 58-59. *Thermosbaena mirabilis* (Monod, 1924), ♂. 58, gnathopod. 59, pereopod 2. Scale indicated 0.1 mm.



Figs. 60-62. *Thermosbaena mirabilis* (Monod, 1924), ♂. 60, pereopod 3 (scale A). 61, pleopod 1. 62, pleopod 2. (figs. 61-62 scale B). Scales indicated 0.1 mm.

(type IIB3) medially and distally on ventral margin, distally one teazel macroseta (type IIB3) on the dorsal margin; propodus with three serrate macrosetae (type IIB1(a)) medially on ventral margin, dorsodistally one teazel (type IIB3) and one subplumose (type IB2) macroseta; dactylus with two teazel macrosetae (type IIB3) on ventral margin, and well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one teazel macroseta (type IIB3) medially and one subplumose macroseta (type IB2) subterminally, second segment with three medial, two subterminal, two terminal and three lateral plumose macrosetae (type IB1).

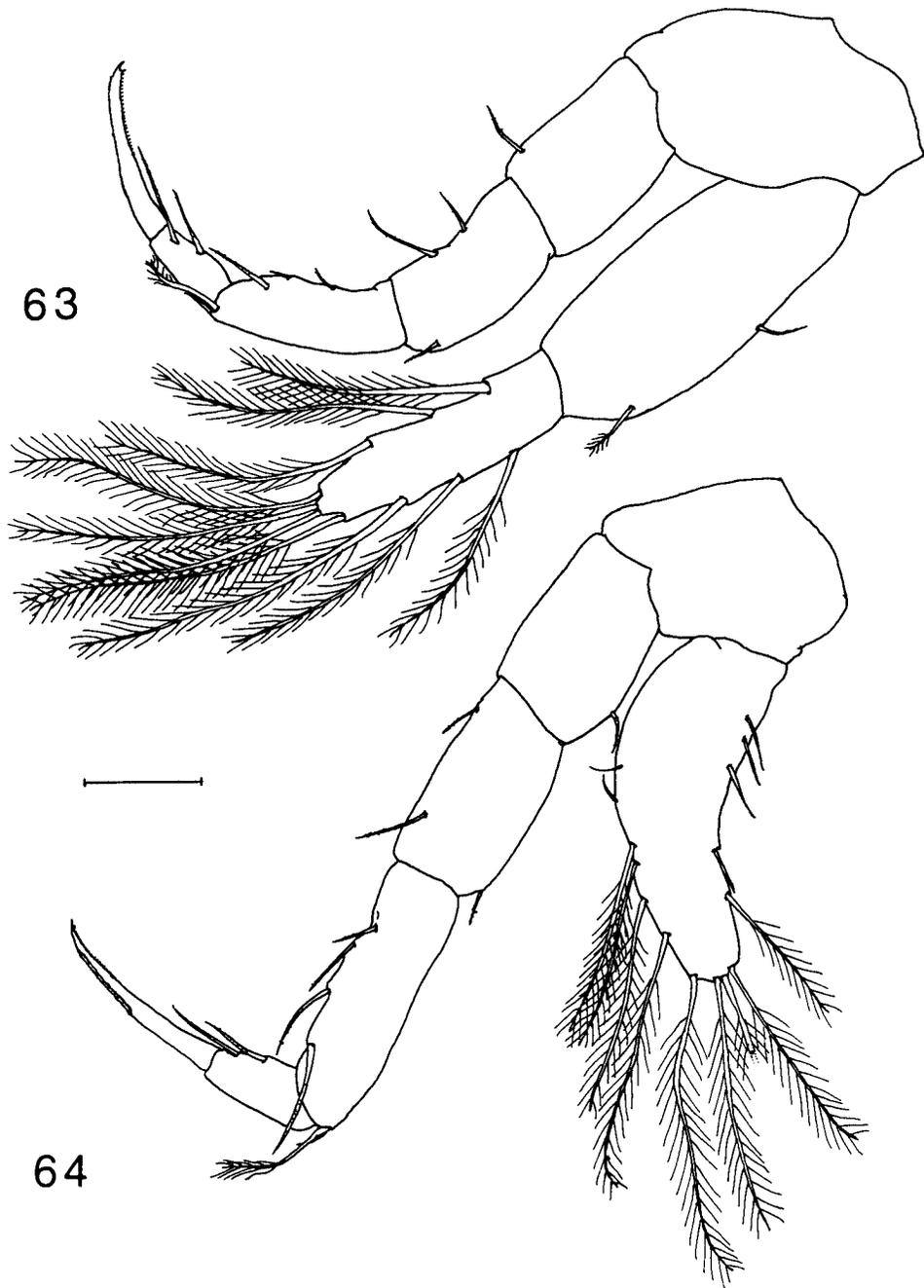
Pereiopod 3: endopodite having ischiomerus distally with teazel macrosetae (type IIB3), one on ventral and one on dorsal margin; carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin, distally with one teazel macroseta (type IIB3) on dorsal margin; propodus with three teazel macrosetae (type IIB3) medially on ventral margin, dorsodistally one teazel (type IIB3) and one subplumose (type IB2) macroseta; dactylus with two teazel macrosetae (type IIB3) on ventral margin, and well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one teazel macroseta (type IIB3) medially and one subplumose macroseta (type IB2) subterminally, second segment with three medial, two subterminal, two terminal and three lateral plumose macrosetae (type IB1).

Pereiopod 4: endopodite having ischiomerus distally with teazel macrosetae (type IIB3), one on ventral and one on dorsal margin; carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin, distally with one teazel macroseta (type IIB3) on dorsal margin; propodus with three teazel macrosetae (type IIB3) medially on ventral margin, dorsodistally one teazel (type IIB3) and one subplumose (type IB2) macroseta; dactylus with two teazel macrosetae (type IIB3) on ventral margin, and well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one teazel macroseta (type IIB3) medially and one subplumose macroseta (type IB2) subterminally, second segment with three medial, two subterminal, two terminal and three lateral plumose macrosetae (type IB1).

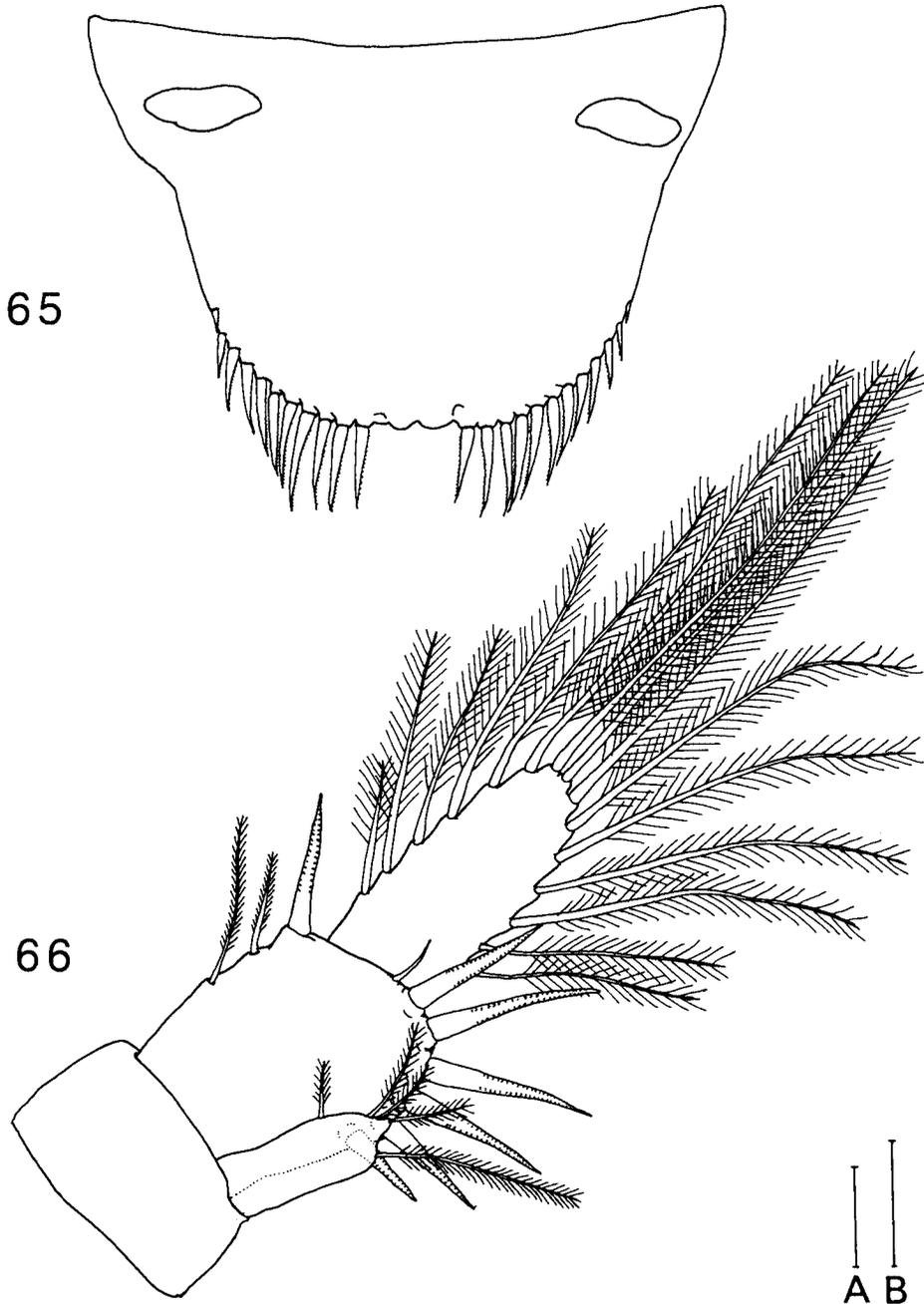
Pereiopod 5: endopodite having ischiomerus distally with teazel macrosetae (type IIB3), one on ventral and one on dorsal margin; carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin, distally one teazel macroseta (type IIB3) on dorsal margin; propodus with four teazel macrosetae (type IIB3) medially on ventral margin, dorsodistally one teazel (type IIB3) and one subplumose (type IB2) macroseta; dactylus with two teazel macrosetae (type IIB3) on ventral margin, and well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; exopodite 1-segmented with two vestigial and four medial plumose macrosetae (type IB1), two subterminal, two terminal, one lateral plumose macrosetae (type IB1), and four vestigial lateral macrosetae.

Thoracomere 8 of male carrying paired short, blunt penial lobes.

First pleopod articulate, 1-segmented, carrying one dorsal, one subterminal, one terminal and one ventral subplumose macroseta (type IB2). Second pleopod articulate, 1-segmented, somewhat longer than first pleopod, carrying two ventral, one terminal and one subterminal subplumose macrosetae (type IB2).



Figs. 63-64. *Thermosbaena mirabilis* (Monod, 1924), ♂. 63, pereopod 4. 64, pereopod 5. Scale indicated 0.1 mm.



Figs. 65-66. *Thermosbaena mirabilis* (Monod, 1924), ♂ and ♀. 65, pleotelson, ♀ (scale A). 66, uropod, ♂ (scale B). Scales indicated 0.1 mm.

Uropod with 2-segmented exopodite and 1-segmented endopodite; segment 1 of exopodite approximately as long as segment 2, segment 1 obliquely triangular, laterally one cuspidate macroseta (type IIA3) and two plumose macrosetae (type IB1), latter absent in female; in female medial armature consisting of six (terminally implanted one smaller) cuspidate macrosetae (type IIA3), in male six or seven (terminally implanted one smaller) cuspidate macrosetae (type IIA3), accompanied by small subplumose macroseta (type IB2); segment 2 with 13-14 plumose macrosetae (type IB1) in female, 15 in male, all along medial, terminal and lateral margins, subterminally two pairs of subplumose macrosetae (type IB2); endopodite two-thirds of length of first segment of exopodite, bearing 3 or 4 plumose macrosetae (type IB1) along medial, terminal and lateral margins, and two short subplumose macrosetae (type IB2), one subterminally and one sublaterally.

Pleotelson with anus opening subterminally, flanked on either side by a small lobe-like swelling that coincides with the distodorsal margin; in female a series of respectively 11 and 12 cuspidate macrosetae (type IIA3) is present on distal corners, in male a series of 13 cuspidate macrosetae (type IIA3) at both distal corners.

Variability.— In the limited number of specimens at my disposal I observed a slight variation in the number of cuspidate macrosetae along the distal corners of the female pleotelson only. At the distal corners there were 11 to 12 pairs of cuspidate macrosetae, or at one side 11, and 12 at the other. Monod (1924, 1927) observed some variability in the number of flagellum segments in both antennae 1 and 2.

Distribution.— The species is known from a limited number of thermal springs at El Hamma, viz. Aïn Baama (destroyed during or shortly after World War II (Dumont, 1978)), Aïn Sidi âbd el Khâdr and Aïn el Bordj (type locality).

Habitat.— Around the thermal springs at El Hamma the Romans build their bathing houses, of which a part is still in use. Except *Thermosbaena mirabilis* no other aquatic fauna is encountered. *Thermosbaena mirabilis* feeds on the blue-green algae *Symploca thermalis* Gom., *Spirulina labyrinthiformis* Gom., *Oscillatoria terebriformis* Ag., *Phormidium tenue* Gom., and *Phormidium papyraceum* Gom. (Monod, 1940: 20). The water at the type locality has a temperature ranging from 44.5 to 48°C (Bruun, 1940; Barker, 1960). The springs lie on one line with a chain of intermittent salt lakes, which are dessicated remnants of a lacustrine period in the Late Pliocene and Pleistocene (Barker, 1960). The water is highly mineralized (Monod, 1924a), and possibly brackish.

#### 4.4. Monodellidae Taramelli, 1954

Monodellidae Taramelli, 1954: 10; Monod, 1960: 528; Straškraba, 1967: 193; Pinkster, 1978: 234; Bousfield, 1982: 241; Schram, 1986: 222; Bowman & Iliffe, 1988: 221; Wagner, 1988: 1st page; Wagner, 1990: 123; Cals & Monod, 1991: 177; Pretus, 1991: 235; Wagner, 1992: 79.

Diagnosis.— Thermosbaenaceans with a elongate body. Transverse groove separates circa anterior one-third of carapace from posterior part. Rostrum pointed, but obscure. Small eye-stalks (ocular scales) absent. Main flagellum of antenna 1 6- to 12-segmented; accessory flagellum 5-segmented. Flagellum of antenna 2 5-(rarely 6-) segmented. Mandible with one plumidenticulate macroseta on second segment of palp; left pars incisiva 6-dentate, right pars incisiva 4-dentate; lacinia mobilis present

in left mandible; pars molaris blunt, robust and rounded, molar surface with spini-form processes. Maxilla 1 with 2- or 3-segmented palp; basipodal endite with seven toothed macrosetae. Basipodal endite 1 of maxilla 2 with simply built plumidenticulate macrosetae; basipodal endite 2 with single row of rake-like serrate macrosetae; basipodal endite 3 with two rows of rake-like serrate macrosetae; endopodite 2-segmented; exopodite reduced to triangular lobe with one simple macroseta, situated between basipodal endite 3 and endopodite. Maxilliped with three simple setulated pappose macrosetae on coxopodite; (sub)terminal margin of basipodite with two rows of plumidenticulate macrosetae; endopodite absent; epipodite well-developed. Seven pairs of legs; gnathopod biramous, basis and ischium coalesced, demarcation between these two segments obscure or absent, propodus with bicuspidate "spur", one serrulate macroseta forming "unguis"; pereopods 2 to 7 biramous, exopodite 2-segmented in pereopods 2 to 5, 1-segmented in pereopods 6 and 7; ovate microsetae on ischiomerus, propodus, dactylus, and exopodites; penis on eighth thoracomere medially of pereopod 7, long, blunt. First pleopod basally articulate, with five subplumose macrosetae; second pleopod articulate, longer than first, with five or more subplumose macrosetae; pleopods 3 to 5 absent. First segment of uropodal exopodite slightly shorter than endopodite, distomedially with three to five cuspidate macrosetae, distolaterally with two cuspidate and one subplumose macrosetae. Telson not fused with pleonite 6, two or three pairs of cuspidate macrosetae on the distal corners.

Discussion.— The family Monodellidae comprises two genera, viz. the monotypic genus *Monodella*, and the widespread polytypic genus *Tethysbaena*. In order to facilitate identification several keys are provided below to the generic level and to the species groups distinguished. The tables 1 and 2 will enable the identification of the species of the more complex species groups.

Key to the genera of Monodellidae  
based on characters visible without dissection

1. Antenna 1 with 10-segmented main flagellum; carpus of gnathopod with four long teazel macrosetae; second segment of exopodite of pereopod 5 without medial and lateral plumose macrosetae; telson with group of two cuspidate macrosetae on the distal corners ..... *Monodella* Ruffo, 1949 (p. 51)  
- Antenna 1 with 6- to 12-segmented main flagellum; carpus of gnathopod with three long teazel macrosetae; second segment of exopodite of pereopod 5 with medial plumose macroseta and with or without vestigial lateral macroseta; telson with group of three cuspidate macrosetae on the distal corners .....  
..... *Tethysbaena* gen. nov. (p. 63)

4.4.1. *Monodella* Ruffo, 1949

*Monodella* Ruffo, 1949a: 45.

*Monodella* (partim); Delamare Deboutteville, 1957: 66; Gordon, 1958: 1186; Monod, 1960: 528; Delamare Deboutteville, 1960: 244; Vandel, 1964: 143; Maguire, 1964: 932; Schmitt, 1965 (reprinted 1973): 88; Fryer, 1965: 49; Botosaneanu & Delamare Deboutteville, 1967: 22; Green, 1967: 168; Hessler, 1969: R367; Kaestner, 1970: 368; Bowman, 1971: 171; Zilch, 1972: 80; Noodt, 1974: 447;

Schminke, 1976: 295; Stock, 1976: 56; Russell-Hunter, 1979: 274; McLaughlin, 1980: 84, fig. 30A; Abele, 1982: 276; Bousfield, 1982: 241; Chelazzi & Messana, 1982: 161; Sieg, 1983a: 38; Newman, 1983: 113; Watling, 1983: 223; Sieg, 1984: 28; Boutin & Cals, 1985: 267; Cals & Boutin, 1985: 337; Bowman & Iliffe, 1986: 88; Stock, 1986a: 587; Cals & Cals-Usciati, 1986: 464; Schram, 1986: 216; Cals, 1987: 661, fig. 1; Monod & Cals, 1988: 101, pl. 2, fig. 2; Bowman & Iliffe, 1988: 224; Wagner, 1988: 1st page; Cals & Monod, 1988: 342; Wagner, 1989: 8; Wagner, 1990: 123; Stock, 1990: 697; Meštrov & Cals, 1991: 42; Pretus, 1991: 235; Casanova, 1993: 148.

*Modadella* (sic) (partim); Bousfield, 1982: 241.

Type species.— *Monodella stygicola* Ruffo, 1949, by monotypy.

Diagnosis.— Body length (antennae 1 and 2 excluded) up to circa 2.6 mm. Carapace reaching to second pedigerous somite. Third peduncular segment of antenna 1 with three subplumose macrosetae on terminal prominence; main flagellum 10-segmented; accessory flagellum 5-segmented. Flagellum of antenna 2 5-segmented. Left mandible with 3-dentate lacinia mobilis; pars molaris robust, rounded and molar surface covered by hexapartite spiniform processes. Palp of maxilla 1 without ovate microseta, basal segment of palp maxilla 1 entirely fused with second segment; basipodal endite with tall, obscurely digitate toothed macrosetae (two rather similar forms). Coxopodal endite of maxilla 2 with five stout plumose macrosetae; basipodal endite 1 with 5 simply built plumidenticulate macrosetae, tips of which finely pointed with subterminal serrations, and setules at the central portion of setal body. Pappose macrosetae of coxopodite of maxilliped with long, almost simple setules with a few setulettes distally (as in fig. 9); basipodite with submedially implanted plumidenticulate macroseta having a broad base, stout and blunt, basal portion of which with fine setules, setules distally of annulus distinctly larger in size and arranged in four rows slightly turning around macrosetal axis. Legs 1 to 7 biramous; gnathopod with one subplumose macroseta on first segment of exopodite; endopodite with entirely fused baso-ischium; carpus with four long fine teazel macrosetae; propodus with three teazel setae and bicuspidate "spur"; pereiopod 5 without medial and lateral plumose macrosetae on second segment of exopodite; pereiopods 6 and 7 with 1-segmented exopodite. Uropodal endopodite slightly longer than first segment of exopodite; first segment of exopodite with four cuspidate macrosetae on median margin. Telson more or less subquadrangular with group of two cuspidate macrosetae on distal corners.

Description.— As for the type species.

Remarks.— After 41 years new specimens of *M. stygicola* have been collected, and were kindly put at my disposal by Professor S. Ruffo for redescriptive purposes. Several differences with the other "*Monodella*" species lead to the above redefinition of *Monodella* and the creation of a new genus, *Tethysbaena* (vide infra). Primarily the differences can be noted in the number of subplumose macrosetae on the terminal prominence of the third peduncular segment of antenna 1 (*Monodella*: 3; *Tethysbaena*: 4), number of dentitions on the lacinia mobilis of the left mandible (*Monodella*: 3; *Tethysbaena*: 4), shape of the spiniform processes on the molar surface of the mandibular pars molaris (*Monodella*: hexapartite; *Tethysbaena*: tripartite), ovate microsetae on the palp of maxilla 1 (absent in *Monodella*; present in *Tethysbaena*), number of stout plumose macrosetae on the coxopodite of maxilla 2 (*Monodella*: 5; *Tethysbaena*: 2), number of plumose macrosetae on the first segment of the exopodite of the gnatho-

pod (*Monodella*: 1; *Tethysbaena*: none), number of serrate macrosetae on the carpus (*Monodella*: 4; *Tethysbaena*: 3), medial plumose macrosetae on the second segment of the exopodite of pereopod 5 (absent in *Monodella*; present in *Tethysbaena*), number of cuspidate macrosetae on the distal corners of the telson (*Monodella*: 2 pairs; *Tethysbaena*: 3 pairs). As no males are known of *Monodella*, it is not possible to establish if the presence of a well-developed 5-segmented endopodite of the maxilliped in the male of *Tethysbaena* is of generic or familial importance.

Distribution.— *Monodella stygicola* Ruffo, 1949, is the only known representative of this genus, and only known from a few specimens collected. *Monodella stygicola* is thus far known to occur in a limited part of the Salentine Peninsula.

Habitat.— The type material (four juvenile females) was collected in water with a chlorinity of 2.9‰ (Ruffo, 1949a, 1949b), thus from oligohaline waters.

#### 4.4.1.1. *Monodella stygicola* Ruffo, 1949 (figs. 67-88)

*Monodella stygicola* Ruffo, 1949a: 34, figs. 1-5; Ruffo, 1949b: 56, figs. 1-8; Stella, 1951a: 1; Stella, 1951b: 227; Stella, 1953: 226; S.L. Karaman, 1953: 57; Stella & Baschieri Salvadori, 1954: 467; Taramelli, 1954: 10; Stella, 1955: 464; Siewing, 1958: 197; Stella, 1959: 121; Barker, 1959: 209; Monod, 1960: 528; Delamare Deboutteville, 1960: 246, 629, figs. 89, 91b, 92b; Barker, 1960: 253; Pór, 1963: 49; Vandel, 1964: 144; Maguire, 1965: 149; Fryer, 1965: 84; Rouch, 1965: 717; Straškraba, 1967: 193; Green, 1967: 168; Hessler, 1969: R367; Meštrov & Lattinger-Penko, 1969: 111; Kaestner, 1970: 369; Zilch, 1972: 80; Stock, 1976: 56; Pinkster, 1978: 234; Abele, 1982: 276; Chelazzi & Messana, 1982: 170; Boutin & Cals, 1985: 267; Pesce, 1985: 131, 143; Stock, 1986a: 587; Schram, 1986: 221; Cals & Monod, 1988: 342; Meštrov & Cals, 1991: 42; Pretus, 1991: 235.

*Monodella* (partim); Botosaneanu & Delamare Deboutteville, 1967: 22, fig.; Wagner, 1990: 123.

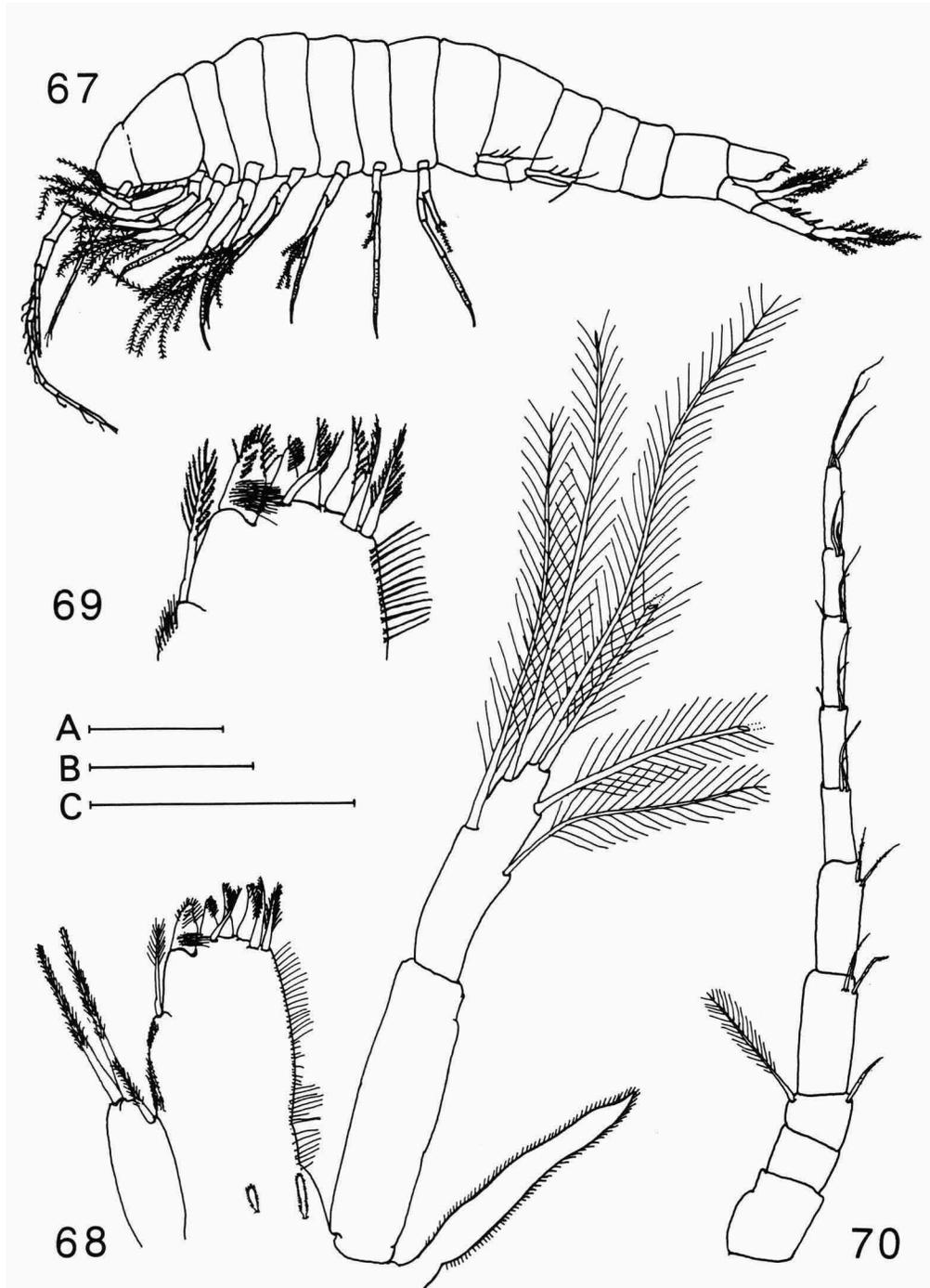
Material.— **Italy**: 5 ♀♀; Prov. Lecce, Puglia, Castro, l'Abisso di Castromarina; collected by S. Inguscio; 26.xii.1989; ZMA coll. no. C.A. 8101 (1 specimen), MCSNV (4 specimens) [topotypes].

- 1 ♀; Prov. Lecce, Puglia, Scraceto Piccola; in well; collected by S. Inguscio; 16.ix.1989; MCSNV.

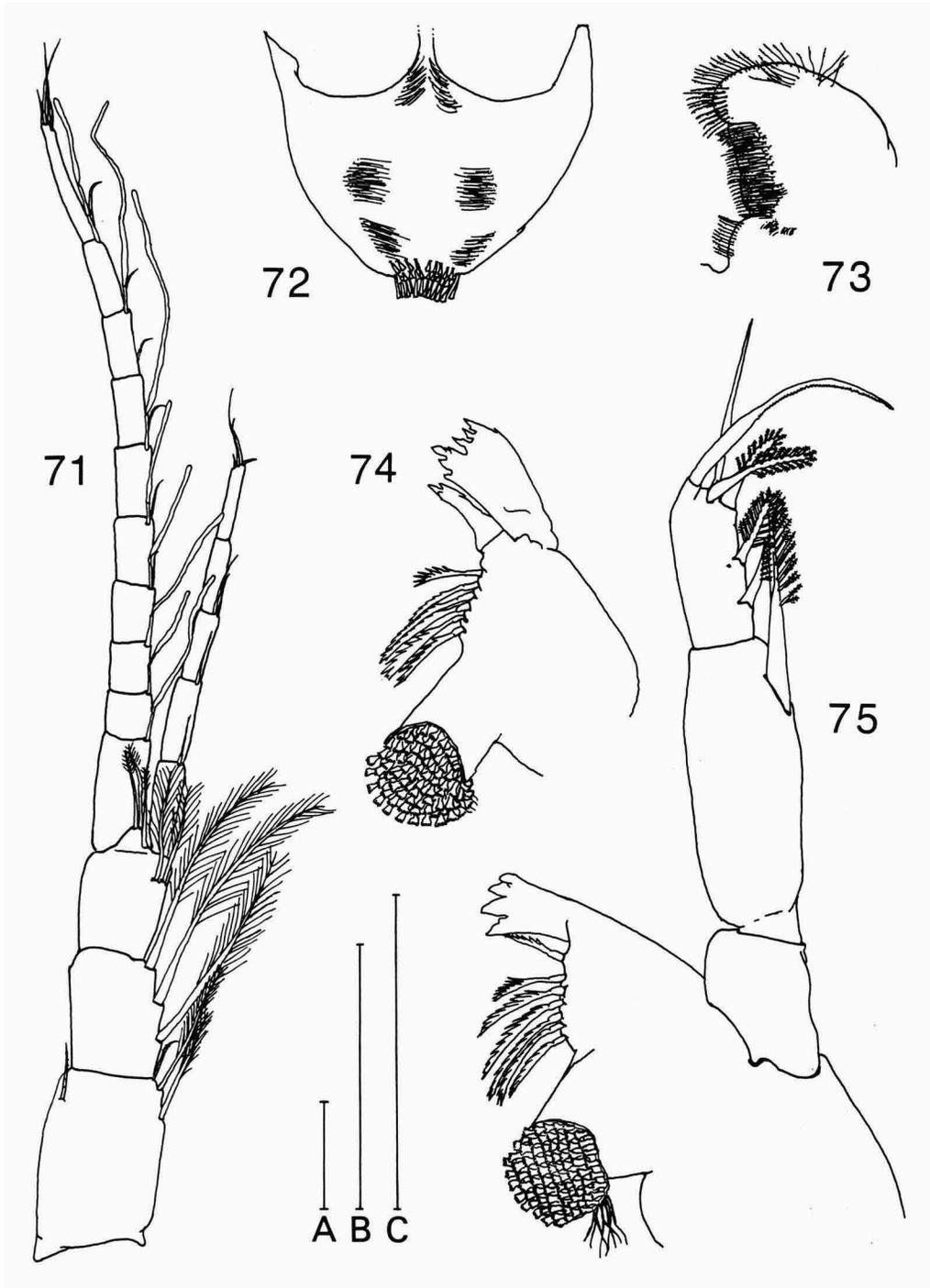
Description.— Body length (antennae 1 and 2 excluded) of female up to 2609 µm in the material studied.

Antenna 1 with 3-segmented peduncle; peduncular segments 1 to 3 with two, three, and two (placed somewhat more mediodorsally) long plumose macrosetae (type IA1) on their median margin; peduncular segment 1 with one teazel macroseta (type IIB3) on both mediobasal and distolateral margin, segment 3 with one subterminal and two terminal subplumose macrosetae (type IB2) on terminal prominence; main flagellum 10-segmented, one aesthetasc (type IIA6) on segments 1 to 6, 8 and 9, segments 4 to 9 with one mediobasal simple macroseta (type IIA1), last segment terminally with one sublateral and three simple macrosetae (type IIA1) of unequal length; accessory flagellum 5-segmented, segments 1 and 2 with one mediobasal simple macroseta (type IIA1), segment 3 with two mediobasal simple macrosetae (type IIA1), segment 4 naked, last segment (sub)terminally with four simple macrosetae (type IIA1) of unequal length.

Antenna 2 uniramous, peduncle 5-segmented, segments 1 and 2 naked, segment 3 with one teazel macroseta (type IIB3) mediobasally, and one plumose macroseta (type IA1) distolaterally, segments 4 and 5 with two teazel macrosetae (type IIB3) on



Figs. 67-70. *Monodella stygicola* (Ruffo, 1949), ♀. 67, lateral view of habitus (2609  $\mu\text{m}$ ). 68, maxilliped (scale B). 69, distal portion of basipodal endite of maxilliped (scale C). 70, antenna 2 (scale A). Scales indicated 0.1 mm.



Figs. 71-75. *Monodella stygicola* (Ruffo, 1949), ♀. 71, antenna 1 (scale A). 72, labrum. 73, lobe of labium (figs. 72-73 scale B). 74, corpus mandibula of left mandible. 75, right mandible. (figs. 74-75 scale C). Scales indicated 0.1 mm.

mediodistal margin; flagellum 5-segmented, segments 1 to 4 each with two simple macrosetae (type IIA1) mediodistally, segments 2 and 3 with one additional simple macroseta (type IIA1) on the dorsolateral margin, segment 5 with three simple macrosetae (type IIA1) of unequal length terminally.

Labrum somewhat longer than wide; its proximal portion with ciliate microsetae (type 2b); apically with ovate microsetae (type 2a).

Mandible with 3-segmented palp, basal palp segment short and unarmed, second segment slender with one plumidenticulate macroseta (type IA3), third segment with five plumidenticulate macrosetae (type IA3), (sub)apically one simple (type IIA1) and one long serrulate macroseta (type IIB1(b)); corpus mandibulae differentiated into pars incisiva, lacinia mobilis (absent in right mandible), cleaning seta (modified type IIB1), row of five (left mandible) or six (right mandible) slender serrate macrosetae (type IIB1(a)), and robust pars molaris having its molar surface covered with spini-form processes with hexapartite tips, and distally circa eight ciliate microsetae (type 2b).

Labium deeply cleft, its two lobes with converging tips, internal distal margin with ciliate microsetae (type 2b), outer distal margin less densely covered by taller ciliate microsetae (type 2b).

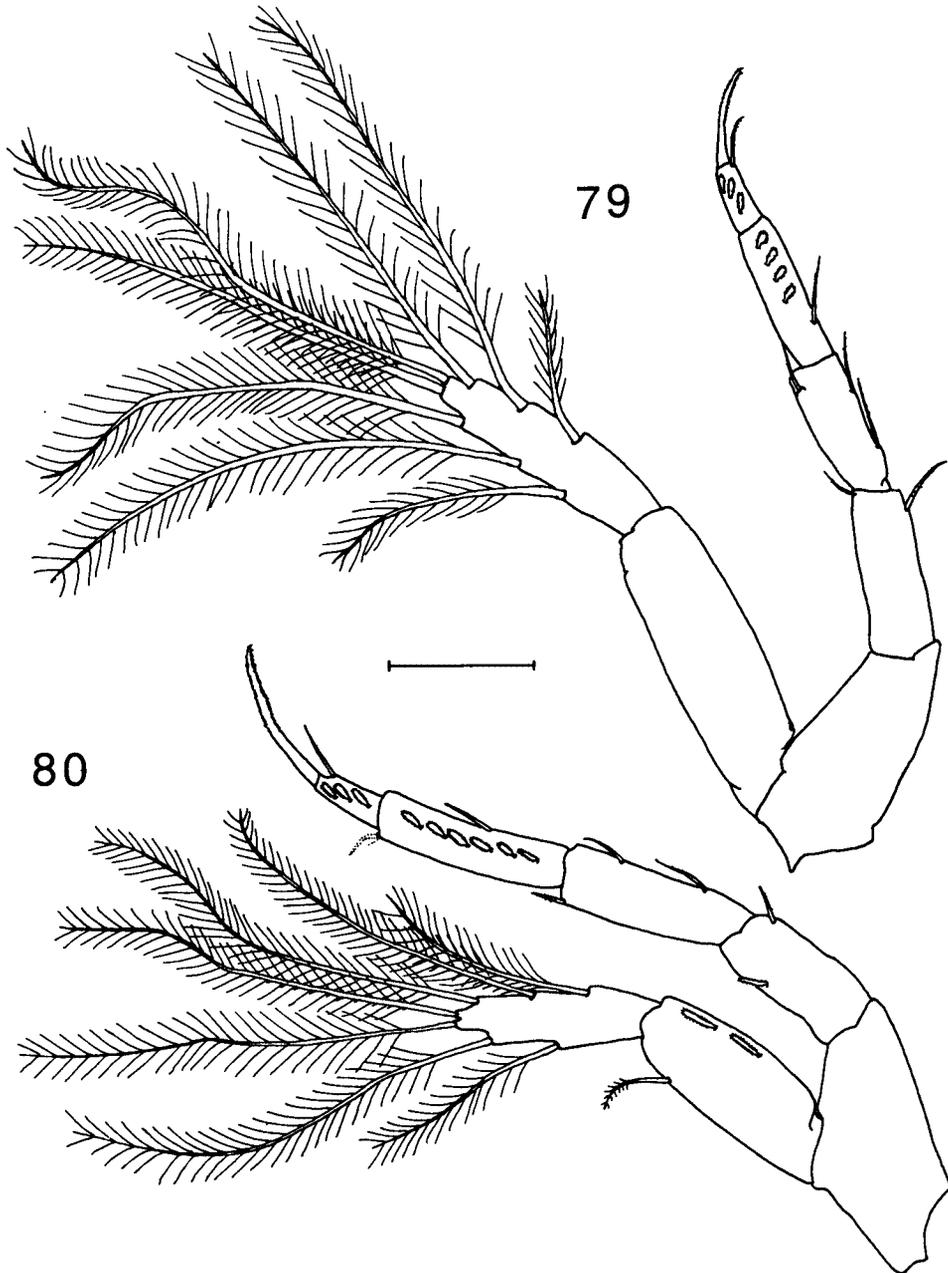
Maxilla 1 differentiated into precoxal endite with medial armature of ten plumidenticulate macrosetae (type IA3) (five medioterminally and five lateroterminally); basipodal endite with distal armature of seven toothed macrosetae (type III1), four slightly bend ending in a sharp pointed tip, three somewhat stouter, less sharply pointed; endopodite forming a 2-segmented palp, original basal segment fused with second segment, fused segment long, with one simple macrosetae (type IIA1), and one comparatively large unisetulate macroseta (type IB3(a)), distal segment small with one distal implanted simple macroseta (type IIA1) and one stout (obscure serrate) unisetulate macroseta (type IB3(a)).

Maxilla 2: complexly built, a coxopodal endite medially with 16 fine plumose macrosetae (type IB1), four rod macrosetae (type IIA2) mediodorsally, and five stout plumose macrosetae (type IB1); three basipodal endites: basipodal endite 1 with five rather simply built plumidenticulate macrosetae (type IA3), tips finely pointed with subterminal serrations, setules at central portion of the setal body; basipodal endite 2 with five rake-like serrate macrosetae (type IIB1(d)) at terminal margin; basipodal endite 3 with seven somewhat more strongly barbed rake-like macrosetae (type IIB1(d)), increasing in size laterally and arranged in two rows of three and four macrosetae, respectively; exopodite reduced to triangular lobe with one simple macroseta (type IIA1); endopodite 2-segmented, with seven simple macrosetae (type IIA1).

Maxilliped: coxopodal endite a tapering lobe with one short and two long pap-pose macrosetae (type IA2) having long almost simple setules with a few setulettes distally (fig. 9); basipodal endite with several differently shaped plumidenticulate macrosetae (type IA3), all with long setules, a tall one medially, three terminal short ones with very broad basis and three taller subterminally, submedially with an additional much stouter plumidenticulate macroseta (type IA3) with a very broad basis, its basal portion with fine setules, setules distally of annulus distinctly larger in size and arranged in four rows slightly turning around the macrosetal axis; exopodite 2-segmented, segment 2 with one medial, two subterminal, two terminal and one later-



Figs. 76-78. *Monodella stygicola* (Ruffo, 1949), ♀. 76, maxilla 2. 77, maxilla 1. (figs. 76-77 scale B). 78, gnathopod (scale A). Scales indicated 0.1 mm



Figs. 79-80. *Monodella stygicola* (Ruffo, 1949), ♀. 79, pereiopod 2. 80, pereiopod 3. Scale indicated 0.1 mm.

al plumose macrosetae (type IB1); epipodite a pointedly tapering lobe with simple microsetae (type 1a) along margin.

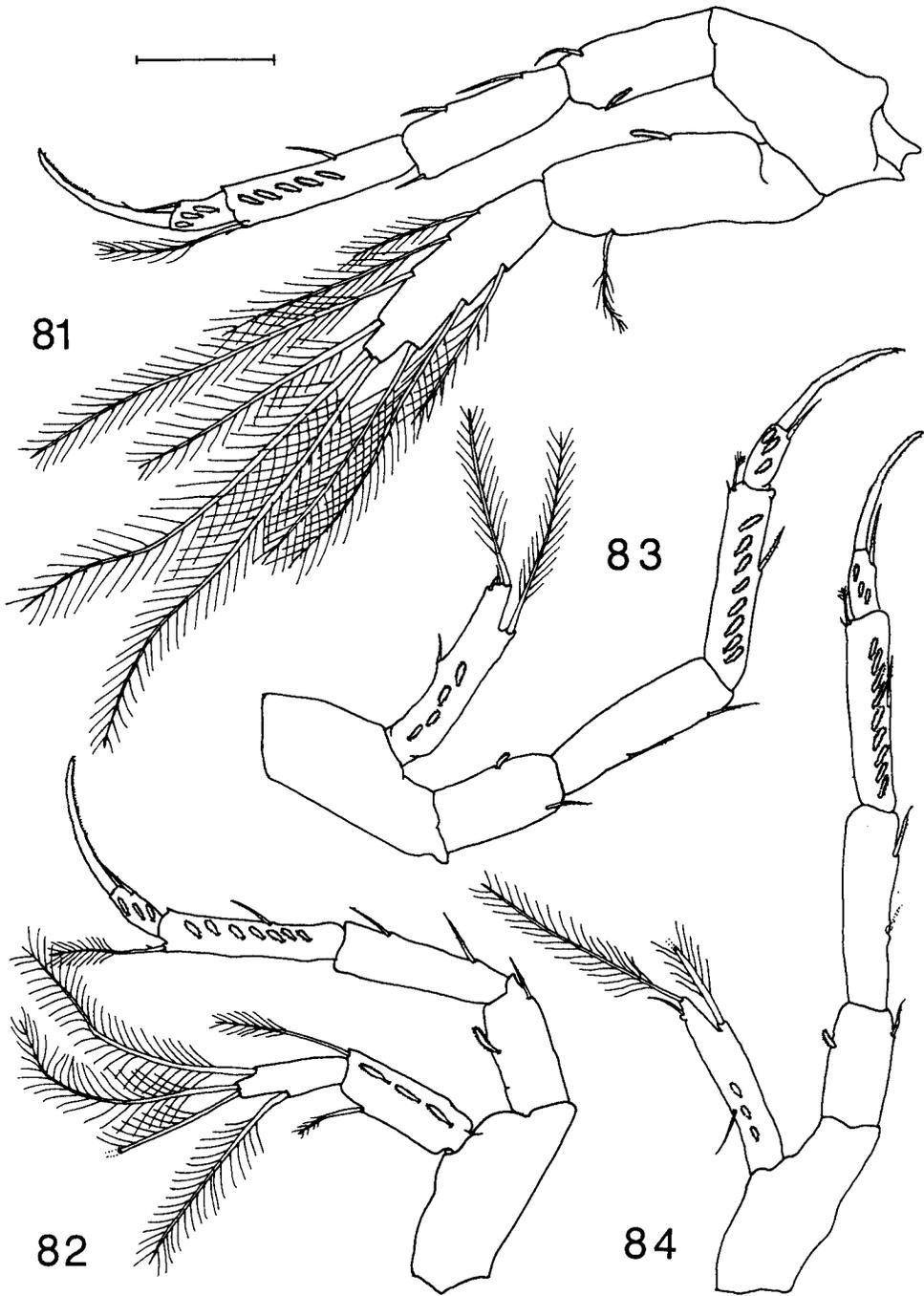
Gnathopod: with naked basal segment; exopodite 2-segmented, proximal segment subterminally with one subplumose macroseta (type IB2), distal segment with two medial, two subterminal, two terminal and two lateral plumose macrosetae (type IB1); merus of endopodite longest segment, unarmed, carpus short, armed with four long teazel macrosetae (type IIB3), two medially and two subterminally, propodus longer, armed with three teazel macrosetae (type IIB3) in distal half, and moreover with long medioterminal bicuspidate "spur", dactylus with two unequal teazel macrosetae (type IIB3) on ventral margin, one on dorsal margin, terminal "unguis" formed by stout serrulate macroseta (type IIB1(b)).

Pereiopod 2: endopodite having ischiomerus with distally teazel macrosetae (type IIB3), one on ventral and one on dorsal margin; carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin, distally one teazel macroseta (type IIB3) on dorsal margin; propodus with one teazel macroseta (type IIB3) medially on ventral margin, female with four to five ovate microsetae (type 2a); dactylus with one teazel macroseta (type IIB3) on ventral margin, three ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite naked, second segment with two medial, two subterminal, two terminal and two lateral plumose macrosetae (type IB1).

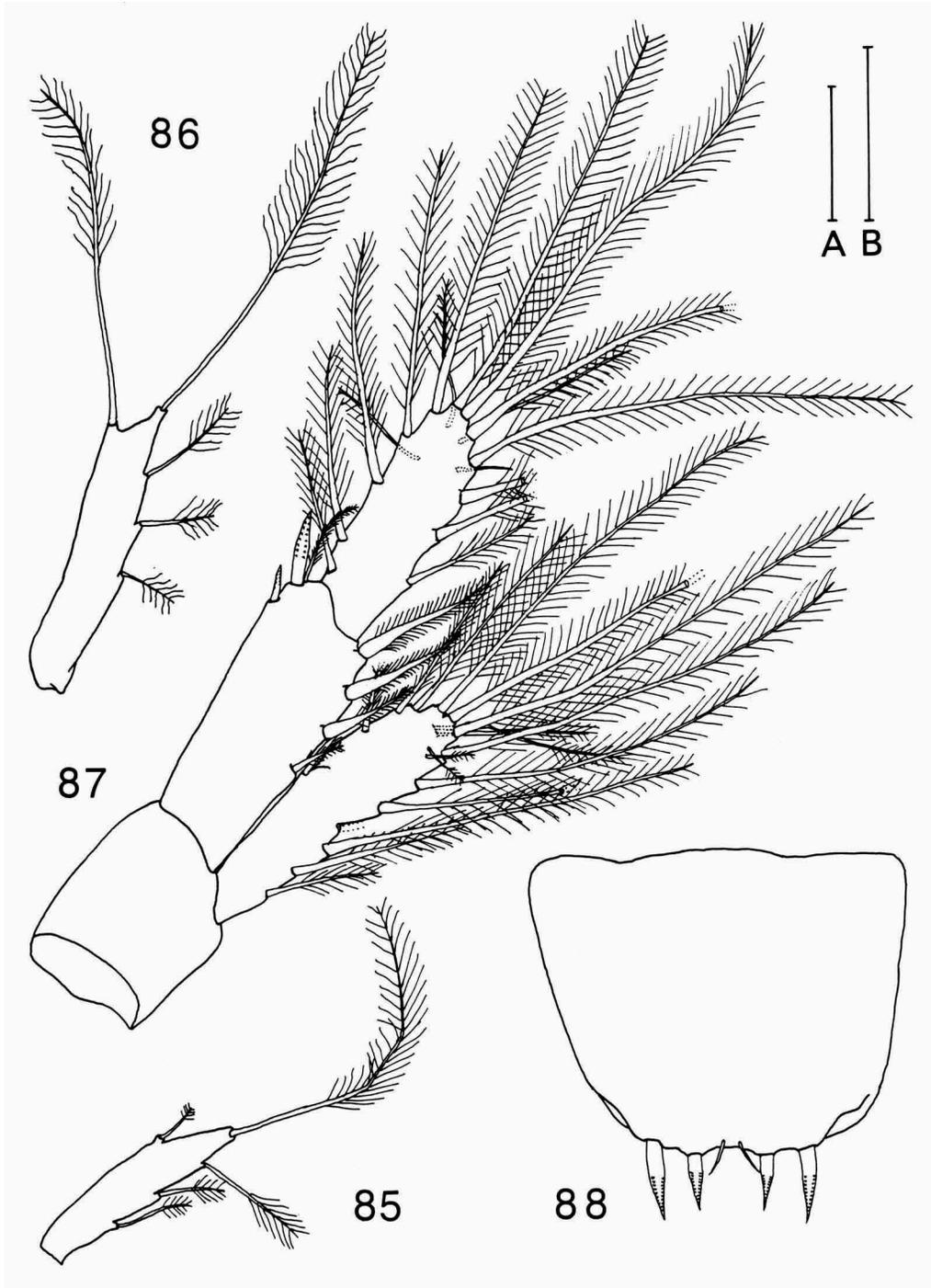
Pereiopod 3: endopodite having distally on ischiomerus one teazel macroseta (type IIB3) on ventral margin, mediodorsally one ovate microseta (type 2a); carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin, distally one teazel macroseta (type IIB3) on dorsal margin; propodus with one teazel macroseta (type IIB3) medially on ventral margin, female with five ovate microsetae (type 2a); dactylus with one teazel macroseta (type IIB3) on ventral margin, three ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subplumose macroseta (type IB2) subterminally and one ovate microseta (type 2a), second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae (type IB1).

Pereiopod 4: endopodite having distally on ischiomerus one teazel macroseta (type IIB3) on ventral margin, mediodorsally one ovate microseta (type 2a); carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin, distally one teazel macroseta (type IIB3) on dorsal margin; propodus with one teazel macroseta (type IIB3) medially on ventral margin, female with six ovate microsetae (type 2a); dactylus with one teazel macrosetae (type IIB3) on ventral margin, three ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subplumose macroseta (type IB2) subterminally, two ovate microseta (type 2a), second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae (type IB1).

Pereiopod 5: endopodite having distally on ischiomerus one teazel macroseta (type IIB3) on ventral margin, mediodorsally one ovate microseta (type 2a); carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin; propodus with one teazel macroseta (type IIB13) medially on ventral margin, female with six to seven ovate microsetae (type 2a); dactylus with one teazel macroseta



Figs. 81-84. *Monodella stygicola* (Ruffo, 1949), ♀. 81, pereopod 4. 82, pereopod 5. 83, pereopod 6. 84, pereopod 7. Scale indicated 0.1 mm.



Figs. 85-88. *Monodella stygicola* (Ruffo, 1949), ♀. 85, pleopod 1. 86, pleopod 2. (figs. 85-86 scale B). 87, uropod. 88, telson. (figs. 87-88 scale A). Scales indicated 0.1 mm.

(type IIB3) on ventral margin, three ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subplumose macroseta (type IB2) subterminally on medial and lateral margin and three ovate microseta (type 2a), second segment with two subterminal and two terminal plumose macrosetae (type IB1).

Pereiopod 6: endopodite having distally on ischiomerus one teazel macroseta (type IIB3) on ventral margin, mediodorsally one ovate microseta (type 2a); carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin; propodus with one teazel macroseta (type IIB3) medially on ventral margin, female with eight to nine ovate microsetae (type 2a); dactylus with one teazel macroseta (type IIB3) on ventral margin, three ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; exopodite 1-segmented with one subterminal and one terminal plumose macrosetae (type IB1), one medial, one subterminal and one terminal vestigial macroseta, four ovate microsetae (type 2a) present.

Pereiopod 7: endopodite having distally on ischiomerus one teazel macroseta (type IIB3) on ventral margin, mediodorsally one ovate microseta (type 2a); carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin; propodus with one teazel macroseta (type IIB3) medially on ventral margin, female with nine ovate microsetae (type 2a), dactylus with one teazel macroseta (type IIB3) on ventral margin, three ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; exopodite 1-segmented with one subterminal and one terminal plumose macrosetae (type IB1), one subterminal and one medial vestigial macroseta, three ovate microsetae (type 2a) present.

First pleopod 1-segmented, carrying three dorsal, one terminal and one subterminal subplumose macrosetae (type IB2). Second pleopod 1-segmented, taller than first pleopod, with three dorsal, one terminal and one subterminal subplumose macrosetae (type IB2).

Uropod 2-segmented exopodite and 1-segmented endopodite; segment 1 of exopodite slightly longer than segment 2, segment 1 laterally with two cuspidate macrosetae (type IIA3) and one plumose macroseta (type IB1), medially with four plumose macrosetae (type IB1), segment 2 with 12 plumose macrosetae (type IB1) all along medial, terminal and lateral margins, subterminally two pairs of subplumose macrosetae (type IB2); distal margin of endopodite not protruding beyond distal margin of first segment of exopodite, bearing 14 plumose macrosetae (type IB1) along medial, terminal and lateral margins, and two pairs of short subplumose macrosetae (type IB2) implanted subterminally and submedially.

Telson subquadrangular in outline, anus subterminally, flanked on either side by lobe-like swellings that do not protrude beyond terminal upper margin, a group of two cuspidate macrosetae (type IIA3) on each distal corner, medially separated by stretch with two glandular simple macrosetae (type IIA1).

Variability.— Not observed.

Distribution.— *Monodella stygicola* was originally found in a cave (l'Abisso) near Castromarina. The recently collected specimens were captured at the type-locality and from a well at Scraceto Piccola, both situated in a restricted part of the Salentine Peninsula, Italy.

Habitat.— Both localities where *M. stygicola* was found are situated close to the coast in deposits of Pliocene age. The water can be characterized as oligohaline. No data of accompanying fauna are known to me.

#### 4.4.2. *Tethysbaena* gen. nov.

*Monodella* (partim); Delamare Deboutteville, 1957: 66; Gordon, 1958: 1186; Monod, 1960: 528; Delamare Deboutteville, 1960: 244; Vandell, 1964: 143; Maguire, 1964: 932; Fryer, 1965: 49; Botosaneanu & Delamare Deboutteville, 1967: 22; Green, 1967: 168; Hessler, 1969: R367; Kaestner, 1970: 368; Bowman, 1971: 171; Zilch, 1972: 80; Noodt, 1974: 447; Schminke, 1976: 295, 298; Stock, 1976: 56; Russell-Hunter, 1979: 274; McLaughlin, 1980: 84, fig. 30A; Watling, 1981: 205; Abele, 1982: 276; Bousfield, 1982: 241; Chelazzi & Messana, 1982: 161; Sieg, 1983a: 38; Newman, 1983: 113; Watling, 1983: 223; Boutin & Cals, 1985: 267; Cals & Boutin, 1985: 337; Bowman & Iliffe, 1986: 88; Stock, 1986a: 587; Cals & Cals-Usciati, 1986: 464; Cals, 1987: 661, fig. 1; Monod & Cals, 1988: 101, pl. 2, fig. 2; Bowman & Iliffe, 1988: 224; Wagner, 1988: 1st page; Cals & Monod, 1988: 342; Anonymous, 1988: 12th page; Wagner, 1989: 8; Wagner, 1990: 123, fig. 1; Stock, 1990: 697; Meštrov & Cals, 1991: 42; Cals & Cals-Usciati: 163, 166, 168; Pretus, 1991: 235; Casanova, 1993: 148.

*Modadella* (sic) (partim); Bousfield, 1982: 241.

Type species.— *Tethysbaena juriaani* spec. nov.

Diagnosis.— Body length (antennae 1 and 2 excluded) up to circa 3.7 mm, but in most species generally between 2 and 3 mm. Carapace reaching to second or third pedigerous somite. Third peduncular segment of antenna 1 with four subplumose macrosetae on terminal prominence; main flagellum 6- to 12-segmented; accessory flagellum 5-segmented. Flagellum of antenna 2 5-(rarely 6)-segmented. Left mandible with 4-dentate lacinia mobilis, pars molaris robust, rounded; molar surface covered with tripartite spiniform processes. Palp of maxilla 1 with ovate microseta, basal segment of palp maxilla 1 more or less fused with second segment, distal margin of basal segment clearly or obscurely demarcated; basipodal endite with distinctly digitate, blunt-tipped toothed macrosetae (two distinct forms). Coxopodal endite of maxilla 2 with two stout plumose macrosetae; basipodal endite 1 with five to seven simply built plumidenticulate macrosetae, tips of which finely pointed with subterminal serrations, and with setules at central portion of setal body. Pappose macrosetae of coxopodite of maxilliped with long, almost simple setules with a few setulettes distally (as in fig. 9); male with endopodite well-developed into a 5-segmented "clasper"; basipodite with submedially implanted, plumidenticulate, tall, stout and pointed macrosetae, basal portion of which with fine setules, setules distally of the annulus distinctly larger in size and arranged in four rows slightly turning around the macrosetal axis. Legs 1 to 7 biramous; gnathopod with naked first exopodite segment, in baso-ischium of endopodite ischium obscurely demarcated; carpus with three long fine teazel macrosetae; propodus with two or three teazel macrosetae and bicuspidate "spur"; pereopod 5 with medial (and often lateral) plumose macrosetae on second segment of exopodite; pereopods 6 and 7 with 1-segmented exopodite. Uropodal endopodite about as long as first segment of exopodite; first segment of exopodite with two to five cuspidate macrosetae on the median margin. Telson subquadrangular with group of three cuspidate macrosetae on distal corners.

Description.— Antenna 1 with 3-segmented peduncle; peduncular segments 1 to 3 with long plumose macrosetae (type IA1) on median margin; peduncular segment 1

mediodorsally with four teazel (type IIB3) and one subplumose macrosetae (type IB2), dorsolaterally with one teazel macroseta (type IIB3) and four subplumose macrosetae (type IB2), segment 2 distodorsally with transverse row of three teazel macrosetae (type IIB3) towards lateral margin, a transverse row of one subplumose (type IB2) and three teazel (type IIB3) macrosetae towards medial margin and one teazel macroseta (type IIB3) accompanying the second to fourth medial plumose macrosetae, segment 3 with one submedial teazel macroseta (type IIB3), two teazel macrosetae (type IIB3) on lateral margin, one subterminal and three terminal subplumose macrosetae (type IB2) on terminal prominence; main flagellum 6- to 12-segmented, in male one aesthetasc (type IIA6) on (nearly) all segments, in female one aesthetasc on segments 4 to distal, segments 2 to 5 with two mediodistal and dorsolateral simple macrosetae (type IIA1), last segment (sub)terminally with simple macrosetae (type IIA1) of unequal length; accessory flagellum 5-segmented, segments 1 to 4 with two mediodistal simple macrosetae (type IIA1), segment 3 with additional distolateral simple macroseta (type IIA1), last segment (sub)terminally with simple macrosetae (type IIA1) of unequal length.

Antenna 2: peduncle 5-segmented, segments 1 and 2 naked, segment 3 dorsolaterally with one subplumose (type IB2) and mediodistally two long teazel macrosetae (type IIB3), segment 4 with three or four, and segment 5 with four teazel macrosetae (type IIB3) on medial and mediodistal margins; flagellum 5- to 6-segmented, segments 1 to 4(-5) each with two simple macrosetae (type IIA1) mediodistally, segments 2 and 3(-4) with one additional simple macroseta (type IIA1) on dorsolateral margin, segment 5 (sub)terminally with simple macrosetae (type IIA1) of unequal length.

Labrum somewhat longer than wide; its proximal portion with ciliate microsetae (type 2b); apically with ovate microsetae (type 2a).

Mandible with 3-segmented palp, basal palp segment short and unarmed, second segment slender with one plumidenticulate macroseta (type IA3), third segment with species-dependant number of plumidenticulate macrosetae (type IA3), (sub)apically one simple (type IIA1) and one long serrulate macroseta (type IIB1(b)); corpus mandibulae differentiated into pars incisiva, lacinia mobilis (absent in right mandible), cleaning seta (modified type IIB1), row of six slender serrate macrosetae (type IIB1(a)), and robust pars molaris having molar surface covered with spiniform processes with tripartite tips, and distally some ciliate microsetae (type 2b).

Labium deeply cleft, its two lobes with converging tips, internal distal margin with ciliate microsetae (type 2b), outer distal margin less densely covered by taller ciliate microsetae (type 2b).

Maxilla 1 differentiated into precoxal endite with medial armature of ten plumidenticulate macrosetae (type IA3), two medially and eight terminally implanted; basipodal endite with distal armature of seven toothed macrosetae (type III1), four distinctly digitate, three with blunt tips; endopodite forming a 2- or 3-segmented palp, basal segment unarmed, its distal margin obscurely or distinctly demarcated from second segment, second segment long with one or two simple macrosetae (type IIA1), one comparatively large unisetulate macroseta (type IB3(a)) with a species dependent number of setules, and an ovate microseta (type 2a), third segment small with one distally implanted simple macroseta (type IIA1) and one obscure or well-developed unisetulate macroseta (type IB3(a)).

Maxilla 2: complexly built, a coxopodal endite medially with 12 fine plumose macrosetae (type IB1), six rod macrosetae (type IIA2) mediodorsally, and two stout plumose macrosetae (type IB1); three basipodal endites: basipodal endite 1 with plumidenticulate macrosetae (type IA3); basipodal endite 2 with rake-like serrate macrosetae (type IIB1(d)) at terminal margin, and two modified longer serrate subterminal macrosetae, of which one has a more developed rake, while the other has its rake strongly reduced to a narrow, pointed tip; basipodal endite 3 with more strongly barbed rake-like macrosetae (type IIB1(d)), increasing in size laterally and arranged in two rows; exopodite reduced to triangular lobe with one simple macroseta (type IIA1); endopodite 2-segmented with simple macrosetae (type IIA1).

Maxilliped sexually dimorphic; female endopodite reduced to a small lobe provided with one stout simple (micro-?)seta (type 1a?), male endopodite well-developed into 5-segmented "clasper", first segment (ischium) with two short mediobasal simple macrosetae (type IIA1), and with or without club microsetae (type 1d), second segment (merus) with 1 medial and 1 medioterminal simple macroseta (type IIA1), and with or without club microsetae (type 1d) on the distal portion, third segment (carpus) with 1 medial and 1 medioterminal simple macroseta (type IIA1) and with or without club microsetae (type 1d), fourth segment (propodus) slightly longer than carpus, with few short lateral simple macrosetae (type IIA1), and with or without club microsetae; coxopodal endite forming tapering lobe with one short and two long pappose macrosetae (type IA2), which have long almost simple setules with a few setulettes distally (as in fig. 9); basipodal endite with several plumidenticulate macrosetae (type IA3) all with long setules, medially, subterminally, and terminally, submedially with one additional much stouter plumidenticulate macroseta (type IA3) with a finely setulated basal portion, setules distad of annulus distinctly larger in size and arranged in four rows slightly turning around macrosetal axis; exopodite 2-segmented, segment 2 with medial, subterminal, terminal and (or) lateral plumose macrosetae (type IB1); epipodite pointed, tapering lobe with simple microsetae (type 1a) along margin.

Gnathopod with plumose macrosetae (type IA1) on basal segment (often broken off); exopodite 2-segmented, proximal segment unarmed, distal segment with medial, subterminal, terminal, and (or) lateral plumose macrosetae (type IB1); basischium of endopodite with indistinct, obscurely or clearly demarcated "free" ischium, merus longest segment with subterminally teazel macrosetae (type IIB3), one on ventral and dorsal margins; carpus short, with three long teazel macrosetae (type IIB3); propodus longer, with ventrally two teazel macrosetae (type IIB3) on distal half, one subplumose macroseta (type IB2) distodorsally, and moreover with a long medioterminal bicuspidate "spur"; dactylus with two unequal teazel macrosetae (type IIB3), one on ventral margin and one on dorsal margin, terminal "unguis" is formed by stout serrulate macroseta (type IIB1(b)).

Pereiopods 2 to 5: endopodite having ischiomerus with distal teazel macrosetae (type IIB3), one on ventral and one on dorsal margin; carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin, dorsodistally one teazel macroseta (type IIB3), mediodorsally with or without one ovate microseta (type 2a); propodus with one or two teazel macrosetae (type IIB3) medially on ventral margin, dorsodistally one teazel (type IIB3) and one subplumose (type IB2) macroseta, spe-

cies- (sometimes also sex-) dependent number of ovate microsetae (type 2a); dactylus with one or two teazel macrosetae (type IIB3) on ventral margin, species-dependent number of ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subplumose macroseta (type IB2) subterminally, with or without ovate microsetae (type 2a), second segment with medial, subterminal, terminal, and (or) lateral plumose macrosetae (type IB1).

Pereiopods 6 to 7: endopodite having ischiomerus with distal teazel macrosetae (type IIB3), one on ventral and one on dorsal margin, mediodorsally with or without one ovate microseta (type 2a); carpus with two teazel macrosetae (type IIB3) medially and distally on ventral margin, dorsodistally one teazel macroseta (type IIB3); propodus with one or two teazel macrosetae (type IIB3) medially on ventral margin, dorsodistally one teazel (type IIB3) and one subplumose (type IB2) macroseta, species- (sometimes also sex-) dependent number of ovate microsetae (type 2a); dactylus with one or two teazel macrosetae (type IIB3) on ventral margin, with a species-dependent number of ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; exopodite 1-segmented with one medial and one subterminal plumose macroseta (type IB1), and (or) vestigial macrosetae, with or without ovate microsetae (type 2a).

In males simple, and rather tall penes medially associated with coxopodite of pereopod 7.

First pleopod 1-segmented, carrying three to four dorsal, one terminal and one subterminal subplumose macrosetae (type IB2). Second pleopod 1-segmented, taller than first pleopod, with three or four dorsal, one terminal, one subterminal, and with or without one additional dorsolateral subplumose macrosetae (type IB2).

Uropod with 2-segmented exopodite and 1-segmented endopodite; first segment of exopodite laterally with cuspidate macrosetae (type IIA3) and plumose macroseta (type IB1), medially with stout cuspidate macrosetae (type IIA3), accompanied by a small subplumose macroseta (type IB2); segment 2 with plumose macrosetae (type IB1) all along medial, terminal and lateral margins, subterminally two pairs of subplumose macrosetae (type IB2) are implanted; endopodite with plumose macrosetae (type IB1) along medial, terminal and lateral margins, and short subplumose subterminal and sublateral macrosetae (type IB2).

Telson subquadrangular with group of three cuspidate (type IIA3) on each distal corner, terminal stretch in between.

Remarks.— When Stella (1951a) described *Monodella argentarii* she provisionally placed the species in the genus *Monodella*, as it was closer to *M. stygicola* than to the only other known species at that time, *Thermosbaena mirabilis*. Ruffo's description seems to be based on immature specimens, so later authors did not question *M. stygicola* and "*M. argentarii*" being congeneric. The generic differences between *Monodella* and *Tethysbaena* have been indicated in detail in the treatment of the former genus.

Distribution.— Known from a considerable number of localities from Somalia, the Mediterranean belt west to the West Indies and Texas (U.S.A.).

Habitat.— Some species are known from pure limnic habitats, but most members of this genus have a salinity preference towards brackish water.

Etymology.— The generic name is a contraction of the Greek words "Τηθύς"

(referring to the ancient mother ocean named Tethys sea) and "βαίπειν" (to walk), referring to these animals as "walkers of the Tethys Sea".

Discussion.— Despite the great similarity existing among the different species, six "groups" of species can be distinguished. In order to facilitate identification of these groups, a key is given below.

Key to the species groups of *Tethysbaena* (♂, ♀)

1. Telson wider than long; anal lobes protruding beyond the terminal stretch of the telson ..... 2
  - Telson longer than wide; anal lobes not protruding beyond the terminal stretch of the telson ..... 3
2. Antennular main flagellum 6- to 7-segmented; maxilliped with eight terminally implanted plumidenticulate macrosetae on basipodite .....
  - ..... "*T. sanctaecrucis* -group" (p. 67)
  - Antennular main flagellum 8-segmented; maxilliped with five terminally implanted plumidenticulate macrosetae on basipodite ..... "*T. relictæ* - group" (p. 142)
3. Terminal stretch of telson convex, without any protuberances .....
  - ..... "*T. atlantomaroccana* -group" (p. 152)
  - Terminal stretch of telson with one or more protuberances ..... 4
4. Glandular macrosetae flanking central protuberance on terminal stretch of telson absent; endopodite of maxilla 2 with four macrosetae; pereopods 2 to 5 without lateral plumose macrosetae on second segment of exopodite .....
  - ..... "*T. texana* -group" (p. 162)
  - Glandular macrosetae flanking central protuberance on terminal stretch of telson present; endopodite of maxilla 2 with six macrosetae; pereopods 2 to 5 with one or two lateral plumose macrosetae on second segment of exopodite ..... 5
5. Terminal stretch of telson with three pointed protuberances; distal margin uropodal endopodite protruding beyond margin of first segment exopodite; lateral armature of first segment of exopodite of uropod with three cuspidate and two plumose macrosetae .....
  - ..... "*T. vinabayesi*-group" (p. 167)
  - Terminal stretch of telson with one central protuberance (flanked with or without lobe-like swellings on both sides) only; distal margin uropodal endopodite not protruding beyond margin of first segment exopodite; lateral armature of first segment of exopodite of uropod with two cuspidate and one plumose macrosetae .....
    - ..... "*T. argentarii* -group" (p. 174)

"*T. sanctaecrucis* -group"

This group of species is characterized by: a 6- to 7-segmented main flagellum of the antenna 1 (exceptions are *T. gaweini* (6- to 8-segmented), *T. haitiensis* and *T. juglandis* (both 8- to 9-segm.)); mandibular palp with six plumidenticulate macrosetae on the second segment (exceptions are *T. haitiensis* with 8, *T. juglandis* with 7, and *T. colubrae* with 5); endopodite of maxilla 2 with four to six simple macrosetae; maxilliped with eight terminally implanted plumidenticulate macrosetae on basipodite; pereopods 2 to 5 with one or two lateral plumose macrosetae on the second segment of

exopodite, number of ovate microsetae on propodus of endopodite of pereopods 2 to 7 alike in both sexes; pleopod 1 with three dorsal subplumose macrosetae; distal margin of the uropodal endopodite not protruding beyond distal margin of the first segment of the exopodite; telson somewhat to distinctly wider than long, anal lobes protruding beyond the terminal stretch; stretch slightly concave, glandular simple macrosetae absent on the stretch.

4.4.2.1. *Tethysbaena juriaani* spec. nov.  
(figs. 89-113)

*Monodella* (partim); Wagner, 1990: 123.

**Material.**— **Hispaniola, Dominican Republic:** 270 ♂♂, 2206 ♀♀ (181 with broodpouch), 10 juveniles, 81 fragmentary specimens; AMEWI sta. 87/523, Distrito Nacional, Guaricano, well of Ramonas Allagracias de Pichardo, Calle Gregorio Luperón # 7, 18°31'41"N 69°56'19"W, 20 m above mean sea level; 3 years old handdug limestone well, covered by concrete cap and square metal lid, well diam. 1.5 m, lid diam. 0.6 m, water table at 6.7 m, water depth 1.9 m, Cvetkov net, temperature 26.6°C, oxygen saturation 53%, electric conductivity 814 µS/cm; collected by H.P. Wagner, N.W. Broodbakker and Chr. Williamson; 31.x.1987; ZMA coll. no. C.A. 8143 [holotype], ZMA coll. no. C.A. 8144; BMNH; MCSNV; MF; MP; MSD; HUI; RMNH G 59; UEKL; ULA; UPCM; UR; USNM; WAM; ZMC [all paratypes].

Accompanying fauna: Crustacea: Isopoda (fragments of terrestrial species), Ostracoda (*Pseudocandona* cf. *antilliana* Broodbakker, 1983), Decapoda (Natantia); Insecta: fragments of various groups; Acari; Oligochaeta.

- 18 ♀♀ (2 with broodpouch), 12 fragmentary specimens; AMEWI sta. 87/524, Distrito Nacional, Guaricano, spring of Maria Esperanza de León, Calle Luise Manuel Caraballo # 22, 18°31'33"N 69°56'25"W, 20 m above mean sea level; spring emerging at the bottom of limestone escarpment, bottom of limestone and sand, covered by concrete and limestone cap and square metal lid, lid diam. 1.0 m, water table at 0.6 m, water depth 0.5 m, Cvetkov net, temperature 26.8°C, oxygen saturation 82%, electric conductivity 542 µS/cm; collected by H.P. Wagner, N.W. Broodbakker and Chr. Williamson; 31.x.1987; ZMA coll. no. C.A. 8145 [paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Cypretta* cf. *sarsi* Brady, 1902); Insecta: fragments of diverse groups; Acari; Tardigrada; Oligochaeta; Mollusca: Gastropoda.

-1 fragmentary specimen; AMEWI sta. 87/525, Distrito Nacional, Guaricano, well of María Sunsion Reyes, Calle Augusto César Sandino # 12, 18°31'31"N 69°56'43"W, 20 m above mean sea level; 6 years old handdug, limestone well, covered by concrete cap and square metal lid, well diam. 2.0 m, lid diam. 0.45 m, water table at 3.7 m, water depth 1.5 m, Cvetkov net, temperature 27.1°C, oxygen saturation 47%, electric conductivity 910 µS/cm; collected by H.P. Wagner, N.W. Broodbakker and Chr. Williamson; 31.x.1987; ZMA coll. no. C.A. 8146 [paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Stenocypris* cf. *major* (Baird, 1859); *Cypretta* cf. *sarsi* Brady, 1902), Copepoda; Insecta: fragments of various groups; Acari; Tardigrada.

- 56 ♂♂, 516 ♀♀ (31 with broodpouch), 23 juveniles, 22 fragmentary specimens; AMEWI sta. 87/711, Distrito Nacional, Guaricano, well of Elena Acosta, Calle Imbert # 75, 18°31'52"N 69°56'18"W, 20 m above mean sea level; handdug well, upper part partially with concrete wall, round concrete covering with metal lid, water surface 1 × 1.2 m, lid diam. 0.4 m, water table at 1.8 m, water depth 3.0 m, Cvetkov net, temperature 26.3°C, oxygen saturation 45%, electric conductivity 716 µS/cm; collected by H.P. Wagner and D. Platvoet; 11.xii.1987; ZMA coll. no. C.A. 8147; RMNH G 63 [all paratypes].

Accompanying fauna: Crustacea: Isopoda (terrestrial), Ostracoda (*Stenocypris* cf. *major* (Baird, 1859)), Copepoda; Insecta: Hymenoptera; Oligochaeta.

- 18 ♂♂, 432 ♀♀ (21 with broodpouch), 22 juveniles, 14 fragmentary specimens; AMEWI sta. 87/712, Distrito Nacional, Guaricano, well of Elridania Guevara, Repalle Nacaone # 91, 18°31'59"N 69°56'15"W, 20 m above mean sea level; handdug, well covered by concrete cap with metal lid, well diam. 1.0 m, lid diam. 0.5 m, water table at 4.2 m, water depth 3.0 m, Cvetkov net, temperature

26.9°C, oxygen saturation 39%, electric conductivity 826  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet; 11.xii.1987; ZMA coll. no. C.A. 8148; RMNH G 64 [all paratypes].

Accompanying fauna: Crustacea: Copepoda; Insecta: Hymenoptera; fragments of Diplopoda; Acari.

- 3 ♂♂, 14 ♀♀, 4 fragmentary specimens; AMEWI sta. 87/713, Distrito Nacional, Guaricano, well of Mariano de Jesus Sanchez, Repalle Nacaone # 26, 18°31'58"N 69°56'17"W, 20 m above mean sea level; handdug, well covered by concrete cap with sink lid, water surface 1.0 × 1.2 m, lid opening 0.5 × 0.6 m, water table at 5.5 m, water depth 3.5 m, Cvetkov net, temperature 26.7°C, oxygen saturation 27%, electric conductivity 853  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet; 11.xii.1987; ZMA coll. no. C.A. 8149 [paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Stenocypris* cf. *major* (Baird, 1859)), Copepoda; Mollusca: Gastropoda.

- 5 ♂♂, 30 ♀♀ (7 with broodpouch); AMEWI sta. 87/715, Distrito Nacional, Guaricano, well of Elsa Encilia of Cafeteria Elsa, Calle Anacoana # 32, 18°31'50"N 69°56'18"W, 20 m above mean sea level; handdug, well covered by concrete cap with metal lid, water surface 1.2 × 1.5 m, lid diam. 0.5 m, water table at 1.8 m, water depth 3.2 m, Cvetkov net, temperature 26.7°C, oxygen saturation 56%, electric conductivity 755  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet; 11.xii.1987; ZMA coll. no. C.A. 8150 [paratypes].

Accompanying fauna: Crustacea: Copepoda; Mollusca: Gastropoda.

- 2 ♂♂, 52 ♀♀, 11 juveniles; AMEWI sta. 88/029 (= same locality as 87/711), Distrito Nacional, Guaricano, well of Elena Acosta, Calle Imbert # 75, 18°31'52"N 69°56'18"W, 20 m above mean sea level; handdug well, upper part partially with concrete wall, round concrete covering with metal lid, water surface 1 × 1.2 m, lid diam. 0.4 m, water table at 1.8 m, water depth 3 m, collected with Cvetkov net; collected by H.P. Wagner and K.A. Guerrero; 14.i.1988; ZMA coll. no. C.A. 8151 [paratypes].

Accompanying fauna: none.

- 1 ♀; AMEWI sta. 87/561, Prov. de San Pedro de Macoris, Boca del Soco, well of family Mabali Rivera, 50 m NW of bridge, 100 m S of road, 18°27'09"N 69°12'38"W, 10 m above mean sea level; well with lower part cut out in limestone, upper part lined in with concrete stones, not covered, well diam. 0.6 m, water table at 5.7 m, water depth 0.3 m, Cvetkov net, temperature 26.7°C, oxygen saturation 100%, electric conductivity 2.26 mS/cm; collected by H.P. Wagner, N.W. Broodbakker and K.A. Guerrero; 7.xi.1987; ZMA coll. no. C.A. 8152. [*Tethysbaena* cf. *juruaani*].

Accompanying fauna: Insecta; Acari.

Description.— Body length (antennae 1 and 2 excluded) of male up to 1882  $\mu\text{m}$  (holotype 1855  $\mu\text{m}$ ), of female up to 1755  $\mu\text{m}$  in the material studied.

Antenna 1: peduncular segments 1 to 3 with three, three, and two long plumose macrosetae on median margin; main flagellum 7-segmented, last segment (sub)terminally with three simple macrosetae of unequal length; accessory flagellum 5-segmented, last segment with three simple (sub)terminal macrosetae of unequal length.

Antenna 2: peduncular segment 4 with three and segment 5 with four teazel macrosetae on the medial and mediodistal margin; flagellum 5-segmented, last segment (sub)terminally with five simple macrosetae of unequal length.

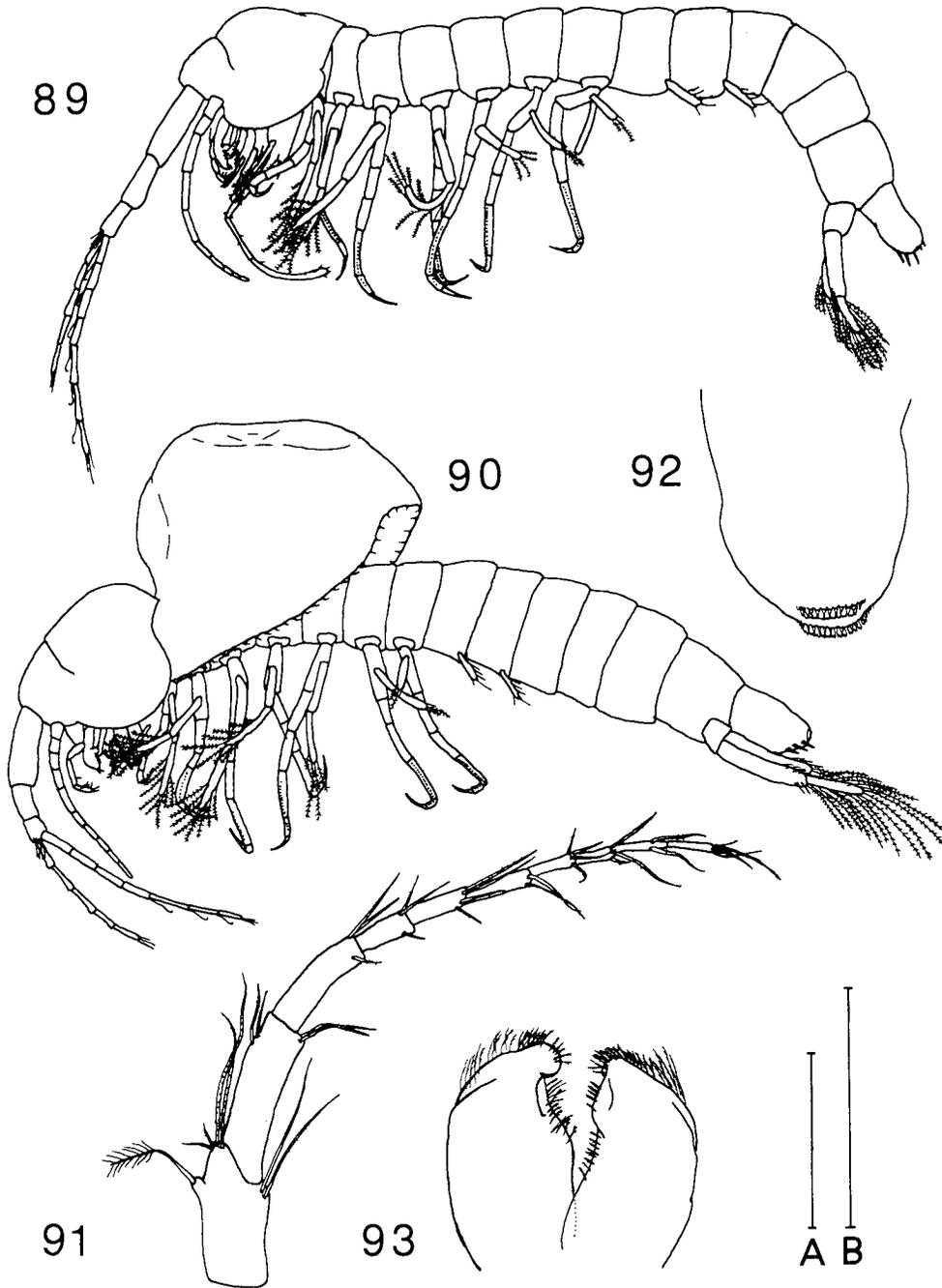
Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

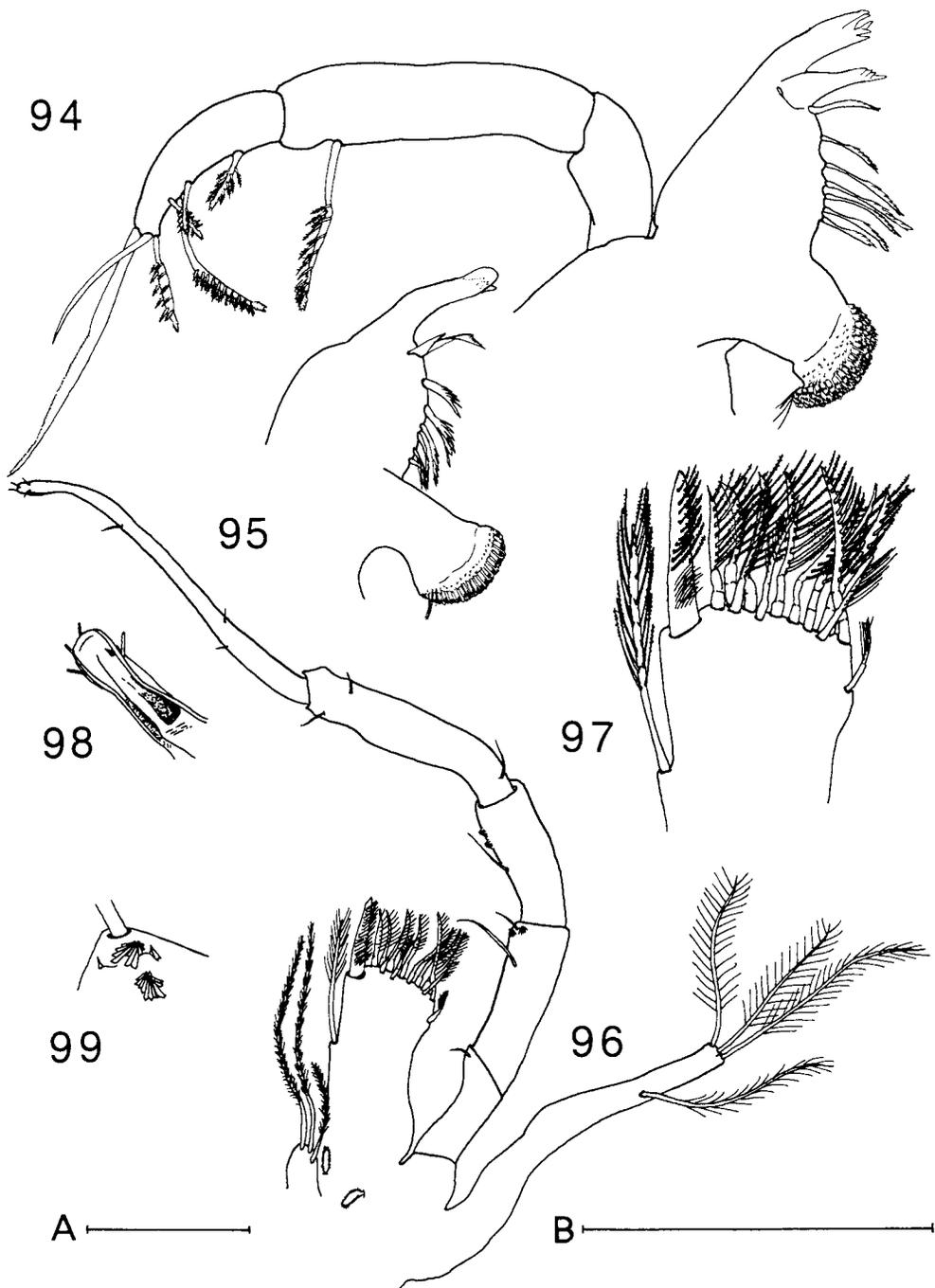
Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with seven setules, third segment with obscurely unisetulate macroseta.

Maxilla 2: basipodal endite 1 with five plumidenticulate macrosetae; basipodal endite 2 with 15 rake-like serrate macrosetae at terminal margin, and two subterminal modified longer serrate macrosetae; basipodal endite 3 with seven more strongly,



Figs. 89-93. *Tethysbaena juriaani* spec. nov., ♂ and ♀. 89, lateral view of habitus, paratype ♂ (1671  $\mu\text{m}$ ). 90, lateral view of habitus, paratype ovigerous ♀ (1645  $\mu\text{m}$ ). 91, antenna 2, holotype ♂ (scale A). 92, labrum, holotype ♂. 93, labium, holotype ♂. (figs. 92-93 scale B). Scales indicated 0.1 mm.



Figs. 94-99. *Tethysbaena juriaani* spec. nov., holotype ♂. 94, left mandible. 95, corpus mandibula of right mandible. 96, maxilliped (scale A). 97, distal portion of basipodal endite of maxilliped. (figs. 94, 95, and 98 scale B). 98, tip of endopodite of maxilliped (extremely enlarged). 99, detail microsetae at distal portion of endopodite segment 2 of maxilliped (extremely enlarged). Scales indicated 0.1 mm.

barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented, bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with two patches of rather short but stout club microsetae (diameter  $\times$  height up to circa  $0.5 \times 2 \mu\text{m}$ ) on the distal portion, third segment with two patches of rather short, but stout club microsetae (diameter  $\times$  height up to circa  $0.5 \times 2 \mu\text{m}$ ), fourth segment without patches of club microsetae; basipodal endite bearing 13 plumidenticulate macrosetae with long setules, a small one medially, eight long ones terminally, three shorter ones subterminally and a small one sublaterally, and an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, one subterminal and one lateral plumose macrosetae.

Gnathopod: basal segment with three plumose macrosetae; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; basischium of endopodite with clearly demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

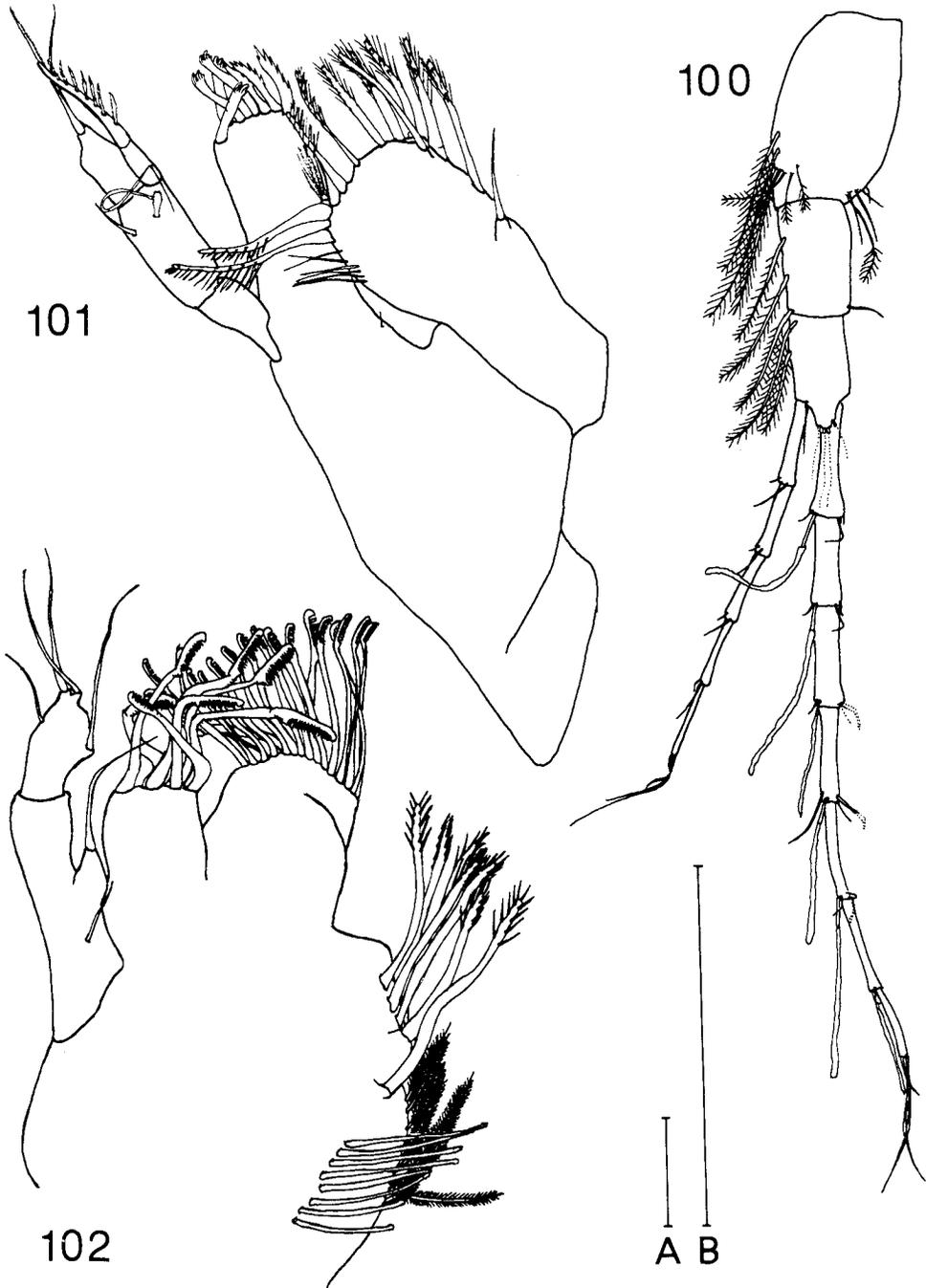
Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with eight to nine ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; first segment of exopodite with one ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with nine ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

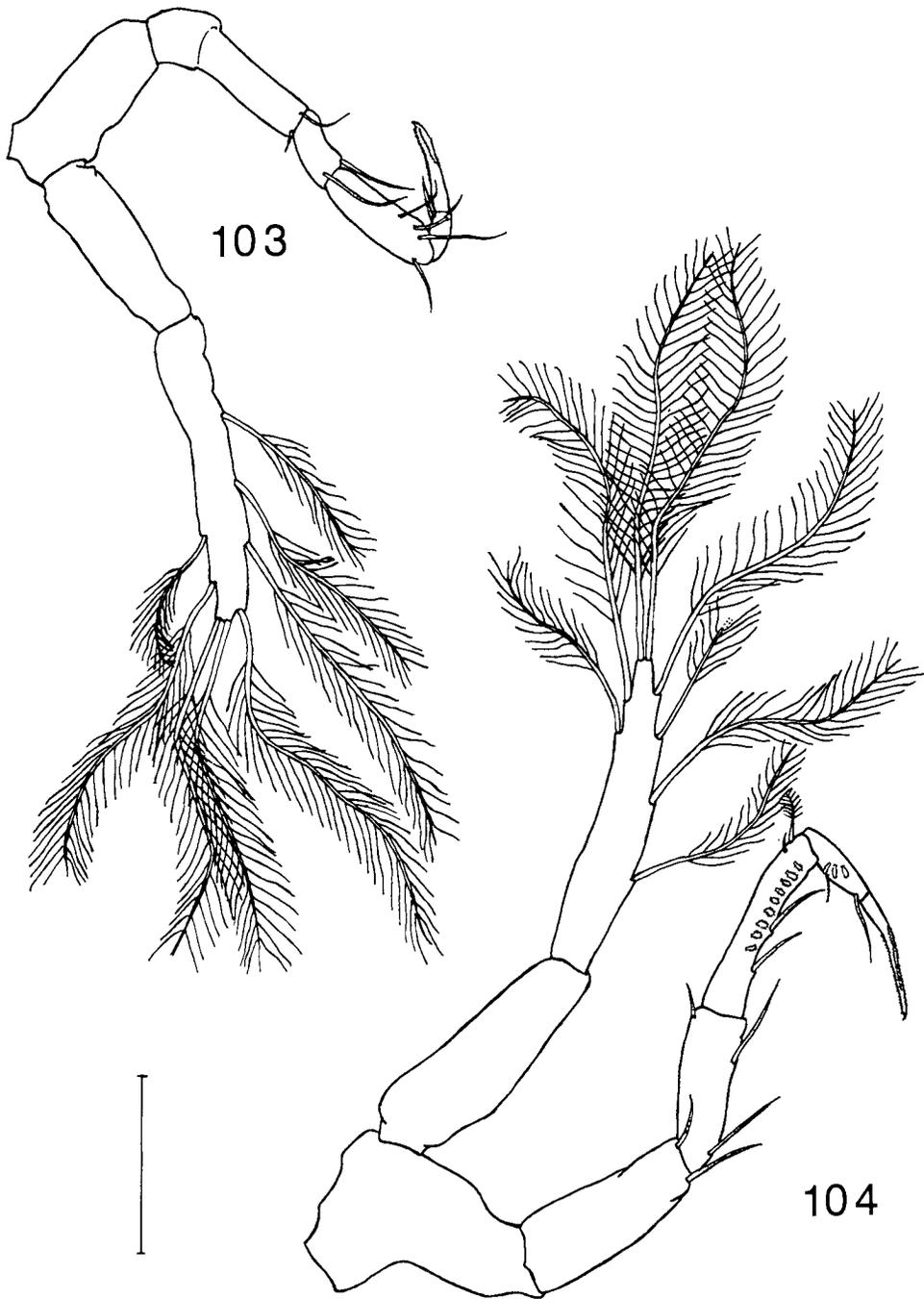
Pereiopod 4: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with one medial, one subterminal and two terminal plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 15 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macroseta and three vestigial macrosetae, one terminal and two lateral, three ovate microsetae present.



Figs. 100-102. *Tethysbaena juriaani* spec. nov., holotype ♂. 100, antenna 1 (scale A). 101, maxilla 1. 102, maxilla 2. (figs. 101-102 scale B). Scales indicated 0.1 mm.



Figs. 103-104. *Tethysbaena juriaani* spec. nov., holotype ♂. 103, gnathopod. 104, pereopod 2. Scale indicated 0.1 mm.

Pereiopod 7: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 16 to 17 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macroseta and one vestigial terminal macroseta, three ovate microsetae present.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of five stout plumose macrosetae, each accompanied by small subplumose macroseta, segment 2 with 16 plumose macrosetae; endopodite bearing 13 plumose macrosetae.

Telson: wider than long, mean width/length ratio 1.28; anal lobes protruding beyond the terminal stretch; stretch slightly concave.

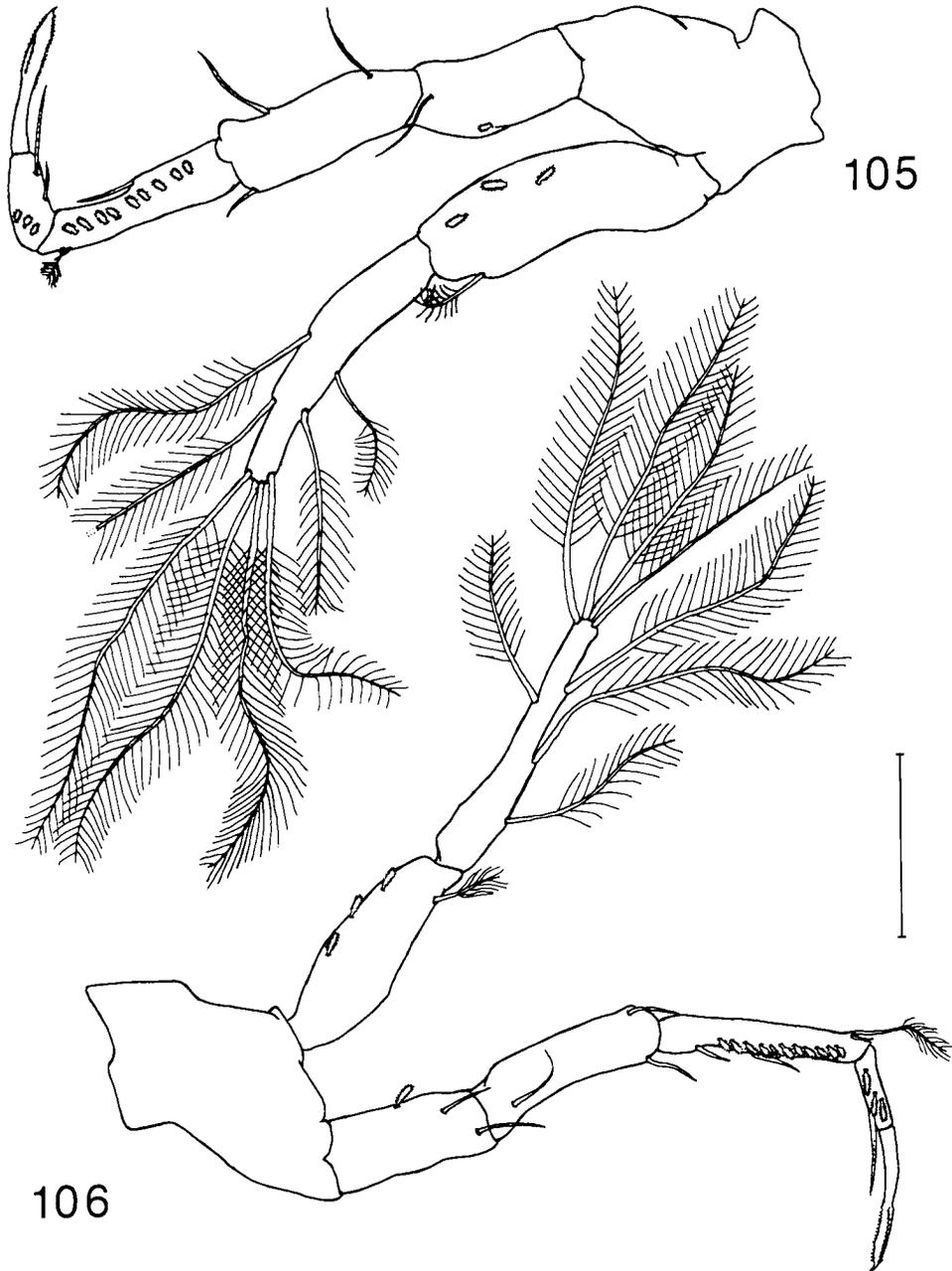
Variability.— Despite the large number of specimens at my disposal the animals show remarkably little variation.

Remarks.— This species closely resembles *T. haitiensis* and *T. gaweini* in several characters. There are, however, substantial differences that warrant distinction at specific level. Compared to *T. gaweini* there are distinct differences in the demarcation of the distal margin of the first segment of the palp of maxilla 1 (distinct in *T. juriaani*; obscure in *T. gaweini*), the number of rake-like macrosetae of basipodal endite 2 of maxilla 2 (*T. juriaani*: 15; *T. gaweini*: 14), the number of plumidenticulate macrosetae of the maxilliped (*T. juriaani*: 14; *T. gaweini*: 13), the shape of the club microsetae and number of patches on the male endopodite of the maxilliped (see text), the demarcation of the ischium in the baso-ischium of the gnathopod (distinct in *T. juriaani*; indistinct in *T. gaweini*), slight differences in the number of ovate microsetae on the pereopods, slight differences in the number of plumose macrosetae on the exopodites of the pereopods, the number of medial cuspidate macrosetae of the uropod (*T. juriaani*: 15 *T. gaweini*: 4), and a quite different mean width/length ratio of the telson. Also the behaviour of the two species is different (*T. juriaani*: essentially swimming; *T. gaweini*: essentially benthic). Compared to *T. haitiensis* there are distinct differences in the number of main flagellar segments of antenna 1 (*T. juriaani*: 7; *T. haitiensis*: 8 to 9), the number of plumidenticulate macrosetae of the maxilliped (*T. juriaani*: 14; *T. haitiensis*: 13), the shape of the club microsetae and number of patches on the male endopodite of the maxilliped (see text), the number of ovate microsetae on the pereopods, the number of medial plumose macrosetae on the uropod (*T. juriaani*: 5 *T. haitiensis*: 4), and the larger number of plumose macrosetae of the uropodal rami in *T. haitiensis*. Noteworthy is the intermediate number of rake-like macrosetae on the basipodal endite of maxilla 2 in *T. haitiensis*. For detailed information on specific differences with the other congeners of this species-group one is referred to table 1 (p. ).

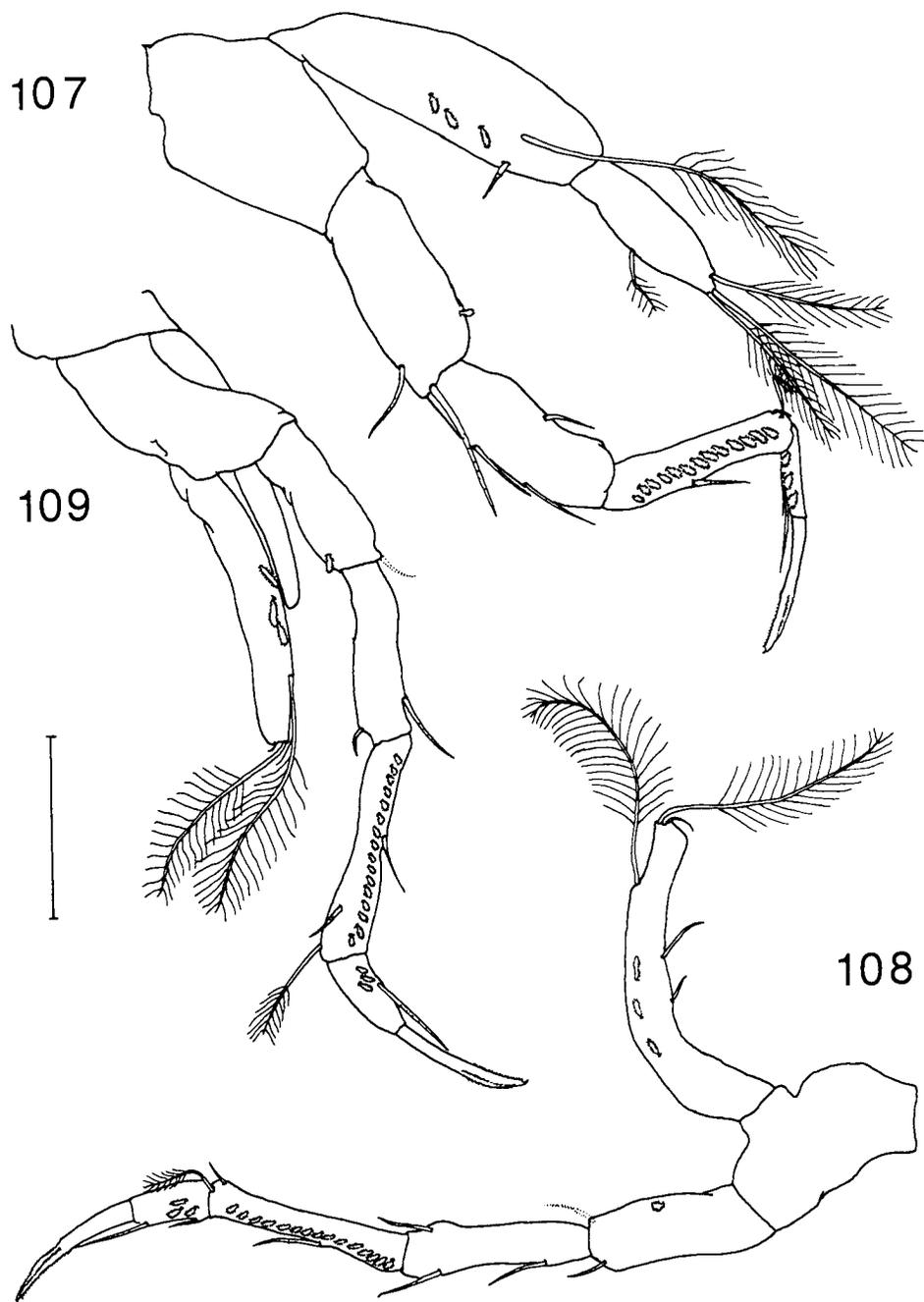
A few specimens, rather damaged, were collected in a well near the coast at Boca del Soco (sta. 87/561), and at a well at Los Bancos de Arena (sta. 87/588), which very well might represent *T. juriaani*.

Etymology.— This species is named after our eldest son Juriaan Elia.

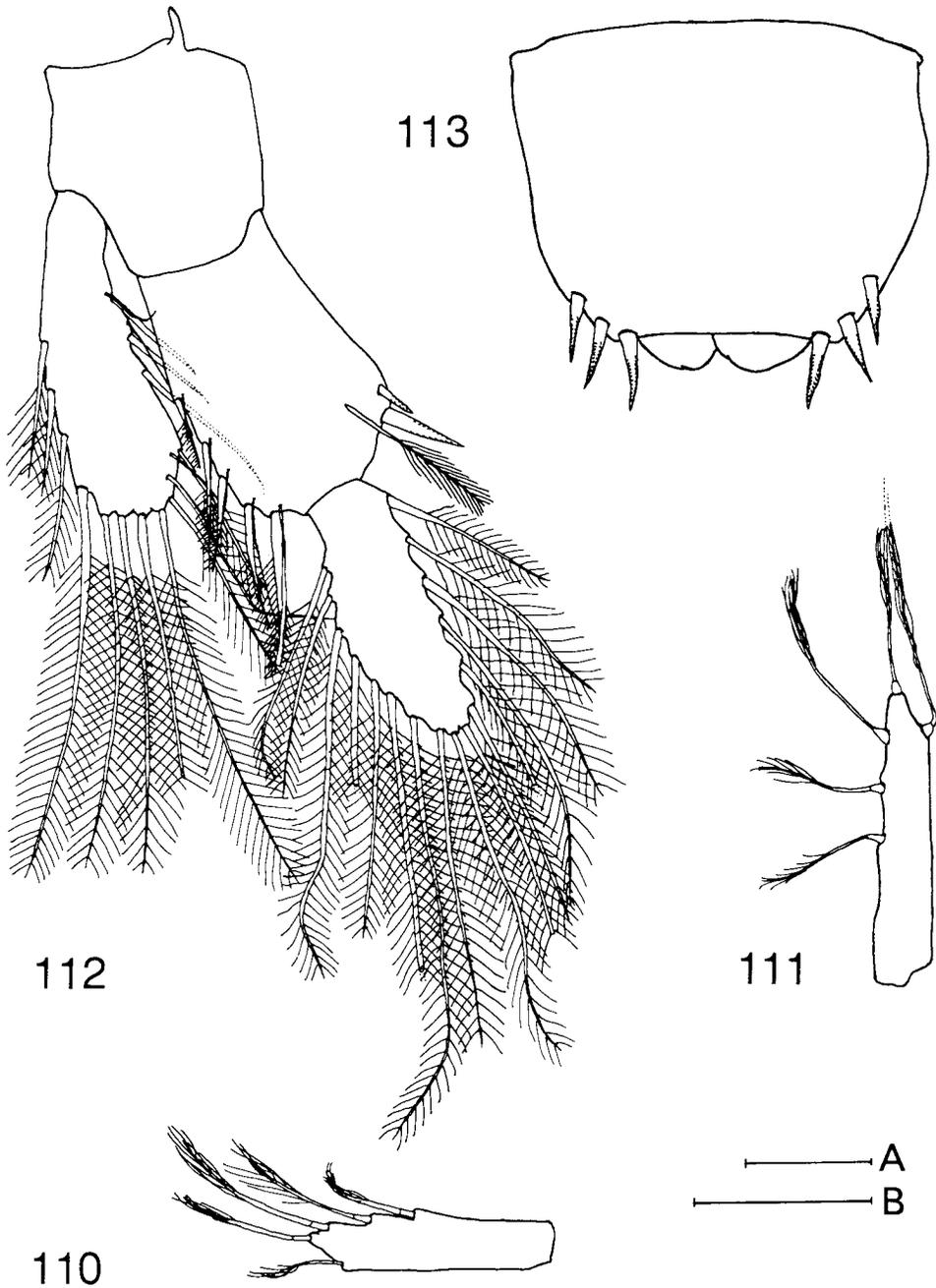
Distribution.— Except for the large number of specimens and samples from



Figs. 105-106. *Tethysbaena juriaani* spec. nov., holotype ♂. 105, pereopod 3. 106, pereopod 4. Scale indicated 0.1 mm.



Figs. 107-109. *Tethysbaena juriaani* spec. nov., holotype ♂. 107, pereopod 5. 108, pereopod 6. 109, pereopod 7. Scale indicated 0.1 mm.



Figs. 110-113. *Tethysbaena juriaani* spec. nov., holotype ♂. 110, pleopod 1. 111, pleopod 2. (figs. 110-111 scale B). 112, uropod. 113, telson. (figs. 112-113 scale A). Scales indicated 0.1 mm.

Guaricano, a little village at circa 2 kilometres north of the capital Santo Domingo, a single specimen has been captured near the mouth of the Río Soco (station 87/561), a part of the southern coast of the southeastern peninsula.

Habitat.— All samples of *Tethysbaena juriaani* come from coralligenous deposits of Pliocene age (Weyl, 1966; Muscio, 1987). Although the species usually lives in fresh waters (electr. conductivity varying between 542  $\mu\text{S}/\text{cm}$  and 910  $\mu\text{S}/\text{cm}$ ) at temperatures of 25.4 to 27.1°C and an oxygen saturation varying between 27% and 82% near the village of Guaricano, it also seems tolerant to oligohaline conditions (conductivities measured of 2.26 mS/cm). Curiously, none of the accompanying faunal elements is a true troglobite, all are epigeal dispersionalists. The groundwater plain at Guaricano is a layer of limnic water situated at circa 20 m above sea level, while station 87/561 is situated at only 10 m above mean sea level and clearly under influence of the nearby sea. It is not unlikely that during sampling an accidental mixture of sea and limnic(?) water was created by the movements of the Cvetkov net. *Tethysbaena juriaani* is essentially a swimming species.

#### 4.4.2.2. *Tethysbaena gaweini* spec. nov. (figs. 114-124)

*Monodella* (partim); Wagner, 1990: 123.

Material.— **Hispaniola, Dominican Republic:** 42  $\delta\delta$ , 2284  $\text{♀♀}$  (1 with broodpouch), 56 juveniles, 26 fragmentary specimens; AMEWI sta. 87/679, Prov. Espaillat, Magante, well of Paulino Almonte, near bent in road, 50 m S of road, 19°36'30"N 70°10'25"W, 20 m above mean sea level; concrete well covered by sink plates, water clear, water table at 6 m, water depth 1.8 m, Cvetkov net, temperature 25.9°C, oxygen saturation 38%, electric conductivity 828  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and N.W. Broodbakker; 1.xii.1987; ZMA coll. no. C.A. 8164; RMNH G 65 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda, Copepoda; Insecta: Diptera, Hymenoptera; Arachnida; Acari; Oligochaeta.

- 43  $\delta\delta$ , 944  $\text{♀♀}$  (116 with broodpouch), 12 fragmentary specimens, 17 juveniles; AMEWI sta. 87/752, Prov. de Salcedo, Campo Los Limones, well of Tranfi Antonio Jimenez Herman, 2.3 km W of roadfork at Cruz de Cenovi, 50 m N of road, 19°17'59"N 70°21'56"W, 100 m above mean sea level; 15 years old well lined with concrete stones, covered with concrete cap and lid, well diam. 1.0 m, lid diam. 0.5 m, water table at 5.75 m, water depth 3.5 m, Cvetkov net, temperature 26.0°C, oxygen saturation 50%, electric conductivity 936  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 21.xii.1987; ZMA coll. no. C.A. 8162 [holotype], ZMA coll. no. C.A. 8163; BMNH; MF; MP; HUJ; RMNH G 60; UEKL; UPMC; USNM; WAM; ZMC [all paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Cyprretta* cf. *sarsi* Brady, 1902); Mollusca: Gastropoda; Polychaeta; Platyhelminthes.

- 2  $\delta\delta$ , 19  $\text{♀♀}$ ; AMEWI sta. 87/753, Prov. de Salcedo, Campo Los Limones, well of Juan Martez, 2.35 km W of roadfork at Cruz de Cenovi, 40 m N of road, 19°17'58"N 70°21'58"W, 100 m above mean sea level; well lined with concrete stones, covered with concrete cap, square opening not covered, well diam. 1.0 m, opening diam. 0.4 m, water table at 3.5 m, water depth 5.0 m, Cvetkov net, temperature 26.2°C, oxygen saturation 42%, electric conductivity 1196  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 21.xii.1987; ZMA coll. no. C.A. 8165 [paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Cyprretta* cf. *sarsi* Brady, 1902), Copepoda; Acari; Polychaeta.

- 1  $\delta$ , 41  $\text{♀♀}$  (2 with broodpouch, 6 fragmentary specimens; AMEWI sta. 87/755, Prov. de Salcedo, Campo Los Limones, well of José Thomas Garcia, 2.41 km W of roadfork at Cruz de Cenovi, 35 m S of road, 19°17'55"N 70°22'01"W, 100 m above mean sea level; well dug 3.vi.1970, lined with concrete stones, covered with concrete cap, square opening covered by large stone, pump used to be connected,

well diam. 1.2 m, lid diam. 0.5 m, water table at 3.25 m, water depth 4.5 m, Cvetkov net, temperature 26.6°C, oxygen saturation 56%, electric conductivity 944  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 21.xii.1987; ZMA coll. no. C.A. 8166 [paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Cypretta* cf. *sarsi* Brady, 1902), Copepoda; Acari; Oligochaeta.

- 5 ♀♀; AMEWI sta. 87/757, Prov. de Salcedo, Campo Los Limones, well of Ventura Alvarez, 2.535 km W of roadfork at Cruz de Cenovi, 30 m N of road, 19°17'56"N 70°22'08"W, 100 m above mean sea level; well lined with concrete stones, covered with concrete cap, square opening not covered, opening diam. 0.45 m, water table at 5.25 m, water depth 6.75 m, Cvetkov net, temperature 25.7°C, oxygen saturation 61%, electric conductivity 1025  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 21.xii.1987; ZMA coll. no. C.A. 8167 [paratypes].

Accompanying fauna: none.

- 1 ♂, 7 ♀♀; AMEWI sta. 87/783, Prov. de Salcedo, San José, well of Ramon Garcias, 400 m E of roadfork, 20 m S of road, 19°20'31"N 70°22'27"W, 160 m above mean sea level; well lined with concrete stones, concrete cap with wooden lid and sink plate construction as extra cap, pump used to be connected before, well diam. 1.2 m, lid diam. 0.5 m, water table at 6.0 m, water depth 1.0 m, collected by Cvetkov net, temperature 25.4°C, oxygen saturation 31%, electric conductivity 908  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 23.xii.1987; ZMA coll. no. C.A. 8168 [no paratypes].

Accompanying fauna: Insecta: Diptera larvae; Acari; Mollusca: Gastropoda; Polychaeta.

- 2 ♀♀; AMEWI sta. 87/803, Prov. de la Vega, Las Yervas la Vega, well of señor Bautido Martez, 20 m W of road, 19°16'48"N 70°27'40"W, 100 m above mean sea level; well dug 31.x.1983, lined with concrete blocks, concrete cap and lid, pump hanging halfway down the well, well diam. 1.5 m, lid diam. 0.5 m, water table at 8.5 m, water depth 2.5 m, collected by Cvetkov net, temperature 26.9°C, oxygen saturation 55%, electric conductivity 1054  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 30.xii.1987; ZMA coll. no. C.A. 8169 [no paratypes].

Accompanying fauna: Mollusca: Gastropoda; Polychaeta.

- 7 ♂♂, 42 ♀♀ (3 with broodpouch); AMEWI sta. 87/804, Prov. de la Vega, Las Yervas la Vega, well of fam. Garcia, 1 km N of sta. 87/803, 20 m E of road, 19°17'15"N 70°27'31"W, 100 m above mean sea level; well dug 7.v.1985, lined with concrete blocks, concrete cap and lid, well diam. 1.5 m, lid diam. 0.5 m, water table at 8.5 m, water depth 3.65 m, collected by Cvetkov net, temperature 26.6°C, oxygen saturation 57%, electric conductivity 798  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 30.xii.1987; ZMA coll. no. C.A. 8170 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda, Ostracoda (*Stenocypris* cf. *major* (Baird, 1859)), Copepoda; Acari.

- 7 ♂♂, 209 ♀♀ (2 with broodpouch), 11 juveniles, 6 fragmentary specimens; AMEWI sta. 87/805, Prov. de la Vega, Las Yervas la Vega, well of Juan Cabrera, 1.04 km N of sta. 87/803, 20 m E of road, 19°17'20"N 70°27'29"W, 100 m above mean sea level; well lined with concrete blocks, concrete cap and lid, well diam. 1.5 m, lid diam. 0.5 m, water table at 8.5 m, water depth 3.5 m, collected by Cvetkov net, temperature 26.4°C, oxygen saturation 64%, electric conductivity 812  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 30.xii.1987; ZMA coll. no. C.A. 8171; RMNH G 66 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983; *Stenocypris* cf. *major* (Baird, 1859)); *Candonopsis hummelincki* Broodbakker, 1983); Mollusca: Gastropoda; Polychaeta; Platyhelminthes.

- 1 ♀; AMEWI sta. 87/808, Prov. Espaillat, Moca, well of Juan Compres, 600 m NE of roadfork, at watertank, 40 m SE of road, 19°24'55"N 70°30'54"W, 200 m above mean sea level; well lined with concrete stones, concrete cap and lid, well diam. 1.2 m, lid diam. 0.6 m, pump connected, water table at 4.5 m, water depth 5.0 m, collected by Cvetkov net, temperature 26.2°C, oxygen saturation 44%, electric conductivity 954  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 31.xii.1987; ZMA coll. no. C.A. 8172 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda; Mollusca: Gastropoda.

- 2 ♂♂, 17 ♀♀, 2 fragmentary specimens; AMEWI sta. 87/809, Prov. Espaillat, Moca, well of Henry Carreras, 650 m NE of roadfork, 40 m S of road, 19°24'55"N 70°30'50"W, 200 m above mean sea level; well lined with concrete stones, concrete cap and lid, well diam. 1.2 m, lid diam. 0.6 m, pump connect-

ed, water table at 4.5 m, water depth 5.0 m, collected by Cvetkov net, temperature 26.0°C, oxygen saturation 49%, electric conductivity 894  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 31.xii.1987; ZMA coll. no. C.A. 8173 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda; Insecta: Diptera larvae, Hymenoptera; Acari; Mollusca: Gastropoda.

- 5  $\delta\delta$ , 23  $\text{f}\text{f}$  (2 with broodpouch), 2 juveniles; AMEWI sta. 87/810, Prov. Espaillat, Moca, well of Ramón Compres, 650 m NE of roadfork, 40 m N of road, 19°24'58"N 70°30'52"W, 200 m above mean sea level; well lined with concrete stones, concrete cap and lid, well diam. 1.2 m, lid diam. 0.6 m, pump connected, water table at 3.8 m, water depth 5.6 m, many cockroaches at inner wall, collected by Cvetkov net, temperature 25.7°C, oxygen saturation 35%, electric conductivity 959  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 31.xii.1987; ZMA coll. no. C.A. 8174 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda; Mollusca: Gastropoda.

- 2  $\delta\delta$ , 68  $\text{f}\text{f}$  (17 with broodpouch), 3 juveniles, 3 fragmentary specimens; AMEWI sta. 87/811, Prov. Espaillat, Moca, well of Rafael Compres, 700 m NE of road fork, 40 m N of road, 19°24'59"N 70°30'49"W, 200 m above mean sea level; well dug 12.xii.1952, lined with concrete stones, concrete cap and lid (lid since 7.viii.1974), well diam. 1.2 m, lid diam. 0.6 m, pump connected, water table at 3.4 m, water depth 5.5 m, collected by Cvetkov net, temperature 25.9°C, oxygen saturation 45%, electric conductivity 884  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 31.xii.1987; ZMA coll. no. C.A. 8175 [no paratypes].

Accompanying fauna: Mollusca: Gastropoda.

- 13  $\delta\delta$ , 41  $\text{f}\text{f}$ ; AMEWI sta. 88/001, Prov. de Santiago, 1 km S of Tamboril, well of William Suarez, 200 m S of roadfork, 75 m W of road, 19°28'37"N 70°36'59"W, 240 m above mean sea level; well lined with concrete half rings, not covered, well diam. 1.0 m, water table at 11.5 m, water depth 2.0 m, collected by Cvetkov net, temperature 25.7°C, oxygen saturation 35%, electric conductivity 5.08 mS/cm; collected by H.P. Wagner and D. Platvoet, 1.i.1988; ZMA coll. no. C.A. 8176 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983); Insecta: Diptera larvae.

- 1  $\text{f}$  (with broodpouch); AMEWI sta. 88/010, Prov. de la Vega, Bacui Arriba, well of Esteban Rojas, 1.92 km SE of roadfork, 25 m S of road, 19°19'04"N 70°27'05"W, 120 m above mean sea level; well dug 10.vii.1981, lined with concrete blocks, concrete cap, covered with steel and sink plates, well diam. 1.5 m, opening diam. 0.5 m, pump installed halfway down the well on wooden frame, water table at 5.0 m, water depth 2.1 m, collected by Cvetkov net, temperature 25.8°C, oxygen saturation 50%, electric conductivity 3.97 mS/cm; collected by H.P. Wagner and D. Platvoet, 1.i.1988; ZMA coll. no. C.A. 8177 [no paratypes].

Accompanying fauna: none.

- 1 fragmentary  $\text{f}$ ; AMEWI sta. 87/797, Prov. de Monseñor Nouel, Juma, well of Leonardo Perez, W side of town, km E of bonao, 30 m S of road, 18°54'54"N 70°24'10"W, 160 m above mean sea level; well lined with stones, concrete cap, opening half covered with concrete poles, pump connected, well diam. 1.2 m, opening diam. 0.5 m, water table at 1.75 m, water depth 1.75 m, collected by Cvetkov net, temperature 25.2°C, oxygen saturation 42%, electric conductivity 237  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner and D. Platvoet, 30.xii.1987; ZMA coll. no. C.A. 8178 [*Tethysbaena* cf. *gaweini*].

Accompanying fauna: Crustacea: Amphipoda; Mollusca: Gastropoda.

Description.— Body length (antennae 1 and 2 excluded) of male up to 1863  $\mu\text{m}$  (holotype), of female up to 1931  $\mu\text{m}$  in the material studied.

Antenna 1: peduncular segments 1 to 3 with four, four, and two long plumose macrosetae on respective median margins; main flagellum 6- to 8-segmented, last segment with seven simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segment 4 with three, and segment 5 with four teazel macrosetae on the medial and mediobasal margin; flagellum 5-segmented, last segment

with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: exopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with six setules, third segment with obscure unisetulate macroseta.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 14 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with a field of scutellae preceding two patches of tall, pointed club microsetae (diameter  $\times$  height up to circa  $0.3 \times 3.5 \mu\text{m}$ ) on the distal portion, third segment with a field of scutellae preceding two rows of two patches of tall, pointed club microsetae (diameter  $\times$  height up to circa  $0.3 \times 3.25 \mu\text{m}$ ), fourth segment without patches of club microsetae; basipodal endite bearing 12 plumidenticulate macrosetae with long setules, a tall one medially, seven long ones terminally, three shorter ones subterminally and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, one subterminal and one lateral plumose macrosetae.

Gnathopod: basal segment with one plumose macroseta; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; basischium of endopodite with indistinct ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with nine ovate microsetae, dactylus with two teazel macrosetae on ventral margin, and two rows of three and four ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with two teazel macrosetae medially on ventral margin, both male and female with ten ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of three and four ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with 12 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with two medial, two subterminal and two terminal plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with two teazel macrosetae medially on ventral margin, both male and female with 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with one medial, one subterminal and two terminal plumose macrosetae.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 15 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macroseta, and one vestigial terminal macroseta, three ovate microsetae present.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 18 ovate microsetae, dactylus with one teazel macroseta on ventral margin, and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macroseta and one vestigial terminal macroseta, three ovate microsetae present.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segments 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of three to four stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 14 to 18 plumose macrosetae; endopodite bearing 10 to 14 plumose macrosetae.

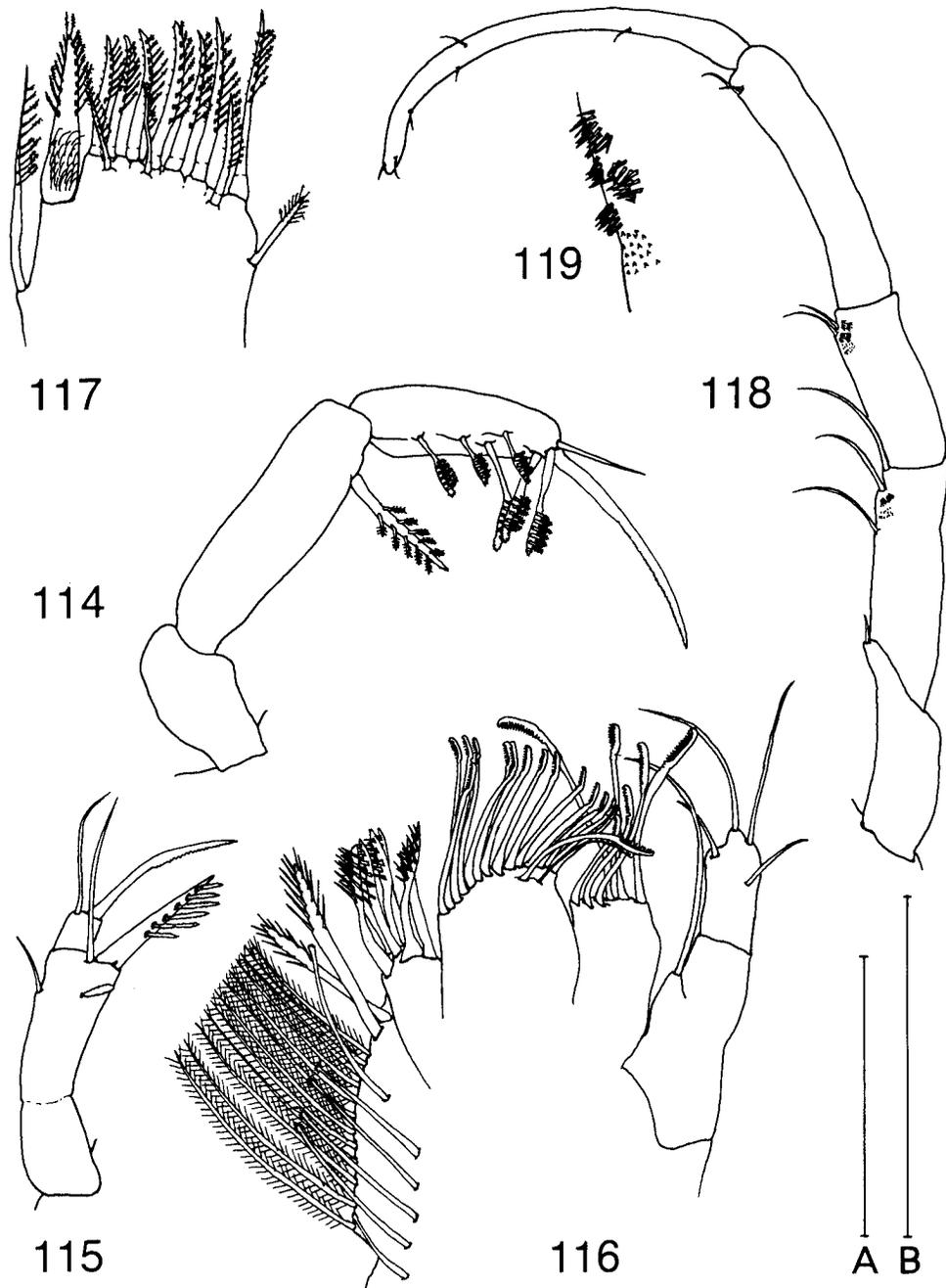
Telson: wider than long, mean width/length ratio 1.20; anal lobes protruding beyond the terminal stretch; stretch slightly concave, straight in centre.

Variability.— The specimens collected in the plain between the upper course of the Río Moca and the Río San Juan show little morphological variation. Among the specimens from the plain between the lower course of the Río Jabo Arriba and Río San Juan (station 87/679) the number of segments of the main flagellum of the antenna 1 varies (up to 8), and peduncular segment 1 bears four to five plumose macrosetae along its medial margin. Also the number of plumose macrosetae on the uropods is generally somewhat higher than in specimens of comparable size from the upper course plain. From a remote area (station 87/797) a single damaged female was collected that looks identical to the type material from the upper course plain that extends from the Río Moca to the Río San Juan; it solely differs in having four plumose macrosetae on the basal segment of the gnathopod instead of the usual one observed in all other specimens dissected.

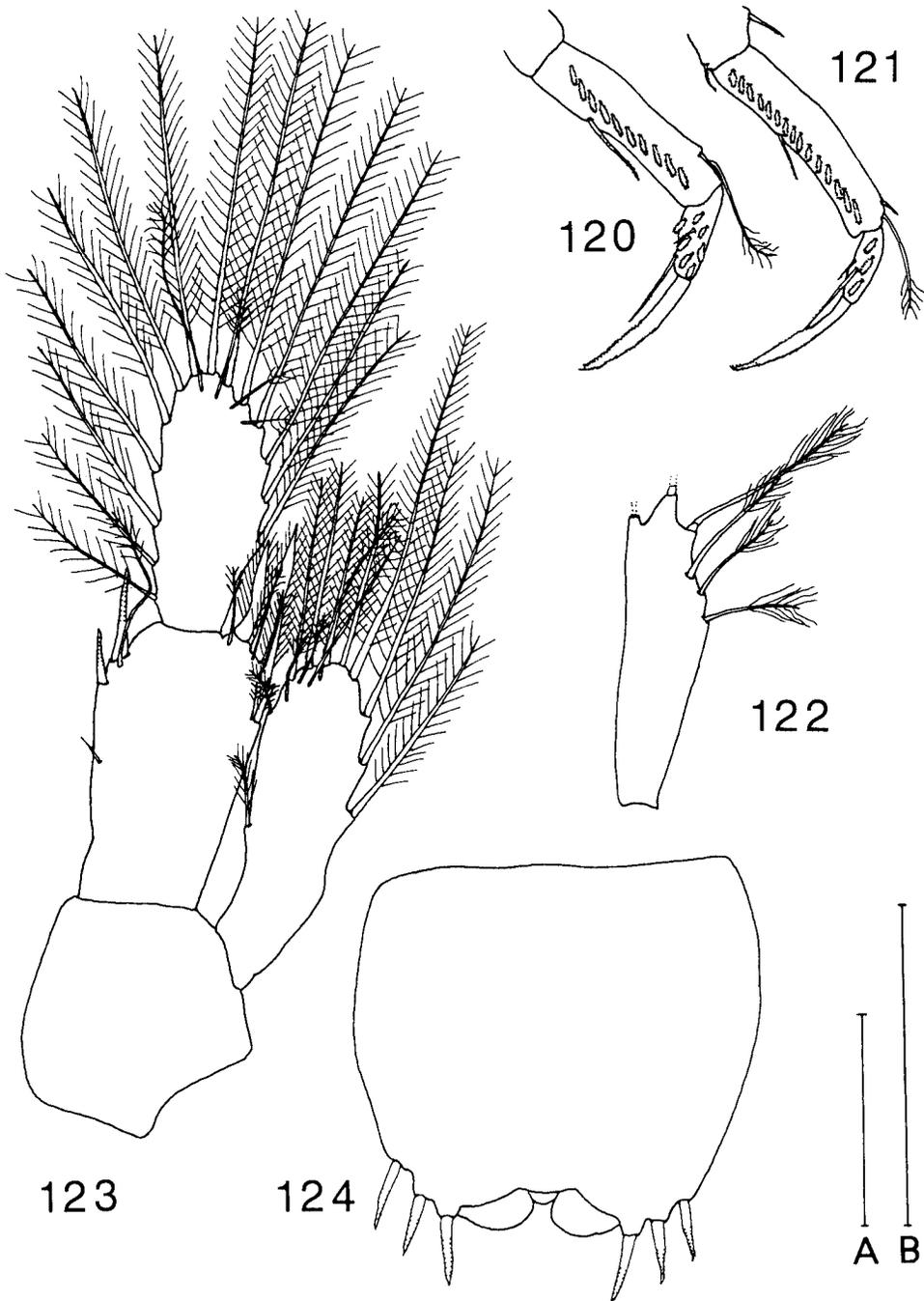
Remarks.— Characters distinctive from the other members of the "*T. sanctaerucis*-group" have been mentioned in the discussion of *T. juriaani*. For detailed information on specific differences with the other congeners of this species-group one is referred to table 1 (p. 140).

Etymology.— This species is named after our youngest son Gawein Willem.

Distribution.— This species seems to be confined to the eastern part of the Valle del Cibao, and a limited area along the northern coast almost exactly between the Río Jabo Arriba and Río San Juan.



Figs. 114-119. *Tethysbaena gaweini* spec. nov., holotype ♂. 114, palp mandible. 115, palp maxilla 1. 116, maxilla 2. 117, distal portion of basipodal endite of maxilliped. (figs. 114-117 scale B). 118, endopodite of maxilliped (scale A). 119, detail microsetae at distal portion of endopodite segment 3 of maxilliped (extremely enlarged). Scales indicated 0.1 mm.



Figs. 120-124. *Tethysbaena gaweini* spec. nov., holotype ♂. 120, distal portion of pereopod 3. 121, distal portion of pereopod 6. 122, pleopod 2 (scale B). 123, uropod. 124, telson. (figs. 120, 121, 123, and 124 scale A). Scales indicated 0.1 mm.

Habitat.— All samples containing *Tethysbaena gaweini* have been taken in alluvial deposits of Holocene age (Weyl, 1966; Muscio, 1987), at altitudes varying between 20 and 240 m above mean sea level. The oxygen saturation of the water varied considerably from 31% to 64%, but the temperature was limited to 25.2 and 26.9°C. The electric conductivity varied mostly between 798  $\mu\text{mS/cm}$  and 1196  $\mu\text{mS/cm}$  (limnic), but an exceptional low electric conductivity of 237  $\mu\text{mS/cm}$  (limnic) was encountered at station 87/797. Two stations contained oligohaline water (stations 88/001 and 88/010) with a electric conductivity of 5.08 mS/cm and 3.97 mS/cm. Except for some occasional captures of blind Amphipoda, most of the other accompanying fauna represented epigeal dispersing taxa. It can not be excluded that the high conductivities encountered in stations 88/001 and 88/010 find their origin in pollution by human interference. *Tethysbaena gaweini* is essentially a benthic species.

#### 4.4.2.3. *Tethysbaena haitiensis* spec. nov. (figs. 125-135)

Thermosbaenacea (partim); Stock, 1979: 64-65; Stock, 1980a: 7; Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1983: 289; Broodbakker, 1984a: 6 table II; Broodbakker, 1984b: 41; Stock, 1986d: 199.

*Monodella*; Notenboom, 1981: 324.

Thermosbaenaceans (partim); Stock, 1983a: 277.

Thermosbaenacea; Broodbakker, 1983: 307, 308, 314.

unident. spp.; Schram, 1986: 221.

*Monodella* (partim); Wagner, 1990: 123.

Material.— **Hispaniola, Haiti:** 1 ♀; AMEWI sta. 78/199, Dépt. de l'Ouest, E of Croix-des-Missions, 18°35'36"N 72°16'53"W; from well, covered, diam. 0.75 m, water table at 4.0 m, water depth 4.5 m, Cvetkov net, chlorinity 80 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 4.v.1978; ZMA coll. no. C.A. 8195 [no paratype].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983); Insecta: Diptera larvae.

- 2 ♀♀; AMEWI sta. 78/201, Dépt. de l'Ouest, between Croix-des-Missions and Croix des-Bouquets, S of road N 102, 18°35'57"N 72°16'14"W; from well, not covered, diam. 0.75 m, in sand, water clear, water table at 7.5 m, water depth 0.5 m, Cvetkov net, chlorinity 10 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 4.v.1978; ZMA coll. no. C.A. 8196 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983).

- 8 ♂♂, 14 ♀♀, 3 juveniles; AMEWI sta. 78/203, Dépt. de l'Ouest, Gressier, N side road D 200, 18°32'23"N 72°31'13"W; from well near house, covered, diam. 1.0 m, water table at 2.5 m, water depth 0.3 m, Cvetkov net, chlorinity 40 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 5.v.1978; ZMA coll. no. C.A. 8197.

Accompanying fauna: Crustacea: Ostracoda (*Caribecandona* (*Caribecandona*) *trapezoidea* Broodbakker, 1983; *Cypretta* spec.), Copepoda (Cyclopidae); Insecta: Diptera larvae; Oligochaeta (*Dero* (*Aulophorus*) *furcata* (Müller, 1773)).

- 3 ♀♀; AMEWI sta. 78/204, Dépt. de l'Ouest, between Gressier and Léogâne, at house near rum factory, 18°32'10"N 72°33'33"W; well partially covered, diam. 1.0 m, in alluvium, water clear, water table at 6.0 m, water depth 2.0 m, Cvetkov net, chlorinity 40 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 5.v.1978; ZMA coll. no. C.A. 8198 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda, Copepoda (Cyclopidae); Insecta: Diptera larvae; Oligochaeta.

- 1 ♀; AMEWI sta. 78/207, Dépt. de l'Ouest, along new road from Léogâne to Jacmel, E of Trouin, estimated position 18°22'35"N 72°35'45"W; from drip-pool at karst source, in sand, altitude ca. 1900 feet, collected with handnet (mesh 0.05 mm), chlorinity 30 mg/l; collected by J.H. Stock, E.S.W. Weinberg

& F. Zijlstra; 5.v.1978; ZMA coll. no. C.A. 8199 [no paratype].

Accompanying fauna: Crustacea: Ostracoda; Insecta: Diptera larvae; Mollusca: Gastropoda; diatoms.

- 1 juvenile; AMEWI sta. 78/216, Dépt. du Sud-Est, Jacmel, house of Dr Abel Gousse, near Rivière des Orangiers, 18°14'31"N 72°32'04"W; from neglected well, covered, water table at 10 m, water depth 0.5 m, Cvetkov net, chlorinity 50 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 5.v.1978; ZMA coll. no. C.A. 8200 [no paratype].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia longula* Broodbakker, 1983), Copepoda (Cyclopidae, Harpacticoida); Oligochaeta (*Dero (Aulophorus) furcata* (Müller, 1773)).

- 8 ♂♂, 82 ♀♀ (1 with broodpouch), 3 juveniles, 4 fragmentary specimens; AMEWI sta. 79/531, Dépt. de l'Ouest, Croix-des-Missions, hamlet of Cazeau, well of Jacques Moyses, 18°35'13"N 72°16'57"W; handdug well in alluvia and soil, not covered, water table at 8.0 m, water depth 1.5 m, Cvetkov net, temperature 27.5°C, chlorinity 42 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xi.1979; ZMA coll. no. C. A. 8201 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Zombiweckelia parvipalpus* Stock, 1985); Polychaeta; Oligochaeta.

- 3 ♀♀; AMEWI sta. 79/532, Dépt. de l'Ouest, Croix-des-Missions, hamlet of Cazeau, well of Saint Aubain Lebrun, 18°35'13"N 72°16'57"W; handdug well in alluvia and soil (less sediment than in sta. 79/531), not covered, water table at 8.0 m, water depth 3.0 m, Cvetkov net, temperature 27.5°C, chlorinity 50 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xi.1979; ZMA coll. no. C. A. 8202 [no paratypes].

Accompanying fauna: Mollusca: Gastropoda.

- 41 ♂♂, 1255 ♀♀ (4 with broodpouch), 234 juveniles, 17 fragmentary specimens; AMEWI sta. 79/533, Dépt. de l'Ouest, Croix-des-Missions, hamlet of Cazeau, Groureau, well of Groureau, 18°34'53"N 72°16'16"W; well not covered, much sediment, water table at 3.0 m, water depth 1.75 m, Cvetkov net, temperature 27.3°C, chlorinity 43 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xi.1979; ZMA coll. no. C. A. 8203; RMNH G 68 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Zombiweckelia parvipalpus* Stock, 1985), Ostracoda (*Caribecandona (Caribecandona) trapezoidea* Broodbakker, 1983; *Chlamydotheca unispinosa* (Baird, 1862)), Copepoda (*Metacyclops (Metacyclops) diana* Pesce, 1985; Harpacticoida); Insecta; Acari; Mollusca: Gastropoda.

- 1 ♂, 1 ♀; AMEWI sta. 79/536, Dépt. de l'Ouest, Croix-des-Missions, hamlet of Cazeau, Groureau, well of Thérèse Celamy, 18°35'03"N 72°16'23"W; handdug well in alluvia, not covered, fine sediments, water table at 3.0 m, water depth 2.75 m, Cvetkov net, temperature 28.3°C, chlorinity 18.0 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xi.1979; ZMA coll. no. C. A. 8204 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (?*Apoweckelia* spec.), Ostracoda (*Strandesia stocki* Broodbakker, 1983; *Stenocypris major* (Baird, 1859); *Chlamydotheca unispinosa* (Baird, 1862)), Copepoda (Cyclopidae); Insecta: Diptera larvae.

- 35 ♂♂, 54 ♀♀ (2 with broodpouch), 2 fragmentary specimens; AMEWI sta. 79/539, Dépt. de l'Ouest, Croix-des-Missions, Marin, well of Gérard Gélan, 18°36'31"N 72°17'31"W; very primitive well, not covered, sediment earthy, water table at 0.4 m, water shallow, Cvetkov net, chlorinity 306 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xi.1979; ZMA coll. no. C. A. 8205 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Cyprretta* spec.; *Strandesia longula* Broodbakker, 1983; *Candonopsis hummelincki* Broodbakker, 1983), Copepoda (Cyclopidae); Acari.

- 15 ♂♂, 62 ♀♀, 1 fragmentary specimen; AMEWI sta. 79/540, Dépt. de l'Ouest, Croix-des-Missions, Marin, well of Mrs Antagras Mifroh, 150 m from sta. 79/539, 18°36'31"N 72°17'31"W; very primitive well, not covered, water table at 1.0 m, water depth 2.0 m, Cvetkov net, temperature 27.5°C, chlorinity 67 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xi.1979; ZMA coll. no. C. A. 8206 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia longula* Broodbakker, 1983), Copepoda (Cyclopidae).

- 5 ♂♂, 24 ♀♀ (2 with broodpouch), 51 fragmentary specimens; AMEWI sta. 79/541, Dépt. de l'Ouest, Gibert, well of Verdier Edouard, close to the centre of the village, 18°36'44"N 72°18'11"W; handdug

well, in clayish ground, not covered, water table at 3.0 m, water depth 1.0 m, Cvetkov net, temperature 27.3°C, chlorinity 56 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xi.1979; ZMA coll. no. C. A. 8207 [no paratypes].

Accompanying fauna: Crustacea: Isopoda (Microcerberidae), Ostracoda (*Strandesia stocki* Broodbakker, 1983), Copepoda (Cyclopidae), Phyllopora; Acari.

- [specimens of this sample lost?]; AMEWI sta. 79/577, Dépt. de l'Ouest, Dumonet, well of Coriolan, between Caiman and Debas and about 200 m from "Trou Caiman", 18°38'58"N 72°06'58"W; well not walled in, not covered, water table at 4.5 m, water depth 1.2 m, Cvetkov net, temperature 27.5°C, chlorinity 594 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 21.xi.1979.

Accompanying fauna: Crustacea: Amphipoda, Ostracoda, Copepoda (Cyclopidae), Phyllopora; Acari; Mollusca: Gastropoda; Hirudinea.

- 2 ♀♀; AMEWI sta. 79/578, Dépt. de l'Ouest, Dumonet, well of Mrs Tissé Coriolan, just opposite of sta. 79/577, about 200 m from "Trou Caiman", 18°38'58"N 72°06'58"W; well made in sandy bottom, water table at 5.1 m, water depth 0.9 m, Cvetkov net, temperature 27.2°C, chlorinity 422 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 21.xi.1979; ZMA coll. no. C. A. 8208 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Bahadzia latipalpus* Stock, 1985), Isopoda (*Anopsilana* spec.), Ostracoda (*Caribecandona* (*Caribecandona*) *auricularia* Broodbakker, 1983; *Chlamydotheca unispinosa* (Baird, 1862); *Physocypria* spec.), Copepoda (*Mesocyclops aspericornis* (Daday, 1906)), Phyllopora; Acari; Mollusca: Gastropoda.

- 1 ♀; AMEWI sta. 79/580, Dépt. de l'Ouest, Debas, well of Eliassin Aldoni, between Caiman and Thomazeau, 18°38'58"N 72°06'34"W; well probably made in sandy bottom, partially covered, water table at 6.0 m, water depth 1.8 m, Cvetkov net, temperature 28.0°C, chlorinity 2330 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 21.xi.1979; ZMA coll. no. C. A. 8209 [no paratype].

Accompanying fauna: Crustacea: Isopoda, Ostracoda, Copepoda (*Mesocyclops aspericornis* (Daday, 1906); *Thermocyclops decipiens* (Kiefer, 1929)), Cladocera; Insecta; Polychaeta.

- 7 ♀♀, 1 fragmentary specimen; AMEWI sta. 79/587, Dépt. de l'Ouest, l'Etang, well of Montezy Imachilis, 18°38'38"N 72°03'48"W; well made in sandy bottom, water table at 5.0 m, water depth 0.9 m, Cvetkov net, temperature 27.8°C, chlorinity 48 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 21.xi.1979; ZMA coll. no. C. A. 8210 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Zombiweeckelia parvipalpus* Stock, 1985; *Crangoweckelia spinicauda* Stock, 1985), Ostracoda, Copepoda (Cyclopidae); Oligochaeta.

- 11 ♀♀ (9 with broodpouch); AMEWI sta. 79/601, Dépt. de l'Artibonite, Dessalines, well of Gaby Gabriel, Rue Jacques 1<sup>er</sup>, 19°15'36"N 72°31'01"W; well dug out in alluvia (sand; gravel), walled in to certain depth, covered, water table at 8.0 m, water depth 3.0 m, Cvetkov net, temperature 28.1°C, chlorinity 143 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 23.xi.1979; ZMA coll. no. C. A. 8211 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Crangoweckelia mixta* Stock, 1985), Ostracoda (*Caribecandona* (*Caribecandona*) *ansa* Broodbakker, 1983), Copepoda (*Mesocyclops aspericornis* (Daday, 1906); *Thermocyclops decipiens* (Kiefer, 1929)); Insecta: Collembola; Acari; Mollusca: Gastropoda; Hirudinea.

- 1 ♀; AMEWI sta. 79/603, Dépt. de l'Artibonite, Dessalines, well of Saimval Luisin, on the corner of Rue Jacques 1<sup>er</sup>, 19°15'36"N 72°31'01"W; well dug in sandy bottom, partially walled in, partially covered, diameter very large, water clear, Cvetkov net, chlorinity 189 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 23.xi.1979; ZMA coll. no. C. A. 8212 [no paratype].

Accompanying fauna: Crustacea: Amphipoda (*Crangoweckelia mixta* Stock, 1985), Ostracoda, Copepoda (*Thermocyclops decipiens* (Kiefer, 1929)), Cladocera; Insecta; Oligochaeta.

- [specimens of this sample lost?]; AMEWI sta. 79/605, Dépt. de l'Artibonite, Dessalines, well of Nord Albert, Rue Charlotin, at the foot of a calcareous mountain, 19°15'36"N 72°31'15"W; well dug out in sand and gravel, covered, clean, water table at 3.5 m, water depth 6.0 m, Cvetkov net, temperature 27.3°C, chlorinity 73 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 23.xi.1979.

Accompanying fauna: Crustacea: Amphipoda (*Crangoweckelia mixta* Stock, 1985), Copepoda (*Thermocyclops decipiens* (Kiefer, 1929)), Cladocera; Acari; Oligochaeta.

- 23 ♂♂, 809 ♀♀ (19 with broodpouch), 25 juveniles, 24 fragmentary specimens; AMEWI sta. 79/609, Dépt. de l'Artibonite, Gonaïves, well of the Royal Hôtel, inner court, about 250 m from the sea; well

walled in to the bottom, covered, clean, pump installed, water table at 0.4 m, water depth 2.0 m, Cvetkov net, temperature 27.5°C, chlorinity 79 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8192; RMNH G 67 [all paratypes].

Accompanying fauna: Crustacea: Amphipoda, Copepoda (*Thermocyclops decipiens* (Kiefer, 1929)); Insecta.

- 5 ♂♂, 40 ♀♀ (2 with broodpouch), 5 fragmentary specimens; AMEWI sta. 79/610, Dépt. de l'Artibonite, Gonaïves, well of the Agricultural Department Office, very close to sta. 79/609, Rue Louverture, about 250 m from the sea; well shadowed, covered, not used for drinking water, pump installed, water table at 1.0 m, water depth 1.1 m, Cvetkov net, temperature 25.8°C, chlorinity 1632 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8193 [paratypes].

Accompanying fauna: Crustacea: Copepoda (*Mesocyclops ellipticus* Kiefer, 1936).

- 89 ♂♂, 648 ♀♀ (8 with broodpouch), 19 juveniles, 16 fragmentary specimens; AMEWI sta. 79/611, Dépt. de l'Artibonite, Gonaïves, well of Mrs Luc Désir, on the national road Gonaïves to Cap Haitien, about 1.5 km from the sea; very primitive well, in fine black sediment, diameter narrow, no drinking water, water table at 0.5 m, water depth 1.0 m, Cvetkov net, temperature 25.8°C, chlorinity 410 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8190 [holotype], ZMA coll. no. C. A. 8191; BMNH; MF; MP; HUI; RMNH G 61; UEKL; UPMG; USNM; WAM; ZMC [all paratypes].

Accompanying fauna: Crustacea: Ostracoda, Copepoda (*Mesocyclops ellipticus* Kiefer, 1936); Insecta; Mollusca: Gastropoda; Oligochaeta.

- 1 ♂; AMEWI sta. 79/613, Dépt. de l'Artibonite, Gonaïves, well of Mérita Justin, quarter Guérin, on the national road to Port-au-Prince, about 1.5 km from the sea; very primitive well, dug in earth, stones on bottom, rather clean, little sediment, water table at 1.0 m, water depth 0.6 m, Cvetkov net, temperature 26.0°C, chlorinity 506 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8194 [paratype].

Accompanying fauna: Crustacea: Ostracoda, Copepoda, Cladocera; Insecta: Diptera, Coleoptera.

- 10 ♂♂, 38 ♀♀ (4 with broodpouch), 11 juveniles; AMEWI sta. 79/616, Dépt. de l'Ouest, Archaïe, well of Henri Sterlin, at the central place of village, about 300 m from the sea, 18°46'08"N 72°30'44"W; well walled in to the bottom, not covered, clean, water table at 0.8 m, water depth 2.4 m, Cvetkov net, temperature 27.5°C, chlorinity 97 mg/l; collected by L. Botosaneanu and J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8213 [no paratypes].

Accompanying fauna: Insecta: aquatic Hemiptera, Diptera; Mollusca: Gastropoda; Oligochaeta.

- 4 ♂♂, 106 ♀♀, 4 juveniles, 1 fragmentary specimen; AMEWI sta. 79/617, Dépt. de l'Ouest, Archaïe, well close to the market, about 100 m from the sea, 18°46'08"N 72°30'44"W; well dug in soil, not covered, murky water, water table at 0.5 m, water depth 0.8 m, Cvetkov net, temperature 26.3°C, chlorinity 145 mg/l; collected by L. Botosaneanu and J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8214; RMNH G 69 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia longula* Broodbakker, 1983), Copepoda (*Mesocyclops aspericornis* (Daday, 1906)), Cladocera; Insecta: Diptera; Oligochaeta.

- 56 ♂♂, 365 ♀♀ (245 with broodpouch), 14 juveniles, 6 fragmentary specimens; AMEWI sta. 79/618, Dépt. de l'Ouest, Archaïe, well of Luc Pierre, Rue Abbé Andelin, not far from the market, about 200 m from the sea, 18°46'08"N 72°30'44"W; well walled into the water level, not covered, relatively clean, water table at 1.5 m, water depth 2.0 m, Cvetkov net, temperature 28.1°C, chlorinity 101 mg/l; collected by L. Botosaneanu and J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8215; RMNH G 70 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia longula* Broodbakker, 1983), Copepoda (*Mesocyclops aspericornis* (Daday, 1906)); Insecta: Acari; Polychaeta; Oligochaeta.

- 22 ♂♂, 278 ♀♀ (11 with broodpouch), 14 juveniles; AMEWI sta. 79/619, Dépt. de l'Ouest, Archaïe, well of Pierre Jeanlouis, section Merotte, about 2 km from the sea, 18°46'51"N 72°31'35"W; well dug out in sand, some gravel, not covered, clean, water table at 8.0 m, water depth 2.0 m, Cvetkov net, temperature 27.6°C, chlorinity 44 mg/l; collected by L. Botosaneanu and J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8216; RMNH G 71 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Zombiweckelia parvipalpus* Stock, 1985), Isopoda, Ostracoda, Copepoda (Cyclopidae), Cladocera; Insecta: Diptera, Coleoptera; Acari.

- 7 ♂♂, 156 ♀♀ (32 with broodpouch), 4 juveniles; AMEWI sta. 79/620, Dépt. de l'Ouest, Arcahaie, well of Boss Raoul Bélizaire, quarter Cortade, much closer to the sea than sta. 79/619, about 18°46'N 72°31'W; well dug in sand, not covered, clean, water table at 3.2 m, water depth 4.0 m, Cvetkov net, temperature 26.9°C, chlorinity 17.2 mg/l; collected by L. Botosaneanu and J.G.M. Notenboom; 24.xi.1979; ZMA coll. no. C. A. 8217; RMNH G 72 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Zombiweckelia parvipalpus* Stock, 1985), Ostracoda (*Strandesia stocki* Broodbakker, 1983), Copepoda (*Mesocyclops aspericornis* (Daday, 1906)); Insecta: Diptera.

- 1 (damaged) ♀; AMEWI sta. 79/622, Dépt. du Centre, River Gimballé, at crossing with road from Croix-des-Bouquets to Mirebalais, alt. ca. 100 m, large metarhithron, 18°46'31"N 72°07'05"W; river interstitia, coarse sand, but with some stones and pebbles, not shadowed, collected with Karaman-Chappuis method, temperature river 23.0°C, temperature sample 24.3°C, chlorinity 16.2 mg/l; collected by L. Botosaneanu and J.G.M. Notenboom; 26.xi.1979; ZMA coll. no. C. A. 8218 [no paratype].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae); Insecta: Diptera; Mollusca: Gastropoda; Polychaeta; Oligochaeta.

- 1 ♂, 8 ♀♀, 1 juvenile, 2 fragmentary specimens; AMEWI sta. 79/623, Dépt. du Centre, River Boucananie, crossing the road from Mirebalais to Croix-des-Bouquets, alt. ca. 100 m, small metarhithron, 18°47'43"N 72°06'48"W; river interstitia, good alluvia, collected with Karaman-Chappuis method, temperature river 27.3°C, temperature sample 26.3°C, chlorinity 11.8 mg/l; collected by L. Botosaneanu and J.G.M. Notenboom; 26.xi.1979; ZMA coll. no. C. A. 8219 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda; Insecta: Hemiptera, Diptera larvae, Coleoptera larvae; Acari; Mollusca: Bivalvia; Polychaeta; Oligochaeta.

- 3 ♂♂, 9 ♀♀ (1 with broodpouch); AMEWI sta. 79/676, Dépt. du Nord, Bénard, sector Milot, well of Rafael Saintfrère, approximate position between 19°37'23"N 72°13'53"W and 19°35'23"N 72°11'30"W; well partially walled, much grey sediment, large diameter, water table at 2.6 m, water depth 1.4 m, Cvetkov net, temperature 24.3°C, chlorinity 383 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xii.1979; ZMA coll. no. C. A. 8220 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983; *Strandesia longula* Broodbakker, 1983), Copepoda (Cyclopidae); Insecta: Hemiptera; Acari; Oligochaeta.

- 8 ♂♂, 31 ♀♀ (5 with broodpouch), 1 juvenile; AMEWI sta. 79/678, Dépt. du Nord, Milot, sector Tassy, well of Deshommes Salvat, approximate position between 19°37'23"N 72°13'53"W and 19°35'23"N 72°11'30"W; well walled to water level, covered, clean, water table at 1.7 m, water depth 4.3 m, Cvetkov net, temperature 25.4°C, chlorinity 31.2 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xii.1979; ZMA coll. no. C. A. 8221 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983; *Strandesia longula* Broodbakker, 1983), Copepoda (Cyclopidae); Insecta: Acari; Mollusca: Gastropoda; Oligochaeta.

- 7 ♀♀ (1 with broodpouch); AMEWI sta. 79/679, Dépt. du Nord, Milot, sector Brossard, well of Narcisus Etienne, approximate position between 19°37'23"N 72°13'53"W and 19°35'23"N 72°11'30"W; well not used anymore, sometimes dry, water table at 2.5 m, water depth 2.0 m, Cvetkov net, temperature 25.6°C, chlorinity 60 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xii.1979; ZMA coll. no. C. A. 8222 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983; *Strandesia longula* Broodbakker, 1983), Copepoda (Cyclopidae); Insecta: diverse larvae, Coleoptera; Acari; Mollusca: Gastropoda.

Description.— Body length (antennae 1 and 2 excluded) of male up to 2059 µm (holotype), of female up to 2202 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with five, four, and two long plumose macrosetae on respective median margins; main flagellum 7- to 9-segmented, last segment with seven simple macrosetae of unequal length (sub)terminally; accessory

flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with four teazel macrosetae on the medial and mediolateral margins; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: eight plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with six to nine setules, third segment with obscure unisetulate macroseta.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 14 rake-like serrate macrosetae at terminal margin in left, 15 in right appendage 2, and two modified longer subterminal serrate macrosetae; basipodal endite 3 with seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented and bears five simple macrosetae.

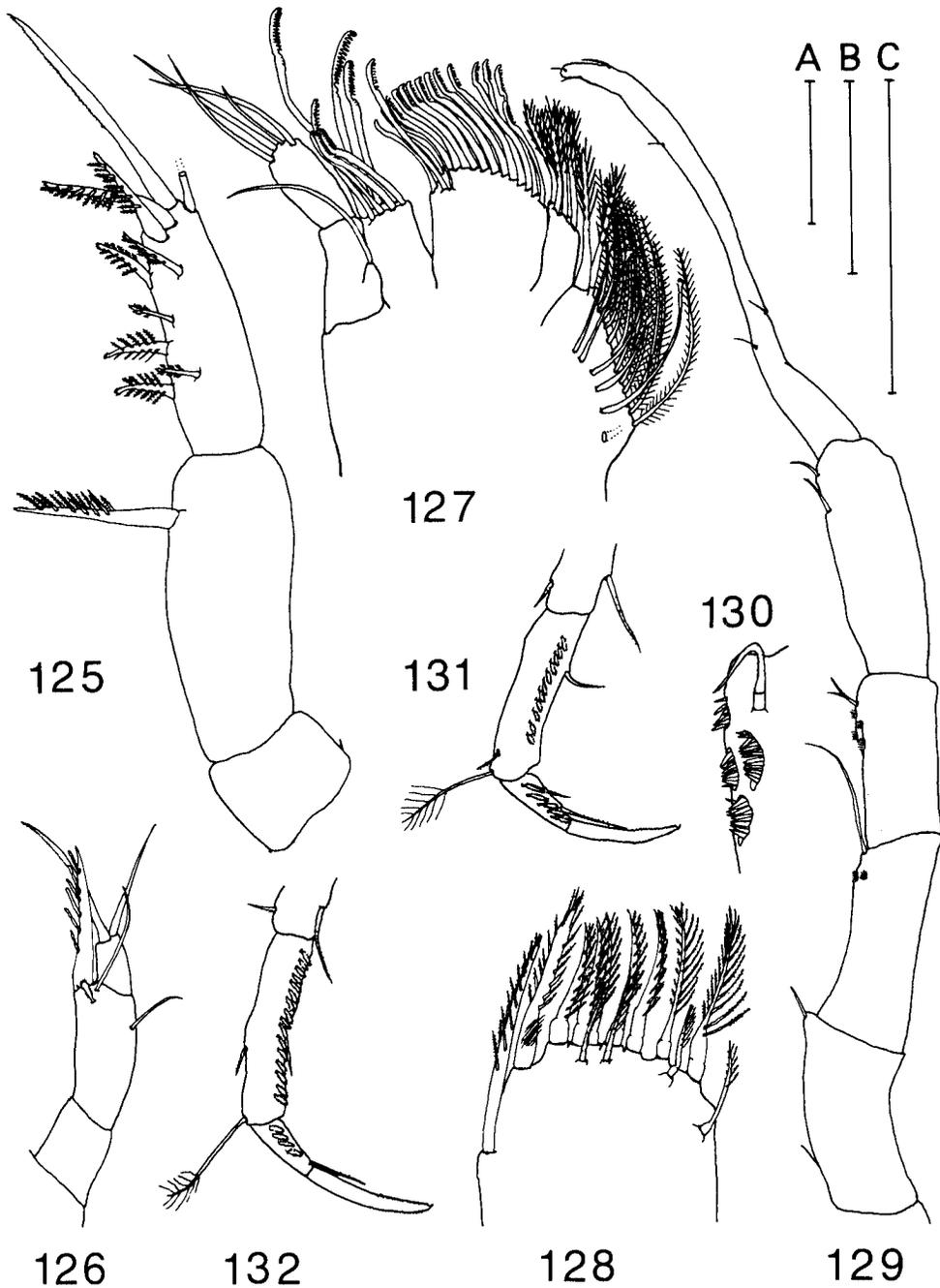
Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with two patches of rather short, but stout club microsetae (diameter  $\times$  height up to circa  $0.5 \times 3.0 \mu\text{m}$ ) on distal portion, third segment with two rows of two patches of tall, more pointed than on second segment, stout club microsetae (diameter  $\times$  height up to circa  $0.5 \times 3.8 \mu\text{m}$ ), fourth segment without patches of club microsetae; basipodal endite bearing 12 plumidenticulate macrosetae with long setules, a tall one medially, seven long ones terminally, three shorter ones subterminally and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, one subterminal and one lateral plumose macrosetae.

Gnathopod: basal segment with three short plumose macrosetae; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; baso-ischium of endopodite with clearly demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

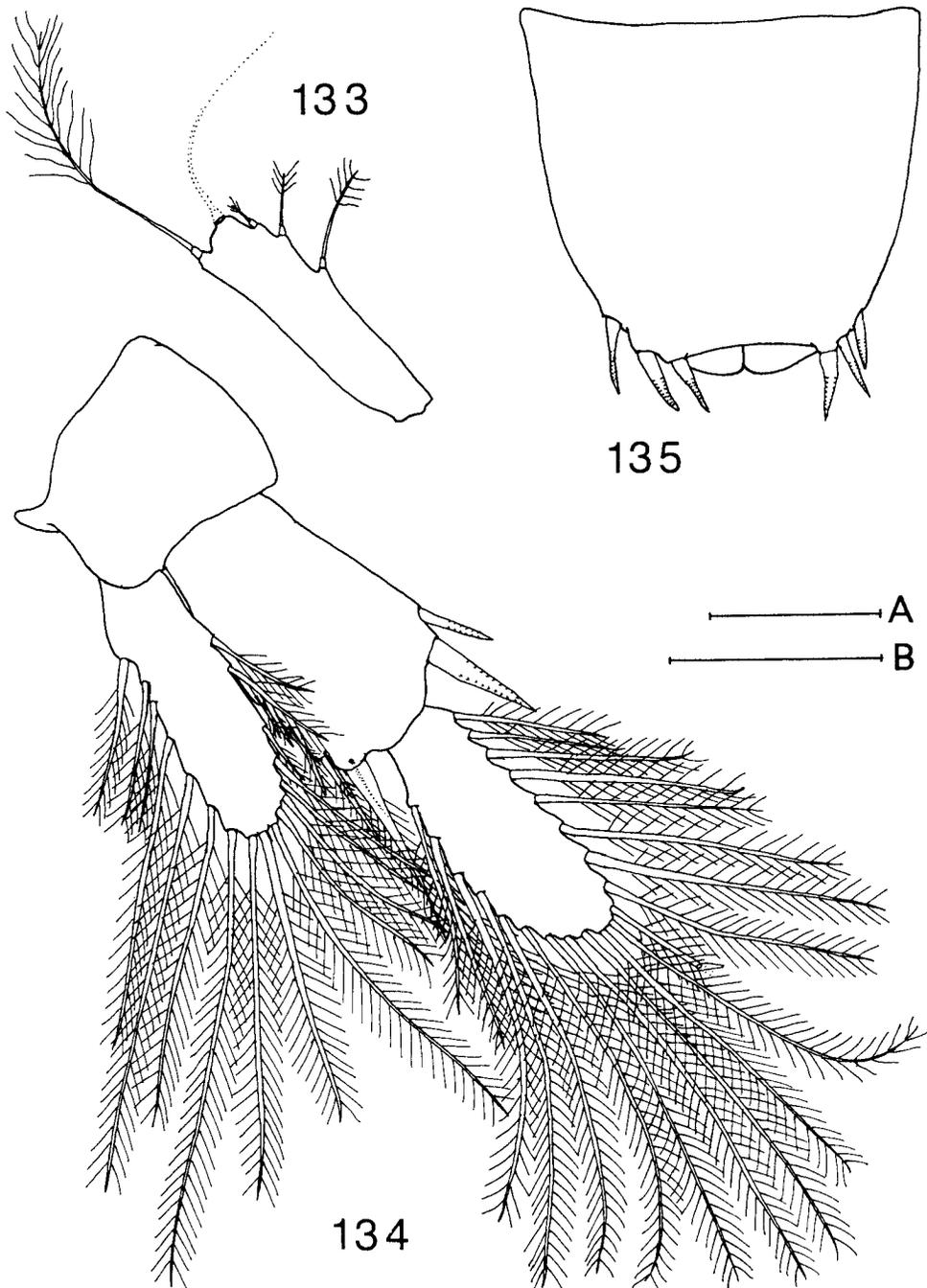
Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with ten ovate microsetae, dactylus with two teazel macrosetae (type IIB1(a)) on ventral margin and five ovate microsetae; first segment of exopodite with one ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and five ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 13 ovate microsetae, dactylus with two teazel macrosetae on ventral



Figs. 125-132. *Tethysbaena haitiensis* spec. nov., holotype ♂. 125, palp mandible. 126, palp maxilla 1. 127, maxilla 2. 128, distal portion of basipodal endite of maxilliped. (figs. 125-128 scale C). 129, endopodite of maxilliped (scale B). 130, detail microsetae at distal portion of endopodite segment 3 of maxilliped (extremely enlarged). 131, distal portion of pereopod 3. 132, distal portion of pereopod 6. (figs. 131-132 scale A). Scales indicated 0.1 mm.



Figs. 133-135. *Tethysbaena haitiensis* spec. nov., holotype and paratype ♂. 133, pleopod 2, holotype. (scale B). 134, uropod, paratype. 135, telson, holotype. (figs. 134-135 scale A). Scales indicated 0.1 mm.

margin and four ovate microsetae; first segment of exopodite with four ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 13 to 14 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and five ovate microsetae; first segment of exopodite with four ovate microsetae, second segment with one medial, one subterminal and two terminal plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 16 ovate microsetae, dactylus with one teazel macroseta on ventral margin and four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macroseta and one vestigial terminal macroseta, four ovate microsetae present.

Pereiopod 7: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 18 ovate microsetae, dactylus with one teazel macroseta on ventral margin and four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macroseta, two vestigial macrosetae, one terminal and one lateral, three ovate microsetae present.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of four stout plumose macrosetae, each accompanied by small subplumose macroseta, segment 2 with 16 to 21 plumose macrosetae; endopodite bearing 14 to 17 plumose macrosetae.

Telson: wider than long, mean width/length ratio 1.21; anal lobes protruding beyond terminal stretch; stretch slightly concave.

Variability.— This species shows a considerable range of variation in the number of segments of the main flagellum of antenna 1 and in the number of plumose macrosetae of the uropodal rami.

Remarks.— Distinctive characters from the other members of the "*T. sanctaerucis*-group" have been mentioned in the discussion of *T. juriaani*. For detailed information on specific differences with the other congeners of this species-group one is referred to table 1 (p. 140).

Etymology.— This species is named after the country of origin.

Distribution.— This is a wide-spread species, found in the subterranean waters of the Plaine du Nord, the entire Vallée de l'Artibonite, Plaine de l'Arcahaie, Plaine du Cul-De-Sac (Étang Saumâtre), Plaine de Léogâne, and the Plaine de Jacmel.

Habitat.— All collecting sites that yielded *Tethysbaena haitiensis* are located in alluvial deposits of Holocene origin (Weyl, 1966). Some of the plains are for the larger part of Pleistocene (Plaine de Jacmel), Miocene (lower reaches of Rivière de l'Artibonite) and Cretaceous origin (north of Plaine de Jacmel), but scattered alluvial deposits of Holocene age are present (stations 78/216, 79/601, 79/603, 79/605, and

78/207). Chlorinity varies from plain to plain: Plaine du Nord (0.03‰ to 0.383‰-limnic to oligohaline), the entire Vallée de l'Artibonite (0.012‰ to 1.632‰-limnic to oligohaline), Plaine de l'Arcahaie (0.017‰ to 0.145‰-limnic), Plaine du Cul-De-Sac (Étang Saumâtre) (0.01‰ to 2.33‰-limnic to oligohaline), Plaine de Léogâne (0.04‰-limnic), and the Plaine de Jacmel (0.03‰ to 0.05‰-limnic). Temperatures range from 24.3 to 28.3°C. Many of the stations were heavily polluted with organic matter (mainly plant detritus). Therefore it is not surprising that a large diversity of accompanying fauna was collected also. Among them several troglobitic Amphipoda and Ostracoda, and epigeal dispersalists (Ostracoda, Copepoda, Phyllopora, Acari, Insecta, Oligochaeta).

#### 4.4.2.4. *Tethysbaena juglandis* spec. nov. (figs. 136-145)

Thermosbaenacea (partim); Stock, 1979: 64-65; Stock, 1980a: 7; Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1984a: 6 table II; Broodbakker, 1984b: 41; Stock, 1986d: 199.

Thermosbaenacea; Spangler, 1981: 380.

Thermosbaenacés; Botosaneanu & Stock, 1982: 20.

Thermosbaenaceans (partim); Stock, 1983a: 277.

unident. spp.; Schram, 1986: 221.

*Monodella* (partim); Wagner, 1990: 123.

Material.— **Hispaniola, Haiti**: 4 ♂♂, 4 ♀♀; AMEWI sta. 78/238, Dépt. du Nord, Limbé, N side road D 100, 19°42'29"N 72°23'53"W; from covered well, diam. 1.0 m, water with filamentous algae, water table at 2.0 m, water depth 1.0 m, Cvetkov net, chlorinity 240 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 10.v.1978; ZMA coll. no. C.A. 8183 [no paratype].

Accompanying fauna: Crustacea: Amphipoda (*Radaweckelia brevicauda* Stock, 1985), Isopoda (*Microcharon* spec.), Ostracoda, Copepoda (Cyclopidae); Insecta: Diptera larvae; Oligochaeta (*Dero (Dero) haitiensis* Dumnicka, 1986; *Dero (Aulophorus) furcata* (Müller, 1773)).

- 3 ♀♀; AMEWI sta. 78/239, Dépt. du Nord, Limbé, S side road D 100, 19°42'05"N 72°23'53"W; from well, not covered, diam. 1.5 m, water table at 2.5 m, water depth 1.5 m, Cvetkov net, chlorinity 100 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 10.v.1978; ZMA coll. no. C.A. 8184 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983), Copepoda (Cyclopidae); Oligochaeta (*Dero (Dero) digitata* Müller, 1773; *Dero (Dero) sawaway* Marcus, 1943; *Dero (Aulophorus) furcata* (Müller, 1773); *Pristina leidy* Smith, 1896).

- 13 ♂♂, 8 ♀♀ (2 with broodpouch), 3 fragmentary specimens; AMEWI sta. 78/241, Dépt. du Nord, Village of Camp-Coq (= S of Limbé), well of school (E side road D 100), 19°40'03"N 72°25'06"W; from square covered well, windpump broken, water table at 2.0 m, water depth 0.5 m, Cvetkov net, chlorinity 200 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 10.v.1978; ZMA coll. no. C.A. 8182 [paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Pintaweckelia grandis* Stock, 1985); Insecta: Coleoptera (*Anommatelemis botosaneanui* Spangler, 1981), Collembola; Oligochaeta (*Dero (Aulophorus) furcata* (Müller, 1773); *Pristina aequisetata* Bourne, 1891).

- 1 ♂; AMEWI sta. 79/681, Dépt. du Nord, Lombard, E of Limbé, well of Mrs Elitess Jeanlouis, 19°42'23"N 72°23'08"W; well walled in to the bottom, water table at 4.1 m, water depth 0.4 m, Cvetkov net, chlorinity 69 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xii.1979; ZMA coll. no. C.A. 8185 [no paratype].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983), Copepoda (Cyclopidae); Insecta: Diptera larvae, Plecoptera, Coleoptera; Acari; Mollusca: Gastropoda; Oligochaeta.

- 1 ♂; AMEWI sta. 79/684, Dépt. du Nord, Limbé, E entrance of town, on the national road, well of

Mrs Antoine Dugrène, 19°42'14"N 72°23'55"W; well walled in to the bottom, water table at 1.8 m, water depth 1.0 m, Cvetkov net, temperature 25.1°C, chlorinity 17.2 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xii.1979; ZMA coll. no. C. A. 8186 [no paratype].

Accompanying fauna: Crustacea: Ostracoda, Copepoda (*Mesocyclops aspericornis* (Daday, 1906); *Thermocyclops decipiens* (Kiefer, 1929)); Insecta: Coleoptera; Oligochaeta; Hirudinea.

- 6 ♀♀ (1 with broodpouch); AMEWI sta. 79/687, Dépt. du Nord, Limbé, sector Canal, well of André Constant, 19°42'14"N 72°23'55"W; well walled in with large stones to the water level, little sediment, rather clean, water table at 2.0 m, water depth 1.1 m, Cvetkov net, temperature 26.0°C, chlorinity 25.8 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xii.1979; ZMA coll. no. C. A. 8187 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda, Copepoda (*Mesocyclops aspericornis* (Daday, 1906)); Insecta; Acari; Oligochaeta.

- 1 ♀; AMEWI sta. 79/688, Dépt. du Nord, Limbé, sector Moulin, well of Mézardié, 19°42'14"N 72°23'55"W; well walled in, very dirty, water table at 4.0 m, water depth 0.4 m, Cvetkov net, temperature 25.4°C, chlorinity 12.4 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 10.xii.1979; ZMA coll. no. C. A. 8188 [no paratype].

Accompanying fauna: Crustacea: Ostracoda (*Strandesia stocki* Broodbakker, 1983), Copepoda (*Mesocyclops ellipticus* Kiefer, 1936); Acari; Oligochaeta; Hirudinea.

- 3 ♂♂, 12 ♀♀; AMEWI sta. 79/689, Dépt. du Nord, Limbé, well of Rectory (Presbytère), 19°42'14"N 72°23'55"W; from well, sandy bottom, clean, pump connected, water table at 2.3 m, water depth 1.2 m, Cvetkov net, temperature 26.5°C, chlorinity 13.8 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 11.xii.1979; ZMA coll. no. C. A. 8189 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Pintaweckelia grandis* Stock, 1985), Isopoda (?*Cyathura* (*Stygocyathura*) *motasi* Botosaneanu & Stock, 1982), Ostracoda (*Strandesia stocki* Broodbakker, 1983), Copepoda (*Mesocyclops ellipticus* Kiefer, 1936); Insecta: Coleoptera (*Anommatelmis botosaneanui* Spangler, 1981); Acari; Oligochaeta.

- 22 ♂♂, 150 ♀♀ (3 with broodpouch), 3 fragmentary specimens; AMEWI sta. 79/693, Dépt. du Nord, Camp-Coq, well of the Community school (one of the two wells in the village), alt. ca. 80 m, 19°38'09"N 72°25'13"W; well walled in to the bottom, covered, sandy bottom, clean, water table at 4.5 m, water depth 0.4 m, Cvetkov net, temperature 26.6°C, chlorinity 13.2 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 11.xii.1979; ZMA coll. no. C. A. 8179 [holotype], ZMA coll. no. C. A. 8180; BMNH; MF; MP; HUJ; UEKL; UR; USNM; WAM; ZMC [all paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Radaweckelia brevicauda* Stock, 1985); Insecta: Coleoptera (*Anommatelmis botosaneanui* Spangler, 1981); Oligochaeta.

- 2 ♂♂, 29 ♀♀, 4 fragmentary specimens; AMEWI sta. 79/694, Dépt. du Nord, Camp-Coq, well of the Rectory (one of the two wells in the village), alt. ca. 80 m, 200 m from sta. 79/693, 19°38'09"N 72°25'13"W; well walled in to the bottom, water table at 3.4 m, water depth 1.1 m, Cvetkov net, temperature 26.6°C, chlorinity 12.8 mg/l; collected by L. Botosaneanu & J.G.M. Notenboom; 11.xii.1979; ZMA coll. no. C. A. 8181 [paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Radaweckelia brevicauda* Stock, 1985), Isopoda (*Cyathura* (*Stygocyathura*) *motasi* Botosaneanu & Stock, 1982); Insecta: Diptera larvae, Coleoptera (*Anommatelmis botosaneanui* Spangler, 1981), Collembola.

Description.— Body length (antennae 1 and 2 excluded) of male up to 1612 µm (holotype), of female up to 1868 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with five, four, and two long plumose macrosetae on respective median margins; main flagellum 8- to 9-segmented, last segment with seven simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with four teazel macrosetae on the medial and mediobasal margins; flagellum 5- to 6-segmented, last segment with five simple

macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: seven plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with four to five setules, third segment with well-developed unisetulate macroseta with three setules.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 15 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae, respectively; endopodite 2-segmented and bears four simple macrosetae.

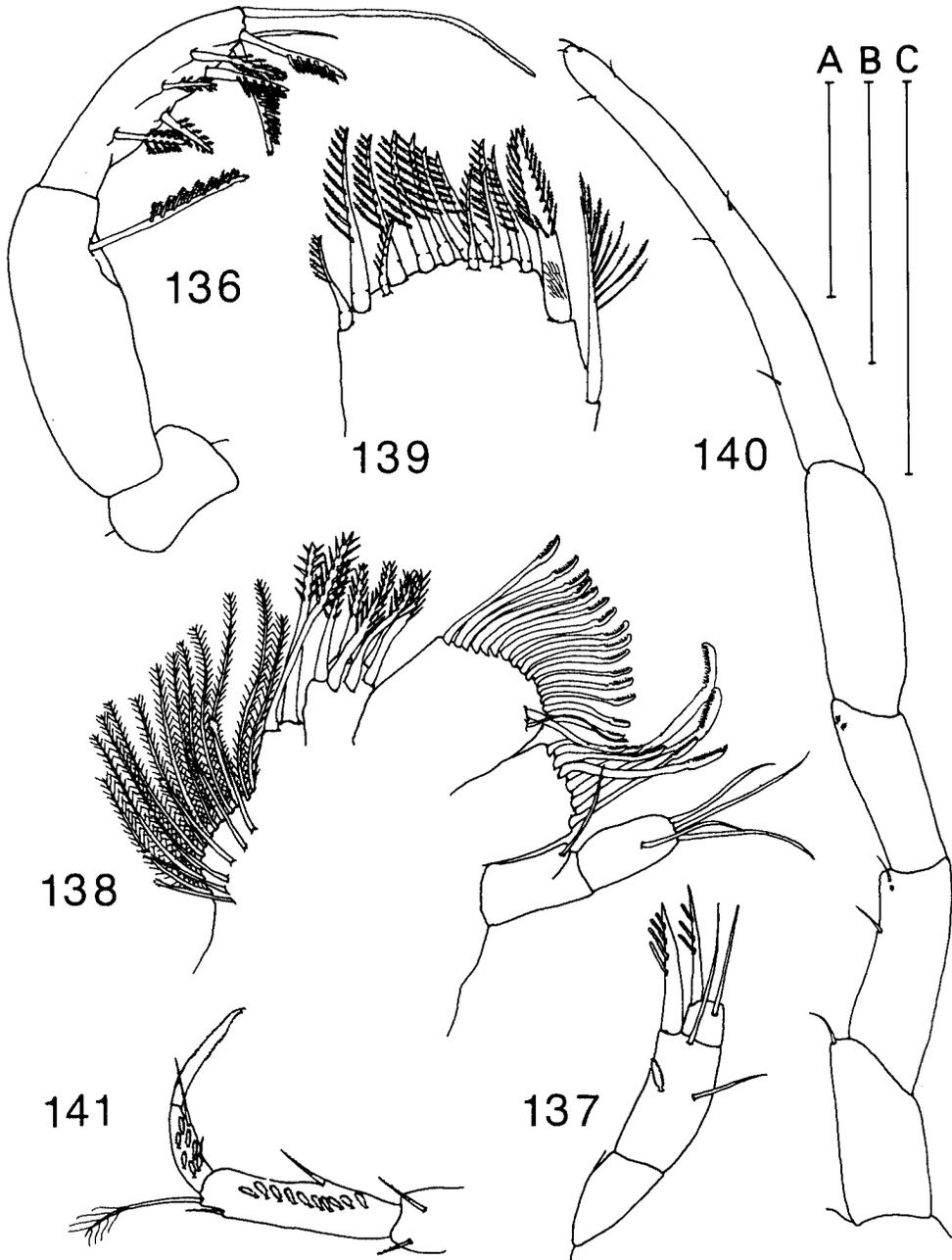
Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with one patch of a few minute club microsetae (diameter  $\times$  height up to circa  $0.3 \times 1 \mu\text{m}$ ) on distal portion, third segment with two patches of a few minute club microsetae (diameter  $\times$  height up to circa  $0.35 \times 1.6 \mu\text{m}$ ), fourth segment without patches of club microsetae; basipodal endite bearing 13 plumidenticulate macrosetae with long setules, a tall one medially, eight long ones terminally, three shorter ones subterminally and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, one subterminal and one lateral plumose macrosetae.

Gnathopod: basal segment with two short plumose macrosetae; exopodite with three medial, two subterminal, two terminal and two lateral plumose macrosetae; baso-ischium of endopodite with indistinct ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

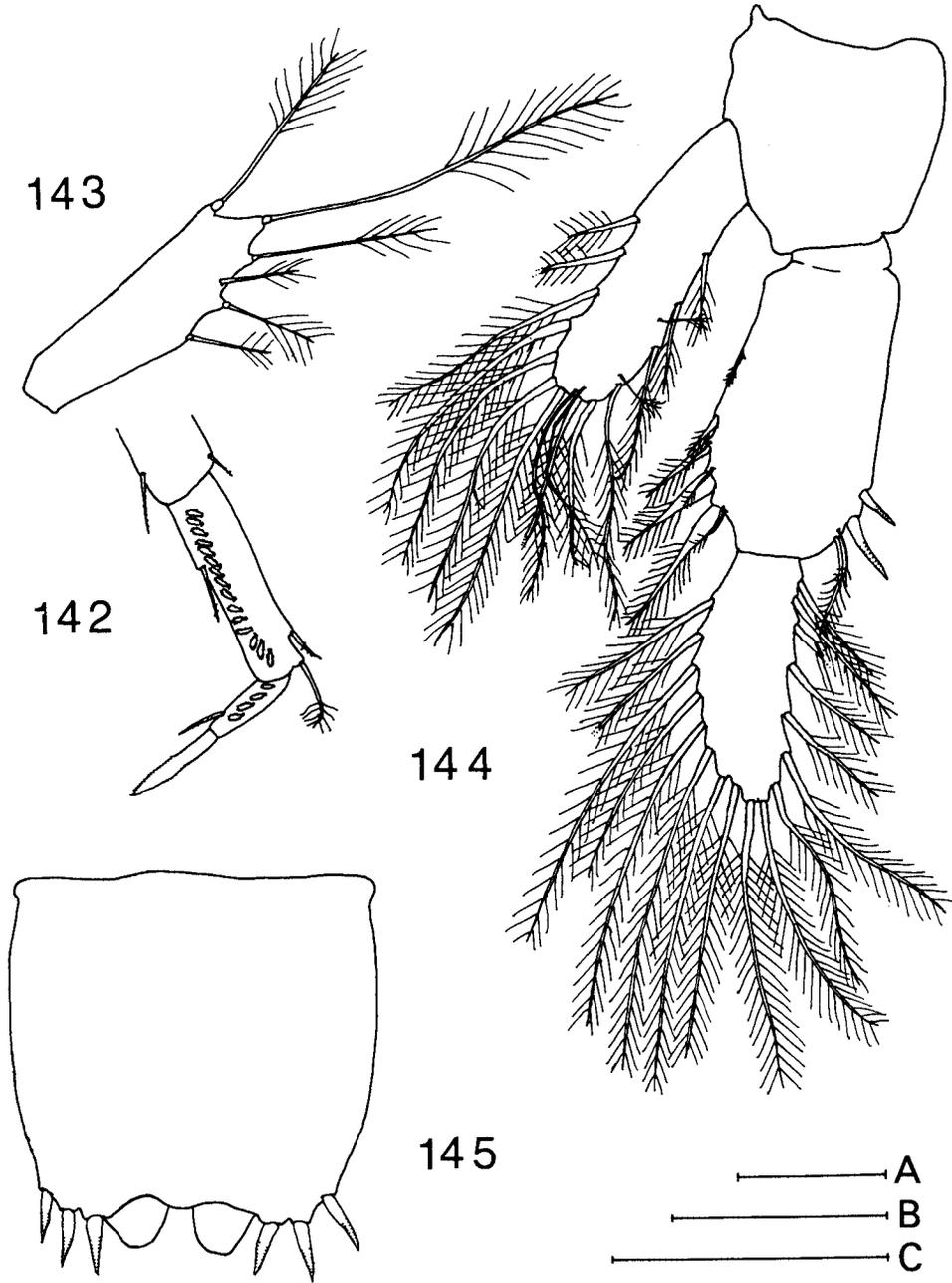
Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with eight to nine ovate microsetae, dactylus with one teazel macroseta (type IIB1(a)) on ventral margin and two rows of three and four ovate microsetae, respectively; first segment of exopodite with one ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one mediobasal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with ten ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of three and four ovate microsetae, respectively; first segment of exopodite with two ovate microsetae, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediobasal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with two medial, two subterminal, two terminal and one lat-



Figs. 136-141. *Tethysbaena juglandis* spec. nov., holotype ♂. 136, palp mandible. 137, palp maxilla 1. 138, maxilla 2. 139, distal portion of basipodal endite of maxilliped. (figs. 136-139 scale C). 140, endopodite of maxilliped (scale B). 141, distal portion of pereiopod 3 (scale A). Scales indicated 0.1 mm.



Figs. 142-145. *Tethysbaena juglandis* spec. nov., holotype ♂ and paratype ♀. 142, distal portion of pereopod 6, holotype. 143, pleopod 2, holotype (scale C). 144, uropod, paratype (scale A). 145, telson, holotype. (figs. 142 and 145 scale B). Scales indicated 0.1 mm.

eral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one mediodistal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with one ovate microseta, second segment with one medial, one subterminal and two terminal plumose macrosetae and one vestigial lateral macroseta.

Pereiopod 6: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 14 to 15 ovate microsetae, dactylus with one teazel macroseta on ventral margin and four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, three vestigial macrosetae, one terminally and two laterally implanted, one ovate microseta present.

Pereiopod 7: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 15 to 16 ovate microsetae, dactylus with one teazel macroseta on ventral margin and four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae and one vestigial terminal macroseta, one ovate microseta present.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of four to six stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 15 to 17 plumose macrosetae; endopodite bearing 12 to 13 plumose macrosetae.

Telson: somewhat wider than long, mean width/length ratio 1.05; anal lobes protruding beyond the terminal stretch; stretch slightly concave with a somewhat convex central part.

Variability.— There exists a slight variation in the number of segments of the main flagellum of the antenna 1 (8 or 9), in the number of plumose macrosetae on the uropod, and remarkably some variation is observed in the number of cuspidate macrosetae on the medial margin of the first segment of the uropodal exopodite.

Remarks.— Considering the large distribution of *Tethysbaena haitiensis* all over Haiti, the discovery of another, closely related species, confined to an isolated part of the Plaine du Nord, came as a surprise to me. In almost all of its specific characters *T. juglandis* resembles most closely *T. haitiensis*. However, it can be distinguished from the latter by the slightly lower number of ovate microsetae on the propodus of the pereiopods, the presence of an additional subplumose macroseta on pleopod 2, a lower number of plumose macrosetae on the uropod, the lower number of plumedenticulate macrosetae on the second segment of the mandibular palp, and a well-developed unisetulate macroseta on the third segment of the palp of maxilla 1. Also the pattern of rugosities on the endopodite of the male maxilliped shows specific differences. The presence of a well-developed unisetulate macroseta is a unique character state for this species within the "*T. sanctaerucis*-group", and excludes any doubt

on the specific status of *T. juglandis*. For more information on specific differences with the other members of this species-group one is referred to table 1 (p. 140).

A similar distribution was observed by Stock (1985: 417), who found only subtle differences between two populations of the amphipod *Radaweckelia brevicauda* Stock, 1985, from the Plain de l'Artibonite and the Rivière du Limbé drainage. As he based his description on damaged specimens, a more careful re-examination of his material, and preferably additional samples of complete specimens, is necessary, as we might deal with two closely related species. Also the presence of other endemics (see below) in the Rivière du Limbé drainage pleads in favour of the independent state of *T. juglandis* at the specific level.

**Etymology.**— The specific epithet is a latinization of the surname of Dr Ir Jos Notenboom (Rijksinstituut voor Volksgezondheid en Milieuhygiëne, Bilthoven, The Netherlands), who is one of the collectors of this new species.

**Distribution.**— This species is restricted to the drainage of the Rivière du Limbé, geologically a more or less isolated part of the Plaine du Nord.

**Habitat.**— With chlorinities of 0.012‰ to 0.069‰ the habitat of *Tethysbaena juglandis* can be defined as limnic. The temperature varies between 25.1 and 26.6°C. The alluvial deposits in which the Rivière du Limbé drainage is situated is of Holocene age (Weyl, 1966). It is not remarkable that this species is endemic to the Rivière du Limbé drainage, like the amphipod *Pintaweckelia grandis* Stock, 1985, the isopod, *Cyathura (Stygocyathura) motasi* Botosaneanu & Stock, 1982, and the elmid beetle *Anommatelmis botosaneanui* Spangler, 1981. There might also be another endemic species, closely related to *Radaweckelia brevicauda* Stock, 1985. The remaining accompanying fauna consists of primarily epigeal dispersionalists only.

#### 4.4.2.5. *Tethysbaena lazarevi* spec. nov. (figs. 146-154)

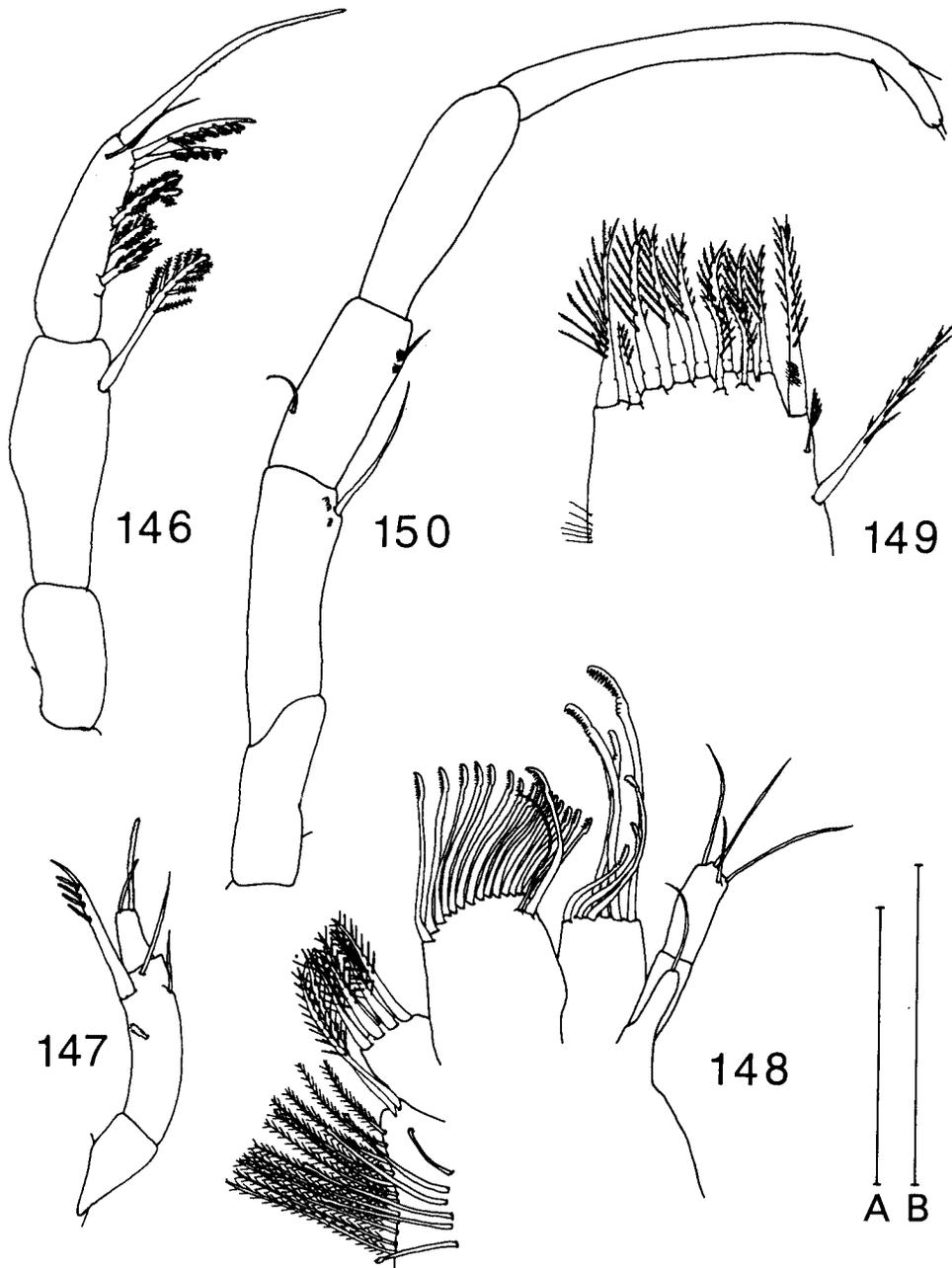
Thermosbaenacea (partim); Orghidan & Nuñez Jimenez, 1977: 12, Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1984b: 41; Stock, 1986d: 199.  
? Thermosbaenacés; Orghidan, Negrea & Viña Bayes, 1977: 30.  
Thermosbaenaceans (partim); Stock, 1983a: 277.  
unident. spp.; Schram, 1986: 221.  
*Monodella* (partim); Wagner, 1990: 123.

**Material.**— **Cuba:** 1 ♂; 2<sup>nd</sup> Cuban-Romanian Exped., Prov. Oriente, Municipio de Mayari, near Mayari Abaso, Arroyo Guayabo; interstitial of gravel bank, 0.3 m depth; collected by L. Botosaneanu; 2.iii.1973; USNM 151476 [holotype].  
- 2 fragmentary specimens; 2<sup>nd</sup> Cuban-Romanian Exped., Prov. Oriente, 200 m off Playa Siboney, Pozo de Agua, from well with electric pump connected (nowadays unused, pump disconnected); collected by L. Botosaneanu; 12-13.iii.1973; ZMA coll. no. C.A. 8153 (= *T. cf. lazarevi*).

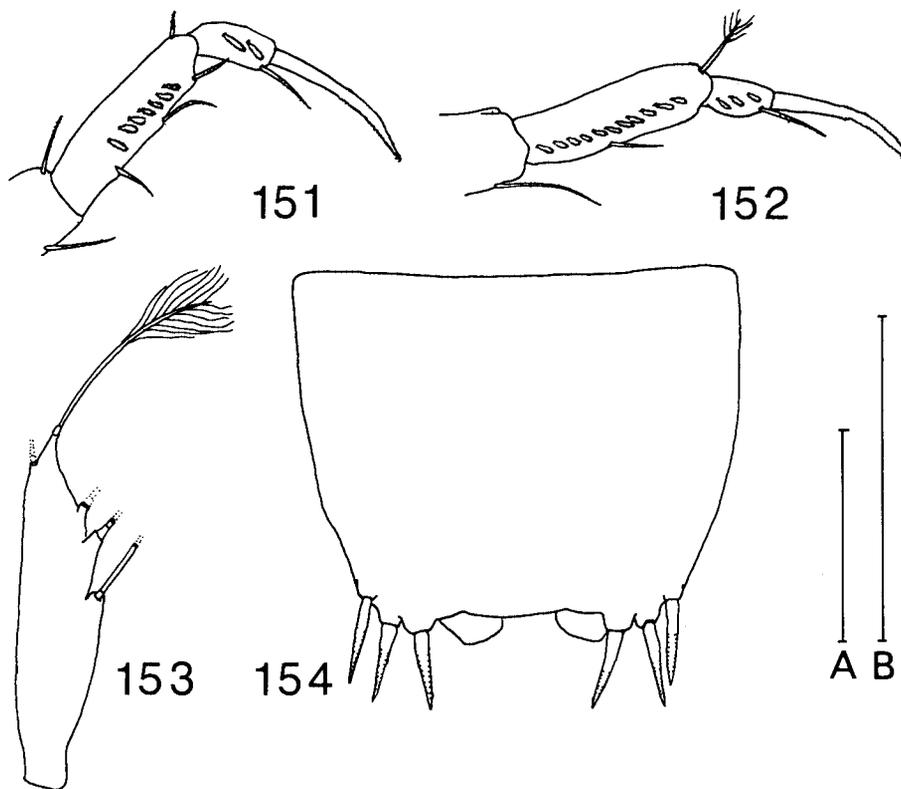
**Description.**— Body length (antennae 1 and 2 excluded) of holotype male 1650 µm.

**Antenna 1:** peduncular segments 1 to 3 with three, three, and two long plumose macrosetae on respective median margins; main flagellum 7-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum partially lost, segments 1 to 3(partim) present only.

**Antenna 2:** all macrosetae broken off, except for a part of segment 4 which carries two teazel macrosetae on the mediodistal margin; flagellum 5-segmented, all macro-



Figs. 146-150. *Tethysbaena lazarei* spec. nov., holotype ♂. 146, palp mandible. 147, palp maxilla 1. 148, maxilla 2. 149, distal portion of basipodal endite of maxilliped. (figs. 146-149 scale B). 150, endopodite of maxilliped (scale A). Scales indicated 0.1 mm.



Figs. 151-154. *Tethysbaena lazarei* spec. nov., holotype ♂. 151, distal portion of pereopod 3. 152, distal portion of pereopod 6. 153, pleopod 2 (scale B). 154, telson. (figs. 151, 152, and 154 scale A). Scales indicated 0.1 mm.

setae broken off on all segments.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta with four setules on second segment, third segment with obscure unisetulate macroseta.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 15, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with two patches of minute club microsetae on the distal portion, third segment with two rows of two patches of minute club microsetae, fourth segment without patches of club microsetae; basipodal endite bearing 12 plumidenticu-

late macrosetae with long setules, none medially, seven long ones terminally, three shorter ones subterminally and one tall and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, two subterminal and one lateral plumose macrosetae.

Gnathopod: exopodite lost; unknown number of plumose macrosetae on basal article (all broken off), baso-ischium of endopodite with indistinctly demarcated ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with one teazel macroseta medially on ventral margin, male with five ovate microsetae, dactylus with two teazel macrosetae (type IIB1(a)) on ventral margin and three ovate microsetae; exopodite lost.

Pereiopod 3: propodus of endopodite with two teazel macrosetae medially on ventral margin, male with seven ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two ovate microsetae; first segment of exopodite with two ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: endopodite lost; first segment of exopodite with one ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: endopodite lost; first segment of exopodite with one ovate microseta, second segment with one subterminal and two terminal plumose macrosetae.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, male with 11 ovate microsetae, dactylus with one teazel macroseta on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one medial and one terminally, one ovate microseta present.

Pereiopod 7: endopodite lost; exopodite 1-segmented with one medial and one subterminal plumose macrosetae and one vestigial terminal macroseta.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: exopodite lost; endopodite bearing 17 plumose macrosetae.

Telson: wider than long, mean width/length ratio 1.29; anal lobes protruding beyond the terminal stretch; stretch slightly concave with a straight centre.

Variability.— Due to the limited number of (damaged) specimens no information on variation is available.

Remarks.— Apart from the material examined Cuban thermosbaenaceans have been collected at Cueva del Agua (Oriente Province), situated in front of Cueva Atabex at El Caney. This sample was mislaid in the period under the care of the late Prof. Cl. Delamare Deboutteville. Cueva del Agua was sampled again during the Cuban-Dutch Biospeleological Expedition (station 89/015), but this time the shrimp *Barbouria cubensis* (von Martens, 1872) was observed only. The two other samples of the Cuban-Romanian Expedition were fortunately available for study, as Dr Lazare Botosaneanu had send the remaining vials (accidentally) to Dr Th. Bowman (Smithsonian Institution, Washington, D.C., U.S.A.) and Dr N. Coineau (Laboratoire Arago, Banyuls-sur-Mer, France), who kindly put them at my disposal. Additional sampling

during the Cuban-Dutch Biospeleological Expedition at the same localities was unsuccessful (stations 89/014 and 89/024). Despite the fact that only one damaged, and two fragmentary specimens were available to me after all, the information provided was sufficient to recognize specific characters in comparison to the other Cuban species, viz. *Tethysbaena tinima* spec. nov., and other congeners of the "*T. sanctaerucis*-group". For detailed information on specific differences one is referred to table 1 (p. 140).

**Etymology.**— The new species is named in honour of Dr Lazare Botosaneanu (Zoölogisch Museum, Amsterdam, The Netherlands), who participated in the Cuban-Romanian Expeditions and the Amsterdam Expeditions to the West Indian Islands.

**Distribution.**— This species is confined to the Valle de Guantanamo, where it is collected in the river interstitia of the Arroyo Guayabo and near the coast at Playa Siboney.

**Habitat.**— At Playa Siboney the habitat consists of a coralligenous bottom of Oligocene age, with a Pleistocene deposit of silt and sand (Weyl, 1966). During the Cuban-Dutch Biospeleological Expedition the water contained a high amount of silty mud with only a few shrimps, copepods and oligochaets, and can be characterized as limnic (electric conductivity 273  $\mu$ S/cm). At Cueva de Agua where this species was probably captured during the second Cuban-Romanian Expedition, the cave has a deep clear lake with a freshwater layer on top, but marine (electric conductivity 37.3 mS/cm) in deeper layers, the bottom is covered with a thin silty layer, and *Barbouria cubensis* (von Martens, 1872) was observed on the rocks in the water. The Arroyo Guayabo was used as a public washing place for cars when I visited the spot, and the interstitia of the sandy banks were filled with silt, and only epigeal fauna was observed. The water can be characterized as oligohaline (2.05 mS/cm). One of the Cuban counterparts (Luis Roberto Pupo Rodriguez) told me that the banks of the stream had been silted during recent years. It used to have coarse sand banks without so much silty mud.

#### 4.4.2.6. *Tethysbaena tinima* spec. nov. (figs. 155-164)

Termogenacea (sic); Labrada Rodriguez, 1989: 4th page.

**Material.**— Cuba: 1 ♀, 1 fragmentary specimen; Cuban-Dutch Biospeleological Exped. sta. 89/008, Prov. Camaguëy, ca. 30 km NNE of Camaguëy, San Juan de la Cruze, near Cueva El Tanque; hand-dug, limestone well, for the larger part (5/6) covered by wooden lid, diam. 1.5 m, water table at 6 m, water depth 2 m, temperature 25.5°C, electric conductivity 702  $\mu$ S/cm; collected by H.P. Wagner, N. Viña Bayes and speleological group "Tinima"; 11.v.1989; ZMA coll. no. 8156 [paratypes].

Accompanying fauna: Crustacea: Mysidacea, Ostracoda; Insecta: (larvae); Oligochaeta; Mollusca: Gastropoda.

- 1 ♂; Cuban-Dutch Biospeleological Exped. sta. 89/011, Prov. Camaguëy, ca. 24 km NNE of Camaguëy, Paso de Lesca; hand-dug, limestone well, covered by wooden plates, diam. 2 m, water table at 10 m, water depth 2 m, temperature 26.6°C, electric conductivity 791  $\mu$ S/cm; collected by H.P. Wagner, N. Viña Bayes and speleological group "Tinima"; 11.v.1989; ZMA coll. no. 8154 [holotype].

Accompanying fauna: Crustacea: Ostracoda (*Chlamydotheca unispinosa* (Baird, 1862)); Insecta: Diptera (mosquito larvae); Polychaeta; Mollusca: Gastropoda.

- 2 ♂♂, 5 ♀♀, 3 fragmentary specimens; Cuban-Dutch Biospeleological Exped. sta. 89/013, Prov.

Camaguëy, ca. 24 km NNW of Camaguëy, Paso Escalera; handdug, limestone well (dug in 1954), half covered by wooden lid, diam. 1.2 m, water table at 8 m, water depth 1.8 m, temperature 25.7°C, electric conductivity 667  $\mu\text{S}/\text{cm}$ ; collected by H.P. Wagner, N. Viña Bayes and speleological group "Tinima"; 11.v.1989; ZMA coll. no. 8155 [paratypes].

Accompanying fauna: Crustacea: Amphipoda, Ostracoda; Insecta (larvae).

**Description.**— Body length (antennae 1 and 2 excluded) of male up to 2466  $\mu\text{m}$  (holotype), of female up to 2155  $\mu\text{m}$  in the material studied.

**Antenna 1:** peduncular segments 1 to 3 with four, four, and one long plumose macrosetae on respective median margins; main flagellum 7-segmented, last segment with seven simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

**Antenna 2:** peduncular segments 4 and 5 with three teazel macrosetae on the medial and mediobasal margin; flagellum 5-segmented, last segment with one medial and three simple macrosetae of unequal length (sub)terminally.

**Labrum:** without peculiarities.

**Mandible:** six plumidenticulate macrosetae on third segment of palp.

**Labium:** without peculiarities.

**Maxilla 1:** endopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with six to seven setules, third segment with obscurely unisetulate macroseta.

**Maxilla 2:** basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 19 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented bearing four simple macrosetae.

**Maxilliped:** first segment of male endopodite without patches of club microsetae, second segment with two patches of minute, but stout pointed club microsetae (diameter  $\times$  height up to circa  $0.3 \times 1.8 \mu\text{m}$ ) on the distal portion, third segment with three patches of minute, but stout pointed club microsetae (diameter  $\times$  height up to circa  $0.3 \times 1.8 \mu\text{m}$ ), fourth segment without patches of club microsetae; basipodal endite bearing 12 plumidenticulate macrosetae with long setules, a tall one medially, seven long ones terminally, three shorter ones subterminally and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, one subterminal and one lateral plumose macrosetae.

**Gnathopod:** basal segment with one short plumose macroseta; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; baso-ischium of endopodite with clearly demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

**Pereiopod 2:** propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with three ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and three to four ovate microsetae, respectively; first segment of exopodite with one ovate microseta, second segment with three medial, two subterminal two terminal and one lateral plumose

macrosetae.

Pereiopod 3: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with six to seven ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and four ovate microsetae, respectively; first segment of exopodite one with ovate microseta, second segment with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with seven to eight ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and four ovate microsetae, respectively; first segment of exopodite with two to three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 12 to 13 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one to four ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with one subterminal and two terminal plumose macrosetae.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 14 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and three ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, one or two ovate microsetae present.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 14 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and three ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and one ovate microseta.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

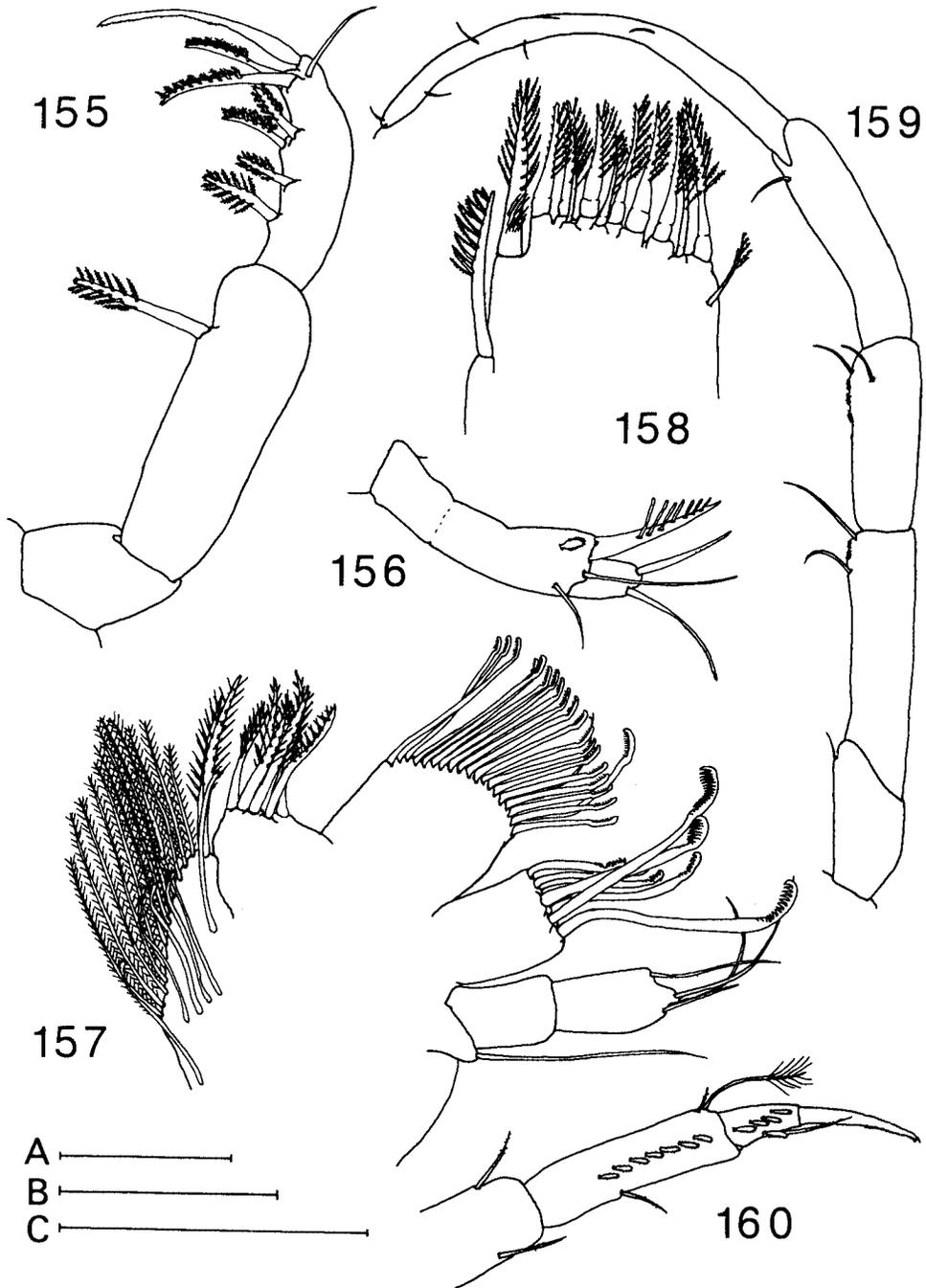
Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of two stout plumose macrosetae, each accompanied by small subplumose macroseta, segment 2 with 16 plumose macrosetae; endopodite bearing 13 plumose macrosetae.

Telson: distinctly wider than long, mean width/length ratio 1.36; anal lobes protruding beyond the terminal stretch; stretch concave.

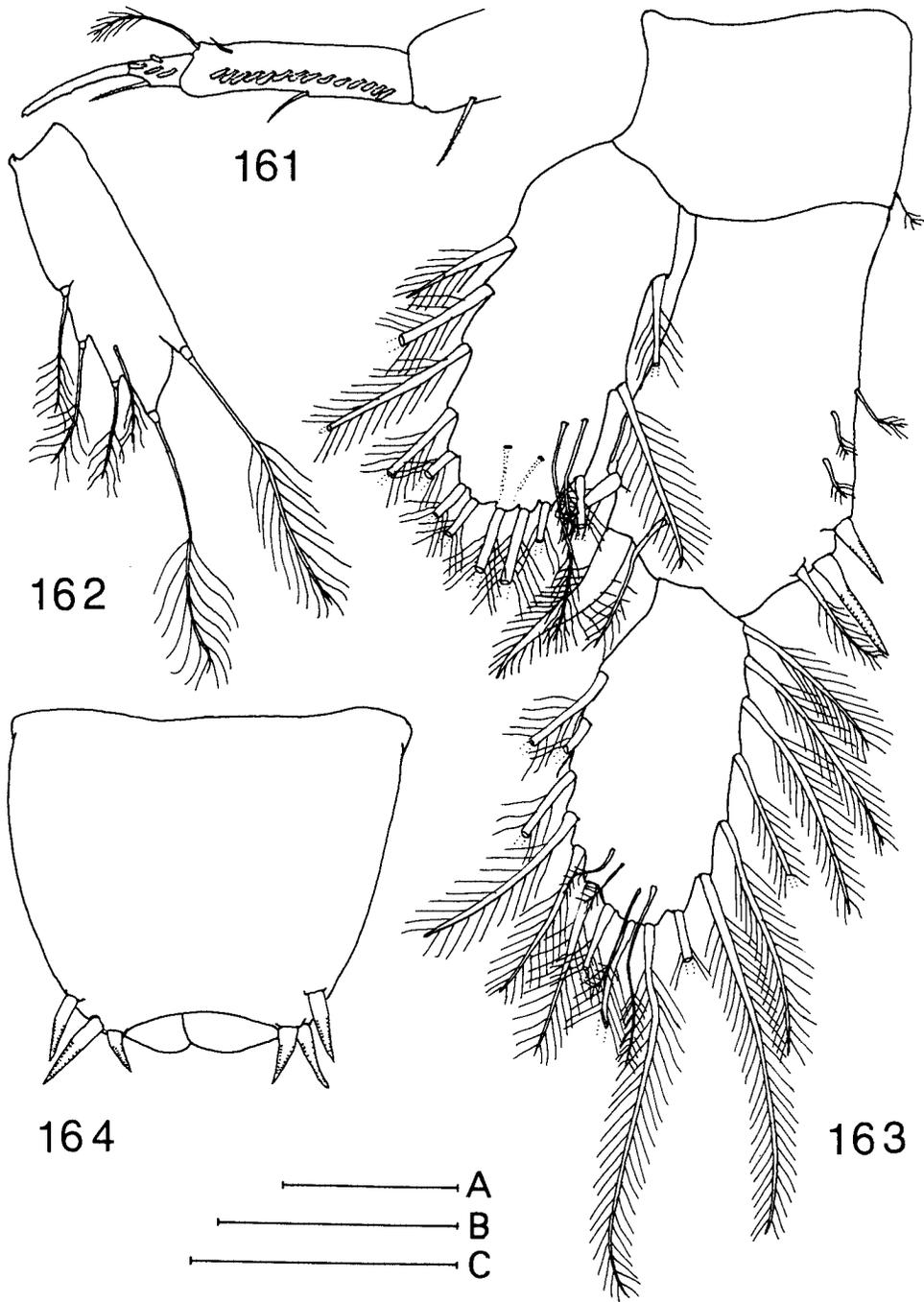
Variability.— Not observed.

Remarks.— The large number of rake-like serrate macrosetae of basipodal endite 2 of maxilla 2 in this species is unique within the "*T. sanctaecrucis*-group". For detailed information on specific differences one is referred to table 1 (p. 140).

Etymology.— This species is named after the speleological group "Tinima" of



Figs. 155-160. *Tethysbaena tinima* spec. nov., holotype ♂. 155, palp mandible. 156, palp maxilla 1. 157, maxilla 2. 158, distal portion of basipodal endite of maxilliped. (figs. 155-158 scale C). 159, endopodite of maxilliped (scale B). 160, distal portion of pereopod 3 (scale A). Scales indicated 0.1 mm.



Figs. 161-164. *Tethysbaena tinima* spec. nov., holotype ♂ and paratype ♀. 161, distal portion of pereopod 6, holotype. 162, pleopod 2, holotype (scale C). 163, uropod, paratype (scale B). 164, telson, paratype. (figs. 161 and 164 scale A). Scales indicated 0.1 mm.

Camaguëy; it is an old Indian name for a nearby river also.

Distribution.— The species has been found in an area between San Juan de la Cruze and Paso Escalera, villages situated at circa 24 to 30 km north of the city Camaguëy, Cuba.

Habitat.— There is a small stretch of limestone deposits of Pleistocene age at circa 24 to 35 km north of Camaguëy (Weyl, 1966) on which the wells that yielded this new species are situated. The stations contained limnic water. Although not all samples taken in the area contained thermosbaenaceans, those with troglobites clearly belong to one hydrographic system, as these elements were also represented in the various samples that did contain thermosbaenaceans. The caves Cueva de Agua de Camaguëy (sta. 89/006) and El Tanque (sta. 89/007) were inhabited by the shrimp *Troglocubanus* spec., which was also present in a well at Vallaga (sta. 89/009, called Pozo de Vallaga). Additional stygobiont crustaceans encountered were amphipods (sta. 89/89/013), isopods (*Troglocirolana* spec.-sta. 89/007), and mysids (sta. 89/008). Other accompanying faunal elements are epigeal dispersionalists (Copepoda, Ostracoda, Insecta (mainly larvae), Oligochaeta, and Polychaeta).

4.4.2.7. *Tethysbaena coqui* spec. nov.  
(figs. 165-174)

Thermosbaenacea (partim); Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1984b: 41; Stock, 1986d: 199.

Thermosbaenaceans (partim); Stock, 1983a: 277.

*Monodella* (partim); Wagner, 1990: 123.

Thermosbaenacea, Stock, 1991b: 18th-19th page.

Material.— U.S.A., Puerto Rico: 4 ♂♂, 9 ♀♀; AMEWI sta. 80/108, E of Palmarejo, 18°02'23"N 67°04'02"W; from pump, 12 m depth, collected with handnet (mesh 0.05 mm); collected by E.S.W. Weinberg; 20.iv.1980; ZMA coll. no. C.A. 8142 [paratypes].

Accompanying fauna: Crustacea: Isopoda, Amphipoda (*Bogidiellidae*, *Hadziidae*); Insecta: Heteroptera; Acari.

- 4 ♂♂, 36 ♀♀ (1 with broodpouch), 1 fragmentary specimen; AMEWI sta. 80/109, E of Palmarejo, about 50 m W of sta. 80/108, 18°02'21"N 67°04'05"W; from pump, 12 m depth, collected with handnet (mesh 0.05 mm); collected by E.S.W. Weinberg; 11 and 20.iv.1980; ZMA coll. no. C.A. 8140 [holotype], ZMA coll. no. C.A. 8141; MF; MP; RMNH G 46; USNM; WAM; ZMC [all paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Bogidiella* spec.); Insecta: Coleoptera, Collembola; Chelicerata: Arachnida; Acari; Oligochaeta.

Description.— Body length (antennae 1 and 2 excluded) of male up to 1660 µm (holotype 1316 µm), of female up to 1553 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with five, four, and one long plumose macrosetae on respective median margins; main flagellum 7-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with three teazel macrosetae on the medial and mediobasal margin; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with six to seven setules, third segment with obscurely unisetulate macroseta.

Maxilla 2: basipodal endite 1 with five plumidenticulate macrosetae; basipodal endite 2 with 14 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment without patches of club microsetae on distal portion, third segment with one large patch of minute, pointed, tall club microsetae (diameter  $\times$  height up to circa  $0.3 \times 1.6 \mu\text{m}$ ), fourth segment without patches of club microsetae; basipodal endite bearing 13 plumidenticulate macrosetae with long setules, a tall one medially, eight long ones terminally, three shorter ones subterminally and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal and one subterminal plumose macrosetae.

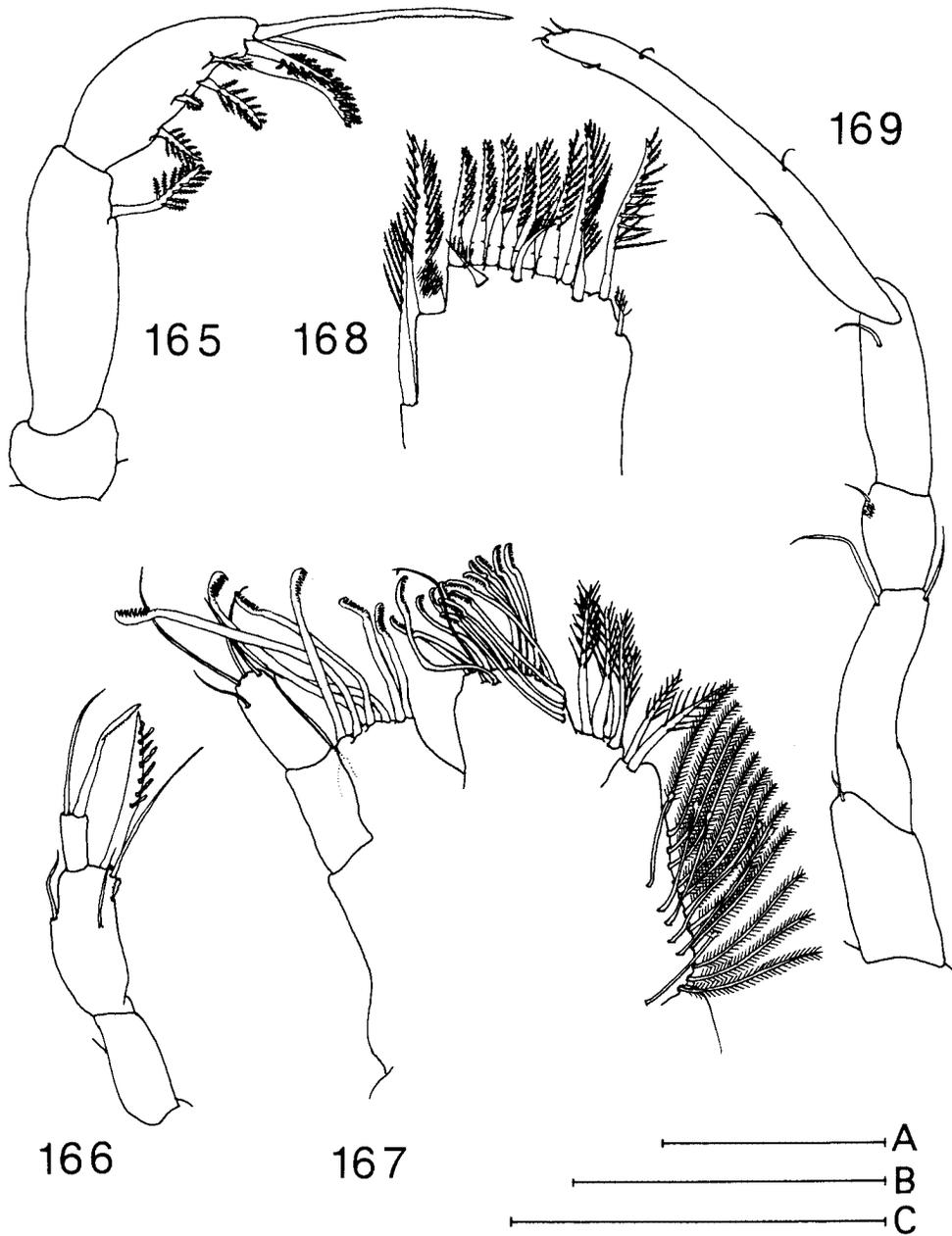
Gnathopod: basal segment with two short plumose macrosetae; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; baso-ischium of endopodite with obscurely demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

Pereiopod 2: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with two teazel macrosetae medially on ventral margin, both male and female with five to six ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two "rows" of one and two ovate microsetae, respectively; first segment of exopodite without ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

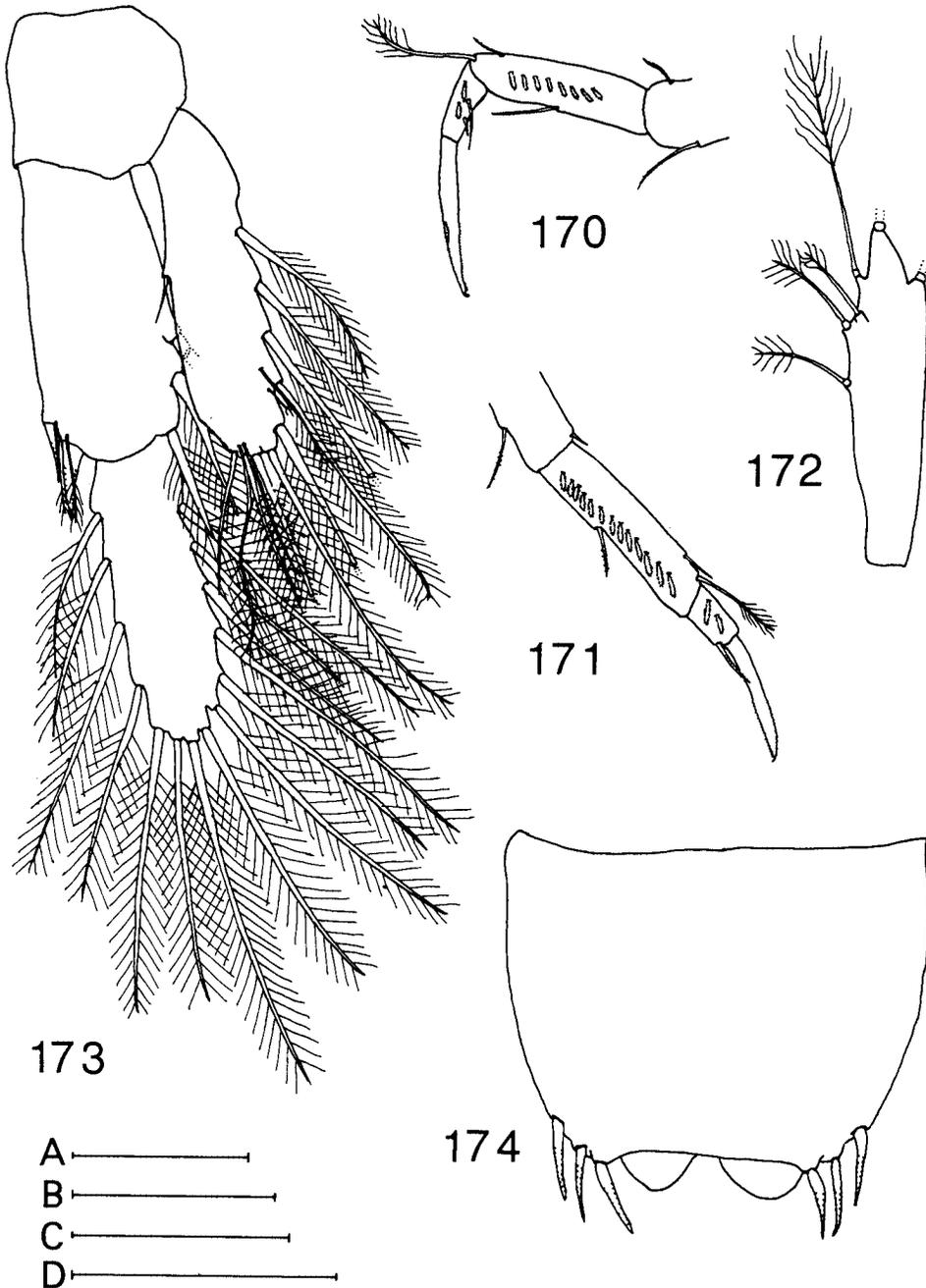
Pereiopod 3: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with eight ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two ovate microsetae; first segment of exopodite with two to three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with eight ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two ovate microsetae; first segment of exopodite with two to three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with eight to nine ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two ovate microsetae; first segment of exopodite with



Figs. 165-169. *Tethysbaena coqui* spec. nov., holotype ♂. 165, palp mandible. 166, palp maxilla 1. 167, maxilla 2. (figs. 165-167 scale C). 168, distal portion of basipodal endite of maxilliped. (scale B). 169, endopodite of maxilliped (scale A). Scales indicated 0.1 mm.



Figs. 170-174. *Tethysbaena coqui* spec. nov., holotype and paratype ♂, paratype ♀. 170, distal portion of pereopod 3, holotype. 171, distal portion of pereopod 7, paratype ♀. (figs. 170-171 scale A). 172, pleopod 2, holotype (scale D). 173, uropod, paratype ♂ (scale C). 174, telson, paratype ♀ (scale B). Scales indicated 0.1 mm.

two ovate microsetae, second segment with one subterminal and two terminal plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, three ovate microsetae present.

Pereiopod 7: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 13 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae and one vestigial terminal macroseta, three ovate microsetae present.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of 3 stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 14 plumose macrosetae; endopodite bearing 10 plumose macrosetae.

Telson: wider than long, mean width/length ratio 1.21; anal lobes protruding beyond the terminal stretch; stretch slightly concave with an almost straight central part.

Variability.— Not observed.

Remarks.— This species shows the greatest resemblance to *T. gaweini* (Dominican Republic) and *T. scitula* (Virgin Gorda, Virgin Islands), but differs in the width/length ratio of the telson, the number of setulettes of the unisetulate macroseta of the palp of maxilla 1, the number of segments of the palp of maxilla 1, the rows of (sub)terminal plumidenticulate macrosetae on the basopodite of the maxilliped. The differences with the other species are more clear. For detailed information on specific differences one is referred to table 1 (p. 140).

Etymology.— "Coqui" was the legendary Indian Chief when the conquistadores conquered Puerto Rico. After his defeat (and death) the Gods decided that a tiny frog would call his name at night to honour his courage. Nowadays this frog (popular name: coqui) is a national symbol of Puerto Rico. The new species, like the frog endemic to this island, is named after this historic hero.

Distribution.— This species is only found at Palmarejo, which is a part of the Valle de Lajas groundwater system, the westernmost part of the Acuíferos de la Costa Sur.

Habitat.— The species was collected from the ground water of alluvial deposits consisting of sand, silt, clay and gravel floodplain deposits of Pleistocene to Holocene age (Briggs & Akers, 1965 (reprinted 1985); Monroe, 1980). The presence of troglobitic amphipods as *Bogidiella* and Hadziidae as accompanying fauna, does not exclude connections to the rest of the Acuíferos de la Costa Sur, and a larger distribution for *T. coqui* can be expected. During the Amsterdam Expedition to the West

Indian Islands of 1987-88, I visited the localities at Palmarejo, but most of the hand-pumps (over 50 years old!) were disconnected, the remaining ones solely giving a limited supply of muddy water without any stygobionts. The electric conductivity was 5.48 mS/cm at the temperature 27.2°C, so the water can be characterized as oligohaline.

4.4.2.8. *Tethysbaena colubrae* spec. nov.  
(figs. 175-184)

Thermosbaenacea (partim); Stock, 1979: 57-58; Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1984b: 41.

Thermosbaenaceans (partim); Stock, 1983a: 277.

*Monodella* (partim); Wagner, 1990: 123.

Material.— U.S.A., Puerto Rico, Isla de Culebra: 1 ♀; AMEWI sta. 78/186, Finca Feliciano, 18°17'38"N 65°17'25"W; round, closed well, diam. 2.5 m, water depth 3.5 m, Cvetkov net, chlorinity 1640 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 2.v.1978; ZMA coll. no. C.A. 8138 [paratypes].

Accompanying fauna: Mollusca: Gastropoda.

- 10 ♂♂, 20 ♀♀, 2 juveniles; AMEWI sta. 78/191, Finca Feliciano, Cerro Balcón, N slope, 18°19'17"N 65°15'40"W; round, closed well, diam 2 m, water table at 2.5 m, water depth 1.5 m, in alluvial sands, Cvetkov net, chlorinity 1280 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 2.v.1978; ZMA coll. no. C.A. 8136 [holotype], ZMA coll. no. C.A. 8137; MF; MP; RMNH G 47; USNM [all paratypes].

Accompanying fauna: Crustacea: Ostracoda; Insecta; Oligochaeta (*Dero (Aulophorus) furcata* (Müller, 1773); Mollusca: Gastropoda (*Pyrgophorus* spec.); Amphibia (frog larvae).

- 1 ♀; AMEWI sta. 78/193, Finca Feliciano, NW of sta. 78/191, 18°19'37"N 65°15'53"W; complex of wells, partly covered, 3 × 6 m, bottom with black (H2S) sand, Cvetkov net, chlorinity 400 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 2.v.1978; ZMA coll. no. C.A. 8139 [paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda, Cladocera; Mollusca: Gastropoda.

Description.— Body length (antennae 1 and 2 excluded) of male up to 2078 µm (holotype), of female up to 1776 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with three, three, and two long plumose macrosetae on respective median margins; main flagellum 7-segmented, last segment with five simple (sub)terminal macrosetae of unequal length; accessory flagellum 5-segmented, last segment with three simple macrosetae of unequal length (sub)terminally.

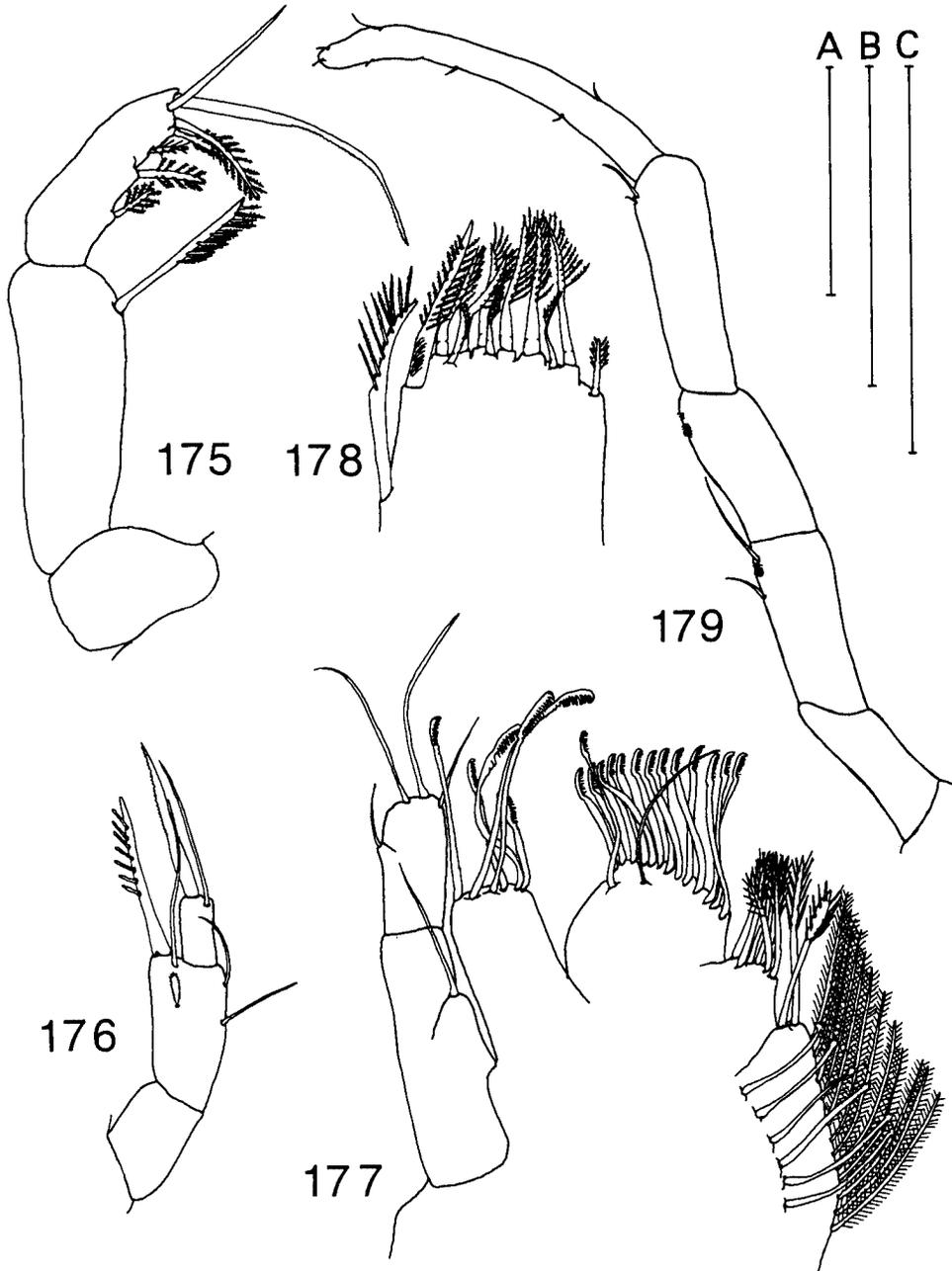
Antenna 2: peduncular segments 4 and 5 with three teazel macrosetae on the medial and mediobasal margins; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

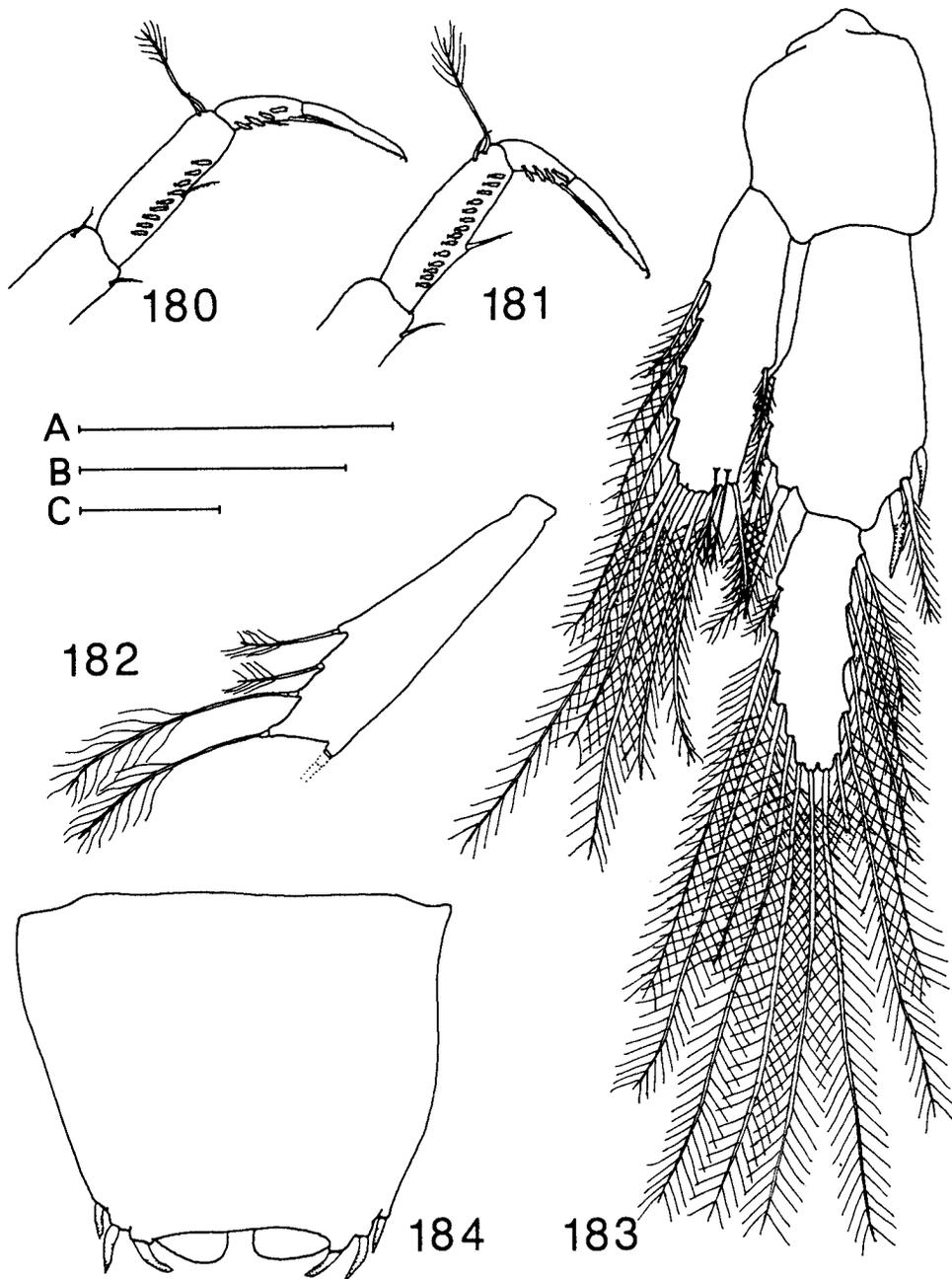
Mandible: five plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with seven to nine setules, third segment with obscurely unisetulate macroseta.



Figs. 175-179. *Tethysbaena colubrae* spec. nov., holotype ♂. 175, palp mandible. 176, palp maxilla 1. 177, maxilla 2. 178, distal portion of basipodal endite of maxilliped. (figs. 175-178 scale B). 179, endopodite of maxilliped (scale A). Scales indicated 0.1 mm.



Figs. 180-184. *Tethysbaena colubrae* spec. nov., holotype ♂ and paratype ♀. 180, distal portion of pereopod 3, paratype. 181, distal portion of pereopod 6, paratype. (figs. 180-181 scale C). 182, pleopod 2, holotype (scale B). 183, uropod, holotype. 184, telson, holotype. (figs. 183-184 scale A). Scales indicated 0.1 mm.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 13 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six strong barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with one large patch of minute pointed club microsetae on the distal portion, third segment with two patches (one large and a smaller more distally) of minute, pointed club microsetae, fourth segment without patches of club microsetae; basipodal endite bearing 11 to 12 plumidenticulate macrosetae with long setules, a tall one medially, seven (six in holotype) long ones terminally, three shorter ones subterminally and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal and one subterminal plumose macrosetae.

Gnathopod: basal segment with two short plumose macrosetae; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; baso-ischium of endopodite with obscurely demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with six ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; first segment of exopodite with one ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with nine ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with two to three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with one teazel macroseta on ventral margin and three ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two ovate microsetae; first segment of exopodite with two ovate microsetae, second segment with one medial, two subterminal and two terminal plumose macrosetae.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 14 ovate microsetae, dactylus with one teazel macroseta on ventral margin and four ovate microsetae; exopodite 1-segmented with

one medial and one subterminal plumose macrosetae and one vestigial terminal macroseta, two ovate microsetae present.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 17 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae and one vestigial terminal macroseta.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of four stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 14 plumose macrosetae; endopodite bearing 11 plumose macrosetae.

Telson: distinctly wider than long, mean width/length ratio 1.38; anal lobes protruding beyond the terminal stretch; stretch slightly concave.

Variability.— Not observed.

Remarks.— *Tethysbaena colubrae* is closely related to *T. scitula* (Virgin Gorda), but shows specific differences primarily in the number of plumidenticulate macrosetae on the mandibular palp, and the number of macrosetae on the basipodal endites 1 and 2 of maxilla 2. For detailed information on specific differences one is referred to table 1 (p. 140).

Etymology.— The name *colubra*, meaning "snake", alludes to (Isla de) Culebra, the type locality sensu lato.

Distribution.— At two areas this new species was found; one is situated on the small island (province Playa Sardinias II) near Culebra city, the other localities are close to each other along the northern slope of the Cerro Balcón (province San Isidro).

Habitat.— The species was collected from wells situated in alluvial deposits of Pleistocene to Holocene age (Weyl, 1966). No other true stygobiont species were found as accompanying fauna. The water can be characterized as oligohaline.

#### 4.4.2.9. *Tethysbaena scitula* spec. nov. (figs. 185-195)

Thermosbaenacea (partim); Stock, 1979: 50; Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1983: 289; Broodbakker, 1984b: 41.

Thermosbaenaceans (partim); Stock, 1983a: 277.

*Monodella* (partim); Wagner, 1990: 123.

Material.— **British Virgin Islands, Virgin Gorda:** 5 ♂♂, 27 ♀♀; AMEWI sta. 78/119, Spanish Town, well near post office, 18°26'42"N 64°26'26"W; open, half natural well, near outcrop rocks, shadowy, water table at 2 m, water depth 1 m, Cvetkov net, chlorinity 640 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 24.iv.1978; ZMA coll. no. C.A. 8119 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda (*Cypretta* spec.); Insecta (various groups, mosquito larvae); Polychaeta.

- 44 ♂♂, 40 ♀♀, 2 juveniles, 2 fragmentary specimens; AMEWI sta. 78/121, Handsome Bay, well in meadow, 18°27'37"N 64°25'34"W; partly closed well, water table at 2 m, water depth 4 m, Cvetkov

net, chlorinity 1680 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 24.iv.1978; ZMA coll. no. C.A. 8120 [male holotype], ZMA coll. no. C.A. 8121; BMNH; MF; MP; RMNH G 48; UEKL; UR; USNM; WAM; ZMC [all paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda; Oligochaeta (*Dero* (*Aulophorus*) *furcata* (Müller, 1773)).

- 1 ♀; AMEWI sta. 78/122, Black Rock Ghut, The Spring (South Sound), 18°29'05"N 64°23'33"W; from spring, open, slowly running into basin, leaves, cows, shadowed, volcanic outcrops, Cvetkov net and handnet (mesh 0.8 mm), chlorinity 1760 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 24.iv.1978; ZMA coll. no. C.A. 8122 [no paratype].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda; Oligochaeta (*Dero* (*Dero*) *sawayai* Marcus, 1943); Mollusca: Gastropoda (*Pyrgophorus* spec.).

Description.— Body length (antennae 1 and 2 excluded) of male up to 2107 µm (holotype), of female up to 2289 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with three, three, and two long plumose macrosetae on respective median margins; main flagellum 7-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segment 4 with three, and segment 5 with four teazel macrosetae on the medial and mediobasal margins; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with eight to nine setules, third segment with obscurely unisetulate macroseta.

Maxilla 2: basipodal endite 1 with five plumidenticulate macrosetae; basipodal endite 2 with 14 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing five simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with one dense patch of fine, long and pointed club microsetae (diameter × height up to circa 0.25 × 4 µm) on the distal portion, third segment with two "rows" of three and one (latter set more mediobasally) dense patches of fine, long and pointed club microsetae (diameter × height up to circa 0.25 × 4 µm), fourth segment without patches of club microsetae; basipodal endite bearing 12 plumidenticulate macrosetae with long setules, a tall one medially, seven long ones terminally, three shorter ones subterminally and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, one subterminal and one lateral plumose macrosetae.

Gnathopod: basal segment with three short plumose macrosetae; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae;

baso-ischium of endopodite with clearly demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with ten ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of four and six ovate microsetae, respectively; first segment of exopodite without ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one mediodistal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 to 12 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two "rows" of one and six ovate microsetae, respectively; first segment of exopodite with three ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediodistal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 12 to 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two "rows" of one and six ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

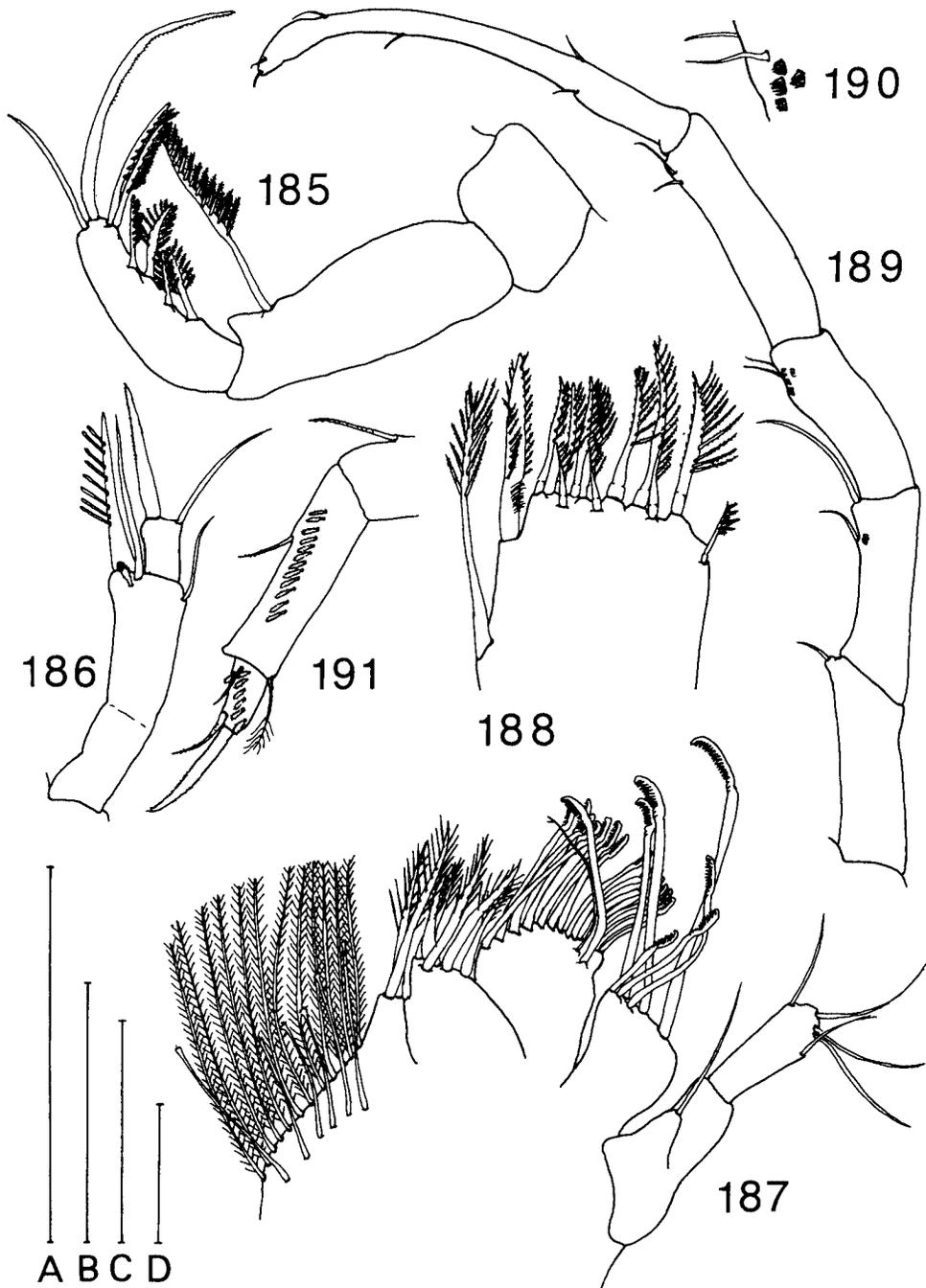
Pereiopod 5: ischiomerus of endopodite with one mediodistal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 15 to 17 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two "rows" of one and six ovate microsetae, respectively; first segment of exopodite with three to five ovate microsetae, second segment with one medial, two subterminal and two terminal plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one mediodistal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 16 to 17 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and six ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, three vestigial macrosetae, one medial, one terminal and one lateral, and two ovate microsetae.

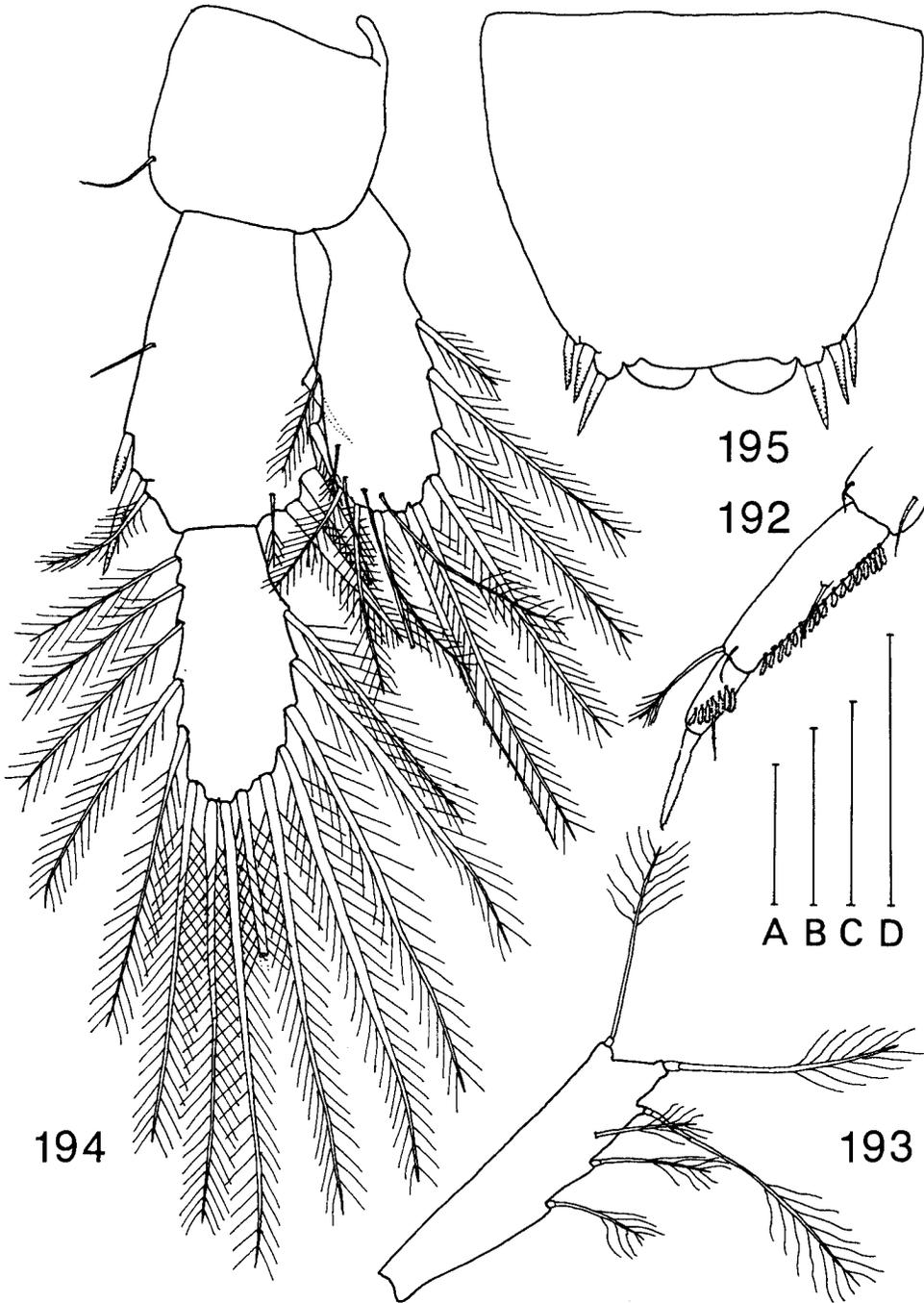
Pereiopod 7: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with 16 to 17 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two "rows" of one and six ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae and one vestigial terminal macroseta.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of four stout plumose macrosetae, each accompanied by small subplumose macroseta, segment 2 with 14 to 15 plumose macrosetae; endopodite bearing 10 to 11



Figs. 185-191. *Tethysbaena scitula* spec. nov., holotype ♂. 185, palp mandible. 186, palp maxilla 1. 187, maxilla 2. (figs. 185-187 scale A). 188, distal portion of basipodal endite of maxilliped. (scale B). 189, endopodite of maxilliped (scale C). 190, detail microsetae at distal portion of endopodite segment 3 of maxilliped (extremely enlarged). 191, distal portion of pereopod 3 (scale D). Scales indicated 0.1 mm.



Figs. 192-195. *Tethysbaena scitula* spec. nov., holotype ♂. 192, distal portion of pereopod 6 (scale A). 193, pleopod 2 (scale D). 194, uropod (scale C). 195, telson (scale B). Scales indicated 0.1 mm.

plumose macrosetae.

Telson: distinctly wider than long, mean width/length ratio 1.36; anal lobes protruding beyond the terminal stretch; stretch slightly concave with laterally and centrally convex bumps (no protuberances!).

Variability.— There is only some variation in the number of plumose macrosetae on the uropodal rami.

Remarks.— This species shows intermediate character states between *T. gaweini*, *T. coqui* and *T. colubrae* on the one hand, and *T. calsi* and *T. stocki* on the other. For detailed information on specific differences one is referred to table 1 (p. 140).

Etymology.— The name *scitula* means "handsome", and alludes to the name of the type locality.

Distribution.— *Tethysbaena scitula* was captured in wells on both western (sta. 78/119) and eastern (sta. 78/121) coastal localities at the southern peninsula of Virgin Gorda, and from a spring near the east coast of the central portion of the island (sta. 78/122).

Habitat.— The samples containing the new species were taken from wells and springs situated in small areas with alluvial deposits of Pleistocene to Holocene age (Weyl, 1966). The water can be characterized as oligohaline. *Tethysbaena scitula* was not found together with other true stygobionts.

#### 4.4.2.10. *Tethysbaena calsi* spec. nov. (figs. 196-206)

Thermosbaenacea (partim); Stock, 1979: 51-54; Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1984b: 41.  
Thermosbaenaceans (partim); Stock, 1983a: 277.  
*Monodella* (partim); Wagner, 1990: 123.

Material.— **British Virgin Islands, Tortola:** 5 ♂♂, 165 ♀♀; AMEWI sta. 78/133, Paraquita Lagoon, 18°25'16"N 64°34'44"W; large (deep) well, covered, Cvetkov net, chlorinity 880 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 25.iv.1978; ZMA coll. no. 8123; RMNH G 73 [no paratypes].

Accompanying fauna: Oligochaeta.

- 11 ♂♂, 53 ♀♀ (1 with broodpouch), 7 juveniles; AMEWI sta. 78/137, House E of East End Police Station, N of road, 18°26'30"N 64°34'10"W; clean well, Cvetkov net, chlorinity 960 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 25.iv.1978; ZMA coll. no. C.A. 8124 [no paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda, Decapoda (larvae of *Macrura*); Oligochaeta; Mollusca: Gastropoda.

- 4 ♀♀; AMEWI sta. 78/140, Josias Bay, in ruined house, 18°26'29"N 64°35'22"W; open, shadowed well, Cvetkov net, chlorinity 1080 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 25.iv.1978; ZMA coll. no. C.A. 8125 [no paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae); Insecta: Diptera (Mosquito larvae).

- 2 ♂♂, 12 ♀♀ (1 with broodpouch), 3 juveniles; AMEWI sta. 78/142, Road Town, well Water Works, ca. 100 m W of Police HQ, 18°25'45"N 64°37'23"W; closed, large well, with electric pump connected, water table at 14 m, water depth 2 m, Cvetkov net, chlorinity 400 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 25.iv.1978; ZMA coll. no. C.A. 8126 [no paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Bogidiella* (*Stygogidiella*) *virginalis* Stock, 1981), Phyllo-poda, Copepoda (Cyclopidae); Oligochaeta (*Pristina foreli* (Piguet, 1906)).

- 3 ♀♀, 1 juvenile; AMEWI sta. 78/144, Duffs Bottom Pond, N side of road, 18°24'42"N 64°37'28"W; from well, troughs, Cvetkov net, chlorinity 720 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 26.iv.1978; ZMA coll. no. C.A. 8127 [no paratypes].

Accompanying fauna: Oligochaeta (*Dero* (*Aulophorus*) *furcata* (Müller, 1773); *Pristina foreli* (Piguet,

1906)); Mollusca: Gastropoda (*Pyrgophorus* spec.).

- 1 ♀; AMEWI sta. 78/145, Albion Ghut, near school, 18°24'46"N 64°37'53"W; open, clean well, collected with Cvetkov net; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 26.iv.1978; ZMA coll. no. C.A. 8128 [no paratype].

Accompanying fauna: Crustacea: Ostracoda; Oligochaeta (*Dero* (*Aulophorus*) *furcata* (Müller, 1773)); Mollusca: Gastropoda (*Pyrgophorus* spec.).

- 9 ♂♂, 93 ♀♀ (1 with broodpouch), 11 juveniles, 1 fragmentary specimen; AMEWI sta. 78/147, Locust Bay, 18°24'00"N 64°38'18"W; small, covered well, water table at 2 m, water depth 0.5 m, Cvetkov net, chlorinity 980 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 26.iv.1978; ZMA coll. no. C.A. 8129; UPMC [no paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda; Mollusca: Gastropoda.

- 1 ♀; AMEWI sta. 78/148, Recovery, 18°23'26"N 64°40'33"W; from well, diatom growth, collected with Cvetkov net; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 26.iv.1978; ZMA coll. no. C.A. 8130 [no paratype].

Accompanying fauna: Crustacea: Ostracoda; Mollusca: Gastropoda (*Pyrgophorus* spec.).

- 3 ♂♂, 4 ♀♀, 2 juveniles, 1 fragmentary specimen; AMEWI sta. 78/149, Frenchman's Cay, Sandy Point, 18°23'13"N 64°42'02"W; covered well, roots, calcite crystals, Cvetkov net, chlorinity 1160 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 26.iv.1978; ZMA coll. no. C.A. 8131 [no paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda; Mollusca: Gastropoda (*Pyrgophorus* spec.).

- 25 ♂♂, 27 ♀♀, 2 juveniles; AMEWI sta. 78/150, Jumbie Ghut, Freshwater Pond, 18°23'38"N 64°40'54"W; complex of wells and troughs, open, diatom growth, Cvetkov net, chlorinity 2440 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 26.iv.1978; ZMA coll. no. C.A. 8132 [no paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda; Insecta (larvae); Oligochaeta; Mollusca: Gastropoda (*Pyrgophorus* spec.).

- 2 ♀♀; AMEWI sta. 78/151, Long Bay Point, well near the sea, 18°23'57"N 64°41'11"W; open, clean well, collected with Cvetkov net; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 26.iv.1978; ZMA coll. no. C.A. 8133 [no paratypes].

Accompanying fauna: Crustacea: Ostracoda.

- 12 ♂♂, 70 ♀♀, 12 juveniles, 2 fragmentary specimens; AMEWI sta. 78/152, ENE of Havers, N side of road, near ruined farm, 18°23'54"N 64°38'22"W; partly covered well, water table at 1 m, water depth 2 m, Cvetkov net, chlorinity 920 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 26.iv.1978; ZMA coll. no. C.A. 8134 [no paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda, Decapoda (*Macrura*); Amphibia (frogs).

**U.S. Virgin Islands, Saint John:** 27 ♂♂, 135 ♀♀ (7 with broodpouch), 15 juveniles; AMEWI sta. 78/156, King well, 18°20'53"N 64°43'06"W; concrete well, diam. 2 m, iron cover, water table at ca. 5 m, water depth 0.3 m, Cvetkov net, chlorinity 360 mg/l; collected by E.S.W. Weinberg & F. Zijlstra; 27.iv.1978; ZMA coll. no. C.A. 8110 [holotype], ZMA coll. no. C.A. 8111; BMNH; HUI; MF; MP; RMNH G 54; UEKL; UPMC; UR; USNM; WAM; ZMC [all paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Bogidiella* (*Stygodiella*) *virginalis* Stock, 1981), Copepoda (Cyclopidae).

- 2 ♂♂, 13 ♀♀ (1 with broodpouch), 1 juvenile; AMEWI sta. 78/157, ca. 100 m E of King Well, 18°20'54"N 64°43'01"W; concrete well, iron cover, water table at ca. 3 m, water depth ca. 2 m, collected with a Cvetkov net, chlorinity 200 mg/l; collected by E.S.W. Weinberg & F. Zijlstra; 27.iv.1978; ZMA coll. no. 8112 [paratypes].

Accompanying fauna: Crustacea: Ostracoda.

Description.— Body length (antennae 1 and 2 excluded) of male up to 2447 µm (holotype 2000 µm), of female up to 2408 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with three, three, and two long plumose

macrosetae on respective median margins; main flagellum 7-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segment 4 with three, and segment 5 with four teazel macrosetae on the medial and mediodistal margins; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with eight setules, third segment with obscurely unisetulate macroseta.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 15 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with four patches of minute stout club microsetae (diameter  $\times$  height up to circa  $0.4 \times 1.5 \mu\text{m}$ ) on the distal portion, third segment with two patches of minute stout club microsetae (diameter  $\times$  height up to circa  $0.4 \times 1.5 \mu\text{m}$ ) fourth segment without patches of club microsetae; basipodal endite bearing 12 plumidenticulate macrosetae with long setules, a very tall one medially, seven long ones terminally, three shorter ones subterminally, and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal and one subterminal plumose macrosetae.

Gnathopod: basal segment with two short plumose macrosetae; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; baso-ischium of endopodite with obscurely demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with eight to nine ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two "rows" of one and five ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with nine to ten ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and five ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and five ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 to 12 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and five ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with two medial, two subterminal and two terminal plumose macrosetae.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 13 to 14 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and five ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, and one vestigial terminal macrosetae, three ovate microsetae present.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 15 to 16 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two "rows" of one and five ovate microsetae, respectively; exopodite 1-segmented with one medial plumose macroseta, two vestigial macrosetae, one subterminal and one terminal, three ovate microsetae present.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae, one plumose macroseta, and 3 additional subplumose macrosetae proximally, medial armature of four stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 15 to 17 plumose macrosetae; endopodite bearing 11 to 13 plumose macrosetae.

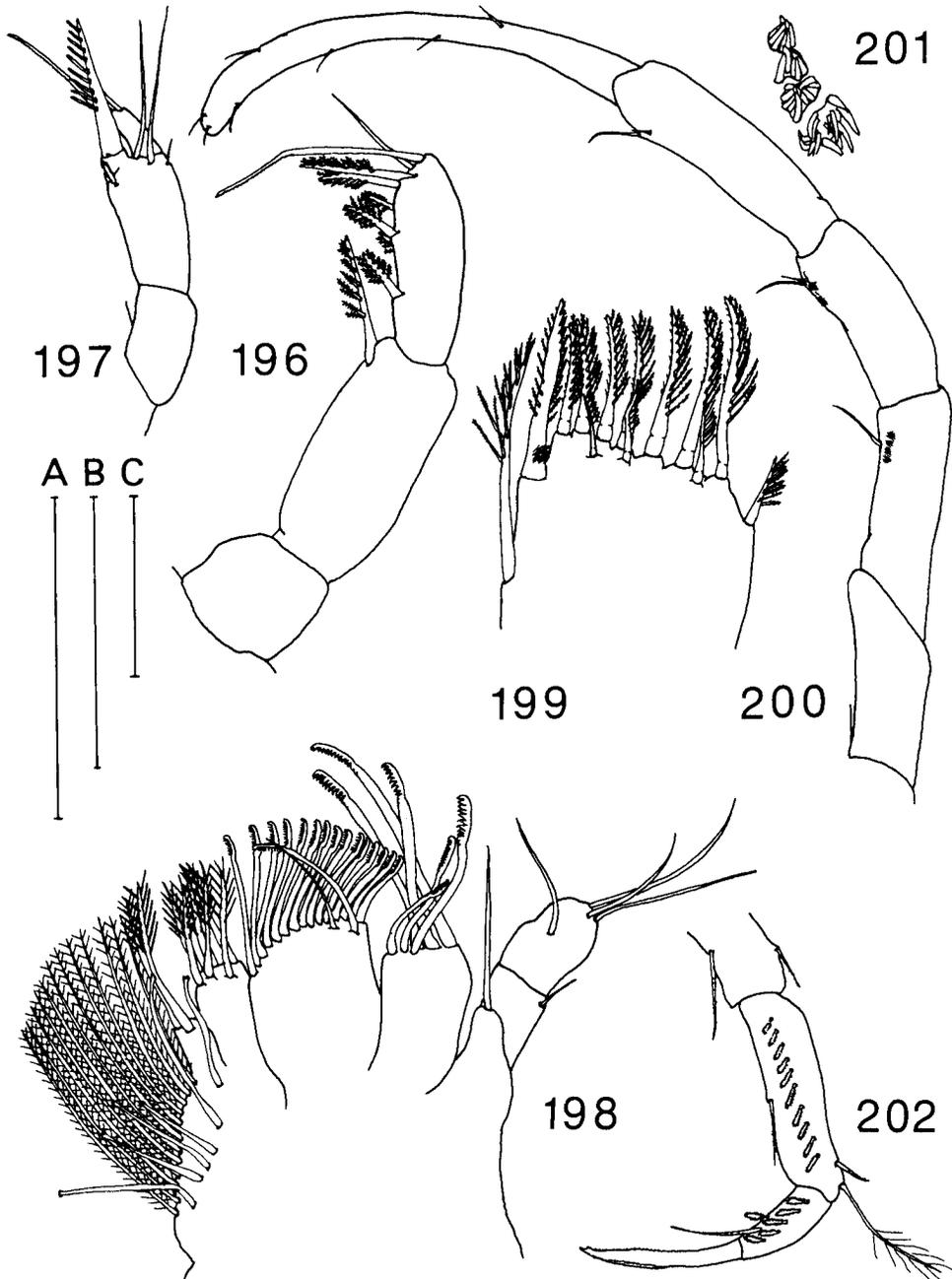
Telson: somewhat wider than long, mean width/length ratio 1.17; anal lobes protruding beyond the terminal stretch; stretch slightly concave, its centre with a convex bump.

Variability.— The holotype specimen has a second plumose macroseta on segment 3 of the right antenna 1. Generally there are eight setulettes on the unisetulate macroseta of the palp of maxilla 1, but sometimes numbers of nine or ten can be encountered within the same individual. As usual the number of plumose macrosetae present on the rami of the uropod varies slightly too. The variability observed can be encountered in any individual from any locality examined.

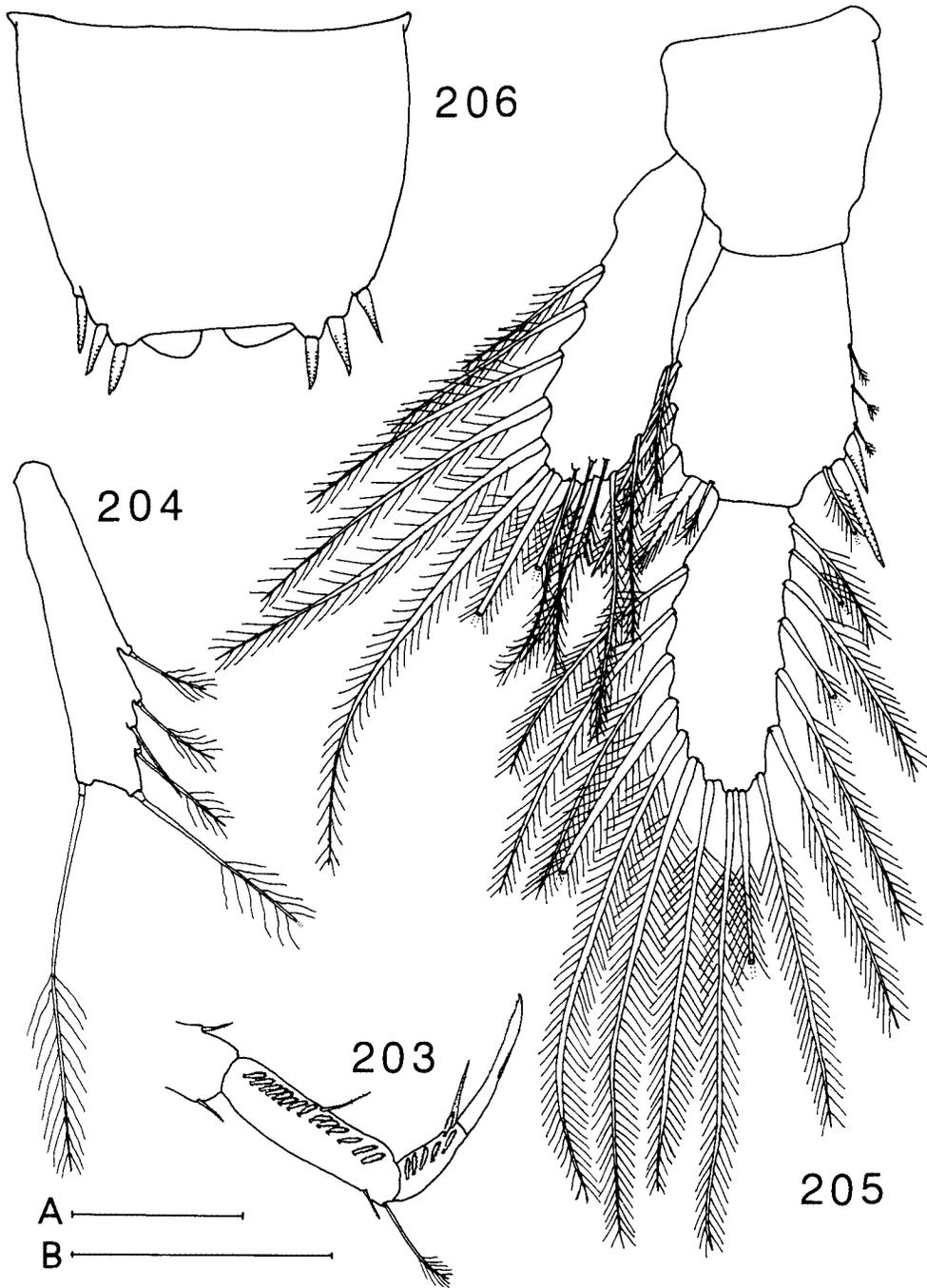
Remarks.— After careful comparison of the materials from Tortola, and St. John, I was unable to distinguish the animals from these two islands. For detailed information on specific differences with its congeners of this species-group one is referred to table 1 (p. 140).

The faunal unity of these islands in biological sense was illustrated before, with the discovery of *Bogidiella (Stygogidiella) virginalis* Stock, 1981.

Etymology.— I take great pleasure in dedicating this new species to Philippe Cals



Figs. 196-202. *Tethysbaena calsi* spec. nov., holotype ♂. 196, palp mandible. 197, palp maxilla 1. 198, maxilla 2. 199, distal portion of basipodal endite of maxilliped. (figs. 196-199 scale A). 200, endopodite of maxilliped (scale B). 201, detail microsetae at distal portion of endopodite segment 2 of maxilliped (extremely enlarged). 202, distal portion of pereopod 3 (scale C). Scales indicated 0.1 mm.



Figs. 203-206. *Tethysbaena calsi* spec. nov., holotype ♂. 203, distal portion of pereopod 6. 204, pleopod 2 (scale B). 205, uropod (scale C). 206, telson (figs. 203, 205, and 206 scale A). Scales indicated 0.1 mm.

(Université Pierre et Marie Curie, Paris, France) as a token of my respect and gratitude for help received.

Distribution.— The species is known from numerous localities scattered over the island of Tortola and from an area near Coral Bay on the island of St. John.

Habitat.— All localities sampled are situated on alluvial deposits of Pleistocene to Holocene age (Weyl, 1966). An abundant accompanying fauna was collected, but except for the amphipod *Bogidiella* (*Stygogidiella*) *virginalis* none of the other animals are true stygobionts. The water characterization varies from limnic (sta. 78/157) to oligohaline (all other stations).

4.4.2.11. *Tethysbaena stocki* spec. nov.  
(figs. 207-217)

Thermosbaenacea (partim); Stock, 1979: 48; Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1984b: 41.

Thermosbaenaceans (partim); Stock, 1983a: 277.

*Monodella* (partim); Wagner, 1990: 123.

Material.— **British Virgin Islands, Anegada:** 9 ♂♂, 221 ♀♀, 34 juveniles; AMEWI sta. 78/99, Lilly Well, near former Crushing Factory, 18°43'31"N 69°18'59"W; open well, shadowy, diam. ca. 1 m, water table at 2.5 m, water depth 0.5 m, Cvetkov net, chlorinity 1680 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 22.iv.1978; ZMA coll. no. C.A. 8113 [holotype], ZMA coll. no. C.A. 8114; BMNH; MF; MP; HJ; RMNH G 51; UEKL; UPMC; UR; USNM; WAM; ZMC [all paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Decapoda (Macrura); Insecta: Collembola, Diptera (Mosquito larvae); Oligochaeta; Mollusca: Gastropoda.

- 1 ♂; AMEWI sta. 78/100, Tamarind well, N of airstrip, 18°43'43"N 64°18'50"W (estimated); two natural crevices in karst plateau, open, water table at 0.2 m, water depth 5 m, Cvetkov net, chlorinity 960 and 1120 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 22.iv.1978; ZMA coll. no. C.A. 8115 [no paratype].

Accompanying fauna: Crustacea: Ostracoda.

- 6 ♀♀, 1 fragmentary specimen; AMEWI sta. 78/102, near The Fountain, approx. 18°44'07"N 64°18'38"W; natural shallow water hole in karst, with grass, Cvetkov net, chlorinity 560 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 22.iv.1978; ZMA coll. no. C.A. 8116 [no paratypes].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae), Ostracoda; Mollusca; Chelicerata: Arachnida (*Solifuga* spec.).

- 6 ♀♀ (1 with broodpouch), 3 juveniles; AMEWI sta. 78/103, Tom Berry Well, 18°43'38"N 64°18'57"W; Cvetkov net, chlorinity 560 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 22.iv.1978; ZMA coll. no. C.A. 8117 [no paratypes].

Accompanying fauna: Crustacea: Isopoda (terrestrial), Copepoda (Cyclopidae), Ostracoda; Insecta; Oligochaeta (*Dero* (*Dero*) *sawayai* Marcus, 1943, *Dero* (*Aulophorus*) *furcata* (Müller, 1773), *Pristina peruviana* Cernovitov, 1939); Mollusca: Gastropoda.

- 1 ♀; AMEWI sta. 78/104, The Settlement Power Station, 18°43'21"N 69°19'05"W; from well, Cvetkov net, chlorinity 2280 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 22.iv.1978; ZMA coll. no. C.A. 8118 [no paratype].

Accompanying fauna: Crustacea: Copepoda (Cyclopidae); Oligochaeta; Mollusca: Gastropoda (*Pyr-gophorus* spec.).

- 1 ♂, 1 ♀; AMEWI sta. 78/111, E side of The Settlement, approximately 18°43'14"N 69°18'46"W; from well, Cvetkov net, chlorinity 680 mg/l; collected by J.H. Stock, E.S.W. Weinberg & F. Zijlstra; 22.iv.1978; ZMA coll. no. C.A. 8241 [no paratypes].

Accompanying fauna: Crustacea: Isopoda (Oniscoidea), Copepoda (Cyclopidae), Phyllopora; Mollusca: Gastropoda (*Pyr-gophorus* spec.).

Description.— Body length (antennae 1 and 2 excluded) of male up to 2058  $\mu\text{m}$  (holotype 2039  $\mu\text{m}$ ), of female up to 1974  $\mu\text{m}$  in the material studied.

Antenna 1: peduncular segments 1 to 3 with three, three, and two long plumose macrosetae on respective median margins; main flagellum 6-segmented, last segment with seven simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with three simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segment 4 with three, and segment 5 with four teazel macrosetae on the medial and mediodistal margins; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with seven to eight setules, third segment with obscure unisetulate macroseta.

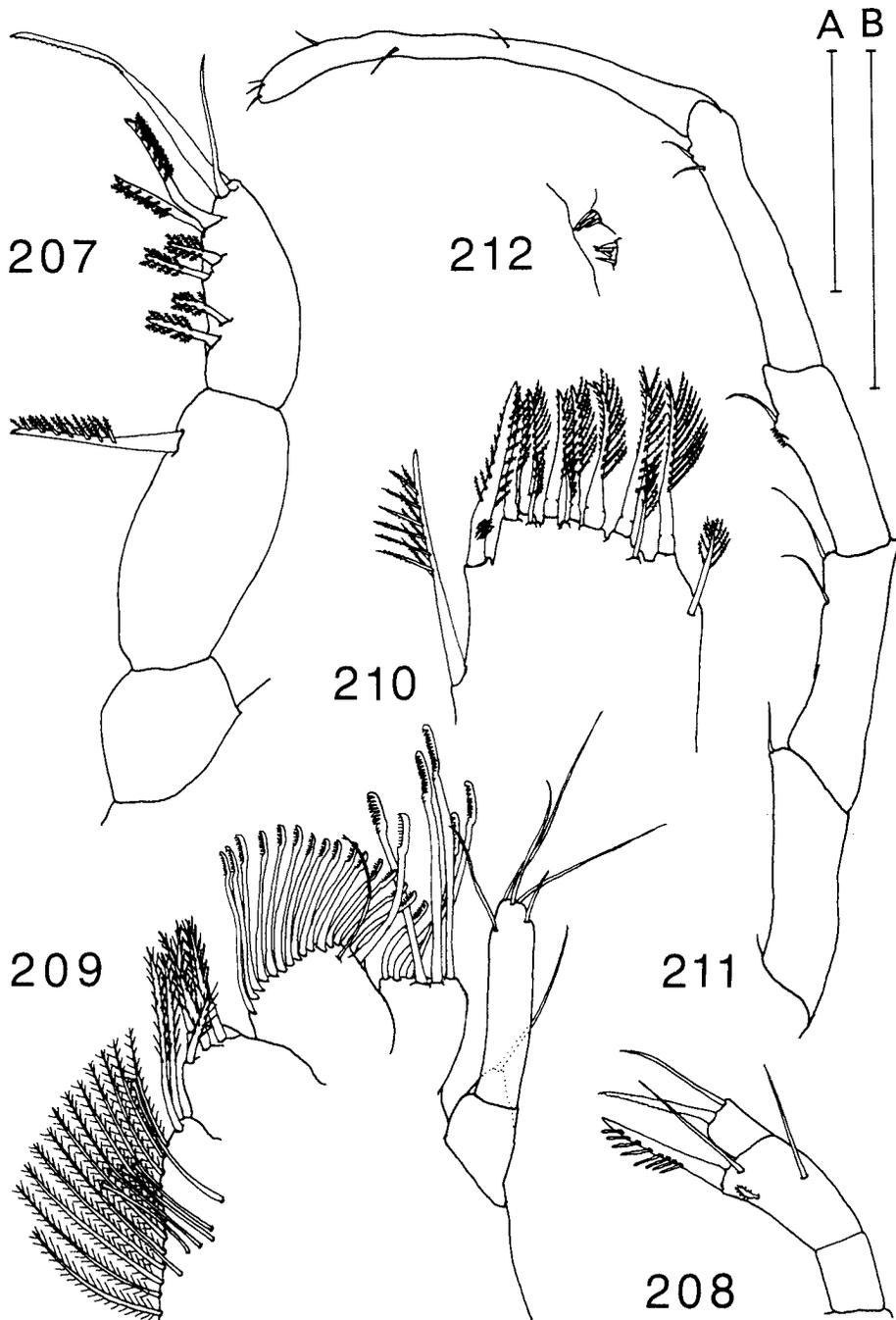
Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 15 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment without patches of club microsetae on the distal portion, third segment with two patches of four to five minute stout club microsetae (diameter  $\times$  height up to circa  $0.5 \times 1.5 \mu\text{m}$ ), fourth segment without patches of club microsetae; basipodal endite bearing 12 plumidenticulate macrosetae with long setules, a tall one medially, seven long ones terminally, three shorter ones subterminally, and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, one subterminal and one lateral plumose macrosetae.

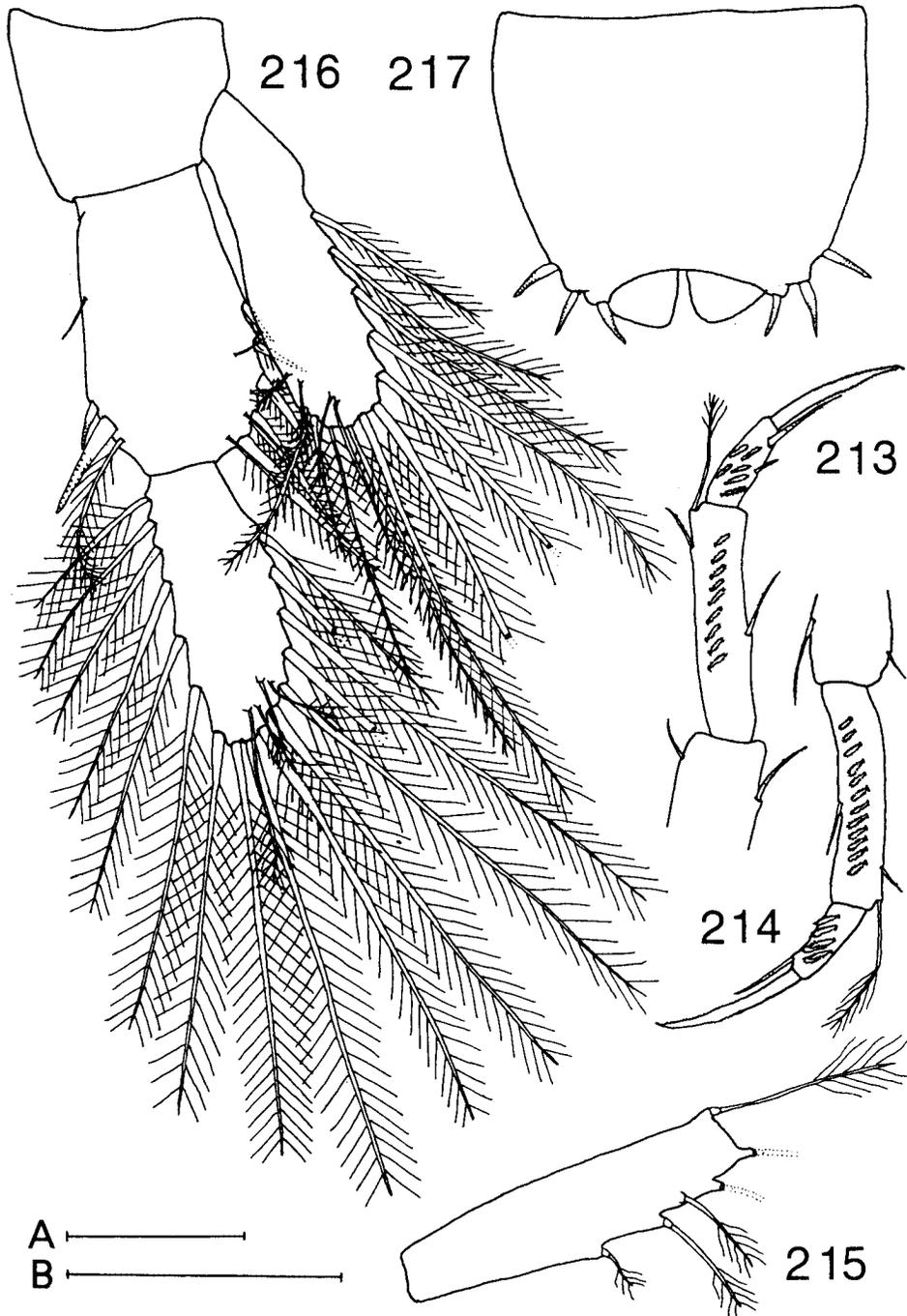
Gnathopod: basal segment with two short plumose macrosetae; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; baso-ischium of endopodite with obscurely demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with nine ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and four ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with nine ovate microsetae, dactylus with two teazel macrosetae on ventral



Figs. 207-212. *Tethysbaena stocki* spec. nov., holotype ♂. 207, palp mandible. 208, palp maxilla 1. 209, maxilla 2. 210, distal portion of basipodal endite of maxilliped. (figs. 207-210 scale B). 211, endopodite of maxilliped (scale A). 212, detail microsetae at distal portion of endopodite segment 3 of maxilliped (extremely enlarged). Scales indicated 0.1 mm.



Figs. 213-217. *Tethysbaena stocki* spec. nov., holotype ♂ and paratype ♀. 213, distal portion of pereopod 3, holotype. 214, distal portion of pereopod 6, holotype. 215, pleopod 2, paratype (scale B). 216, uropod, holotype. 217, telson, holotype (figs. 213-214 and 216-217 scale A). Scales indicated 0.1 mm.

margin and two rows of two and four ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with ten ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and four ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with ten ovate microsetae, dactylus with one teazel macroseta on ventral margin and two rows of two and four ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with one medial, two subterminal and two terminal plumose macrosetae.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 11 to 12 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two rows of two and four ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, and one vestigial terminal macroseta, two ovate microsetae present.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 13 to 14 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two rows of two and four ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, and one vestigial terminal macroseta, two ovate microsetae present.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of four to five stout plumose macrosetae, each accompanied by small subplumose macroseta, segment 2 with 16 to 17 plumose macrosetae; endopodite bearing 11 to 13 plumose macrosetae.

Telson: wider than long, mean width/length ratio 1.19; anal lobes protruding beyond the terminal stretch; stretch concave.

Variability.— Variation is observed in the number of setules of the unisetulate macroseta of the palp of maxilla 1 within the same individual. In the uropod not only the number of plumose macrosetae of both rami varies, but the number of cuspidate macrosetae on the medial margin of the first segment of the exopodite can be either four or five.

Remarks.— A female of 1842  $\mu\text{m}$  body length had a regenerated right pereiopod 4. It therefore seems likely that the animals can moult in the adult phase, like most other crustaceans do after damaging an appendage.

This species shows the greatest similarity to *T. calsi*, but can be distinguished by the lower number of segments of the main flagellum of antenna 1, the generally lower number of setules on the unisetulate macroseta of the palp of maxilla 1, the

indistinct demarcation of the ischium in the baso-ischium of the gnathopod, the slightly lower number of ovate microsetae on the propodus of pereopods 4 to 7, the different configuration of ovate microsetae on the dactylus of the pereopods, the almost complete absence of the rugosities on the endopodal palp of the male maxilliped, and the slightly different width/length ratio of the telson. For detailed information on specific differences one is referred to table 1 (p. 140).

**Etymology.**— The species is named after my supervisor and good friend Prof. Dr Jan H. Stock (Zoölogisch Museum, Amsterdam, The Netherlands), who also collected the material on which the description of this new species is based, and who is the founder of the stygobiological research carried out by the Instituut voor Systematiek en Populatiebiologie, Amsterdam.

**Distribution.**— This species has been found only in the central part of Anegada on several stations between The Settlement and the airport. As limited sampling was carried out in the eastern (and none in the western) part of the island one can not conclude that the species is confined to that area only.

**Habitat.**— The area consists of a karst bottom of Pleistocene age (Weyl, 1966). All accompanying faunal elements encountered are in origin epigeal dispersionalist taxa. The water can be characterized as oligohaline.

#### 4.4.2.12. *Tethysbaena sanctaegrucis* (Stock, 1976) (figs. 218-228)

*Monodella sanctaegrucis* Stock, 1976: 48, figs. 1-26; Abele, 1982: 276; Chelazzi & Messana, 1982: 170; Watling, 1983: 216 fig. 1e, 218 fig. 2e; Boutin & Cals, 1985: 267; Stock, 1986a: 587, fig. 3; Schram, 1986: 220, fig. 17-1A-B; Meštrović & Cals, 1991: 42; Pretus, 1991: 235.

*Monodella*, Stock, 1979: 24.

Thermosbaenaceans (partim); Stock, 1983a: 277.

Thermosbaenacea (partim); Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1984b: 41; Stock, 1986d: 199.

*Monodella sanctae-crucis*; Cals & Monod, 1988: 342.

*Monodella* (partim); Wagner, 1990: 123.

**Material.**— U.S. Virgin Islands, Saint Croix: 2 ♂♂, 2 ♀♀, 2 juveniles (1 ♂, 1 ♀); AMEWI sta. 75/31, Estate Union & Mount Washington, about 1 km N of the shore of Great Pond (a salt pond), 17°44'23"N 64°39'33"W; deep well (6" drill hole) in a meadow W of road, behind a low dam, provided with a ramshackled windmill, alt. 20 m, water level -15 m, chlorinity 990 mg/l; collected by J.H. Stock; 20.xi.1975; ZMA coll. no. C.A. 8001 [female holotype], ZMA coll. no. C.A. 8002 [male allotype], ZMA coll. no. 8003 [paratypes].

Accompanying fauna: Crustacea: Isopoda (*Cyathura* spec.); Insecta: Collembola; Oligochaeta.

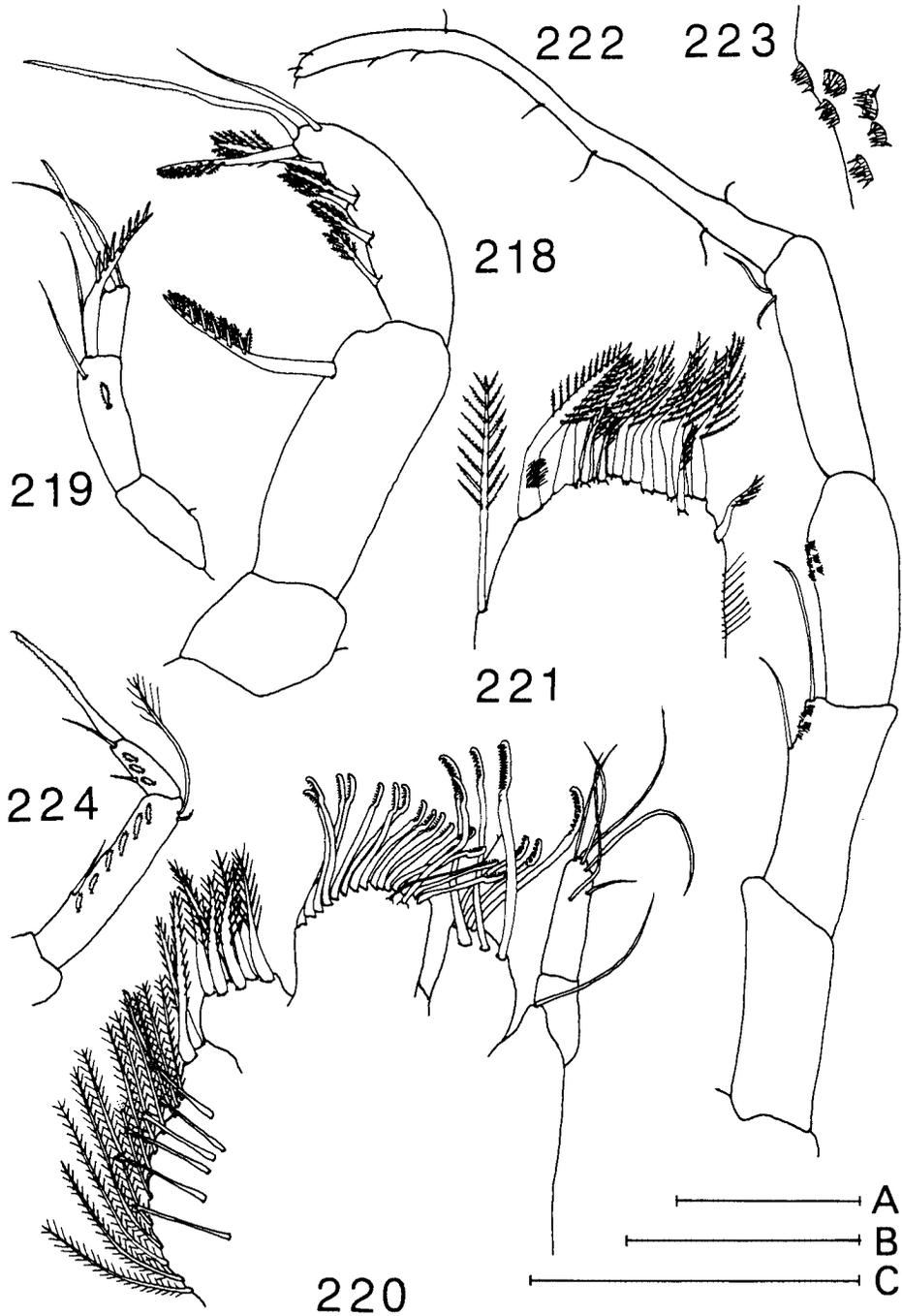
- 1 ♂; same locality as sta. 75/31; collected by Mr D. Holt; i.1976; ZMA coll. no. C.A. 8011 [topotype].

- 2 fragmentary specimens; Estate Solitude, Mr Roebuck's meadow, 17°45'22"N 64°38'04"W; deep well provided with an electric, submersible pump, placed at -48 m depth, alt. 24 m, 500-600 m from the sea, chlorinity 540-580 mg/l; collected by Mr D. Holt; i.1976; ZMA coll. no. C.A. 8010.

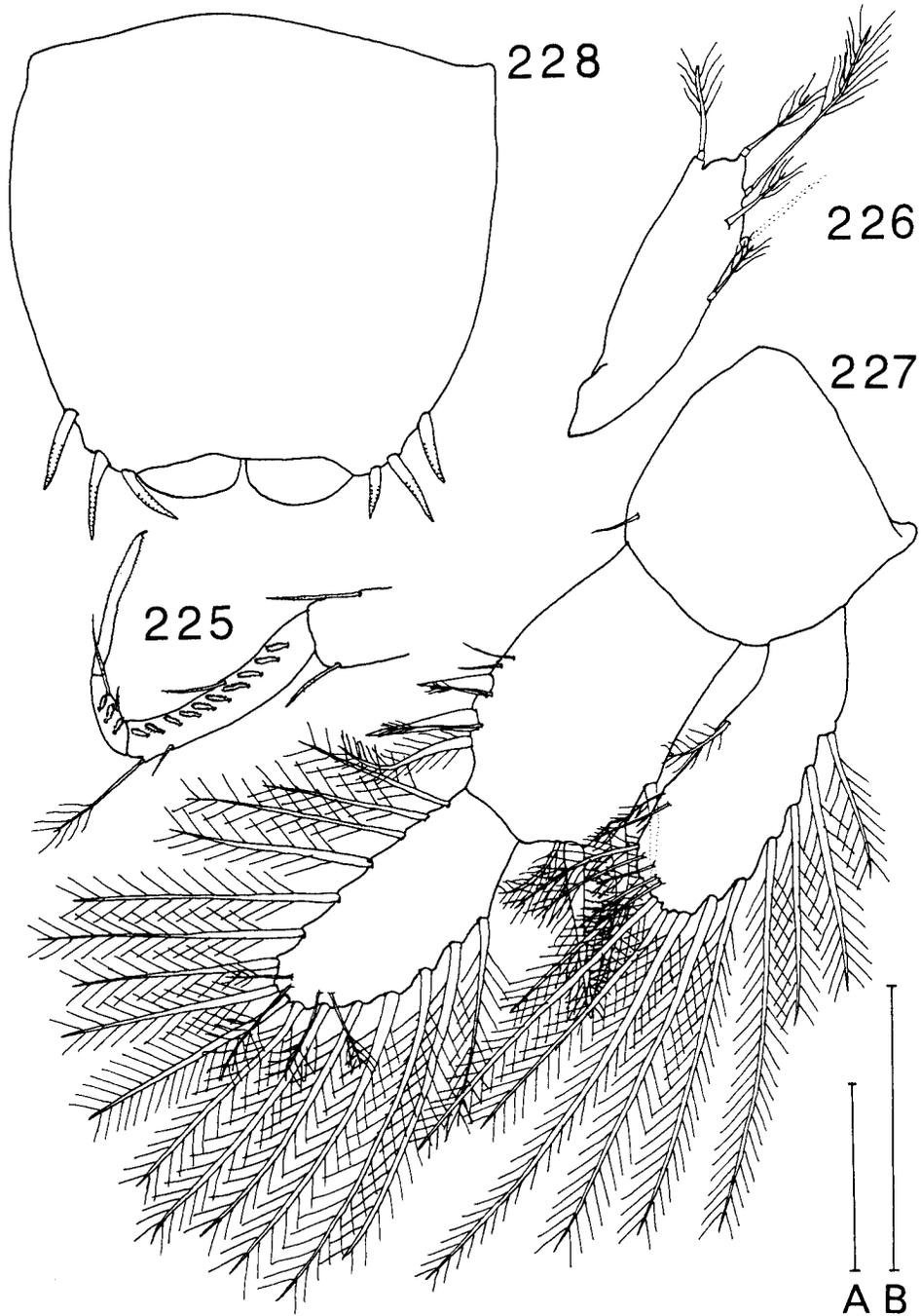
Accompanying fauna: Crustacea: Isopoda (*Cyathura* spec.), Amphipoda (*Metaniphargus beattyi* Shoemaker, 1942).

**Description.**— Body length (antennae 1 and 2 excluded) of male up to 2352 µm, of female up to 2295 µm (holotype) in the material studied.

Antenna 1: peduncular segments 1 to 3 with four, four, and three long plumose



Figs. 218-224. *Tethysbaena sanctaerucis* (Stock, 1976), paratype ♂ and ♀. 218, palp mandible, ♂. 219, palp maxilla 1, ♂. 220, maxilla 2, ♂. 221, distal portion of basipodal endite of maxilliped, ♂. (figs. 218-221 scale C). 222, endopodite of maxilliped (scale B), ♂. 223, detail microsetae at distal portion of endopodite segment 3 of maxilliped (extremely enlarged), ♂. 224, distal portion of pereopod 3, ♀ (scale A). Scales indicated 0.1 mm.



Figs. 225-228. *Tethysbaena sanctaerucis* (Stock, 1976), paratype ♂ and ♀. 225, distal portion of pereopod 6, ♂. 226, pleopod 2, ♀ (scale B). 227, uropod, ♂. 228, telson, ♀ (figs. 225 and 227-228 scale A). Scales indicated 0.1 mm.

macrosetae on respective median margins; main flagellum 7-segmented, last segment with seven simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with three teazel macrosetae on the medial and mediiodistal margins; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with seven setules, third segment with obscurely unisetulate macroseta.

Maxilla 2: basipodal endite 1 with six plumidenticulate macrosetae; basipodal endite 2 with 15 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing six simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment two rows of two patches of tall, pointed club microsetae (diameter  $\times$  height up to circa  $0.4 \times 2.5 \mu\text{m}$ ) on the distal portion, third segment with two rows of three patches of tall, pointed club microsetae (diameter  $\times$  height up to circa  $0.4 \times 2.5 \mu\text{m}$ ) fourth segment without patches of club microsetae; basipodal endite bearing 12 plumidenticulate macrosetae with long setules, a tall one medially, seven long ones terminally, three shorter ones subterminally, and a small one sublaterally, and with an additional much stouter submedial plumidenticulate macroseta; exopodite 2-segmented, distal segment with two terminal, two subterminal and one lateral plumose macrosetae.

Gnathopod: basal segment with three short plumose macrosetae; exopodite with three medial, two subterminal, two terminal and two lateral plumose macrosetae; baso-ischium of endopodite with clearly demarcated "free" ischium, propodus with three teazel macrosetae on distal half, and dactylus with two unequal teazel macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with six ovate microsetae, dactylus with two teazel macrosetae on ventral margin and five ovate microsetae; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one mediiodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with six ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one mediiodorsal ovate microseta,

propodus with one teazel macroseta medially on ventral margin, both male and female with eight ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with five ovate microsetae, second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one mediodorsal ovate microseta, propodus with one teazel macroseta medially on ventral margin, both male and female with eight ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with two medial, two subterminal and two terminal plumose macrosetae.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with ten ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and three ovate microsetae.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and three ovate microsetae.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of three stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 16-17 plumose macrosetae; endopodite bearing 10 to 12 plumose macrosetae.

Telson: somewhat wider than long, mean width/length ratio 1.12; anal lobes protruding beyond the terminal stretch; stretch slightly concave, somewhat convex centrally.

Variability.— Some variation was noted in the number of plumose macrosetae on the uropodal rami, the number of specimens examined was too limited to establish any further variability.

Remarks.— For detailed information on specific differences one is referred to table 1 (p. 140).

Distribution.— Thus far this species has been recorded from a limited area southwest of the Seven Hills in the eastern part of St. Croix.

Habitat.— The specimens were collected in alluvial deposits from Pleistocene to Holocene age (Weyl, 1966). Besides *T. sanctaerucis*, other stygiobionts like the isopod *Cyathura* spec. and the amphipod *Metaniphargus beattyi* Shoemaker, 1942, were found as accompanying fauna. The water can be characterized as oligohaline.

Table 1. Salient differences between the species of the "*Tethysbaena sanctaecrucis*-group"

	<i>T. juriaani</i> spec. nov.	<i>T. gaweini</i> spec. nov.	<i>T. haitiensis</i> spec. nov.	<i>T. juglandis</i> spec. nov.	<i>T. lazarei</i> spec. nov.
Antenna 1:					
# segm. main flagellum 3	7	6-8	8-9	8-9	7
# plumose m.s. segm. 1, 2, 3	3,3,2	4,3,2	5,4,2	5,4,2	4,4,2
Mandible:					
# plumidenticulate m.s. segm. 2	6	6	8	7	6
Maxilla 1:					
distal margin segm. 1	distinct	indistinct	distinct	distinct	distinct
# setules uniset. m.s. segm. 2	7	6	6-9	4-5	4
setules of uniset. m.s. segm. 3	obscure	obscure	obscure	developed	obscure
Maxilla 2:					
# plumidenticulate m.s. b.e.1	5	7	7	7	7
# rake-like m.s. b.e.2	15	14	l: 14; r: 15	15	15
# rake-like m.s. b.e.3	7	6	7	6	7
# simple m.s. end.	4	4	4	4	4
Maxilliped:					
total # plumidenticulate m.s.	14	13	13	14	13
# plumose m.s. ex.	4	4	4	4	5
# patches segm. 2, 3 end. male	2,2	2,4	2,4	1,2	2,2
Gnathopod:					
demarcation ischium	distinct	indistinct	distinct	indistinct	indistinct
# plumose m.s. exopodite	8	8	8	9	?
Pereiopod 2:					
# ovate microsetae propodus	8-9	9	10	8-9	5
# ovate microsetae dactylus	3	3 + 4	5	3 + 4	3
# ovate microsetae exopodite	1	0	1	0	?
# plumose m.s. exopodite	9	8	9	9	?
Pereiopod 3:					
# ovate microsetae ischiomerus	1	1	1	1	0
# ovate microsetae propodus	9	10	11	10	7
# ovate microsetae dactylus	3	3 + 4	5	3 + 4	2
# ovate microsetae exopodite	3	3	3	2	2
# plumose m.s. exopodite	8	8	8	9	8
Pereiopod 4:					
# ovate microsetae propodus	11	12	13	11	?
# ovate microsetae dactylus	3	4	4	4	?
# ovate microsetae exopodite	3	3	4	3	3
# plumose m.s. exopodite	8	6	8	7	8
Pereiopod 5:					
# ovate microsetae propodus	13	13	13-14	13	?
# ovate microsetae dactylus	3	4	5	4	?
# ovate microsetae exopodite	3	3	4	1	1
# plumose m.s. exopodite	4	4	4	4 + 1v	3
Pereiopod 6:					
# ovate microsetae ischiomerus	1	0	1	0	0
# ovate microsetae propodus	15	15	16	14-15	11
# ovate microsetae dactylus	3	3	4	4	3
# ovate microsetae exopodite	3	3	4	1	1
# plumose m.s. exopodite	2 + 3v	2 + 1v	2 + 1v	2 + 1v	2 + 2v

<i>T. tinima</i> spec. nov.	<i>T. coqui</i> spec. nov.	<i>T. colubrae</i> spec. nov.	<i>T. scitula</i> spec. nov.	<i>T. calsi</i> spec. nov.	<i>T. stocki</i> spec. nov.	<i>T. sanctaegrucis</i> (Stock, 1976)
7 4,4,1	7 5,4,1	7 3,3,2	7 3,3,2	7 3,3,2	6 3,3,2	7 4,4,3
6	6	5	6	6	6	6
indistinct 6-7 obscure	distinct 6-7 obscure	distinct 7-9 obscure	indistinct 8-9 obscure	distinct 8-10 obscure	distinct 7-8 obscure	distinct 7 obscure
7 19 7 4	5 14 7 4	7 13 6 4	5 14 6 5	7 15 6 4	5 15 6 5	6 15 6 6
13 4 2,3	14 3 0,1	12-13 3 1,2	13 4 1,4	13 3 4,2	13 4 0,2	13 5 4,6
distinct 8	indistinct 8	indistinct 8	indistinct 8	indistinct 8	indistinct 8	distinct 9
3 1+4 1 8	5-6 1+2 0 8	6 3 1 8	10 4+6 0 8	8-9 1+5 0 9	9 2+4 0 8	6 5 0 9
1 6 1+4 1 8	1 8 2 2-3 8	1 9 4 3 8	1 11-12 1+6 3 8	1 9-10 1+5 3 8	1 9 2+4 3 8	1 6 5 3 9
7-8 1+4 2-3 8	8 2 2-3 8	11 4 3 8	12-13 1+6 3 8	11 1+5 3 8	10 2+4 3 8	8 4 5 7
12-13 1+4 3 3	8-9 2 2 3	11 2 3 5	15-17 1+6 3-5 5	11-12 1+5 3 6	10 2+4 5 5	8 4 3 6
0 14 1+4 1-2 2+2v	1 11 2 3 2+2v	0 14 4 2 2+1v	1 16-17 1+6 2 2+3v	0 13-14 1+5 3 2+1v	0 11-12 2+4 2 2+1v	1 10 3 3 2+2

Table 1 (continued)

	<i>T. juriaani</i> spec. nov.	<i>T. gaweini</i> spec. nov.	<i>T. haitiensis</i> spec. nov.	<i>T. juglandis</i> spec. nov.	<i>T. lazarei</i> spec. nov.
Pereiopod 7:					
# ovate microsetae ischiomerus	1	0	1	0	?
# ovate microsetae propodus	16-17	18	18	15-16	?
# ovate microsetae dactylus	3	3	4	4	?
# ovate microsetae exopodite	3	3	1	1	0
# plumose m.s. exopodite	2 + 1v	2 + 1v	2 + 2v	2 + 1v	2 + 1v
Pleopod 2:					
# dorsolateral subplumose m.s.	0	1	0	1	0
Uropod:					
# medial plumose m.s.	5	4	4	4-6	?
# plumose m.s. segm. 2 ex.	16	14-18	16-21	15-17	?
# plumose m. s. end.	13	10-14	14-17	12-13	11
Telson:					
mean width/length ratio	1.28	1.20	1.21	1.05	1.29

abbreviations: b.e. = basipodal endite; end. = endopodite; ex. = exopodite; m.s. = macroseta(e); segm. =

#### "*T. relicta* -group"

This group of species is characterized by: the presence of a 8-segmented main flagellum of the antenna 1; mandibular palp with seven plumidenticulate macrosetae on the second segment; unisetulate macroseta of third segment of the palp of maxilla 1 well-developed and with five setules; endopodite of maxilla 2 with six simple macrosetae; maxilliped with five or six terminally implanted plumidenticulate macrosetae on basipodite; pereopods 2 to 5 with one lateral plumose macrosetae on second segment of exopodite, number of ovate microsetae on propodus of endopodite of pereopods 2 to 7 not different between the sexes; pleopod 1 with three dorsal subplumose macrosetae; distal margin of uropodal endopodite not protruding beyond distal margin of first segment of the exopodite; telson wider than long, anal lobes protruding beyond terminal stretch; stretch concave with centrally a bump, glandular simple macrosetae absent on stretch.

#### 4.4.2.13. *Tethysbaena relicta* (Pór, 1962) (figs. 229-237)

*Monodella relicta* Pór, 1962: 304, figs. 2-4, pl. 7; Pór, 1963: 49, fig. 1; Vandel, 1964: 144; Maguire, 1965: 149; Fryer, 1965: 83; Rouch, 1965: 717; Straškrabá, 1967: 193; Green, 1967: 168; Meštrov & Lattinger-Penko, 1969: 112; Kaestner, 1970: 369; Tsumamal & Pór, 1971: 221, pl. 69 fig. 3; Zilch, 1972: 81; Schminke, 1976: 295; Stock, 1976: 56; McLaughlin, 1980: fig. 30C; Abele, 1982: 276; Chelazzi & Messana, 1982: 170; Boutin & Cals, 1985: 267; Stock, 1986a: 587, fig. 2; Schram, 1986: 221; Cals & Monod, 1988: 342; Meštrov & Cals, 1991: 42; Dimentman & Pór, 1991: 156 fig. 1, 157; Pretus, 1991: 235.

*Monodella* (partim); Botosaneanu & Delamare Debutteville, 1967: 22; Wagner, 1990: 123.

<i>T. tinima</i> spec. nov.	<i>T. coqui</i> spec. nov.	<i>T. colubrae</i> spec. nov.	<i>T. scitula</i> spec. nov.	<i>T. calsi</i> spec. nov.	<i>T. stocki</i> spec. nov.	<i>T. sanctaerucis</i> (Stock, 1976)
0	1	0	0	0	0	1
14	13	17	16-17	15-16	13-14	11
1 + 4	2	2	1 + 6	1 + 5	2 + 4	3
1	3	0	0	3	2	3
2 + 2v	2 + 1v	2 + 1v	2 + 1v	1 + 2v	2 + 1v	2 + 2v
1	1	0	1	1	1	1
2	3	4	4	4	4-5	3
16	14	14	14-15	15-17	16-17	16-17
13	10	11	10-11	10-13	11-13	10-12
1.36	1.21	1.38	1.36	1.17	1.19	1.12

segment(s); uniset. = unisetulate; v = vestigial macroseta; # = number of...

Material.— **Israel:** 1 fragmentary specimen; Hamei Zohar, W of Dead Sea; from thermo-mineral spring; collected by F. D. Pór; 12.xii.1960; ZMA coll. no. 8105 [syntype].

- 1 ♂, 2 ♀; Kinneret ?; collected by F. D. Pór, 14.xii.1966; ZMA coll. no. C.A. 8106 ( male specimen), HUJ.

Description.— Body length (antennae 1 and 2 excluded) of male up to 1778 µm, of female up to 2042 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with four, four, and two long plumose macrosetae on respective medial margins; main flagellum 8-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with four teazel macrosetae on medial and mediiodistal margins; flagellum 5-segmented, last segment with one medial, one lateral, and five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with four setules, third segment with well-developed unisetulate macroseta with five setulettes.

Maxilla 2: basipodal endite 1 with five plumidenticulate macrosetae; basipodal endite 2 with 14 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with eight more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of

appendage, arranged in two rows of three and five macrosetae, respectively; endopodite 2-segmented bearing six simple macrosetae.

Maxilliped: male endopodite lost in the specimen examined (see remarks below); basipodal endite bearing 10 plumidenticulate macrosetae with long setules, a tall one medially, five long ones terminally, three variable sized ones subterminally, and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal and two subterminal plumose macrosetae.

Gnathopod: basal segment with an unknown number of plumose macrosetae (broken off in all specimens examined); exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; baso-ischium of endopodite with obscurely demarcated "free" ischium, propodus with three fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with five ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of three and seven ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with eight ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of three and seven ovate microsetae, respectively; first segment of exopodite with two ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with eight to nine ovate microsetae, dactylus with one teazel macroseta on ventral margin and six ovate microsetae; first segment of exopodite with two ovate microsetae, second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with ten ovate microsetae, dactylus with one teazel macroseta on ventral margin and six ovate microsetae; first segment of exopodite with two ovate microsetae, second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with 11 ovate microsetae, dactylus with one teazel macroseta on ventral margin and four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one laterally implanted, and four ovate microsetae.

Pereiopod 7: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both

male and female with 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, one vestigial terminal macroseta, and two ovate microsetae.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, and two additional lateral macrosetae; segment 2 with 16 to 19 plumose macrosetae; endopodite bearing 11 to 13 plumose macrosetae.

Telson: distinctly wider than long, mean width/length ratio 1.25; anal lobes protruding beyond terminal stretch; stretch concave with central bump.

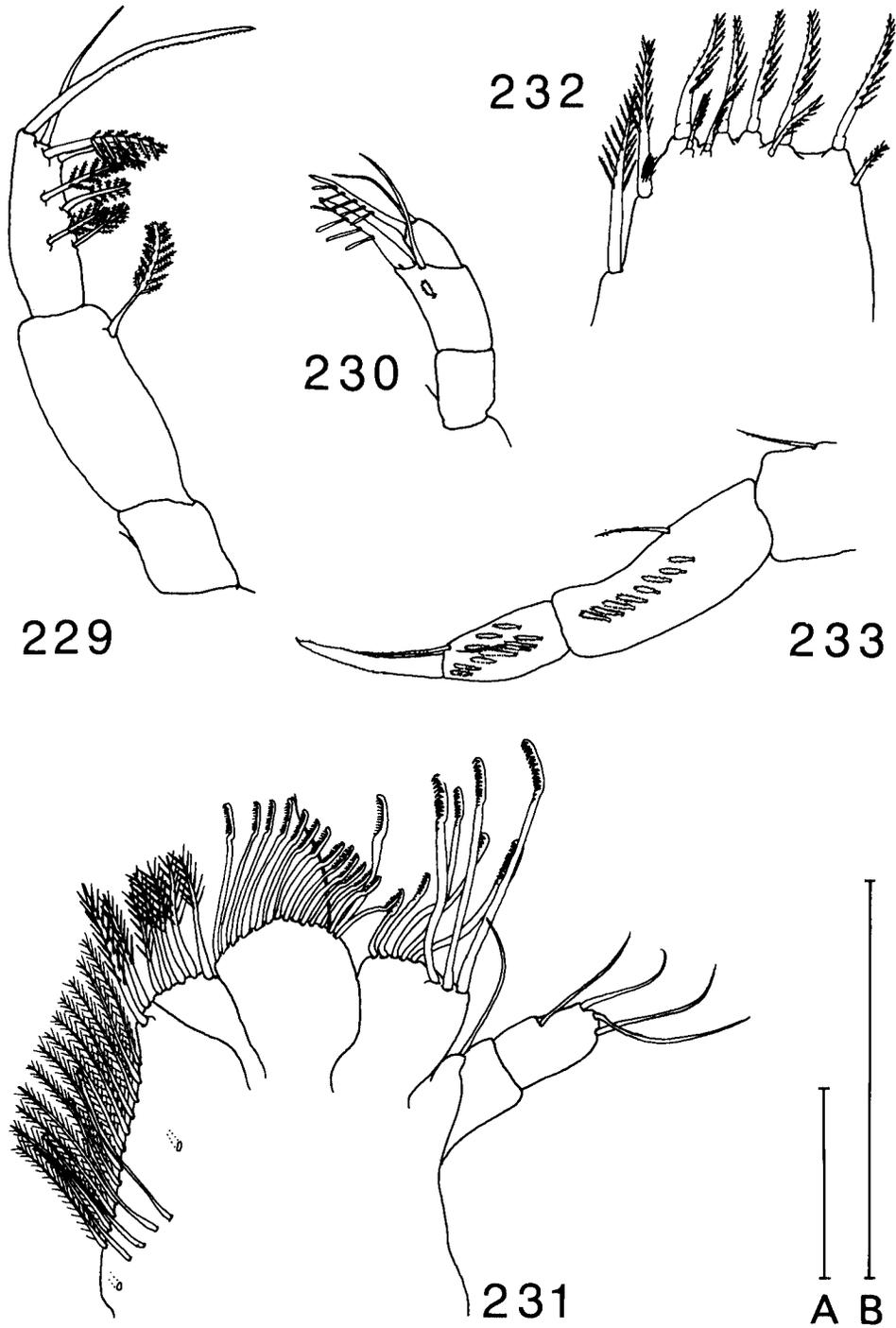
Variability.— Due to the limited number and state of the specimens at my disposal, only some variability in the number of plumose macrosetae of the uropodal rami could be established.

Remarks.— This species can not be confused with any of the other known representatives of the genus, with the exception of *T. somala* (Chelazzi & Messina, 1982). Both *T. relictata* and *T. somala* clearly represent a separate cluster, which can be distinguished by the above-mentioned species-group characters. Distinctive characters between the two species exist in the number of plumidenticulate macrosetae of segment 2 of the mandibular palp (*T. relictata*: 6; *T. somala*: 7), the number of setules of the unisetulate macroseta on segment 2 of the maxilla 1 (*T. relictata*: 4; *T. somala*: 5 to 6), the number of terminally implanted plumidenticulate macrosetae of the basipodal endite 1 of maxilla 2 (*T. relictata*: 5; *T. somala*: 7), the number of rake-like macrosetae on basipodal 3 of the maxilla 2 (*T. relictata*: 8; *T. somala*: 7), the demarcation between the ischium and the basis in the gnathopodal baso-ischium (*T. relictata*: obscure; *T. somala*: distinct), the absence of an additional dorsolateral subplumose macroseta on pleopod 2 in *T. relictata*, a slightly lower number of plumose macrosetae on the uropod of *T. relictata* (*T. relictata*: 13 to 14; *T. somala*: 14 to 16), and the mean width/length ratio of the telson (*T. relictata*: 1.25; *T. somala*: 1.13). Slight differences in the number of ovate microsetae of the propodus and of the serrate macrosetae on propodus and dactylus are present as well.

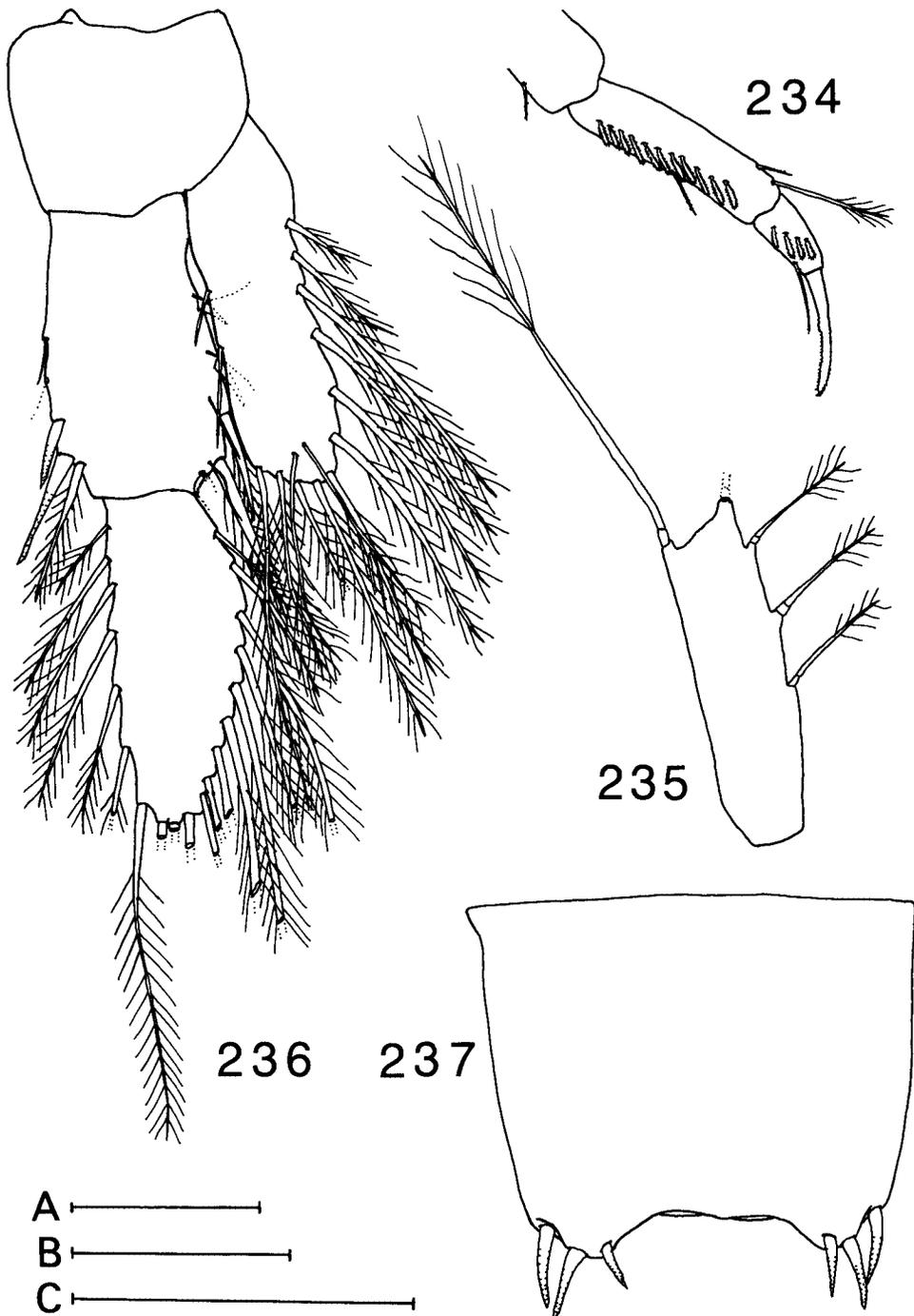
Unfortunately no information can be provided about the club microsetal patterns present on the male maxillipedal endopodite, due to the fact that the only remnant maxilliped present in the single (somewhat damaged) male at my disposal was lost during critical point drying in order to prepare it for SEM study.

Distribution.— This species was originally described from the thermo-mineral spring of Hamei Zohar, near the Dead Sea shore, and later reported from the warm sulphur spring En-Nur on the northern shore of Lake Tiberias, all in Israel (Tsurumal & Pór, 1971; [as Lake Kinneret in] Dimentman & Pór, 1991).

Habitat.— The type locality is a highly mineralized spring with hyperhaline water and a temperature of 31°C, while En-Nur is a slightly cooler (temperature 29.5°C) oligohaline sulphur spring. The occurrence of *Bogidiella hebraea* Ruffo, 1963 as accompanying fauna at both localities supports the theory of a supposed link between Lake Tiberias and the Dead Sea as an originally continuous marine gulf, that became iso-



Figs. 229-233. *Tethysbaena relictus* (Pór, 1962), ♂ and ♀. 229, palp mandible, ♂. 230, palp maxilla 1, ♂. 231, maxilla 2, ♂. 232, distal portion of basipodal endite of maxilliped, ♀. (figs. 229-232 scale B). 233, distal portion of pereiopod 3, fragmentary syntype (scale A). Scales indicated 0.1 mm.



Figs. 234-237. *Tethysbaena relicta* (P6r, 1962), ♂. 234, distal portion of pereopod 6 (scale A). 235, pleopod 2 (scale C). 236, uropod. 237, telson (figs. 236-237 scale B). Scales indicated 0.1 mm.

lated quite recently (Tsuramal & Pór, 1971). In the Jordan Rift Valley *Tethysbaena relict*a is found in groundwaters in sediments of Pliocene age (Pór, 1963; Tsuramal & Pór, 1971; Dimentman & Pór, 1991). Besides the amphipod *Bogidiella hebraea* Ruffo, 1963, the accompanying fauna reported consisted of the copepod *Nitocra balnearia* Pór, 1964 at Hamei Zohar, of the shrimp *Typhlocaris galilea* Calman, 1909, and the bathynellid *Cteniobathynella calmani* (Pór, 1968) at Lake Tiberias (Dimentman & Pór, 1991).

4.4.2.14. *Tethysbaena somala* (Chelazzi & Messana, 1982)  
(figs. 238-248)

*Monodella* n. sp.; Messana, 1980: 6; Ercolini, Berti, Chelazzi & Messana, 1982: 235.

*Monodella somala* Chelazzi & Messana, 1982: 162, figs. 2-6; Messana, 1982: 17 fig.; Chelazzi & Messana, 1985: 53; Messana & Chelazzi, 1986: 346; Stock, 1986a: 587; Cals & Monod, 1988: 342; Pretus, 1991: 235.

*Monodella* (partim); Wagner, 1990: 123.

Material.— **Somalian Democratic Republic**: 5 ♂♂, 6 ♀♀; Rahole, 02°07'N 42°36'E; 7.vi.1978; ZMA coll. no. C.A. 8107 [topotypes]; RMNH G 49.

Description.— Body length (antennae 1 and 2 excluded) of male up to 1776 µm, of female up to 2342 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with four, four, and two long plumose macrosetae on respective medial margins; main flagellum 8-segmented, last segment with seven simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with four teazel macrosetae on the medial and mediobasal margin; flagellum 5-segmented, last segment with one medial, one lateral, and five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: seven plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with five to six setules, third segment with well-developed unisetulate macroseta with five setulettes.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 14 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented bearing six simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment two fields of scutellae preceding three transverse "bands" of two, four, and four patches of tall, pointed (diameter × height up to circa 0.5 × 2.5 µm) club microsetae on distal portion, third segment with one field of scutellae preceding

two pairs of patches of tall, pointed club microsetae (diameter  $\times$  height up to circa  $0.4 \times 2.0 \mu\text{m}$ ), fourth segment without patches of club microsetae; basipodal endite bearing 11 plumidenticulate macrosetae with long setules, a tall one medially, five long ones terminally, three variable-sized ones subterminally, and a small one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal and two subterminal plumose macrosetae.

Gnathopod: basal segment with three to four plumose macrosetae; exopodite with three medial, two subterminal, two terminal and one lateral plumose macrosetae; baso-ischium of endopodite with clearly demarcated "free" ischium, propodus with three fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, both male and female with five ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; first segment of exopodite with two ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

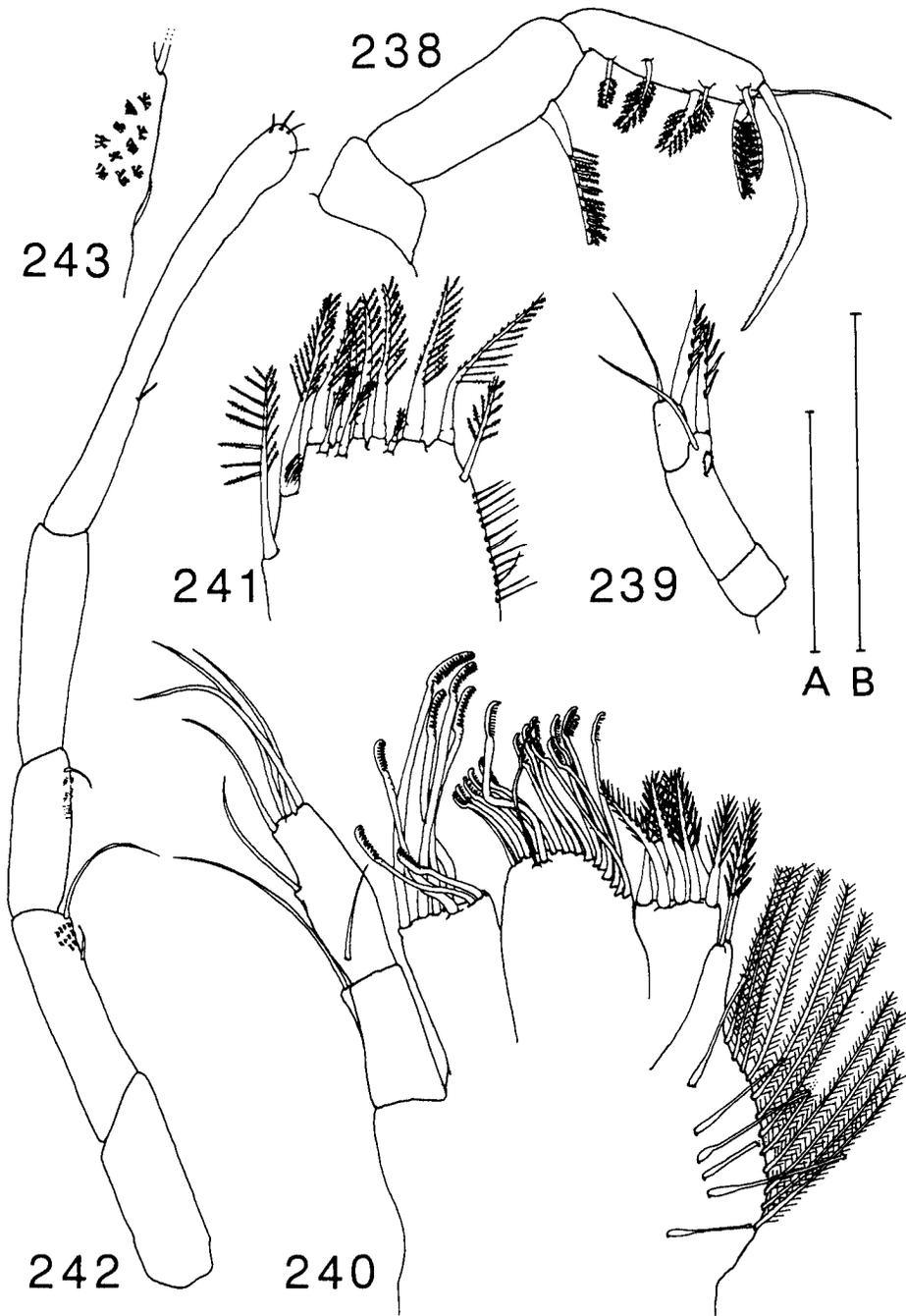
Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with seven ovate microsetae, dactylus with one teazel macroseta on ventral margin and three ovate microsetae; first segment of exopodite with five ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one to two ovate microsetae mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with seven ovate microsetae, dactylus with one teazel macroseta on ventral margin and three ovate microsetae; first segment of exopodite with five ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

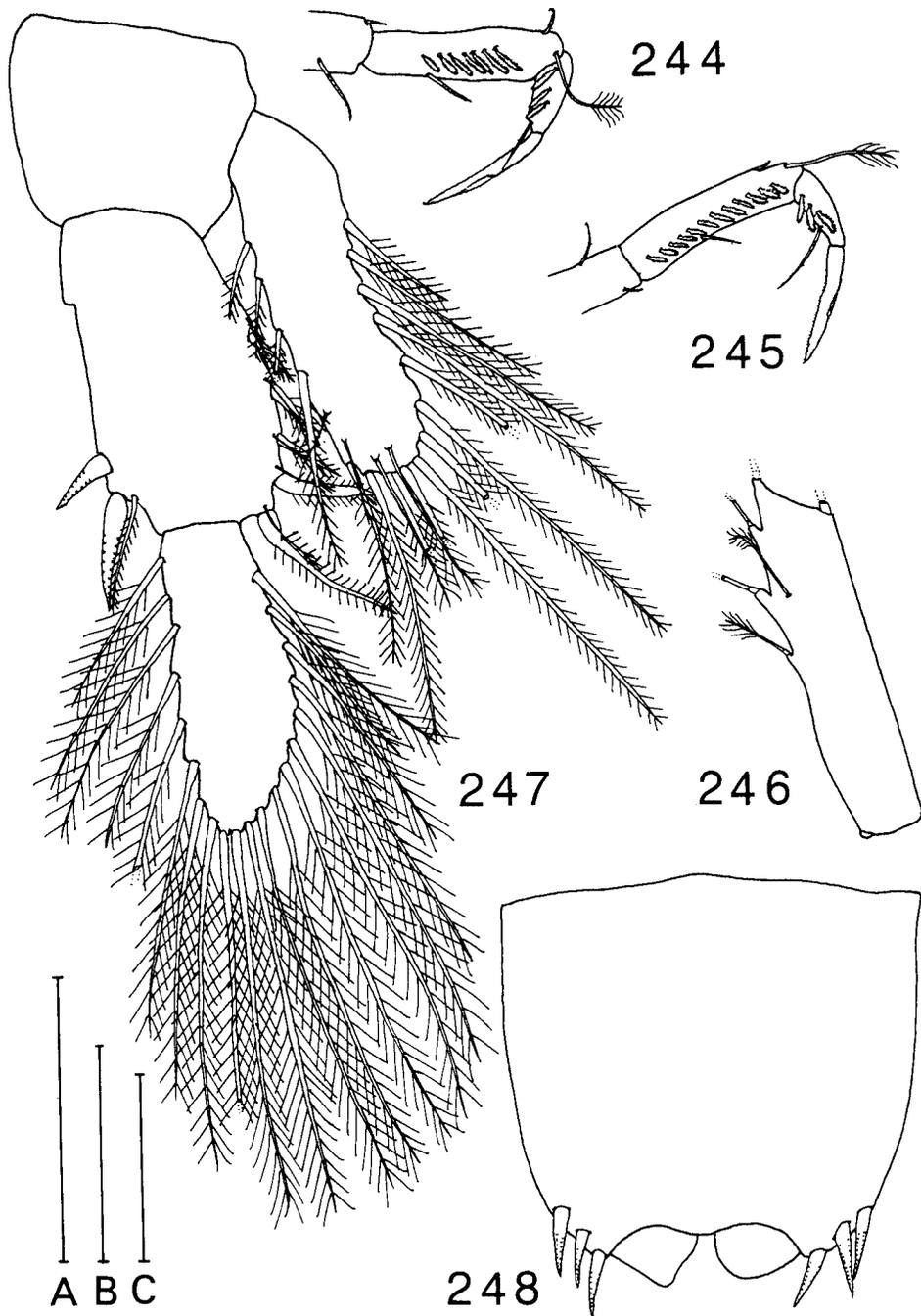
Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with eight to nine ovate microsetae, dactylus with one teazel macroseta on ventral margin and three ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with 12 ovate microsetae, dactylus with one teazel macroseta on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and three ovate microsetae.

Pereiopod 7: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with 15 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal



Figs. 238-243. *Tethysbaena somala* (Chelazzi & Messina, 1982), ♂ and ♀. 238, palp mandible, ♂. 239, palp maxilla 1, ♂. 240, maxilla 2, ♀. 241, distal portion of basipodal endite of maxilliped, ♂. (figs. 238-241 scale B). 242, endopodite of maxilliped (scale A), ♂. 243, detail microsetae at distal portion of endopodite segment 2 of maxilliped (extremely enlarged), ♂. Scales indicated 0.1 mm.



Figs. 244-248. *Tethysbaena somala* (Chelazzi & Messina, 1982), ♂. 244, distal portion of pereopod 3. 245, distal portion of pereopod 6 (figs. 244-245 scale C). 246, pleopod 2 (scale A). 247, uropod. 248, telson (figs. 247-248 scale B). Scales indicated 0.1 mm.

and one lateral, and three ovate microsetae.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and one additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, and three additional subplumose macrosetae, segment 2 with 17 to 20 plumose macrosetae; endopodite bearing 14 to 16 plumose macrosetae.

Telson: wider than long, mean width/length ratio 1.13; anal lobes protruding beyond terminal stretch; stretch concave with central bump.

Variability.— One of the females examined showed an aberrant appendage, viz., an "unguis" formed by two terminal serrulate macrosetae in the left pereopod 2. A similar aberrant state was reported previously by Stock & Longley (1981: 574, fig. 17) for *T. texana* (Maguire, 1965). Further the variation is limited to the number of plumose macrosetae on the uropodal rami.

Remarks.— This species closely resembles *T. relictata* only. For detailed distinctive characters one is referred to the remarks under *T. relictata*.

Chelazzi & Messana (1982: 164) mention a maximal number of 22 flagellar segments for the main flagellum of the antenna 1, and up to 12 for the accessory flagellum. I seriously doubt the validity of their observation; probably another species was mistakenly identified as *T. somala*.

Distribution.— *Tethysbaena somala* was initially found in the Mesopotamic region between the Scebeli and Giuba rivers at Rahole, El Dere, El Ali, El Messri, and El Uarre (Chelazzi & Messana, 1982), south Somalia, later also north of the Scebeli river at Bud Bud, central Somalia (Messana & Chelazzi, 1986).

Habitat.— The wells from where this species was procured are located in limestone sediments of Cretaceous age (Chelazzi & Messana, 1982; Messana & Chelazzi, 1986). The temperatures of the water varies between 26 and 31°C, and the water is oligohaline to mixohaline (salinity: 0.3 g/l at Bud Bud and 1.7 to 3.7 g/l at the other localities). Messana & Chelazzi (1986: 341) reported for the same hydrographic unit the isopod *Stenasellus costai* Lanza, Chelazzi & Messana, 1970, and the amphipod *Afridiella somala* (Ruffo, 1970) as accompanying fauna. Accompanying fauna at Bud Bud is represented by the isopod *Acanthastenasellus forficuloides* Chelazzi & Messana, 1985, the amphipod *Afridiella pectinicauda* Ruffo, 1982, and the cyprinid fish *Phreatichthys andruzzii* Vinciguerra, 1924 (Chelazzi & Messana, 1985).

#### "*T. atlantomaroccana* -group"

This group of species is characterized by: a 7-segmented main flagellum of the antenna 1; mandibular palp with five plumidenticulate macrosetae on the second segment; endopodite of maxilla 2 with four simple macrosetae; maxilliped with eight terminally implanted plumidenticulate macrosetae on basipodite; pereopods 2 to 5 with one lateral plumose macrosetae on second segment of exopodite, number of ovate microsetae on propodus of endopodite of pereopods 2 to 7 sexually different; pleopod 1 with three dorsal subplumose macrosetae; distal margin of uropodal

endopodite not protruding beyond distal margin of first segment of exopodite; telson somewhat longer than wide, anal lobes not protruding beyond terminal stretch, stretch straight with two small glandular simple macrosetae.

4.4.2.15. *Tethysbaena atlantomaroccana* (Boutin & Cals, 1985)  
(figs. 249-259)

*Monodella atlantomaroccana* Boutin & Cals, 1985: 267, figs. A-D; Pretus, 1991: 237.

*Monodella atlantomaroccana* Cals (sic); Stock, 1986a: 588.

*Monodella* (partim); Wagner, 1990: 123.

*Monodella*; Pretus, 1991: 236.

Material.— **Morocco**: 2 ♂♂, 2 ♀♀, 20 specimens; near Qued Tensift; from well; collected by Cl. Boutin; v.1984; ZMA coll. no. C.A. 8044; UPMC [all syntypes].

Description.— Body length (antennae 1 and 2 excluded) of male up to 2872 µm, of female up to 1891 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with four, four, and two long plumose macrosetae on respective medial margins; main flagellum 7-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with two teazel macrosetae on medial and mediodistal margins; flagellum 5-segmented, last segment with one medial, one lateral, and five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

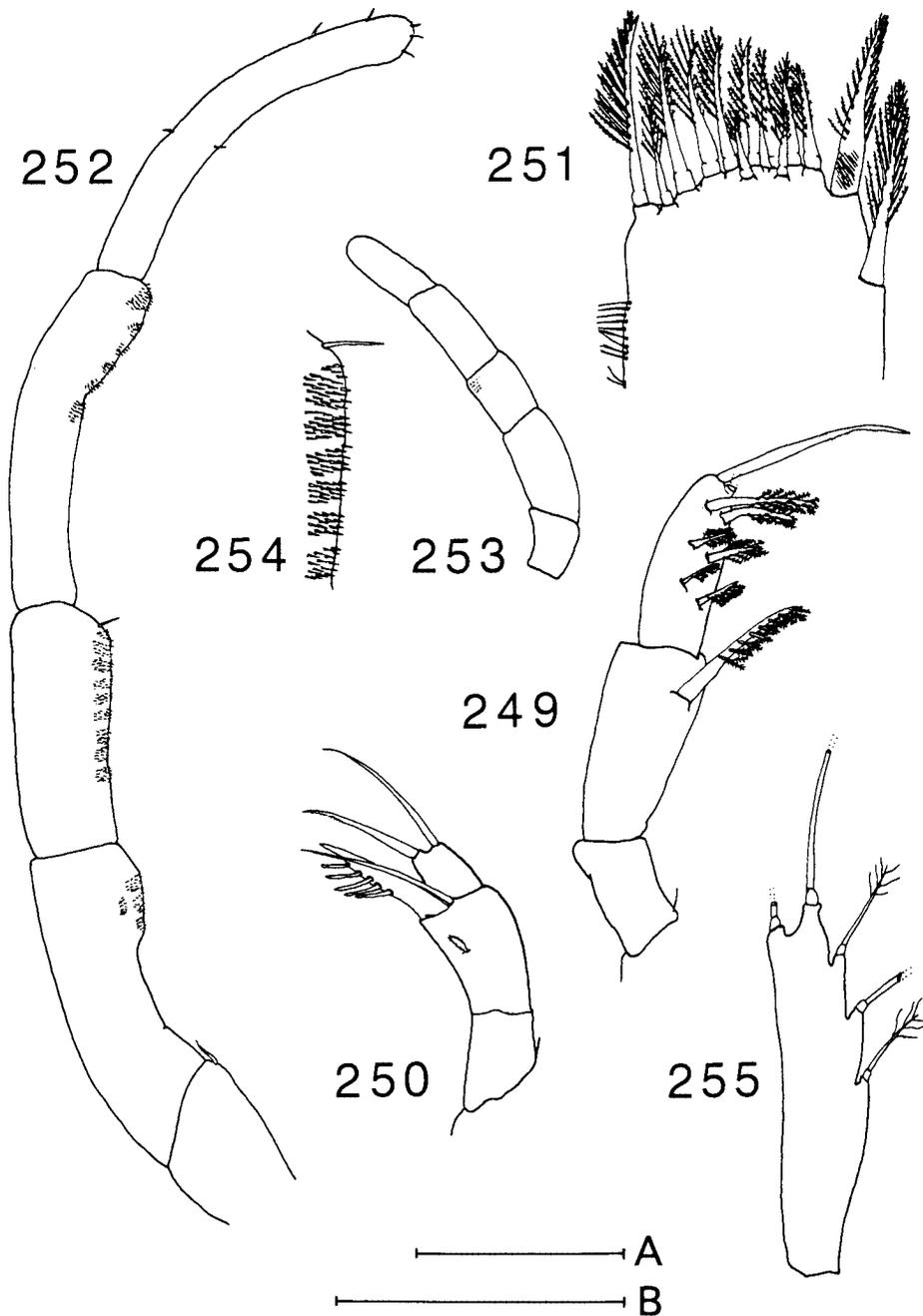
Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with four to five setules, third segment with one obscurely unisetulate macroseta.

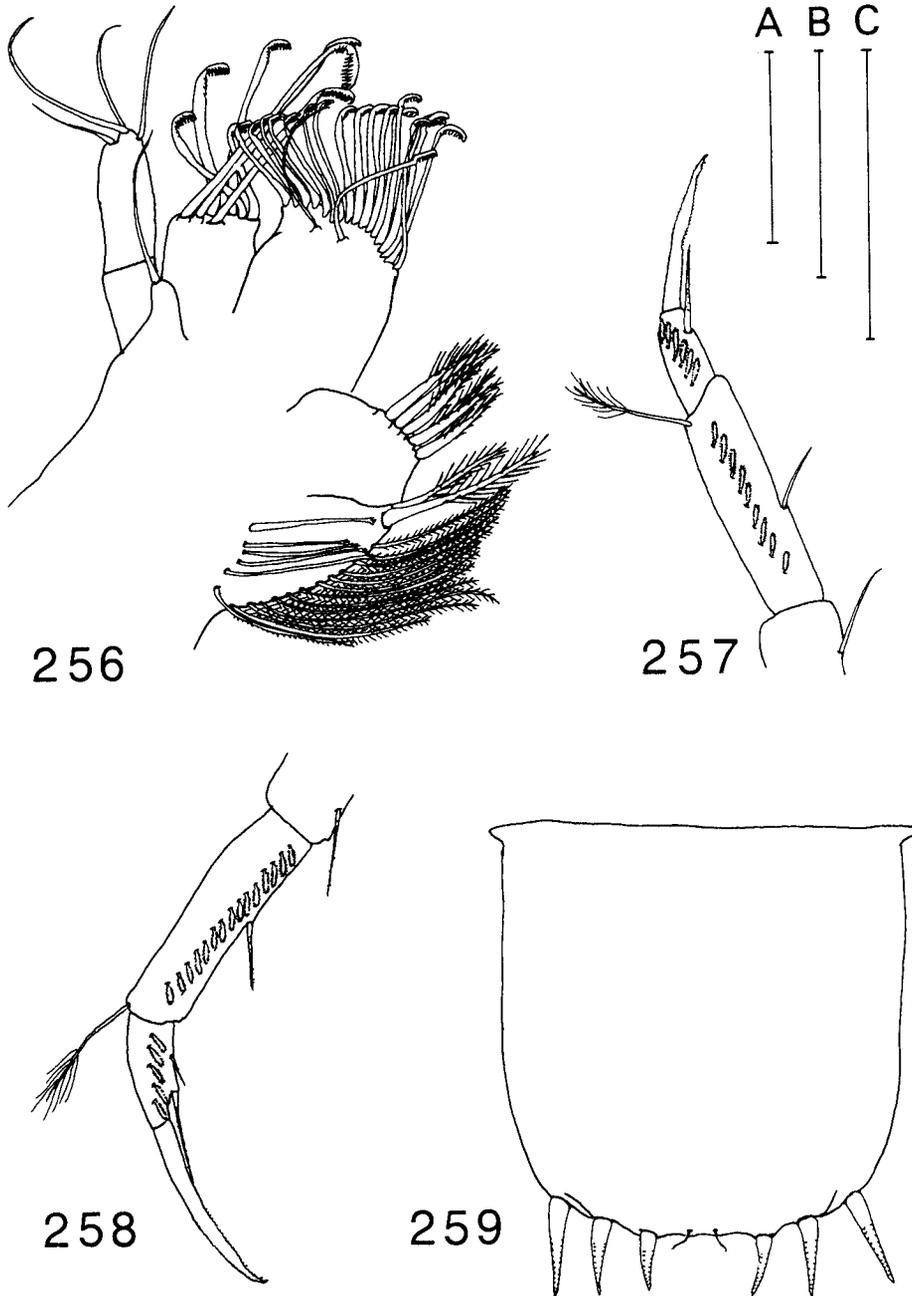
Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 17 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with four patches of club microsetae on the distal portion, third segment with nine patches of club microsetae, fourth segment with six patches of club microsetae; basipodal endite bearing 12 plumidenticulate macrosetae with long setules, a tall one medially, eight long ones terminally, three shorter ones subterminally, none sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal and one subterminal plumose macrosetae.

Gnathopod: basal segment with two plumose macrosetae; exopodite with three



Figs. 249-255. *Tethysbaena atlantomaroccana* (Boutin & Cals, 1986), syntype ♂ and ♀. 249, palp mandible, ♀. 250, palp maxilla 1, ♀. 251, distal portion of basipodal endite of maxilliped, ♀. (figs. 249-251 scale B). 252, endopodite of maxilliped, ♂. 253, regenerated endopodite of maxilliped (figs. 252-253 scale A), ♂. 254, detail microsetae at distal portion of endopodite segment 3 of maxilliped, ♂ (extremely enlarged). 255, pleopod 2, ♂ (scale B). Scales indicated 0.1 mm.



Figs. 256-259. *Tethysbaena atlantomaroccana* (Boutin & Cals, 1986), syntype ♂ and ♀. 256, maxilla 2, ♀ (scale C) 257, distal portion of pereopod 3, ♀. 258, distal portion of pereopod 6, ♂ (figs. 257-258 scale A). 259, telson, ♂ (scale B). Scales indicated 0.1 mm.

medial, two subterminal, two terminal and one lateral plumose macrosetae; basoischium of endopodite with obscurely demarcated "free" ischium, propodus with two fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with one teazel macroseta medially on ventral margin, male with four ovate microsetae, female with four to five ovate microsetae, dactylus with one teazel macroseta on ventral margin and two rows of three and six ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with nine ovate microsetae, dactylus with one teazel macroseta on ventral margin and six ovate microsetae; first segment of exopodite with two ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one to two ovate microsetae mediadorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 11 ovate microsetae, female with 12 ovate microsetae, dactylus with one teazel macroseta on ventral margin and six ovate microsetae; first segment of exopodite with two ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediadorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 13 ovate microsetae, female with 14 ovate microsetae, dactylus with one teazel macroseta on ventral margin and five ovate microsetae; first segment of exopodite with two ovate microsetae, second segment with one subterminal and one terminal plumose macrosetae, two vestigial macrosetae, one medial and one subterminal.

Pereiopod 6: ischiomerus of endopodite with one ovate microseta mediadorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 15 ovate microsetae, female with 16 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and five ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, one vestigial terminal macroseta, and three ovate microsetae.

Pereiopod 7: both endopodite and exopodite lost in the material examined.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and one additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 15 plumose macrosetae; endopodite bearing 10 plumose macrosetae.

Telson: somewhat longer than wide, mean width/length ratio 0.98; anal lobes not protruding beyond terminal stretch; stretch straight with two small glandular simple macrosetae.

Variability.— The limited number of specimens examined did not reveal any infor-

mation on variation.

Remarks.— *T. atlantomaroccana* is most closely related to *T. tarsiensis* spec. nov. (described below), the two forming a species-group. Both can be distinguished from the other congeners by the above-mentioned species-group characters. Distinctive characters between the two species are discussed under *T. tarsiensis*.

Distribution.— Qued Tensift, Marrakech, Morocco.

Habitat.— The well at Qued Tensift is located in the alluvial plain of Marrakech, deposits of which date back to Pliocene age. No information is given by Boutin and Cals (1985, MS) on temperature, water condition and accompanying fauna.

#### 4.4.2.16. *Tethysbaena tarsiensis* spec. nov. (figs. 260-268)

*Monodella* sp.; Bou, 1975: 109; Notenboom, 1988b: 111.

*Monodella* spec. 1 (partim); Pinkster, 1978: 234.

unident. spp.; Schram, 1986: 221.

Bathynellacea; Notenboom, 1988a: 80.

*Monodella* (partim); Wagner, 1990: 123.

*Monodella*; Notenboom, 1988c: 199; Pretus, 1991: 236.

Material.— **Spain**: 13 ♀♀, 1 fragmentary ♀; sta. A85- 6/51, Prov. Sevilla, Cantillana, Los Pajares (UTM coordinates TG498670); from well, alt. 30 m, temperature 19.8°C, electric conductivity 4900 µS/cm, oxygen contents 6.9 mg/l, pH 6.59, chlorinity 120 mg/l; collected by P. van den Hurk & R. Leys; 30.vi.1985; ZMA coll. no. C.A. 8108 [holotype]; ZMA coll. no. C.A. 8109; RMNH G 55 [all paratypes].  
Accompanying fauna: Crustacea: Amphipoda (*Salentinella angelieri* Ruffo & Delamare Deboutteville, 1952; *Metahadzia unispina* Notenboom, 1988), Isopoda (*Stenasellus* spec.; *Microcharon* cf. *marinus* Chapuis & Delamare Deboutteville, 1954), Copepoda (Cyclopoida), Ostracoda; Insecta; Mollusca: Gastro-poda.

Description.— Body length (antennae 1 and 2 excluded) of female up to 2373 µm (holotype) in the material studied; male unknown.

Antenna 1: peduncular segments 1 to 3 with four, four, and three long plumose macrosetae on respective medial margins; main flagellum 7-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segment 4 with three, and segment 5 with four teazel macrosetae on the medial and mediodistal margin; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: five plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment distinctly demarcated from second segment, large unisetulate macroseta on second segment with five to seven setules, third segment with one obscurely unisetulate macroseta.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 25 rake-like serrate macrosetae at terminal margin, and two modified

longer serrate subterminal macrosetae; basipodal endite 3 with six or seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and three or four macrosetae, respectively; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: male endopodite unknown; basipodal endite bearing 14 plumidenticulate macrosetae with long setules, a tall one medially, nine long ones terminally, three shorter ones subterminally, and one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal and one subterminal plumose macrosetae.

Gnathopod: basal segment with three plumose macrosetae; exopodite with two medial, two subterminal, two terminal and two lateral plumose macrosetae; basischium of endopodite with obscurely demarcated "free" ischium, propodus with two fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with one teazel macroseta medially on ventral margin, female with six to seven ovate microsetae, dactylus with one teazel macroseta on ventral margin and three to four ovate microsetae; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: propodus of endopodite with one teazel macroseta medially on ventral margin, female with seven to eight ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite without ovate microseta, second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: propodus of endopodite with one teazel macroseta medially on ventral margin, female with eight ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: propodus of endopodite with one teazel macroseta medially on ventral margin, female with ten ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; first segment of exopodite with three ovate microsetae, second segment with one subterminal and one terminal plumose macrosetae, two vestigial macrosetae, one medial and one subterminal.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, female with 11 to 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, one vestigial terminal macroseta, and one ovate microseta.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, female with 13 to 14 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three to four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, and one vestigial terminal macroseta.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of four stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 14 to 16 plumose macrosetae; endopodite bearing 10 to 13 plumose macrosetae.

Telson: somewhat longer than wide, mean width/length ratio 0.95; anal lobes not protruding beyond terminal stretch; stretch straight with two small glandular simple macrosetae.

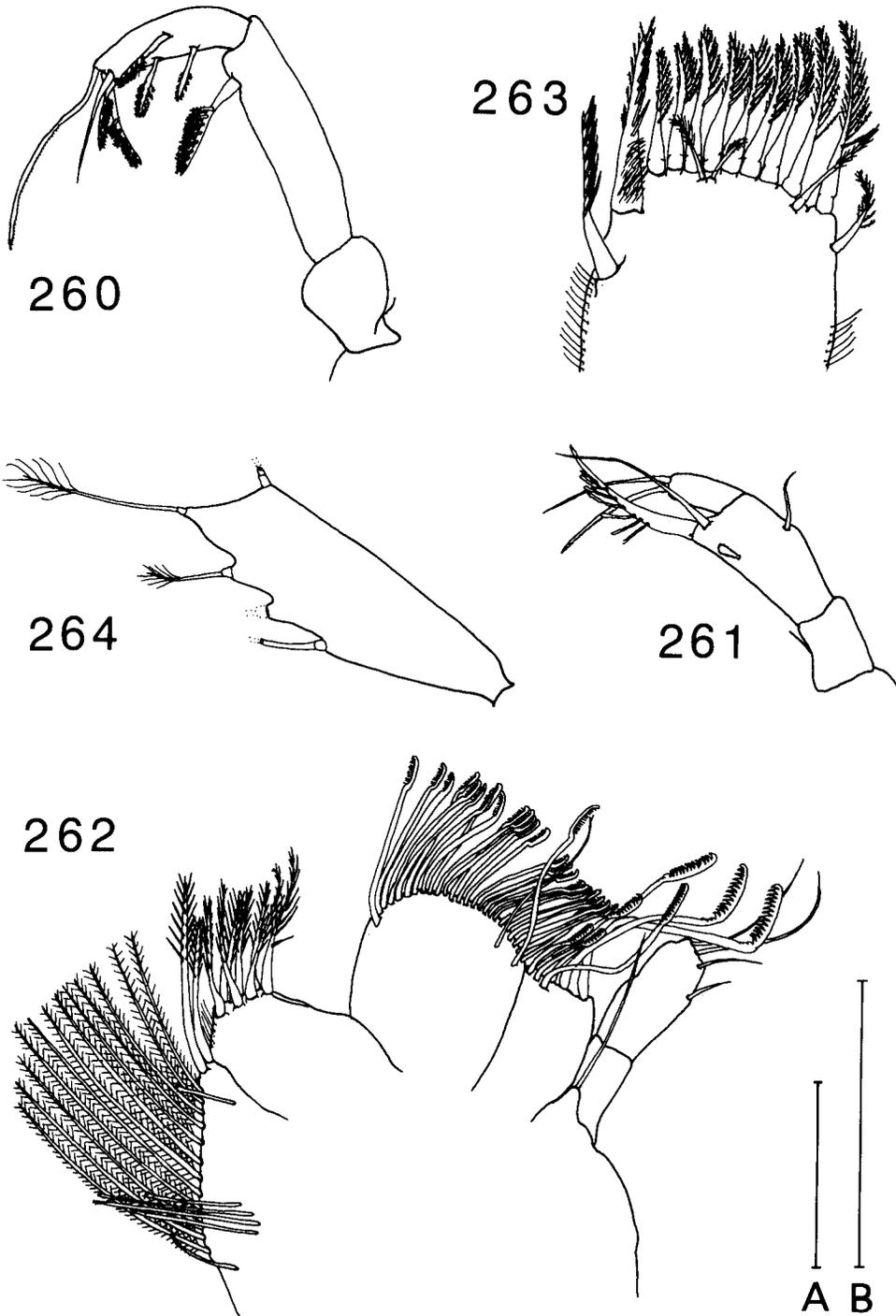
Variability.— In addition to the usual variation in the number of plumose macrosetae of the uropodal rami, remarkable variation is noted in the number of rake-like macrosetae on basipodal endite 3 of maxilla 2. In 50% of all maxillae 2 examined there were 6 rake-like macrosetae present; the other 50% of the maxillae 2 had 7 rake-like macrosetae. This variation was even observed in contralateral appendages of the same individual!

Remarks.— As remarked above *T. tarsiensis* and *T. atlantomaroccana* are closely akin. Distinctive characters between the two species exist in the number of plumid-enticulate macrosetae of segment 2 of the mandibular palp (*T. atlantomaroccana*: 6; *T. tarsiensis*: 5), the number of setules of the unisetulate macroseta on segment 2 of the maxilla 1 (*T. atlantomaroccana*: 4 to 5; *T. tarsiensis*: 5 to 7), the number of rake-like macrosetae of basipodal endite 2 of the maxilla 2 (*T. atlantomaroccana*: 17; *T. tarsiensis*: 25), the number of rake-like macrosetae on basipodal endite 3 of the maxilla 2 (*T. atlantomaroccana*: 7; *T. tarsiensis*: 6 or 7), the lower number of ovate microsetae on the propodus of the pereopods of *T. tarsiensis*, the different number of ovate macrosetae on both dactylus and exopodite, the absence of an additional dorsolateral subplumose macroseta on pleopod 2 in *T. tarsiensis*, the different number of plumose macrosetae on the medial margin of the first segment of the uropodal exopodite (*T. atlantomaroccana*: 5; *T. tarsiensis*: 4), and a different mean width/length ratio of the telson (*T. atlantomaroccana*: 0.98; *T. tarsiensis*: 0.95).

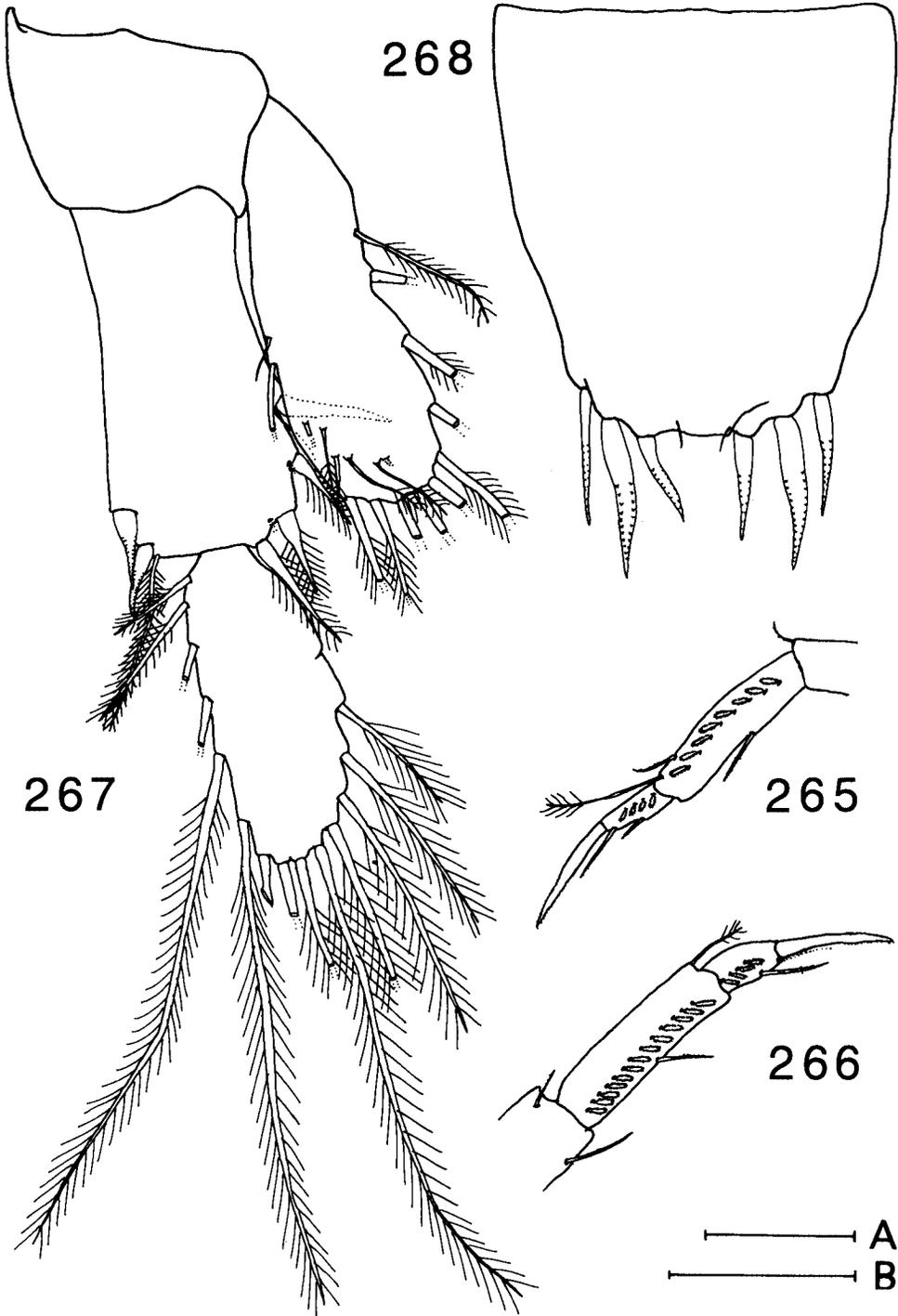
Etymology.— This species is named after the Phoenician empire *Tarsis* (eight and seventh century B.C.), that extended from the mouth of the Guadalquivir to Cape Nao.

Distribution.— *Tethysbaena tarsiensis* seems a rare endemic species of the Guadalquivir drainage in southern Spain.

Habitat.— The well at Los Pajares is located in an alluvial deposit of Pliocene age (Notenboom, 1988a, 1988c). The water can be characterized as limnic (chlorinity 120 mg/l). Accompanying fauna consist of the amphipods *Salentinella angelieri* Ruffo & Delamare Deboutteville, 1952, *Metahadzia uncispina* Notenboom, 1988; the isopods *Microcharon* cf. *marinus* Chappuis & Delamare Deboutteville, 1954, *Stenasellus* spec., *Proasellus* spec.; copepods, ostracods, insects, and gastropods. For the whole Guadalquivir drainage area the following endemics have been reported (updated after Notenboom, 1988b): Amphipoda: *Metahadzia uncispina* Notenboom, 1988, *Parapseudoniphargus baetis* Notenboom, 1988, *Pseudoniphargus latipes* Notenboom, 1987, *P. illustris* Notenboom, 1987, *P. cazorlae* Notenboom, 1987, *P. granadensis* Notenboom, 1987, *P. affinis* Notenboom, 1987; Isopoda: *Stenasellus bragai* Magniez, 1976, *Stenasellus escolai* Magniez, 1977, *Proasellus escolai* Henry & Magniez, 1982, *Proasellus espanoli* Henry & Magniez, 1982; Copepoda, Harpacticoida: *Parapseudoleptomesochra almohadensis*



Figs. 260-264. *Tethysbaena tarsiensis* spec. nov., holotype and paratype ♀. 260, palp mandible, holotype. 261, palp maxilla 1, holotype. 262, maxilla 2, holotype. 263, distal portion of basipodal endite of maxilliped, paratype. (figs. 261-263 scale A). 264, pleopod 2, paratype (scale B). Scales indicated 0.1 mm.



Figs. 265-268. *Tethysbaena tarsiensis* spec. nov., holotype and paratype ♀. 265, distal portion of pereopod 3, holotype. 266, distal portion of pereopod 6, holotype (figs. 265-266 scale A). 267, uropod, paratype. 268, telson, paratype (figs. 267-268 scale B). Scales indicated 0.1 mm

Rouch, 1986, *P. almoravidensis* Rouch, 1986, *P. balnearia* Rouch, 1986. Notenboom's interpretation of *Pseudoniphargus vomeratus* Notenboom, 1987, as endemic of the Guadalquivir drainage area is not shared by me, as in my view the species rather represents an endemic of the upper course of the Río Segura drainage area, a system that underwent an isolated Pliocene Atlantic influence, as figured by Notenboom (1988c: fig. 25).

"*T. texana* -group"

This group of species is characterized by: a 7- to 9-segmented main flagellum of the antenna 1; mandibular palp with eighth plumidenticulate macrosetae on second segment; unisetulate macroseta of third segment of the palp of maxilla 1 well-developed and with six to seven setules; basipodal endite 2 of maxilla 2 with sexually different number of rake-like serrate macrosetae, endopodite of maxilla 2 with four simple macrosetae; maxilliped with eight terminally implanted plumidenticulate macrosetae on basipodite; pereopods 2 to 5 without lateral plumose macrosetae on the second segment of exopodite, number of ovate microsetae on propodus of endopodite of pereopods 2 to 7 sexually different; pleopod 1 with three dorsal subplumose macrosetae; distal margin of uropodal endopodite slightly protruding beyond distal margin of first segment of exopodite; telson somewhat longer than wide, anal lobes not protruding beyond terminal stretch; stretch with one distinct protuberance, glandular simple macrosetae absent on stretch.

4.4.2.17. *Tethysbaena texana* (Maguire, 1965)  
(figs. 269-279)

*Monodella*; Maguire, 1964: 931, fig. 1; Fryer, 1965: 90.

*Monodella texana* Maguire, 1965: 149, figs. 1-3, pl. 3; Green, 1967: 168; Meštrov & Lattinger-Penko, 1969: 112; Reddell, 1970: 397; Kaestner, 1970: 369; Zilch, 1972: 81; Stock, 1976: 56; Karnei, 1978: 38, fig. 15; Holsinger & Longley, 1980: 1; Longley, 1981: 126; Stock & Longley, 1981: 570, figs. 1-21; Abele, 1982: 276; Chelazzi & Messana, 1982: 170; Boutin & Cals, 1985: 267; Stock, 1986a: 587; Schram, 1986: 220; Cals & Monod, 1988: 342; Kroschewsky, 1990: 219; Meštrov & Cals, 1991: 42; Pretus, 1991: 235.

*Monadella* (sic) *texana*; Longley, 1978: 23.

*Monodella* (partim); Wagner, 1990: 123.

Material.— U.S.A., Texas: 7 ♂♂, 17 ♀♀, 2 fragmentary specimens; San Marcos, Hays County, Edwards Aquifer Research and Data Center Aquatic station; from artesian well; collected by G. Longley et al.; diverse data in 1975-1977; ZMA coll. no. C.A. 8033, ZMA coll. no. C.A. 8034 (2 specimens); RMNH G 45.

- 6 ♀♀, 1 fragmentary specimen; Uvalde County, George Ligoocky Farm well no. H-5-158, 29°11'37"N 99°48'38"W; collected by R. C. Wiedenfeld; 14 .iii-9.v.1980; ZMA coll. no. C.A. 8035.

Description.— Body length (antennae 1 and 2 excluded) of male up to 2000 µm, female up to 2474 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with six, three, and two long plumose macrosetae on respective medial margins; main flagellum 7- to 9-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with four simple macrosetae of unequal length

(sub)terminally.

Antenna 2: peduncular segments 4 and 5 with two teazel macrosetae on the medial and mediodistal margin; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: eight plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with six to seven setules, third segment with one well-developed unisetulate macroseta with six setules.

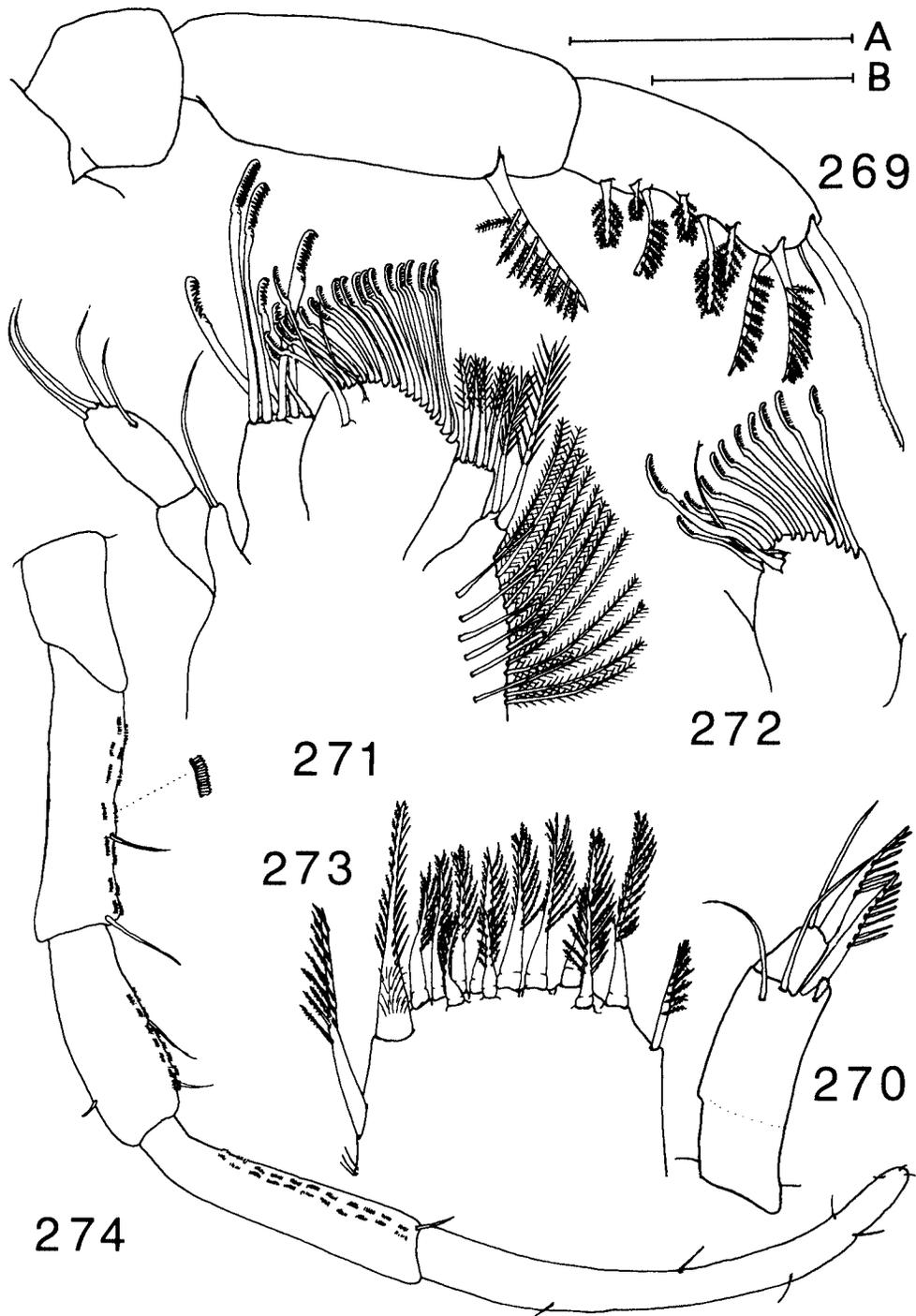
Maxilla 2: basipodal endite 1 with five plumidenticulate macrosetae; basipodal endite 2 with sexually dimorphic number of rake-like serrate macrosetae at terminal margin (female: 10 to 11 in right, 11 in left maxilla 2; male: 18 in right, 19 in left maxilla 2), and two modified longer serrate subterminal macrosetae; basipodal endite 3 with seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three and four macrosetae, respectively; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment from proximal to distal two rows of seven linear patches of rectangularly shaped club microsetae (diameter  $\times$  height up to circa  $0.3 \times 1.25 \mu\text{m}$ ) on the distal portion, third segment from proximal to distal two rows of seven linear patches of rectangularly shaped club microsetae (diameter  $\times$  height up to circa  $0.3 \times 1.25 \mu\text{m}$ ), fourth segment from proximal to distal two rows of 11 linear patches of rectangularly shaped club microsetae (diameter  $\times$  height up to circa  $0.3 \times 1.25 \mu\text{m}$ ); basipodal endite bearing 13 plumidenticulate macrosetae with long setules, a small one medially, eight long ones terminally, three shorter ones subterminally, and one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal and one subterminal plumose macrosetae.

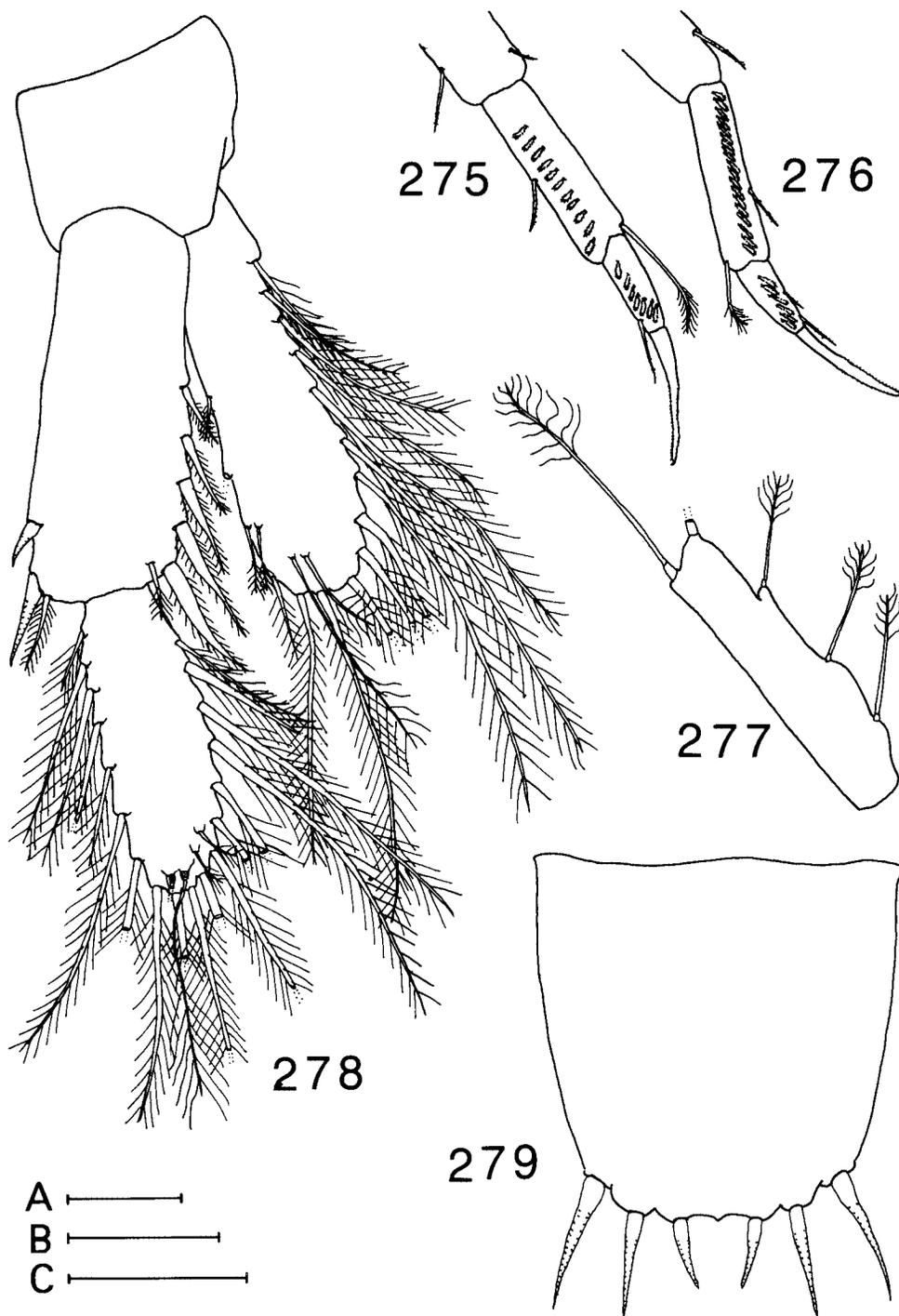
Gnathopod: basal segment with three plumose macrosetae; exopodite with two medial, two subterminal and two terminal, plumose macrosetae, two vestigial macrosetae on the lateral margin; baso-ischium of endopodite with obscurely demarcated "free" ischium, propodus with two fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with one teazel macroseta medially on ventral margin, male with five ovate microsetae, female with five to six ovate microsetae, dactylus with one teazel macroseta on ventral margin and three rows of two, two, and six ovate microsetae, respectively; first segment of exopodite with one ovate microseta, second segment with three medial, two subterminal and two terminal plumose macrosetae, lateral armature lacking.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with nine ovate microsetae, female with 10 to 11 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and five ovate microsetae, respectively; first segment of exopodite with two ovate microsetae, second segment



Figs. 269-274. *Tethysbaena texana* (Maguire, 1965), ♂ and ♀. 269, palp mandible, ♀. 270, palp maxilla 1, ♀. 271, maxilla 2, ♂. 272, maxilla 2, ♀. 273, distal portion of basipodal endite of maxilliped, ♀. (figs. 269-273 scale A). 274, endopodite of maxilliped, ♂. (scale B). Scales indicated 0.1 mm.



Figs. 275-279. *Tethysbaena texana* (Maguire, 1965), ♀. 275, distal portion of pereopod 3. 276, distal portion of pereopod 6 (figs. 275-276 scale A). 277, pleopod 2 (scale C). 278, uropod. 279, telson (figs. 278-279 scale B). Scales indicated 0.1 mm.

with three medial, two subterminal and two terminal plumose macrosetae, lateral armature lacking.

Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 12 ovate microsetae, female with 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and seven to eight ovate microsetae; first segment of exopodite with five ovate microsetae, second segment with three medial, two subterminal and two terminal plumose macrosetae, lateral armature lacking.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 15 ovate microsetae, female with 15 to 16 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and seven to eight ovate microsetae; first segment of exopodite with six to seven ovate microsetae, second segment with two medial, one subterminal and two terminal plumose macrosetae, lateral armature lacking.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, male with 18 to 19 ovate microsetae, female with 19 to 20 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and six to eight ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and five ovate microsetae.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 19 to 20 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and five to six ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and four ovate microsetae.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 18 plumose macrosetae; endopodite bearing 13 to 16 plumose macrosetae.

Telson: somewhat longer than wide, mean width/length ratio 0.97; anal lobes not protruding beyond terminal stretch; stretch with distinct central protuberance.

Variability.— A slight variation exists in the number of plumose macrosetae of the uropodal exopodite. In one female an aberrant second pereiopod was present with two instead of one terminally implanted serrulate macrosetae (see also Stock & Longley, 1981: 574, fig. 17).

Remarks.— With the redescription by Stock and Longley (1981) many questionable observations by Maguire (1965) were clarified, but these authors overlooked one very peculiar feature of this species, viz., male and female have a different number of rake-like macrosetae on the basipodal endite 2 of the maxilla 2. The materials examined by Stock & Longley formed the majority of the material at my disposal, and the maxillae 2 of their slides showed indeed the sexual dimorphism noted above. This species shows great resemblance to *T. vinabayesi* spec. nov., but can be distinguished

instantly by the lower number of protuberances at the distal stretch of the telson (*T. texana*: 1; *T. vinabayesi*: 3) and the presence of a well-developed unisetulate macroseta on segment 3 of the palp of maxilla 1. More details to distinguish *T. texana* from *T. vinabayesi* are discussed below under the latter species. Further resemblance exists to members of the "*T. argentarii* -group" in the shape of the telson, except for the absence of glandular macrosetae, the presence of a well-developed unisetulate macroseta on segment 3 of the palp of maxilla 1, and the absence of lateral plumose macrosetae on the pereopodal exopodites in *T. texana*, are three major differences that put this species apart.

Distribution.— The species has been reported from the Edwards Aquifer (Texas): Ezells Cave at San Marcos (type-locality) (Maguire, 1964, 1965), Verstraeten Well No. 1 in Bexar County and City Water Board Artesian Pump Station Well in Bexar County (Karnei, 1978), Artesian Well of the Southwest Texas State University Aquatic Station at San Marcos (Longley, 1978), and the George Ligocky Farm Well No. H-5-158 in Uvalde County (Stock & Longley, 1981).

Habitat.— Thus far *Tethysbaena texana* has been captured in small quantities in the Artesian zone of the Edwards Aquifer. This aquifer is named for the geological formation and associated limestones, which are of Cretaceous age (Kroschewsky, 1990). The subterranean water plain, and subsequently its fauna, is of younger age (Kroschewsky, pers. comm.). Since *T. texana* shows such a large distribution throughout the whole Edwards Aquifer it can be expected to be found together with a large variety of other troglobites. In total the fauna of the Edwards Aquifer consists of at least 35 to 40 troglobitic invertebrate and vertebrate species (for species lists see Reddell, 1970; Longley, 1981; Kroschewsky, 1990), of which several new species have been described in the past decade (Holsinger & Longley, 1980; Hershler & Longley, 1986a; 1986b; 1987a; 1987b; Bowman, 1992). Information on the accompanying fauna procured while capturing the specimens examined is not available to me. Together with the type material of *T. texana*, Maguire (1965) only mentions the capture of copepods. The water is characterized as "fresh and cool" (limnic) by Maguire (1965).

#### "*T. vinabayesi* -group"

This group of species is characterized by: a 7- to 8-segmented main flagellum of the antenna 1; a mandibular palp with six plumidenticulate macrosetae on the second segment; an obscure unisetulate macroseta of third segment of the palp of maxilla 1; endopodite of maxilla 2 with six simple macrosetae; maxilliped with seven to eight terminally implanted plumidenticulate macrosetae on basipodite; pereopods 2 to 5 with one lateral plumose macroseta on the second segment of exopodite, number of ovate microsetae on propodus of endopodite of pereopods 2 to 7 sexually different; pleopod 1 with four dorsal subplumose macrosetae; distal margin of uropodal endopodite slightly protruding beyond distal margin of first segment of exopodite; telson somewhat longer than wide, anal lobes not protruding beyond terminal stretch; stretch with three distinct protuberances, central protuberance flanked at either side by a glandular simple macroseta.

4.4.2.18. *Tethysbaena vinabayesi* spec. nov.  
(figs. 280-291)

*Monodella* sp.; (Orghidan), 1977: frontpage and photo 6.

Thermosbaenacea (partim); Orghidan & Nuñez Jimenez, 1977: 12; Stock, 1981b: 34; Stock, 1983b: 235; Broodbakker, 1984b: 41.

Thermosbaenacés; Orghidan, Negrea & Viña Bayes, 1977: 17.

Thermosbaenacea; Juberthie, Delamare Deboutteville, Viña Bayes & Aminot, 1977: 44; Decou, 1981: 11.

Thermosbaenaceans (partim); Stock, 1983a: 277.

*Monodella* (partim), Wagner, 1990: 123.

Material.— Cuba, Isla de Juventud (= Isla de Pinos): 6 ♂♂, 29 ♀♀ (6 with broodpouch), 3 fragmentary specimens; Cuban-Dutch Biospeleological Exped. sta. 89/027, Cueva de Agua, near Nueva Gerona, Sierra de Casas; in lake at end of deep siphon, in fine mud and guano with vegetable detritus at bottom of lake, water table at 20 m, water depth to 3.5 m, temperature 26.9°C, electric conductivity 720 µS/cm, Cvetkov net; collected by H.P. Wagner and N. Viña Bayes; 23.v.1989; ZMA coll. no. C.A. 8157 [holotype], ZMA coll. no. C.A. 8158; COBEC; RMNH G 56 [all paratypes].

Accompanying fauna: Crustacea: Ostracoda, Copepoda; Oligochaeta.

Description.— Body length (antennae 1 and 2 excluded) of male up to 2513 µm (holotype 2365 µm), of female up to 2539 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with four, three, and two long plumose macrosetae on respective medial margins; main flagellum 7- to 8-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with five teazel macrosetae on the medial and mediodistal margin; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: six plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with six to seven setules, third segment with one obscurely unisetulate macroseta.

Maxilla 2: basipodal endite 1 with five plumidenticulate macrosetae; basipodal endite 2 with 13 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing six simple macrosetae.

Maxilliped: first segment of male endopodite with three patches of tall and pointed club microsetae (diameter × height up to circa 0.3 × 4.25 µm) distolaterally, second segment without club microsetae, third segment with two rows of two and four (more dorsally) patches of tall and pointed club microsetae (diameter × height up to circa 0.3 × 4.25 µm), fourth segment without club microsetae; basipodal endite bear-

ing 13 to 14 plumidenticulate macrosetae with long setules, a tall one medially, seven to eight long ones terminally, three shorter ones subterminally, and one or two sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, one subterminal and one medial plumose macrosetae.

Gnathopod: basal segment with one plumose macroseta; exopodite with two medial, two subterminal and two terminal, plumose macrosetae, and two vestigial macrosetae on the lateral margin; baso-ischium of endopodite with indistinct ischium, propodus with two fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with one teazel macroseta medially on ventral margin, male with seven ovate microsetae, female with seven to nine ovate microsetae, dactylus with one teazel macroseta on ventral margin and two rows of three and four ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: propodus of endopodite with one teazel macroseta medially on ventral margin, male with 11 ovate microsetae, female with 12 to 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two "rows" of one and six ovate microsetae, respectively; first segment of exopodite with three ovate microseta, second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, both male and female with 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two "rows" of one and six ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 13 ovate microsetae, female with 13 to 14 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and five to six ovate microsetae; first segment of exopodite with four to five ovate microsetae, second segment with one medial, one subterminal and two terminal plumose macrosetae, and one vestigial lateral macroseta.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, male with 14 to 15 ovate microsetae, female with 15 to 16 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three to four ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and three ovate microsetae.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, both male and female with 15 to 16 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and three ovate microsetae.

First pleopod with four dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of three cuspidate macrosetae and two plumose macrosetae, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 15 to 17 plumose macrosetae; endopodite bearing 11 to 13 plumose macrosetae.

Telson: somewhat longer than wide, mean width/length ratio 0.97; anal lobes not protruding beyond terminal stretch; stretch with three distinct pointed central protuberances, the central one flanked at either side by a glandular simple macroseta (type IIA1).

Variability.— Apart from the slight variability of the plumose macrosetae on the uropodal rami, slight fluctuation in the number of plumidenticulate macrosetae on the basipodal endite of the maxilliped was noted (13 to 14, the large stouter plumidenticulate macroseta excluded).

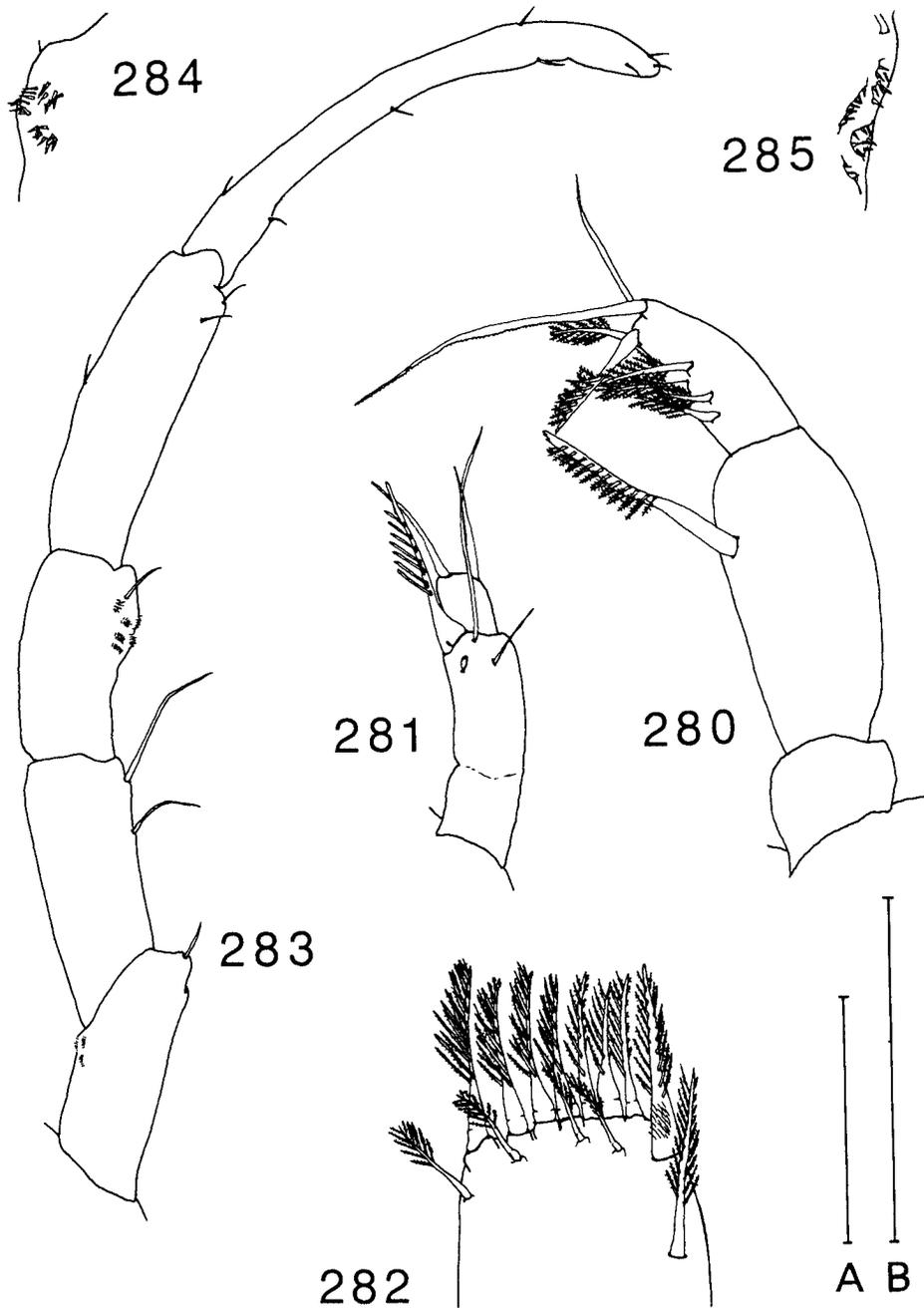
Remarks.— As remarked above *T. texana* shows a close morphological resemblance to *T. vinabayesi*. Except for the larger number of protuberances on the terminal stretch of the telson, the presence of an obscurely unisetulate macroseta on segment 3 of the palp of maxilla 1, and the absence of sexual dimorphism in the number of plumidenticulate macrosetae on the basipodal endite of the maxilliped, more differentiating character states can be noted in the number of plumidenticulate macrosetae on segment 2 of the mandibular palp (*T. texana*: 8; *T. vinabayesi*: 6), armature of the endopodite of the male maxilliped, presence of lateral plumose macrosetae on the pereopodal exopodites, the (sometimes slightly) different number of ovate microsetae on propodus, dactylus, and exopodites of the pereopods, the number of dorsal subplumose macrosetae on the pleopod 1 (*T. texana*: 3; *T. vinabayesi*: 4), the number of cuspidate macrosetae on segment 1 of the uropodal exopodite (*T. texana*: 5; *T. vinabayesi*: 3), the lower number of plumose macrosetae on both uropodal rami in *T. vinabayesi*, and the presence of two glandular macrosetae on the terminal stretch of the telson of *T. vinabayesi* (absent in *T. texana*). The only other species that shows some resemblance to *T. vinabayesi* in telson shape is *T. aiakos* spec. nov., also with three protuberances on the terminal stretch, but for the rest is quite distinct in several other specific characters. The lateral protuberances on the terminal stretch of *T. aiakos*, however, are not pointed, but small lobelike swellings; the three pointed protuberances on the terminal stretch prove to be a unique character to distinguish this species from all its congeners.

Etymology.— I have much pleasure to name this new species after Dr Nicasio Viña Bayes (Centro Oriental de Biodiversidad y Ecosistemas, Santiago de Cuba, Cuba), who was my counterpart during the Cuban-Dutch Biospeleological Expedition.

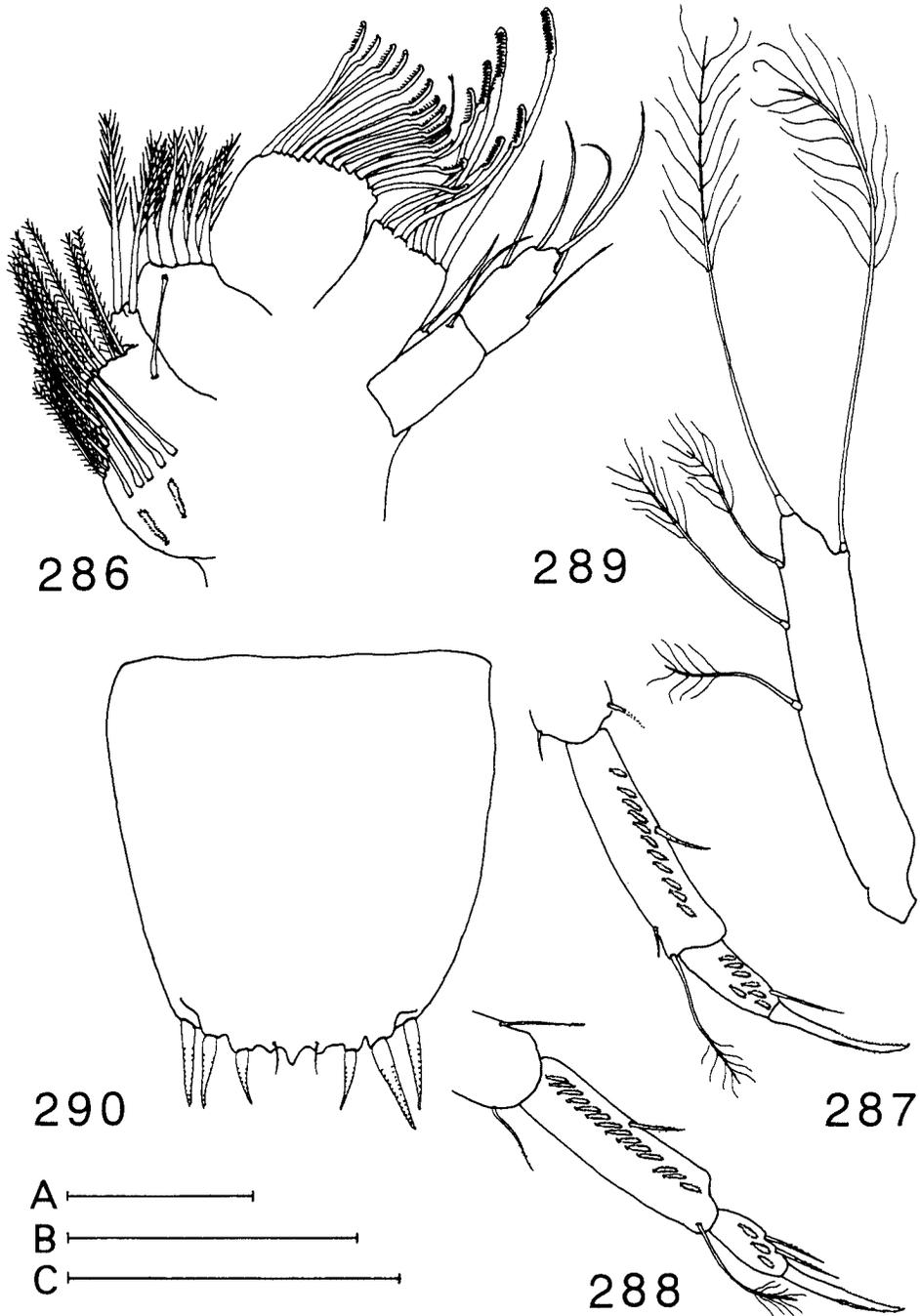
Distribution.— Thus far *T. vinabayesi* has been found in one Cuban locality only, the Cueva de Agua, near Nueva Gerona, Isla de Juventud (= Isla de Pinos).

Habitat.— The cave is located in the karstic area in the north of the island, and is of Pliocene age (Weyl, 1966; Nuñez Jiménez et al., 1972). The cave itself is very humid, the water temperature reached 26.9°C at an aerial temperature of 26.0°C.

When the second Cuban-Romanian Expedition visited the Cueva de Agua, an



Figs. 280-285. *Tethysbaena vinabayesi* spec. nov., holotype ♂. 280, palp mandible, ♂. 281, palp maxilla 1, ♂. 282, distal portion of basipodal endite of maxilliped, ♂ (figs. 280-282 scale B). 283, endopodite of maxilliped, ♂ (scale A). 284, detail microsetae at distal portion of endopodite segment 1 of maxilliped (extremely enlarged), ♂. 285, detail microsetae at distal portion of endopodite segment 3 of maxilliped (extremely enlarged), ♂. Scales indicated 0.1 mm.



Figs. 286-290. *Tethysbaena vinabayesi* spec. nov., holotype ♂. 286, maxilla 2 (scale C). 287, distal portion of pereopod 3. 288, distal portion of pereopod 6. 289, pleopod 2 (scale B). 290, telson (figs. 287-288 and 290 scale A). Scales indicated 0.1 mm.

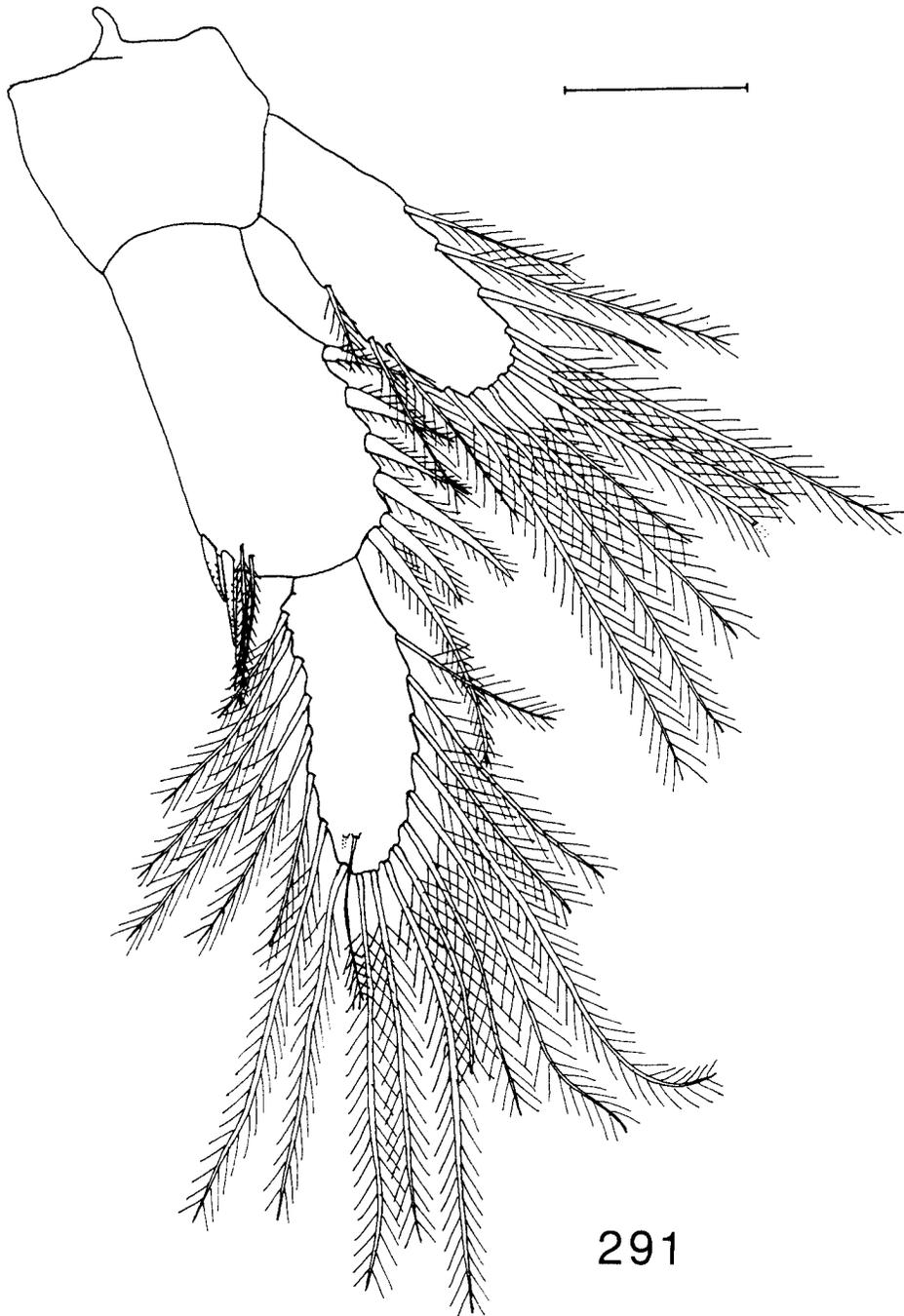


Fig. 291. *Tethysbaena vinabayesi* spec. nov., uropod, paratype  $\delta$ . Scale indicated 0.1 mm.

immense population of thermosbaenaceans was encountered (Orghidan et al., 1977; Juberthie et al., 1977; Decou, 1981). Also the bat *Nyctiellus* (= *Natalus lepidus* (Gervais, 1837)?) was abundantly present (Viña Bayes, pers. comm.). When the Cuban-Dutch Biospeleological Expedition visited the cave, no bats were observed, and the lake was polluted with bottles, plastic, and even a car-battery was observed in the water. According to Mr Augusto Martinez (president of the Speleological Society of Isla de Juventud) the bats were gone for some time, and the amount of guano at the bottom of the lake was distinctly less than before. Therefore it was no surprise that visually no animal life was observed. The stygobionts presumably had retreated deeper (inaccessible) into the groundwater plain. Fortunately, after our intensive sampling some animals have been encountered in the guano sampled at the bottom of the lake. The accompanying fauna collected by the Cuban-Dutch Biospeleological Expedition consisted of Ostracoda, Copepoda, and Oligochaeta. Orghidan et al., 1977, also reported the occurrence of Cladocera (Crustacea), Copepoda (Crustacea), Diptera (Insecta), Coleoptera (Insecta), and *Typosyllis* sp. (Polychaeta). The water can be characterized as limnic. As all the specimens of *T. vinabayesi* were found in the guano sample only, it is most likely a benthic species.

“*T. argentarii*-group”

This group of species is characterized by: a 9- to 12-segmented main flagellum of the antenna 1; a mandibular palp without a fixed number of plumidenticulate macrosetae on the second segment; second segment of endopodite of maxilla 1 with one simple macroseta; endopodite of maxilla 2 with four to six simple macrosetae; maxilliped with eight or more terminally implanted plumidenticulate macrosetae on basipodite; pereopods 2 to 5 with none, one or two lateral plumose macrosetae on the second segment of exopodite; number of ovate microsetae on propodus of endopodite of pereopods 2 to 7 sexually different; pleopod 1 with three dorsal subplumose macrosetae; distal margin of uropodal endopodite not protruding beyond distal margin of first segment of exopodite; telson somewhat longer than wide, anal lobes not protruding beyond terminal stretch; stretch with distinct central protuberance, flanked at either side by one glandular simple macroseta.

4.4.2.19. *Tethysbaena argentarii* (Stella, 1951)  
(figs. 292-301)

*Monodella argentarii* Stella, 1951a: 2, figs. 1-21; Stella, 1951b: 227, figs. 1-4; Stella, 1953: 226, figs. 1-9; S.L. Karaman, 1953: 57; Stella & Baschieri Salvadori, 1954: 441, 467, pl. 1 fig. 2; Taramelli, 1954: 10, 12; Stella, 1955: 464; Siewing, 1958: 197; Stella, 1959: 121, figs. 1-6, pls. 1-2; Barker, 1959: 209; Monod, 1960: 528; Delamare Deboutteville, 1960: 248, 630, figs. 91d, 92d; Barker, 1960: 253; Pór, 1963: 49; Gordon, 1964: 153 figs. 1B-B'; Vandell, 1964: 144; Maguire, 1965: 149; Fryer, 1965: 49, figs. 1-22; Straškraba, 1967: 193; Green, 1967: 168; Meštrov & Lattinger-Penko, 1969: 112; Kaestner, 1970: 369; Zilch, 1972: 81, fig. 1b; Sieg, 1983a: 36; Sieg, 1984: 27; Pesce, 1985: 131, 144; Stock, 1986a: 587; Schram, 1986: 219; Meštrov & Cals, 1991: 42; Pretus, 1991: 235, figs. 3.11e, 3.11g; Casanova, 1993: 145, figs. 1a-c.

*Monodella argentarii* (partim); Rouch, 1965: 726; Stock, 1976: 56; Pinkster, 1978: 234; Abele, 1982: 276; Chelazzi & Messana, 1982: 170; Stock, 1986a: 588; Schram, 1986: 221; Cals & Monod, 1988: 342.

*Monodella* (partim); Wagner, 1990: 123.

**Material.**— **Italy:** 1 ♂, 2 ♀♀; Prov. Toscana, Grotta di Monte Argentario; collected by E. Stella; ZMA coll. no. C.A. 8004 [topotypes].

- 2 ♀♀; same locality; collected by R. Zilch; viii.1969; ZMA coll. no. C.A. 8102 (1 specimen) [topotypes].

- 5 ♀♀; same locality; 1971; collection Cl. Delamare Deboutteville; MP Th. 30 to MP Th. 32 (set of 13 slides with wholemounts and partially dissected specimens) [topotypes].

**Description.**— Body length (antennae 1 and 2 excluded) of male up to 2000 µm, of female up to 3364 µm in the material studied.

**Antenna 1:** peduncular segments 1 to 3 with five, five, and two long plumose macrosetae on respective medial margins; main flagellum 10-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with four simple macrosetae of unequal length (sub)terminally.

**Antenna 2:** peduncular segments 4 and 5 with four teazel macrosetae on the medial and mediiodistal margin; flagellum 5- to 6-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

**Labrum:** without peculiarities.

**Mandible:** nine plumidenticulate macrosetae on third segment of palp.

**Labium:** without peculiarities.

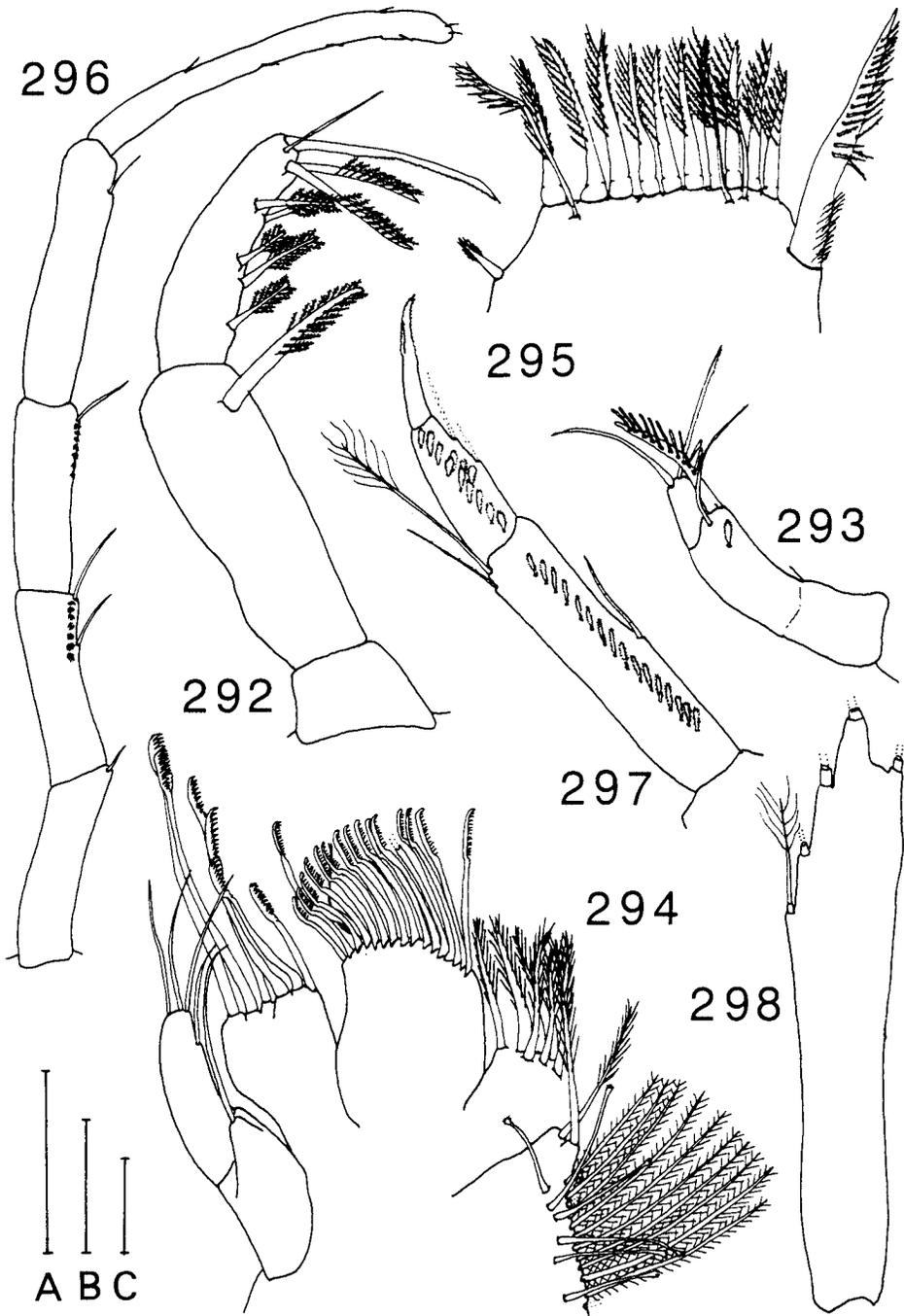
**Maxilla 1:** endopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with 10 to 11 setules, third segment with one obscurely unisetulate macroseta.

**Maxilla 2:** basipodal endite 1 with six plumidenticulate macrosetae; basipodal endite 2 with 16 to 17 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing six simple macrosetae.

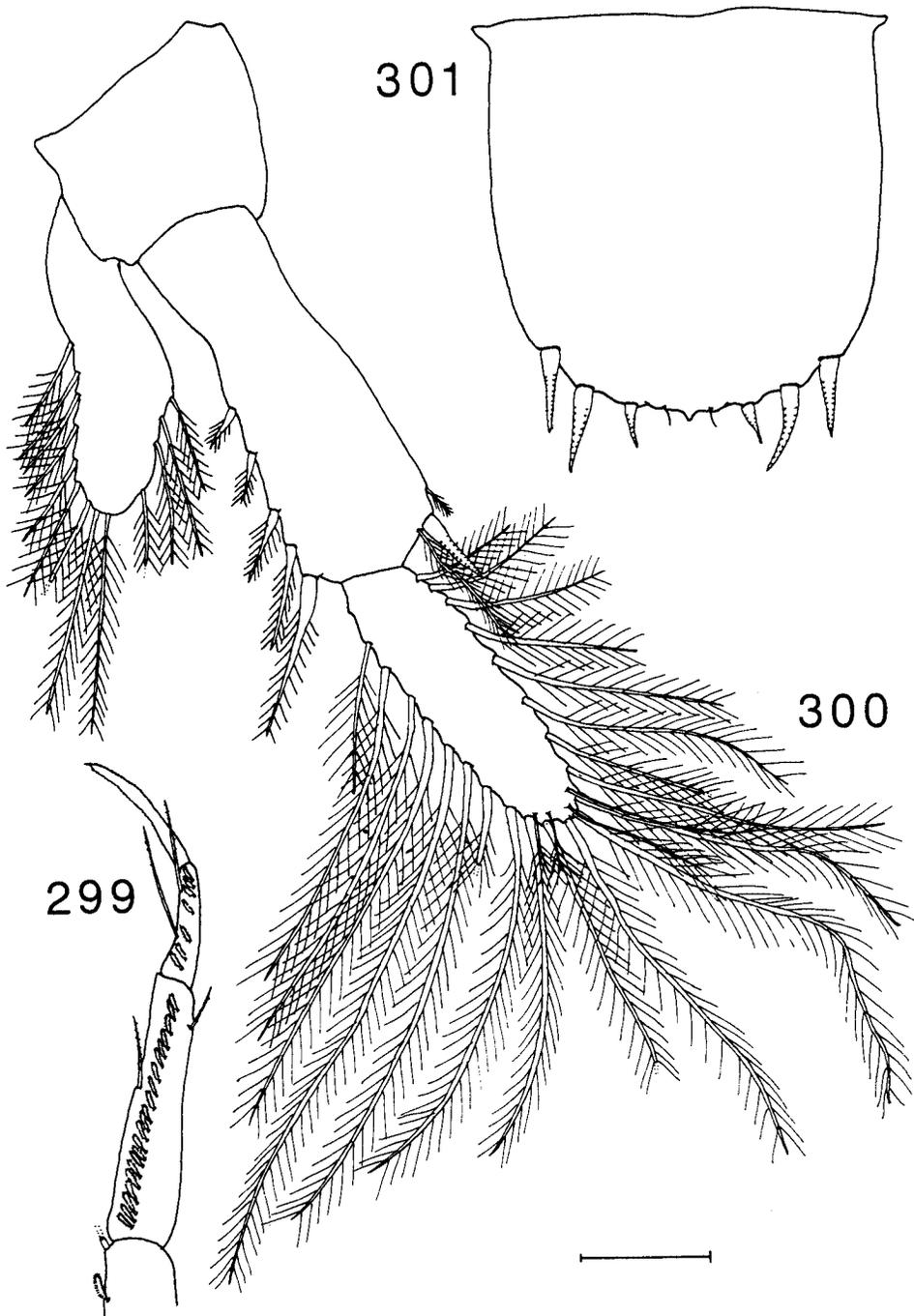
**Maxilliped:** first segment of male endopodite without patches of club microsetae, second segment with seven patches of tall pointed club microsetae (diameter × height up to circa 0.5 × 2.5 µm) on the distal portion, third segment with seven patches of tall pointed club microsetae (diameter × height up to circa 0.5 × 2.5 µm), fourth segment without patches of club microsetae; basipodal endite bearing 12 to 14 plumidenticulate macrosetae with long setules, none medially, eight to ten long ones terminally, three shorter ones subterminally, and one or two sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, two subterminal and one medial plumose macrosetae.

**Gnathopod:** basal segment with up to three plumose macrosetae; exopodite with three medial, two subterminal, two terminal and two lateral plumose macrosetae; baso-ischium of endopodite with obscurely demarcated “free” ischium, propodus with two fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

**Pereiopod 2:** ischiomerus of endopodite with one ovate microseta mediadorsally



Figs. 292-298. *Tethysbaena argentarii* (Stella, 1951), ♂ and ♀. 292, palp mandible, ♀. 293, palp maxilla 1, ♀. 294, maxilla 2, ♀. 295, distal portion of basipodal endite of maxilliped, ♀. 296, endopodite of maxilliped, ♂ (scale C). 297, distal portion of pereopod 3, ♀ (scale B). 298, pleopod 2, ♂ (figs. 292 - 295 and 298 scale A). Scales indicated 0.1 mm.



Figs. 299-301. *Tethysbaena argentarii* (Stella, 1951), ♀. 299, distal portion of pereopod 6. 300, uropod. 301, telson. Scale indicated 0.1 mm.

implanted, propodus with two teazel macrosetae medially on ventral margin, male with 13 ovate microsetae, female with 14 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of three and ten ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 13 ovate microsetae, female with 16 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of three and nine ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 13 to 14 ovate microsetae, female with 17 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of three and eight ovate microsetae, respectively; first segment of exopodite with four ovate microsetae, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 14 to 15 ovate microsetae, female with 21 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of three and eight ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 16 ovate microsetae, female with 21 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and seven ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macroseta, two vestigial macrosetae, one terminal and one lateral, and three ovate microsetae.

Pereiopod 7: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 17 ovate microsetae, female with 22 to 23 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and six ovate microsetae; exopodite 1-segmented with one medial and one subterminal plumose macroseta, one vestigial terminal macroseta, and three ovate microsetae.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macroseta.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of one cuspidate macroseta and two plumose macrosetae, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 20 to 22 plumose macrosetae; endopodite bearing 11 to 16 plumose macrosetae.

Telson: somewhat longer than wide, mean width/length ratio 0.98; anal lobes not protruding beyond terminal stretch; stretch with distinct central protuberance, flanked at either side by one glandular simple macroseta.

Variability.— Slight variation was observed in the number of flagellum segments of antenna 1, the number of setules on segment 2 of maxilla 1, the number of rake-like macrosetae of basipodal endite 2 of maxilla 2, the number of terminal plumidenticulate macrosetae on the basipodite of the maxilliped, and the number of plumose macrosetae on the uropodal rami.

Remarks.— Actually the five species of the “*T. argentarii*-group” fall apart into two sub-groups. With the aid of the SEM, or after staining the cuticula with Black Chlorazol B, one can reveal the presence or absence of scutellated scales on the body. In *Tethysbaena argentarii* (Stella, 1951a), *T. halophila* (S.L. Karaman, 1953), and *T. aiakos* spec. nov., scutellated scales are absent. In *T. scabra* (Pretus, 1991) and *T. siracusae* spec. nov. these scales cover the whole body. Rouch (1965) synonymized *T. halophila* with *T. argentarii*, and also considered specimens from the Peleponnesos (Greece) identical, having overlooked some subtle but important differences. There are, however, differences in the number of plumidenticulate macrosetae on segment 2 of the mandibular palp, the number of setules on the unisetulate macroseta of the palp of maxilla 1, the absence of a plumidenticulate macroseta on the medial margin of the maxilliped in *T. argentarii* (present in *T. halophila* and *T. aiakos*), the rugosities present on the endopodite of the male maxilliped, the (slightly different) number of ovate microsetae on the pereopods, and the mean width/length ratio of the telson. For detailed information on specific differences of the members of this species-group one is referred to table 2 (p. 202).

Distribution.— So far this species was collected only in the lakes in «Punta degli Stretti», Grotta di Monte Argentario, Tuscany Province, Italy.

Habitat.— The lakes in which *T. argentarii* occurs are situated in a karstic cave of Pliocene to Pleistocene age (Ducci & Segre, 1950). The water is oligohaline (based on Fryer, 1965: table 1), but the animals even can survive to some extent euhaline environments under laboratory conditions (Fryer, 1965: 55). During the year the temperature of the lakes varies between 13 and 19°C (Stella, 1951b). Stella & Baschieri Salvadori (1954) published an account of all species found at the cave. The following have been found together with *T. argentarii*: the amphipod *Salentinella denticulata* Baschieri Salvadori, 1952, the ostracods *Notodromas persica* Gurney, 1921, *?Cavernocypris subterranea* (Wolf, 1919), the copepods *Tropocyclops prasinus* (Fischer, 1860), *Paracyclops fimbriatus* (Fischer, 1853), *Diacyclops crassicaudis cosana* Stella & Baschieri Salvadori, 1954 (originally described as variety) *Nitocra lacustris* (Schmankevich, 1875), and the hydroid *Chlorohydra viridissima* (Pallas, 1766). *T. argentarii* is essentially a benthic organism.

Important information on reproduction and development was published by Stella (1955; 1959) and an anatomical study has been done by Taramelli (1954).

#### 4.4.2.20. *Tethysbaena halophila* (S.L. Karaman, 1953) (figs. 302-312)

*Monodella halophila* S.L. Karaman, 1953: 57, 1 pl., figs. 1-24; Stella & Baschieri Salvadori, 1954: 468; Taramelli, 1954: 10; Siewing, 1958: 197, figs. 40D-E; Stella, 1959: 121; Barker, 1960: 209; Monod,

1960: 528, fig. 3; Delamare Deboutteville, 1960: 248, 630, figs. 91c, 92a, 93; Barker, 1960: 253; Pór, 1962: 306; Pór, 1963: 49; Vandel, 1964: 144, fig. 20; Maguire, 1965: 149; Fryer, 1965: 50; Straškraba, 1967: 193; Green, 1967: 168; Hessler, 1969: fig. 183; Meštrov & Lattinger-Penko, 1969: 112; Kaestner, 1970: 367, 369; Zilch, 1972: 81; Sieg, 1983a: 39; Sieg, 1984: 29; Meštrov & Cals, 1991: 42; Pretus, 1991: 235.

*Monodella argentarii* (partim); Rouch, 1965: 726; Stock, 1976: 56; Pinkster, 1978: 234; Abele, 1982: 276; Chelazzi & Messana, 1982: 170; Stock, 1986a: 588; Schram, 1986: 221; Cals & Monod, 1988: 342.

*Monodella argentarii*; Sket, 1986: 327, 329, 330, 334; Sket, 1988a: 66, 69. [non Stella, 1951]

*Monodella* (partim); Botosaneanu & Delamare Deboutteville, 1967: 22; Wagner, 1990: 123.

Thermosbaenacea (partim); Sket et al., 1991: 43.

Material.— **Croatia**: 1 ♂, 1 juvenile; Prov. Dalmatia, Cavtat, Aesculapius cave; collected with the aid of a Cvetkov net in lake; collected by J.H. Stock; 17.vi.1961; ZMA coll. no. C.A. 8005 [topotypes].

- 7 ♂♂, 43 ♀♀ (1 with broodpouch), 6 juveniles; Prov. Dalmatia, Kornati Archipelago, Kukuljar Island; in small cave, at 5 m depth, salinity 35‰; collected by B. Sket; 8.viii.1977; ZMA coll. no. C.A. 8103; RMNH G 52; UEKL.

- 11 ♂♂, 64 ♀♀ (5 with broodpouch), 1 juvenile; Prov. Dalmatia, Korcula Island, Vrbovica; in well, salinity 18‰; vii.1975; ZMA coll. no. C.A. 8104; RMNH G 53; UEKL.

Description.— Body length (antennae 1 and 2 excluded) of male up to 2951 µm, of female up to 3645 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with four, five, and two long plumose macrosetae on respective medial margins; main flagellum 9-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segment 4 with three, and segment 5 with four teazel macrosetae on the medial and mediiodistal margin; flagellum 5- to 6-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

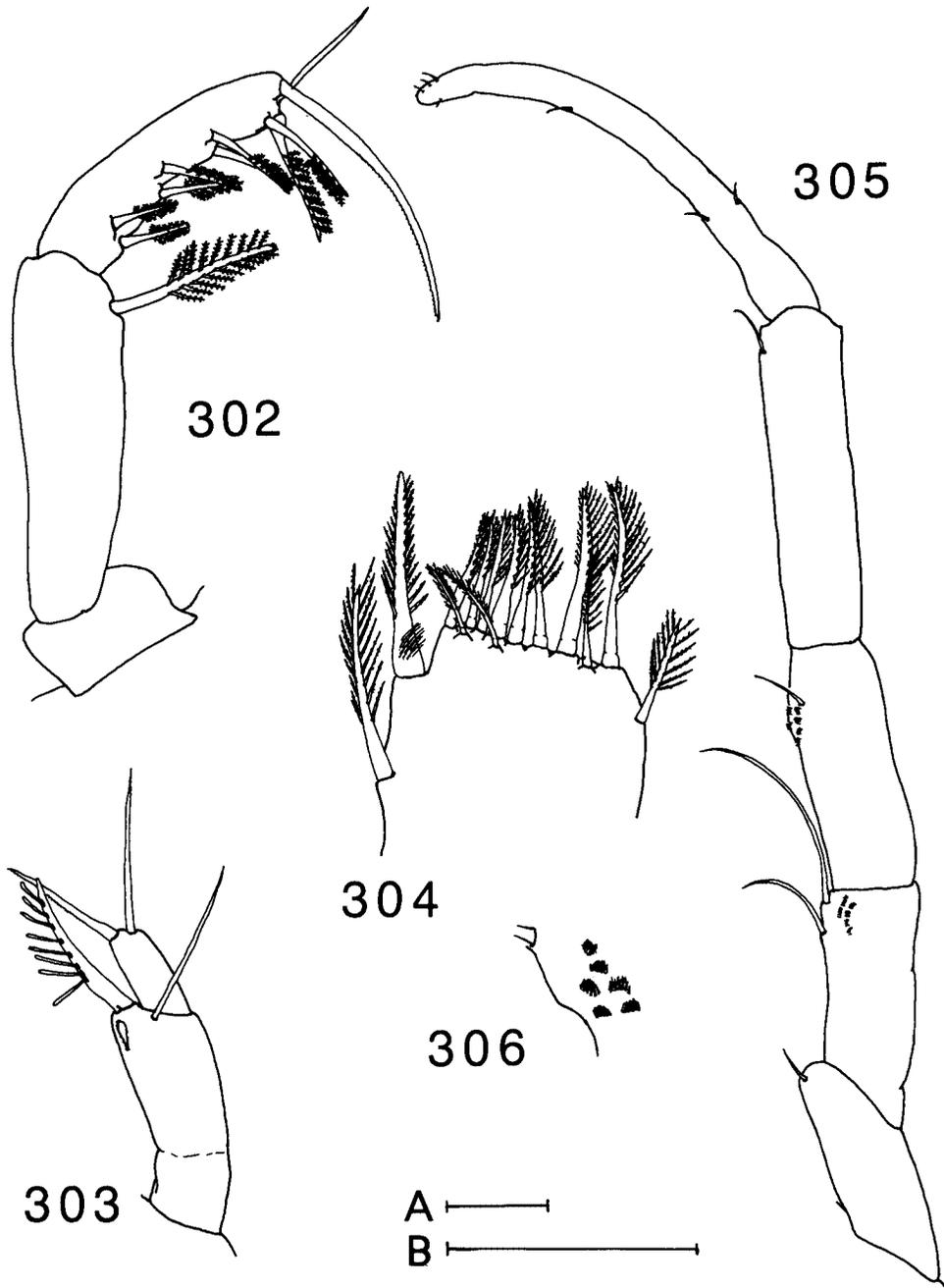
Mandible: eight plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

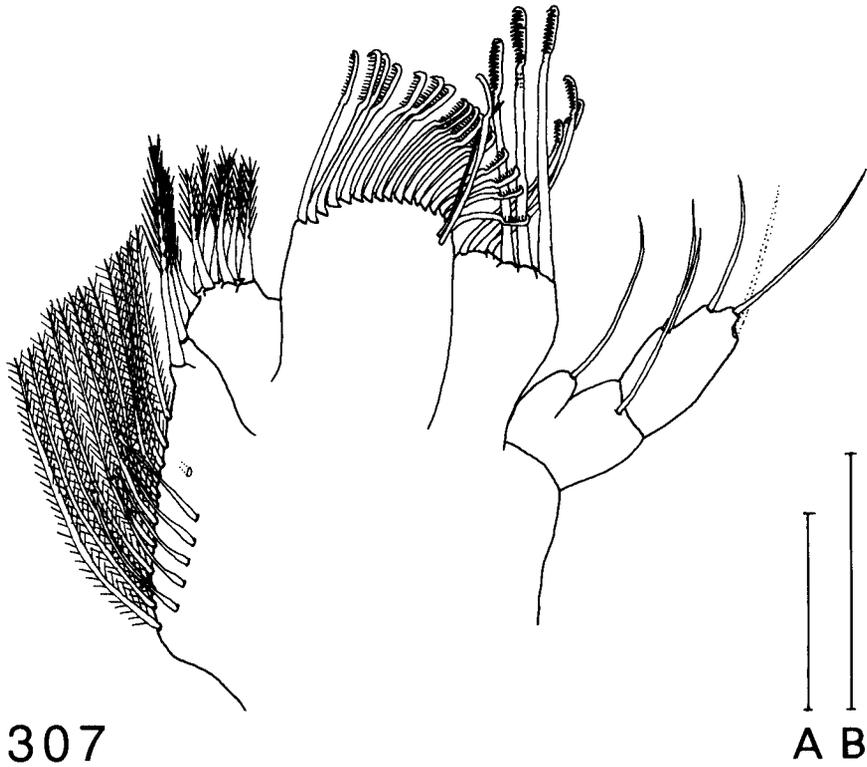
Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with seven to eight setules, third segment with one obscurely unisetulate macroseta.

Maxilla 2: basipodal endite 1 with six plumidenticulate macrosetae; basipodal endite 2 with 15 (in topotypic material examined) to 17 (in very large individuals from Korcula) rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with seven more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing five simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with two rows of two and four (somewhat more dorsal) patches of tall pointed club microsetae (diameter × height up to circa 0.5 × 3.0 µm) on distal portion, third segment with two rows of two and four (somewhat more dorsal) patches of tall pointed club microsetae (diameter × height up to circa 0.5 × 2.5 µm), fourth segment without patches of club microsetae; basipodal endite bearing 13 plumiden-

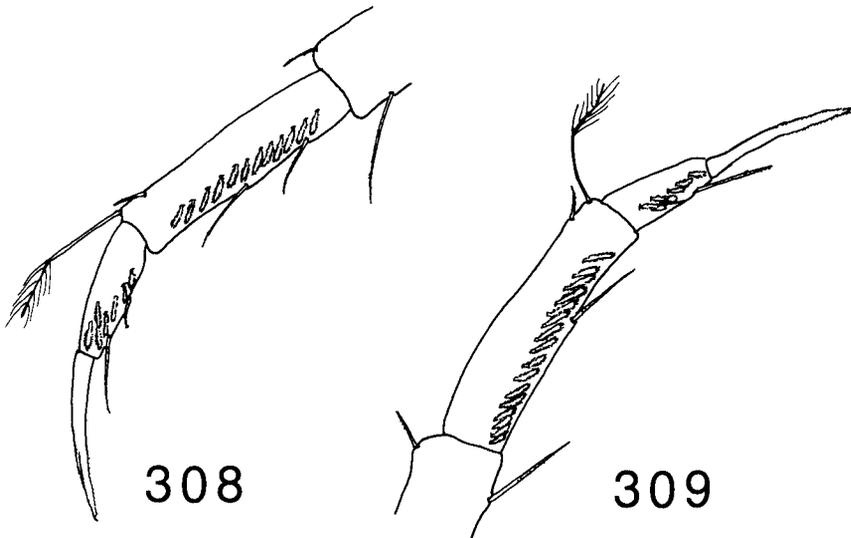


Figs. 302-306. *Tethysbaena halophila* (S.L. Karaman, 1953), ♂. 302, palp mandible. 303, palp maxilla 1, ♂. 304, distal portion of basipodal endite of maxilliped (figs. 302-304 scale B). 305, endopodite of maxilliped (scale A). 306, detail microsetae at distal portion of endopodite segment 3 of maxilliped (extremely enlarged). Scales indicated 0.1 mm.



307

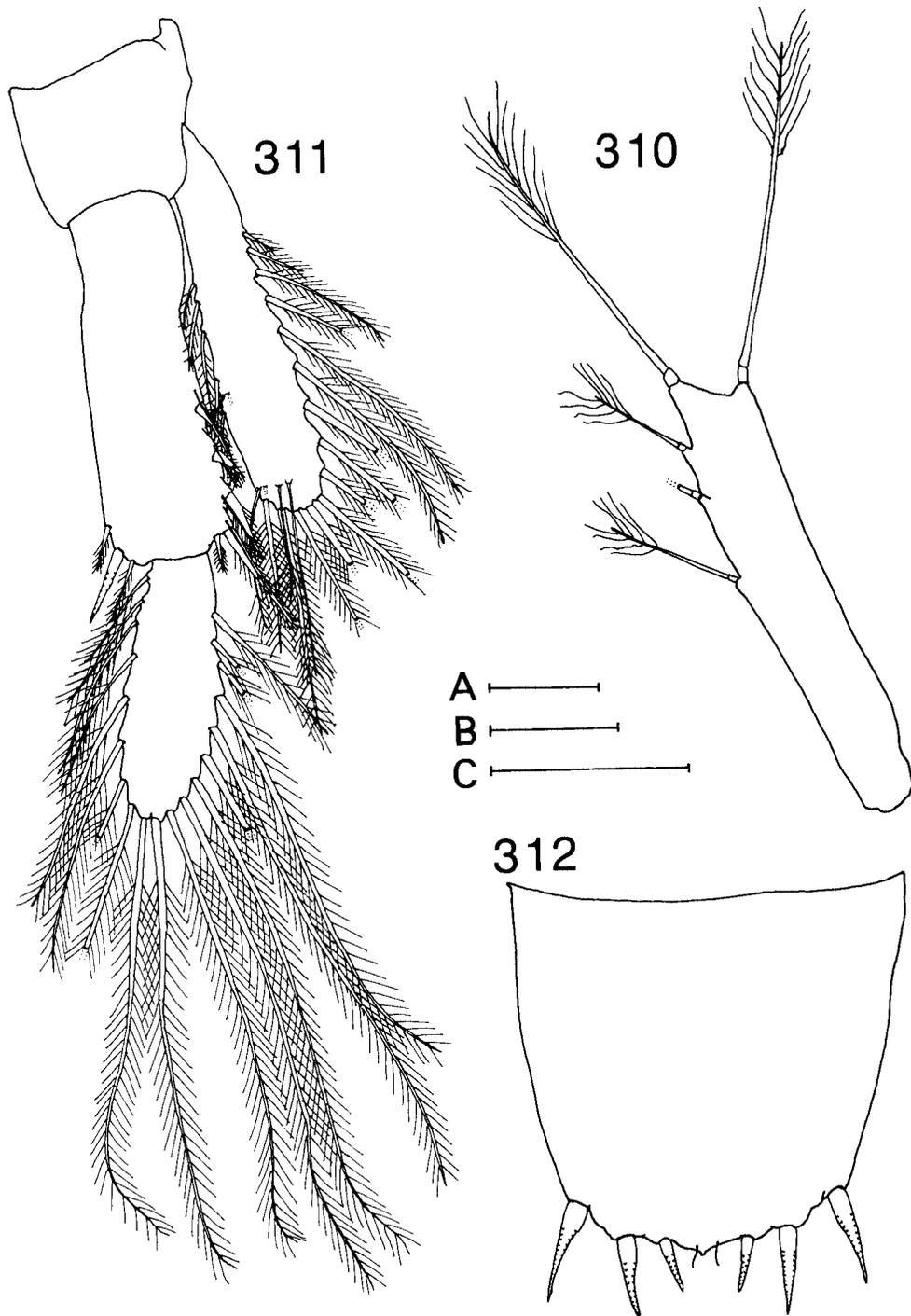
A B



308

309

Figs. 307-309. *Tethysbaena halophila* (S.L. Karaman, 1953), ♂. 307, maxilla 2 (scale B). 308, distal portion of pereopod 3. 309, distal portion of pereopod 6 (figs. 308-309 scale A). Scales indicated 0.1 mm.



Figs. 310-312. *Tethysbaena halophila* (S.L. Karaman, 1953), ♂. 310, pleopod 2 (scale C). 311, uropod (scale A). 312, telson (scale B). Scales indicated 0.1 mm.

ticulate macrosetae with long setules, a tall one medially, eight long ones terminally, three shorter ones subterminally, and one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, two subterminal and one medial plumose macrosetae.

Gnathopod: basal segment with up to three plumose macrosetae; exopodite with three medial, two subterminal, two terminal and two lateral plumose macrosetae; baso-ischium of endopodite with indistinct ischium, propodus with three fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, male with 12 ovate microsetae, female with 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and five ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with two teazel macroseta medially on ventral margin, male with 12 to 13 ovate microsetae, female with 14 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and five ovate microsetae, respectively; first segment of exopodite with three ovate microsetae, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with two teazel macrosetae medially on ventral margin, male with 13 to 15 ovate microsetae, female with 16 to 17 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and five ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 15 to 16 ovate microsetae, female with 20 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and five ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male with 16 ovate microsetae, female with 21 to 22 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and five ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and four ovate microsetae.

Pereiopod 7: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with one teazel macroseta medially on ventral margin, male

with 18 ovate microsetae, female with 24 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and five ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial macrosetae, one terminal and one lateral, and three ovate microsetae.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of one cuspidate macrosetae and two plumose macrosetae, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 19 to 22 plumose macrosetae; endopodite bearing 19 to 21 plumose macrosetae.

Telson: somewhat longer than wide, mean width/length ratio 0.92; anal lobes not protruding beyond terminal stretch; stretch with distinct central protuberance, flanked at either side by one glandular simple macroseta.

Variability.— A remarkable variation exists in the number of rake-like macrosetae on basipodal endite 2 of maxilla 2. In most of the material 17 rake-like macrosetae were observed, but 15 or 16 have been observed in some. The topotypic (immature) male showed 15 rake-like macrosetae, but no further differences could be found between this specimen and the materials from Kukuljar Island and Korcula Island. In general some variation exists in the number of flagellum segments of antenna 1.

Remarks.— Distinctive characters from the other members of the "*T. argentarii*-group" have been mentioned in the discussion of *T. argentarii*. For more information on specific differences with the other members of this species-group one is referred to table 2 (p. 202).

Distribution.— Apart from the type locality, the Aesculapius Cave at Cavtat, near Dubrovnik, the species is also reported from the Kornati Islands (Sket, 1986): Losinj Island, Kornati Island and Zut Island, Kvarner Islands (Sket, 1988a), all on the Adriatic coast of the former Yugoslavia.

Habitat.— The wells and caves on the mainland and the Kvarner Islands where *T. halophila* was found, are located in deposits of Pliocene age. The islands were separated from the continent by the post-pleistocene marine transgression (Sket, 1988a). This species seems to have a preference for environments with apparently quite unfavourable conditions, with a near absence of oxygen and a lot of H<sub>2</sub>S. The salinity of the water varies from 0.5 to 30‰, thus can be characterized as oligohaline to polyhaline. Under polyhaline conditions (salinity 18-30‰) populations are quite dense, but under mesohaline conditions (salinity 5-18‰) *T. halophila* reaches exceptional densities and is the sole inhabitant of this realm with the exception of an occasional amphipod (*Niphargus salonitanus* S.L. Karaman, 1950 and *N. hebereri* Schellenberg, 1933). Under oligohaline conditions (salinity 0.5-5‰) only a few isolated specimens were captured by Sket (1986). In the same paper Sket also gives an account of the fauna accompanying *T. halophila*. In polyhaline waters he mentions copepods from Kukuljar; in oligohaline waters occur dense populations of the amphipods *Hadzia* spec. and *Niphargus* spec., and the copepod *Diacyclops* spec. Less abundant are oligochaetes of the family Enchytraeidae and gastropod molluscs of the genus *Hauffenia*, as well as occasional specimens of the amphipod *Niphargus salonitanus* S.L.

Karaman, 1950, the copepods *Acanthocyclops gordani* Petkovski, 1971 and *Diacyclops bicuspidatus odessanus* (Schmankevich, 1873), the ostracod *Cypria lacustris* G.O. Sars, 1890, the isopod *Proasellus coxalis* (Dollfus, 1892) (= subspecies *lucifugus* (Deeleman-Reinhold, 1965)?) and the oligochaete *Trichodrilus* spec.

4.4.2.21. *Tethysbaena aiakos* spec. nov.  
(figs. 313-323)

*Monodella argentarii*; Rouch, 1965: 718, figs. 1-17; Pesce & Maggi, 1983: 17, 25; Pretus, 1991: 235. [non Stella, 1951]

Thermosbaenacés; Bou, 1975: 106, 109.

*Monodella argentarii* (partim); Pinkster, 1978: 234; Schram, 1986: 221.

*Monodella* (partim); Botosaneanu & Delamare Deboutteville, 1967: 22; Wagner, 1990: 123.

Material.— **Greece**: 12 ♂♂, 61 ♀♀ (many damaged); St. n.G/109, Peleponnesos, Ghiton, well at ca. 10 m from seashore; coarse sand, organic clay, water table at 5.9 m, water depth 0.6 m, salinity 3.8‰, pH 7.2, aerial temp. 22.4°C, water temp. 19.5°C; collected by G. L. Pesce, D. Maggi & G. Silverii; 11.iv.1978; ZMA coll. no. C. A. 8237 [holotype]; ZMA coll. no. C. A. 8238, RMNH G 50; ULA [all paratypes].

Accompanying fauna: Crustacea: Amphipoda (*Salentinella angelieri* Ruffo & Delamare Deboutteville, 1952; *Niphargus* spec.); Ostracoda (Cytheridae); Copepoda (*Halicyclops* cf. *rotundipes* (Kiefer, 1935), *Tropocyclops prasinus* (Fischer, 1860), *Thermoscyclops oblongatus* (G. O. Sars, 1927), *Attheyella* (*Attheyella*) *crassa* (G. O. Sars, 1863), *Canthocamptus staphylinus* (Jurine, 1820)); Insecta: Diptera larvae; Oligochaeta (Tubificidae); Hydrachnida.

Description.— Body length (antennae 1 and 2 excluded) of male up to 2794 µm (holotype), of female up to 3324 µm in the material studied.

Antenna 1: peduncular segments 1 to 3 with five, five, and two long plumose macrosetae on respective medial margins; main flagellum 11- to 12-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with five teazel macrosetae on the medial and mediodistal margin; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: seven plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: endopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with seven to nine setules, third segment with one obscure unisetulate macroseta in male, in female more developed (less, however, than in *T. juglandis*, the "*T. relicta*-group", and the "*T. texana*-group") unisetulate macroseta with three setules.

Maxilla 2: basipodal endite 1 with six plumidenticulate macrosetae; basipodal endite 2 with 15 to 16 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: first segment of male endopodite without patches of club microsetae, second segment with four patches of club microsetae on the distal portion, third segment with four patches of club microsetae, fourth segment without patches of club microsetae; basipodal endite bearing 13 plumidenticulate macrosetae with long setules, a tall one medially, eight long ones terminally, three shorter ones subterminally, and one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, two subterminal, one medial, and one lateral plumose macrosetae.

Gnathopod: basal segment with one plumose macroseta; exopodite with three medial, two subterminal, two terminal and two lateral plumose macrosetae; basischium of endopodite with indistinct ischium, propodus with three fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

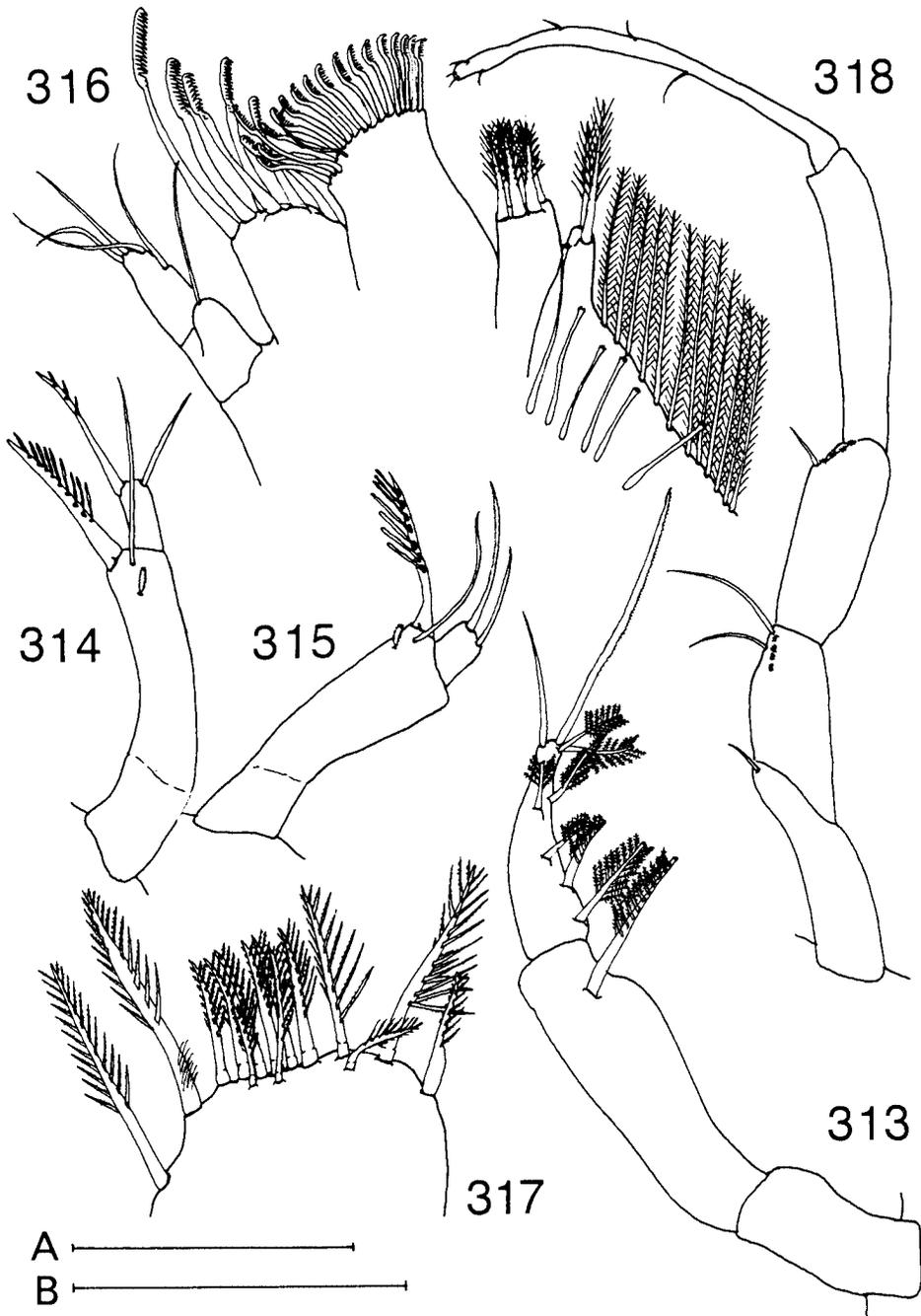
Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, male with 13 ovate microsetae, female with 10 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two rows of four and five ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, moreover carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 13 to 14 ovate microsetae, female with 11 to 12 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of four and five ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

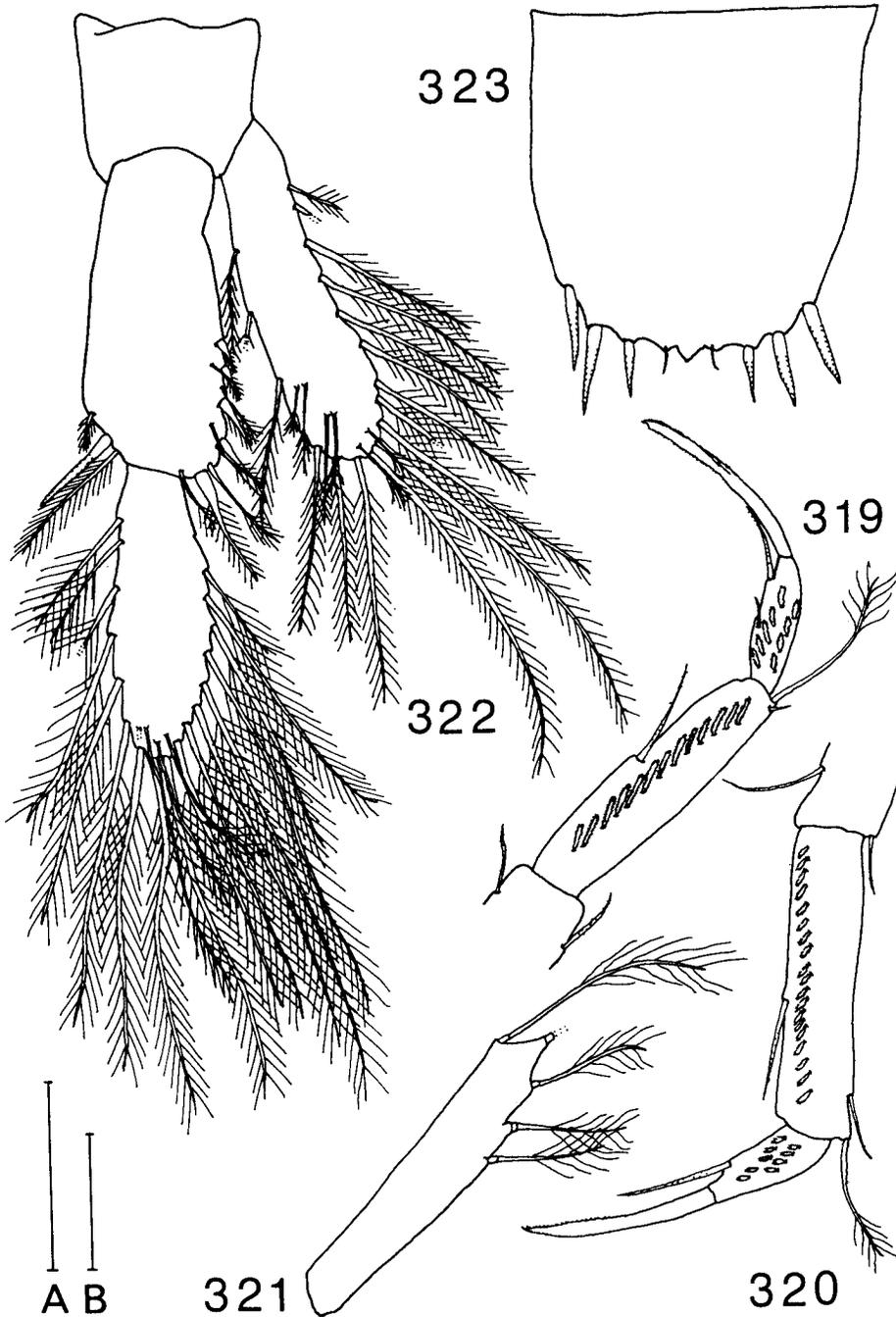
Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, moreover carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 14 to 15 ovate microsetae, female with 13 to 14 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of four and five ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, moreover carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 15 to 16 ovate microsetae, female with 15 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of four and five ovate microsetae, respectively; first segment of exopodite with four ovate microsetae, second segment with two or three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, moreover carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 19 to 20 ovate microsetae, female with 15 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two rows of four and five ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, two vestigial



Figs. 313-318. *Tethysbaena aiakos* spec. nov., holotype ♂ and paratype ♀. 313, palp mandible, ♂. 314, palp maxilla 1, ♀. 315, palp maxilla 1, ♂. 316, maxilla 2, ♂. 317, distal portion of basipodal endite of maxilliped, ♂ (figs. 313-317 scale A). 318, endopodite of maxilliped, ♂ (scale B). Scales indicated 0.1 mm.



Figs. 319-323. *Tethysbaena aiakos* spec. nov., holotype ♂. 319, distal portion of pereopod 3. 320, distal portion of pereopod 6. 321, pleopod 2 (figs. 319-321 scale A). 322, uropod. 323, telson (figs. 322-323 scale B). Scales indicated 0.1 mm.

macrosetae, one terminal and one lateral, and three ovate microsetae.

Pereiopod 7: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, moreover carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 21 to 22 ovate microsetae, female with 16 to 17 ovate microsetae, dactylus with one teazel macroseta on ventral margin and two rows of two and five ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macrosetae, one vestigial terminal macroseta, and two ovate microsetae.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of one cuspidate macroseta and two plumose macrosetae, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 16 to 17 plumose macrosetae; endopodite bearing 17 to 23 plumose macrosetae.

Telson: somewhat longer than wide, mean width/length ratio 0.96; anal lobes not protruding beyond terminal stretch; stretch with three protuberances, viz. a pointed central protuberance and two lobe-like swellings at the distolateral corners, central one flanked at either side by a glandular simple macroseta.

Variability.— Some peculiar variation is observed in several specific characters. The first peduncular segment of antenna 1 has generally five (but six in one female) plumose macrosetae along its medial margin. The same female showing this feature, also has a tiny tenth setule on the unisetulate macroseta of the right maxilla 1. By contrast the holotype has 16 rake-like macrosetae on basipodal endite 2 of its left maxilla 2. The holotype had eight plumose macrosetae on the exopodite of pereopod 5 instead of the usual number of seven. No exception to the rule formed the uropod, with a variable number of plumose macrosetae on its rami.

Remarks.— Characters distinguishing *T. aiakos* from the other members of the "*T. argentarii*-group" can be found in the distinctly larger number of segments of antenna 1, the lower number of ovate microsetae on the propodus of the pereopods in the female (usually the number in the male is lower than in the female), and a lobe-like swelling present at the distolateral corners of the stretch of the telson, so that the terminal stretch shows three protuberances (one pointed, two blunt) in contradiction to the usual central single pointed one in the other species of the "*T. argentarii*-group". For detailed information on specific differences with the other members of this species-group one is referred to table 2 (p. 202).

Although Rouch (1965) found several of the characteristic differences I observed too, he did not recognize their importance as discriminative among species. I can imagine that the specific characters were not recognized at that time, seen in the light that all species were considered belonging to *Monodella*, the characters of the type species being quite distinct from the species that are now considered to represent *Tethysbaena*.

The specimens at my disposal have first antennae with a main flagellum of at least 11 segments. The largest number counted by me was 12, but the distal portion of the terminal segment was incomplete, so it very well might be possible that more segments were present. Rouch (1965: 720) counted in one of his specimens 14 seg-

ments.

**Etymology.**— This species is named after Aiakos, who in Greek mythology was the son of Zeus and the nymph Aigina, and became after his death gatekeeper of the Hades.

**Distribution.**— *Tethysbaena aiakos* is known from a well at Ghiton, Peloponnesos, Greece. Most probably specimens of this new species have been collected before by H. Coiffait from lakes in the Glyfada Cave at the Bay of Dirou, Peloponnesos (Rouch, 1965), but these specimens were unfortunately lost (Rouch, in litt. 15-X-1988). Bou (1975) collected additional specimens at the Glyfada cave, and reports finding "*Monodella argentarii*" in the nearby situated cave Alépotrypa no. 923. This material was not available for my study.

**Habitat.**— The area from which *T. aiakos* was collected originated most probably at the end of the Pliocene to lower Pleistocene (Dermitzakis, 1990; Kemperman, 1992). With a salinity of 3.8‰, the water can be characterized as oligohaline. Sket (1986: 334) suggests the water of the Glyfada cave is oligohaline. Most of the accompanying fauna collected at the type locality of *T. aiakos* are epigean dispersionalists. Only a few true stygobionts were collected: the amphipods *Salentinella angelieri* Ruffo & Delamare Deboutteville, 1952, and *Niphargus* spec. Bou (1975) mentions the amphipod *Salentinella angelieri*, and copepods (Cyclopidae and Harpacticoidae) as accompanying faunal elements at the Glyfada cave. In the Alépotrypa cave the amphipods *Salentinella angelieri* and *Bogidiella cerberus* Bou & Ruffo, 1979 form the accompanying fauna.

#### 4.4.2.22. *Tethysbaena scabra* (Pretus, 1991) (figs. 324-333)

*Monodella* sp.; Orghidan, Dumitresco & Georgesco, 1975: 13, 15; Stock, 1978: 89; Gourbault & Lescher-Moutoué, 1979: 49, 50; Pretus, 1982: 239, fig. 37.

*Monodella* spec. 3; Pinkster, 1978: 234.

*Monodella argentarii*; Fornós et al., 1989: 59; Pretus, 1989: 63. [non Stella, 1951]

*Monodella argentarii* (partim); Cals & Monod, 1988: 342.

*Monodella* (partim); Wagner, 1990: 123.

*Monodella scabra* Pretus, 1991: 237, figs. 3.6-3.7, 3.11a-d, 3.11f, 3.12-3.13.

**Material.**— **Spain, Balearic Islands, Menorca:** 7 ♂♂, 123 ♀♀, 8 juveniles; Sant Lluís, Cova de ses Figueres; electric conductivity 745-2240 µS/cm, chlorinity 2-6 mg/l; collected by J. Ll. Pretus, M. Trias, J. Damians and Ll. Garcia; 27.vi.1987; ZMA coll. no. C. A. 8223; RMNH G 57 [all syntypes].

Accompanying fauna: Crustacea: Amphipoda (*Metacrangonyx longipes* Chevreux, 1909), Isopoda (*Typhlocirolana moraguesi* Racovitza, 1905).

**Spain, Balearic Islands, Mallorca:** 5 ♂♂, 24 ♀♀, 6 fragmentary specimens; Grotte du Port Majorque; 13.ii.1970; collection Cl. Delamare Deboutteville; MP th. 6 to MP th. 29 (set of 32 slides with whole-mounts and partially dissected specimens).

- 2 ♂♂, 74 ♀♀ (or fragmented specimens); Cueva del Drach; 30.v.1971; collection Cl. Delamare Deboutteville; MP.

- 16 ♂♂, 44 ♀♀ (6 with broodpouch), 6 juveniles; sta. PMX 4, Sa Porassa, E of Aeroclub Bar (W of Magaluf); well with ruined mill, water table close under mowing field, sandy water, water depth 2.5 m, chlorinity 2400 mg/l; collected by J.H. Stock; 28.xii.1977; ZMA coll. no. C. A. 8224.

Accompanying fauna: Crustacea: Isopoda (*Typhlocirolana moraguesi* Racovitza, 1905), Copepoda (Cyclopidae); Insecta (Diptera).

- 7 ♂♂, 126 ♀♀; sta. PMX 21, Can Pastilla, well near "Sometimes" (small side-road from road PMV-6012), at unmetalled side of the road; well with windpump, water table directly under mowing field, water depth 0.4 m, chlorinity 2900 mg/l; collected by J.H. Stock, 5.i.1978; ZMA coll. no. C. A. 8225; RMNH G 74.

Accompanying fauna: Crustacea: Amphipoda (*Metacrangonyx longipes* Chevreux, 1909), Copepoda (Cyclopidae).

- 6 ♀♀, 6 juveniles, 2 fragmentary specimens; sta. 83-09, well 4 km NW of Salines (roadfork roads C604 and C6014); well with ruined mill, pump connected, water table at 1.5 fathoms, water depth 0.3 m, Cvetkov net, salinity 8‰, temperature 17.9°C; collected by J.H. Stock; 1.v.1983; ZMA coll. no. C. A. 8226.

Accompanying fauna: Crustacea: Amphipoda (*Metacrangonyx longipes* Chevreux, 1909), Isopoda (*Typhlocirolana moraguesi* Racovitza, 1905), Ostracoda, Copepoda (Cyclopidae); Mollusca: Gastropoda (Hydrobiidae); Oligochaeta.

- 5 ♂♂, 47 ♀♀, 4 juveniles; sta. 83-10, Baños de San Juan, well near Edificio Thermal; well with ruined windpump, Cvetkov net, salinity 9‰, temperature 19.5°C; collected by J.H. Stock; 1.v.1983; ZMA coll. no. C. A. 8227.

Accompanying fauna: Crustacea: Amphipoda (*Metacrangonyx longipes* Chevreux, 1909), Isopoda (*Typhlocirolana moraguesi* Racovitza, 1905), Ostracoda; Mollusca: Gastropoda (Hydrobiidae); Oligochaeta.

- 10 ♀♀, 11 fragmentary specimens; sta. 83-11, Baños de San Juan, well with ruined windpump, covered, water table at 2.5 fathoms, water depth 0.1 m, Cvetkov net, salinity 8.5‰, temperature 17.1°C; collected by J.H. Stock; 1.v.1983; ZMA coll. no. C. A. 8228.

Accompanying fauna: Crustacea: Amphipoda (*Metacrangonyx longipes* Chevreux, 1909), Isopoda (*Typhlocirolana moraguesi* Racovitza, 1905; *Sphaeroma* spec.); Mollusca: Gastropoda (Hydrobiidae).

- 2 ♀♀; sta. 83-12, well E of road from Sercelles to Inca, along dry ditch, just N. of Sercelles; well not covered, clean, water table at 2.0 fathoms, water depth 4.5 fathoms, Cvetkov net, salinity 2‰, temperature 15.7°C; collected by J.H. Stock; 2.v.1983; ZMA coll. no. C. A. 8229.

Accompanying fauna: Crustacea: Amphipoda (*Metacrangonyx longipes* Chevreux, 1909), Isopoda (*Typhlocirolana moraguesi* Racovitza, 1905; juv. *Sphaeroma* spec.; div. Asellids); Mollusca: Gastropoda (Hydrobiidae).

- 3 ♂♂, 15 ♀♀, 1 juvenile; sta. 83-37, well along road Campos to Sant Jordi; well with ruined windpump, clean, water table at 3.0 fathoms, water depth 0.3 m, Cvetkov net, salinity 5.5‰, temperature 18.5°C; collected by J.H. Stock; 5.v.1983; ZMA coll. no. C. A. 8230.

Accompanying fauna: Oligochaeta.

- 9 (damaged) ♀♀; sta. 83-38, well NE of Colonia Sant Jordi; well with square opening, pump connected (not working), bottom with clean coarse sand, water table at 2.0 m, water depth 0.5 m, Cvetkov net, salinity 7‰, temperature 18.0°C; collected by J.H. Stock; 5.v.1983; ZMA coll. no. C. A. 8231.

Accompanying fauna: Crustacea: Amphipoda (*Metacrangonyx longipes* Chevreux, 1909; *Salentinella* spec.), Isopoda (*Typhlocirolana moraguesi* Racovitza, 1905), Copepoda (Cyclopidae, Harpacticidae); Oligochaeta.

- 1 ♀; sta. 83-62, W of S'Aranjassa; well with windpump, half open, water table at 2 fathoms, water depth 1 fathom, Cvetkov net, salinity 12‰, temperature 16.5°C; collected by J.H. Stock; 7.v.1983.

Accompanying fauna: Crustacea: Isopoda (Assellid), Ostracoda, Copepoda (Cyclopidae); Mollusca: Gastropoda (Hydrobiidae); Oligochaeta; Insecta (Diptera).

- 19 ♀♀; sta. 83-76, Porto Cristo, noria s'Hort d'en Servera; ruined well, partially covered, electric pump connected (not working), water table at 4.5 fathoms, water depth 0.4 m, Cvetkov net, salinity 6‰, temperature 18.1°C; collected by J.H. Stock; 9.v.1983; ZMA coll. no. C. A. 8232.

Accompanying fauna: Crustacea: Amphipoda (*Metacrangonyx longipes* Chevreux, 1909; *Salentinella angelieri* Ruffo & Delamare Deboutteville, 1952); Oligochaeta.

- 6 ♂♂, 18 ♀♀; sta. 88-100, well ca. 500 m NE of Puerto de Andraitx; water table at 1.5 fathoms, water depth 0.3 m, Cvetkov net, salinity 4‰; collected by J.H. Stock; 17.viii.1988; ZMA coll. no. C. A. 8233.

Accompanying fauna: Crustacea: Amphipoda (*Rhipidogammarus varicauda* Stock, 1978), Isopoda (Asellota), Copepoda (Cyclopidae).

- 2 ♂♂, 4 ♀♀; sta. 88-101, W of Andraitx, at 1 km along road PM-103 (from Andraitx to San Telmos) at city border, well in small house; H<sub>2</sub>S rich mud at bottom, water table at 3.5 fathoms, water depth 1.5 fathoms, Cvetkov net, salinity 3‰; collected by J.H. Stock; 17.viii.1988; ZMA coll. no. C. A. 8234.

Accompanying fauna: Crustacea: Isopoda (Asellota), Copepoda (Cyclopidae).

- 1 ♀, 2 fragmentary specimens; sta. 88-102, Andraitx, well just S of school; water table at 5.5 fathoms, water depth 1.5 fathoms, Cvetkov net; collected by J.H. Stock; 17.viii.1988; ZMA coll. no. C. A. 8235.

Accompanying fauna: Crustacea: Isopoda (Asellota, micro-oculate (terrestrial?) isopods), Copepoda (Cyclopidae).

- 2 ♀♀; sta. 88-117, Puerto de Andraitx, well in small house near pontoons; clean water, electrical pump connected, water table at 2 fathoms, water depth 1 fathom, salinity 8‰; collected by J.H. Stock; 27.viii.1988; ZMA coll. no. C. A. 8236.

Accompanying fauna: none.

**Description.**— Body length (antennae 1 and 2 excluded) of male up to 2961 µm, of female up to 3146 µm in the material studied. Body covered with scutellated scales (see fig. 45).

**Antenna 1:** peduncular segments 1 to 3 with five, five, and two long plumose macrosetae on respective medial margins; main flagellum 10-segmented, last segment with seven simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

**Antenna 2:** peduncular segment 4 with five, and segment 5 with four teazel macrosetae on the medial and mediodistal margin; flagellum 6-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

**Labrum:** without peculiarities.

**Mandible:** seven plumidenticulate macrosetae on third segment of palp.

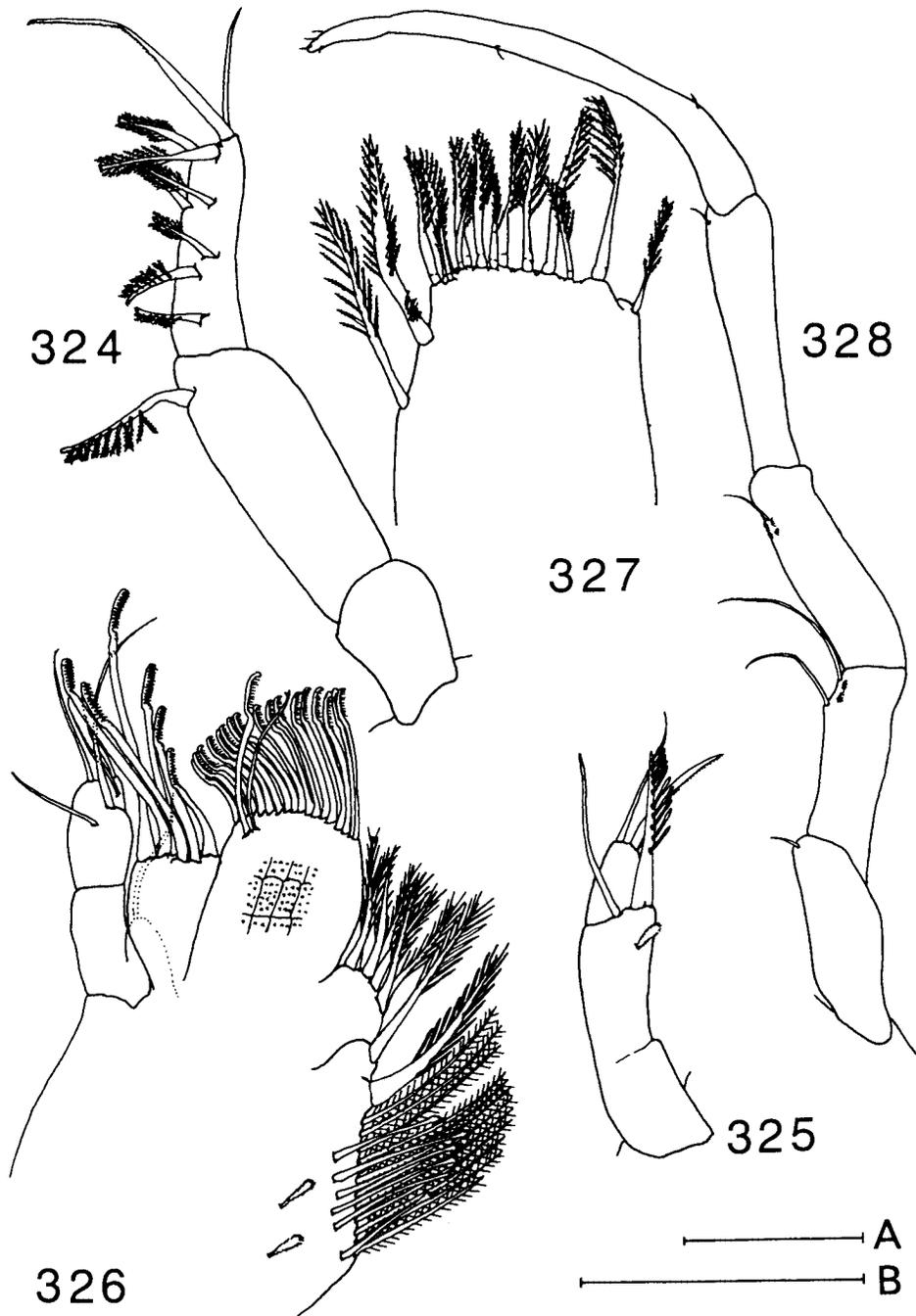
**Labium:** without peculiarities.

**Maxilla 1:** exopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with ten setules, third segment with one obscurely unisetulate macroseta.

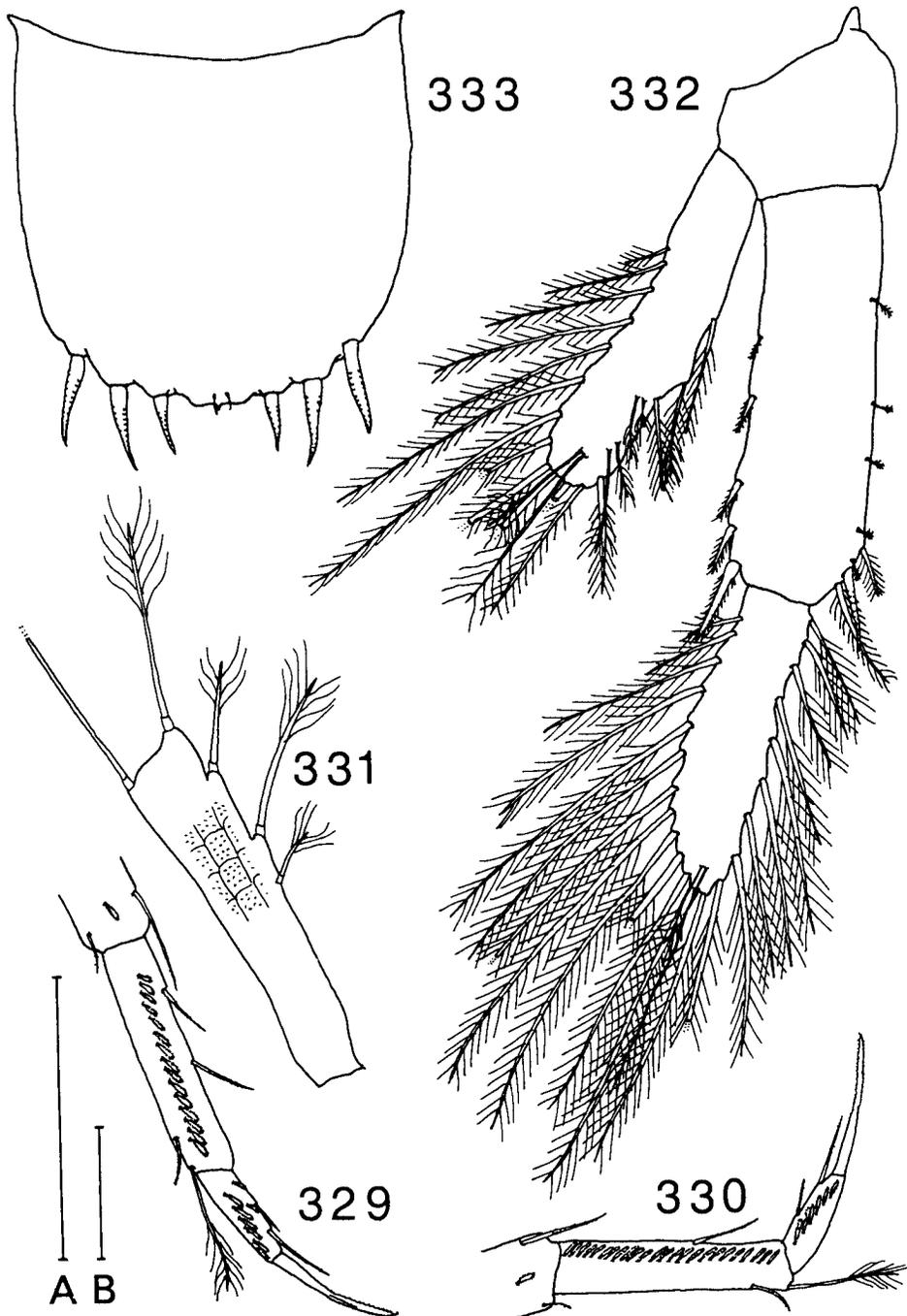
**Maxilla 2:** basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 17 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards lateral margin of appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing five simple macrosetae.

**Maxilliped:** first segment of male endopodite without patches of club microsetae, second segment with two patches of very tall and pointed club microsetae (diameter × height up to circa 0.5 × 4.5 µm) on the distal portion, third segment with two rows of two patches of tall, pointed club microsetae (diameter × height up to circa 0.4 × 4.5 µm), fourth segment without patches of club microsetae; basipodal endite bearing 13 to 17 plumidenticulate macrosetae with long setules, a tall one medially, 8 to 11 (in right maxilliped) and 12 (left maxilliped) long ones terminally, three or four shorter ones subterminally, and one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite 2-segmented, distal segment with two terminal, two subterminal and one medial plumose macrosetae.

**Gnathopod:** basal segment with up to four plumose macrosetae; exopodite with three medial, two subterminal, two terminal and two lateral plumose macrosetae;



Figs. 324-328. *Tethysbaena scabra* (Pretus, 1991), ♂ and syntype ♀. 324, palp mandible, ♀. 325, palp maxilla 1, ♀. 326, maxilla 2, ♀. 327, distal portion of basipodal endite of maxilliped, ♂ (figs. 324-327 scale B). 328, endopodite of maxilliped, ♂ (scale A). Scales indicated 0.1 mm.



Figs. 329-333. *Tethysbaena scabra* (Pretus, 1991), syntype ♀. 329, distal portion of pereopod 3. 330, distal portion of pereopod 6. 331, pleopod 2 (scale A). 332, uropod. 333, telson (figs. 329-330 and 332-333 scale B). Scales indicated 0.1 mm.

baso-ischium of endopodite with indistinct ischium, propodus with three fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on ventral margin, male with 11 ovate microsetae, female with 15 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and three rows with two, six and eight ovate microsetae, respectively; first segment of exopodite with one ovate microseta, second segment with three medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, moreover carpus with one ovate microseta distodorsally, propodus with two teazel macrosetae medially on ventral margin, male with 11 ovate microsetae, female with 15 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and six ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 14 ovate microsetae, female with 16 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and six ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 5: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 15 ovate microsetae, female with 22 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and six ovate microsetae, respectively; first segment of exopodite with five ovate microsetae, second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, moreover carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 16 ovate microsetae, female with 24 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and six ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macroseta, two vestigial macrosetae, one terminal and one lateral, and four ovate microsetae.

Pereiopod 7: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, moreover carpus with one ovate microseta distodorsally, propodus with one teazel macroseta medially on ventral margin, male with 17 ovate microsetae, female with 24 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and six ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macroseta, two vestigial macrosetae, one terminal and one lateral, and four ovate microsetae.

First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal and one subterminal subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of one cuspidate macroseta and two plumose macrosetae, medial armature of four stout plumose macrosetae, each accompanied by a small subplumose macroseta, and four additional subplumose macrosetae laterally, segment 2 with 19 to 22 plumose macrosetae; endopodite bearing 18 to 25 plumose macrosetae.

Telson: somewhat longer than wide, mean width/length ratio 0.97; anal lobes not protruding beyond terminal stretch; stretch with distinct central protuberance, flanked at either side by one glandular simple macroseta.

Variability.— In all specimens examined hardly any variation could be established, except for the number of plumose macrosetae of the uropodal rami, and in one female the presence of four (instead of the usual three) macrosetae on the carpus of the left pereopod 6.

Remarks.— As remarked at the discussion under *T. argentarii*, the species of the “*T. argentarii*-group” fall apart into two sub-groups, when studied with SEM, or after staining the cuticula with Black Chlorazol B, making the presence or absence of scutellated scales on the body visible. Two species of this group, viz. *T. scabra* (Pretus, 1991) and *T. siracusae* spec. nov., show these scutellated scales, and indeed also have more characters in common with each other than with the other members of the sub-group (see table 2, p. 202).

Distribution.— In recent years the species was reported from several localities in the Balearic Islands (Menorca, Mallorca and Dragonera) (Orghidan et al., 1975; Stock, 1978; Gourbault & Lescher-Moutoué, 1979; Ginés, 1983; Pretus, 1989, 1991).

Habitat.— *Tethysbaena scabra* is known from caves and wells all situated near the coast and in the lower part of the islands where deposits of Early Miocene and Pliocene age rose above sealevel during the last marine regressions in the Pleistocene (Riba Arderiu, 1981, Pretus, 1988). The water varies from oligohaline to mixohaline, the species being more abundant under the latter conditions. Several species have been found as accompanying fauna: the amphipods *Metacrangonyx longipes* Chevreux, 1909, *Salentinella angelieri* Ruffo & Delamare Deboutteville, 1952, *Salentinella* spec., and *Rhipidogammarus variicauda* Stock, 1978; the isopods *Typhlocirolana moraguezi* Racovitza, 1905, *Sphaeroma* spec., and various asellids; copepods (Cyclopidae and Harpacticoidea); ostracods; molluscs (gastropod family Hydrobiidae); oligochaetes; and insects (mainly Diptera). Fornós et al. (1989) and Pretus (1989, 1991) reported the amphipod *Bogidiella (Bogidiella) balearica* Dancau, 1973, the isopod *Jaera italica* Kessel-yak, 1938, and the copepod *Thermocyclops dybowskii* (Landé, 1890) co-occurring with *T. scabra* at Cova de sa Gleda, Mallorca.

#### 4.4.2.23. *Tethysbaena siracusae* spec. nov. (figs. 334-342)

Termosbenacei; Cottarelli & Fasano, 1979: 187.

*Monodella* sp.; Caruso & Costa, 1979: 441.

*Monodella* spec.; Pesce, 1985: 144, 152.

*Monodella* (partim); Wagner, 1990: 123.

*Monodella*; Pretus, 1991: 236.

Material.—Italy: 1 ♀; Sicily, Siracusa Province, Porto Palo (= Portopalo di Capo Passero), Guardiani; in artesian well; collected by R. Argano; 16.ix.1978; UR [holotype].

Accompanying fauna: Crustacea: Amphipoda (*Sarothrogammarus catacumbae* (G.S. Karaman & Ruffo, 1977)), Isopoda (*Typhlocirolana moraguesi* Racovitza, 1905), Copepoda (*Nitocrella stammeri* Chappuis, 1938).

- 1 ♀ (immature); st. n.Si/43, Sicily, Siracusa Province, Pachino; well, organic sandstone, water table at 12 m, water depth 4.0 m, salinity 4.5‰, pH 6.5, temperature 18.0°C; ULA [paratype].

Accompanying fauna: Crustacea: Amphipoda, Ostracoda, Copepoda (Cyclopidae); Oligochaeta.

- 1 ♀ (immature); st. n.Si/44, Sicily, Siracusa Province, Pachino; ZMA coll. no. C. A. 8239 [paratype].

Description.— Body length (antennae 1 and 2 excluded) female up to 3350 µm (holotype) in the material studied. Body covered with scutellated scales (as in fig. 45).

Antenna 1: incomplete in holotype, only first two peduncular segments present, peduncular segments 1 to 2 with five, and six long plumose macrosetae on respective medial margins. In immature female paratype: peduncular segments 1 to 3 with three, three, and two long plumose macrosetae on respective medial margins; main flagellum 8-segmented, last segment with five simple macrosetae of unequal length (sub)terminally; accessory flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Antenna 2: peduncular segments 4 and 5 with five teazel macrosetae on the medial and mediodistal margin; flagellum 5-segmented, last segment with five simple macrosetae of unequal length (sub)terminally.

Labrum: without peculiarities.

Mandible: eight plumidenticulate macrosetae on third segment of palp.

Labium: without peculiarities.

Maxilla 1: exopodite forming a 3-segmented palp, distal margin of basal segment obscurely demarcated from second segment, large unisetulate macroseta on second segment with six to eight setules, third segment with one rather well-developed (though less so than in *T. juglandis*, the "*T. relictata*-group", and the "*T. texana*-group") unisetulate macroseta with four setules.

Maxilla 2: basipodal endite 1 with seven plumidenticulate macrosetae; basipodal endite 2 with 15 rake-like serrate macrosetae at terminal margin, and two modified longer serrate subterminal macrosetae; basipodal endite 3 with six more strongly barbed rake-like macrosetae, which increase in size towards the lateral margin of the appendage, arranged in two rows of three macrosetae; endopodite 2-segmented bearing four simple macrosetae.

Maxilliped: male endopodite unknown; basipodal endite bearing 13 plumidenticulate macrosetae with long setules, a tall one medially, eight long ones terminally, three shorter ones subterminally, and one sublaterally, and with an additional much stouter plumidenticulate macroseta implanted submedially; exopodite lost.

Gnathopod: basal segment with three plumose macrosetae; exopodite with three medial, two subterminal, two terminal and two lateral plumose macrosetae; basischium of endopodite with indistinct ischium, propodus with three fine serrate macrosetae on distal half, and dactylus with two unequal, fine serrate macrosetae on ventral margin.

Pereiopod 2: propodus of endopodite with two teazel macrosetae medially on

ventral margin, female with 12 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of five and seven ovate microsetae, respectively; first segment of exopodite without ovate microseta, second segment with three medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 3: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with two teazel macrosetae medially on ventral margin, female with 12 to 13 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of five and seven ovate microsetae, respectively; first segment of exopodite (in immature female) with one ovate microseta, second segment with two medial, two subterminal and two terminal plumose macrosetae, lateral armature lacking.

Pereiopod 4: ischiomerus of endopodite with one ovate microseta mediodorsally implanted, propodus with two teazel macrosetae medially on ventral margin, female with 15 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and seven ovate microsetae, respectively; first segment of exopodite (in immature female) with five ovate microsetae, second segment with two medial, two subterminal and two terminal plumose macrosetae, lateral armature lacking.

Pereiopod 5: endopodite holotype (and dissected immature female) lost; first segment of exopodite (in immature female) with five ovate microsetae, second segment with two medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 6: propodus of endopodite with one teazel macroseta medially on ventral margin, female with 17 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and seven ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macroseta and one vestigial terminal macroseta, two ovate microsetae present.

Pereiopod 7: propodus of endopodite with one teazel macroseta medially on ventral margin, female with 19 ovate microsetae, dactylus with two teazel macrosetae on ventral margin and two rows of two and seven ovate microsetae, respectively; exopodite 1-segmented with one medial and one subterminal plumose macroseta and one vestigial terminal macroseta, one ovate microseta present.

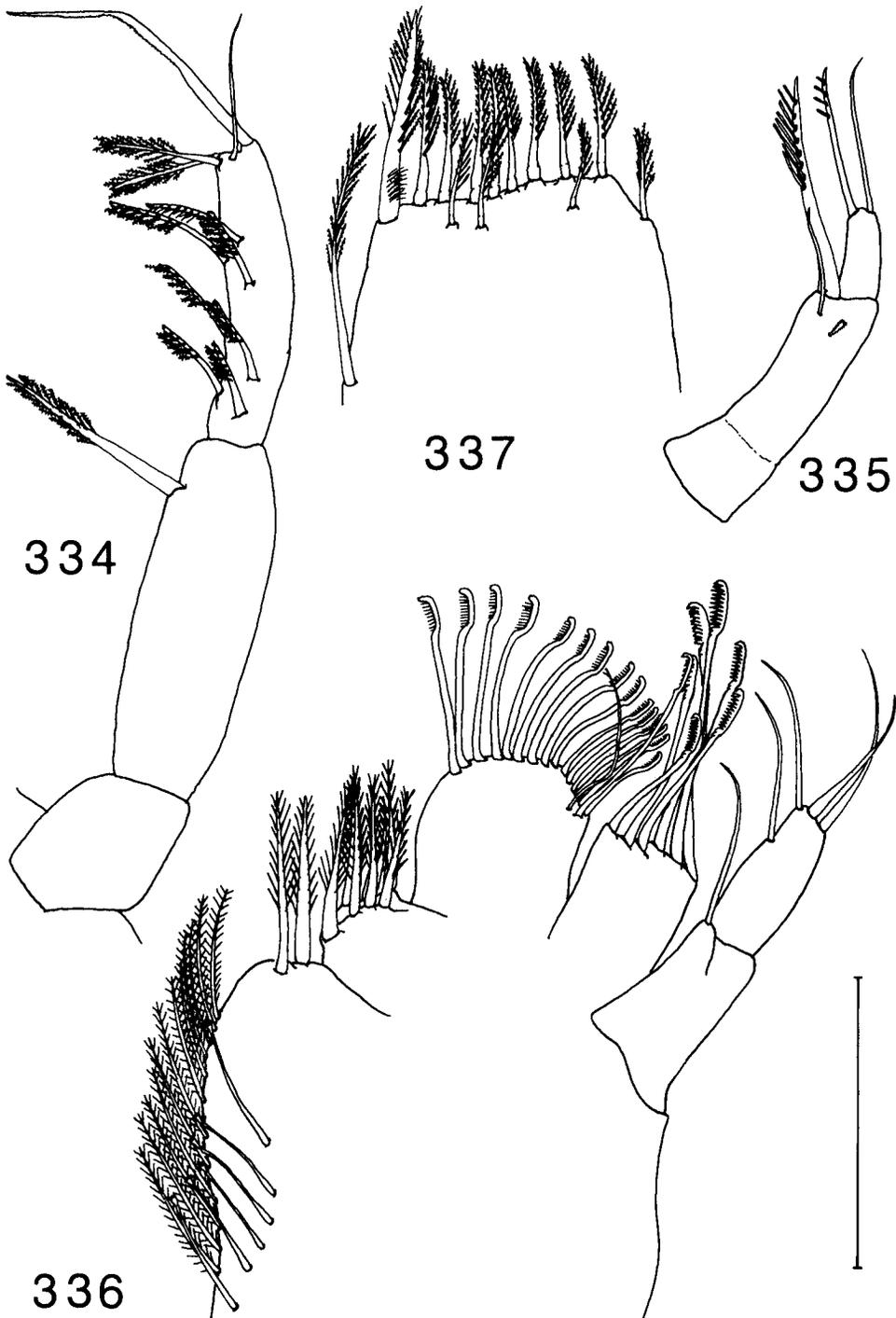
First pleopod with three dorsal subplumose macrosetae. Second pleopod with three dorsal, one terminal, one subterminal and an additional dorsolateral subplumose macrosetae.

Uropod: segment 1 of exopodite slightly longer than segment 2, segment 1 with lateral armature of two cuspidate macrosetae and one plumose macroseta, medial armature of five stout plumose macrosetae, each accompanied by a small subplumose macroseta, segment 2 with 14 (in immature female) to 22 plumose macrosetae; endopodite bearing 12 (in immature female) to 14 plumose macrosetae.

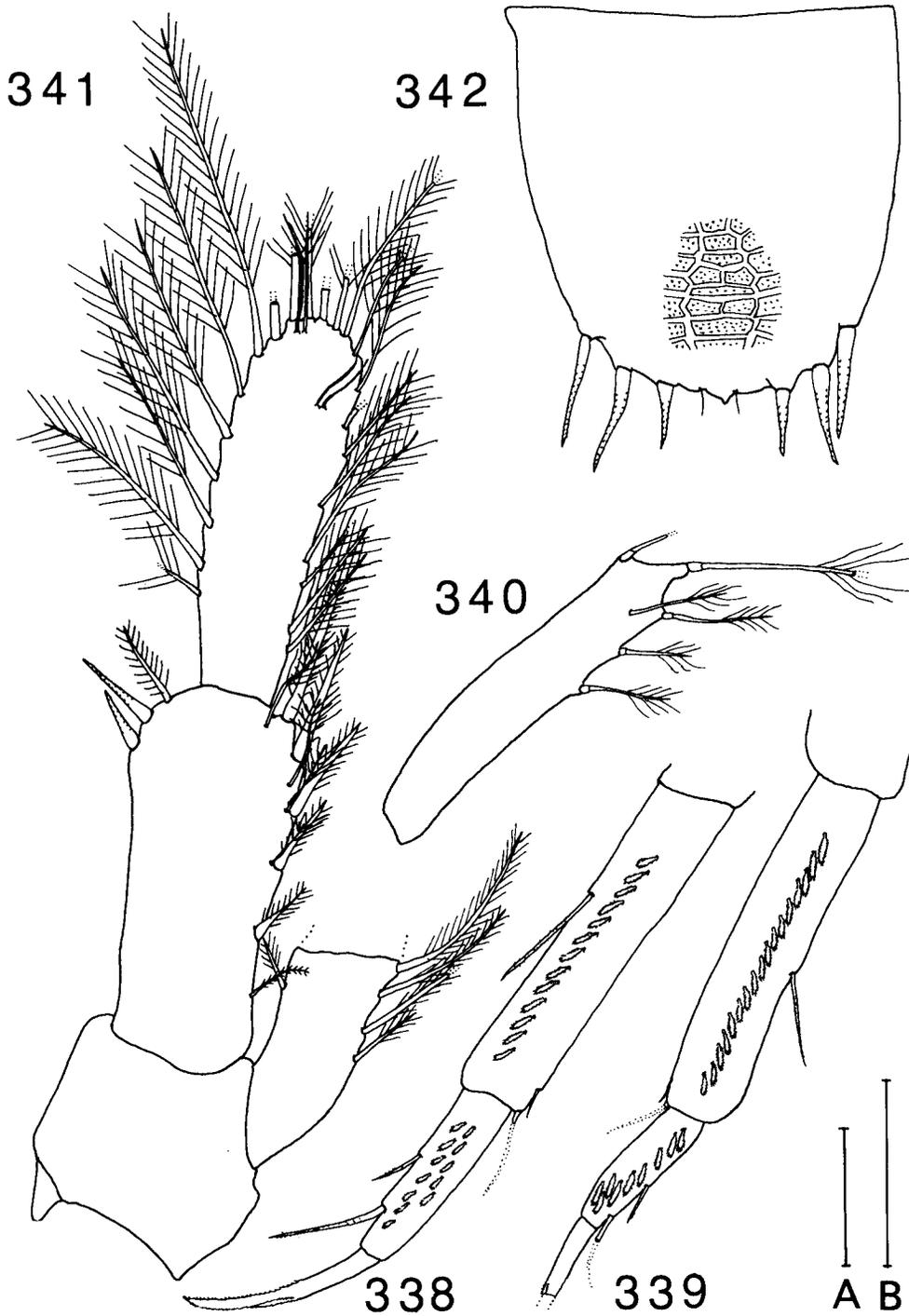
Telson: as long as wide, mean width/length ratio 1.00; anal lobes not protruding beyond terminal stretch; stretch with distinct central protuberance, flanked at either side by one glandular simple macroseta.

Variability.— Due to the limited number of specimens and state of development (only one adult available), it is not possible to establish the variation.

Remarks.— Since several remarks have been made above under the treatment of other members of the "*T. argentarii*-group" one is referred to table 2 (p. 202) for detailed



Figs. 334-337. *Tethysbaena siracusae* spec. nov., holotype ♀. 334, palp mandible. 335, palp maxilla 1. 336, maxilla 2. 337, distal portion of basipodal endite of maxilliped. Scale indicated 0.1 mm.



Figs. 338-342. *Tethysbaena siracusae* spec. nov., holotype ♀. 338, distal portion of pereopod 3. 339, distal portion of pereopod 6. 340, pleopod 2 (figs. 338-340 scale B). 341, uropod. 342, telson (figs. 341-342 scale A). Scales indicated 0.1 mm.

Table 2. Salient differences between the species of the "*Tethysbaena argentarii*-group"

	<i>T. argentarii</i> (Stella, 1951)	<i>T. halophila</i> (S.L. Karaman, 1953)	<i>T. aiakos</i> spec. nov.	<i>T. scabra</i> (Pretus, 1991)	<i>T. siracusae</i> spec. nov.
Body:					
scutellated scales	absent	absent	absent	present	present
Antenna 1:					
# segm. main flagellum	10	9	11-12(+)	10	8 (juv.)
# plumose m.s. segm. 1, 2, 3	5, 5, 2	4, 5, 3	5, 5, 2	5, 5, 2	5, 6, ?
Mandible:					
# plumidenticulate m.s. segm. 3	9	8	7	7	8
Maxilla 1:					
# setules uniset. m.s. segm. 2	10-11	7-8	7-9	10	6-8
uniset. m.s. segm. 3	m&f:obscure	m&f:obscure	m:obscure f:dev. m: 0; f:3	m&f:obscure	m: ? f:dev. 4
# setules uniset. m.s. segm. 3	0	0		0	4
Maxilla 2:					
# plumidenticulate m.s. b.e.1	6	7	6	7	7
# rake-like m.s. b.e.2	16-17	17	15-16	17	15
# rake-like m.s. b.e.3	6	5	6	6	6
# simple m.s. end.	6	5	4	5	4
Maxilliped:					
total # plumidenticulate m.s.	13-15	14	14	14-18	14
# plumose m.s. ex.	5	5	6	5	?
# patches segm. 2, 3 end. male	7, 7	6, 6	4, 4	2, 4	?
Gnathopod:					
demarcation ischium	obscure	indistinct	indistinct	indistinct	indistinct
Pereiopod 2:					
# ovate microsetae carpus	0	0	0	1	0
# ovate microsetae propodus	m:13; f:14	m:12; f:13	m:13; f:10	m:11; f:15	f:12
# ovate microsetae dactylus	10 + 3	5 + 2	5 + 4	6 + 2 + 8	5 + 7
# ovate microsetae exopodite	0	2	0	1	0
# plumose m.s. exopodite	9	9	9	8	8
Pereiopod 3:					
# ovate microsetae carpus	0	0	1	1	0
# ovate microsetae propodus	m:13; f:16	m:12-13; f:14	m:14; f:11-12	m:11; f:15	f:12-13
# ovate microsetae dactylus	9 + 3	5 + 2	5 + 4	6 + 2	5 + 7
# ovate microsetae exopodite	3	3	5	5	1
# plumose m.s. exopodite	9	9	9	8	6(juv.)
Pereiopod 4:					
# ovate microsetae carpus	0	0	1	1	0
# ovate microsetae propodus	m:13-14; f:17	m:13-15; f:16-17	m:14-15; f:13-14	m:14; f:16	f:15
# ovate microsetae dactylus	8 + 3	5 + 2	5 + 4	6 + 2	7 + 2
# ovate microsetae exopodite	4	5	5	5	5
# plumose m.s. exopodite	9	9	9	8	6(juv.)
Pereiopod 5:					
# ovate microsetae carpus	0	0	1	1	0
# ovate microsetae propodus	m:14-15; f:21	m:15-16; f:20	m:15-16; f:15	m:15; f:22	?
# ovate microsetae dactylus	8 + 3	5 + 2	5 + 4	6 + 2	?
# ovate microsetae exopodite	5	5	4	5	?
# plumose m.s. exopodite	8	8	7-8	7	7(juv.)

Table 2 (continued)

Pereiopod 6:					
# ovate microsetae ischiomerus	1	1	1	0	0
# ovate microsetae carpus	0	0	1	1	0
# ovate microsetae propodus	m:16; f:21	m:16; f:21-22	m:19-20; f:15	m:16; f:24	f:17
# ovate microsetae dactylus	7	5 + 2	5 + 4	6 + 2	7 + 2
# ovate microsetae exopodite	3	4	3	4	2
# plumose m.s. exopodite	2 + 2v	2 + 2v	2 + 2v	2 + 2v	2 + 1v(juv.)
Pereiopod 7:					
# ovate microsetae ischiomerus	1	0	1	0	0
# ovate microsetae carpus	0	0	1	1	0
# ovate microsetae propodus	m:17; f:22-23	m:18; f:24	m:21-22; f:16-17	m:17; f:24	f:19
# ovate microsetae dactylus	6	5 + 2	5 + 4	6 + 2	7 + 2
# ovate microsetae exopodite	3	3	2	4	1
# plumose m.s. exopodite	2 + 1v	2 + 2v	2 + 1v	2 + 2v	2 + 1v(juv.)
Pleopod 2:					
# dorsolateral subplumose m.s.	0	0	0	0	1
Uropod:					
# plumose m.s. segm. 2 ex.	20-22	19-22	16-17	19-22	14(juv.) -22
# plumose m. s. end.	11-16	19-21	17-23	18-25	12(juv.) -14
Telson:					
mean width/length ratio	0.98	0.92	0.96	0.97	1.00

abbreviations: b.e. = basipodal endite; dev. = developed; end. = endopodite; ex. = exopodite; f = female; juv. = juvenile; m = male; m.s. = macroseta(e); segm.= segment(s); uniset. = unisetulate; v = vestigial; # = number of...

information on the specific differences.

**Etymology.**— This species is named after the province of origin.

**Distribution.**— The only material available to me was found in Porto Palo and Pachino, both villages in the Siracusa Province, Sicily.

**Habitat.**— The age of the deposits in the wells from which *T. siracusae* was procured is unknown to me. With a salinity of 4.5‰ as measured at Pachino, the water can be characterized as oligohaline. Accompanying fauna consisted of Amphipoda, Copepoda (Cyclopidae), Ostracoda, and Oligochaeta. Accompanying fauna of the type locality consisted of the endemic amphipod *Sarothrogammarus catacumbae* (G.S. Karaman & Ruffo, 1977), the isopod *Typhlocirolana moraguesi* Racovitza, 1905, and the harpacticoid copepod *Nitocrella stammeri* Chappuis, 1938 (Caruso & Costa, 1979).

#### 4.5. Tulumellidae fam. nov.

**Diagnosis.**— Thermosbaenaceans with elongate body. Carapace distinctly enlarged. Rostrum obscure, more or less triangularly lobe. Small eye-stalks (ocular scales) present. Peduncular segments of antenna 1 with long plumose macrosetae along medial margin; main flagellum of antenna 1 8- to 24-segmented; accessory flagellum 8- to 16-segmented. Antenna 2 with large scale on third peduncular segment;

flagellum of antenna 2 7- to 13-segmented. Mandible with several plumidenticulate macrosetae on second segment of palp; left pars incisiva 5-dentate, right pars incisiva 4-dentate; lacinia mobilis present on left mandible or absent; pars molaris slender and conical, molar surface with serrate spiniform processes. Maxilla 1 with 2-segmented palp, basal palp segment not fused with second segment; basipodal endite with nine toothed macrosetae. Basipodal endite 1 of maxilla 2 with simply built plumidenticulate macrosetae; basipodal endites 2 and 3 with row of spoon-shaped serrate macrosetae; endopodite 1-segmented; exopodite with several plumose macrosetae, laterally implanted. Maxilliped with two or three simple setulated pappose macrosetae on coxopodite; (sub)terminal margin of basipodite with two rows of plumidenticulate macrosetae; endopodite lobate, with plumose macrosetae; exopodite lobate, with plumose macrosetae; epipodite well-developed. Seven pairs of biramous legs; exopodites 2-segmented; gnathopod with basis and ischium coalesced, demarcation between these two segments absent, dorsal margin with numerous long plumose macrosetae, propodus and dactylus ventrally with long plumose macrosetae, dactylus with three spatulate serrate macrosetae forming a claw; ovate microsetae on dactylus of pereopods 2 to 7. First pleopod a broadly pyriform unarticulate lobe, with subplumose macroseta(e); second pleopod articulate, elongate, with five to six subplumose macrosetae; pleopods 3 to 5 absent. First segment of uropodal exopodite distinctly shorter than endopodite, distomedially with two to four cuspidate macrosetae, distolaterally with three to four cuspidate macrosetae, each accompanied by subplumose macroseta. Telson not fused with pleonite 6, three to six pairs of cuspidate macrosetae on the posterior margin.

Discussion.— The family Tulumellidae only includes the genus *Tulumella*. Classification of this genus in a separate family is warranted on the basis of some peculiar apomorphies, e.g., segments of main flagellum of antenna 1 with two aesthetascs, generally quite differently shaped chaetotaxic elements on mouthparts and gnathopodal endopodite, the shape of pleopods 1 and 2; and plesiomorphies, e.g., large scale on third peduncular segment of antenna 2, laterally implanted exopodite of maxilla 2. In its other characters this family shows intermediate states between Thermosbaenidae and Monodellidae on the one hand (long plumose macrosetae on medial margin of the peduncular segments of antenna 1, spiniform processes present on the molar surface of the mandible, one and two rows of serrate macrosetae on basipodal endites 2 and 3 of maxilla 2, respectively, general shape of pereopods 2 to 5, and general outline of telson), and Halosbaenidae on the other hand (ocular scales, numerous plumidenticulate macrosetae on second segment of mandibular palp, 2-segmented palp of maxilla 1, distally developed claw in the gnathopod, non-articulate first pleopod, general outline of uropods). The unique, differently shaped macrosetae of the mouthparts in particular (for example the spoon-shaped serrate macrosetae versus rake-like macrosetae in all other thermosbaenacean families), the lobate exopodites of maxilla 2 and maxilliped (not present in the other families), the scale on peduncular segment 3 of antenna 2, and the presence of two aesthetascs on some flagellar segments of antenna 1, places *Tulumella* so apart from the other thermosbaenaceans that the creation of a separate family for this taxon is in my view justified.

4.5.1. *Tulumella* Bowman & Iliffe, 1988

*Tulumella* Bowman & Iliffe in Yager, 1988: 374. [nomen nudum]

*Tulumella* Bowman & Iliffe, 1988: 221; Wagner, 1988: 1st page; Cals & Monod, 1988: 342; Holsinger, 1989: 25; Wagner, 1990: 125, fig. 1; Cals & Monod, 1991: 176; Casanova, 1993: 145.

Type species.— *Tulumella unidens* Bowman & Iliffe, 1988.

Diagnosis.— Body length (antenna 1 and 2 excluded) up to 5.2 mm. Carapace reaching to the last pedigerous somite. Third peduncular segment of antenna 1 with four subplumose macrosetae on terminal prominence. Mandible with three to four serrate macrosetae, merging into six to nine serrate spiniform processes towards and on the molar process, distal portion of molar process dentate. Two compactly built serrulate macrosetae distally on palp of maxilla 1; basipodal endite with stout, relatively compact, digitate toothed macrosetae. Coxopodal endite of maxilla 2 with two stout plumose macrosetae; basipodal endite 1 with nine simply built plumidenticulate macrosetae, tips finely pointed, subterminally obscurely digitate, with setules at distal half of setal body. Maxilliped with two or three long, simple setulate pappose macrosetae on coxopodite; basipodite with submedial plumidenticulate, tall, stout and pointed macroseta, basal portion of which with two opposite rows of fine setules, slightly turning around the macrosetal axis, setules distad of the annulus distinctly larger in size and arranged in two parallel rows. Pereiopods 1 to 7 biramous; gnathopod with naked first exopodite segment, in baso-ischium of endopodite demarcation of ischium indistinct; propodus without "spur"; in pereiopods 2 to 7 ischium free. First segment of exopodite of uropod with oblique terminal margin. Telson fundamentally subquadrangular, towards tip slightly trapezoid, with three to six pairs of cuspidate macrosetae.

Description.— Antenna 1 with 3-segmented peduncle; peduncular segments 1 to 3 with long plumose macrosetae (type IA1) on medial margin; peduncular segment 1 with two teazel macrosetae (type IIB3) on mediodorsal margin, three teazel (type IIB3) and one subplumose macrosetae (type IB2) distally on lateral margin, and transverse row of four teazel macrosetae (type IIB3) on dorsal margin, segment 2 with one teazel macroseta (type IIB3) accompanying last medial plumose macroseta, and transverse row of three teazel macrosetae (type IIB3) on dorsal margin, segment 3 with transverse row of two teazel macrosetae (type IIB3) accompanying last medial plumose macroseta, one subterminal and three terminal subplumose macrosetae (type IB2) on terminal prominence; main flagellum 8- to 24-segmented, one or two aesthetascs (type IIA6) on fourth and more distal segments, last three segments excepted, if one aesthetasc present it is accompanied by two simple macrosetae (type IIA1), if two aesthetascs are present they are accompanied by one simple macroseta (type IIA1), last segment with two medial, two subterminal and three terminal simple macrosetae (type IIA1) of unequal length; accessory flagellum 8- to 16-segmented, segments with up to four mediodistal simple macrosetae (type IIA1), last segment with five simple macrosetae (type IIA1) of unequal length (sub)terminally.

Antennae 2 uniramous, peduncle 5-segmented, segments 1 and 2 naked, segment 3 with one teazel macroseta (type IIB3) mediodistally, and well-developed scale with plumose macrosetae (type IA1) distolaterally, segments 4 and 5 without or with two teazel macrosetae (type IIB3) on mediodistal margin, three teazel macrosetae (type

IIB3) distally on medial margin; flagellum 7- to 14-segmented, segments 1 to penultimate each with two simple macrosetae (type IIA1) mediodistally, last segment with five simple macrosetae (type IIA1) of unequal length terminally.

Labrum approximately 1.3 times broader than long; proximal portion with ciliate microsetae (type 2b); apically with ovate microsetae (type 2a).

Mandible with 3-segmented palp, basal palp segment rectangular and unarmed, second segment slender with several plumidenticulate macrosetae (type IA3), third segment with several plumidenticulate macrosetae (type IA3), (sub)apically one simple (type IIA1) and one long serrulate macroseta (type IIB1(b)); corpus mandibulae differentiated into pars incisiva, 5-dentate left, 4-dentate right, with or without lacinia mobilis in left mandible (absent in right mandible), row of three to four slender serrate macrosetae (type IIB1(a)), and robust pars molaris having its molar surface covered with six to nine serrate spiniform processes, distal portion of molar process dentate.

Labium deeply cleft, its two lobes with rounded tips, internal distal margin with ciliate microsetae (type 2b), outer distal margin more densely covered by taller ciliate microsetae (type 2b).

Maxilla 1 differentiated into precoxal endite with medial armature of 12 or 16 plumidenticulate macrosetae (type IA3) (six stout medioterminally and six or ten latero-terminally); basipodal endite with distal armature of nine stout, relatively compact, digitate toothed macrosetae (type III), of which four somewhat more strongly dentate (as in fig. 36); exopodite forming a 2-segmented palp, first segment naked, second segment with one serrulate macroseta (type IIB1(a)) and four stout, relatively compact, unisetulate macrosetae (type IB3(a)), with thick, stout setules, giving them a rake-like appearance.

Maxilla 2 complexly built: a coxopodal endite medially with numerous fine plumose macrosetae (type IB1), four rod macrosetae (type IIA2) mediodorsally and two stout plumose macrosetae (type IB1); three basipodal endites: basipodal endite 1 with nine rather simply built plumidenticulate macrosetae (type IA3), tips finely pointed, subterminally obscurely digitate, dense patch of setules starting in distal direction at central portion of setal body; basipodal endite 2 with row of spoon-shaped serrate macrosetae (type IIB1) at terminal margin, and two modified (longer one with more developed spoon, short one with spoon strongly reduced to narrow tip) serrate macrosetae (type IIB1); basipodal endite 3 with a row of somewhat more strongly developed spoon-shaped macrosetae (type IIB1(d)), increasing in size laterally; endopodite 1-segmented, with simple macrosetae (type IIA1); exopodite a distinct lobe with plumose macroseta (type IB1).

Maxilliped: coxopodal endite a tapering lobe with or without one short, but with two long pappose macrosetae (type IA2), having long almost simple setules with few setulettes distally (as in fig. 9); basipodal endite with two or three rows of plumidenticulate macrosetae (type IA3) rather similar in shape, all with fine setules, a tall one medially, and with an additional much stouter plumidenticulate macroseta (type IA3) with very broad basis is implanted submedially, its distal portion with two parallel rows of long, but fine setules (as in fig. 13); endopodite lobate, unarticulate, with five plumose macrosetae (IB1); exopodite lobate, 1-segmented, with three plumose macrosetae (type IB1); epipodite a broad tapering lobe with simple microsetae (type

1a) along margin.

Gnathopod with plumose macrosetae (type IA1) dorsally on basal segment, one teazel macroseta (type IIB3) distally on ventral margin; exopodite 2-segmented, proximal segment naked, distal segment with two medial, two subterminal, two terminal and two to three lateral plumose macrosetae (type IB1); merus of endopodite with one to four teazel macrosetae (type IIB3) on ventral margin, one teazel (type IIB3) and one subplumose macroseta (type IB2) distodorsally; carpus short, armed with several very long serrate macrosetae (type IIB1) on ventral margin; propodus short also, armed with several very long serrate macrosetae (type IIB1) on ventral margin, dactylus with three serrate macrosetae (type IIB1(a)) on ventral margin, one on dorsal margin, terminal "unguis" formed by one short simple (type IIA1) and three stout serrate macroseta (type IIB1) of unequal length.

Pereiopod 2: with or without precoxal gill-like structure; ischium of endopodite with one teazel macroseta (type IIB3) on ventral margin; merus with one teazel macroseta (type IIB3) on ventral margin; carpus with two or three teazel macrosetae (type IIB3) medially and distally on ventral margin; propodus with three teazel macrosetae (type IIB3) medially and distally on ventral margin, one small teazel macroseta (type IIB3) on distodorsal margin; dactylus with teazel macroseta (type IIB3) on ventral margin, several species-dependent ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite naked, second segment with three medial, two subterminal, two terminal and three lateral plumose macrosetae (type IB1).

Pereiopods 3 to 7: pereiopods 3 and 4 with or without precoxal gill-like structure; ischium of endopodite with one teazel macroseta (type IIB3) on ventral margin; merus with one teazel macroseta (type IIB3) on ventral margin; carpus with two or three teazel macrosetae (type IIB3) medially and distally on ventral margin, one teazel macroseta (type IIB3) distodorsally; propodus with three (occasionally four) teazel macrosetae (type IIB3) medially and distally on ventral margin, one small teazel (type IIB3) and one subplumose macroseta (type IB2) on distodorsal margin; dactylus with teazel macroseta (type IIB3) on ventral margin, several species-dependent ovate microsetae (type 2a), and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subplumose macroseta (type IB2) subterminally, second segment with three medial, two subterminal, two terminal and three lateral plumose macrosetae (type IB1).

First pleopod unarticulate, broad, pyriform, with one large medial and several small subplumose macrosetae (type IB2) towards the lateral margin. Second pleopod 1-segmented, articulate, elongate, with four to five dorsal and one terminal subplumose macrosetae (type IB2).

Uropod with 2-segmented exopodite and 1-segmented endopodite; first segment of exopodite distinctly longer than segment 2, distal margin of segment 1 oblique, laterally with three to four cuspidate macrosetae (type IIA3) each accompanied by a subplumose macroseta (type IB2), medially with four to five cuspidate macrosetae (type IIA3), segment 2 with several plumose macrosetae (type IB1) all along medial, terminal and lateral margins, subterminally two pairs of subplumose macrosetae (type IB2); distal margin of endopodite projecting beyond distalmost margin of first segment of exopodite, bearing several plumose macrosetae (type IB1) along medial,

terminal and lateral margins, and two pairs of subterminal short subplumose macrosetae (type IB2).

Telson essentially subquadrangular in outline, towards posterior end slightly trapezoid, width/length ratio approximately 0.8 in all species, three to six pairs of cuspidate macrosetae (type IIA3) along distal margin, with or without dorsal simple macrosetae (type IIA1).

Distribution.— Known from Mexico (Yucatan Peninsula, Cozumel Island), and the Bahamas.

Habitat.— All species are known from caves where fresh and marine waters meet, and live just above or just below the density interface of the halocline in waters that are of oligohaline to euhaline nature.

Discussion.— When the genus and species of *Tulumella* were established, a small nomenclatorial problem arose. Initially *T. unidens* was intended to be the first species published, but unfortunately the paper by Dr Jill Yager was published a month earlier. This confronted me with a possible nomenclatorial problem. As Yager compared her species with *T. unidens*, referring to specific characters of that species one could interpret her as actual author of this species. However, according to the French definition of article 13(a)(i) of the ICZN the name *Tulumella unidens* Bowman & Iliffe in Yager, 1988, must be considered a nomen nudum (Bowman, in litt. 17.vi.1988), as Yager clearly did not intend to describe *T. unidens*. The authorship of the generic name forms no nomenclatorial problem, as Yager did not connect a name of a type species to her definition of the genus (sensu article 13(b) of the ICZN). Thus Bowman & Iliffe, 1988, remain the authors of *Tulumella* as actually was intended. *Tulumella unidens* Bowman & Iliffe, 1988, is type species by original designation.

#### 4.5.1.1. *Tulumella unidens* Bowman & Iliffe, 1988 (figs. 343-364)

Thermosbaenaceans; Bowman, 1987: 662; Yager, 1987b: 165; Kornicker & Iliffe, 1989: 15.

*Tulumella unidens* Bowman & Iliffe in Yager, 1988: 377 [nomen nudum-see remarks above].

*Tulumella unidens* Bowman & Iliffe, 1988: 221, figs. 1-2; Cals & Monod, 1988: 342, fig. 1A; Holsinger, 1989: 26; Holsinger, 1990: 103.

*Tulumella*; Holsinger, 1990: 103.

Material.— **Mexico**: 2 ♀♀ (1 damaged); Quintana Roo, about 10 km S of Tulúm, pueblo on cross-road # 307, Najaron (Naharon) Cenote; collected by J. Bozanic; 17.ii.1986; USNM 235279 [topotypes].

Description.— Body length (antennae 1 and 2 excluded) female up to 2157 µm (Bowmann & Iliffe, 1988: holotype 2.9 mm) in the material studied.

Antenna 1: peduncular segments 1 to 3 with three, six and three long plumose macrosetae on respective medial margins; main flagellum 18- to 22-segmented, one aesthetasc on segments 5, 7, 9, and 11 (13 to 15), two aesthetascs on segments 4, 6, 8, and 10 (and 12); accessory flagellum 14-segmented.

Antennae 2: scale on peduncle segment 3 with 11 plumose macrosetae, segments 4 and 5 with two teazel macrosetae on mediodistal margin; flagellum 10-segmented, segments 1 to 9 each with two simple macrosetae.

Labrum: without peculiarities.

Mandible: second palp segment with five plumidenticulate macrosetae, third segment with eight plumidenticulate macrosetae; lacinia mobilis absent in left mandible, row of three slender serrate macrosetae, pars molaris with six serrate spiniform processes.

Labium: without peculiarities.

Maxilla 1: precoxal endite with medial armature of 16 plumidenticulate macrosetae, of which six stout medioterminally and ten tall ones laterotermally.

Maxilla 2: coxopodal endite medially with 27 fine plumose macrosetae, four rod macrosetae mediodorsally and two stout plumose macrosetae; basipodal endite 2 with nine spoon-shaped serrate macrosetae, and two modified serrate macrosetae; basipodal endite 3 with seven somewhat more strongly developed spoon-shaped macrosetae, increasing in size towards the lateral margin of the appendage; endopodite with four simple macrosetae; exopodite with three plumose macrosetae.

Maxilliped: coxopodal endite a tapering lobe with one short, and two long pap-pose macrosetae; basipodal endite with two rows of four and nine plumidenticulate macrosetae, respectively, varying in size, but all with fine setules, a tall one medially, and submedially and with an additional much stouter plumidenticulate macroseta.

Gnathopod: baso-ischium with six plumose macrosetae dorsally, one teazel macroseta distally on ventral margin, merus of endopodite with three teazel macrosetae on ventral margin, one teazel and one subplumose macroseta distodorsally; carpus with eight very long serrate macrosetae on ventral margin; propodus with seven very long serrate macrosetae on ventral margin; exopodite 2-segmented, distal segment with two medial, two subterminal, two terminal and two to three lateral plumose macrosetae.

Pereiopods 2 to 7: shape (size excluded) and chaetotaxy uniform, but endopodite having dactylus with variable number of ovate microsetae: pereiopod 2 with 10; pereiopod 3 with 11; pereiopod 4 with 12; pereiopod 5 with 13; pereiopods 6 and 7 with 11. Pereiopods 2 to 4 without precoxal gill-like structures.

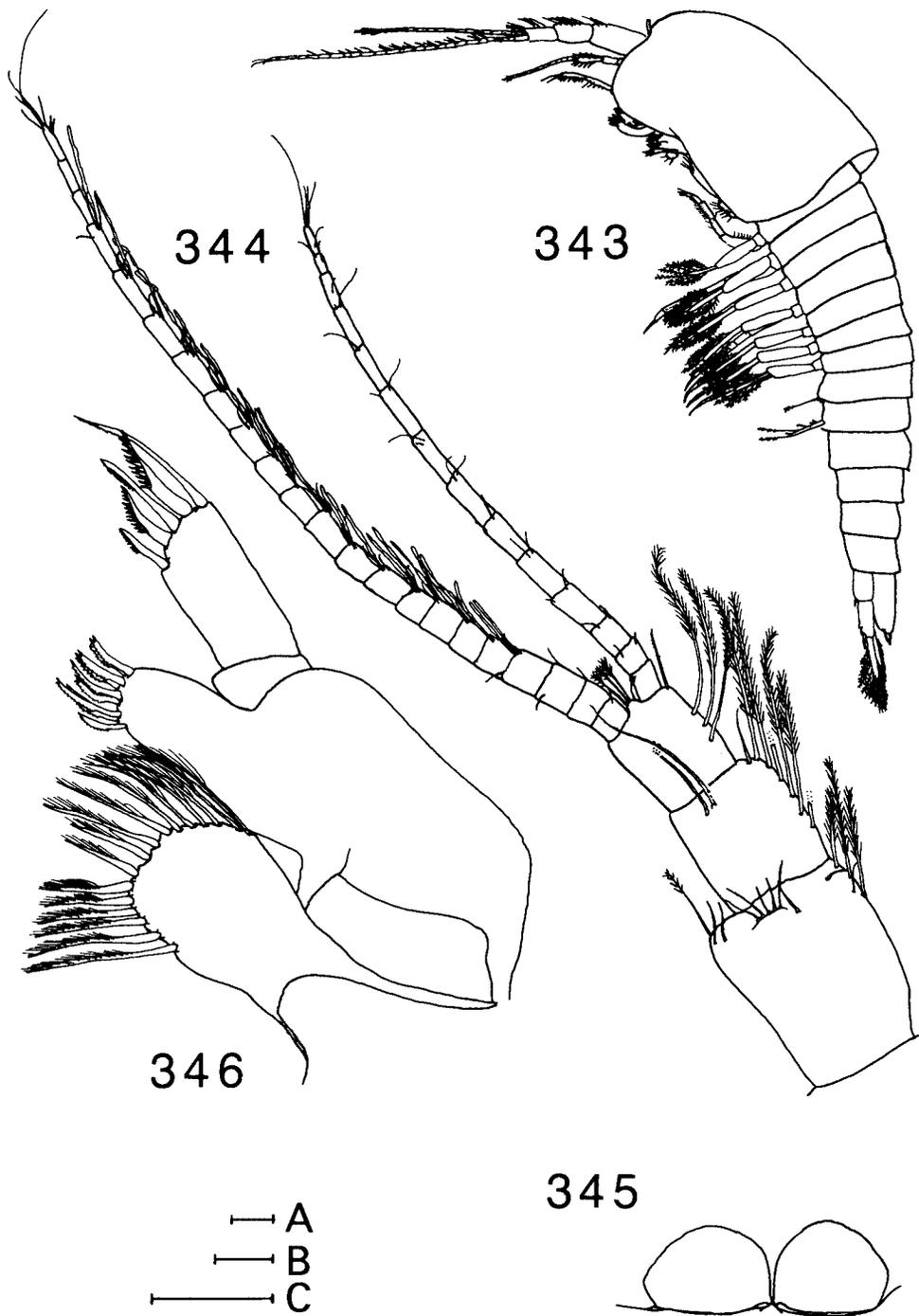
First pleopod: with one large medial and nine small subplumose macrosetae towards lateral margin.

Second pleopod: with five dorsal and one terminal subplumose macrosetae.

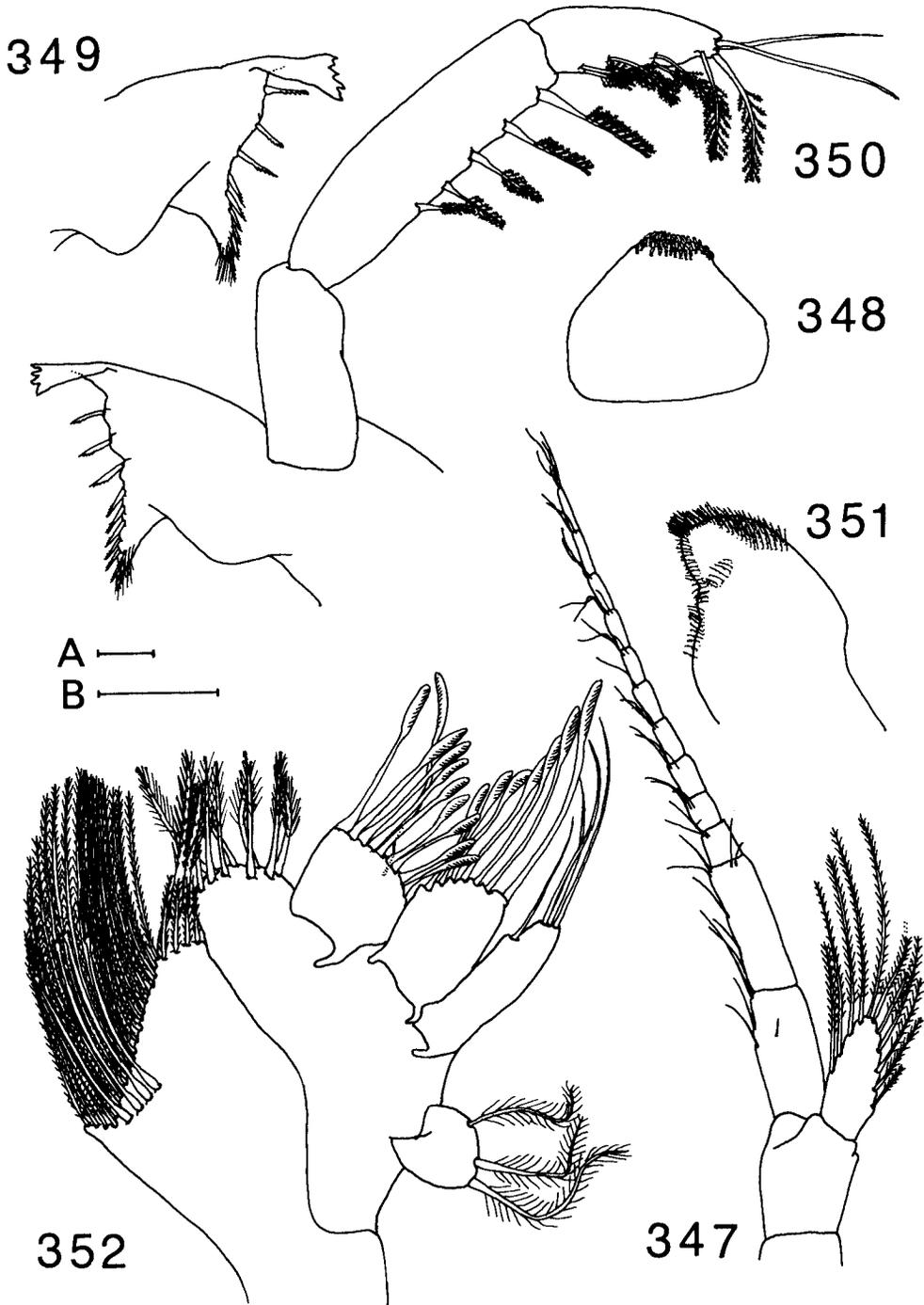
Uropod: segment 1 of exopodite laterally with four cuspidate macrosetae each accompanied by subplumose macroseta, medially with five cuspidate macrosetae, segment 2 with 18 plumose macrosetae all along medial, terminal and lateral margins; endopodite with 22 plumose macrosetae along medial, terminal and lateral margins.

Telson: width/length ratio 0.82, three pairs of cuspidate macrosetae along distal margin, dorsal simple macrosetae absent.

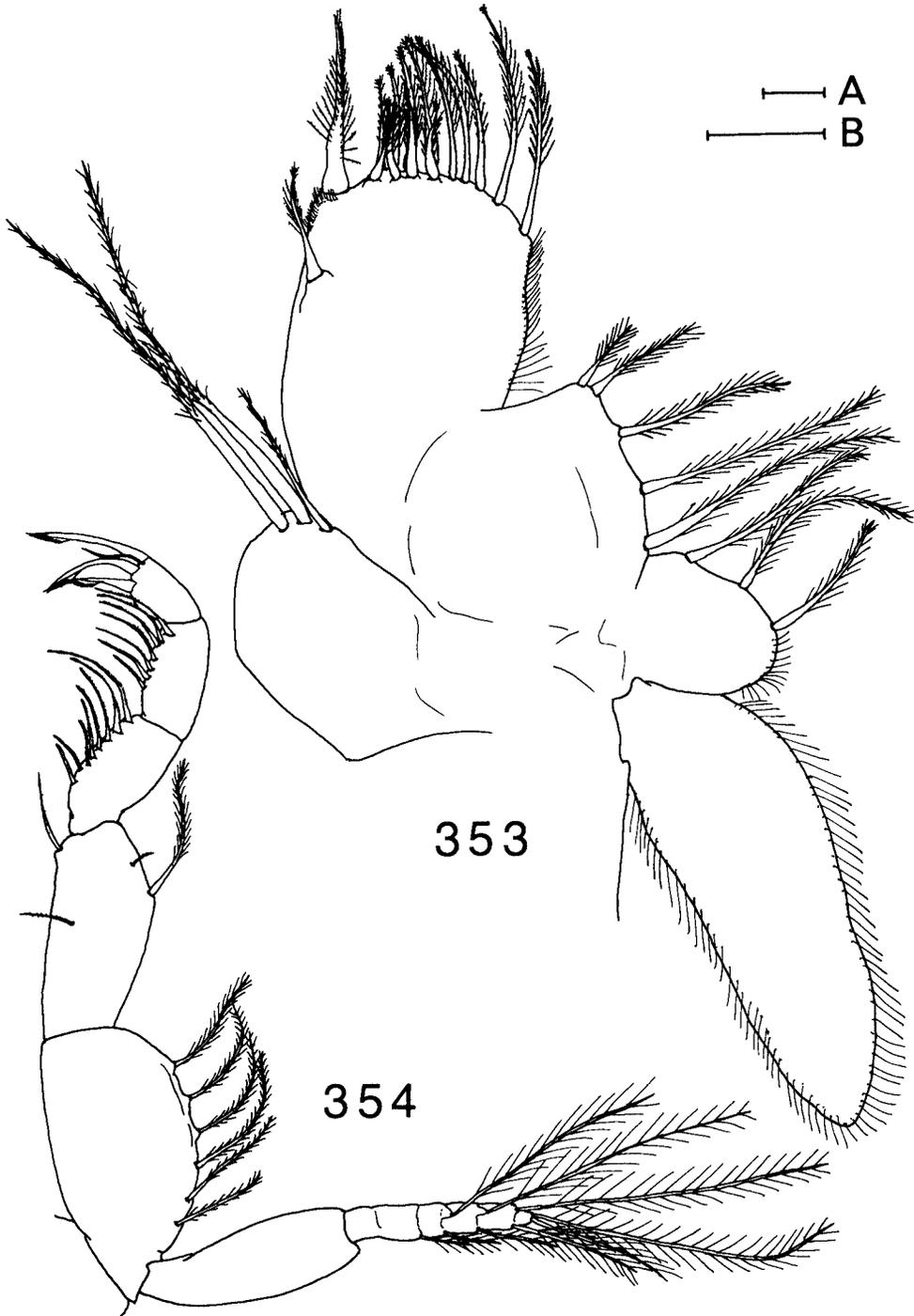
Variability.— As only one of the two specimens at my disposal was complete, the above description leaves no space to establish any variation. Compared to the original description of this taxon (Bowman & Iliffe, 1988) a few observations were made that could refer to variation. The number of flagellar segments of the main flagellum of antenna 1, plumose macrosetae medially on the peduncular segments of antenna 1, the number of plumose macrosetae on the scale of antenna 2, and the number of plumose macrosetae on the uropodal rami are in my opinion typically variable characters for the species. All other characters that show differences compared to the



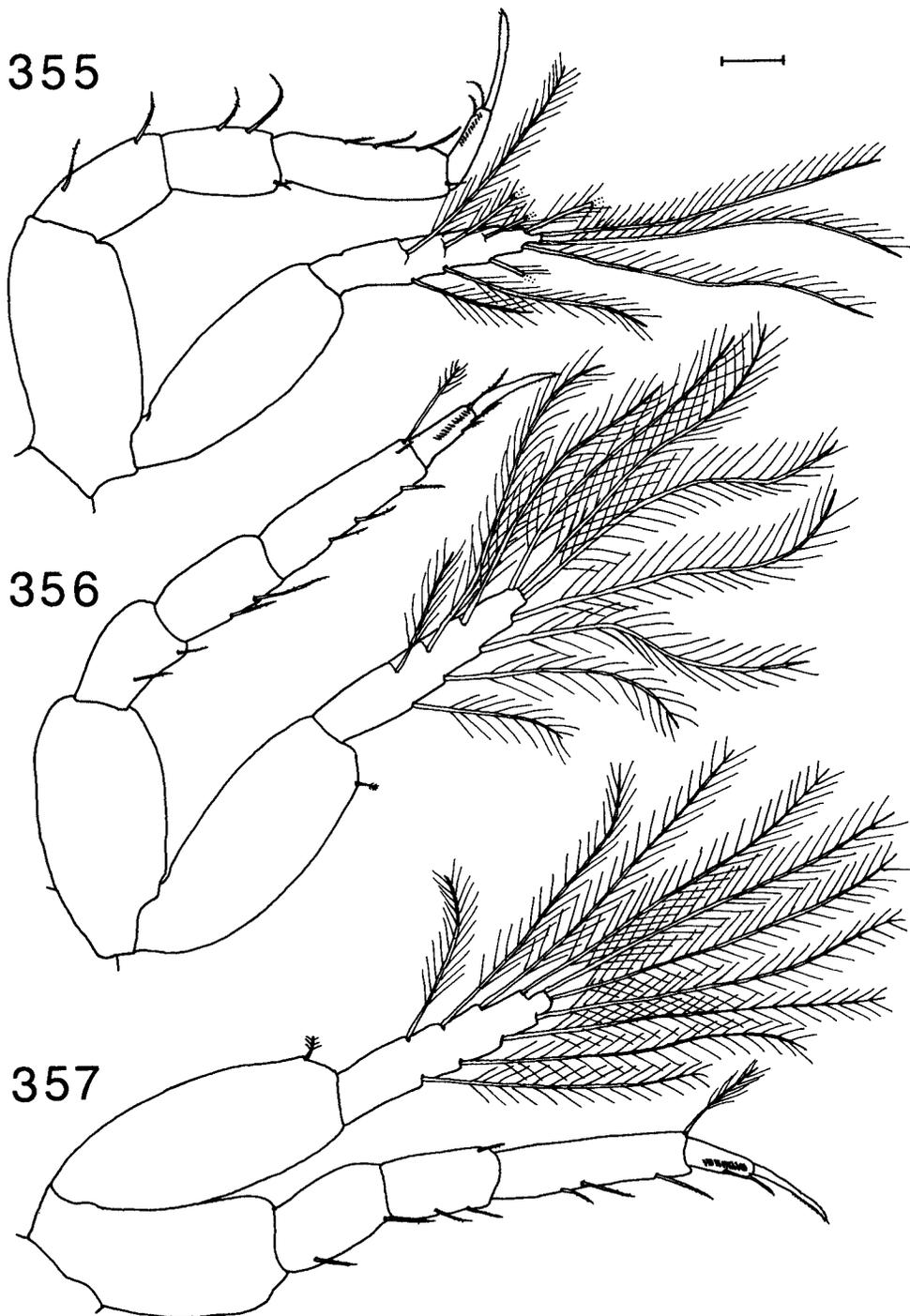
Figs. 343-346. *Tulumella unidens* Bowman & Iliffe, 1988, ♀. 343, lateral view of habitus (2157  $\mu\text{m}$ ). 344, antenna 1 (scale A). 345, ocular scales (scale B). 346, maxilla 1 (scale C). Scales indicated 0.1 mm.



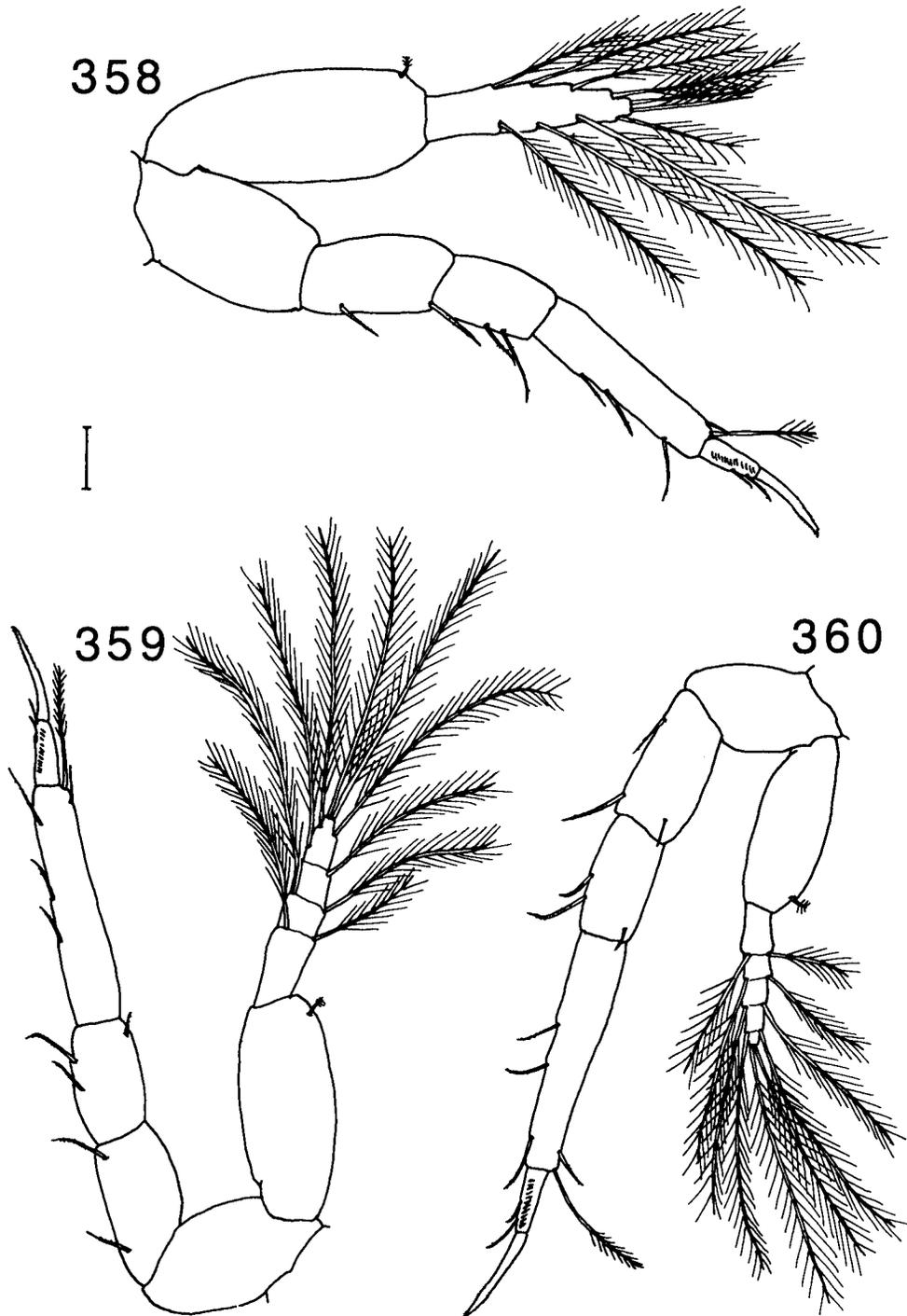
Figs. 347-352. *Tulumella unidens* Bowman & Iliffe, 1988, ♀. 347, antenna 2 (scale A). 348, labrum. 349, corpus mandibula of right mandible. 350, left mandible. 351, lobe of labium. 352, maxilla 2 (figs. 348-352 scale B). Scales indicated 0.1 mm.



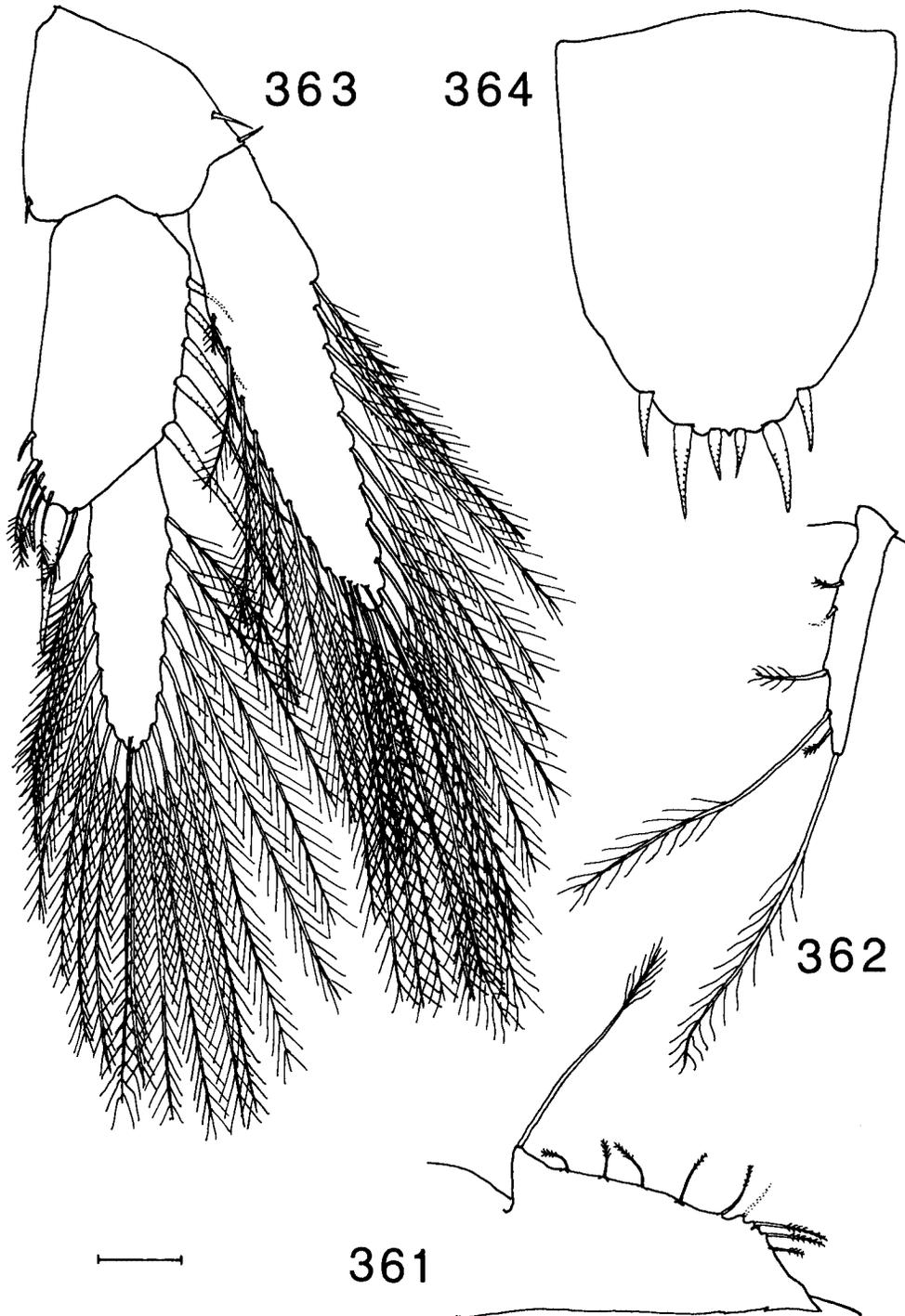
Figs. 353-354. *Tulumella unidens* Bowman & Iliffe, 1988, ♀. 353, maxilliped (scale B). 354, gnathopod (scale A). Scales indicated 0.1 mm.



Figs. 355-357. *Tulumella unidens* Bowman & Iliffe, 1988, ♀. 355, pereiopod 2. 356, pereiopod 3. 357, pereiopod 4. Scale indicated 0.1 mm.



Figs. 358-360. *Tulumella unidens* Bowman & Iliffe, 1988, ♀. 358, pereopod 5. 359, pereopod 6. 360, pereopod 7. Scale indicated 0.1 mm.



Figs. 361-364. *Tulumella undens* Bowman & Iliffe, 1988, ♀. 361, pleopod 1. 362, pleopod 2. 363, uropod. 364, telson. Scale indicated 0.1 mm.

original description are dubious, as a part of them is not easily visible without the Black Chlorazol B cuticular staining that even makes the tiniest macroseta visible.

Remarks.— *Tulumella unidens* shows a closer (general) similarity to *T. grandis* Yager, 1988, than to *T. bahamensis* Yager, 1988. However, it is quite distinct from both species in having one aesthetasc on the odd flagellar segments of antenna 1 and two aesthetascs on the even flagellar segments, by the absence of a lacinia mobilis in the left mandible, the absence of precoxal gill-like structures on pereopods 2 to 4, and the distinctly lower number of pairs of cuspidate macrosetae on the telson. For detailed information on specific differences with its congeners one is referred to table 4.

Distribution.— This species is known only from the vicinity of Tulum at the Yucatan Peninsula. Originally the species is described from the Najaron (=Naharon) Cenote, but it is also reported from Cueva Quebrada (Bowman, 1987), Carwash Cenote (Yager, 1987b; Holsinger, 1990), Mayan Blue Cave (Kornicker & Iliffe, 1989), and Temple of Doom Cenote (Holsinger 1990).

Habitat.— The Najaron (Naharon) cave is a completely underwater limestone cenote of Pleistocene Age (Back et al., 1986). There is a halocline present at approximately 15 metres depth, and the salinities of the water vary between 1.5‰ (at -14 m.) and 32.5‰ (at -15m) to 35‰ (at -20m.). Most of the animals were observed just above the holocline in oligohaline water (Bowman & Iliffe, 1988). A large diversity of accompanying fauna (mainly crustaceans) is encountered: remipedes (*Speleonectes tulumensis* Yager, 1987), amphipods (*Mayaweckelia cenotocola* Holsinger, 1977, *Tuluweckelia cernua* Holsinger, 1990, *Bahadzia bozanici* Holsinger, 1992, *Bahadzia setodactylus* Holsinger, 1992), isopods (*Creaseriella anops* (Creaser, 1936), *Bahalana mayana* Bowman, 1987), the mysid *Anthromysis* (*Anthromysis*) *cenotensis* Creaser, 1936, copepods, the ostracod *Danielopolina mexicana* Kornicker & Iliffe, 1989, shrimps (*Procaris* spec., *Typhlatya* spec., *Creaseria morleyi* (Creaser, 1936), and the brotulid cave fish *Ogilbia pearsei* (Hubbs, 1938).

#### 4.5.1.2. *Tulumella grandis* Yager, 1988 (figs. 365-376)

unident. spp.; Schram, 1986: 221.

Thermosbaenacea (partim); Stock, 1983b: 235; Holsinger & Yager, 1985: 290; Stock, 1986b: 926 (partim).

Thermosbaenaceans (sic); Cunliffe, 1985: 106, 108.

?Thermosbaenacea; Stock, 1986b: 926 (partim).

undescribed species (partim); Yager, 1987a: 310, 316.

*Tulumella grandis* Yager, 1988: 374, figs. 1-2; Cals & Monod, 1988: 342; Holsinger, 1989: 26; Cals & Monod, 1991: 173, figs. 1-4.

Thermosbaenaceans (partim); Kornicker, Yager & Williams, 1990: 2.

Material.— U.S.A., Bahamas: 2 ♀♀; Grand Bahama Island, Lucayan National Park, Lucayan Cavern; collected by D. Williams; 5.xi.1983; ZMA coll. no. C.A. 8160 (1 specimen) [topotypes].

- 2 ♀♀; Abaco Island, Dan's Cave; collected by J. Yager; 24.xii.1984; ZMA coll. no. C.A. 8159 [paratypes].

Description.— Body length (antennae 1 and 2 excluded) female up to 5153 µm (Yager, 1988: holotype 4.8 mm) in the material studied.

Antenna 1: peduncular segments 1 to 3 with three, eight and five long plumose

macrosetae on respective medial margins; main flagellum 24-segmented, one aesthetasc on segments 8, 10, 12, 14, and 16 to 21, two aesthetascs on segments 7, 9, 11, 13, and 15; accessory flagellum 16-segmented.

Antennae 2: scale on peduncle segment 3 with 16 plumose macrosetae, segments 4 and 5 without teazel macrosetae on mediodistal margin; flagellum 13-segmented, segments 1 to 12 each with two simple macrosetae.

Labrum: without peculiarities.

Mandible: second palp segment with six plumidenticulate macrosetae, third segment with 11 plumidenticulate macrosetae; lacinia mobilis present in left mandible, row of four slender serrate macrosetae, pars molaris with eight serrate spiniform processes.

Labium: without peculiarities.

Maxilla 1: precoxal endite with medial armature of 16 plumidenticulate macrosetae, of which six stout medioterminally and ten tall lateroterminally.

Maxilla 2: coxopodal endite medially with 22 fine plumose macrosetae, four rod macrosetae mediodorsally and two stout plumose macrosetae; basipodal endite 2 with 21 spoon-shaped serrate macrosetae, and two modified serrate macrosetae; basipodal endite 3 with 12 somewhat more strongly developed spoon-shaped macrosetae, increasing in size towards the lateral margin of the appendage; endopodite with two simple macrosetae; exopodite with four plumose macrosetae.

Maxilliped: coxopodal endite tapering lobe with two long pappose macrosetae; basipodal endite with three rows of five, seven and four plumidenticulate macrosetae, respectively, varying in size, but all with fine setules, a tall one medially, and submedially and with an additional much stouter plumidenticulate macroseta.

Gnathopod: baso-ischium with ten plumose macrosetae dorsally, one teazel macroseta distally on ventral margin, merus of endopodite with four teazel macrosetae on ventral margin, one teazel and one subplumose macroseta distodorsally; carpus with six very long serrate macrosetae on ventral margin; propodus with nine very long serrate macrosetae on ventral margin; exopodite 2-segmented, distal segment with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopods 2 to 7: shape (size excluded) and chaetotaxy uniform, but endopodite having dactylus with variable number of ovate microsetae: pereiopod 2 with 9; pereiopod 3 with 10; pereiopod 4 with 11; pereiopods 5 and 6 with 12 and pereiopod 7 with 8. Pereiopods 2 to 4 with precoxal gill-like structures, diminishing in size from anterior to posterior.

First pleopod: with one large medial and 14 small subplumose macrosetae towards lateral margin.

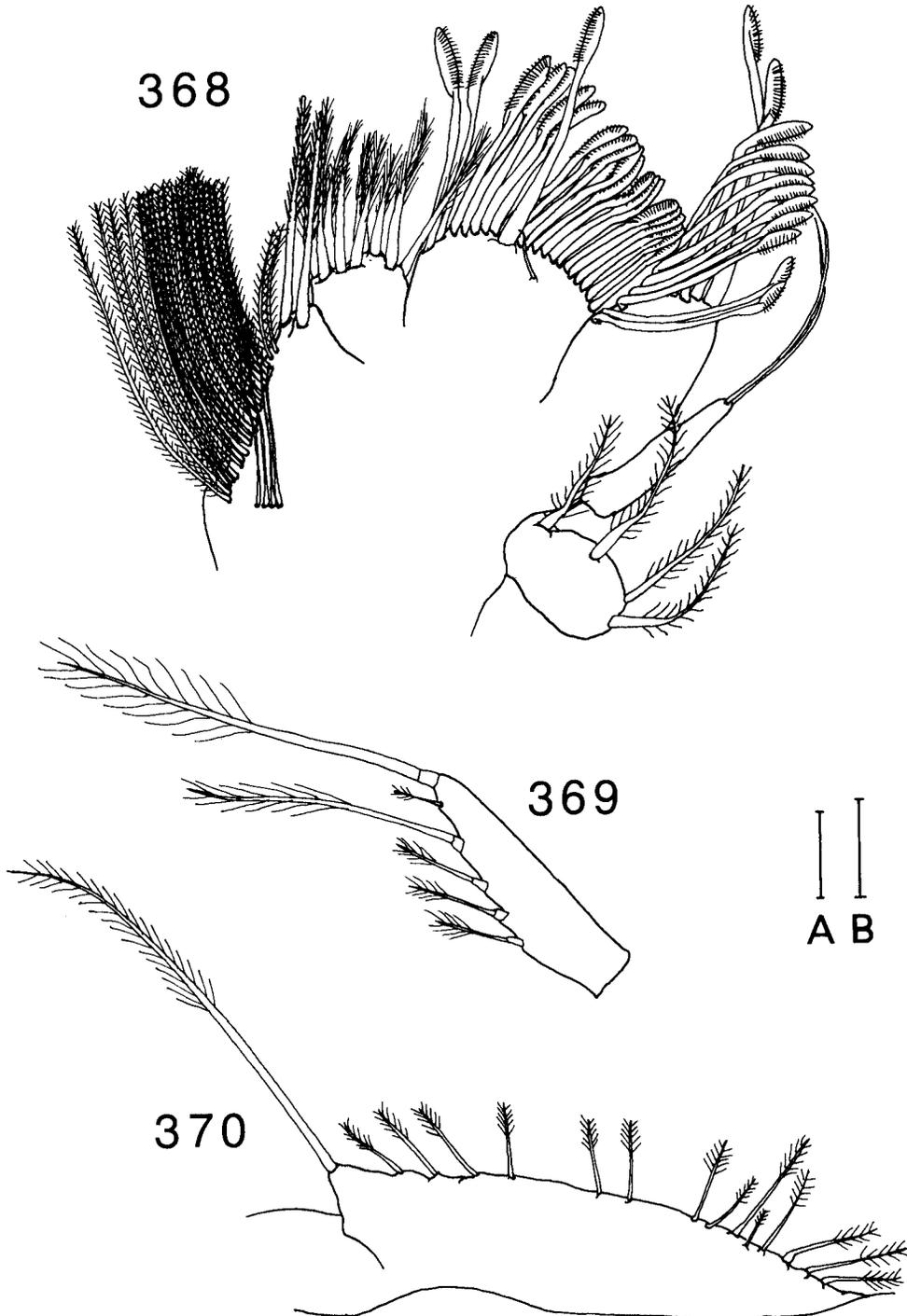
Second pleopod: with five dorsal and one terminal subplumose macrosetae.

Uropod: segment 1 of exopodite laterally with four cuspidate macrosetae, each accompanied by a subplumose macroseta, medially with four cuspidate macrosetae, segment 2 with 22 plumose macrosetae all along medial, terminal and lateral margins; endopodite with 26 plumose macrosetae along medial, terminal and lateral margins.

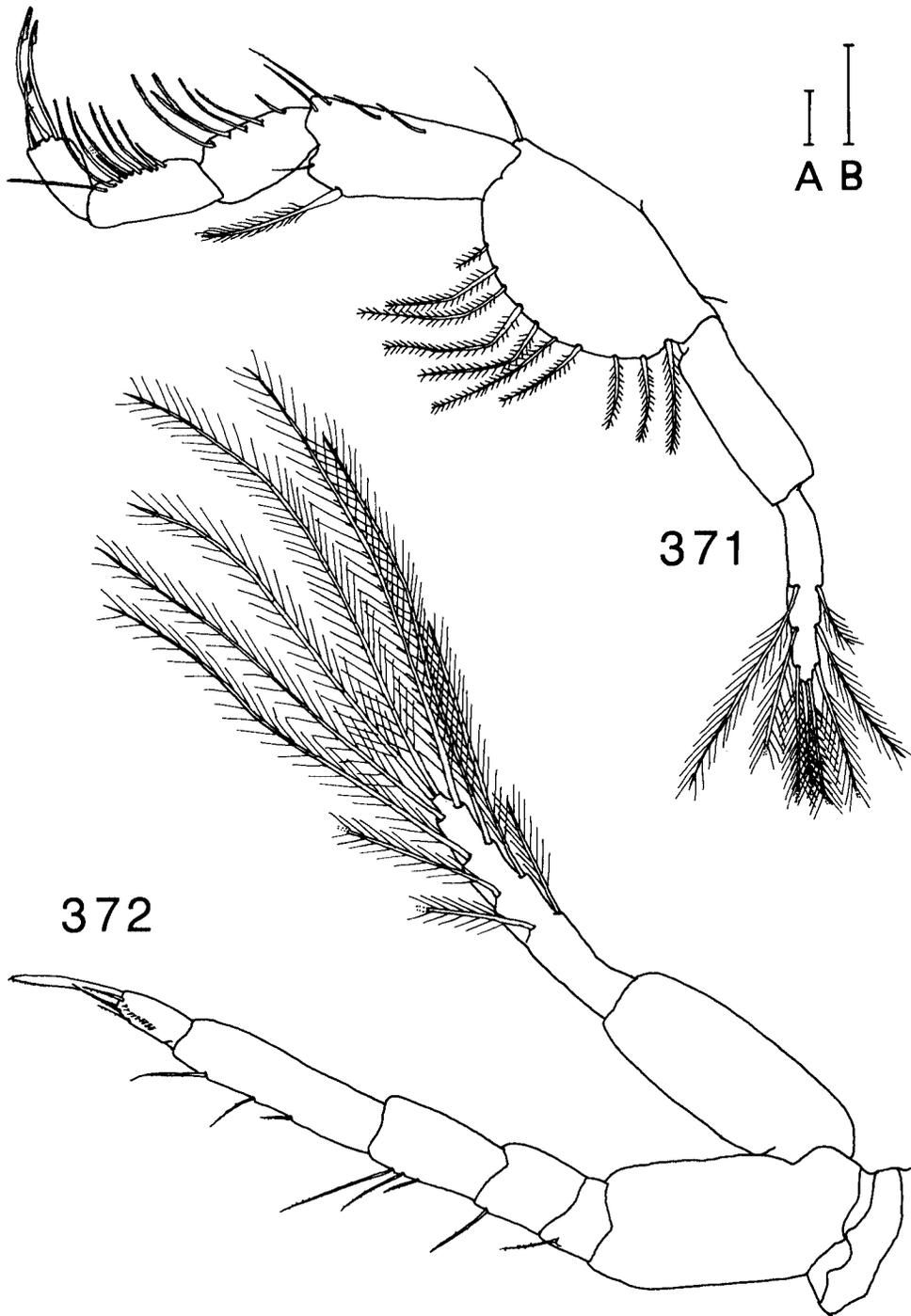
Telson: width/length ratio 0.79, six pairs of cuspidate macrosetae along distal margin, three simple macrosetae dorsally, of which one at the right and two at the left side.



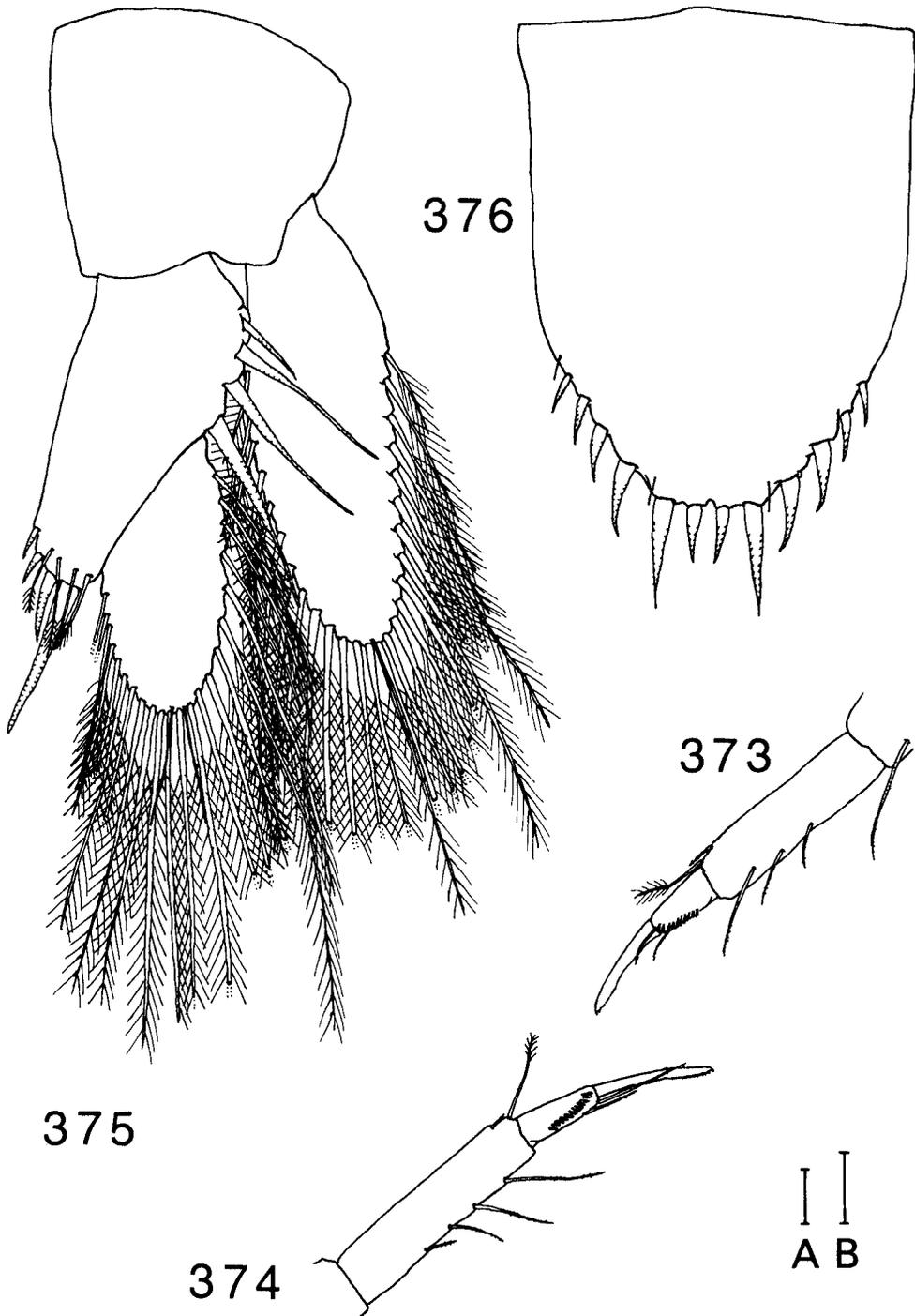
Figs. 365-367. *Tulumella grandis* Yager, 1988, ♀. 365, scale of antenna 2 (scale A). 366, left mandible. 367, coxopodal and endopodal endite of maxilliped (figs. 366-367 scale B). Scales indicated 0.1 mm.



Figs. 368-370. *Tulumella grandis* Yager, 1988, ♀. 368, maxilla 2 (scale A). 369, pleopod 1. 370, pleopod 2 (figs. 369-370 scale B). Scales indicated 0.1 mm.



Figs. 371-372. *Tulumella grandis* Yager, 1988, ♀. 371, gnathopod (scale B). 372, pereopod 2 (scale A). Scales indicated 0.1 mm.



Figs. 373-376. *Tulumella grandis* Yager, 1988, ♀. 373, distal portion of pereopod 3. 374, distal portion of pereopod 6 (figs. 373-374 scale A). 375, uropod. 376, telson (figs. 375-376 scale B). Scales indicated 0.1 mm.

Table 3. Accompanying fauna of *Tulumella* in the Bahamas

	GR. BAHAMA					ABACO	S. ANDROS		CAT ISL.	LONG ISL.	
	1	2	3	4	5	6	7	8	9	10	11
REMIPEDIA											
<i>Speleonectes lucayensis</i> Yager, 1981	x	x	x				x	x		x	
<i>S. benjamini</i> Yager, 1987		x	x				x				
<i>Speleonectes</i> spec.				x							
<i>Cryptocorynetes haptodiscus</i> Yager, 1987		x			x	x					
<i>Godzillius robustus</i> Schram, Yager & Emerson, 1986		x					x			x	
<i>Pleomothra aplocheles</i> Yager, 1989		x			x	x					
<i>Godzillioognomus frondosus</i> Yager, 1989		x	x	x			x			x	
THERMOSBAENACEA											
<i>Tulumella grandis</i> Yager, 1988	x	x	x	x	x		x	x			
<i>T. bahamensis</i> Yager, 1988	x					x	x	x			
unidentified specimens										x	x
AMPHIPODA											
<i>Bahadzia williamsi</i> Holsinger, 1985	x	x	x	x			x				
<i>B. setimana</i> Stock, 1986								x			
<i>B. obliqua</i> Stock, 1986										x	
unidentified hadzoid species											x
<i>Spelaeonicippe</i> cf. <i>provo</i> Stock & Vermeulen, 1982							x				
<i>Grandidierella</i> cf. <i>bonnieroides</i> Stephenson, 1947	x										
unidentified species			x								
ISOPODA											
<i>Bahalana geracei</i> Carpenter, 1981		x	x	x			x	x			
MYSIDACEA											
<i>Stygiomysis holthuisi</i> (Gordon, 1958)	x	x	x								
COPEPODA											
unidentified species	x	x							x		
OSTRACODA											
<i>Deeveya styrax</i> Kornicker, 1990		x					x				
<i>D. hirpex</i> Kornicker, 1990							x				
<i>D. medix</i> Kornicker, 1990			x				x				
<i>Deeveya</i> spec.		x									
<i>Speleoccia sagax</i> Kornicker, 1990			x								
<i>S. styx</i> Kornicker, 1990								x			
unidentified species		x						x		x	
NEBALIACEA											
unidentified species							x				
DECAPODA											
unidentified shrimps							x			x	
OLIGOCHAETA											
free-swimming species								x			
PISCES											
<i>Lucifuga spelaeotes</i> Cohen & Robbins, 1970	x	x	x				x	x			
<i>Eleotris pisonis</i> (Gmelin, 1788)	x						x				

This table is based on data published by Bowman, Iliffe & Yager (1984), Holsinger & Yager (1985), Schram, Yager & Emerson (1986), Stock (1986b), and Yager (1987a, 1988, and 1989).

Localities: 1. Lucayan Caverns; 2. Asgard Cave; 3. Sagittarius Cave; 4. Bahama Cement Cave; 5. Lucy's Cave; 6. Mermaid's Lair; 7. Dan's Cave; 8. Stargate Blue Hole; 9. El Dorado Cave; 10. Big Fountain Blue Hole; 11. locality unknown.

Variability.— Because the number of specimens at my disposal was rather limited, I could not establish any variation among the specimens dissected and examined with SEM. In comparison with the description given by Yager (1988) some differences (and variation) are found in the number of segments of the flagellum of antennae 1 and 2, and in the number of plumose macrosetae on the medial margin of the peduncular segments 2 and 3 of antenna 1. The number of plumose macrosetae on the scale of antenna 2 and the uropods, and the number of pairs of cuspidate macrosetae of the telson show some variation too. The variation found in the chaetotaxy of mandible, maxilla 2, maxilliped, and gnathopod must be regarded with some reserve, as a part of the information in table 4 is derived from the rather diagrammatic drawings by Yager. She also gives in her descriptive text approximate numbers (“... at least...”), which indicate that her observations are not necessarily accurate.

Remarks.— As remarked and discussed above in detail, *T. grandis* shows a closer relationship to *T. unidens* Bowman & Iliffe, 1988, than it does to *T. bahamensis* Yager, 1988. It can in general be distinguished from *T. bahamensis* by the distinctly larger number of micro- and macrosetae on the appendages, its larger size, and the presence of precoxal gill-like structures on pereopods 2 to 4. For detailed information on specific differences with its congeners one is referred to table 4.

Distribution.— This species has been reported from a number of localities in the Bahamas, viz., Grand Bahama (Lucayan Caverns (type locality), Asgard Cave, Sagittarius Cave, Bahama Cement Cave, Lucy's Cave, and Mermaid's Lair), Abaco Island (Dan's Cave), and South Andros Island (El Dorado Cave). Stock (1986b) reported thermosbaenaceans from Big Fountain Blue Hole on Cat Island, but the this material was not available to me. Yager (1988: 381) mentions a record of *Tulumella* from Long Island.

Habitat.— The anchihaline cave systems in which these thermosbaenaceans occur find their origin in the Pleistocene (Cunliffe, 1985). *Tulumella grandis* is a relatively euhaline nectic species that lives near the density interface of the halocline (Yager, 1988). Initially Yager mentions the species from marine passages below the density interface, later she states that it occurs just above and below the interface. In the Lucayan Caverns (Grand Bahama), Dan's Cave (Abaco Island) and the Stargate Blue Hole (South Andros Island) it occurs sympatrically with *T. bahamensis*. The density of the populations of both species at Lucayan Caverns is estimated at 20 individuals per m<sup>3</sup>; they are the most abundant animal in the water column (Yager, 1988). In table 3 a review is given of the fauna accompanying *T. grandis* and *T. bahamensis*.

#### 4.5.1.3. *Tulumella bahamensis* Yager, 1988 (figs. 377-388)

unident. spp.; Schram, 1986: 221.

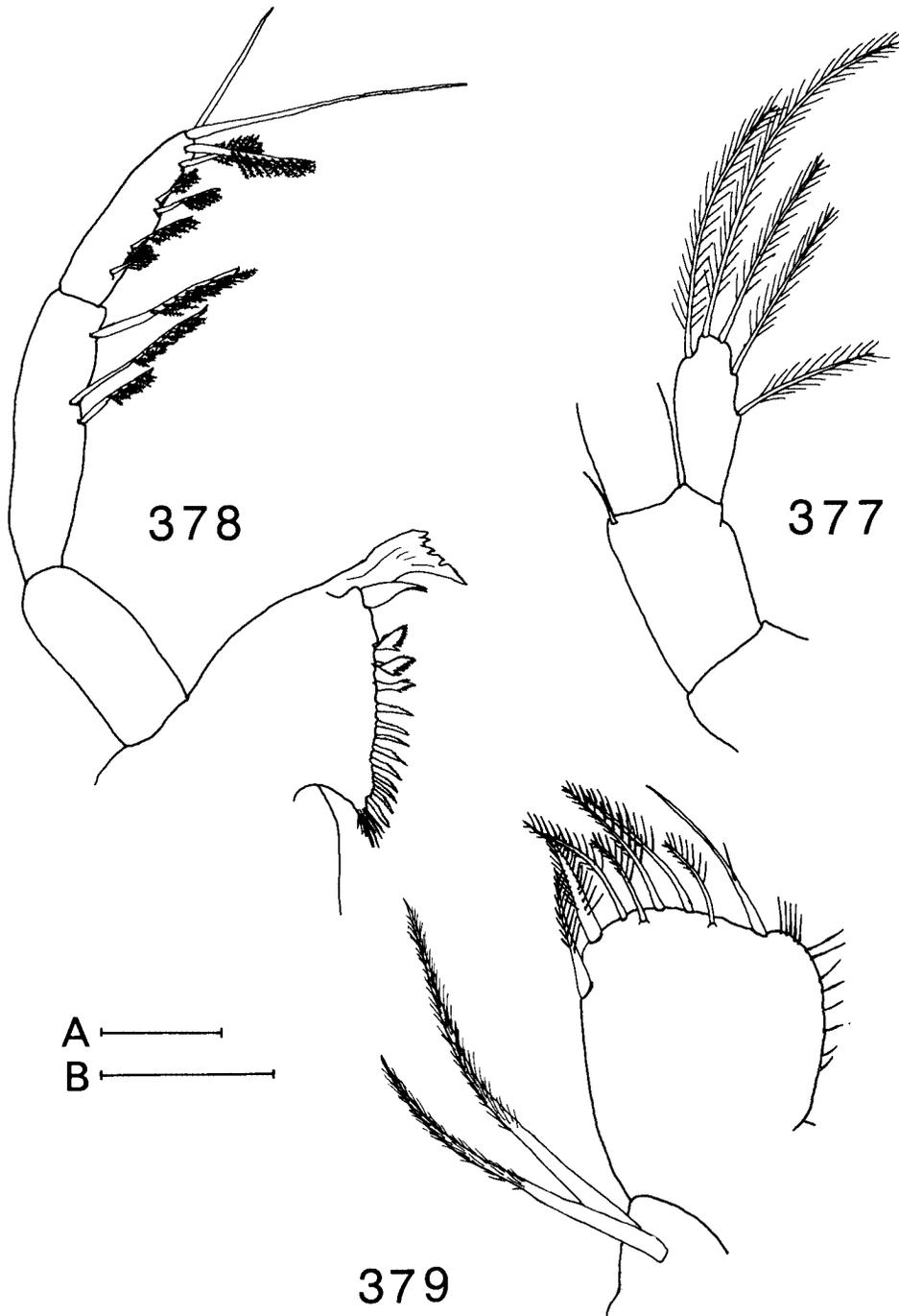
Thermosbaenacea (partim); Stock, 1983b: 235; Holsinger & Yager, 1985: 290; Stock, 1986b: 926 (partim).

?Thermosbaenacea; Stock, 1986b: 926 (partim).

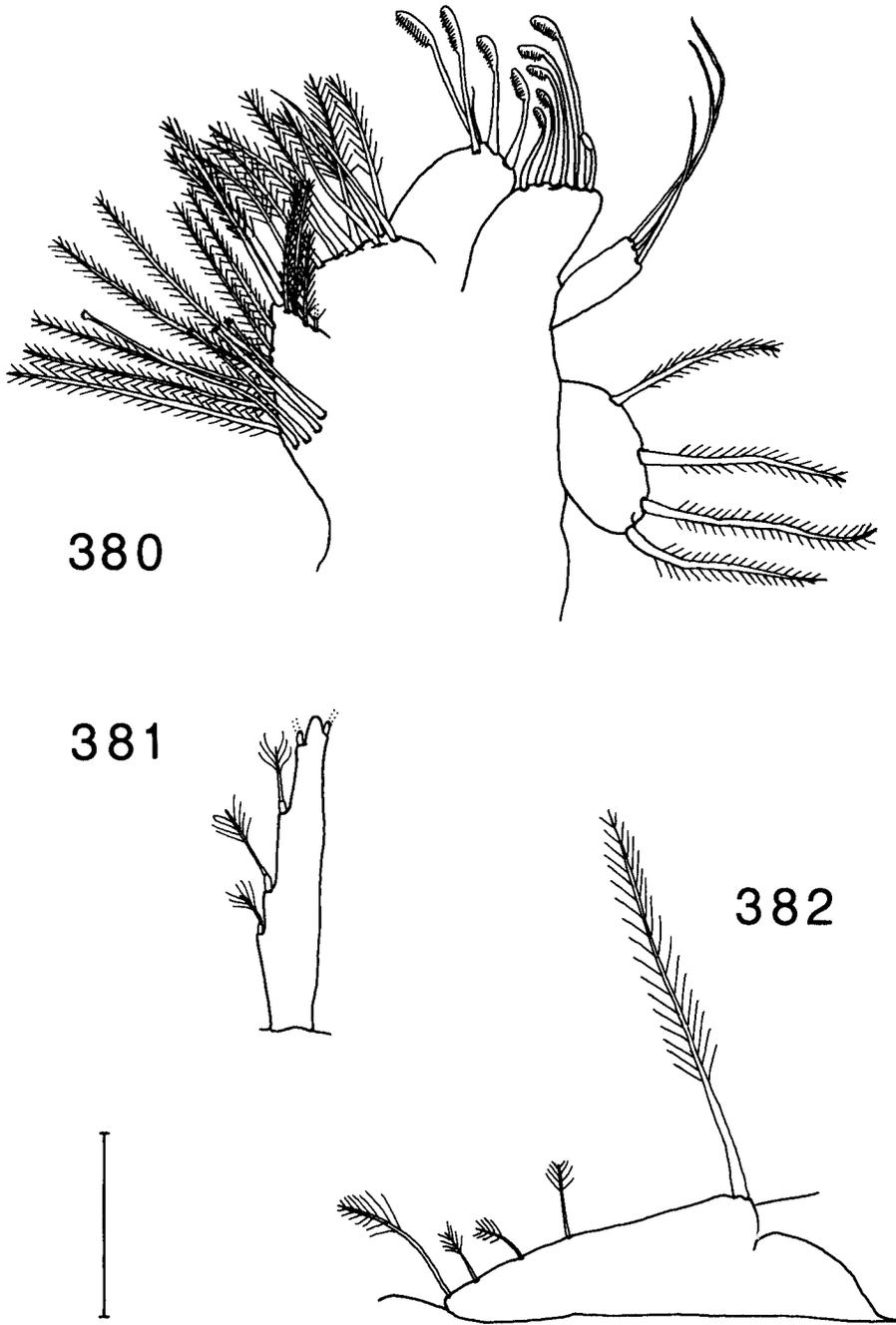
undescribed species (partim); Yager, 1987a: 310, 316.

*Tulumella bahamensis* Yager, 1988: 378, figs. 3-4; Cals & Monod, 1988: 342; Holsinger, 1989: 26; Kornicker, Yager & Williams, 1990: 2; Cals & Monod, 1991: 176.

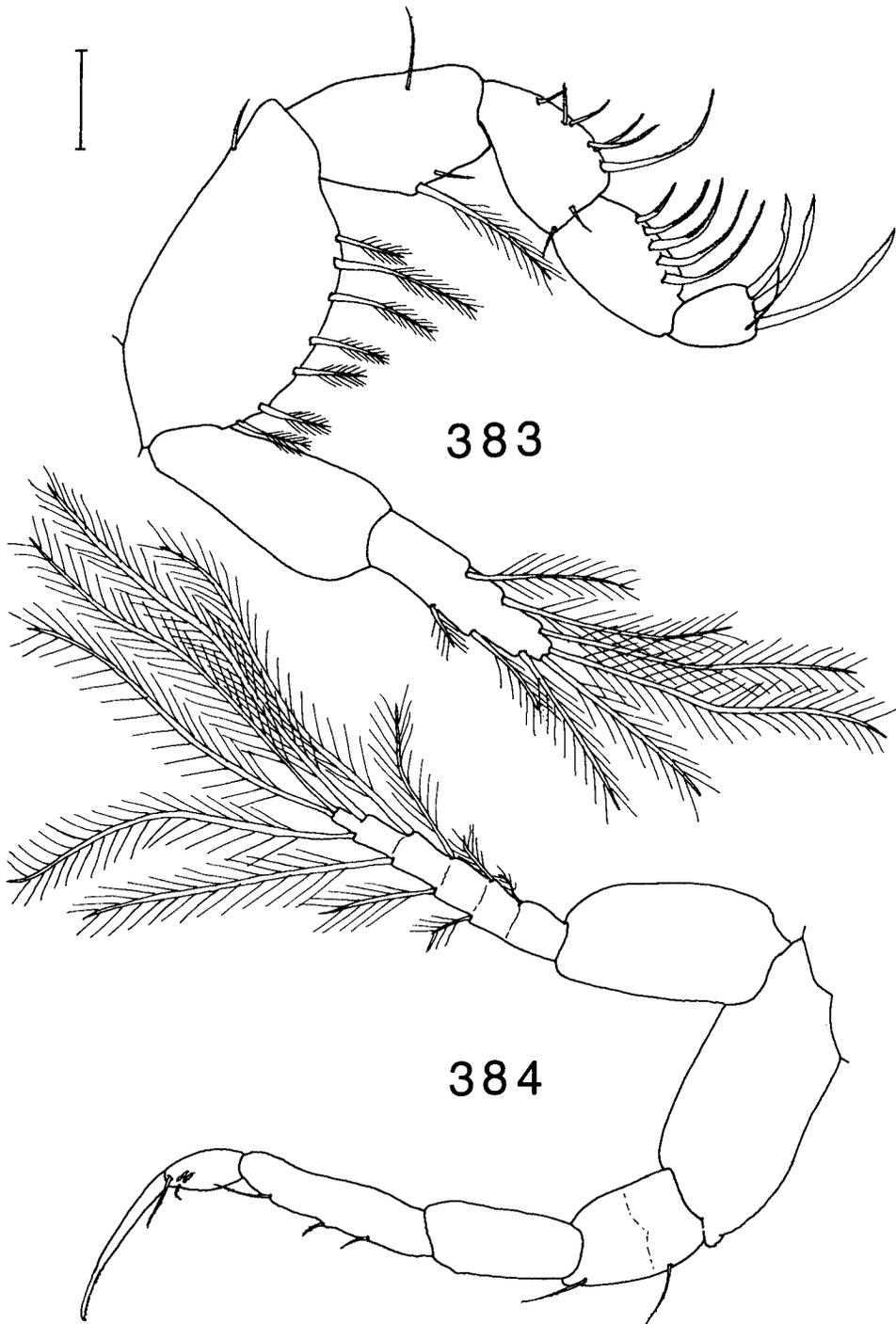
Thermosbaenaceans (partim); Kornicker, Yager & Williams, 1990: 2.



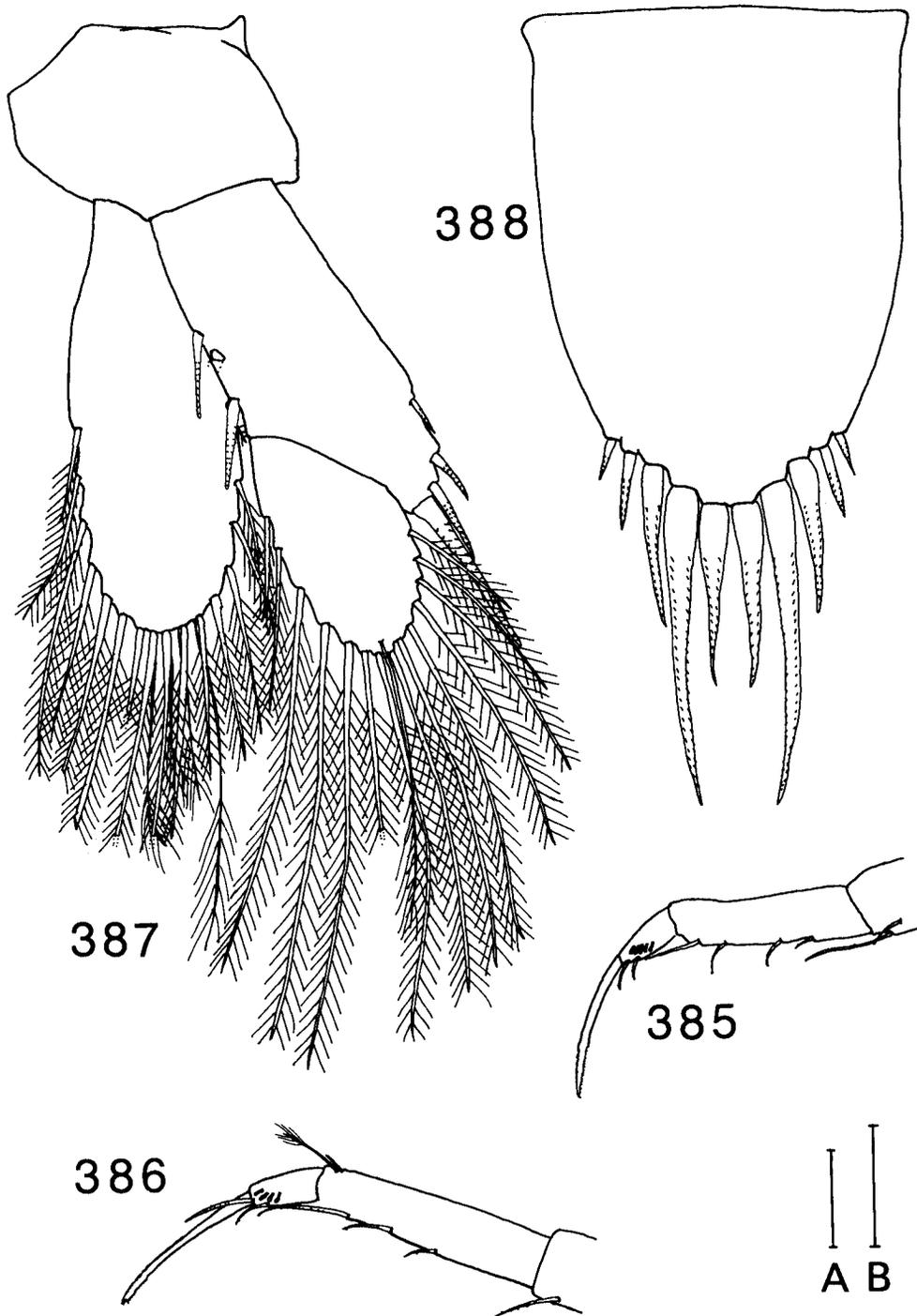
Figs. 377-379. *Tulumella bahamensis* Yager, 1988, ♀. 377, scale of antenna 2 (scale A). 378, left mandible. 379, coxopodal and endopodal endite of maxilliped (figs. 378-379 scale B). Scales indicated 0.1 mm.



Figs. 380-382. *Tulumella bahamensis* Yager, 1988, ♀. 380, maxilla 2. 381, pleopod 1. 382, pleopod 2. Scale indicated 0.1 mm.



Figs. 383-384. *Tulumella bahamensis* Yager, 1988, ♀. 383, gnathopod. 384, pereopod 2 (scale A). Scale indicated 0.1 mm.



Figs. 385-388. *Tulumella bahamensis* Yager, 1988, ♀. 385, distal portion of pereopod 3. 386, distal portion of pereopod 6 (figs. 385-386 scale A). 387, uropod. 388, telson (figs. 387-388 scale B). Scales indicated 0.1 mm.

Material.— U.S.A., Bahamas: 2 ♀♀; South Andros Island, El Dorado Cave; collected by D. Williams; 19.x.1986; ZMA coll. no. C.A. 8161 [topotypes].

Description.— Body length (antennae 1 and 2 excluded) female up to 3028  $\mu\text{m}$  (Yager, 1988: holotype 3.1 mm) in the material studied.

Antenna 1: peduncular segments 1 to 3 with two, six and three long plumose macrosetae on respective medial margins; main flagellum 11-segmented, one aesthetasc on segments 4, 6, 8, and 9, two aesthetascs on segments 5 and 7; accessory flagellum 8-segmented.

Antennae 2: scale on peduncle segment 3 with 5 plumose macrosetae, segments 4 and 5 without teazel macrosetae on mediodistal margin; flagellum 7-segmented, segments 1 to 6 each with two simple macrosetae.

Labrum: without peculiarities.

Mandible: second palp segment with three plumidenticulate macrosetae, third segment with six plumidenticulate macrosetae; lacinia mobilis present in left mandible, row of three slender serrate macrosetae, pars molaris with nine serrate spiniform processes.

Labium: without peculiarities.

Maxilla 1: precoxal endite with medial armature of 12 plumidenticulate macrosetae, of which six stout mediotermally and six tall laterotermally.

Maxilla 2: coxopodal endite medially with 7 fine plumose macrosetae, four rod macrosetae mediodorsally and two stout plumose macrosetae; basipodal endite 2 with three spoon-shaped serrate macrosetae, and two modified serrate macrosetae; basipodal endite 3 with six somewhat more strongly developed spoon-shaped macrosetae, increasing in size towards the lateral margin of the appendage; endopodite with three simple macrosetae; exopodite with four plumose macrosetae.

Maxilliped: coxopodal endite a tapering lobe with one short and two long papose macrosetae; basipodal endite with two rows of two and four plumidenticulate macrosetae, respectively, varying in size, but all with fine setules, a tall one medially, and submedially and with an additional much stouter plumidenticulate macroseta.

Gnathopod: basal segment with seven plumose macrosetae dorsally, one teazel macroseta distally on ventral margin, merus of endopodite with one teazel macroseta on ventral margin, one teazel and one subplumose macroseta distodorsally; carpus with six very long serrate macrosetae on ventral margin; propodus with five very long serrate macrosetae on ventral margin; exopodite 2-segmented, distal segment with two medial, two subterminal, two terminal and two to three lateral plumose macrosetae.

Pereiopods 2 to 7: shape (not size) and chaetotaxy uniform, but endopodite having dactylus with variable number of ovate microsetae: pereiopod 2 with 2; pereiopods 3 and 4 with 5; pereiopods 5 and 6 with 4 and pereiopod 7 with 2. Pereiopods 2 to 4 without precoxal gill-like structures.

First pleopod: with one large medial and four small subplumose macrosetae towards the lateral margin.

Second pleopod: with four dorsal and one terminal subplumose macrosetae.

Uropod: segment 1 of exopodite laterally with three cuspidate macrosetae each

accompanied by subplumose macroseta, medially with four cuspidate macrosetae, segment 2 with 14 plumose macrosetae all along medial, terminal and lateral margins; endopodite with 16 plumose macrosetae along medial, terminal and lateral margins.

Telson: width/length ratio 0.80, five pairs of cuspidate macrosetae along distal margin, dorsal simple macrosetae absent.

Variability.— Of this species only two specimens were at my disposal, so I could not establish any variation. In comparison with the description given by Yager (1988) only minor differences have been observed in the number of segments of the flagellum of antennae 1 and 2, and in the number of plumose macrosetae of the uropods. The number of pairs of cuspidate macrosetae of the telson shows some variation too. For the same reasons mentioned in the discussion of the variation of *T. grandis*, the variation found in the chaetotaxy of mandible, maxilla 2, maxilliped, and gnathopod must be regarded with some reservation.

Remarks.— For detailed information on specific differences with its congeners one is referred to table 4.

Distribution.— This species has been reported from a number of localities in the Bahamas, e.g. Grand Bahama (Lucayan Caverns (type locality), and Mermaid's Lair), Abaco Island (Dan's Cave), and South Andros Island (Stargate Blue Hole, and El Dorado Cave). Stock (1986b) reported thermosbaenaceans from Big Fountain Blue Hole on Cat Island, but this material was not available to me. Yager (1988: 381) also mentions *Tulumella* to be present at Long Island.

Habitat.— The anchihaline karstic cave systems in which these thermosbaenaceans occur find their origin in the Pleistocene (Cunliffe, 1985). *Tulumella bahamensis* is a relatively euhaline nectic species that lives near the density interface of the halocline (Yager, 1988). Initially Yager mentioned the species from marine passages below the density interface, but later she states that it occurs just above and below the density interface. In the Lucayan Caverns (Grand Bahama), Dan's Cave (Abaco Island) and the Stargate Blue Hole (South Andros Island) it occurs sympatrically with *T. grandis*. The density of the populations of both species at Lucayan Caverns is estimated at 20 individuals per m<sup>3</sup>, they are the most abundant animal in the water column (Yager, 1988). In table 3 a review is given of the fauna accompanying *T. grandis* and *T. bahamensis*.

#### 4.6. Halosbaenidae Monod & Cals, 1988

Halosbaenidae Monod & Cals, 1988: 101; Wagner, 1988: 1st page; Cals & Monod, 1988: 343; Wagner, 1990: 123; Cals & Monod, 1991: 177.

Halosbaenidea (sic); Bowman & Iliffe, 1988: 226.

Diagnosis.— Thermosbaenaceans with elongate body. Rostrum short, broad, and indistinct. Small eye-stalks (ocular scales) present. Peduncular segments of antenna 1 without long plumose macrosetae along medial margin; main flagellum of antenna 1 3- to 29-segmented; accessory flagellum 3- to 14-segmented. Flagellum of antenna 2 5- to 7-segmented. Mandible with several plumidenticulate macrosetae on second segment of palp; left pars incisiva 3- or 5-dentate, right pars incisiva 2-, 6- or 9-dentate; lacinia mobilis present on left mandible; pars molaris pointedly triangular or ensiform, molar surface with ciliate microsetae only. Maxilla 1 with 2-segmented palp,

Table 4. Salient differences between the species of *Tulumella*

	<i>T. unidens</i> Bowman & Iliffe, 1988	<i>T. grandis</i> Yager, 1988	<i>T. bahamensis</i> Yager, 1988
<b>Antenna 1:</b>			
# segments main flagellum	[18]-22	[18-22]-24	[8 -] 11
# segments accessory flagellum	14	[14 -] 16	8
# plumose macrosetae segments 1,2,3	3, 6, 3[5]	3, [6]-8, 5[6]	2, 6, 3
1 aesthetasc on flagellar segment no.	5, 7, 9, 11, 13-19	8, 10, 12, 14, 16-21	4, 6, 8, 9
2 aesthetascs on flagellar segment no.	4, 6, 8, 10, 12	7, 9, 11, 13, 15	5, 7
<b>Antenna 2:</b>			
# plumose macrosetae on scale	[10 -] 11	[12 -] 16	5
# medial m.s. peduncular segm. 4 and 5	2	0	0
# segments flagellum	10	[12-14] 13	7 [8-10]
<b>Mandible:</b>			
# plumidenticulate m.s. palp segm. 2	[4 -] 5	6	3-[4]
# plumidenticulate m.s. palp segm. 3	8	[10]-11	6 [-8]
lacinia mobilis in left mandible	absent	present	present
# serrate m.s. left /right mandible	3 / 3	4 / 4	3 / 3
# serrate spiniform processes molar	6	8	9
<b>Maxilla 1:</b>			
# tall + stout m.s. coxopodal endite	10 + 6	10 + 6	6 + 6
<b>Maxilla 2:</b>			
# plumose m.s. coxopodal endite	[22]-27	22-[24]	7-[15]
# spoon-shaped m.s. b.e.2	9-[11]	21 [± 20]	3 [± 6]
# spoon-shaped m.s. b.e.3	[6]-7	12 [± 12]	6 [± 6]
# simple m.s. endopodite	4	2	3-[4]
# plumose m.s. exopodite	3-[4]	4	4-[5]
<b>Maxilliped:</b>			
total # plumidenticulate m.s.	[14]-15	[12-14]-18	8 [-10]
# pappose m.s. coxopodite	3	2	2
<b>Gnathopod:</b>			
# plumose m.s. baso-ischium	6-[8]	[± 9] 10	[± 5]-7
# ventral teazel m.s. merus	3	[2]-4	[0]-1
# serrate m.s. carpus	[5]-8	6 [±6]	[4]-6
# serrate m.s. propodus	7-[10]	[±6] 9	5-[6]
# plumose m.s. exopodite	8-9	8	8-9
<b>Pereiopods 2 to 4:</b>			
precoxal gill-like structures	absent	present	absent
<b>Pereiopod 2:</b>			
# ovate microsetae dactylus	10	9	2
<b>Pereiopod 3:</b>			
# ovate microsetae dactylus	11	10	5
<b>Pereiopod 4:</b>			
# ovate microsetae dactylus	12	11	5
<b>Pereiopod 5:</b>			
# ovate microsetae dactylus	13	12	4
<b>Pereiopod 6:</b>			
# ovate microsetae dactylus	11	12	4
<b>Pereiopod 7:</b>			
# ovate microsetae dactylus	11	8	2
<b>Pleopod 1:</b>			
# subplumose m.s.	1 large + [8] 9 small	1 large + 14 small	1 large + 4 small

Table 4 (continued).

Pleopod 2:			
# dorsal subplumose m.s.	5	5	4
Uropod:			
# plumose m.s. endopodite	[18]-22	[20-24]-26	[11]-16
# cusp. m.s. med. margin ex. segm. 1	[4]-5	[3 -] 4	[3]-4
# cusp. m.s. lat. margin ex. segm. 1	[3]-4	[3 -] 4	[2]-3
# plumose m.s. ex. segm. 2	18	[15+]-22	[12]-14
Telson:			
# pairs of cuspidate m.s.	3	[5]-6	[4]-5
# (dorsal) simple m.s.	0	3 (1 right, 2 left)	0
mean width/length ratio	0.82	0.79	0.80

abbreviations: b.e. = basipodal endite; cusp. = cuspidate; end. = endopodite; ex. = exopodite; lat. = lateral; med. = medial; m.s. = macroseta(e); no. = number; plum. = plumose; segm. = segment; # = number of....; [...] = character state in original description or figure(s).

basal segment of palp not fused with second segment; basipodal endite with seven to eight toothed macrosetae. Basipodal endite 1 of maxilla 2 with one long, five obscurely serrate and six modified plumidenticulate macrosetae, tip of modified type flattened, ovate and terminally digitate, a ring of stout setules around basis of flattened portion (as in fig. 12); basipodal endite 2 with two rows of rake-like serrate macrosetae; basipodal endite 3 with numerous rake-like macrosetae arranged in oblique rows, thus forming triangular field of macrosetae; endopodite 2-segmented; exopodite absent. Maxilliped with three to six complexly setulated pappose macrosetae on coxopodite; (sub)terminal margin of basipodite with three rows of (modified) plumidenticulate macrosetae; endopodite reduced, with ciliate microsetae; exopodite lobate, with ciliate microsetae; epipodite lobate or well-developed. Seven pairs of pereopods; gnathopod uniramous, in baso-ischium of endopodite demarcation of ischium obscure, dorsal margin naked or with numerous fine simple microsetae, dactylus with three to four (modified) serrulate macrosetae forming a claw; pereopods 2 to 6 biramous, exopodites 2-segmented; pereopod 7 uniramous or biramous, exopodite (when present) 1- or 2-segmented. First pleopod unarticulate, fused with first pleonite, forming a protrusion with subplumose and simple macrosetae; second pleopod articulate, more or less triangular to elongate, with three to four subplumose macrosetae; pleopods 3 to 5 absent, but in some genera small simple macrosetae is left. Endopodite of uropod longer than first segment of exopodite or longer than entire exopodite, medial margin of endopodite with serrate cuspidate macrosetae; first segment of exopodite distomedially with three to six cuspidate macrosetae, distolaterally with five to nine macrosetae, each accompanied by a subplumose macroseta. Telson not fused with pleonite 6, tongue-shaped, with four to sixteen cuspidate macrosetae at either side on the posterolateral margin.

Discussion.— The family Halosbaenidae comprises three genera, viz. *Limnosbaena*, the nominal genus *Halosbaena*, and the monotypic genus *Theosbaena*. In order to facilitate identification at the generic level a key is provided below.

Key to the genera of Halosbaenidae  
based on characters visible without dissection

1. Main flagellum of antenna 1 4-segmented, accessory flagellum 3-segmented; gnathopod with one serrate macroseta on ventral margin; pereopod 7 uniramous; distomedial margin of first segment of uropodal exopodite with cuspidate macroseta ..... *Limnosbaena* Stock, 1976 (p. 232)  
- Main flagellum of antenna 1 more than 8-segmented, accessory flagellum more than 4-segmented; gnathopod with three or four serrate macrosetae on ventral margin; pereopod 7 biramous; distomedial margin of first segment of uropodal exopodite with plumose macroseta ..... 2
2. Main flagellum of antenna 1 9- to 16-segmented, accessory flagellum 4- to 7-segmented; gnathopod with four serrate macrosetae on ventral margin; exopodite of pereopod 7 2-segmented; pleonites 3 to 6 with simple macrosetae ventrally; medial margin of uropodal endopodite with stout serrate macrosetae; telson with four pairs of cuspidate macrosetae and three to five serrate macrosetae along posterolateral margin ..... *Halosbaena* Stock, 1976 (p. 247)  
- Main flagellum of antenna 1 29-segmented, accessory flagellum 14-segmented; gnathopod with three serrate macrosetae on ventral margin; exopodite of pereopod 7 1-segmented; pleonites 3 to 6 without simple macrosetae ventrally; medial margin of uropodal endopodite with scale-like serrate macrosetae; telson with 13 to 16 cuspidate macrosetae along posterolateral margin ..... *Theosbaena* Cals & Boutin, 1985 (p. 279)

4.6.1. *Limnosbaena* Stock, 1976

*Limnosbaena* Stock, 1976: 64; McLaughlin, 1980: 84; Abele, 1982: 277; Stock, 1986a: 587; Cals, 1987: 661; Monod & Cals, 1988: 101, pl. 2, fig. 2; Wagner, 1988: 1st page; Bowman & Iliffe, 1988: 225; Wagner, 1990: fig. 1; Meštrov & Cals, 1991: 41; Cals & Monod, 1991: 174.  
Termosbenacei; Gasparo, Minelli & Brandmayr, 1984: 51.

Type species.— *Limnosbaena finki* (Meštrov & Lattinger-Penko, 1969).

Diagnosis.— Body length (antenna 1 and 2 excluded) up to 2.1 mm. Carapace reaching to the fourth pedigerous somite. Third peduncular segment of antenna 1 with three subplumose macrosetae on terminal prominence; main flagellum 4-segmented; accessory flagellum 3-segmented. Flagellum of antenna 2 5-segmented. Ocular scales evenly rounded anteriorly. Mandible with two plumidenticulate macrosetae on second segment of palp; left pars incisiva 3-dentate, right pars incisiva 2-dentate (of which one with five lobate protrusions distally); lacinia mobilis with six lobate protrusions (absent in right mandible); row of three serrate macrosetae in left mandible, row of four serrate macrosetae in right mandible; pars molaris ensiform, molar surface covered by five very long ciliate microsetae. Palp of maxilla 1 with two long bisetulate macrosetae (sub)terminally; basipodal endite with seven tall and sharply dentate toothed macrosetae. Coxopodal endite of maxilla 2 with 18 long plumose, six rod and two stout plumose macrosetae; basipodal endite 1 with one long (tip pointed, dentations obscure), five obscurely setulate and six stout (modified) plumidenticulate macrosetae. Maxilliped with three complexly setulated pappose macrosetae on coxopodal endite, setules with flattened distal portion (with LM no

detailed structures visible); subterminal margin with three rows of differently shaped plumidenticulate macrosetae, a ventral row of curved macrosetae, a central row of long macrosetae with foliaceous setules and a dorsal row of short, stout, and distally densely setulate macrosetae, submedially a modified (e.g., with partially reduced elements) "plumidenticulate" macroseta is implanted, being faintly S-shaped, and naked, except for a short setule present on top of each prominence, these prominences arranged in two closely set parallel rows of 14 prominences on distal half. Gnathopod propodus with one teazel macroseta ventrally; dactylus with three unequally long serrulate macrosetae with somewhat flattened rake-like tips forming a claw terminally; pereiopod 7 uniramous. First pleopod a rounded process with six subplumose macrosetae flanked by two simple macrosetae medially; second pleopod almost rectangular with three subplumose macrosetae, flanked by simple macrosetae laterally; long and short simple macrosetae lying in the extension of pleopod 2 on pleonites 3 to 5 probably representing remnants of pleopods 3 to 5 and their accompanying simple macrosetae. Uropodal endopodite somewhat longer or shorter than exopodite, medial margin with cuspidate macrosetae; first segment of exopodite distomedially with a single cuspidate macroseta, distolaterally with three cuspidate macrosetae and two subplumose macrosetae. Telson posteriorly with three to four pairs of cuspidate macrosetae on distal corners, two to three pairs of serrate macrosetae somewhat more dorsally.

Description.— As for the type species.

Remarks.— There has been some confusion about the taxonomic position of *Limnosbaena* in the past. Initially based on the original description of the type species, Monod & Cals (1988) erected the subfamily Limnosbaeninae as they believed *Limnosbaena* showed intermediate characters between *Monodella* (well-developed endopodite in male maxilliped) and *Halosbaena* (great similarity in general morphology of remaining mouthparts, pereiopods, pleopods, and telson). After examining a number of dissected specimens from Comaria at my disposal, Cals agreed with me that the confusion was based on the misinterpretation of the gnathopod being treated as endopodite of the maxilliped (Meštrov & Cals, 1991: 47). With this major problem solved, there is no doubt that *Limnosbaena* is a typical member of the Halosbaenidae as defined above.

Distribution.— Representatives of this genus are known from limnic waters in Bosnia and in the Italian part of Comaria, and from the vicinity of Senas, northwest of Marseille, southern France.

Habitat.— The only data available pertain to *Limnosbaena finki*, which inhabits purely limnic waters.

#### 4.6.1.1. *Limnosbaena finki* (Meštrov & Lattinger-Penko, 1969) (figs. 389-411)

*Monodella finki* Meštrov & Lattinger-Penko, 1969: 113, figs. 1-16.

*Limnosbaena finki*; Stock, 1976: 66; Pinkster, 1978: 234; Abele, 1982: 276; Stock, 1986a: 587; Schram, 1986: 220; Cals & Monod, 1988: 342; Wagner, 1990: 123; Meštrov & Cals, 1991: 42, figs. 1-4; Pretus, 1991: 235.

Thermosbaenacea (partim); Sket et al., 1991: 43.

Material.— **Bosnia-Hercegovina:** 1 ♂; Bosnia, Zenica, 50 m from the river Bosna; pumped from alluvia, at 7 m depth, temperature 8°C, pH 6.8, salinity 1.2 mg/l, CO<sub>2</sub> 7.2 mg/l; collected by M. Mestrov and R. Lattinger-Penko; 30.vi.1965; UZC [holotype].

Accompanying fauna: Crustacea: Isopoda (*Stenasellus skolpjensis skolpjensis* (S.L. Karaman, 1936), *Microcharon* spec.), Amphipoda (*Niphargus* spec.).

**Italy:** 5 ♂♂, 1 ♀, 2 fragmentary specimens; Doberdo di Lago (=Doberdob), Comaria (=Komarje), Grotta di Comaria (=Jama pri Komarjih); fresh water; collected by F. Gasparo & F. Stoch; diverse data in 1983-1986; ZMA coll. no. C.A. 8097; UEKL; UR.

Description.— Body length (antennae 1 and 2 excluded) up to circa 2050 µm in the material studied.

Antenna 1 with 3-segmented peduncle; peduncular segment 1 three teazel macrosetae (type IIB3) of unequal length on medial margin, one medially, two distally, dorsolateral margin with a transverse row of seven fine plumose macrosetae (type IA1); peduncular segment 2 distally with one teazel macroseta (type IIB3) on dorsomedian margin, one teazel macroseta (type IIB3) on ventromedian margin, one teazel macroseta (type IIB3) on dorsolateral margin, one teazel macroseta (type IIB3) on ventrolateral margin; peduncular segment 3 with one teazel macroseta (type IIB3) on distomedial margin, one teazel macroseta (type IIB3) on mediolateral margin, terminal prominence with three subplumose macrosetae (type IB2); main flagellum 4-segmented, distally with one simple macroseta (type IIA1) on lateral margin, a longitudinal row of six aesthetascs (type IIA6) on medial margin of first segment, segments 2 and 3 with one aesthetasc (type IIA6) medially; accessory flagellum 3-segmented, segments with one simple macroseta (type IIA1) laterally, two simple macrosetae (type IIA1) medially, last segment (sub)terminally with three simple macrosetae (type IIA1) of unequal length.

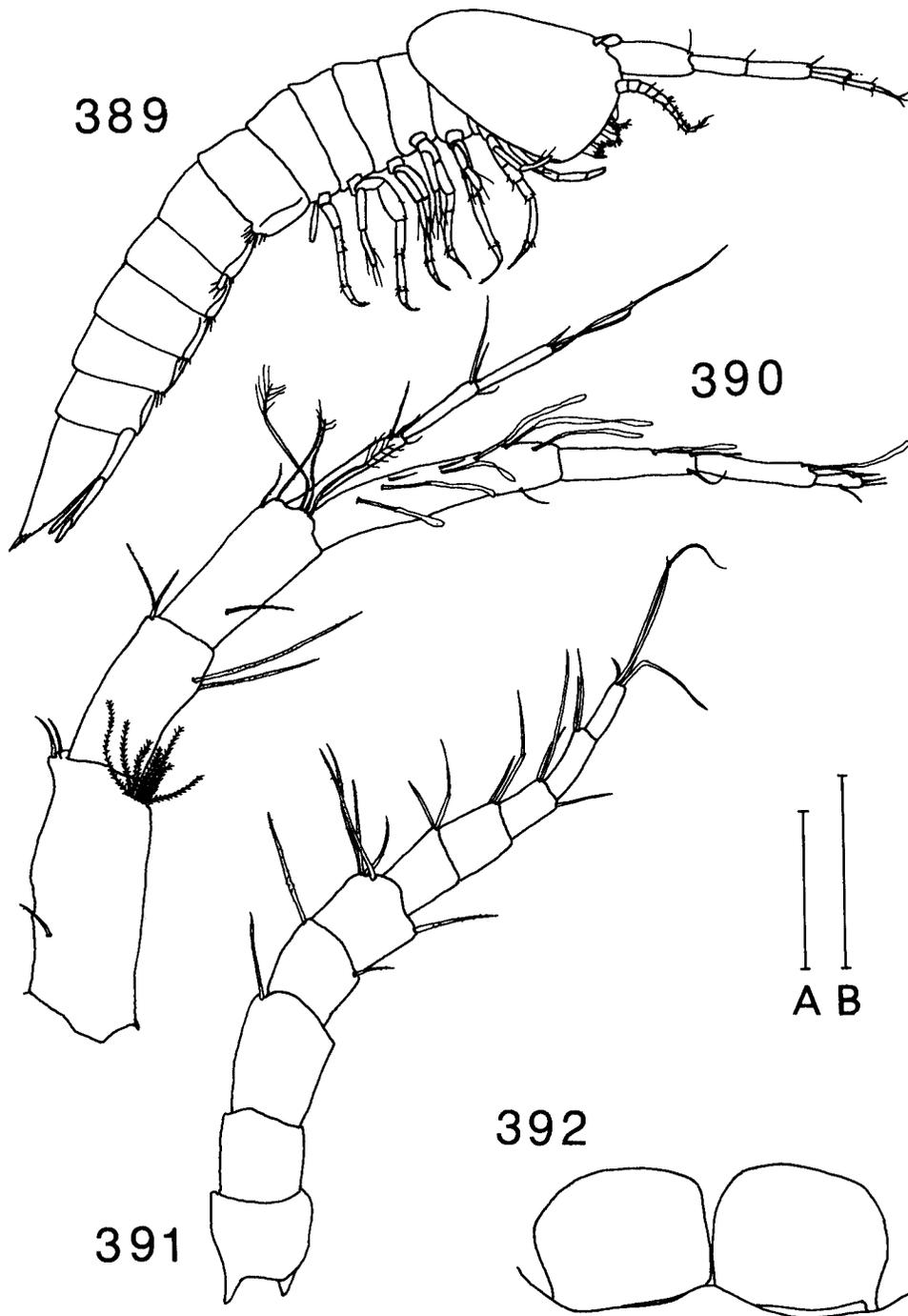
Antenna 2 uniramous, peduncle 5-segmented; segments 1 and 2 naked, segment 3 with one teazel macroseta (type IIB3) distomedially, segment 4 with one teazel macroseta (type IIB3) distomedially and one teazel macroseta (type IIB3) distolaterally, segment 5 with one lateral and four medial teazel macrosetae (type IIB3) distally; flagellum 5-segmented, segments 1 to 4 with two simple macrosetae (type IIA1) on medial margin, segment 3 one simple macroseta (type IIA1) on distolateral margin, last segment with four simple macrosetae (type IIA1) (sub)terminally.

Labrum 1.6 times broader than long, its proximal portion densely covered with ciliate microsetae (type 2b), apically with ovate microsetae (type 2a).

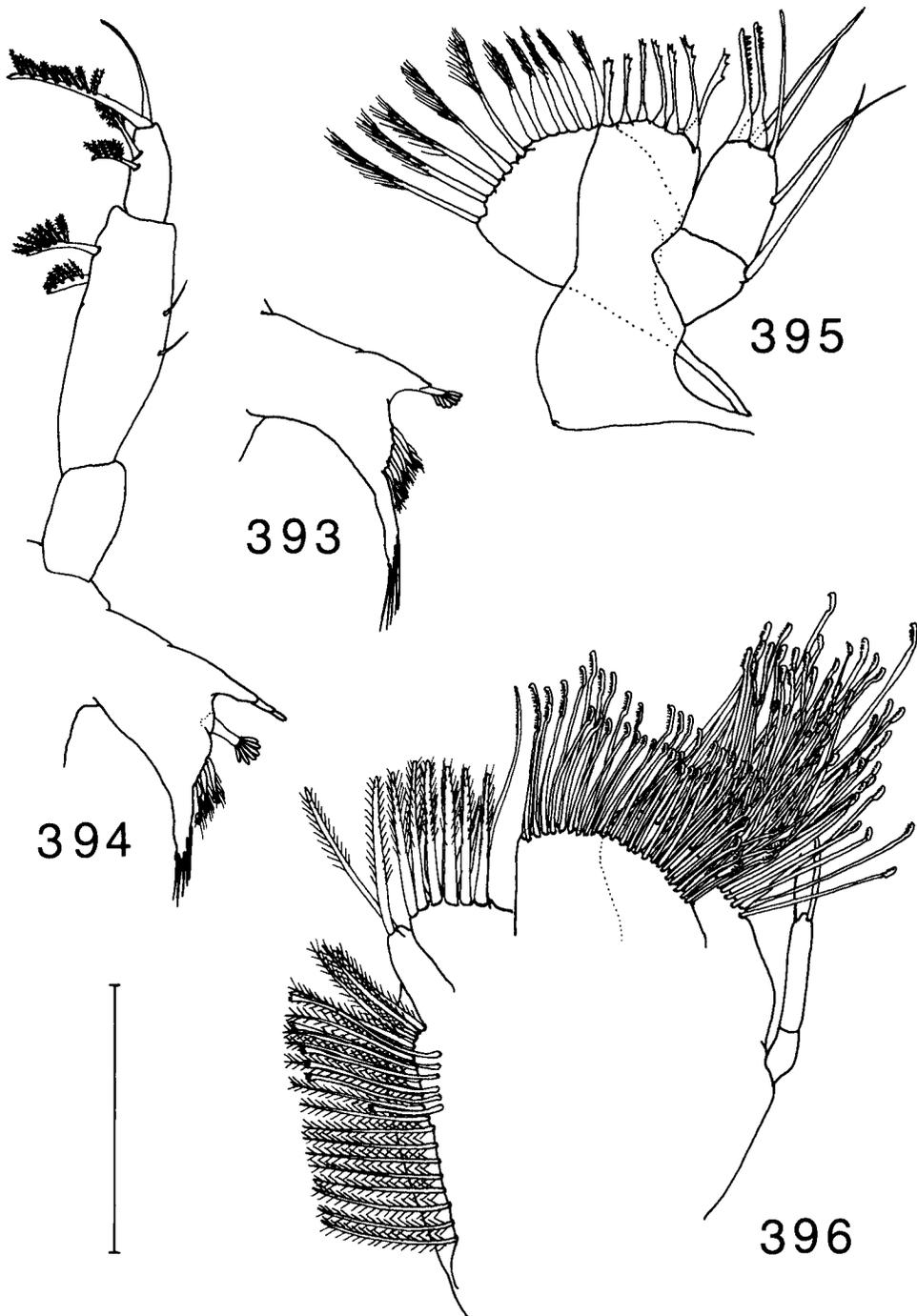
Mandible with well-developed 3-segmented palp; basal palp segment rectangular and unarmed; second segment with two simple (type IIA1) and two plumidenticulate macrosetae (type IA3); third segment with three plumidenticulate macrosetae (type IA3), (subapically) and 1 long serrulate macroseta (type IIB1(b)); corpus mandibula differentiated into pars incisiva, lacinia mobilis (absent in right mandible), row of three (left mandible) or four (right mandible) serrate macrosetae (type IIB1), and ensiform pars molaris having its molar surface covered by five very long ciliated microsetae (type IIB).

Labium deeply cleft, its lobes with rounded converging tips, internal distal margin with ciliate microsetae (type IIB), outer distal margin less densely covered by taller ciliate microsetae (type IIB).

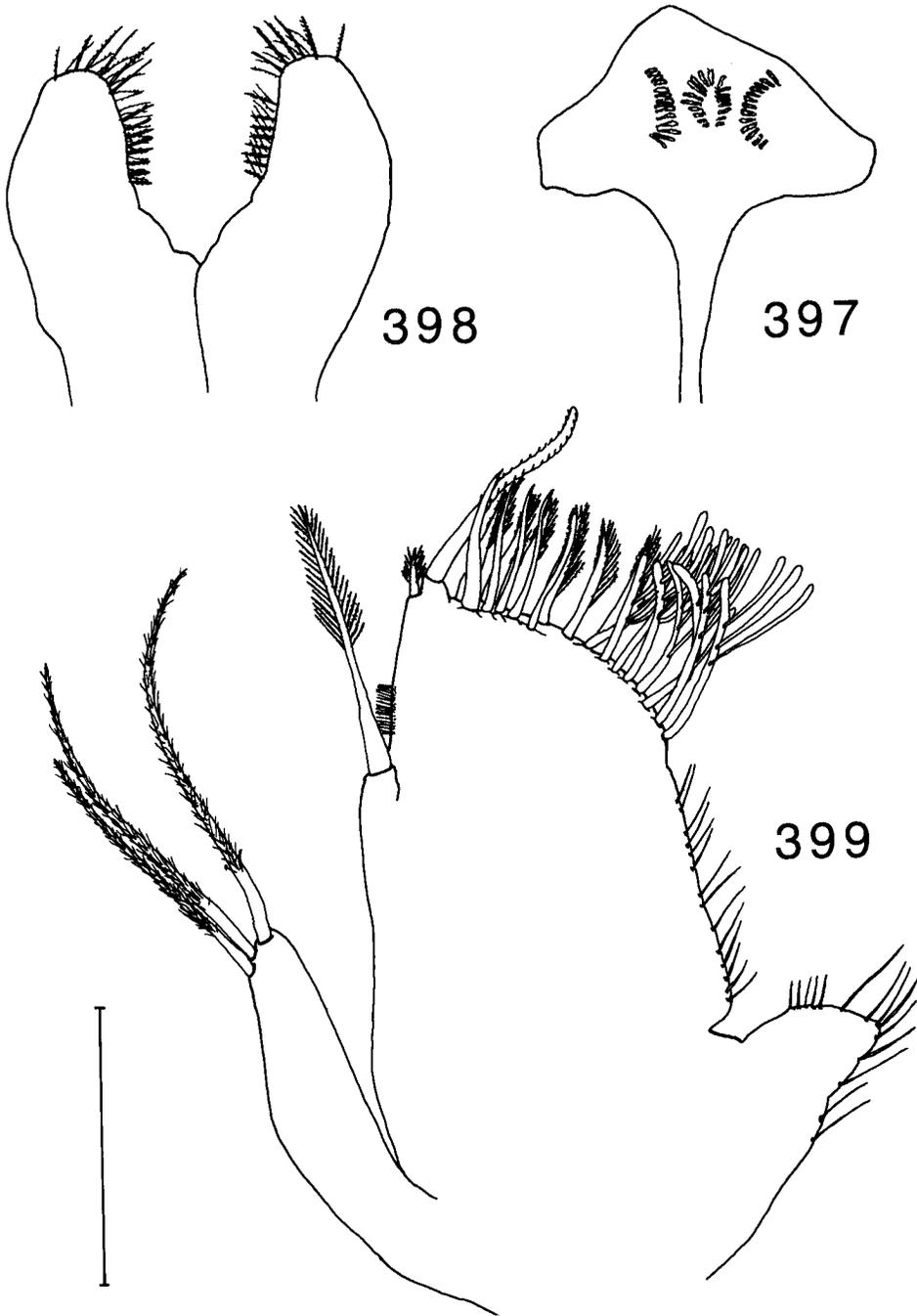
First maxilla differentiated into precoxal endite with a distomedial armature of



Figs. 389-392. *Limnosbaena finki* (Meštrov & Lattinger-Penko, 1969), ♂. 389, lateral view of habitus (2050  $\mu$ m). 390, antenna 1, holotype (scale A). 391, antenna 2. 392, ocular scales (figs. 391-392 scale B). Scales indicated 0.1 mm.



Figs. 393-396. *Limnosbaena finki* (Meštrov & Lattinger-Penko, 1969), ♂. 393, corpus mandibula of left mandible. 394, right mandible. 395, maxilla 1. 396, maxilla 2. Scale indicated 0.1 mm.



Figs. 397-399. *Limnosbaena finki* (Meštrov & Lattinger-Penko, 1969), ♂. 397, labrum. 398, labium. 399, maxilliped. Scale indicated 0.1 mm.

two rows of five tall and five stout plumose macrosetae (type IB1), respectively; a basipodal endite with distal armature of seven toothed macrosetae (type III); endopodite forming a rather short 2-segmented palp, first segment with one long simple macroseta (type IIA1), second segment with one simple macroseta (type IIA1) laterally, three simple macrosetae (type IIA1) (sub)apically, and two larger bisetulate macrosetae (type IB3(b)).

Maxilla 2 complexly built: coxopodal endite with 18 long plumose macrosetae (type IA1), six rod macrosetae (type IIA2) and two stout plumose macrosetae (type IB1); three basipodal endites: basipodal endite 1 with 12 plumidenticulate macrosetae (type IA3): one long, five obscurely serrate, and six stout macrosetae; basipodal endite 2 with two transverse rows of 23 rake-like serrate macrosetae (type IIB1) at terminal margin increasing in size and denticulation towards the medial margin of the appendage, and two modified (longer one with a more developed rake, short one with rake strongly reduced to narrow tip) serrate subterminal macrosetae; basipodal endite 3 with 55 rake-like serrate macrosetae (type IIB1) increasing in size and dentation medially, and arranged in 10, somewhat triangular, oblique rows of 1+2+3+4+5+6+7+8+9+10; endopodite 2-segmented, first segment with one long simple macroseta (type IIA1), segment 2 with one simple macroseta (type IIA1) and one serrulate macroseta (type IIB1(b)); exopodite absent.

Maxilliped: coxopodal endite a tapering lobe with one subterminal and two terminal pappose macrosetae (type IA2) with complex setules (as in fig. 10?); basipodal endite with three rows of plumidenticulate macrosetae (type IA3), ventral row of five curved macrosetae, central row of eight long macrosetae with foliaceous setules, and dorsal row of six short, stout, and distally densely setulate macrosetae, submedially an additional large modified "plumidenticulate" naked faintly S-shaped macroseta (type IA3) with short setules on prominences arranged in two close-set parallel rows, medially two plumidenticulate macrosetae (type IA3), of which small one in front of base of naked plumidenticulate macroseta and large one at central portion of medial margin; endopodite fused with exopodite and basipodal endite, platelike with a row of long fine simple microsetae (type Ia) along its margin; exopodite a non-articulating, tapering, blunt lobe, with simple microsetae (type Ia); epipodite a bow-shaped tapering lobe with simple microsetae (type Ia), apically a short stout macroseta (type could not be established with LM).

Gnathopod: baso-ischium longest segment, naked; merus with one subterminal teazel macroseta (type IIB3) on ventral margin; carpus with one subterminal teazel macroseta (type IIB3) on ventral margin; propodus with one teazel macroseta (type IIB3) distally on both dorsal and ventral margin, dactylus with claw formed by three (modified) serrulate macrosetae (type IIB1), having somewhat flattened rake-like distal portions.

Pereiopod 2: ischiomerus of endopodite with two teazel macrosetae (type IIB3) on ventral margin; carpus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins; propodus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins; dactylus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins, and well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one plumose macroseta (type IB1) subterminally, second segment with one

medial, two terminal and one lateral plumose macrosetae (type IB1).

Pereiopods 3 to 6: ischiomerus of endopodite with two teazel macrosetae (type IIB3) on ventral margin, of which one medially and one distally; carpus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins; propodus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins, and one subplumose macroseta (type IB2); dactylus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins, and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one plumose macroseta (type IB1) subterminally, second segment with one medial, two terminal and one lateral plumose macrosetae (type IB1).

Pereiopod 7: ischiomerus of endopodite with two teazel macrosetae (type IIB3) on ventral margin, one medially and one distally; carpus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins; propodus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins, and one subplumose macroseta (type IB2); dactylus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins, and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; exopodite absent.

In males penial lobes simple, long, distal half slightly bend, medially associated with coxopodite of pereiopod 7.

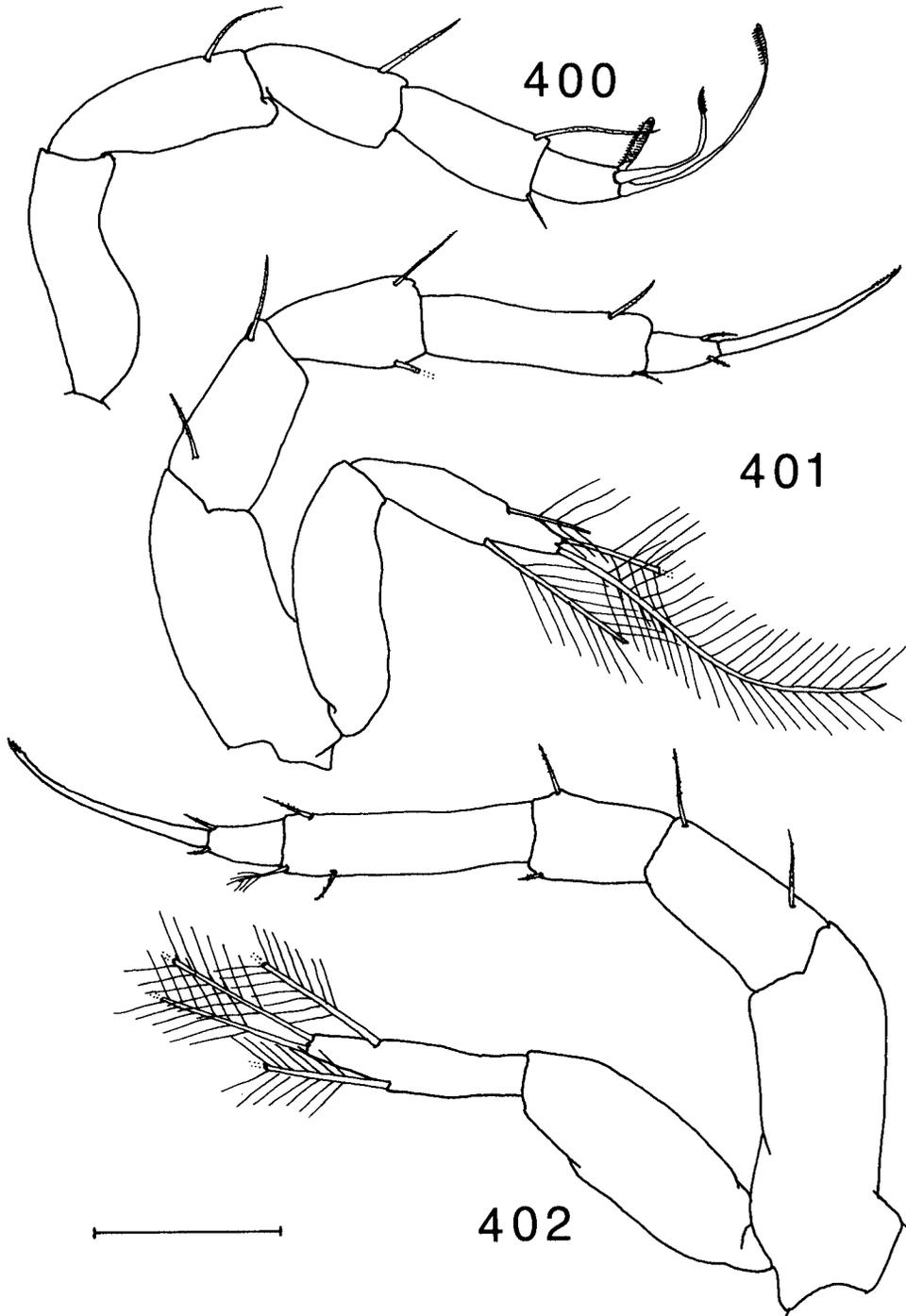
First pleopod an unarticulate rounded process with six subplumose macrosetae (type IB2), flanked by two simple macrosetae (type IIA1) medially. Second pleopod 1-segmented, almost rectangular, with two dorsal and one terminal subplumose macrosetae (type IB2). Pleonites 3 to 5 ventrally with two long and two short simple macrosetae (type IIA1) at either side.

Uropod with 2-segmented exopodite and 1-segmented endopodite; first segment of exopodite distinctly longer than segment 2, segment 1 laterally with three cuspidate macrosetae (type IIA3) and two subplumose macroseta (type IB2); medially with one to two cuspidate macrosetae (type IIA3), segment 2 with six plumose macrosetae (type IB1) all along distolateral to terminal margins; endopodite distinctly longer than exopodite, seven to eight cuspidate macrosetae (type IIA3) along medial margin, five stout plumose macrosetae (type IB1) along distomedial and terminal margins, one pair of subplumose macrosetae (type IB2) implanted distolaterally, accompanied by long simple macroseta (type IIA1), and lateral margin with four fine plumose macrosetae (type IB1), of which distalmost accompanied by small simple macroseta (type IIA1).

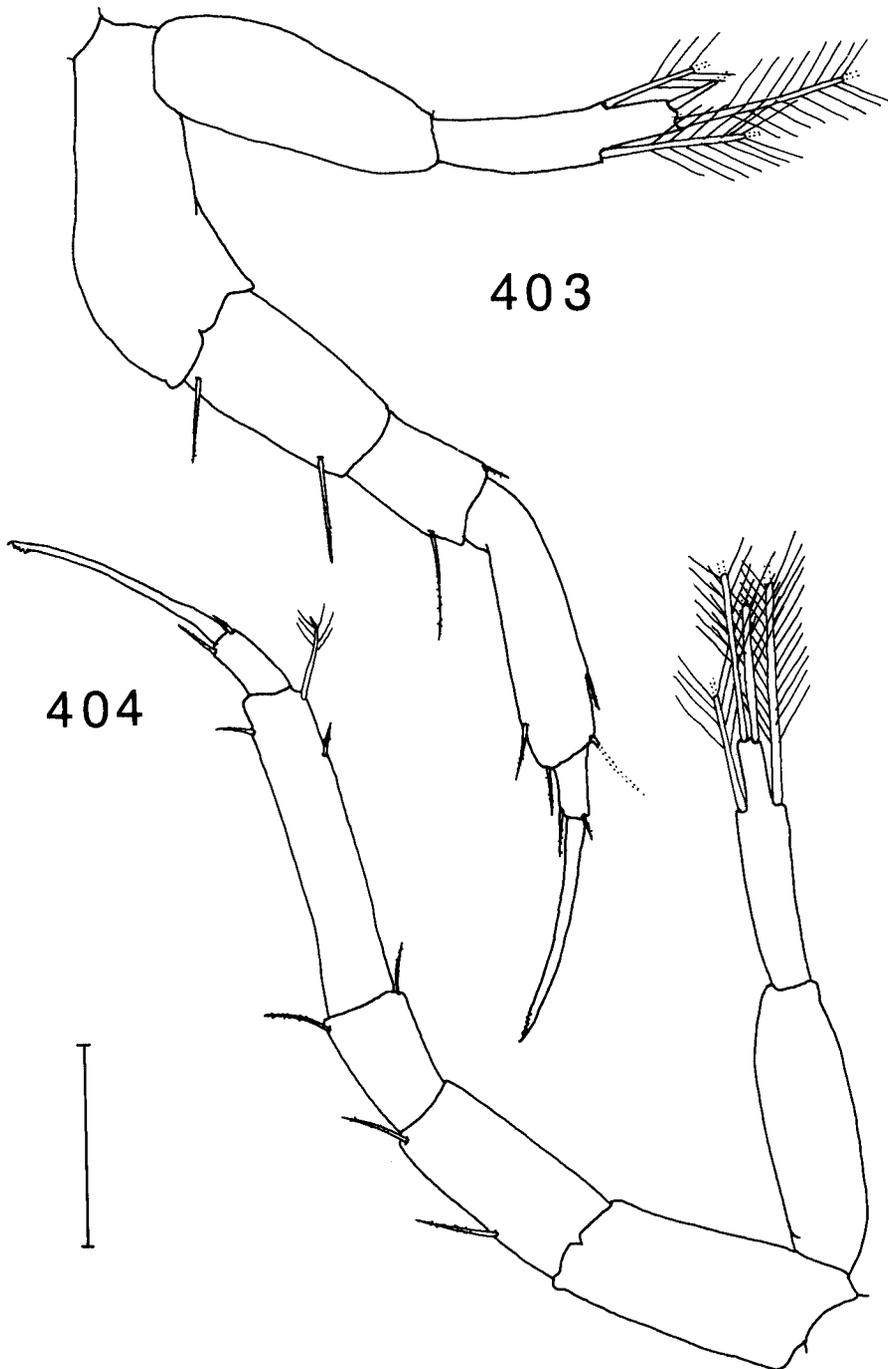
Telson longer than wide, width/length ratio varying between 0.78 and 0.82, tapering, terminal margin almost straight, posterior lateral margins with four pairs of cuspidate macrosetae (type IIA3), three pairs of serrate macrosetae (type IIB1) implanted somewhat more dorsally, one pair laterally, two pairs between second and third pair of cuspidate macrosetae.

Variability.— Except for a slight variation in the number of cuspidate macrosetae on the uropodal rami, no variation has been observed in the other appendages.

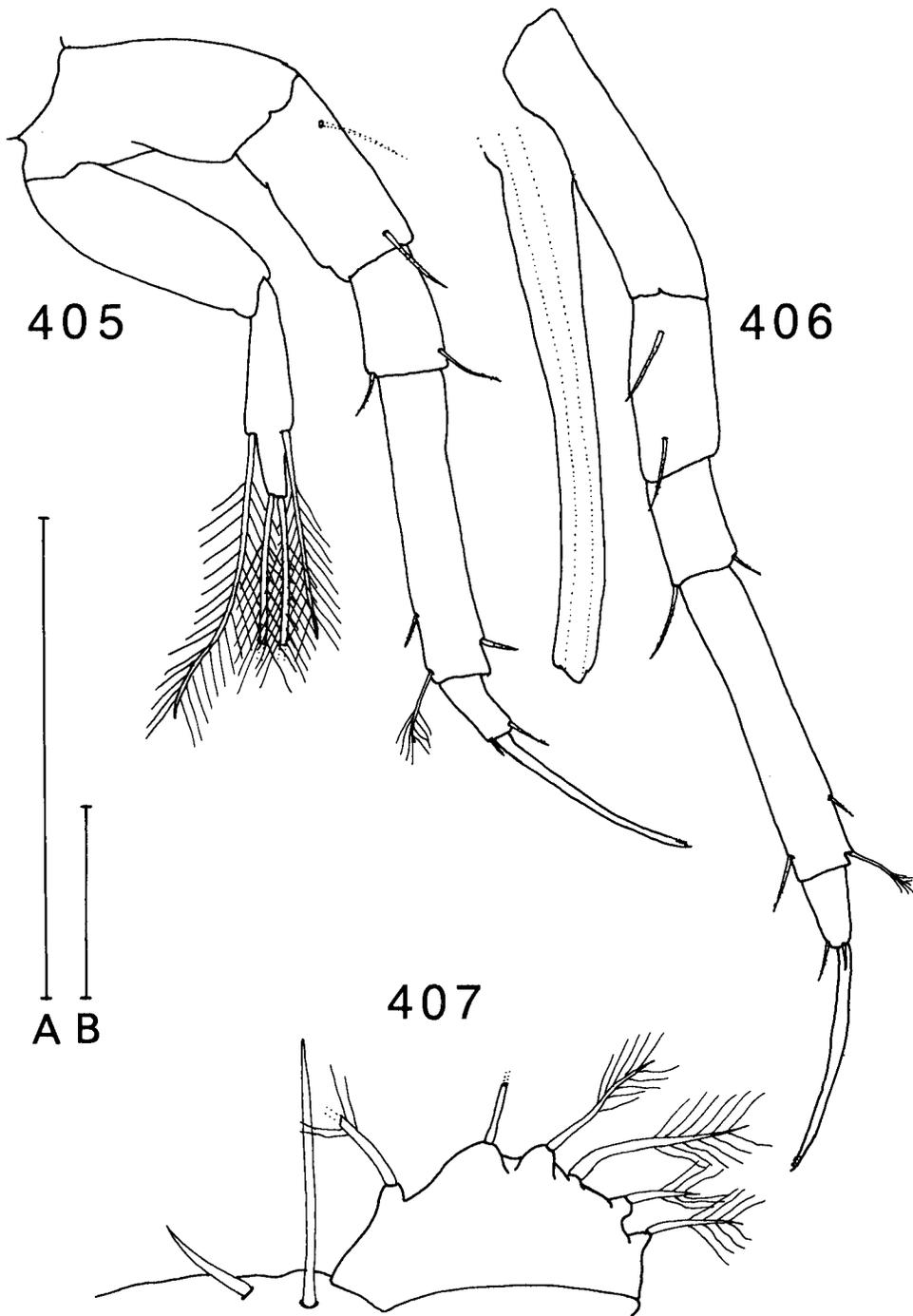
Remarks.— The first segment of the main flagellum of antenna 1 is distinctly longer compared to the other segments. The longitudinal row of six aesthetascs seems to indicate a fusion of the original first six segments of the main flagellum. With the aid of the Black Chlorazol B cuticular staining (although faintly visible) it was possible to



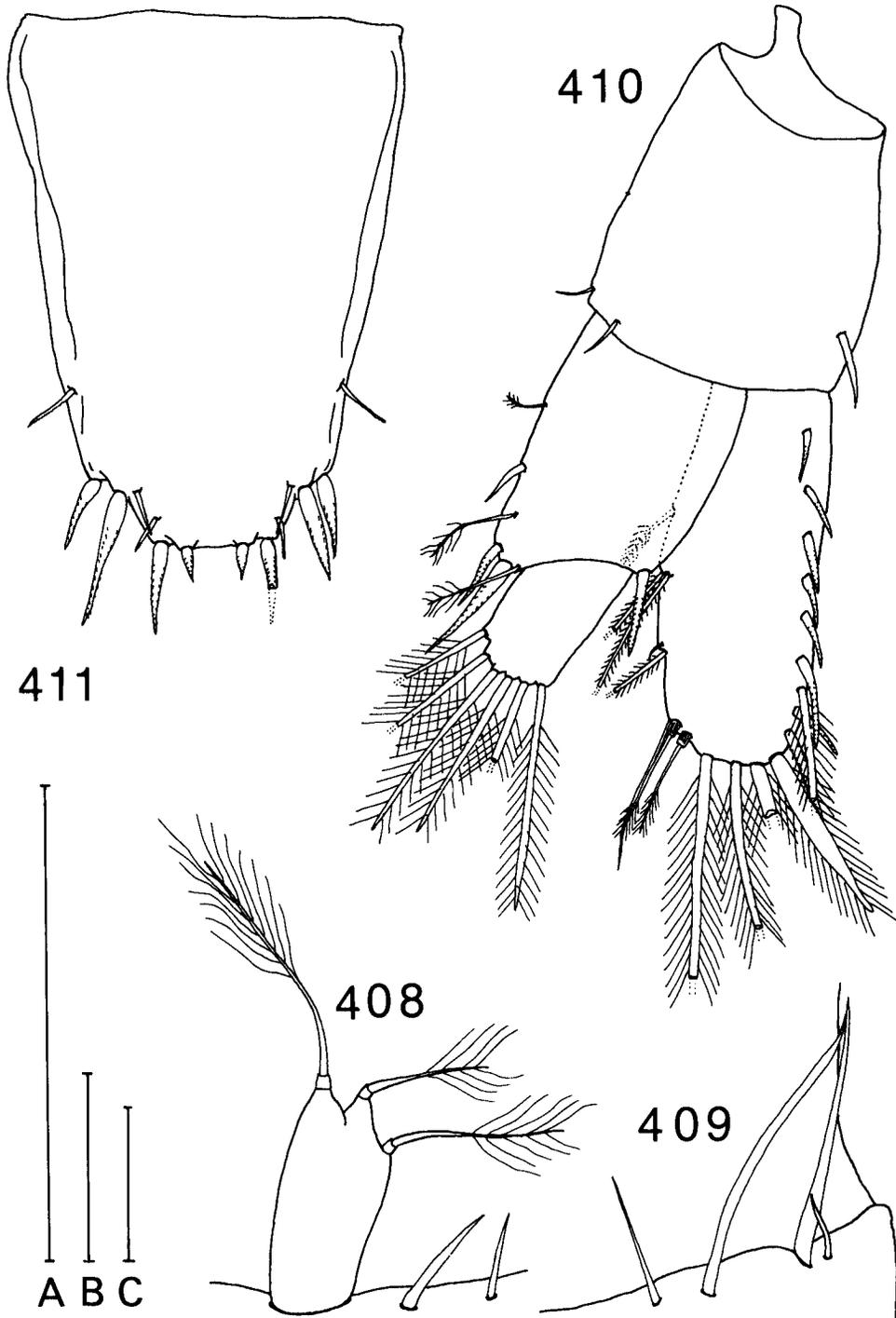
Figs. 400-402. *Limnosbaena finki* (Meštrov & Lattinger-Penko, 1969), ♂. 400, gnathopod. 401, pereopod 2. 402, pereopod 3. Scale indicated 0.1 mm.



Figs. 403-404. *Limnosbaena finki* (Meštrov & Lattinger-Penko, 1969), ♂. 403, pereopod 4. 404, pereopod 5. Scale indicated 0.1 mm.



Figs. 405-407. *Limnosbaena finki* (Meštrov & Lattinger-Penko, 1969), ♂. 405, pereiopod 6. 406, pereiopod 7 (figs. 405-406 scale B). 407, pleopod 1 (scale A). Scales indicated 0.1 mm.



Figs. 408-411. *Limnosbaena finki* (Meštrović & Lattinger-Penko, 1969), ♂. 408, pleopod 2. 409, detail of pleonite 3 (figs. 408-409 scale A). 410, uropod (scale B). 411, telson (scale C). Scales indicated 0.1 mm.

distinguish the six sclerites that form the first segment of the main flagellum in the specimen of *Limnosbaena* spec. described below. As in Tulumellidae the two aesthetascs per segment are implanted transversely near the distal margin, a situation that is not homologous to that of *Limnosbaena*. In this respect *Limnosbaena*, indeed, is a typical member of the Halosbaenidae too, as fundamentally it has one aesthetasc per segment.

Distribution.— *Limnosbaena finki* is known from limnic water from the interstitial of alluvia of the Bosna river near Zenica (Bosnia) and from a cave lake situated in the Italian part of Comaria.

Habitat.— As accompanying fauna of *Limnosbaena finki* the amphipod *Niphargus* spec., and the isopods *Stenasellus skolpjensis skolpjensis* (S.L. Karaman, 1936), and *Microcharon* spec. have been reported by Meštrov & Lattinger-Penko (1969: 112). From Comaria Gasparo et al. (1984: 51) mention the isopod *Sphaeromides* spec. as accompanying faunal element. No geological data are known to me.

#### 4.6.1.2. *Limnosbaena* spec. (figs. 412-415)

*Monodella* (partim); Botosaneanu & Delamare Deboutteville, 1967: 22; Wagner, 1990: 123.

Thermosbaenacés; Bou, 1975: 109.

*Monodella* spec. 1 (partim); Pinkster, 1978: 234.

*Monodella* spec. 2; Pinkster, 1978: 234.

unident. spp.; Schram, 1986: 221.

*Monodella*; Pretus, 1991: 236.

Material.— **France**: 1 (damaged) ♀; sta. Pt D2, Bouches-du-Rhône (Département 13), from tube-shaped well along road to Senas; collected by Cl. Bou; xi.1967; MP Thb. 5.

Description.— Body length (antennae 1 and 2 excluded) of the female studied is 1450 µm.

As the specimen is so severely damaged, not all appendages could be studied in detail.

Antenna 1: as in *L. finki*.

Antenna 2: as in *L. finki*.

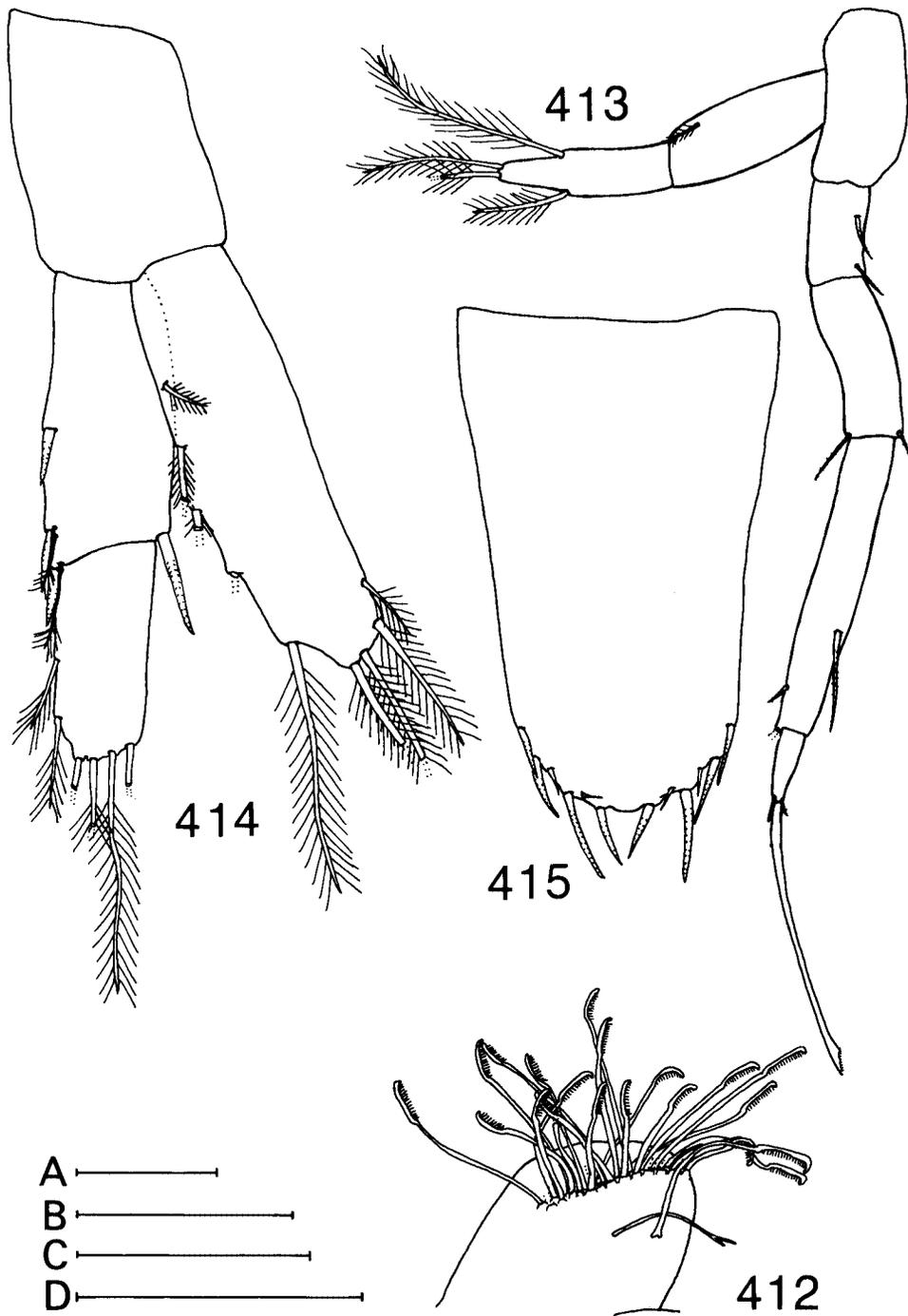
Labrum: without peculiarities.

Mandible: lost, except for the palp of the right mandible. Without peculiarities.

Labium: lost.

Maxilla 1: without peculiarities.

Maxilla 2: coxopodal endite with 18 long plumose macrosetae, six rod macrosetae and two stout plumose macrosetae; three basipodal endites: basipodal endite 1 with 12 plumidenticulate macrosetae (type IA3): one long, five obscurely serrate, and six stout macrosetae; basipodal endite 2 with two transverse rows of approximately 13 rake-like serrate macrosetae at terminal margin increasing in size and denticulation towards the medial margin of the appendage, and two modified serrate subterminal macrosetae; basipodal endite 3 with an estimated number of 55 rake-like serrate macrosetae, approximately 10, somewhat triangularly configured, oblique rows of 1+2+3+4+5+6+7+8+9+10 could be counted (majority of macrosetae broken



Figs. 412-415. *Limnosbaena* spec., ♀. 412, basipodal endite 2 of maxilla 2 (scale D). 413, pereopod 3 (scale B). 414, uropod (scale C). 415, telson (scale A). Scales indicated 0.1 mm.

off); endopodite 2-segmented, first segment with one long simple macroseta, segment 2 with one simple macroseta and one serrulate macroseta; exopodite absent.

Maxilliped: severely damaged, but appears identical with that of *L. finki* in number of macrosetae.

Gnathopod: lost.

Pereiopod 2: lost.

Pereiopods 3 to 6: only the right pereiopod 3 and left pereiopods 5 and 6 are present; ischiomerus of endopodite with two teazel macrosetae on ventral margin, of which one medially and one distally; carpus with one teazel macroseta subterminally on both ventral and dorsal margins; propodus with one teazel macroseta subterminally on both ventral and dorsal margins, and one subplumose macroseta; dactylus with one teazel macroseta subterminally on both ventral and dorsal margins, and a well-developed serrulate macroseta forming terminal "unguis"; first segment of exopodite with one plumose macroseta subterminally, second segment with one medial, two terminal and one lateral plumose macrosetae.

Pereiopod 7: ischiomerus of endopodite with two teazel macrosetae on ventral margin, of which one medially and one distally; carpus with one teazel macroseta subterminally on both ventral and dorsal margins; propodus with two teazel macrosetae medially and subterminally on ventral margins and one teazel and one subplumose macroseta subterminally on dorsal margin; dactylus with one teazel macroseta subterminally on both ventral and dorsal margins, and a well-developed serrulate macroseta forming terminal "unguis".

Pleopods 1 and 2 lost. Pleonites 3 to 5 ventrally with "scars" of three simple macrosetae at either side.

Uropod with 2-segmented exopodite and 1-segmented endopodite; first segment of exopodite distinctly longer than segment 2, segment 1 laterally with three cuspidate macrosetae, and two subplumose macrosetae; medially with one cuspidate macroseta, segment 2 with six plumose macrosetae all along distolateral to terminal margins; endopodite somewhat shorter than exopodite, four fine plumose macrosetae along lateral margin, five stout plumose macrosetae along distomedial and terminal margins, subplumose macrosetae not observed.

Telson longer than wide, width/length ratio of 0.68, tapering, terminal margin more or less halfround, posterior lateral margins with four pairs of cuspidate macrosetae, two pairs of serrate macrosetae implanted somewhat more dorsally, one pair near the second pair of cuspidate macrosetae, other pair situated halfway third and fourth pair of cuspidate macrosetae.

Variability.— As one (incomplete) specimen is available only, it is not possible to establish the variation.

Remarks.— When Professor Delamare Debutteville passed away, only a small part of his collection of slides with thermosbaenaceans was recovered by Professor J. Forest of the Paris Museum. Through his kindness I was able to examine this material. On all slides partially dissected or complete specimens were "crushed" under coverglasses. One slide contained a specimen belonging to the genus *Limnosbaena*. Under the pressure of the coverglass, the animal was badly damaged, for the mayor part dried out, and almost completely devoid of its pereiopods. As the mouthparts were severely damaged, and the pereiopods of the various species of Halosbaenidae

known so far show some specific characteristics, I am reluctant to name the present material. Until more specimens become available, which make a (nearly) complete description possible it seems best to leave this specimen unnamed.

Distribution.— Known from a single specimen only captured near Senas, Bouches-du-Rhône, southern France.

Habitat.— The specimen was found in a well in the vicinity of Senas. Dr C. Bou unfortunately did not provide any information about the exact locality.

#### 4.6.2. *Halosbaena* Stock, 1976

*Halosbaena* Stock, 1976: 56; McLaughlin, 1980: 84; Watling, 1981: 208; Stock, 1982: 195 table 2; Stock, 1986a: 587; Stock, 1986b: 932; Schram, 1986: 216, figs. 17-1C, 17-2; Cals, 1987: 661; Monod & Cals, 1988: 101, pl.2, fig. 2; Wagner, 1988: 1st page; Bowman & Iliffe, 1988: 225; Wagner, 1990: 123, fig. 1; Stock, 1990: 697; Meštrov & Cals, 1991: 42; Cals & Monod, 1991: 174. género aparte; Pretus, 1991: 235.

Type species.— *Halosbaena acanthura* Stock, 1976.

Diagnosis.— Body length (antennae 1 and 2 excluded) up to 2.5 mm. Carapace reaching up to the sixth pedigerous somite. Third peduncular segment of antenna 1 with four subplumose macrosetae on terminal prominence; main flagellum 7- to 16-segmented; accessory flagellum 4- to 9-segmented. Flagellum of antenna 2 4- to 7-segmented. Ocular scales anteriorly evenly rounded, rounded or pointed mediodistally. Mandible with three to four plumidenticulate macrosetae on second segment of palp; left pars incisiva with 2 processes, in total 6-dentate, right pars incisiva 6-dentate; left lacinia mobilis 5-dentate (absent in right mandible); row of four to five serrate macrosetae in left mandible, row of six serrate macrosetae in right mandible; pars molaris pointedly triangular, molar surface covered by numerous long ciliate microsetae. Palp of maxilla 1 with two long bisetulate macrosetae (sub)terminally; basipodal endite with seven tall sharply serrate toothed macrosetae, of which three are somewhat more strongly dentate. Coxopodal endite of maxilla 2 with numerous long plumose, six rod, and two stout plumose macrosetae; basipodal endite 1 with one long (tip pointed, dentations obscure), five obscurely serrate, and six stout (modified) plumidenticulate macrosetae. Maxilliped with five to six complexly setulated pappose macrosetae on coxopodal endite, setules with flattened distal portion, terminally bearing setulettes (as in fig. 10); subterminal margin with three rows of differently shaped plumidenticulate macrosetae, a ventral row of curved macrosetae with two stout setules medially and a bifurcated distal portion, a central row of strongly dentate and curiously setulate macrosetae (see figs. 15 and 16), and a dorsal row of long, finely setulate macrosetae with finely bifurcated portions (as in fig. 17), submedially a modified (viz., with partially reduced elements) curved, tall and stout plumidenticulate macroseta, the basal portion with two, three or four short, stiff setules, the distal portion with two closely set parallel rows of serrations (as in fig. 14). Gnathopod with obscurely demarcated ischium in baso-ischium of endopodite; propodus with four teazel macrosetae ventrally; dactylus with four serrate macrosetae, two of equal length having rake-like tips, the remaining two obscurely serrulate and of unequal length, the four forming a terminal claw. Pereiopods 2 to 7 biramous, exopodites 2-segmented, gradually decreasing in size from anterior to posterior. Thorac-

omeres 6 to 8 and pleonites 1 to 6 with a pair of simple macrosetae distodorsally; pleonites 1 to 6 also a with medial pair of simple macrosetae ventrally. First pleopod rather complex, formed by two processes with subplumose and simple macrosetae; second pleopod elongate with four subplumose macrosetae, and flanked at either side by simple macrosetae; five simple macrosetae placed in the extension of pleopod 2 on pleonites 3 to 5, probably representing remnants of pleopods 3 to 5 and their accompanying simple macrosetae. Uropodal endopodite distinctly longer than first segment of exopodite, medial margin with up to six cuspidate macrosetae; first segment of exopodite distomedially with five to six plumose macrosetae, distolaterally with seven to nine cuspidate macrosetae, each cuspidate macroseta accompanied by subplumose macroseta. Telson posteriorly with four pairs of cuspidate macrosetae, laterally with three to five serrate macrosetae.

Description.— Antenna 1 with 3-segmented peduncle; peduncular segment 1 one teazel macroseta, one plumose macroseta (type IA1) and three teazel macrosetae (type IIB3) on medial margin, one teazel macroseta (type IIB3) on lateral margin, two transverse rows of four and three fine plumose macrosetae (type IA1), respectively, on dorsal margin; peduncular segment 2 distally with three teazel macrosetae (type IIB3) on medial margin, two teazel macrosetae (type IIB3) on ventromedial margin, a transverse row of one plumose macroseta (type IA1) and six teazel macrosetae (type IIB3) on dorsomedial margin, a transverse row of five teazel macrosetae (type IIB3) on dorsolateral margin; peduncular segment 3 with two teazel macrosetae (type IIB3) on distomedial margin, one teazel macroseta (type IIB3) on mediolateral margin, terminal prominence with four subplumose macrosetae (type IB2); main flagellum 7- to 16-segmented, segment 1 with one simple macroseta (type IIA1) medially on medial margin, all segments distally with one simple macroseta (type IIA1) on lateral margin, one aesthetasc (type IIA6) and one simple macroseta (type IIA1) distomedially; accessory flagellum 4- to 9-segmented, segments with one simple macroseta (type IIA1) laterally, two simple macrosetae (type IIA1) medially, last segment (sub)terminally with five simple macrosetae (type IIA1) of unequal length.

Antenna 2 uniramous, peduncle 5-segmented; segment 1 naked, segment 2 with one medial and two lateral teazel macrosetae (type IIB3), segment 3 with one teazel macroseta (type IIB3) on lateral margin, three teazel macrosetae (type IIB3) on medial margin, two medially and one distally, segment 4 with one teazel macroseta (type IIB3) on distolateral margin, three teazel macrosetae (type IIB3) on medial margin, one medially and two distally, and one teazel macroseta (type IIB3) on dorsal margin, medial margin of segment 5 with two distally and one medially implanted teazel macrosetae (type IIB3); flagellum 4- to 7-segmented, segments 1 to 3 (-6) with three simple macrosetae (type IIA1) on medial margin, segments 1, 3 and 5 without or with one simple macroseta (type IIA1) on distolateral margin, last segment with five simple macrosetae (type IIA1) (sub)terminally.

Ocular scales anteriorly evenly rounded, rounded or pointed mediolaterally.

Labrum approximately 1.5 times broader than long; proximal portion densely covered with ciliate microsetae (type 2b); apically with ovate microsetae (type 2a).

Mandible with well-developed 3-segmented palp; basal palp segment rectangular and unarmed; second segment with three to four plumidenticulate macrosetae (type IA3); third segment with two to four plumidenticulate macrosetae (type IA3) and

one long serrulate macroseta (type IIB1(b)); corpus mandibulae differentiated into pars incisiva, lacinia mobilis (absent on right mandible), row of four to five (left mandible) or six (right mandible) serrate macrosetae (type IIB1), and pointedly triangular pars molaris having its molar surface densely covered by numerous ciliated microsetae (type IIB).

Labium deeply cleft, each lobe with rounded converging tip, internal distal margin with ciliate microsetae (type IIB), outer distal margin less densely covered by taller ciliate microsetae (type IIB).

First maxilla differentiated into precoxopodal endite with a distomedial armature of two rows of eight and four stout but tall plumose macrosetae (type IB1), respectively; basipodal endite with distal armature of seven toothed macrosetae (type III); endopodite forming a 2-segmented palp, first segment with one long and one short simple macroseta (type IIA1), second segment with two simple (type IIA1) and one serrulate macrosetae (type IIB1(b)) laterally, and (sub)apically with one serrulate macroseta (type IIB1(b)) and two stout bisetulate macrosetae (type IB3(b)).

Maxilla 2 complexly built: coxopodal endite with numerous long plumose macrosetae (type IA1), six rod macrosetae (type IIA2), and two stout plumose macrosetae (type IB1); three basipodal endites: basipodal endite 1 with one long and five rather simple and six complex (modified) plumidenticulate macrosetae (type IA3); basipodal endite 2 with two transverse rows of numerous small and large rake-like serrate macrosetae (type IIB1) at terminal margin increasing in size and denticulation towards the medial margin of the appendage, and two modified (longer one with a more developed rake, short one with rake strongly reduced to narrow tip) serrate subterminal macrosetae; basipodal endite 3 with numerous rake-like serrate macrosetae (type IIB1) increasing in size and dentation towards the medial margin of the appendage, arranged in somewhat triangularly configured oblique rows of 1+2+3+....(etc.) macrosetae; endopodite 2-segmented, first segment naked, segment 2 with two simple macrosetae (type IIA1) medially, two simple macrosetae (type IIA1) subterminally and one obscurely serrulate macroseta (type IIB1(b)); exopodite absent.

Maxilliped: coxopodal endite a tapering lobe with one or two medial, one subterminal, two terminal and one lateral pappose macrosetae (type IA2), with complex setules (as in fig. 10); basipodal endite with three rows of plumidenticulate macrosetae (type IA3), ventral row of four to seven curved macrosetae, central row of eight long macrosetae with stout setules and dorsal row of nine tall and finely setulate macrosetae, submedially an additional large modified plumidenticulate curved macroseta (type IA3), with two, three or four short stiff setules on basal portion, and two closely set parallel rows of serrations distally, one long stout plumidenticulate macroseta (type IA3) at central portion of medial margin; endopodite fused with exopodite and basipodal endite, plate-like with a row of long fine simple microsetae (type Ia) near margin; exopodite a non-articulating, tapering blunt lobe with two short stout simple macrosetae (type IIA1) and numerous simple microsetae (type Ia); epipodite a short, blunt, tapering lobe with simple microsetae (type 1a) along lateral margin.

Gnathopod: baso-ischium longest segment, with or without simple microsetae (type 1a) proximally on dorsal margin, one teazel macroseta (type IIB3) distally on

ventral margin, with or without one teazel macroseta (type IIB3) on distodorsal margin; merus with one subterminal teazel macroseta (type IIB3) distally on both ventral and dorsal margins; carpus with three subterminal teazel macrosetae (type IIB3) on ventral margin, one medially and two distally; propodus with teazel macrosetae (type IIB3), one medially and three distally on ventral margin, one distally on dorsal margin; dactylus with claw formed by four (modified) serrate macrosetae (type IIB1), two of equal length with rake-like tips and two obscurely serrulate of unequal length.

Pereiopod 2: ischiomerus of endopodite with two teazel macrosetae (type IIB3) on ventral margin, one proximally and one distally; carpus with or without one teazel macroseta (type IIB3) medially on ventral margin and one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins; propodus with one or two teazel macrosetae (type IIB3) medially on ventral margin, one teazel macroseta (type IIB3) distodorsally; dactylus with two teazel macrosetae (type IIB3) medially on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one plumose macroseta (type IB1) subterminally, second segment with one or two medial, two subterminal, two terminal and one or two lateral plumose macrosetae (type IB1).

Pereiopods 3 to 5: ischiomerus of endopodite with two teazel macrosetae (type IIB3) on ventral margin, with or without two teazel macrosetae (type IIB3) on dorsal margin, one proximally and one distally; carpus with one teazel macroseta (type IIB3) medially on ventral margin and one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins; propodus with one or two teazel macrosetae (type IIB3) medially on ventral margin, one teazel macroseta (type IIB3) and one subplumose macroseta (type IB2) distodorsally; dactylus with two teazel macrosetae (type IIB3) medially on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one plumose macroseta (type IB1) subterminally, second segment with one or two medial, two subterminal, two terminal and two lateral plumose macrosetae (type IB1).

Pereiopod 6: ischiomerus of endopodite with two teazel macrosetae (type IIB3) on ventral margin, one proximally and one distally; carpus with or without one teazel macroseta (type IIB3) medially on ventral margin and one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins; propodus with one or two teazel macrosetae (type IIB3) medially on ventral margin, one teazel macroseta (type IIB3) and one subplumose macroseta (type IB2) distodorsally; dactylus with two teazel macrosetae (type IIB3) medially on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one plumose macroseta (type IB1) subterminally, second segment with one or two medial, two subterminal, two terminal and one or two lateral plumose macrosetae (type IB1).

Pereiopod 7: ischiomerus of endopodite with two teazel macrosetae (type IIB3) on ventral margin, one proximally and one distally; carpus with one teazel macroseta (type IIB3) subterminally on both ventral and dorsal margins; propodus with one or two teazel macrosetae (type IIB3) medially on ventral margin, one teazel macroseta (type IIB3) and one subplumose macroseta (type IB2) distodorsally; dactylus with two teazel macrosetae (type IIB3) medially on ventral margin and a well-developed

serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one plumose macroseta (type IB1) subterminally, second segment no or one medial, two subterminal, two terminal and without or with one lateral plumose macroseta (type IB1).

Male penial lobes simple, naked, tall, almost straight, medially associated with coxopodite of pereopod 7.

Thoracomeres 6 to 8 with a pair of simple macrosetae distodorsally.

Pleonites 1 to 6 with a pair of simple macrosetae distodorsally; pleonites 1 to 6 also a medial pair of simple macrosetae ventrally; pleonite 6 with two distolateral simple macrosetae (type IIA1). First pleopod non-articulate, rather complex, formed by two processes, one rounded with five to six subplumose macrosetae (type IB2) and one tapering with a subplumose macroseta (type IB2), both protrusions flanked by simple macrosetae (type IIA1) in a species-dependent configuration. Second pleopod 1-segmented, elongate, with three dorsal and one terminal subplumose macrosetae (type IB2), flanked by one or two simple macrosetae laterally and one medially (= central one).

Uropod with 2-segmented exopodite and 1-segmented endopodite; first segment of exopodite distinctly longer than segment 2, segment 1 laterally with several cuspidate macrosetae (type IIA3), partly accompanied by subplumose macroseta (type IB2); medially with up to six plumose macrosetae (type IB1), segment 2 with up to 12 plumose macrosetae (type IB1) all along distolateral to terminal (or to medial) margins; endopodite distinctly longer than first segment of exopodite, up to eight cuspidate macrosetae (type IIA3) along medial margin, up to six stout plumose macrosetae (type IB1) along distomedial and/or terminal margins, pairs of subplumose macrosetae (type IB2) on lateral and distolateral margins, and lateral and/or terminal margins with a few fine plumose macrosetae (type IB1).

Telson longer than wide, width/length ratio species-dependent, tapering, distally rounded, posterior lateral margins with four pairs of cuspidate macrosetae (type IIA3), three to five serrate (type IIB1) macrosetae laterally on each side, with or without dorsal simple macrosetae (type IIA1).

Remarks.— The interpretation by Stock (1976) and Bowman and Iliffe (1986) of an exopodite between basipodal endite 3 and endopodite of the maxilla 2 finds its origin in the folds that are formed when pressing the coverglass while embedding the appendage. As the distal portion of basipodal endite 3 is rather globose, the subterminal naked part laterad of the field of rake-like serrate setae gets an appearance as drawn by Stock (1976: fig. 45) and Bowman & Iliffe (1986: fig. 1L). That it is an artefact created by the embedding of the appendage, could be verified in the type series of *Halosbaena acanthura* Stock, 1976, and examination of not yet embedded appendages with LM, and SEM studies of the mouthparts in situ and dissected state.

Distribution.— Representatives of *Halosbaena* have been found on a number of Caribbean islands, on Lanzarote (Canary Islands), and recently in tropical, continental Western Australia.

Habitat.— *Halosbaena* is known from shallow marine sands, the marine interstitium and marine caves (the island of San Andres, Colombia and Lanzarote, Canary Islands) and a freshwater cave lake (North West Cape, Western Australia).

4.6.2.1. *Halosbaena acanthura* Stock, 1976  
(figs. 416-438)

Thermosbaenacea; Botosaneanu, Decou & Negrea, 1973: 14; Orghidan, 1973: 48.  
*Halosbaena acanthura* Stock, 1976: 56, figs. 27-54; Abele, 1982: 276; Stock, 1986a: 587, fig. 1; Schram, 1986: 220; Bowman & Iliffe, 1986: 84; Wilkens, Parzefall & Iliffe, 1986: 227; Cals & Monod, 1988: 342; Sket, 1988b: 78; Meštrov & Cals, 1991: 42; Wagner, 1992: 79.  
 Thermosbaenacea (partim); Orghidan & Nuñez Jimenez, 1977: 12; Stock, 1981b: 34; Stock, 1983b: 235.  
*Halosbaena*; Stock, 1979: 7-9, 69-71; Stock, 1980b: 379.  
*Halosbaena acanthrua* (sic); Abele, 1982: 276.  
 Thermosbaenaceans (partim); Stock, 1983a: 277.  
*Halosbaena* spec.; Stock, 1986a: 587, 588.  
*Halosbaena acanthura* ssp.; Sket, 1988b: 79.  
 mysids (partim?); Kornicker & Iliffe, 1992: 3.

Material.— **Venezuela, Aves Islands:** 2 (damaged) ♀♀, 16 fragmentary specimens; AMEWI sta. 88/216, Sotavento; in coral debris at beach, 2 m off waterline, Bou-Rouch biophreatical pump, pipe depth 0.7 m, temperature 26.6 °C, oxygen 6.6 mg/l; collected by R. Vonk; 8.iii.1988; ZMA coll. no. 8064.

Accompanying fauna: Crustacea: Copepoda (Cyclopoida), Ostracoda; Mollusca: Gastropoda (*Caecum* spec.).

**Netherlands Antilles, Curaçao:** 4 ♂♂, 8 ♀♀; AMEWI sta. 73/3, S shore of lagoon Zakitó, along John F. Kennedy Boulevard, approx. 12°07'02"N 68°57'33"W; muddy, much plant debris, partly rotting, interstitial, Bou-Rouch biophreatical pump, chlorinity 35640 mg/l; collected by J.H. Stock; 20.xi.1973; ZMA coll. no. C.A. 8006 [female holotype], ZMA coll. no. C.A. 8007 [male paratype (allotype)], ZMA coll. no. C.A. 8008 [1 male, 2 females], ZMA coll. no. 8009 [2 males, 5 females].

Accompanying fauna: Crustacea: Amphipoda (*Saliweckelia emarginata* Stock, 1977).

- 1 ♀; AMEWI sta. 73/11, Piscadera Innerbay, E side of mouth, about 100 m inland of the shack of "American Rent a Boat", approx. 12°07'35"N 68°58'01"W; coral sand, rubble, partly artificial, beach interstitial, Bou-Rouch biophreatical pump, chlorinity 35046 mg/l; collected by J.H. Stock; 30.xi.1973; ZMA coll. no. C.A. 8014.

Accompanying fauna: none.

- 1 ♀; AMEWI sta. 73/14, Santa Marta Bay, inside of coral rubble wall facing a small lagoon, just in front of (former) "Coral Cliff Hotel", approx. 12°16'13"N 69°07'30"W; coral rubble, clean, interstitial, Bou-Rouch biophreatical pump, chlorinity 32670 mg/l; collected by J.H. Stock; 16.xii.1973; ZMA coll. no. C.A. 8015.

Accompanying fauna: none.

- 1 ♂; AMEWI sta. 73/16, W side of Jan Thiel Bay, shore of brackish (probable temporary) pool, approx. 12°04'49"N 68°52'37"W; very clean coral debris, interstitial, Bou-Rouch biophreatical pump, chlorinity 23760 mg/l; collected by J.H. Stock; 22.xii.1973; ZMA coll. no. C.A. 8016.

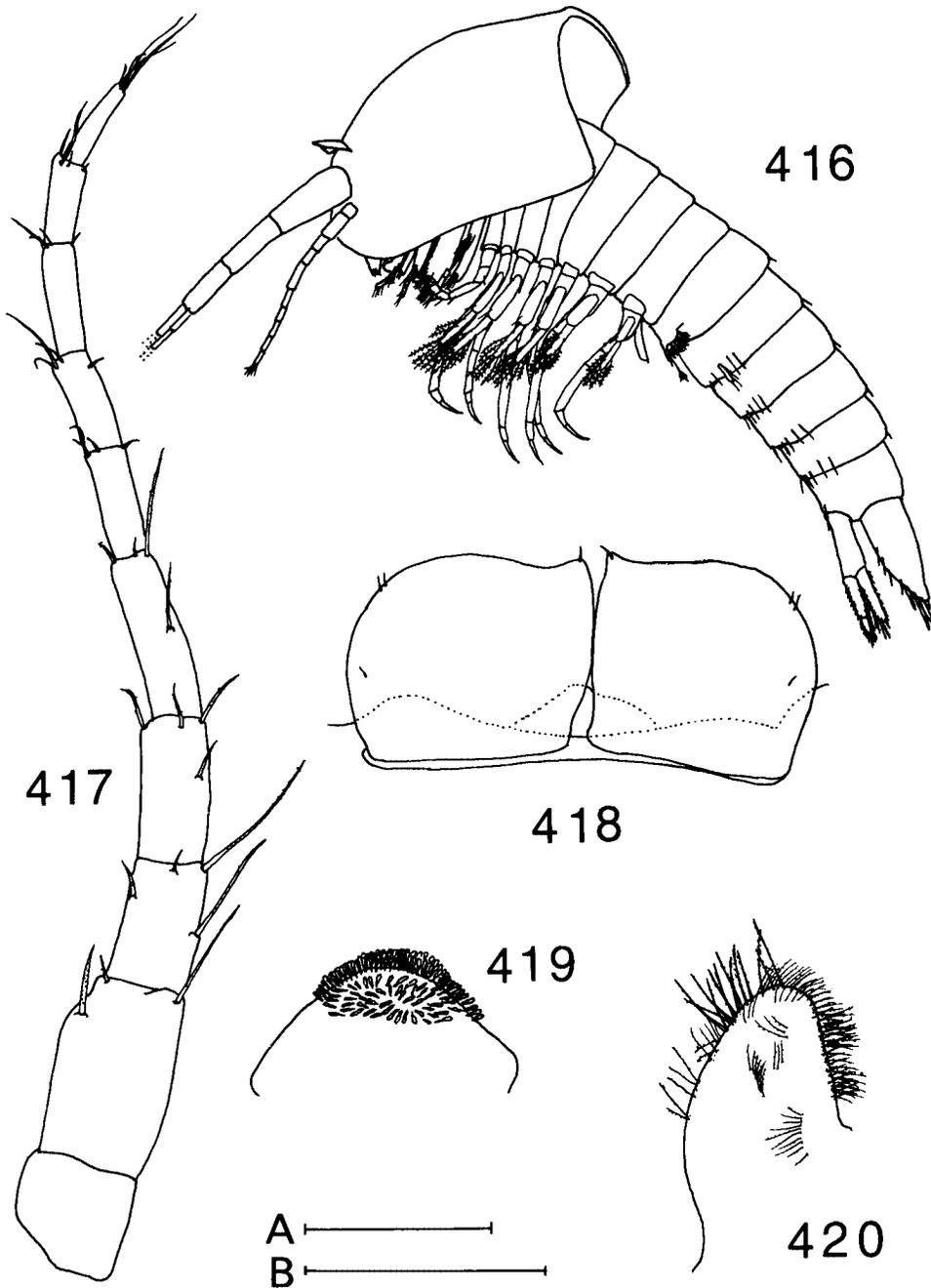
Accompanying fauna: none.

- 1 ♂, 1 damaged specimen; AMEWI sta. 73/17, Blauw Bay, in supralittoral (spray zone), just in front of the entrance of Blauw Bay cave, approx. 12°08'19"N 68°59'05"W; clean, not much sand, interstitial, Bou-Rouch biophreatical pump, chlorinity 17820 mg/l; collected by J.H. Stock; 28.xii.1973; ZMA coll. no. C.A. 8012.

Accompanying fauna: Crustacea: Amphipoda (*Metaniphargus curassavicus orientis* Stock, 1977).

- 3 ♂♂, 6 ♀♀ (1 with broodpouch), 12 juveniles; AMEWI sta. 78/305, Boca Tabla, in dry gully below entrance of sea cave, 12°22'19"N 69°06'49"W; very coarse sand and gravel, 1 m above tide line rarely reached by the waves, interstitial, Bou-Rouch biophreatical pump, chlorinity 4990 mg/l; collected by J.H. Stock, E.S.W. Weinberg and F. Zijlstra; 19.v.1978; ZMA coll. no. 8065.

Accompanying fauna: Crustacea: Amphipoda (Hadziidae, *Ingolfiella* (*Gevgeliella*) *tabularis* Stock, 1977), Ostracoda, Copepoda (Harpacticoida, Cyclopoida); Polychaeta (*Typosyllis* (*Typosyllis*) *lutea* Hartman-Scröder, 1960; *Typosyllis* (*Langerhansia*) *botosaneanui* Hartman-Scröder, 1973; *Typosyllis* (*Langerhansia*)



Figs. 416-420. *Halosbaena acanthura* (Stock, 1976), ♂, San Andres Island. 416, lateral view of habitus (1742  $\mu\text{m}$ ). 417, antenna 2. 418, ocular scales (figs. 417-418 scale A). 419, labrum. 420, lobe of labium (figs. 419-420 scale B). Scales indicated 0.1 mm.

*broomensis* Hartman-Scröder, 1979; *Heteromastus filiformis* (Claparède, 1864)); Oligochaeta; Mollusca: Gastropoda (*Caecum* spec.).

- 7 ♀♀, 7 juveniles; AMEWI sta. 78/308, Blauw Bay, below entrance of Blauw Bay Cave, 12°08'20"N 68°59'05"W; sand, gravel, rock, 3 m from the sea, interstitial, Bou-Rouch biophreatical pump, chlorinity 18840 mg/l; collected by J.H. Stock, E.S.W. Weinberg and F. Zijlstra; 20.v.1978; ZMA coll. no. 8066.

Accompanying fauna: Crustacea: Isopoda (Microcerberidae, Anthuridae, *Microjaera* spec., *Stenetrium* spec.), Amphipoda (Hadziidae, Bogidiellidae, *Ingolfiella* (*Gevgeliella*) *tabularis* Stock, 1977), Tanaidacea, Ostracoda, Copepoda (Harpacticoida, Cyclopoida); Polychaeta (*Microphthalmus stocki* Hartman-Schröder, 1980; *Typosyllis* (*Typosyllis*) *lutea* Hartman-Scröder, 1960; *Namanereis pontica* (Bobretsky, 1872); *Goniadides* spec.); Oligochaeta; Archiannelida; Mollusca: Gastropoda (*Caecum* spec.).

- 3 ♀♀ (all with broodpouch); AMEWI sta. 78/309, Blauw Bay Cave, in cave pool, 12°08'20"N 68°59'05"W; hole dug in sand of bank of subterranean lake, loamy, semi-dark, handnet (mesh 0.05 mm), chlorinity 9400 mg/l; collected by J.H. Stock, E.S.W. Weinberg and F. Zijlstra; 20.v.1978; ZMA coll. no. 8067.

Accompanying fauna: Crustacea: Isopoda (*Cyathura* spec.), Amphipoda (*Psammodon caesicolus* Stock, 1980), Copepoda (Harpacticoida, Cyclopoida); Polychaeta (*Namanereis pontica* (Bobretsky, 1872)); Oligochaeta.

- 1 juvenile; AMEWI sta. 78/315, Piscadera, first buoy, approx. 12°07'42"N 68°58'18"W; coarse coral sand, collected by SCUBA divers at a depth of 4 m, top layer of substrate washed, marine interstitial, handnet (mesh 0.05 mm), marine; collected by J.H. Stock, E.S.W. Weinberg and F. Zijlstra; 20.v.1978; ZMA coll. no. 8068.

Accompanying fauna: Crustacea: Isopoda (Microparasellidae), Amphipoda (*Ingolfiella* (*Hanseniella*) *quadridentata* Stock, 1979), Cumacea, Copepoda (Cyclopoida; Harpacticoida: *Ellucana secunda* Coull, 1971; *Laophonte plana* Fiers, 1986; *Cletopsyllus rotundifera* Fiers, 1986), Decapoda (Macrura); Nematoda; Mollusca: Gastropoda (*Caecum* spec.); Hemichordata (*Amphioxus* spec.).

- 3 ♂♂, 28 ♀♀ (6 with broodpouch), 3 fragmentary specimens; AMEWI sta. 84/75, Santa Marta Bay behind house of Nat. Sci. Workgroup, ca. 8 m off the shore of the inner bay, 12°16'19"N 69°07'37"W; in coral debris, Bou-Rouch biophreatical pump, pipe depth 0.6 m, chlorinity 29779 mg/l; collected by J.H. Stock and J. Vermeulen; 20 May 1984; ZMA coll. no. C.A. 8074.

Accompanying fauna: Crustacea: Isopoda (Anthuridae), Amphipoda, Copepoda (Calanoida); Polychaeta; Sipunculida; Mollusca: Gastropoda (*Caecum* spec.).

- 3 fragmentary specimens; AMEWI sta. 84/76, Santa Marta (Boca), ca 40 cm off the shore of the inner bay, 12°16'19"N 69°07'37"W; sandy upper layer with fine coral debris, interstitial, Bou-Rouch biophreatical pump, water depth 0.25 m, pipe depth 0.6 m, chlorinity 27231 mg/l; collected by J.H. Stock and J. Vermeulen; 20.v.1984; ZMA coll. no. C.A. 8069.

Accompanying fauna: Crustacea: Isopoda (Anthuridae), Amphipoda, Cumacea, Ostracoda, Copepoda (Harpacticoida, Lichomolgidae); Polychaeta; Sipunculida; Mollusca: Gastropoda (*Caecum* spec.).

- 2 ♂♂, 3 ♀♀ (1 with broodpouch); AMEWI sta. 84/86A, Santa Marta Bay behind house of Nat. Sci. Workgroup, 7 m W of jetty, 12°16'19"N 69°07'37"W; coral debris on sand, interstitial, Bou-Rouch biophreatical pump, pipe depth 0.8 m; collected by J.H. Stock and J. Vermeulen; 22.v.1984; ZMA coll. no. C.A. 8070.

Accompanying fauna: Crustacea: Isopoda (Anthuridae), Amphipoda, Copepoda (Harpacticoida, Cyclopoida); Polychaeta; Sipunculida; Mollusca: Gastropoda (*Caecum* spec.); Cnidaria; Foraminifera.

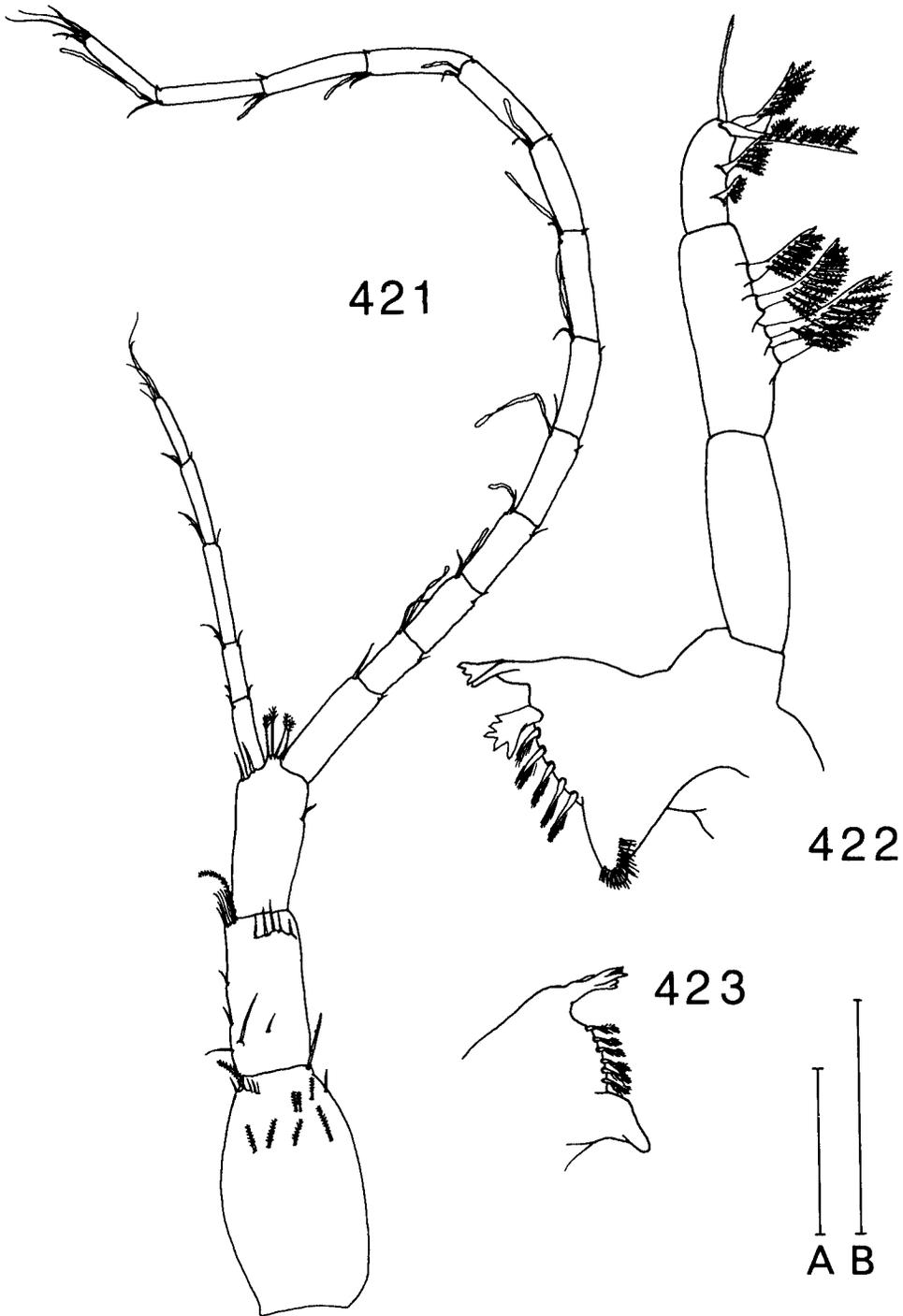
- 2 ♀♀; AMEWI sta. 84/86B, same locality as sta. 84/86A; coral debris on sand, interstitial, vacuum pump; collected by J.H. Stock and J. Vermeulen; 22.v.1984; ZMA coll. no. C.A. 8071.

Accompanying fauna: Crustacea: Isopoda (Anthuridae, Microparasellidae), Amphipoda (blind), Ostracoda, Copepoda (Harpacticoida, Cyclopoida, Calanoida (blind)); Polychaeta; Oligochaeta; Mollusca: Gastropoda (*Caecum* spec.); Foraminifera.

- 1 ♂, 13 ♀♀ (2 with broodpouch); AMEWI sta. 84/86C, same locality as sta. 84/86A; coral debris on sand, interstitial, Bou-Rouch biophreatical pump; collected by J.H. Stock and J. Vermeulen; 22.v.1984; ZMA coll. no. C.A. 8072.

Accompanying fauna: Crustacea: Isopoda (Anthuridae); Mollusca: Gastropoda (*Caecum* spec.).

- 2 ♂♂, 16 ♀♀ (11 with broodpouch), 2 juveniles, 3 fragmentary specimens; AMEWI sta. 84/87, Santa



Figs. 421-423. *Halosbaena acanthura* (Stock, 1976), ♂, San Andres Island. 421, antenna 1 (scale A). 422, left mandible. 423, corpus mandibula of right mandible (figs. 422-423 scale B). Scales indicated 0.1 mm.

Marta Bay, behind house and laboratory of Nat. Sci. Workgroup, 12°16'19"N 69°07'37"W; hard coral rock, interstitial, collected with the aid of a Bou-Rouch biophreatical pump, pipe depth 0.75 m, chlorinity 26611 mg/l; collected by J.H. Stock and J. Vermeulen; 22.v.1984; ZMA coll. no. C.A. 8073.

Accompanying fauna: Crustacea: Isopoda (Anthuridae), Amphipoda (blind), Ostracoda, Copepoda (Calanoida); Insecta; Polychaeta; Mollusca: Gastropoda.

- 14 ♀♀ (1 with broodpouch), 2 fragmentary specimens; AMEWI sta. 84/98, Lagoon Jan Thiel, 12°05'04"N 68°53'07"W; resurgence of (sea?)water in Saliña, bottom with jagged stones and sand, water depth 4 m, Bou-Rouch biophreatical pump, chlorinity 80000 mg/l; collected by J.H. Stock and J. Vermeulen; 24.v.1984; ZMA coll. no. C.A. 8075.

Accompanying fauna: Insecta: Diptera (mosquito larvae); Mollusca: Gastropoda.

- 146 damaged specimens (4 ♀♀ with broodpouch); AMEWI sta. 84/113, John F. Kennedy Boulevard, ca. 500 m E of Concorde Hotel, at shore of a small lagoon on debris barrier, 12°07'13"N 68°57'50"W; sand and coral debris, deeper layer rich of H<sub>2</sub>S, water depth 6 m, Bou-Rouch biophreatical pump, chlorinity 29963 mg/l; collected by J.H. Stock and J. Vermeulen; 27.v.1984; ZMA coll. no. C.A. 8076; RMNH G 75.

Accompanying fauna: Crustacea: Isopoda (Microparasellidae), Amphipoda (Hadziidae), Copepoda (Harpacticoida); Sipunculida.

- 1 ♂, 6 ♀♀ (2 with broodpouch); AMEWI sta. 84/114, John F. Kennedy Boulevard, ca. 500 m E of Concorde Hotel, at seaside of debris-barrier of small lagoon, near water line, 12°07'13"N 68°57'50"W; Bou-Rouch biophreatical pump, chlorinity 29399 mg/l; collected by J.H. Stock and J. Vermeulen; 27.v.1984; ZMA coll. no. C.A. 8077.

Accompanying fauna: Crustacea: Isopoda (oculate), Amphipoda (Hadziidae), Ostracoda; Pycnogonida (*Hedgpethius interstitialis* Stock, 1989); Polychaeta; Oligochaeta; Sipunculida; Mollusca: Gastropoda (*Caecum* spec.).

- 2 (damaged) ♀♀; AMEWI sta. 84/118, Boca Tabla, ca. 1 m above waterline, 12°22'19"N 69°06'49"W; upper surface with coarse sand, deeper layer of loam, little water, Bou-Rouch biophreatical pump, pipe depth 0.95 m, chlorinity 27878 mg/l; collected by J.H. Stock and J. Vermeulen; 28.v.1984; ZMA coll. no. C.A. 8078.

Accompanying fauna: Crustacea: Isopoda (terrestrial), Amphipoda (Ingolfiellidea, *Nuuanu curvata* Vonk, 1988); Polychaeta; Oligochaeta; Mollusca: Gastropoda (*Caecum* spec.).

- 2 ♀♀; AMEWI sta. 84/126A, John F. Kennedy Boulevard, at -2 m on the high water line, 12°07'13"N 68°57'50"W; little underlying sediment, coarse sand, marine, Bou-Rouch biophreatical pump, pipe depth 0.5 m, water depth 0.2 m, marine; collected by J.H. Stock and J. Vermeulen; 29.v.1984; ZMA coll. no. C.A. 8079.

Accompanying fauna: Crustacea: Isopoda (Anthuridae), Amphipoda (oculate), Ostracoda, Tanaidacea; Polychaeta; Oligochaeta; Sipunculida; Mollusca: Gastropoda (*Caecum* spec.).

- 5 ♀♀, 2 fragmentary specimens; AMEWI sta. 84/127, John F. Kennedy Boulevard, at +1 m landward of high water line, 12°07'13"N 68°57'50"W; little underlying sediment, Bou-Rouch biophreatical pump, pipe depth 0.5 m, chlorinity 28449 mg/l; collected by J.H. Stock and J. Vermeulen; 29.v.1984; ZMA coll. no. C.A. 8080.

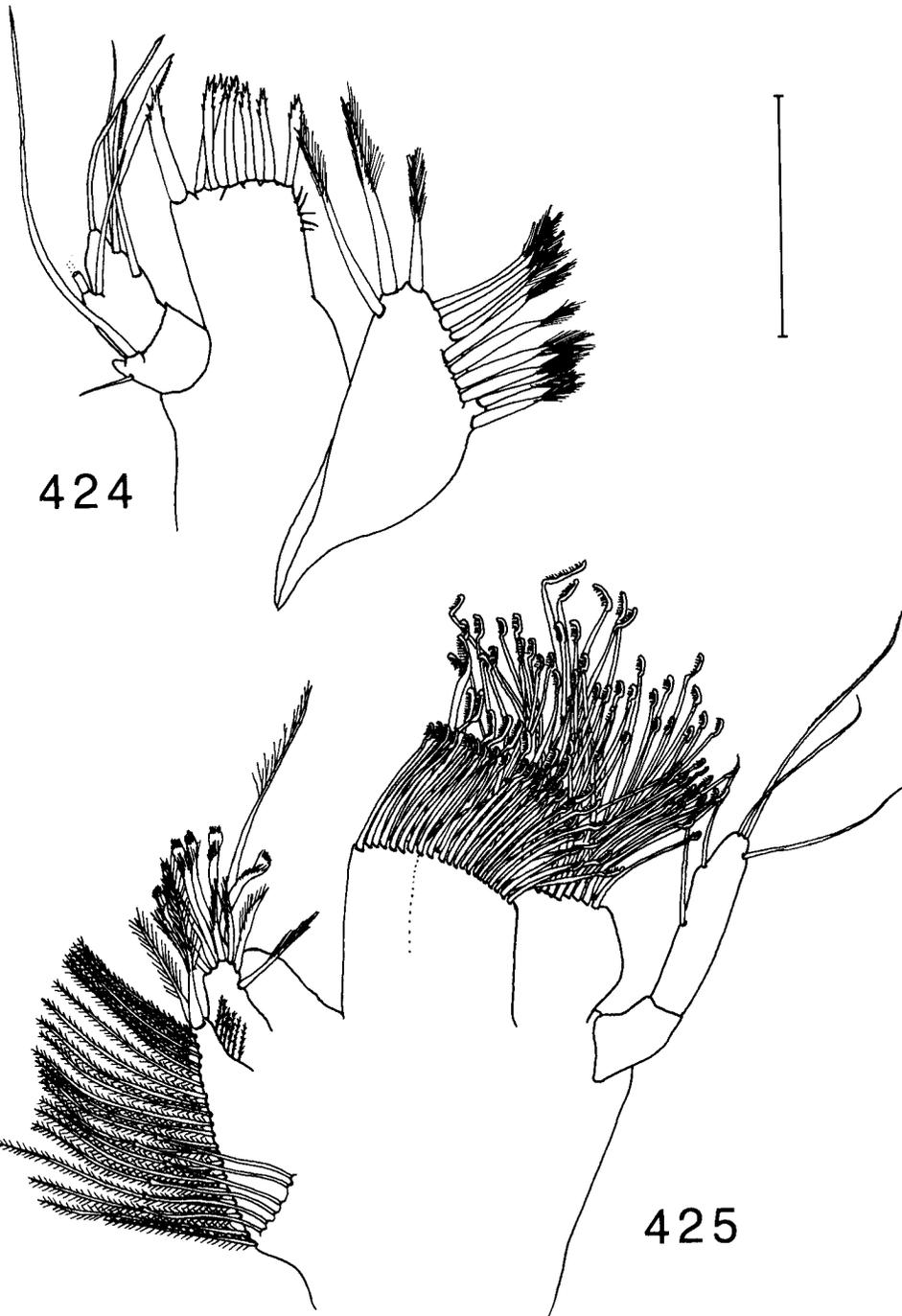
Accompanying fauna: Crustacea: Isopoda (Anthuridae), Amphipoda (Hadziidae); Polychaeta; Oligochaeta; Sipunculida; Mollusca: Gastropoda (*Caecum* spec.).

- 2 ♂♂, 36 ♀♀ (3 with broodpouch), 3 juveniles, 2 fragmentary specimens; AMEWI sta. 84/128, John F. Kennedy Boulevard, at +5 m landward of high water line, 12°07'13"N 68°57'50"W; smell of H<sub>2</sub>S, Bou-Rouch biophreatical pump, pipe depth 0.7 m, chlorinity 28195 mg/l; collected by J.H. Stock and J. Vermeulen; 29.v.1984; ZMA coll. no. C.A. 8081.

Accompanying fauna: Crustacea: Amphipoda (Hadziidae), Ostracoda, Copepoda (Cyclopidea); Insecta: Collembola; Pycnogonida; Polychaeta; Oligochaeta.

- 26 ♂♂, 118 ♀♀ (15 with broodpouch), 3 juveniles, 24 fragmentary specimens; AMEWI sta. 84/132, John F. Kennedy Boulevard, at +2 m landward of high water line, 12°07'13"N 68°57'50"W; little underlying sediment, Bou-Rouch biophreatical pump, chlorinity 27657 mg/l; collected by J.H. Stock and J. Vermeulen; 30.v.1984; ZMA coll. no. C.A. 8082; BMNH; RMNH G 76; WAM.

Accompanying fauna: Crustacea: Isopoda (Anthuridae), Amphipoda (Hadziidae), Tanaidacea; Poly-



Figs. 424-425. *Halosbaena acanthura* (Stock, 1976), ♂, San Andres Island. 424, maxilla 1. 425, maxilla 2. Scale indicated 0.1 mm.

chaeta; Oligochaeta.

- 6 ♂♂, 94 ♀♀ (13 with broodpouch), 2 juveniles, 9 fragmentary specimens; AMEWI sta. 84/133, John F. Kennedy Boulevard, at +3 m landward of high water line, 12°07'13"N 68°57'50"W; underlying sediment of coarse sand, Bou-Rouch biophreatical pump, pipe depth 0.75 m, chlorinity 29526 mg/l; collected by J.H. Stock and J. Vermeulen; 30.v.1984; ZMA coll. no. C.A. 8083.

Accompanying fauna: Crustacea: Amphipoda (Hadziidae), Tanaidacea, Copepoda (Harpacticoida, Cyclopidae), Decapoda (*Salmonesus arubae* (Schmitt, 1936)); Oligochaeta; Mollusca: Gastropoda (*Caecum* spec.).

- 3 ♂♂, 100 ♀♀ (8 with broodpouch), 19 fragmentary specimens; AMEWI sta. 84/134, John F. Kennedy Boulevard, at +4 m landward of high water line, 12°07'13"N 68°57'50"W; coarse sediment, smell of H<sub>2</sub>S, Bou-Rouch biophreatical pump, pipe depth 0.7 m, chlorinity 29272 mg/l; collected by J.H. Stock and J. Vermeulen; 30.v.1984; ZMA coll. no. C.A. 8084; RMNG G 77.

Accompanying fauna: Crustacea: Amphipoda (Hadziidae), Ostracoda, Copepoda (Harpacticoida, Cyclopidae); Polychaeta; Oligochaeta; Nematoda.

- 7 ♂♂, 31 ♀♀ (14 with broodpouch), 4 fragmentary specimens; AMEWI sta. 84/136, John F. Kennedy Boulevard, between +2 and +4 m landward of high water line, 12°07'13"N 68°57'50"W; coral debris and coarse sand, Karaman-Chappuis method, chlorinity 29526 mg/l; collected by J.H. Stock and J. Vermeulen; 31.v.1984; ZMA coll. no. C.A. 8085.

Accompanying fauna: Crustacea: Isopoda (Anthuridae, Sphaeromatiidae, terrestrial), Amphipoda (Hadziidae, *Bogidiella* spec.), Tanaidacea, Ostracoda; Insecta: Collembola; Pycnogonida; (*Hedgpeithius interstitialis* Stock, 1989) Chelicerata: Pseudoscorpionida; Polychaeta; Oligochaeta; Sipunculida; Nematoda; Mollusca: Gastropoda (*Caecum* spec.).

- 2 ♂♂, 10 ♀♀ (3 with broodpouch); AMEWI sta. 84/139, John F. Kennedy Boulevard, between +2 and +4 m landward of high water line, 12°07'13"N 68°57'50"W; "production-drilling", Bou-Rouch biophreatical pump, pipe depth 0.75 m; collected by J.H. Stock and J. Vermeulen; 1.vi.1984; ZMA coll. no. C.A. 8086.

Accompanying fauna: Crustacea: Amphipoda (Hadziidae, *Bogidiella* spec., *Psammogammarus* spec.), Ostracoda, Copepoda (Harpacticoida, Cyclopidae), Decapoda (*Macrura*); Pycnogonida (*Hedgpeithius interstitialis* Stock, 1989); Polychaeta; Oligochaeta; Nematoda.

- 1 ♀, 1 fragmentary specimen; AMEWI sta. 84/146, Boca Wandomi, NW of Boca Tabla, behind protecting barrier of beachrock, 12°22'31"N 69°07'12"W; coarse sand, on edge of water line, first loamy, Bou-Rouch biophreatical pump, pipe depth 0.35 m, marine; collected by J.H. Stock and J. Vermeulen; 2.vi.1984; ZMA coll. no. C.A. 8087.

Accompanying fauna: Crustacea: Isopoda (*Microcerberus* spec.), Amphipoda (Melitidae); Polychaeta; Oligochaeta; Nematoda; Mollusca: Gastropoda (*Caecum* spec., *Philine* spec.).

- 5 ♂♂, 17 ♀♀ (5 with broodpouch); AMEWI sta. 84/167, Fuik Bay, NW land tongue of the second lagoon, at the shore, 12°03'30"N 68°50'16"W; coarse sand, Bou-Rouch biophreatical pump, pipe depth 0.5 m, chlorinity 25597 mg/l; collected by J.H. Stock and J. Vermeulen; 4.vi.1984; ZMA coll. no. C.A. 8088.

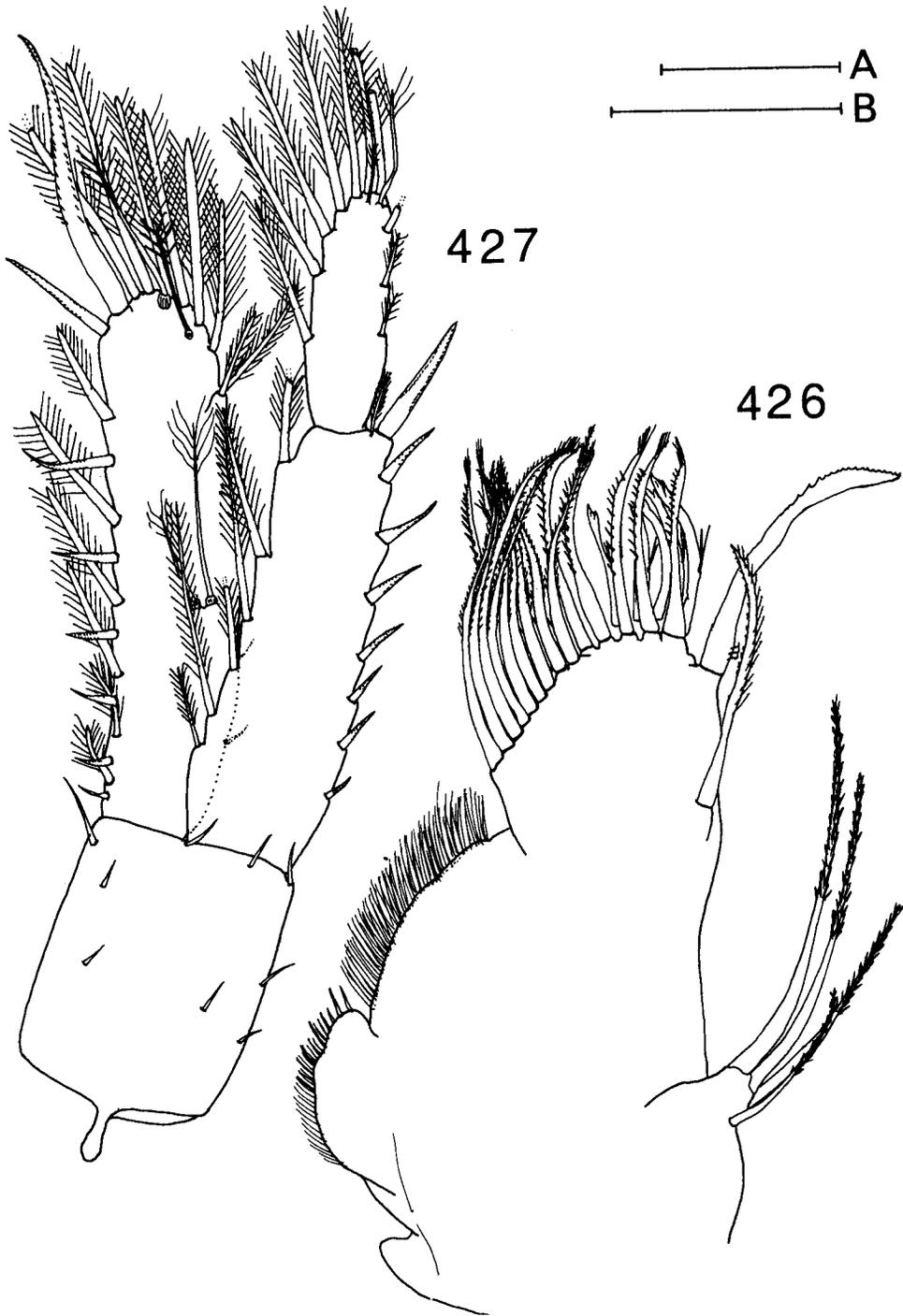
Accompanying fauna: Crustacea: Amphipoda (Hadziidae, *Psammogammarus* spec.); Polychaeta; Oligochaeta; Sipunculida.

**Netherlands Antilles, Bonaire:** 2 ♂♂, 70 ♀♀; AMEWI sta. 84/205, Estate Washington, Plaj'i (Playa) Funchi, 12°17'08"N 68°24'41"W; small resurgence ("trickle") on inner side of the coral debris and beachrock barrier, grey coarse and fine sand, Bou-Rouch biophreatical pump, pipe depth 0.5 m, chlorinity 26104 mg/l; collected by J.H. Stock and J. Vermeulen; 9.vi.1984; ZMA coll. no. C.A. 8089; RMNH G 78.

Accompanying fauna: Crustacea: Isopoda (*Curassanthura halma* Kensley, 1981), Amphipoda (*Bogidiella* spec., *Psammogammarus caesicolus* Stock, 1980, *Saliweckelia emarginata* Stock, 1977, oculate species), Ostracoda, Barnchiopoda; Polychaeta; Nematoda; Mollusca: Gastropoda (*Caecum* spec.).

- 1 ♂; AMEWI sta. 84/206, Estate Washington, Playa Bengé, 12°17'36"N 68°24'37.3"W; on waterline, on stones with sand and loam underneath, Bou-Rouch biophreatical pump, pipe depth 0.45 m, chlorinity 28385 mg/l; collected by J.H. Stock and J. Vermeulen; 9.vi.1984; ZMA coll. no. C.A. 8090.

Accompanying fauna: Crustacea: Amphipoda (*Bogidiella* spec.), Ostracoda; Insecta; Polychaeta; Oligo-



Figs. 426-427. *Halosbaena acanthura* (Stock, 1976), ♂, San Andres Island. 426, distal portion of coxopodal and basipodal endites of maxilliped (scale A). 427, uropod (scale B). Scales indicated 0.1 mm.

chaeta; Sipunculida; Nematoda; Mollusca: Gastropoda (*Caecum* spec.).

- 13 ♂♂, 97 ♀♀, 17 fragmentary specimens; AMEWI sta. 84/209, Saliña Bartol, a few m SW of drill hole on shore, 1 m above waterline, 12°28'01"N 68°23'46"W; in coral debris, Bou-Rouch biophreatical pump, pipe depth 0.45 m, chlorinity 33327 mg/l; collected by J.H. Stock and J. Vermeulen; 9.vi.1984; ZMA coll. no. C.A. 8091.

Accompanying fauna: Crustacea: Amphipoda (Talitridae; *Psammogammarus caesicolus* Stock, 1980, *Sal- iweckelia holsingeri* Stock, 1977), Copepoda (Cyclopidae), Ostracoda; Insecta; Polychaeta; Oligochaeta; Nematoda; Mollusca: Gastropoda.

- 1 (damaged) specimen; AMEWI sta. 84/213, ca. 2.3 km E of Beneden Bolivia, ca. 8 m E of well of Estate Bolivia, 12°14'04"N 68°15'28"W; narrow natural crevice with drinking trough, outside the coral, H<sub>2</sub>S smell, decomposing wood, muddy bottom, handnet, water depth 0.3 m, chlorinity 13401 mg/l; collected by J.H. Stock and J. Vermeulen; 10.vi.1984; ZMA coll. no. C.A. 8092.

Accompanying fauna: Crustacea: Isopoda; Insecta: Collembola; Acari; Oligochaeta; Nematoda; Mol- lusca: Gastropoda.

**Colombia:** 17 ♂♂, 34 ♀♀ (29 with broodpouch), 8 juveniles; San Andres Island, Schooner Bight Cave; salinity ca. 27‰; collected by B. Sket; vi.1984; ZMA coll. no. C.A. 8093, RMNH G 43; UEKL.

**Cuba:** 1 ♀, 3 fragmentary specimens; Cuban-Dutch Biospeological Exped. sta. 89/005, Prov. Matanzas, «grieta» near Cueva La Pluma, 1 km E of Lighthouse; open natural crevice in calcareous bottom, opening hidden by bushes, water table 4 m, water depth 0.5-1 m, Cvetkov net, temperature 25.9 °C, electric conductivity 27.9 mS/cm; collected by H.P. Wagner; 7.v.1989; ZMA coll. no. C.A. 8094.

Accompanying fauna: Crustacea: Isopoda, Amphipoda (oculate), Decapoda (*Barbouria cubensis* (Von Martens, 1872), larvae); Mollusca: Gastropoda.

- 1 ♂, 3 ♀♀, 1 fragmentary specimen; same locality; collected by C. Delamare Deboutteville; MP.

- 1 damaged ♀; same locality; 1 November 1970; MP.

**Jamaica:** 2 ♂♂, 1 ♀; Iliffe sta. 90-008, St. Ann Parish, Discovery Bay, air strip cave #3 & 5; limestone cave, anchihaline water, at 0-3 m, salinity 26-29.5 ppt; collected by Th.M. Iliffe and S. Sarbu; 13.vi.1990; USNM.

Accompanying fauna: Crustacea: Mysidaacea (partim?), Tanaidacea, Ostracoda (halocyprids and pod- ocopids), Copepoda, Decapoda (Natantia).

- 1 ♂, 1 ♀; Iliffe sta. 90-016, Clarendon Parish, Jackson Bay, anchihaline sinkhole #2; limestone cave, anchihaline water, at 0-1 m, salinity 23 ppt; collected by Th.M. Iliffe and S. Sarbu; 19.vi.1990; USNM.

- 1 ♀; Iliffe sta. 90-036, St. Ann Parish, Discovery Bay, air strip cave #2; limestone cave, anchihaline water, at 0-5 m, salinity 25 (surface)-28 (bottom) ppt; 280 µm mesh plankton net, from the water col- umn; collected by Th.M. Iliffe and S. Sarbu; 30.vi.1990; USNM.

Accompanying fauna: Crustacea: Mysidaacea (partim?), Tanaidacea, Ostracoda (*Spelaeoecia jamaicensis* Kornicker & Iliffe, 1992, and podocopids), Copepoda.

**Description.**— Body length (antennae 1 and 2 excluded) of male up to 2132 µm, of female up to 2460 µm (holotype 1.7 mm) in the material studied.

**Antenna 1:** main flagellum 7- to 13-segmented; accessory flagellum 4- to 6-seg- mented.

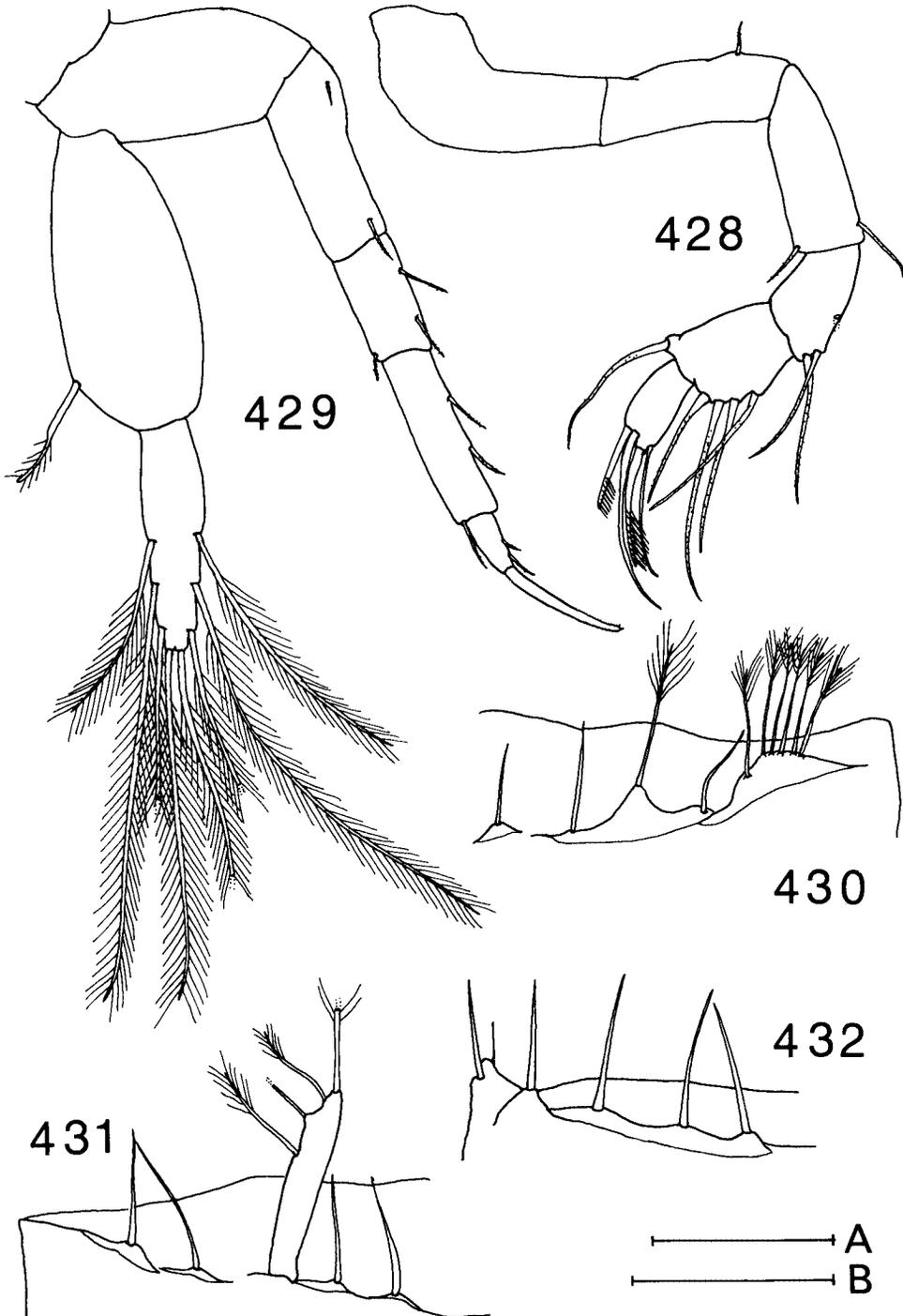
**Antenna 2:** flagellum 5- to 6-segmented, segments 1 to 3 with three simple macro- setae on medial margin, segments 1, 3 and 5 with one simple macroseta on distolat- eral margin.

**Ocular scales:** anteriorly evenly rounded, mediodistal angle pointed.

**Labrum:** without peculiarities

**Mandible:** second segment of palp with four plumidenticulate macrosetae; third segment with two plumidenticulate macrosetae, one short simple and one long ser- rulate macroseta; corpus mandibula with row of five serrate macrosetae in left man- dible.

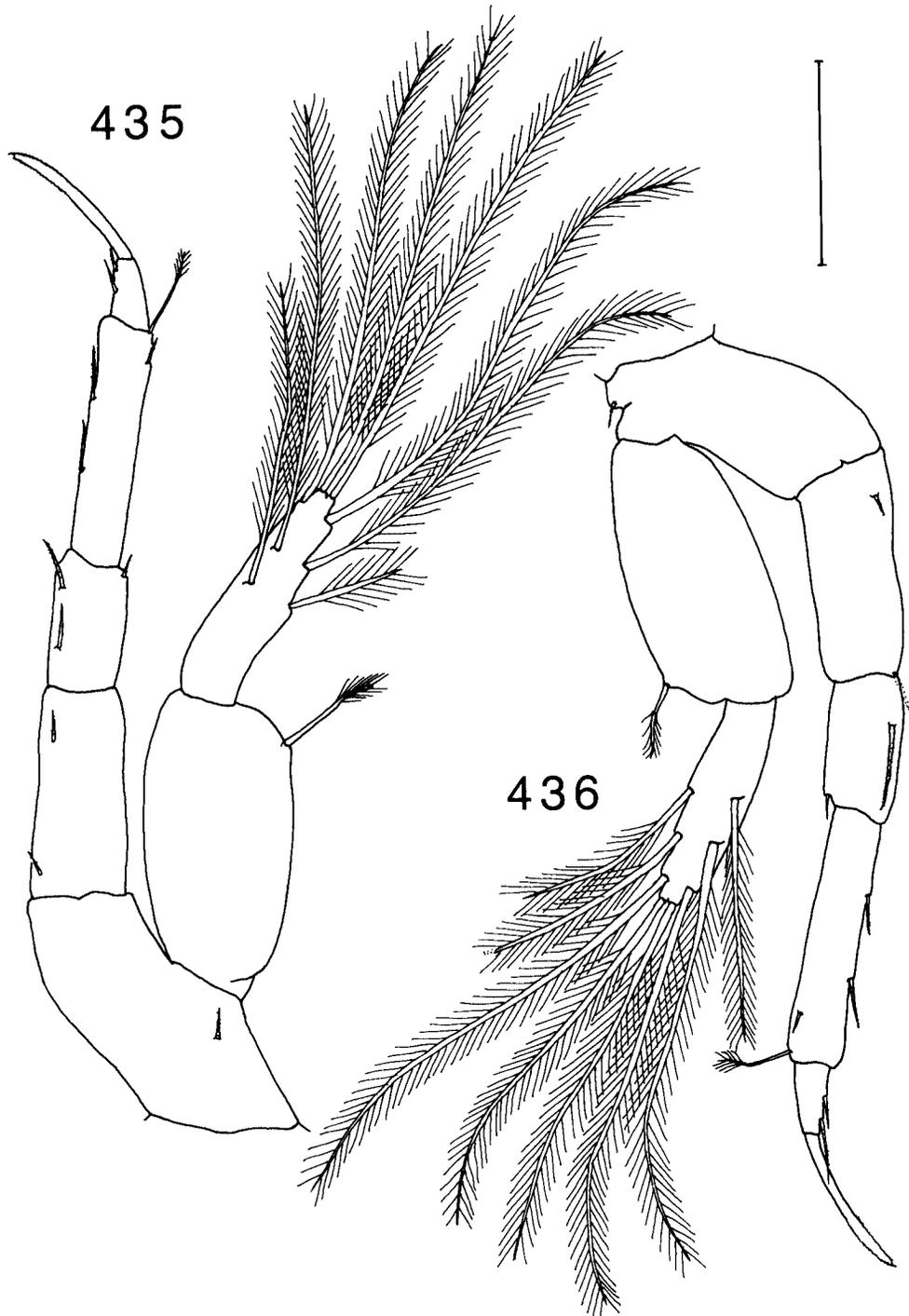
**Labium:** without peculiarities.



Figs. 428-432. *Halosbaena acanthura* (Stock, 1976), ♂, San Andres Island. 428, gnathopod. 429, pereopod 2 (figs. 428-429 scale B). 430, pleopod 1. 431, pleopod 2. 432, pleonite 5 (figs. 430 - 432 scale A). Scales indicated 0.1 mm.



Figs. 433-434. *Halosbaena acanthura* (Stock, 1976), ♂, San Andres Island. 433, pereopod 3 (scale B). 434, telson (scale A). Scales indicated 0.1 mm.



Figs. 435-436. *Halosbaena acanthura* (Stock, 1976), ♂, San Andres Island. 435, pereopod 4. 436, pereopod 5. Scale indicated 0.1 mm.

Maxilla 1: without peculiarities.

Maxilla 2: coxopodal endite with 20 long plumose macrosetae, six rod macrosetae and two stout plumose macrosetae; basipodal endite 2 with two transverse rows of 21 small and 14 large, and two modified serrate subterminal macrosetae; basipodal endite 3 with 55 to 78 rake-like serrate macrosetae increasing in size and dentation towards the medial margin of the appendage, arranged in 10 to 12 somewhat triangularly configurated oblique rows of 1+2+3+4+5+6+7+8+9+10(+11+12) macrosetae.

Maxilliped: coxopodal endite a tapering lobe with one medial, one subterminal, two terminal and one lateral pappose macrosetae; basipodal endite with three rows of plumidenticulate macrosetae, ventral row of five curved macrosetae, central row of eight (lateralmost one reduced) macrosetae with stout setules, and dorsal row of nine tall and finely setulate macrosetae, submedially an additional large modified plumidenticulate macroseta with three or four short stiff setules on basal portion.

Gnathopod: baso-ischium with simple macroseta proximally on dorsal margin, but without teazel macroseta on distodorsal margin.

Pereiopod 2: carpus of endopodite with one teazel macroseta subterminally on both ventral and dorsal margins; propodus with two teazel macrosetae medially on ventral margin, one teazel macroseta distodorsally; second segment of exopodite with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopods 3 to 5: ischiomerus of endopodite with two teazel macrosetae on ventral margin, one proximally and one distally; carpus with one teazel macroseta medially on ventral margin and one teazel macroseta subterminally on both ventral and dorsal margins; propodus with two teazel macrosetae medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with two teazel macrosetae on ventral margin, one proximally and one distally; carpus with two teazel macrosetae medially on ventral margin and one teazel macroseta subterminally on both ventral and dorsal margins; propodus with two teazel macrosetae medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite with one or two medial, two subterminal, two terminal and one or two lateral plumose macrosetae.

Pereiopod 7: ischiomerus of endopodite with two teazel macrosetae on ventral margin, one proximally and one distally; carpus with one teazel macroseta subterminally on both ventral and dorsal margins; propodus with two teazel macrosetae medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite with one medial, two subterminal, two terminal and one lateral plumose macrosetae.

Male penial lobes simple, naked, tall, almost straight, medially associated with coxopodite.

First pleopod: two processes, one rounded with five to six subplumose macrosetae, and one tapering with a subplumose macroseta that is flanked medially by two simple macrosetae, in between processes with two additional simple macrosetae.

Second pleopod: with subplumose macrosetae flanked by two simple macrosetae

laterally, and two medially (medialmost being the central one).

Pleonites 3 to 5: five simple macrosetae are implanted at either side, one laterally, and four ventrally.

Uropod: protopodite with three medial and three lateral simple macrosetae and two simple macrosetae dorsotermally; segment 1 of exopodite laterally with eight cuspidate macrosetae, some accompanied by subplumose macroseta; medially with five plumose macrosetae, segment 2 with 11 to 12 plumose macrosetae all along distolateral to medial margins; endopodite with eight cuspidate macrosetae along medial margin, five stout plumose macrosetae along distomedial margin, lateral and terminal margins with 10 to 11 plumose macrosetae.

Telson: width/length ratio 0.90, lateroposterior margin with four pairs of cuspidate macrosetae, three to five serrate macrosetae laterally on each side, and one to three small serrate macrosetae implanted dorsally.

Variability.— Two groups of variable characters have been observed; size-dependent and non-size-dependent. Typical size-dependent variation concerns the number of flagellum segments of antennae 1 and 2, and to some extent in the number of rake-like macrosetae of basipodal endite 3 of maxilla 2. Non-size-dependent variation was observed in the number of plumose macrosetae present on segment 2 of the exopodite of pereopod 6, the number of plumose macrosetae of the endopodite of the uropod, and in the number of laterally and dorsally implanted serrate macrosetae of the telson.

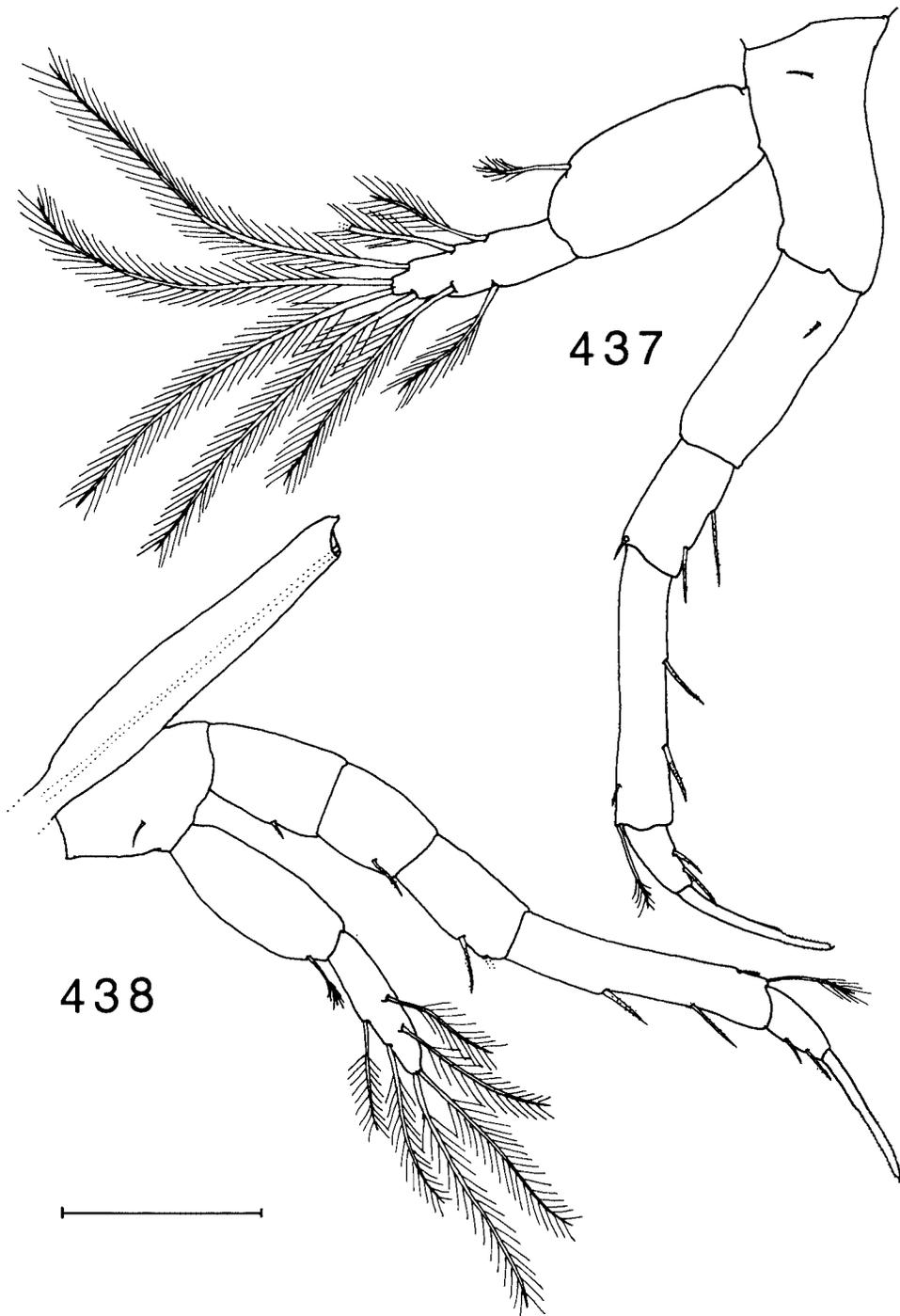
Remarks.— The (unstained) paratypes dissected, described and figured by Stock (1976) were re-examined and found to match the above redescription. In Stock's figure 35 one of the lateral serrate macrosetae of the telson (central one left in drawing) actually is not present (nor is an implantation pit visible). Also, the chaetotaxy of the palp of maxilla 1 (Stock, 1976: fig. 44) is misinterpreted, probably due to the condition (unstained and with internal musculature present) of the material.

Examination of over 40 specimens from several islands throughout the Caribbean, showed no perceptible variation between the various populations. Any variation observed occurred among individuals of each of these populations. Specimens from Cuba, Jamaica and Colombia are generally somewhat larger in size than those from Curaçao, Bonaire and the Aves Islands, but in the former localities the specimens were collected in marine cave lakes, and not in the less spacious interstitium.

*Halosbaena fortunata* Bowman & Iliffe, 1986, is the species most closely related to *H. acanthura*. It shows more similarity in segmentation of the flagellum of antenna 2, shape of the ocular scales, and in the chaetotaxy of its mandible, pleonites 3 to 5, and uropod, to *H. acanthura* or *H. fortunata* than either of these two do to *H. tulki* Poore & Humphreys, 1992. For detailed information on specific differences with the other congeners one is referred to table 5 (p. 280).

Distribution.— This species is widely distributed throughout the Caribbean. It is reported from the Netherlands Antilles: Curaçao (Stock, 1976) and Bonaire (Stock, 1986a), the Aves Islands, Venezuela (as Islote Aves by Wagner, 1990), San Andres Island, Colombia (Stock, 1986a; Sket, 1988b), Cuba and Jamaica.

Habitat.— *Halosbaena acanthura* has been found mainly in the coastal interstitium of Curaçao, but in recent years it has been reported too from shallow marine sands (Stock, 1986a), and marine cave lakes at Curaçao (Stock, 1979) and San Andres Island



Figs. 437-438. *Halosbaena acanthura* (Stock, 1976), ♂, San Andres Island. 437, pereopod 6. 438, pereopod 7. Scale indicated 0.1 mm.

(Sket, 1988b). Recently Dr Thomas Iliffe (Texas A. & M. University, Galveston, U.S.A.) collected *H. acanthura* from an anchihaline sinkhole and cave lake at Jamaica. The specimens from the Aves Islands originate from the marine interstitial, and the material collected in Cuba comes from a marine lake at the bottom of a «grieta» (= an opening in the karstic bottom). All these localities are situated in limestone deposits. Those from Jamaica and San Andres Island, Colombia, date back to Miocene or Pleistocene age (Weyl, 1966; Sket, 1988b). The «grieta» in Matanzas, Cuba, is situated in karstic rocks formed between the Pliocene and Holocene (Weyl, 1966), while in Curaçao and Bonaire all localities are in limestone deposits of Pliocene to Pleistocene age (Beets, 1972; Stock, 1976) or in coral shingle of holocene age (De Buissonjé, 1974; Stock, 1976). The geology of the Aves Islands is comparable to that of Curaçao and Bonaire.

With such diverse localities and habitats a diversity in accompanying fauna can be expected and, indeed, has been observed. For detailed information, one is referred to the extensive material list above.

#### 4.6.2.2. *Halosbaena fortunata* Bowman & Iliffe, 1986 (figs. 439-449)

*Halosbaena* n. sp.; Stock, 1986a: 588.

*Halosbaena fortunata* Bowman & Iliffe, 1986: 84, figs. 1-2; Wilkens, Parzefall & Iliffe, 1986: 224, 227; Cals & Monod, 1988: 342; Meštrov & Cals, 1991: 43.

*Halosbaena*; Rondé-Broekhuizen & Stock, 1987: 27; Stock, 1987: 169.

Material.— **Spain, Canary Islands:** 2 ♀♀; Canary Islands Exped. sta. 85/86, Lanzarote, Ponta Chica; old windpump of salt pit, water table 11 m, water depth 0.25 m, temperature 20.4°C, conductivity 39.7 mS/cm; collected by J.H. Stock and B.L.M. Rondé-Broekhuizen; 20.v.1985; ZMA coll. no. C.A. 8095.

Accompanying fauna: Crustacea: Amphipoda (*Liagoceradocus acutus* Andres, 1978), Copepoda (Calanoida).

- 1 ♀; Canary Islands Exped. sta. 85/100, Lanzarote, Jameos del Agua, Lago Mayor; washed from sand and gravel and taken free-swimming with a dipnet in the great cave lake, water depth 0-0.5 m, temperature 18.4°C, conductivity 40.1 mS/cm; collected by J.H. Stock and B.L.M. Broekhuizen; 21.v.1985; ZMA coll. no. C.A. 8096 [topotype].

Accompanying fauna: Crustacea: Mysidacea (*Heteromysoides cotti* (Calman, 1932)), Amphipoda (*Liagoceradocus acutus* Andres, 1978; *Bogidiella (Stygogidiella) uniramosa* Stock & Rondé-Broekhuizen, 1987; *Parhyale multispinosa* Stock, 1987), Copepoda (Cyclopidae; Harpacticoidea), Cladocera, Anomura (*Munidopsis polymorpha* Koelbel, 1892); Polychaeta (*Typosyllis (Langerhansia) cornuta* (Rathke, 1843)); Sipunculida.

Description.— Body length (antennae 1 and 2 excluded) female up to 2252 µm (holotype 2.2 mm) in the material studied.

Antenna 1: main flagellum up to 16-segmented; accessory flagellum 7- to 9-segmented.

Antenna 2: flagellum 5- to 7-segmented, segments 1 to 3 with three simple macrosetae on medial margin, segments 1, 3 and 5 with one simple macroseta on distolateral margin.

Ocular scales: anteriorly evenly rounded, mediolateral angle pointed.

Labrum: without peculiarities.

Mandible: second segment of palp with four plumidenticulate macrosetae; third

segment with two plumidenticulate macrosetae, one short simple and one long serrulate macroseta; corpus mandibula with row of five serrate macrosetae in left mandible.

Labium: without peculiarities.

Maxilla 1: without peculiarities.

Maxilla 2: coxopodal endite with 22 long plumose macrosetae, six rod macrosetae and two stout plumose macrosetae; basipodal endite 2 with two transverse rows of 40 small and 18 large, and two modified serrate subterminal macrosetae; basipodal endite 3 with 66 to 105 rake-like serrate macrosetae increasing in size and dentation towards the medial margin of the appendage, arranged in 11 to 14 somewhat triangularly configured oblique rows of 1+2+3+4+5+6+7+8+9+10+11(+12+13+14) macrosetae.

Maxilliped: coxopodal endite a tapering lobe with two medial, one subterminal, two terminal and one lateral pappose macrosetae; basipodal endite with three rows of plumidenticulate macrosetae, ventral row of seven curved macrosetae, central row of eight (lateralmost one reduced) macrosetae with stout setules, and dorsal row of nine tall and finely setulate macrosetae, submedially an additional large modified plumidenticulate macroseta with four short stiff setules on basal portion.

Gnathopod: baso-ischium without simple macroseta proximally on dorsal margin, but with teazel macroseta on distodorsal margin.

Pereiopod 2: carpus of endopodite with one teazel macroseta subterminally on both ventral and dorsal margins; propodus with one teazel macroseta medially on ventral margin, one teazel macroseta distodorsally; second segment of exopodite with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopods 3 to 5: ischiomerus of endopodite with two teazel macrosetae on ventral margin, one proximally and one distally; carpus with one teazel macroseta medially on ventral margin and one teazel macroseta subterminally on both ventral and dorsal margins; propodus with one teazel macroseta medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite with two medial, two subterminal, two terminal and two lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with two teazel macrosetae on ventral margin, one proximally and one distally; carpus with one teazel macroseta medially on ventral margin and one teazel macroseta subterminally on both ventral and dorsal margins; propodus with one teazel macroseta medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite with one medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 7: ischiomerus of endopodite with two teazel macrosetae on ventral margin, one proximally and one distally; carpus with one teazel macroseta subterminally on both ventral and dorsal margins; propodus with one teazel macroseta medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite two subterminal and two terminal plumose macrosetae.

First pleopod: with two processes, one rounded with five to six subplumose

macrosetae, and one tapering with a subplumose macroseta that is flanked medially by two simple macrosetae, in between processes with two additional simple macrosetae.

Second pleopod: with subplumose macrosetae flanked by one simple macroseta laterally, and one medially (= central one).

Pleonites 3 to 5: four simple macrosetae are implanted at either side, one laterally and three ventrally.

Uropod: protopodite with three medial and three lateral simple macrosetae; segment 1 of exopodite laterally with six cuspidate macrosetae, some accompanied by subplumose macroseta; medially with six plumose macrosetae, segment 2 with 12 plumose macrosetae all along distolateral to medial margins; endopodite with eight cuspidate macrosetae along medial margin, six stout plumose macrosetae along distomedial margin, lateral and terminal margins with 11 plumose macrosetae.

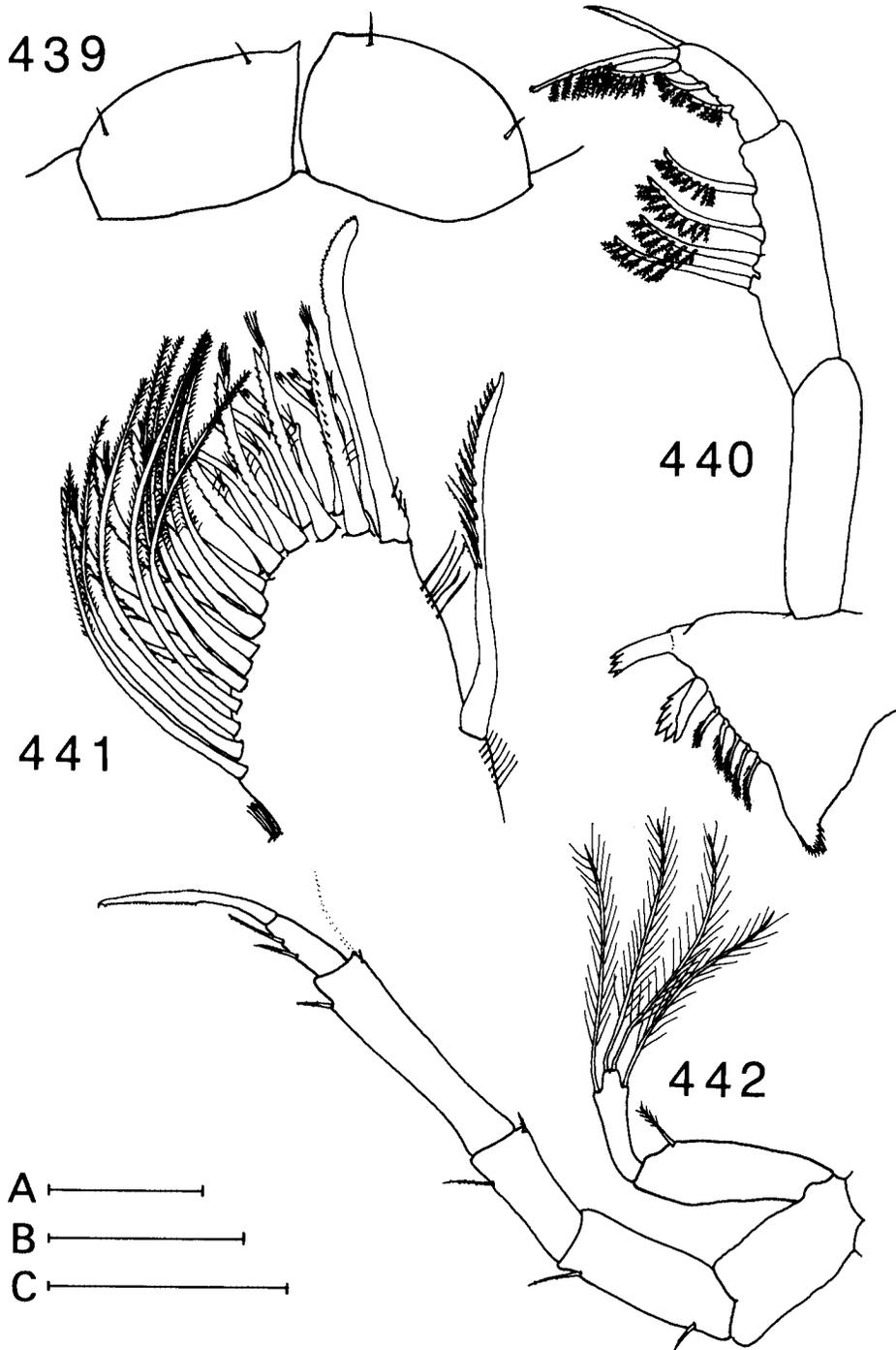
Telson: width/length ratio 0.66, lateroposterior margin with four pairs of cuspidate macrosetae, three to five serrate macrosetae laterally on each side, without dorsal simple macrosetae.

Variability.— Due to the limited number of specimens available I only observed some variation in the number of flagellum segments of antennae 1 and 2, and in the number of rake-like macrosetae on basipodal endite 3 of maxilla 2.

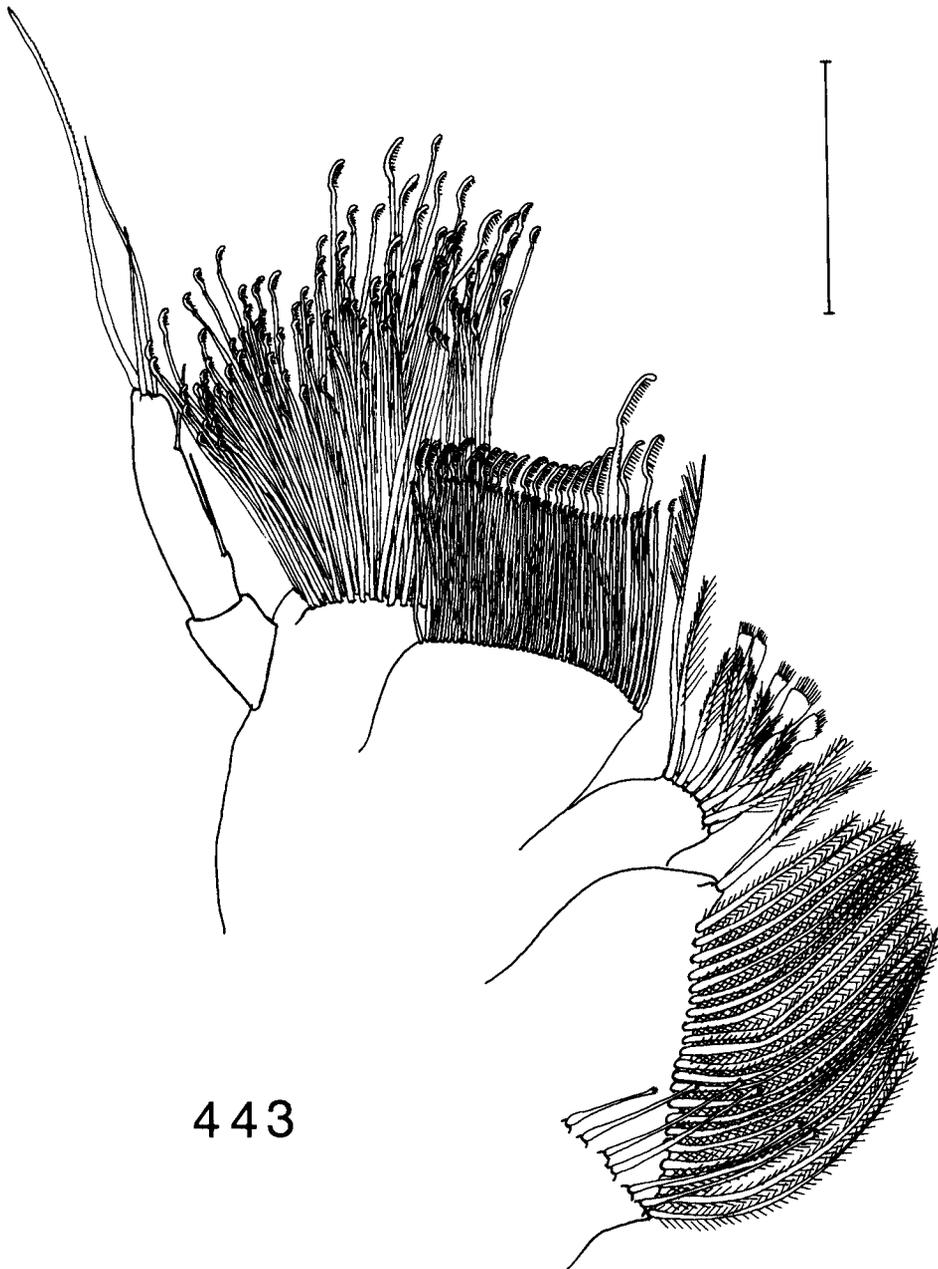
Remarks.— The tabulated diagnosis given by Bowman & Iliffe (1986) to describe this species matches this re-description perfectly, with the sole exception of the number of "spines" (plumose macrosetae) of the precoxal endite of maxilla 1. This erroneous observation is probably due to the examination of unstained material. For detailed information on specific differences with the other congeners one is referred to table 5 (p. 280).

Distribution.— *Halosbaena fortunata* is found in the Jameos del Agua marine lava cave (type locality) and several wells pumping up saline waters for salinas (salt-works) on Lanzarote, Canary Islands.

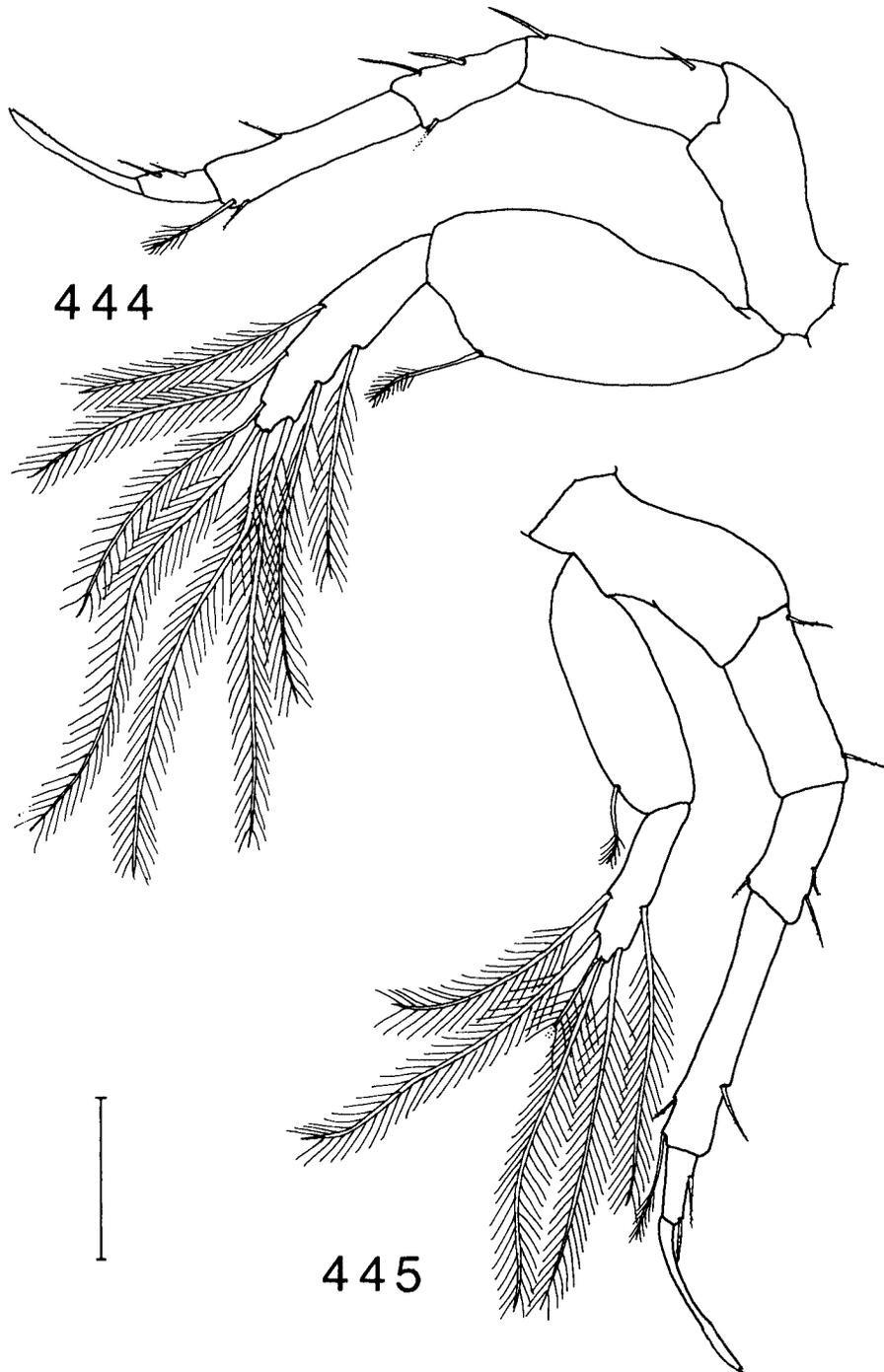
Habitat.— The Jameos del Agua lava tube was formed by an eruption of the volcano Monte Corona about 3000 to 5000 years BP (Wilkins & Parzefall, 1974; Bowman & Iliffe, 1986). The saltpits, where the wells that provided *H. fortunata* are situated, are located on nearcoastal lava outcrops of Holocene age. For the wells a normal marine salinity (35‰) has been reported by Wilkins, Parzefall & Iliffe (1986). The accompanying fauna living in the lava tunnel consists of the remiped *Speleonectes ondinae* (García-Valdecasa, 1984); the amphipods *Spelaeonicippe buchi* (Andres, 1975), *Liagoceradocus acutus* Andres, 1978, *Bogidiella (Stygogidiella) uniramosa* Stock & Rondé-Broekhuizen, 1987, and *Parhyale multispinosa* Stock, 1987; the isopod *Curassanthura canariensis* Wägele, 1985; the mysid *Heteromysoides cotti* (Calman, 1932); the ostracod *Danielopolina wilkensi* Hartman, 1985; the galatheid *Munidopsis polymorpha* Koelbel, 1892; copepods (Cyclopidae and Harpactoidea), cladocerans, the polychaetes *Typosyllis (Langerhansia) cornuta* (Rathke, 1843) and *Gesiella jameensis* Hartman-Schröder, 1974; and sipunculids. From the wells the following species have been found as accompanying fauna: the amphipods *Liagoceradocus acutus* Andres, 1978; the mysid *Heteromysoides cotti* (Calman, 1932); the ostracod *Danielopolina wilkensi* Hartman, 1985; copepods (Calanoida); and the galatheid *Munidopsis polymorpha* Koelbel, 1892.



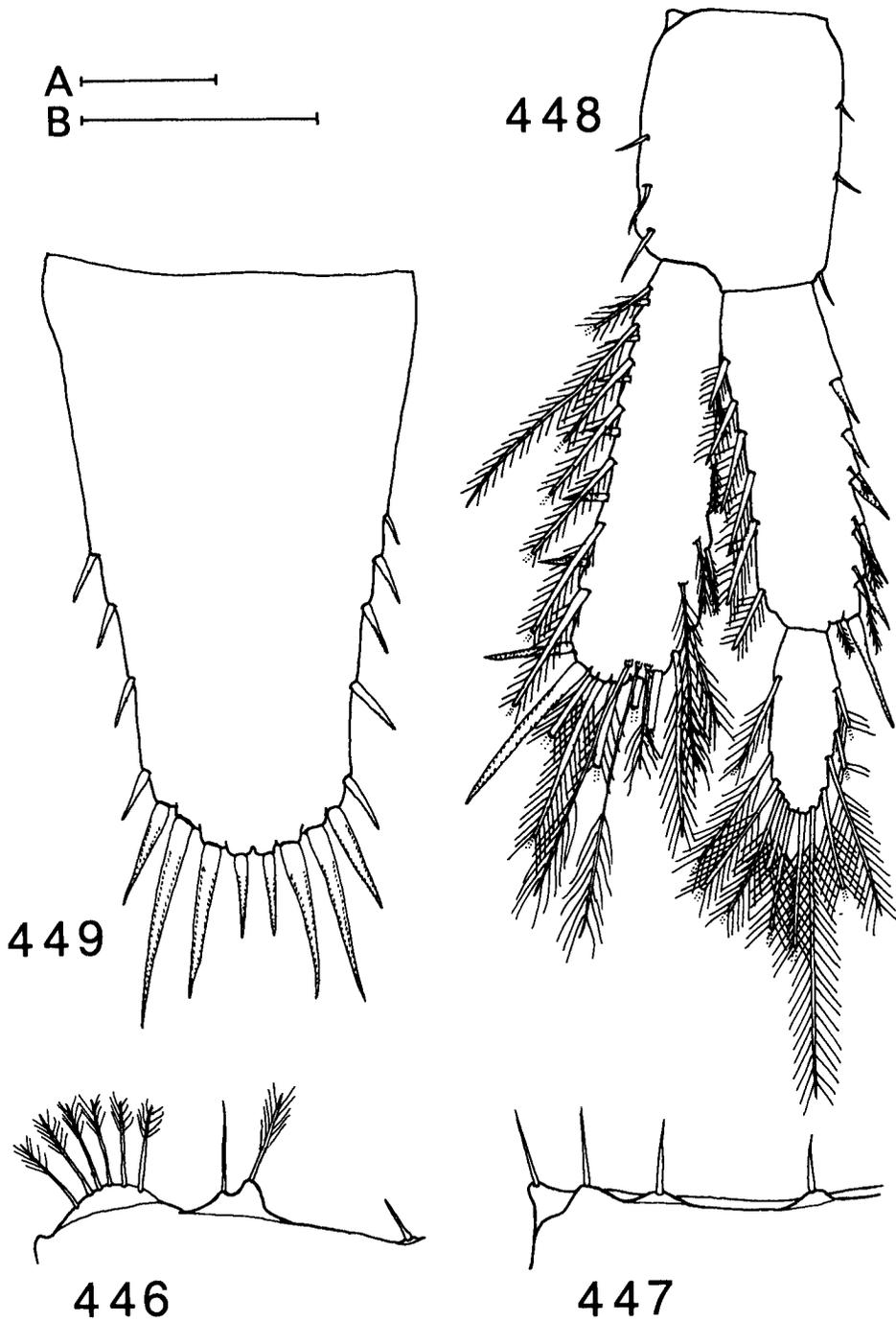
Figs. 439-442. *Halosbaena fortunata* Bowman & Iliffe, 1986, ♀. 439, ocular scales (scale B). 440, left mandible. 441, distal portion of basipodal endite of maxilliped (figs. 440-441 scale C). 442, pereiopod 7 (scale A). Scales indicated 0.1 mm.



Figs. 443. *Halosbaena fortunata* Bowman & Iliffe, 1986, ♀, maxilla 2. Scale indicated 0.1 mm.



Figs. 444-445. *Halosbaena fortunata* Bowman & Iliffe, 1986, ♀. 444, pereopod 3. 445, pereopod 6. Scale indicated 0.1 mm.



Figs. 446-449. *Halosbaena fortunata* Bowman & Iliffe, 1986, ♀. 446, pleopod 1. 447, pleonite 4 (figs. 446-447 scale B). 448, uropod. 449, telson (figs. 448-449 scale A). Scales indicated 0.1 mm.

4.6.2.3. *Halosbaena tulki* Poore & Humphreys, 1992  
(figs. 450-460)

*Halosbaena tulki* Poore & Humphreys, 1992: 721, fig. 1.

**Material.**— **Australia, Western Australia:** 3 ♂♂, 3 ♀♀ (1 with broodpouch); North West Cape, western slope of Cape Range (22°02'S 113°56'E), cave C-215; in standing water, Tulki limestones; water depth 1 m, air temperature 22.9°C, surface salinity 1.6 ppt, bottom salinity 1.7 ppt; collected by W.F. Humphreys; 16.x.1991; ZMA coll. no. C. A. 8240 [paratypes].

Accompanying fauna: Crustacea: Decapoda (*Stygiocaris* spec.); Pisces (*Milyeringia veritas* Whitley, 1945)

**Description.**— Body length (antennae 1 and 2 excluded) of male up to 1452 µm, of female up to 1653 µm (holotype 2.1 mm) in the material studied.

Antenna 1: main flagellum 7- to 9-segmented; accessory flagellum 4-segmented.

Antenna 2: flagellum 4-segmented, segments 1 with one, and segments 2 and 3 with three teazel macrosetae on medial margin, segments 1 and 3 without simple macroseta on distolateral margin.

Ocular scales: anteriorly evenly rounded, mediodistal angle rounded too.

Labrum: without peculiarities

Mandible: second segment of palp with three plumidenticulate macrosetae; third segment with two plumidenticulate macrosetae, one short simple and one long serrulate macroseta; corpus mandibula with row of four serrate macrosetae in left mandible.

Labium: without peculiarities.

Maxilla 1: without peculiarities.

Maxilla 2: coxopodal endite with 16 long plumose macrosetae, six rod macrosetae and two stout plumose macrosetae; basipodal endite 2 with two transverse rows of 15 small and 12 large, and two modified serrate subterminal macrosetae; basipodal endite 3 with 45 to 55 rake-like serrate macrosetae increasing in size and dentation towards the medial margin of the appendage, arranged in 9 to 10 somewhat triangularly configurated oblique rows of 1+2+3+4+5+6+7+8+9(+10) macrosetae.

Maxilliped: coxopodal endite a tapering lobe with one medial, one subterminal, two terminal and one lateral pappose macrosetae; basipodal endite with three rows of plumidenticulate macrosetae, ventral row of four curved macrosetae, central row of seven (lateralmost one reduced) macrosetae with stout setules, and dorsal row of nine tall and finely setulate macrosetae, submedially an additional large modified plumidenticulate macroseta with two short stiff setules on basal portion.

Gnathopod: baso-ischium with simple macroseta proximally on dorsal margin, but without teazel macroseta on distodorsal margin.

Pereiopod 2: carpus of endopodite with one teazel macroseta subterminally on both ventral and dorsal margin; propodus with one teazel macroseta medially on ventral margin, one teazel macroseta distodorsally; second segment of exopodite with one medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopods 3 to 5: ischiomerus of endopodite with two teazel macrosetae on ventral margins, one proximally and one distally; carpus with one teazel macroseta medially on ventral margin and one teazel macroseta subterminally on both ventral

and dorsal margins; propodus with one teazel macroseta medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite with one medial, two subterminal, two terminal and one lateral plumose macrosetae.

Pereiopod 6: ischiomerus of endopodite with two teazel macrosetae on ventral and dorsal margins, one proximally and one distally; carpus with one teazel macroseta medially on ventral margin and one teazel macroseta subterminally on both ventral and dorsal margins; propodus with one teazel macroseta medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite with one short medial, two subterminal, two terminal and one short lateral plumose macrosetae.

Pereiopod 7: ischiomerus of endopodite with two teazel macrosetae on ventral and dorsal margins, one proximally and one distally; carpus with one teazel macroseta subterminally on both ventral and dorsal margins; propodus with one teazel macroseta medially on ventral margin, one teazel macroseta and one subplumose macroseta distodorsally; second segment of exopodite two subterminal and two terminal plumose macrosetae.

Male penial lobes simple, naked, somewhat club-shaped, almost straight, the distal portion slightly broadened; medially associated with coxopodite.

First pleopod: with two processes, one rounded with six subplumose macrosetae, and one tapering with a subplumose macroseta that is flanked medially by one simple macroseta, in between processes with an additional simple macroseta.

Second pleopod: with subplumose macrosetae flanked by one simple macroseta laterally and one medially (= central one).

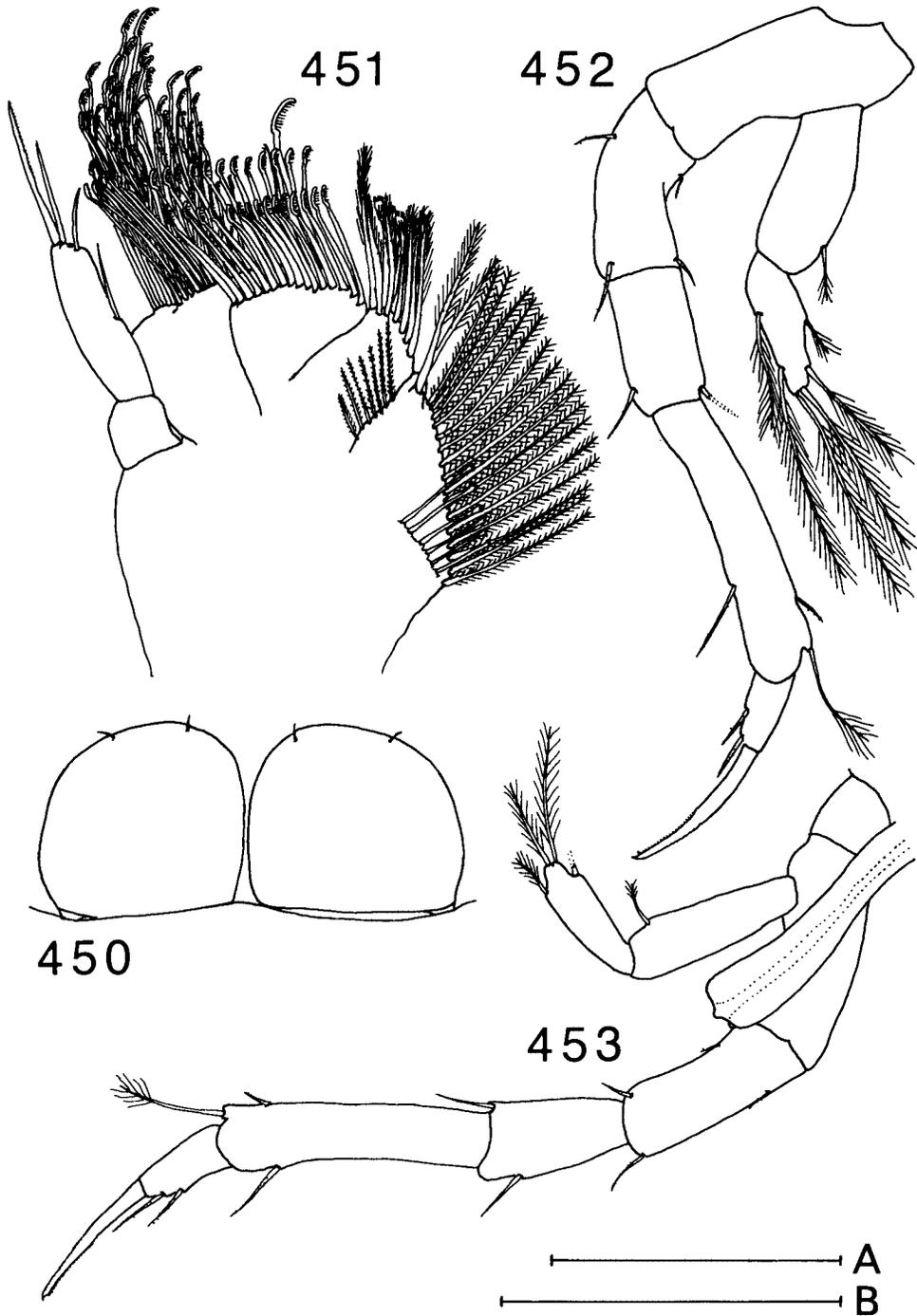
Pleonites 3 to 5: two simple macrosetae are implanted at either side, one laterally and one ventrally.

Uropod: protopodite with two medial and two lateral simple macrosetae; segment 1 of exopodite laterally with five cuspidate macrosetae, some accompanied by subplumose macroseta; medially with four (proximal one very small) plumose macrosetae, segment 2 with seven plumose macrosetae all along distolateral and terminal margins; endopodite with four (to five) cuspidate macrosetae along medial margin, five stout plumose macrosetae along distomedial margin, lateral and terminal margins with 9 to 10 plumose macrosetae.

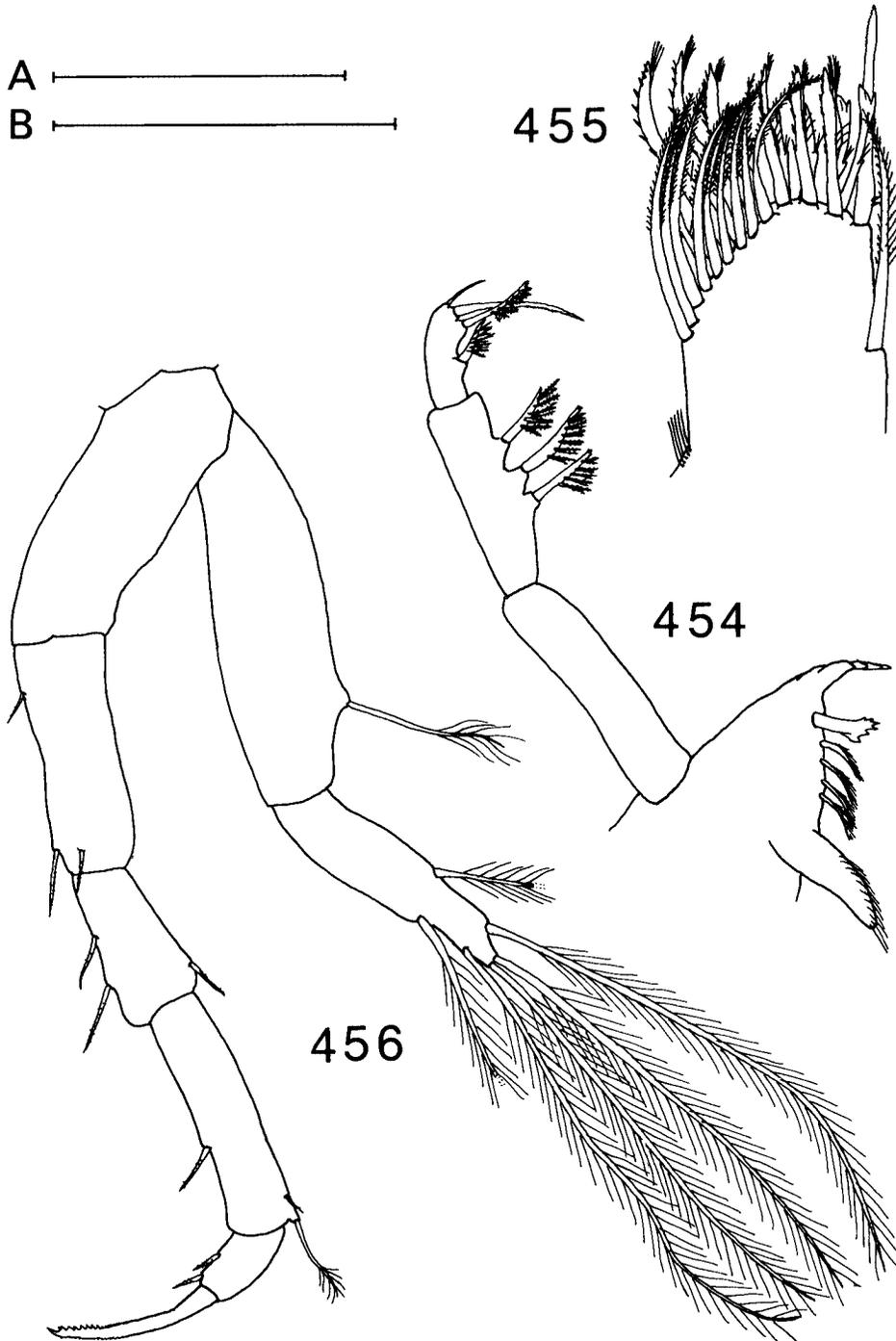
Telson: width/length ratio 0.92, lateroposterior margin with four pairs of cuspidate macrosetae, four to five serrate macrosetae laterally on each side, without dorsal simple macrosetae.

Variability.— Variation was noted in the number of segments of the main flagellum of antenna 1 (size-dependent), in the number of rake-like macrosetae of basipodal endite 3 of maxilla 2, in the number of plumose macrosetae of the uropodal endopodite, and in the number of serrate macrosetae along the lateral margins of the telson.

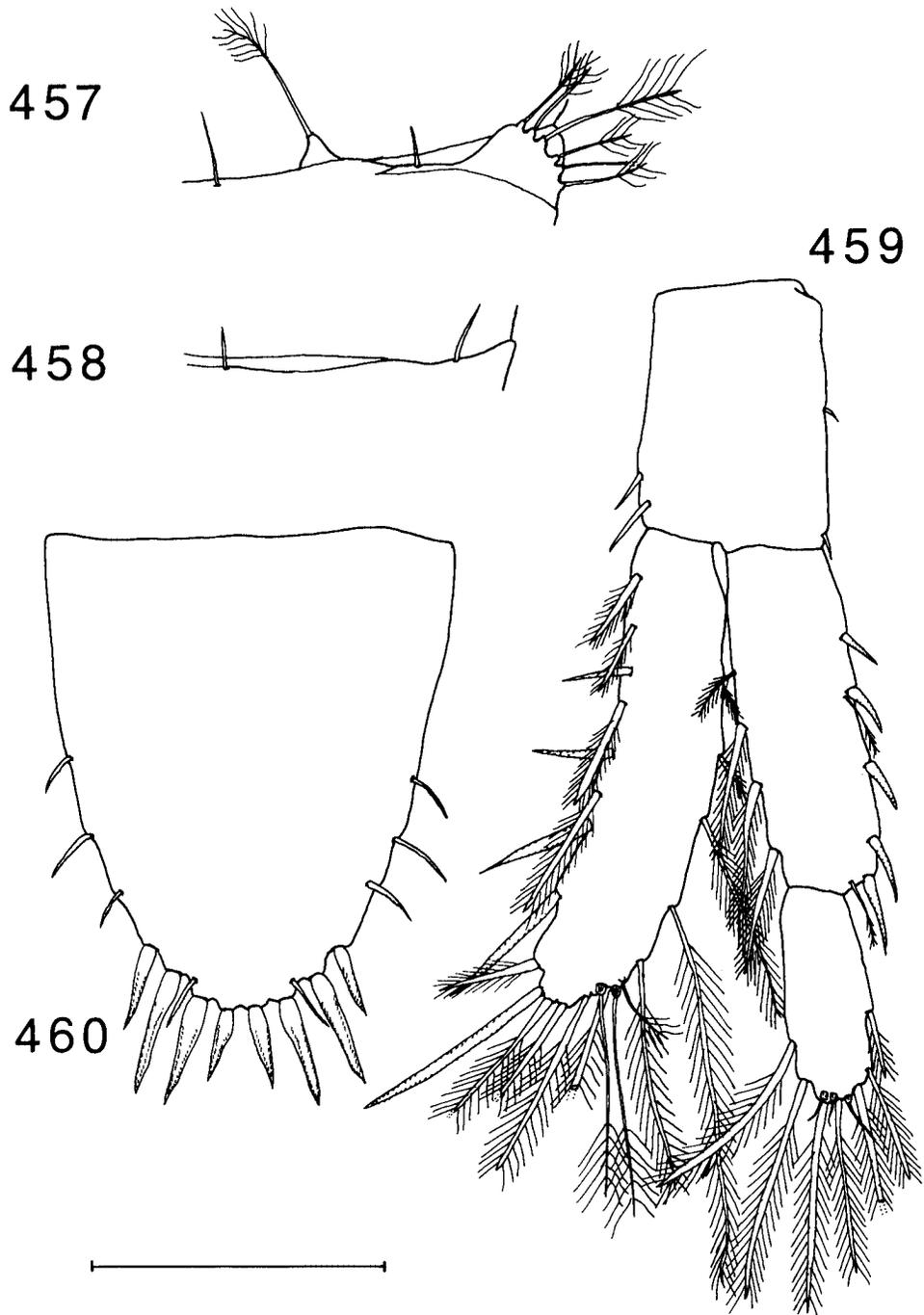
Remarks.— *Halosbaena tulki* shows in comparison with *H. acanthura* and *H. fortunata* some remarkable "reductions" in the number of the various macrosetae present on the mandible, maxilla 2, maxilliped, exopodites of pereopods 2 to 5, uropod, and ventrally on pereionites 3 to 5. Also, the absence of a pointed mediodistal angle of the ocular scale, distinguishes this species from *H. acanthura* and *H. fortunata*. For



Figs. 450-453. *Halosbaena tulki* Poore & Humphreys, 1992, paratype ♂. 450, ocular scales. 451, maxilla 2 (scale B). 452, pereopod 6. 453, pereopod 7 (figs. 450, 452-453 scale A). Scales indicated 0.1 mm.



Figs. 454-456. *Halosbaena tulki* Poore & Humphreys, 1992, paratype ♂. 454, left mandible. 455, distal portion of basipodal endite of maxilliped (figs. 454-455 scale B). 456, pereiopod 3 (scale A). Scales indicated 0.1 mm.



Figs. 457-460. *Halosbaena tulki* Poore & Humphreys, 1992, paratype ♂. 457, pleopod 1. 458, pleonite 4. 459, uropod. 460, telson. Scale indicated 0.1 mm.

detailed information on specific differences with the other congeners one is referred to table 5 (p. 280).

Distribution.— Thus far *Halosbaena tulki* is only known from its type locality, cave C-215, at the western slope of Cape Range (22°02'S 113°56'E), North West Cape, Western Australia.

Habitat.— The Cape Range system, with its highly cavernous Tulki Limestones, is an anticline of Lower Miocene Age (Poore & Humphreys, 1992). Poore & Humphreys (1992: 723) suggest that as recently as the Late Pleistocene the present troglotic fauna colonized the North West Cape peninsula. The water in which *H. tulki* lives is almost fresh. As accompanying fauna of *H. tulki*, Poore & Humphreys mention shrimps of the genus *Stygiocaris*, and the gudgeon *Milyeringia veritas* Whitley, 1945 (Pisces).

#### 4.6.3. *Theosbaena* Cals & Boutin, 1985

*Theosbaena* Cals & Boutin, 1985: 337; Cals, 1987: 661; Bowman & Iliffe, 1988: 225; Wagner, 1988: 1st page; Wagner, 1990: fig. 1; Meštrov & Cals, 1991: 42; Cals & Monod, 1991: 174.

Type species.— *Theosbaena cambodjiana* Cals & Boutin, 1985, by monotypy.

Diagnosis.— Body length (antennae 1 and 2 excluded) up to 3.65 mm. Carapace reaching up to the second pedigerous somite. Third peduncular segment of antenna 1 with four subplumose macrosetae on terminal prominence; main flagellum 29-segmented; accessory flagellum 14-segmented. Flagellum of antenna 2 5-segmented. Ocular scales evenly rounded anteriorly. Mandible with seven to nine plumidenticulate macrosetae on second segment of palp; left pars incisiva with 2 processes, its tips in total 5-dentate (one 4-dentate, other 1-dentate), right pars incisiva with 5 processes, its tips in total 12-dentate (central one 4-dentate, marginal ones 2-dentate); left lacinia mobilis 4-dentate; row of three serrate macrosetae in left, row of four serrate macrosetae in right mandible; pars molaris pointedly triangular, molar surface covered with numerous long ciliate microsetae. Palp of maxilla 1 with one long and one short bisetulate macroseta (sub)terminally; basipodal endite with eight fine, but distinctly dentate toothed macrosetae, of which three are somewhat more strongly dentate. Coxopodal endite of maxilla 2 with numerous long plumose, six rod, and two stout plumose macrosetae; basipodal endite 1 with one long (tip blunt, dentations well-developed), five obscurely setulate and six stout (modified) plumidenticulate macrosetae. Maxilliped with five complexly setulate pappose macrosetae on coxopodite, setules with flattened distal portion (with LM no detailed structure visible); subterminal margin with three rows of plumidenticulate macrosetae, with long setules in all rows, submedially a modified (i.e., with partially reduced elements) "plumidenticulate" macroseta, being tall, stout and blunt, naked, except for two oblique crenulate ridges on distal portion. Baso-ischium of endopodite of gnathopod with distinctly demarcated ischium; propodus with three serrate macrosetae ventrally; dactylus with three bow-shaped serrulate macrosetae of more or less equal length, forming terminal claw; pereopods 2 to 7 biramous, exopodites 2-segmented in pereopods 2 to 6, 1-segmented in pereopod 7. First pleopod a bump with six subplumose macrosetae; second pleopod short, somewhat triangular, with three or four

Table 5. Salient differences between the species of *Halosbaena*.

	<i>H. acanthura</i> Stock, 1976	<i>H. fortunata</i> Bowman & Iliffe, 1986	<i>H. tulki</i> Poore & Humphreys, 1992
Antenna 1:			
# segments main flagellum	7-13	?-16	7-9
# segments accessory flagellum	4-6	7-9	4
Antenna 2:			
# segments flagellum	5-6	5-7	4
Ocular scales:			
shape mediiodistal angle	pointed	pointed	rounded
Mandible:			
# plumidenticulate m.s. segm. 2	4	4	3
# serrate macrosetae left mandible	5	5	4
Maxilla 2:			
# plumose m.s. coxopodal endite	20	22	16
# rake-like m.s. ventral row b.e.2	21	40	15
# rake-like m.s. dorsal row b.e.2	14	18	12
# rake-like m.s. b.e.3	55-78 (10-12 rows)	66-105 (11-14 rows)	45-55 (9-10 rows)
Maxilliped:			
# curved plumidenticulate m.s.	5	5	4
# basal setules large modified m.s.	3-4	7	2
Gnathopod:			
# dorsal teazel m.s. baso-ischium	absent	present	absent
proximal simple m.s. baso-ischium	present	absent	present
Pereiopod 2:			
# ventral teazel m.s. carpus	2	1	1
Pereiopods 2 to 5:			
# ventral teazel m.s. propodus	2	1	1
# plumose m.s. exopodite	8	8	6
Pereiopod 6:			
# ventral teazel m.s. carpus	2	1	2
# ventral teazel m.s. propodus	2	1	1
# plumose m.s. exopodite	6-8	6	4 + 2v
Pereiopod 7:			
# ventral teazel m.s. propodus	2	1	1
# plumose m.s. exopodite	6	4	4
Pleopod 1:			
# subplumose and simple m.s.	5 to 6sp-2s-1sp-2s	6sp-1s-1sp-1s	6sp-1s-1sp-1s
Pleonites 3 to 5:			
# simple macrosetae	1 lat., 4 ventral	1 lat., 3 ventral	1 lat., 1 ventral
Uropod:			
# m.s. protopodite med., lat., dorsal	3, 3, 2	3, 3, 0	2, 2, 0
# cuspidate m.s. endopodite	8	8	4-5
# large + small plum. m.s. end.	13-14 + 2	14 + 3	12-13 + 2
# cuspidate m.s. ex. segm.1	8	6	5
total # plumose m.s. ex. segm. 1	7	10	7
# plumose m.s. ex. segm. 2	11-12	12	7
Telson:			
# lateral serrate m.s.	3-5	3-5	4-5
# dorsal serrate m.s.	1-3	0	0
mean width/length ratio	0.90	0.66	0.92

abbreviations: b.e. = basipodal endite; cusp. = cuspidate; end. = endopodite; ex. = exopodite; lat. = lateral; med. = medial; m.s. = macroseta(e); plum. = plumose; s = simple macroseta(e); segm. = segment; sp = subplumose macroseta(e); v = vestigial; # = number of....

subplumose macrosetae; small simple macrosetae absent on pleonites 3 to 5. Uropodal endopodite distinctly longer than first segment of exopodite, medial margin with serrate scale-like macrosetae; first segment of exopodite distomedially with six plumose macrosetae, distolaterally with nine cuspidate macrosetae, of which distal cuspidate macroseta accompanied by subplumose macroseta. Telson posteriorly with 13 to 16 cuspidate macrosetae at either side.

Description.— As for the type species.

Distribution.— Specimens of *Theosbaena cambodjiana*, and probably conspecific material, have been collected in the Kompong Trach mountain, Kampot Province, Cambodia and north of Chum Phae, Khon Kaen Province, Thailand.

Habitat.— *Theosbaena* is known from cave pools. At the type locality *Theosbaena* lives in fresh water.

#### 4.6.3.1. *Theosbaena cambodjiana* Cals & Boutin, 1985 (figs. 461-486)

Thermosbaenacea; Boutin, 1971: 178.

*Theosbaena cambodjiana* Cals & Boutin, 1985: 337, 339 figs. A-C; Cals & Monod, 1988: 342; Wagner, 1990: 123; Meštrov & Cals, 1991: 43.

Thermosbaenacés; Boutin & Magniez, 1985: 42.

*Theobaena* (sic) *cambodjiana* (sic); Stock, 1986a: 588.

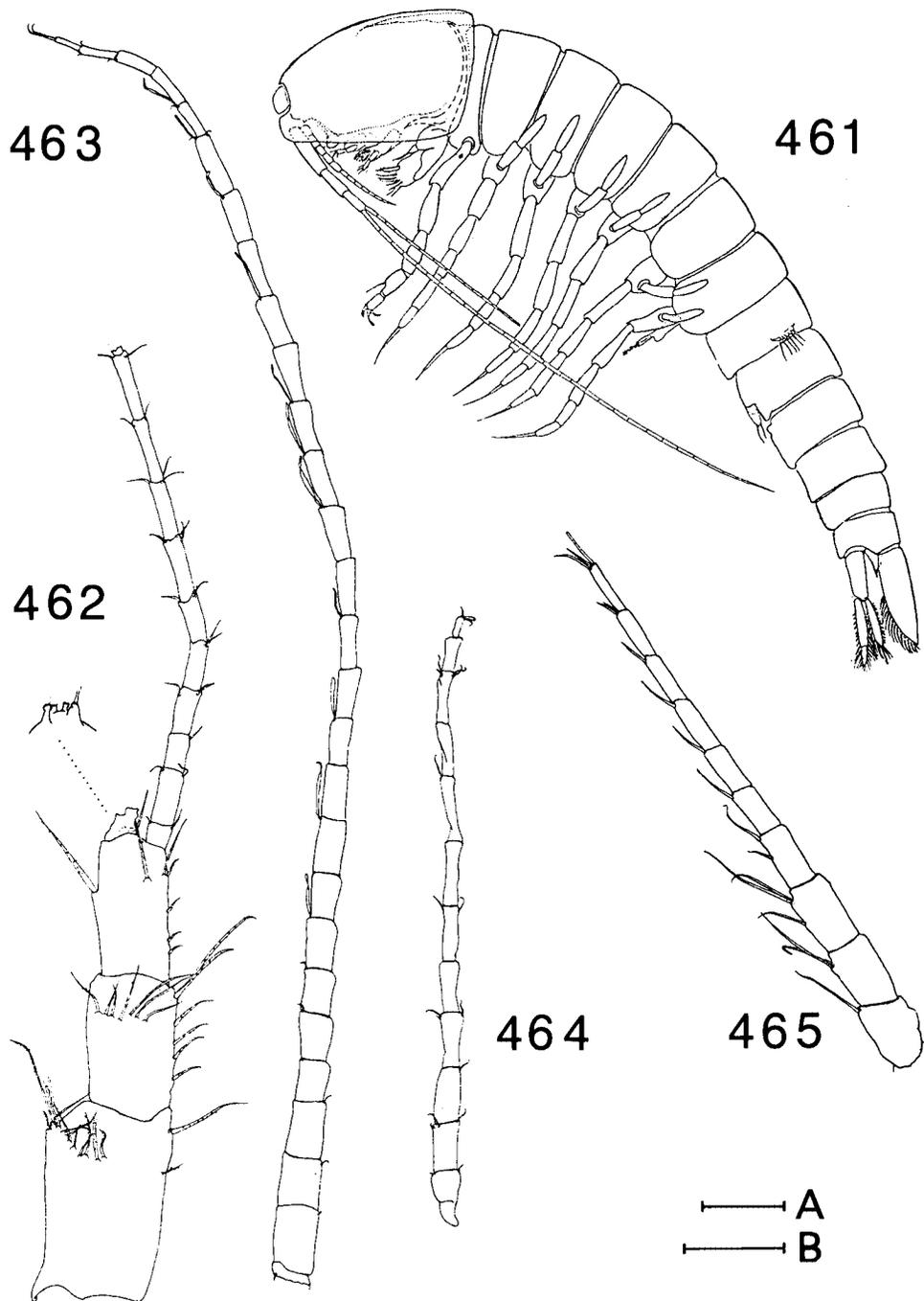
nuevo género; Pretus, 1991: 236.

Material.— **Cambodia:** 3 ♂♂; Kampot Province, Kompong Trach mountain, 15 km South of the China Sea, Leg. Cl. Boutin, x-xi 1968, MP [lectotype (labelled specimen B) and paralectotype], ZMA Cr. A. 8045 [paralectotype].

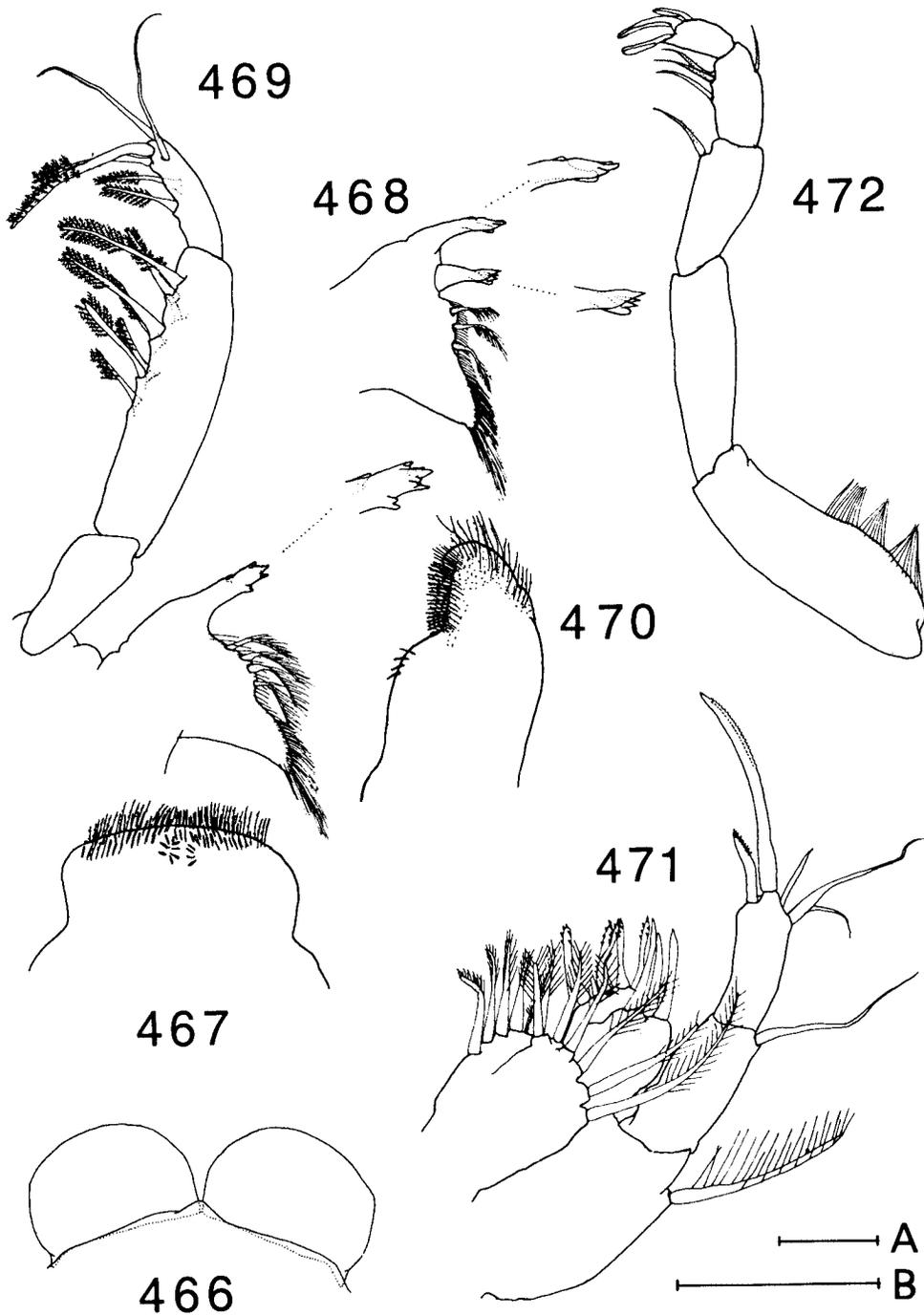
**Thailand:** 2 ♂♂; Thai-Maros Exped. sta. 87-KKC, Khon Kaen Province, N of Chum Phae, Tham (=cave) "Kubio"; in pool; collected by D. Rigal & L. Deharveng; 13.vi.1987; ZMA coll. no. C.A. 8098, USA. [*Theosbaena* cf. *cambodjiana* Cals & Boutin, 1985].

Description.— Body length (antennae 1 and 2 excluded) of lectotype 3.65 mm (MP), and of the paralectotypes (estimated) 3.22 mm (in ZMA) and 3.30 mm (MP), respectively.

Antenna 1 with 3-segmented peduncle; peduncular segment 1 with two teazel macrosetae (type IIB3) of unequal length on medial margin, dorsolateral margin with oblique row of one subplumose (type IB2) and seven simple macrosetae (type IB3), flanked more dorsally by two pairs of transversely placed simple macrosetae (type IB3), ventrolateral margin with one teazel macroseta (type IIB3); peduncular segment 2 with five teazel macrosetae (type IIB3) on dorsomedian margin, one teazel macroseta (type IIB3) on ventromedian margin, two groups of three and four simple macrosetae (type IB3) dorsally; peduncular segment 3 with four teazel macrosetae (type IIB3) on medial margin and two teazel macrosetae (type IIB3) somewhat more dorsally, terminal prominence with four subplumose macrosetae (type IB2); main flagellum 29-segmented, in general with two simple distal macrosetae (type IIA1) on lateral margin and one (type IIA1) on medial margin, aesthetasc (type IIA6) on segments 9, 11, 13, 15, 17 to 19, 21, and 23 to 25; accessory flagellum 14-segmented, segments with (0-)1-4 simple macrosetae (type IIA1), last segment with apical papillate macroseta (type IIA5).



Figs. 461-465. *Theosbaena cambodjiana* Cals & Boutin, 1985, lectotype and paralectotype ♂. 461, lateral view of habitus, lectotype (3.65 mm) (after Cals & Boutin, 1985). 462, antenna 1 (incomplete), paralectotype. 463, main flagellum of antenna 1, lectotype. 464, accessory flagellum of antenna 1, lectotype (figs. 462-464 scale B). 465, antenna 2, paralectotype (scale A). Scales indicated 0.1 mm.



Figs. 466-472. *Theosbaena cambodjiana* Cals & Boutin, 1985, paralectotype ♂. 466, ocular scales. 467, labrum. 468, corpus mandibula of left mandible. 469, right mandible. 470, lobe of labium. 471, maxilla 1 (figs. 466-471 scale B). 472, gnathopod (scale A). Scales indicated 0.1 mm.

Antenna 2 uniramous, peduncle 5-segmented; distomedian margin of segment 1 with one long teazel macroseta (type IIB3), distomedian margin of segment 2 with two long teazel macrosetae (type IIB3), segments 3 and 4 with one teazel macroseta (type IIB3) medially and two teazel macrosetae (type IIB3) distally on medial margin, distomedian margin of segment 5 with one distal teazel macroseta (type IIB3); flagellum 5-segmented, segments 1 to 3 with one simple macroseta (type IIA1); segment 4 with two simple macrosetae (type IIA1), one situated dorsally and one ventrally on medial margin; last segment with two simple macrosetae (type IIA1) and apical papillate macroseta (type IIA5).

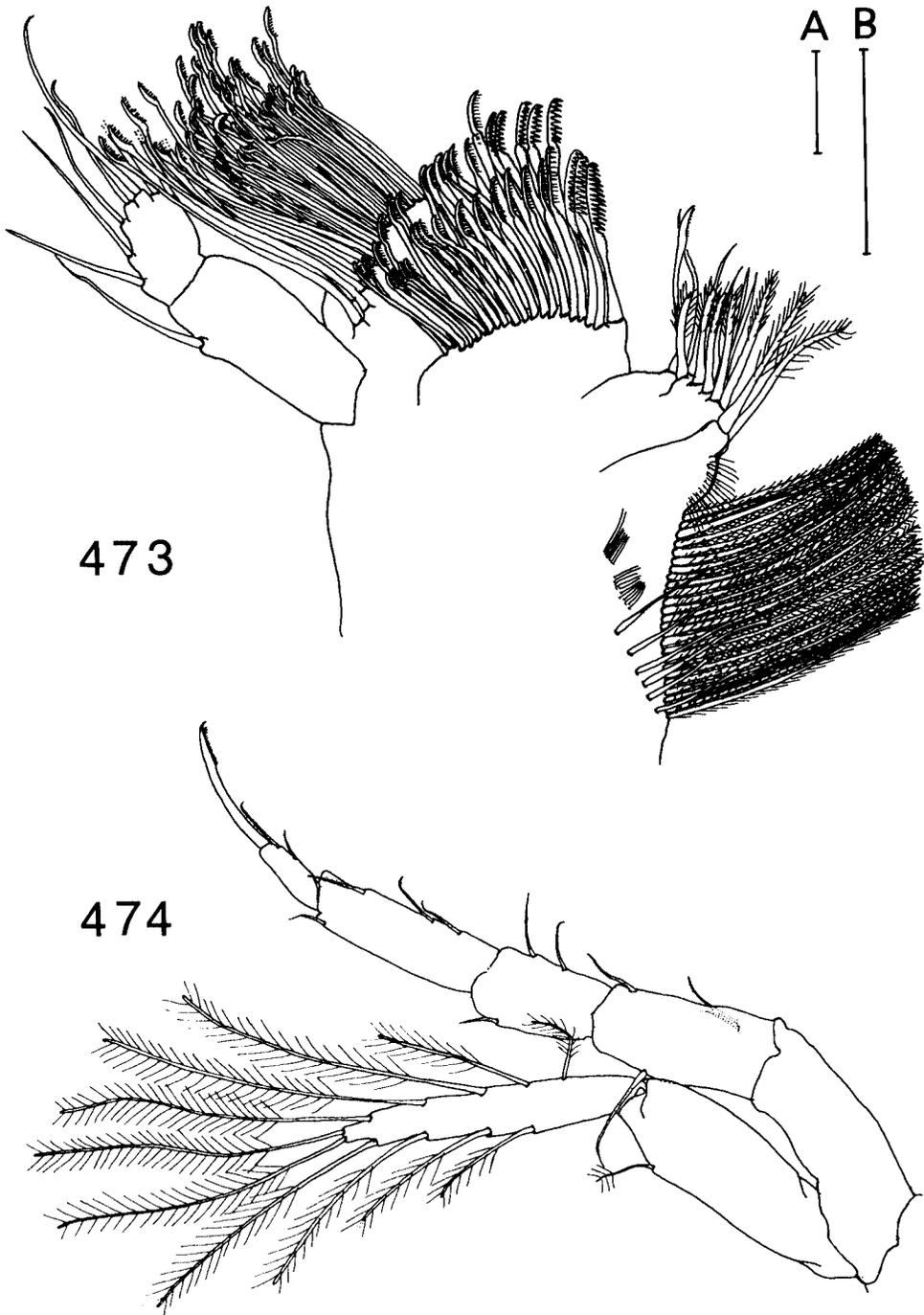
Labrum 2.3 times broader than long; proximal portion densely covered with ciliate microsetae (type 2b); apically with ovate microsetae (type 2a).

Mandible having a well-developed 3-segmented palp; basal palp segment elongate-triangular and unarmed; second segment with seven to eight plumidenticulate macrosetae (type IA3) in transversely oblique arranged configuration 1-1-2-3 or 1-2-2-3, increasing in size in distal and dorsal direction of the appendage; third segment with four plumidenticulate macrosetae (type IA3), (subapically) 1 simple macroseta (type IIA5) and 1 long serrulate macroseta (type IIB1(b)); corpus mandibula differentiated into pars incisiva, lacinia mobilis with one 3-dentate and one 1-dentate process (absent in right mandible, but row of ciliate microsetae (type 2b) instead), row of three (left mandible) or four (right mandible) serrate macrosetae (type IIB1), and pointedly triangular pars molaris with its molar surface densely covered by numerous ciliated microsetae (type IIB).

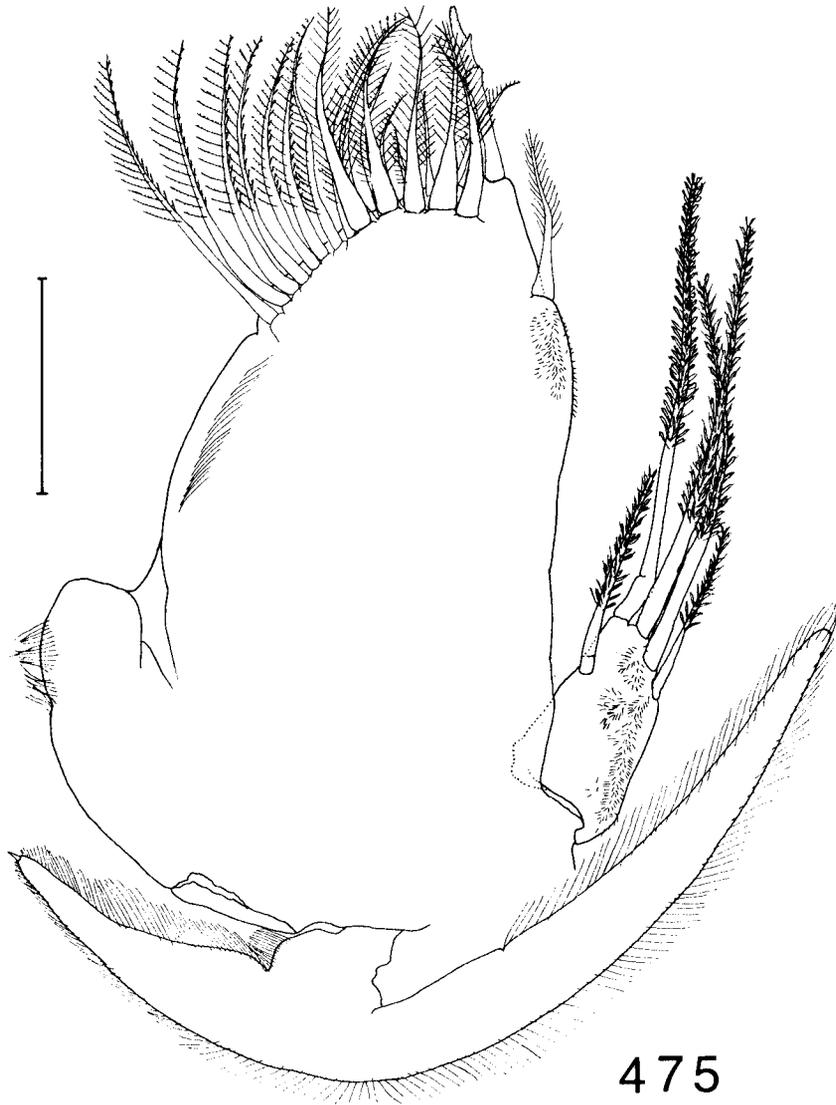
Labium deeply cleft, lobe with fine converging tips, internal distal margin with ciliate microsetae (type IIB), outer distal margin less densely covered by taller ciliate microsetae (type IIB).

Maxilla 1 differentiated into precoxal endite with distomedial armature of two rows of five and six plumose macrosetae (type IB1), respectively; basipodal endite with distal armature of eight toothed macrosetae (type III) arranged in two rows of five and, somewhat more proximally, three macrosetae; endopodite forming 2-segmented palp, first segment with one simple macroseta (type IIA1), second segment (sub)apically with three simple (type IIA1), one small and one larger bisetulate macroseta (type IB3(b)).

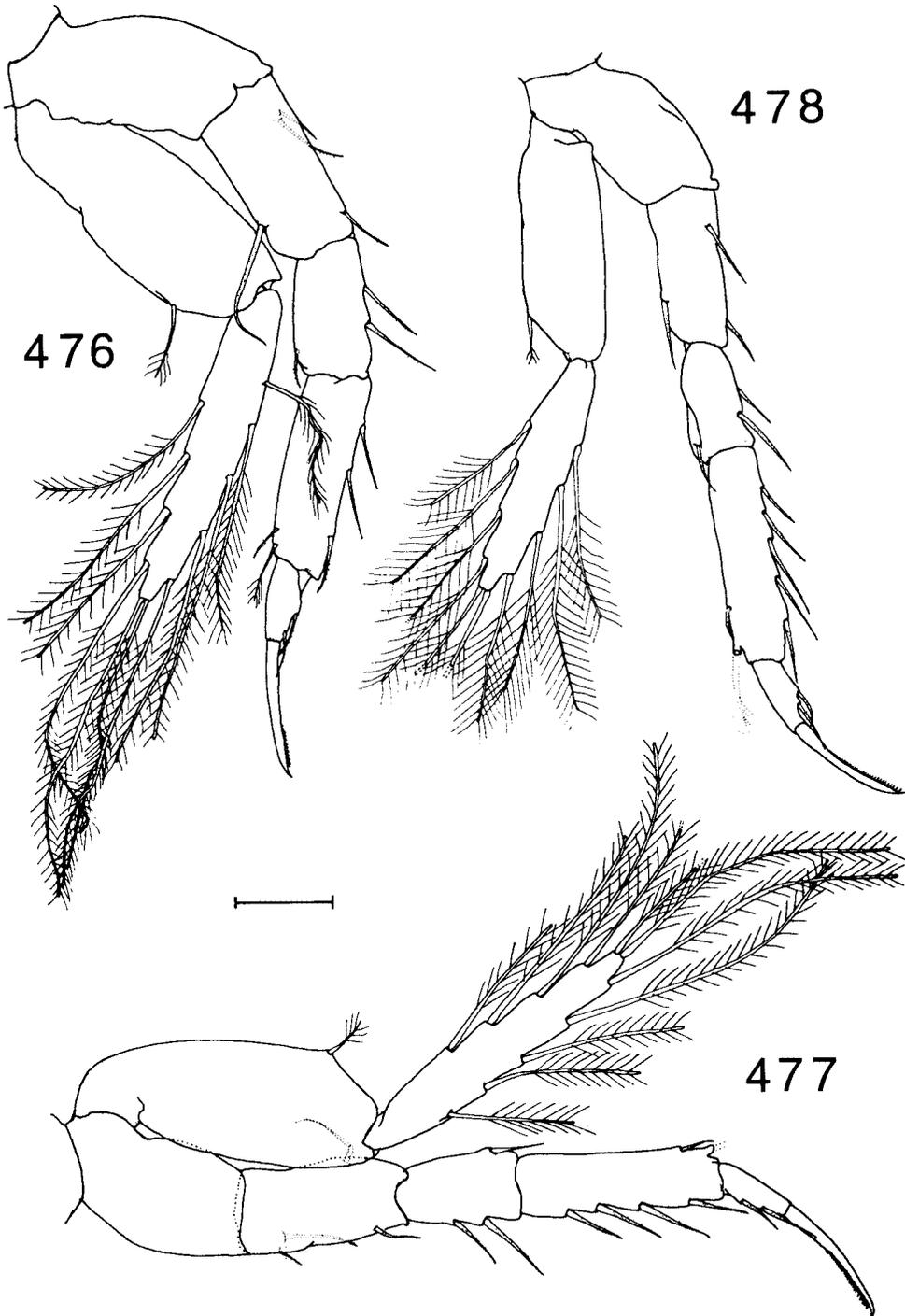
Maxilla 2 complexly built: coxopodal endite with 25 to 33 long plumose macrosetae (type IA1) followed distally by simple microsetae (type Ia), six rod macrosetae (type IIA2), two bundles of simple microsetae (type Ia) mediodorsally and two stout plumose macrosetae (type IB1); three basipodal endites: basipodal endite 1 with three groups of plumidenticulate macrosetae (type IA3): one long, five obscurely serrate, and six stout macrosetae; basipodal endite 2 with two transverse rows of 17 to 18 rake-like serrate macrosetae (type IIB1) at terminal margin increasing in size and denticulation towards the medial margin of the appendage, and two modified (longer one with a more developed rake, short one with rake strongly reduced to narrow tip) serrate subterminal macrosetae; basipodal endite 3 with 55 to 91 rake-like serrate macrosetae (type IIB1) increasing in size and dentation medially, and arranged in 10 to 13, somewhat triangularly configured, oblique rows of 1+2+3+4+5+6+7+8+9+10 (+11+12+13) macrosetae; endopodite 2-segmented, first segment with one long simple macroseta (type IIA1), segment 2 with seven simple macrosetae (type IIA1); exo-



Figs. 473-474. *Theosbaena cambodjiana* Cals & Boutin, 1985, paralectotype ♂. 473, maxilla 2 (scale B). 474, pereopod 2 (scale A). Scales indicated 0.1 mm.



Figs. 475. *Theosbaena cambodjiana* Cals & Boutin, 1985, maxilliped, paralectotype ♂. Scale indicated 0.1 mm.



Figs. 476-478. *Theosbaena cambodjiana* Cals & Boutin, 1985, paralectotype ♂. 476, pereopod 3. 477, pereopod 5. 478, pereopod 6. Scale indicated 0.1 mm.

podite absent.

Maxilliped: coxopodal endite a tapering lobe with one medial, one subterminal, two terminal and one lateral pappose macrosetae (type IA2), with complex setules (as in fig. 10); basipodal endite with three rows of plumidenticulate macrosetae (type IA3), ventral row of five stout macrosetae, central row of eight long macrosetae with foliaceous setules, and dorsal row of six finely setulate macrosetae, submedially an additional large modified "plumidenticulate" macroseta (type IA3) which is naked, except for two crenulate ridges on distal portion, medially another plumidenticulate macroseta (type IA3) with an area of simple microsetae (type Ia) in front of its implantation; endopodite fused with exopodite and basipodal endite, plate-like with a row of long fine simple microsetae (type Ia) near margin; exopodite non-articulating elongate blunt lobe, with simple microsetae (type Ia); epipodite bow-shaped, tapering lobe with simple microsetae (type Ia), apically with short stout macroseta (type could not be established with LM).

Gnathopod: baso-ischium longest segment, with simple microsetae (type Ia) on ventral margin; merus naked (except for left merus of a paralectotype having one subterminal teazel macroseta (type IIB3) on ventral margin); carpus with one subterminal teazel macroseta (type IIB3) on ventral margin; propodus with one subterminal fine plumose macroseta (type IA1) on dorsal margin, and three teazel macrosetae (type IIB3) distoventrally, of which distalmost two situated subterminally next to each other; dactylus distally widened and somewhat flattened, with claw formed by three bow-shaped (modified) serrulate macrosetae (type IIB1) with a prominent membrane ventrally.

Pereiopod 2: ischiomerus of endopodite with three teazel macrosetae (type IIB3) on ventral margin, two medially and one distally, and one teazel macroseta (type IIB3) dorsally; carpus with two teazel macrosetae (type IIB3) medially on ventral margin and one subterminally on dorsal margin; propodus with three teazel macrosetae (type IIB3) on ventral margin, dorsodistally one teazel macroseta (type IIB3); dactylus with two teazel macrosetae (type IIB3) on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one plumose macroseta (type IB1) subterminally, second segment with three to four medial, two subterminal, two terminal and three lateral plumose macrosetae (type IB1).

Pereiopod 3: ischiomerus of endopodite with three teazel macrosetae (type IIB3) on ventral margin, two medially and one distally, and one teazel macroseta (type IIB3) dorsally; carpus with two teazel macrosetae (type IIB3) medially on ventral margin and one subterminally on dorsal margin; propodus with three teazel macrosetae (type IIB3) on ventral margin, dorsodistally one teazel macroseta (type IIB3) and one subplumose macroseta (type IB2); dactylus with two teazel macrosetae (type IIB3) on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subterminal plumose macroseta (type IB1), second segment with four to five medial, two subterminal, two terminal and three to four lateral plumose macrosetae (type IB1).

Pereiopod 4: ischiomerus of endopodite with three teazel macrosetae (type IIB3) on ventral margin, two medially and one distally, and one teazel macroseta (type IIB3) dorsally; carpus with two teazel macrosetae (type IIB3) medially on ventral

margin and one subterminally on dorsal margin; propodus with four teazel macrosetae (type IIB3) on ventral margin, dorsodistally one teazel macroseta (type IIB3) and one subplumose macroseta (type IB2); dactylus with two teazel macrosetae (type IIB3) on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subterminal plumose macroseta (type IB1), second segment with four to five medial, two subterminal, two terminal and three to four lateral plumose macrosetae (type IB1).

Pereiopod 5: ischiomerus of endopodite with three teazel macrosetae (type IIB3) on ventral margin, two medially and one distally, and one teazel macroseta (type IIB3) dorsally; carpus with two teazel macrosetae (type IIB3) medially on ventral margin and one subterminally on dorsal margin; propodus with four teazel macrosetae (type IIB3) on ventral margin, dorsodistally one teazel macroseta (type IIB3) and one subplumose macroseta (type IB2); dactylus with two teazel macrosetae (type IIB3) on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subterminal plumose macroseta (type IB1), second segment with three to four medial, two subterminal, two terminal and three to four lateral plumose macrosetae (type IB1).

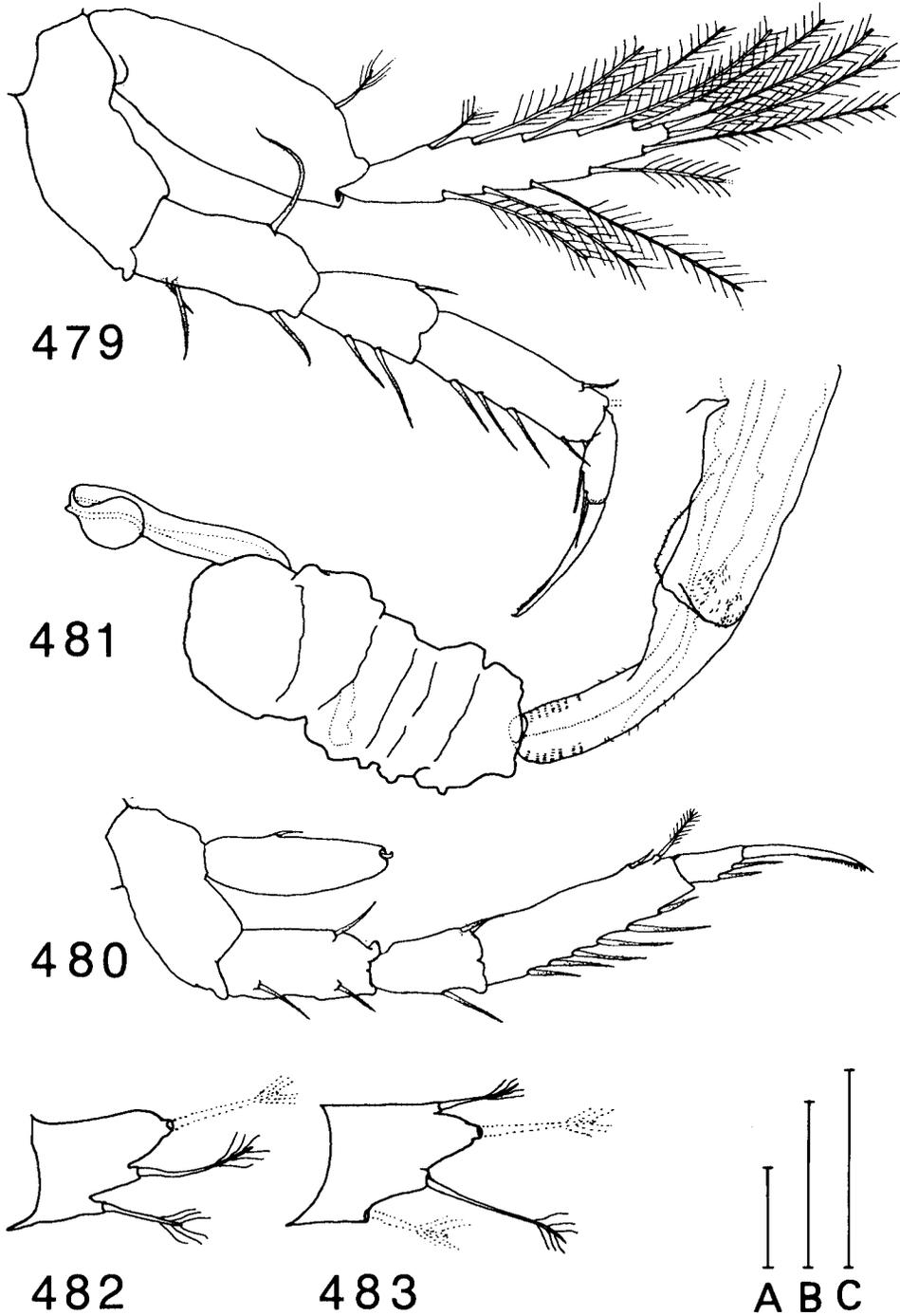
Pereiopod 6: ischiomerus of endopodite with three teazel macrosetae (type IIB3) on ventral margin, two medially and one distodorsally and one teazel macroseta (type IIB3) dorsally; carpus with two teazel macrosetae (type IIB3) medially on ventral margin and one subterminally on dorsal margin; propodus with four (to five) teazel macrosetae (type IIB3) on ventral margin, dorsodistally one teazel macroseta (type IIB3) and one subplumose macroseta (type IB2); dactylus with two teazel macrosetae (type IIB3) on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; first segment of exopodite with one subterminal plumose macroseta (type IB1), second segment with four medial, two subterminal, two terminal and three lateral plumose macrosetae (type IB1).

Pereiopod 7: ischiomerus of endopodite with two teazel macrosetae (type IIB3) on ventral margin and one teazel macroseta (type IIB3) dorsally; carpus with one teazel macroseta (type IIB3) subterminally on ventral margin and one teazel macroseta (type IIB3) subterminally on dorsal margin; propodus with six teazel macrosetae (type IIB3) on ventral margin, dorsodistally one teazel macroseta (type IIB3) and one subplumose macroseta (type IB2); dactylus with two teazel macrosetae (type IIB3) on ventral margin and a well-developed serrulate macroseta (type IIB1(b)) forming terminal "unguis"; exopodite with two vestigial macrosetae, one terminal and one laterally implanted.

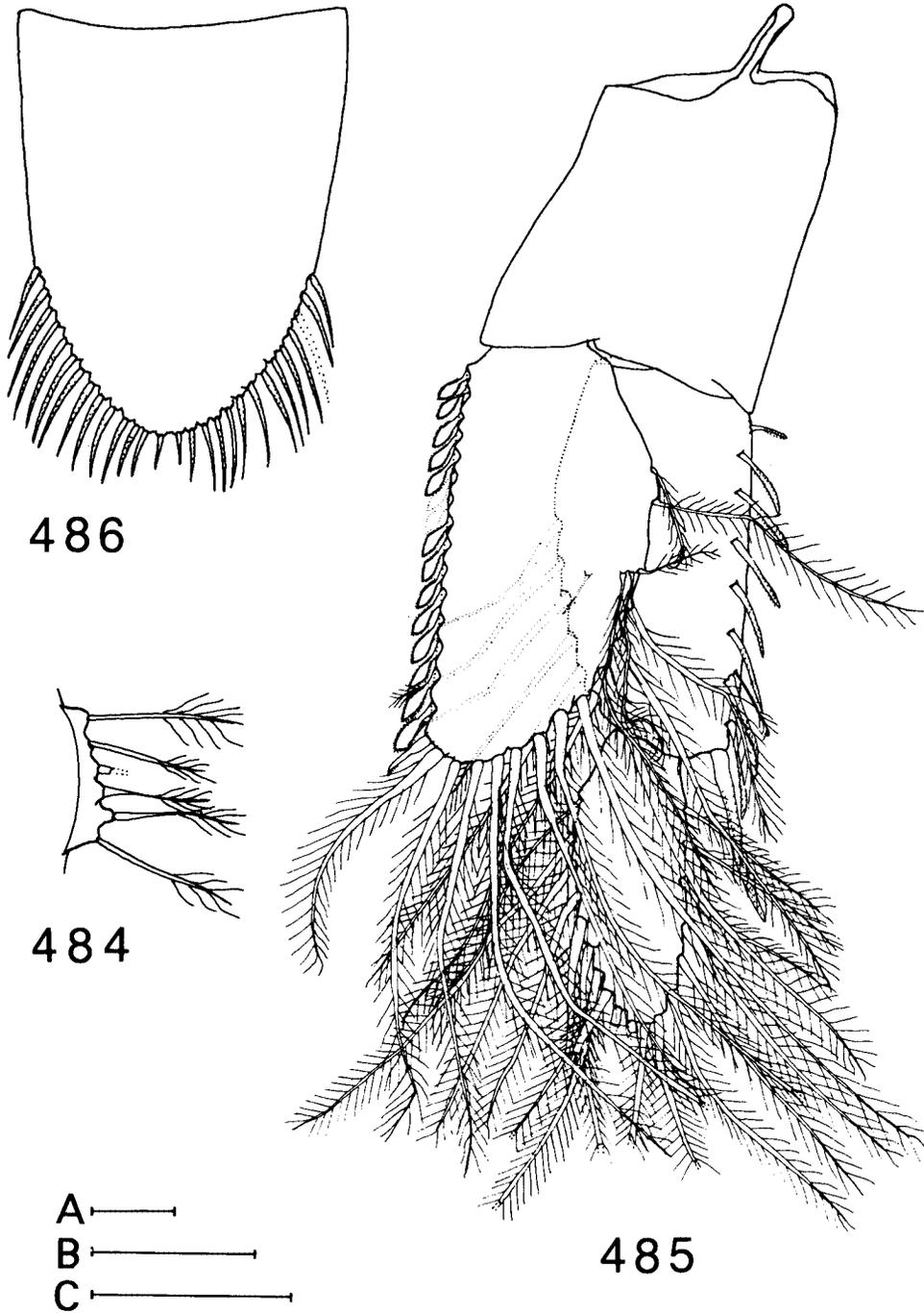
Male penial lobes simple, proximal half slightly bend, with rows of short simple microsetae (type Ia) medially and subapically; medially associated with coxopodite. Spermatophore initially spiralized, ending in turned, broad and flat "castanette"-shaped tip.

First pleopod non-articulate bump with six subplumose macrosetae (type IB2). Second pleopod 1-segmented, more or less triangular, with two dorsal, and one terminal subplumose macrosetae (type IB2). One paralectotype has an additional subterminal macroseta on ventral margin of left pleopod 2.

Uropod: 2-segmented exopodite and 1-segmented endopodite; segment 1 of exopodite distinctly longer than segment 2, segment 1 laterally with nine cuspidate mac-



Figs. 479-483. *Theosbaena cambodjiana* Cals & Boutin, 1985, paralectotype ♂. 479, pereiopod 4. 480, pereiopod 7 (figs. 479-480 scale A). 481, penial lobe (scale C). 482, left pleopod 2. 483, right pleopod 2 (figs. 482-483 scale B). Scales indicated 0.1 mm.



Figs. 484-486. *Theosbaena cambodjiana* Cals & Boutin, 1985, paralectotype ♂. 484, pleopod 1 (scale B). 485, uropod (scale C). 486, telson (scale A). Scales indicated 0.1 mm.

rosetae (type IIA3) and one subplumose macroseta (type IB2); medially with six plumose macrosetae (type IB1), and one subplumose macroseta (type IB2) dorsomedially, segment 2 with 18 plumose macrosetae (type IB1) all along medial, terminal and lateral margins, subterminally two pairs of subplumose macrosetae (type IB2); distal margin of endopodite distinctly protruding beyond distal margin of first segment of exopodite, with 14 plumose macrosetae (type IB1) along medial, terminal and lateral margins, one pair of subplumose macrosetae (type IB2) implanted laterally, medial margin with 15 scale-like serrate macrosetae (type IIB1), and dorsomedially one serrate macroseta (type IIB1).

Telson longer than wide, width/length ratio 0.80, tapering and distally rounded, posterior lateral margins with 13 to 16 cuspidate macrosetae (type IIA3) at either side; macrosetae from proximal to distal initially increasing in size, then constant and then decreasing in size.

Variability.— Some variation was found in the number of macrosetae of certain appendages, which may well be related to size and maturity of the specimens examined. Generally eight plumidenticulate macrosetae are present on the second segment of the mandibular palp, but in one of the paralectotypes (measuring 3.30 mm) the left mandibula shows only seven plumidenticulate macrosetae. The number of rake-like serrate macrosetae on the basipodal endite 3 of the maxilla 2 varies considerably; the lectotype has 12 rows (78 macrosetae in total) both left and right, one paralectotype (measuring 3.30 mm) has 12 rows (78 macrosetae in total) on the right, and 13 rows (91 macrosetae in total) on the left maxilla 2, while the other paralectotype (measuring 3.22 mm) has 10 rows (55 macrosetae in total) on the right, and 11 rows (66 macrosetae in total) on the left maxilla 2. There are 18 rake-like serrate macrosetae on the basipodal endite 2 of the maxilla 2 in both the lectotype and the largest paralectotype, while the small paralectotype has 17 only. The number of plumose macrosetae on the coxopodal endite increases with the size of the specimen examined, from 25 in the smallest paralectotype to 33 in the lectotype. The number of plumose macrosetae on the second segment of the exopodites, too, increases with the body size of the animals. On the propodus of the left pereopod 6 of the smallest paralectotype five macrosetae are present on the ventral margin. This in contrast to the right pereopod 6 of the same individual that bears the usual four macrosetae. The same paralectotype has on its endopodite of the right uropod an aberrant (bipinnate) plumose macroseta distomedially. Along the posterolateral margin of the telson the number of these macrosetae varies in the type material; the lectotype has 13 pairs, the smallest paralectotype 14 pairs, and the larger paralectotype 15 and 16 conate macrosetae, respectively.

Material from Thailand differs in having seven plumidenticulate macrosetae on the second segment of the mandibular palp; a row of 16 plumidenticulate macrosetae on the basipodite of the maxilliped (further chaetotaxy identical); nine simple macrosetae on the second segment of the endopodite of maxilla 2, in contrast to the lectotype which has seven.

Remarks.— The original paper wherein this taxon was established mentions three specimens only. However, fragments of a fourth (and fifth?) specimen appear to exist also, but as these were not mentioned by Cals & Boutin (1985); these do not represent type specimens. One of these fragments represents pereopods only, and these do not

differ from those of the type series. Of a (questionable) fifth specimen a single mandibula was found, that -contrary to the type series- has nine plumidenticulate macrosetae on the second segment of the palp.

Cals & Boutin did not select a holotype, thus all three specimens are syntypes. The largest specimen, partially preserved as a wholemount, is here selected as lectotype.

During the Thai-Maros Expedition in Thailand, three specimens (one is lost) of *Theosbaena* were collected north of Chum Phae, Khon Kaen Province, Thailand. As on the one hand only a few specimens of this species are known to date from Cambodia, and on the other hand the variation of the Thailand material only reveals slight differences with the type material, I provisionally consider all to represent one species. As the differences between the specimens from Cambodia and Thailand could be assigned to individual or clinal variation in maxilla 2 and maxilliped, it seems best to regard these specimens conspecific until more material becomes available.

Distribution.— Known from caves in the Kompong Trach mountain, Kampot Province, Cambodia and north of Chum Phae, Khon Kaen Province, Thailand. Boutin (1971: 178) also mentions Thermosbaenacea from the Battambang region. Unfortunately this sample has been lost, and the same holds for additional samples taken in the vicinity of the type locality (Boutin, pers. comm.).

Habitat.— The type locality is situated in an alluvial plain along the western coast of Cambodia. Its fauna is supposed to have colonized the cave in the Holocene (Boutin & Magniez, 1985). With an electric conductivity of 570  $\mu\text{S}/\text{cm}$  at a water temperature of 22°C *Theosbaena cambodjiana* lives in fresh water. The sole accompanying faunal element collected is the isopod *Stenasellus cambodianus* Boutin & Magniez, 1985.

## 5. Phylogeny

### 5.1. Introduction

As Tethyan relicts the Thermosbaenacea form an important link in gaining knowledge on the biogeography of stygobiont animals on the one hand, and the geological events that happened during and since the formation of the Atlantic Ocean and the Mediterranean basin, on the other. Prior to a discussion on the biogeography of the Thermosbaenacea (chapter 6) it is here attempted to explore the phylogenetic relationships of this order using phylogenetic numerical techniques. Previously, similar studies have been carried out for amphipods (Stock, 1980a; Notenboom, 1988c; Boutin & Coineau, 1988; Holsinger, 1992), and provided explanations for the present distributions of stygobionts, i.e., having been evolved directly from marine ancestors in the brackish and fresh insular and continental ground waters (the "Regression model"). The relationship between my hypothesized cladogram and the paleogeography of the species will be treated extensively in the next chapter. The present chapter is devoted to developing a cladogram of the Thermosbaenacea.

However, it must be remarked that an important obstacle in re-constructing a phylogenetic tree of the Thermosbaenacea exists. Like all animals adapted to subterranean life, thermosbaenaceans exhibit typical "cave" dependent morphological modifications (sensu Notenboom, 1988c), which means that their morphology is hardly comparable to any other group of crustaceans. Moreover, because neither fossil records nor epigeal forms of this group are known to date, it is not well possible to

indicate with any degree of certainty a sister-group beforehand.

## 5.2. Material and methods

In order to study the cladistic relationships between the peracarid taxa in general, and those of the Thermosbaenacea in particular, I analyzed several sets of morphological character states. This analysis was carried out with the aid of the PAUP (Phylogenetic Analysis Using Parsimony) computer program of D. L. Swofford (version 3.0-released in 1990) as compiled for Macintosh (APPLE) personal computers (Swofford, 1989). The goal of this analysis was to find the most parsimonious tree(s) in terms of minimum tree length (minimal number of character state changes) and reversals required.

PAUP trees were produced with a 10-taxon, 39-character discontinuous multistate data matrix for the analysis of the Peracarida (§ 5.3.1), while for the analysis of the Thermosbaenacea and its sister-group (provided by the analysis of the Peracarida) a 9-taxon, 49-character combined binary-discontinuous multistate data matrix was used (§ 5.4.1). A third analysis (§ 5.5.1) was carried out for the species-groups within *Tethysbaena*, with *Monodella* serving as a sister-group, by the use of a 7-taxon, 11-character mixed binary-discontinuous multistate data matrix.

At the specific level an alternative use of the PAUP program was made, in order to obtain a hypothetical model for the phylogeny of the Thermosbaenacea as a whole. This method will be discussed in detail below, preceding the proposed hypothetical model (§ 5.6).

To obtain the peracarid PAUP tree an ordered analysis was performed, based on "polarized" character states derived from a fully plesiomorphic interpretation of the caridoid "facies" as the out-group. Polarities were thus determined using Calman (1904), with corrections and additions argued by Dahl (1976, 1983); Watling (1981, 1983); Schram (1984); Bowman (1984); Schram, Yager & Emerson (1986); Notenboom (1988c); and Platvoet & Pinkster (1992). Although the accent lies on the out-group analysis, an unordered (in-group) analysis for the Peracarida was performed too, thus using the 9-taxon, 39-character continuous multistate data matrix, with the caridoid "facies", which had served as an out-group, omitted. For the "directed" PAUP trees of the Thermosbaenacea and *Tethysbaena*, their respective sister-groups derived from this general peracarid analysis were defined as out-group, such in order to assess character state polarity (out-group comparison sensu Watrous & Wheeler, 1981). Additional information was obtained by performing unordered analyses where the sister-groups were not defined as out-groups. For all three analyses the "all trees" option was employed. The branch and bound option, a method implementing the Hendy-Penney algorithm (Hendy & Penney, 1982) for finding the shortest trees was used as well in all analyses.

Character states of the Thermosbaenacea were determined on the basis of the previously observed and discussed external morphology (see Chapters 2 to 4), while those of the remaining peracarid groups were based on personal observations and data provided by literature (McLaughlin, 1980; Watling, 1981, 1983; Schram, 1984; Sieg, 1984; Pires, 1987). Although geographical data are available I refused to use these as phylogenetic characters, preferring to check my phylogenetic hypotheses

later with the distributional data. Also the unique characters, so-called autapomorphies, of a taxon have been excluded from the data matrices as they do not contribute information when it comes to the relationship with sister-taxa. The multistate data matrices have been composed instead of synapomorphies (advanced character states shared by at least two taxa) only.

### 5.3. Phylogenetic relationships within the Peracarida

When Calman (1904) created the Peracarida, he did so to provide a synthesis for a debate about the relationships between the various malacostracan groups that had lasted for several decades (Boas, 1883; Claus, 1885; Grobben, 1892; Hansen, 1893; Haeckel, 1896). Although the monophyly of the Peracarida was not questioned until the past decade (Schram, 1981, 1986; Watling, 1981, 1983) the position of the Thermosbaenacea as a part of this taxon was subject to debate quite soon after their discovery.

Initially, the Thermosbaenacea were considered to represent one of the orders of the superorder, or division, Peracarida (Monod, 1924a, 1927a, 1927b, 1940; Calman (Anonymous, 1924a); Spandl, 1926; Zimmer, 1927; Gordon, 1958; Barker, 1959, 1960, 1962; Fryer, 1965; Green, 1967; Hessler, 1969; Kukulova-Peck, 1973; Stock, 1976; McLaughlin, 1980; Bousfield, 1982; Bowman et al., 1985; Cals & Monod, 1988). The first ones to propose an alternative grouping were Chappuis (1927) and G. O. Sars (1929), combining Thermosbaenacea and Bathynellacea into the Anostraca. This grouping was rejected, as it was supposed to be based on mere convergence, rather than true affinity (Fryer, 1965). Also the suggested relation of Thermosbaenacea with the Stomatopoda (Glaessner, 1957) did not find any support. Nor did the curious classification of the Thermosbaenacea into the division Thermosbaenida by Russel-Hunter (1979). That the idea of some relation to the Bathynellacea was not completely rejected was illustrated by Stella (1953, 1959) and Taramelli (1954) who placed the Thermosbaenacea between the Syncarida (Bathynellacea) and Peracarida. Their ideas found support by Siewing (1958) who went as far as to create the new division Pancarida for them. A considerable, and wide acceptance of the division Pancarida followed (Siewing, 1963; Monod, 1960; Schmitt, 1965; Botosaneanu & Delamare Deboutteville, 1967; Straškraba, 1967; Kaestner, 1970; Zilch, 1975; Pinkster, 1978; Dahl & Hessler, 1982; Bowman & Abele, 1982; Schram, 1982; Newman, 1983; Sieg, 1983a, 1984; Pires, 1987).

The discussion as to the question whether the Peracarida represent a monophyletic group, resulted in several alternative classifications of the Eumalacostraca (Schram, 1981, 1984, 1986; Watling, 1981, 1983; Cals & Monod, 1991). Although it certainly is not within the scope of this monograph to discuss the validity of the Peracarida, it was essential for me to carry out a phylogenetic analysis of the Peracarida *sensu* Calman (1904) including the Thermosbaenacea and Mictacea. Such an analysis is unavoidable, as thus far in studies in which the Thermosbaenacea are treated as a component of the "Peracarida", the Mictacea were not included. Up till now, four groups (given in order of branching sequence) have been indicated as a sister-group: (1) the cluster Spelaeogriphacea-Tanaidacea-Isopoda (Fryer, 1965), (2) the cluster Spelaeogriphacea-Cumacea-Tanaidacea (Schram, 1981; Watling, 1983), (3) Mysidacea (Watling, 1981), and (4) the cluster Cumacea-Tanaidacea-Spelaeogriphacea (Schram, 1984, 1986). Since the discovery of the Mictacea (Bowman et al., 1985), Pires (1987)

Table 6. Character transformation series used in the phylogenetic analysis of the Peracarida. 0 = plesiomorphous state; 1-3 = apomorphous states in transformation series; 1' = alternative apomorphous state.

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<p>1. Hatching embryo:            0 : having all pereopods            1 : not all pereopods present [manca]</p>	<p>10. Eyes:            0 : sessile            1 : (sessile or) ocular scales            2 : stalked</p>
<p>2. Bloodsystem (sensu Watling, 1983):            0 : type I            1 : type II            2 : type III            3 : type IV</p>	<p>11. Antenna 1:            0 : strongly biramous            1 : uniramous or one ramus reduced</p>
<p>3. Foregut:            0 : pyloric funnel of the gastric mill and a pyloric bristle chamber            1 : simple unelaborated</p>	<p>12. Antenna 2: antennal gland in adult            0 : present            1 : reduced            2 : absent</p>
<p>4. Midgut: epithelium            0 : multicellular            1 : syncytial</p>	<p>13. Antenna 2:            0 : biramous            1 : uniramous</p>
<p>5. Testes:            0 : in thorax            1 : under carapace</p>	<p>14. Antenna 2: exopodal scale            0 : always present            1 : present or absent            2 : always absent</p>
<p>6. Vas deferens:            0 : reaching into the abdomen            1 : in thorax only</p>	<p>15. Mandible:            0 : rolling, dual-purpose type with large boat-like basal portion            1 : transverse biting type with short basal portion</p>
<p>7. Carapace:            0 : short, covering anterior part of cephalothorax            1 : long, covering cephalothorax completely            1': absent</p>	<p>16. Mandible: hinge            0 : oblique            1 : horizontal</p>
<p>8. Body:            0 : dorsoventrally compressed            1 : laterally compressed</p>	<p>17. Mandible: molar process            0 : well-developed, columnar            1 : not developed, rounded</p>
<p>9. Eyes:            0 : compound            1 : not compound (cave adapted?)</p>	<p>18. Mandible: serrate macrosetae (lifting spines)            0 : close proximity            1 : short, low numbered            2 : absent</p>
	<p>19. Mandible: incisor and molar process            0 : widely separated            1 : close proximity</p>

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| 20. Maxilla 1: maxillary gland in adult<br>0 : present<br>1 : reduced<br>2 : absent  | 30. Pereiopods: exopodites<br>0 : unspecialized<br>1 : specialized<br>1': absent                                     |
| 21. Maxilla 1: palp<br>0 : elongate<br>1 : reduced to seta-like article  | 31. Pereiopods: coxal plates<br>0 : absent<br>1 : present  |
| 22. Maxilla 2: number of endites<br>0 : 1 to 2<br>1 : 3  | 32. Pereiopod 1:<br>0 : pediform or claw-like<br>1 : often chelate<br>1': modified into additional maxilliped        |
| 23. Maxilliped: coxal endite<br>0 : present<br>1 : absent  | 33. Pleopods:<br>0 : multi-articulate<br>1 : bi-articulate<br>2 : uni-articulate                                     |
| 24. Maxilliped: number of pairs<br>0 : no pereopod modified for maxillipedal function<br>1 : one pereopod modified for maxillipedal function | 34. Pleopods: number of pairs<br>0 : 5<br>1 : 1 to 3 (not in both sexes)   |
| 25. Maxilliped: epipodite<br>0 : present<br>1 : absent   | 35. Abdomen:<br>0 : without pleura<br>1 : with pleura  |
| 26. Maxilliped: exopodite<br>0 : basically present<br>1 : absent   | 36. Uropods:<br>0 : flattened<br>1 : cylindrical   |
| 27. Maxilliped: endopodite<br>0 : elongate<br>1 : short, (or) strongly modified  | 37. Uropods: number of segments exopodite<br>0 : 2<br>1 : 1  |
| 28. Pereiopods:<br>0 : with epipods<br>1 : without epipods   | 38. Uropods: number of segments endopodite<br>0 : 2 or more<br>1 : 1   |
| 29. Pereiopods:<br>0 : neutral orientation<br>1 : tagmosis into groups   | 39. Telson:<br>0 : always free from pleonites<br>1 : sometimes fused with pleonites<br>2 : always forming pleotelson |
- 

carried out a phylogenetic analysis, but defined the Thermosbaenacea as out-group (Pancarida) on the basis of only one autapomorphic character state (viz., the dorsal broodpouch). In her analysis, nearly half of the characters of the data matrix are autapomorphies. However, Schram (1983) showed, as an example with only three characters (uniramous or biramous thoracopods, presence or absence of subthoracic broodpouches, absence or degree of development of a carapace), various "paper animals" to illustrate possible "Baupläne" within the Eumalacostraca. The fact that

Table 7. Distribution of character states in Peracarida. Unknown states are indicated with "?" (see

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
'Caridoid'	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda	0	2	0	0	0	1	1'	1	0	0	1	0	1	2	1	1	0	0	1
Isopoda	1	3	1	1	0	0	1'	0	0	0	1	1	1	0	1	1	0	0	1
Cumacea	1	1	1	1	0	1	1'	0	0	0	1	2	1	2	0	0	0	0	0
Tanaidacea	1	1	1	1	0	1	0	0	0	1	0	2	0	0	0	0	0	1	0
Thermosbaenacea	1	1	0	0	1	0	0	0	1	1	0	2	1	1	0	0	0	0	0
Mictacea	1	1	0	0	1	0	0	0	1	1	0	2	1	0	0	0	0	0	0
Spelaeogriphacea	?	1	0	0	?	?	0	1	1	2	0	2	0	0	0	0	0	0	0
Lophogastrida	0	0	0	0	0	1	1	1	0	2	0	0	0	0	0	0	1	2	1
Mysida	0	0	0	0	0	1	1	1	0	2	0	0	0	0	0	0	1	1	1

the larger part of these "paper animals" indeed exist is proof of the outstanding scale of natural, evolutionary experiments that takes place in the Crustacea, or even in the Arthropoda as a whole. All this means, that only one autapomorphic state, such as the dorsal broodpouch, is in my opinion not sufficient to exclude the Thermosbaenacea from the Peracarida. Another item is the division of the Mysidacea into Mysida and Lophogastrida: this has been based on reasons discussed by previous authors (e.g. Sieg, 1983a; Schram, 1984), as well as on practical reasons exemplified by the data matrix (table 7).

### 5.3.1. Character analysis

The 39 characters which differentiate the various peracarid orders and which are used in the numerical analysis are listed in table 6. The ordering of characters is based on traditional morphological order of treatment rather than on their branching sequence in the analysis. No cladograms have been constructed with the aid of weighted characters. In general, quantitative counts of characters are grouped in such a manner that (a) non-overlapping classes are achieved, under the restriction that (b) intraspecific variation is restricted within such a class. The majority of the characters used are of a qualitative nature, generally based on the presence or absence, or on differences in morphology of, certain features.

In four characters, some overlap occurs (characters 10, 14, 26, and 39) as both character states are represented in the same (monophyletic) group. In the case of sessile eyes (plesiomorphic state according to Bowman, 1984) versus stalked eyes (apomorphic state), three groups, viz. Thermosbaenacea, Mictacea and Tanaidacea, have either sessile eyes (or -except for ocular nerves- none at all), or ocular scales (character 10). A similar problem occurs regarding the exopodal scale of antenna 2 (character 14): The Thermosbaenacea form the intermediate group between the Cumacea and the Amphipoda at the one hand, which lack the exopodal scale, and the remaining peracarid orders on the other, which possess this scale. Also in the condition of the telson, i.e., being free or fused with one (or more) pleonite(s) (character 39), the Thermosbaenacea, this time with the Isopoda, link the two extremes together. In

table 6 for description of characters and explanation of character numbers).

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	1	0	1	1	0	0	1	1'	1	1	0	1	1	1	1	1	0
0	1	0	1	0	1	1	1	1	1	1'	1	1	2	0	1	0	1	1	1
0	1	0	1	1	0	1	1	1	1	0	0	1'	1	1	0	1	1	1	0
0	1	0	1	0	0	1	1	1	1	0	0	1	2	0	1	1	1	0	2
0	0	1	0	0	0	0	1	1	0	0	0	0	2	1	0	0	0	1	1
0	1	1	0	0	1	1	0	1	0	0	0	0	2	0	0	0	0	0	0
0	0	1	1	0	0	1	0	1	1	1	0	0	2	0	0	0	0	1	0
1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0

order to solve this problem a transformation series of character states is proposed here too. In the case of the presence or absence of an exopodite on the maxilliped (character 26) the decision was not in favour of a transformation series, since in the Halosbaenidae (the sole exception) traces of a reduced exopodite can be indicated, while this is not the case or hardly so in the other groups which lack an exopodite.

Transformation series have also been indicated for five other characters (characters 2, 12, 18, 20, and 33). Watling (1983) distinguishes four main types of blood systems (here character 2), two of which show reductions (types II and III) compared to the plesiomorphic state (type I); one other is elaborate (type IV). I also judged it best to indicate presence, absence, as well as the intermediate state (reduced), and of an antennal gland in the antenna 2 (character 12), and a maxillary gland in maxilla 1 (character 20) of the adult animals. The same argument applies to the lifting spines of the mandible (character 18), which can either be present, sparsely present and very short, or absent. In case of the number of segments of the pleopods (character 33) the Cumacea represent an intermediate between those groups with multi-segmented pleopods and those with only 1-segmented pleopods. Defining a transformation series seemed the best solution to me, although a definition that grouped 1-segmented and 2-segmented pleopods into one class is not reflected in the trees obtained.

In a number of characters (characters 7, 30, and 32) the apomorphic condition could be clearly divided in two separate alternative states derived from the ancestral (plesiomorphic) state.

In all other instances the characters could be defined as binary, i.e., simply into one plesiomorphic and one (syn)apomorphic state.

### 5.3.2. Cladistic analysis

Following the selection of characters and combining these into a data matrix (table 7), cladograms were constructed following the methodology described above (§ 5.2), and eventually three trees were obtained (fig. 487). The strict consensus of these trees (fig. 488) has a consistency index of 0.750, and shows a polytomy with Thermosbaenacea, Mictacea, Spelaeogriphacea, and a clade formed by the Tanaidacea, Cumacea,

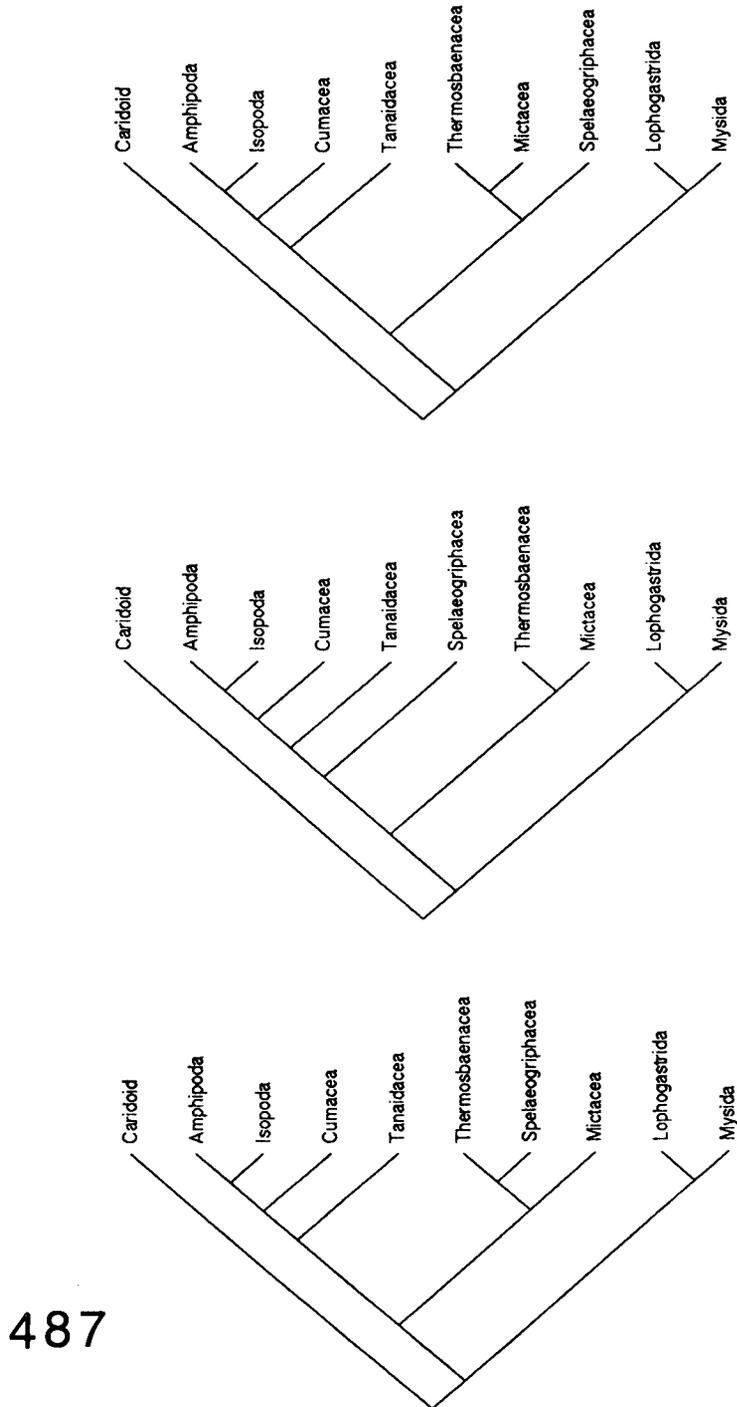
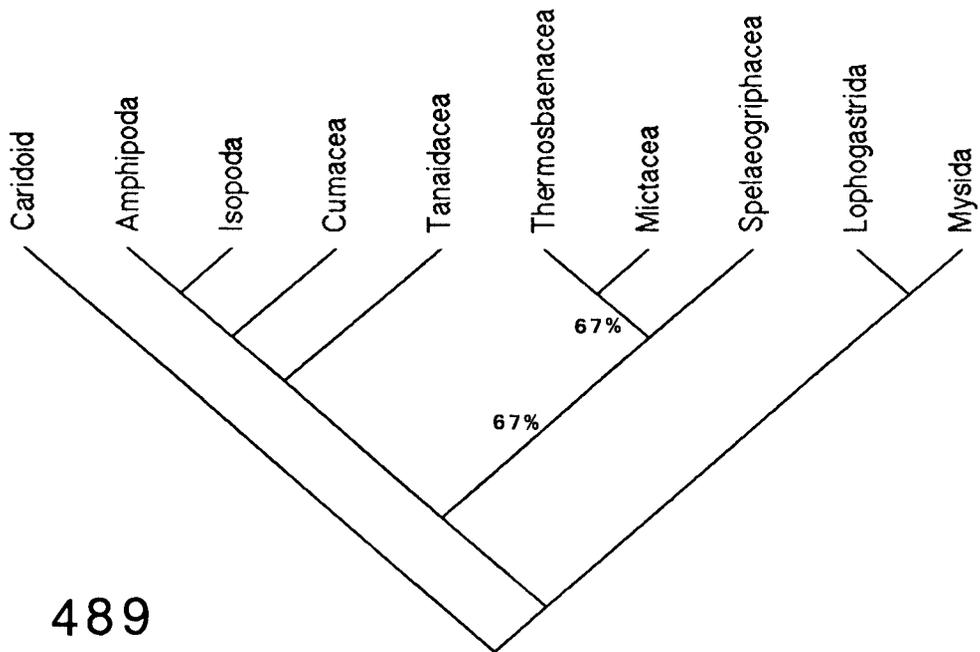
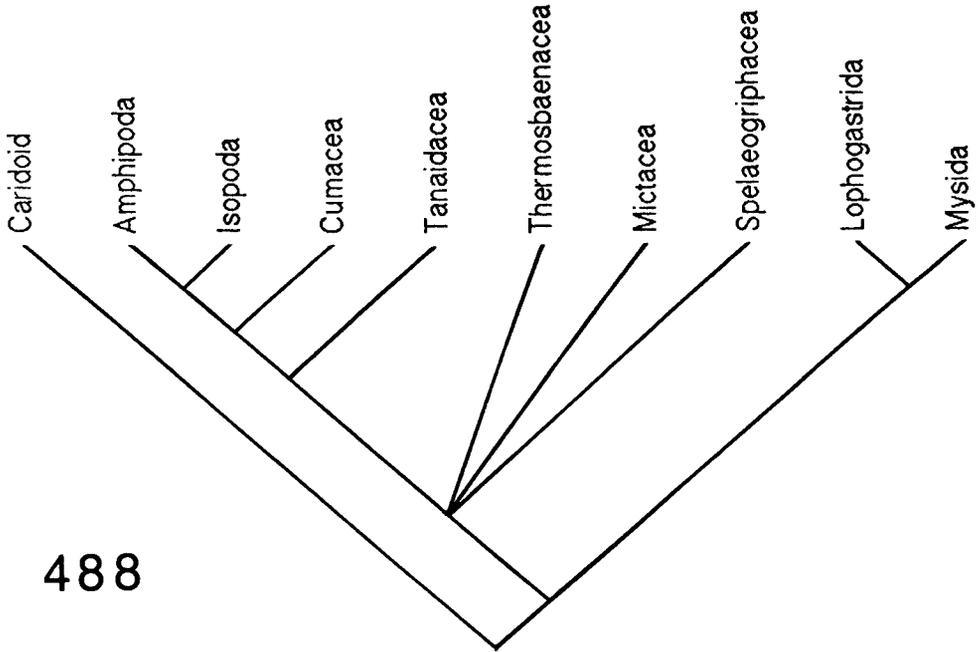


Fig. 487. Shortest and most parsimonious trees found for the phylogeny of the Peracarida.



Figs. 488-489. Consensus cladograms of the Peracarida. 488, strict consensus; 489, 50% majority-rule.

Isopoda, and Amphipoda. A complete solution of the consensus tree into dichotomies was achieved by calculating the 50% majority-rule consensus option of PAUP, having a consistency index of 1.000. This consensus tree (fig. 489) shows the Mictacea as the most probable sister-group. Complete dichotomy was reached until calculating a 66% majority-rule consensus tree.

An unordered analysis (without a defined out-group) resulted in two equally parsimonious trees. Both the strict consensus tree and the 50% majority-rule consensus tree were strongly polytomous and reached not further than the low consistency index of 0.429. Only two combinations of sister-groups were obtained in the respective trees, viz. Lophogastrida-Mysida, and Thermosbaenacea-Mictacea.

Based on these results, I chose the Mictacea (viz., the genera *Mictocaris* and *Hirsutia*), to serve as an out-group for the analysis of the Thermosbaenacea at the generic level (§5.4) as it was selected the most often as the sister-group (66%).

#### 5.4. Phylogenetic relationships within the Thermosbaenacea

To date only Monod and Cals (Monod & Cals, 1988; Cals & Monod, 1988) have addressed the issue of the relationships within the Thermosbaenacea. Their first tree (Monod & Cals, 1988) is only a pictorial representation of their identification key. As a result of the discovery of *Tulumella*, Cals & Monod (1988) presented a new tree with *Tulumella* incorporated. This time the tree showed several unexplained empty side-branches, and a polytomy for *Limnosbaena*, *Tulumella*, *Theosbaena*, and *Halosbaena*. Both trees were based on nine characters, and it is not clear whether a computer based cladistic analysis was carried out.

##### 5.4.1. Character analysis

In the present analysis 49 characters have been used to differentiate the various genera of the Thermosbaenacea and its sister-group the Mictacea (listed in table 8). Here also, the characters have been ordered in traditional morphological order of treatment.

In contrast to the matrix of the Peracarida, this data matrix (table 9) yields a considerably larger number of quantitative characters. In order to achieve non-overlapping classes, the interpretation of the number of segments of the main flagellum of antenna 1 (character 41) required an alternative method of grouping. Of each genus the average number of segments over all species was calculated. Three classes were obtained. Platvoet & Pinkster (1992) argued that a large number of segments can be considered plesiomorphic, allowing definition of a transformation series running from a high to low number of segments.

Apart from character 41, transformation series have been defined for some other characters as well (characters 43, 50, 62, 63, 65, 68, 69, 71, 81, 82, and 84). Transformation series have been used to define classes within the decline in number of macrosetae on the distal prominence of peduncle segment 3 of antenna 1 (character 43), segmentation of the exopodites of pereopods 6 (character 81) and 7 (character 82), or the decline in development of the maxillipedal endopodite

Table 8. Character transformation series used in the phylogenetic analysis of the Thermosbaenacea and Mictacea. 0 = plesiomorphous state; 1 - 2 = apomorphous states in transformation series; 1' = alternative apomorphous state.

<p>40. Antenna 1: plumose macrosetae on median margin of the peduncular segments 0 : present 1 : absent</p>	<p>49. Mandible: number of cusps on the right pars incisiva 0 : 4 1 : 6 or more 1' : 2</p>
<p>41. Antenna 1: average number of segments of the main flagellum 0 : <math>\geq 18</math> 1 : 7 to 11 2 : 4</p>	<p>50. Mandible: lacinia modilis in left mandible 0 : always present 1 : absent or present 2 : always absent</p>
<p>42. Antenna 1: number of segments of the accessory flagellum 0 : 8 or more 1 : 7 or less</p>	<p>51. Mandible: number of cuspidations in the left lacinia mobilis 0 : 3 to 4 1 : 5 to 6 1' : absent</p>
<p>43. Antenna 1: number of macrosetae on distal prominence of last peduncular segment 0 : 4 1 : 3</p>	<p>52. Mandible: number of serrate macrosetae in the ('spine') row of the left mandible 0 : 6 or more 1 : 3 to 5</p>
<p>44. Antenna 2: "epipodal" scale on peduncular segment 2 0 : present 1 : absent</p>	<p>53. Mandible: number of serrate macrosetae in the ('spine') row of the right mandible 0 : 6 or more 1 : 3 to 4</p>
<p>45. Ocular scales: 0 : absent 1 : present</p>	<p>54. Mandible: shape of the pars molaris 0 : pointedly triangular 1 : robust 1' : ensiform</p>
<p>46. Mandible: number of plumidenticulate macrosetae on palp segment 2 0 : 1  1 : 2 or more</p>	<p>55. Mandible: pars molaris (ex. ciliate microsetae) 0 : naked 1 : with multi-partite spiniform processes 1' : with serrate spiniform processes</p>
<p>47. Mandible: number of plumidenticulate macrosetae on palp segment 3 0 : 2 - 4 (0 in Hirsutia ?) 1 : 5 or more</p>	<p>56. Maxilla 1: number of toothed macrosetae on the basal endite 0 : 7 1 : 8 or more 1' : 6</p>
<p>48. Mandible: number of cusps on the left pars incisiva 0 : 4 or less 1 : 5 or more</p>	

57. Maxilla 1: number of forms of toothed macrosetae  
0 : 1  
1 : 2
58. Maxilla 1: palp segments 1 and 2  
0 : free  
1 : coalesced  
1': absent
59. Maxilla 1: palp segments 2 and 3  
0 : free  
1 : segment 3 reduced or absent
60. Maxilla 1: type of setulate macrosetae on segment 2 of the palp  
0 : unisetulate  
1 : bisetulate  
1': absent
61. Maxilla 1: number of setulate macrosetae on the distal palp segment  
0 : 1  
1 : 2 or more  
1': absent
62. Maxilla 1: setulate macrosetae on the distal palp segment  
0 : always obscurely setulate  
1 : obscurely setulate or well-developed  
2 : always well-developed  
1': absent
63. Maxilla 2: position exopod  
0 : lateral  
1 : at base of palp  
2 : reduced
64. Maxilla 2: number of rows of serrate macrosetae on basal endite 2  
0 : 1  
1 : 2
65. Maxilla 2: number of rows of serrate macrosetae on basal endite 3  
0 : 1  
1 : 2  
2 : 9 to 14
66. Maxilliped: number of pappose macrosetae on the coxopodite  
0 : 2 to 3  
1 : 5 to 6  
1': absent
67. Maxilliped: setules of pappose macrosetae  
0 : simple  
1 : complex  
1': absent
68. Maxilliped: number of setal rows on the distal margin of the basal endite  
0 : 2  
1 : 2 to 3  
2 : 3
69. Maxilliped: number of forms of plumidenticulate macrosetae on the distal margin of the basal endite  
0 : 1  
1 : 2  
2 : 3
70. Maxilliped: large medio-distal plumidenticulate macrosetae  
0 : with setules  
1 : setules reduced or absent, terminal portion naked with knobs or serrations
71. Maxilliped: endopodite  
0 : well-developed (multi-segmented)  
1 : lobate  
2 : reduced or absent
72. Maxilliped: epipodite  
0 : present  
1 : absent
73. Maxilliped: broodpouch  
0 : ventral, oostegites  
1 : dorsal outgrowth of carapace
74. Gnathopod: exopodite  
0 : present  
1 : absent
75. Gnathopod: number of ungues  
0 : 1  
1 : 3 to 4

- |   |  |
|---|--|
| <p>76. Gnathopod: "spur" on propodus<br/>0 : absent<br/>1 : present</p>                           | <p>83. Pleopod 1:<br/>0 : articulate<br/>1 : non-articulate</p>  |
| <p>77. Pereiopods 2 to 7: ovate microsetae on propodus<br/>0 : present<br/>1 : absent</p>         | <p>84. Pleopods 3 to 5:<br/>0 : present, articulate<br/>1 : present, rudimentary<br/>2 : absent</p>                                |
| <p>78. Pereiopods 2 to 7: ovate microsetae on dactylus<br/>0 : present<br/>1 : absent</p>         | <p>85. Uropod: endopod<br/>0 : 2- or more segmented<br/>1 : 1-segmented</p>  |
| <p>79. Pereiopods 3 to 6: ovate microsetae on ischio-merus<br/>0 : present<br/>1 : absent</p>     | <p>86. Telson: shape<br/>0 : tongueshaped<br/>1 : subquadrangular<br/>1': pleotelson by fusion with pleonite 6</p>                 |
| <p>80. Pereiopods 3 to 7: ovate microsetae on exopodite<br/>0 : present<br/>1 : absent</p>        | <p>87. Telson: position cuspidate macrosetae<br/>0 : distolaterally<br/>1 : distally and along entire lateral margin</p>           |
| <p>81. Pereiopod 6: exopodite<br/>0 : 2- or more segmented<br/>1 : 1-segmented<br/>2 : absent</p> | <p>88. Telson: number of different macrosetal types<br/>0 : cuspidate macrosetae only<br/>1 : cuspidate and serrate macrosetae</p> |
| <p>82. Pereiopod 7: exopodite<br/>0 : 2- or more segmented<br/>1 : 1-segmented<br/>2 : absent</p> |  |
- 

(character 71), and pleopods 3 to 5 (character 84). A development from a simple row of serrate macrosetae to numerous rows of serrate macrosetae on basipodal endite 3 of maxilla 2 (character 65), as well as the increase in number of forms of plumidenticulate macrosetae on the distal margin of the basal endite of the maxilliped (character 69), each fall into three classes, thus a transformation series is proposed. Intermediate classes were found for four characters (characters 50, 62, 68, and 84) and solved likewise as done as in § 5.3.1, for characters 10, 14, 26, and 39. Besides the transformation series in character 62, also an alternative apomorphy could be defined for both *Hirsutia* and *Mictocaris*,

Table 9. Distribution of character states in genera of Thermosbaenacea and Mictacea. Unknown states

	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
<i>Hirsutia</i>	1	2	1	2	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1'	1	1'	1'	1'	2
<i>Mictocaris</i>	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1'	1	1'	1'	1'	2
<i>Thermosbaena</i>	0	1	0	1	1	0	0	0	0	0	2	1'	0	0	1	0	1'	1	1	0	0	0	2	1
<i>Monodella</i>	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	2	1
<i>Tethysbaena</i>	0	1	1	0	1	0	0	1	1	0	0	0	0	1	1	1	0	0	1	0	0	0	1	1
<i>Tulumella</i>	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1'	1	0	0	1	0	1	0	0
<i>Limnosbaena</i>	1	2	1	1	1	1	1	0	0	1'	0	1	1	1	1'	0	0	1	0	1	1	1	0	2
<i>Halosbaena</i>	1	1	1	0	1	1	1	0	1	1	0	1	0	1	0	0	0	1	0	1	1	1	0	2
<i>Theosbaena</i>	1	0	0	0	1	1	1	0	1	1	0	0	1	1	0	0	1	1	0	1	1	1	0	2

as both are devoid of a setulate macroseta on the distal palp segment of maxilla 1. A transformation series was defined also as a solution for the position of the exopod of maxilla 2 (character 63), as a part of the taxa concerned have their exopod reduced.

In quite a large number of characters (characters 49, 51, 54, 55, 56, 58, 60, 61, 62, 66, 67, and 86), alternative apomorphic states derived from the same ancestral (plesiomorphic) state were inevitable, i.e., resulting in non-linear transformation series. The typical "cave" dependent requirements, giving selection pressure on all taxa concerned, most probably play an important role in the development of alternative apomorphies, as does the apparent sensitivity of Crustacea in general to be involved in new "evolutionary experiments" (§ 5.3).

In all other instances the remaining characters could be easily defined binary, i.e., in two classes: plesiomorphic and (syn)apomorphic.

#### 5.4.2. Cladistic analysis

Following the same method as described in paragraph 5.2 parsimony cladograms were constructed, with *Mictocaris* and *Hirsutia* defined as out-groups in order to obtain ordered trees. Eventually, three trees were obtained with a calculated length of 117 (fig. 490). The strict consensus of these trees (fig. 491) has a consistency index of 0.714. In this consensus tree two polytomies occur, one at the familial level between the Thermosbaenidae-Monodellidae, the Tulumellidae, and the Halosbaenidae; the other at the generic level of the Halosbaenidae. Calculating the 50% majority-rule consensus tree (fig. 492) solved the polytomies satisfactorily, and even reached a consistency index of 1.000. This complete dichotomy was achieved until calculating a 66% majority-rule consensus tree.

The unordered analysis performed gave the same solution of the relationships within the Thermosbaenacea and Mictacea (the latter now having been defined as in-group). Both *Mictocaris* and *Hirsutia* were segregated immediately from the thermosbaenacean genera. The consistency indices found were equal to that of the ordered analyses also.

Due to its high (maximal) consistency index the 50% majority-rule consensus tree (fig. 492) is chosen to represent the most probable phylogenetic tree of the Thermosbaenacea.

are indicated with “?” (see table 8 for description of characters and explanation of character numbers).

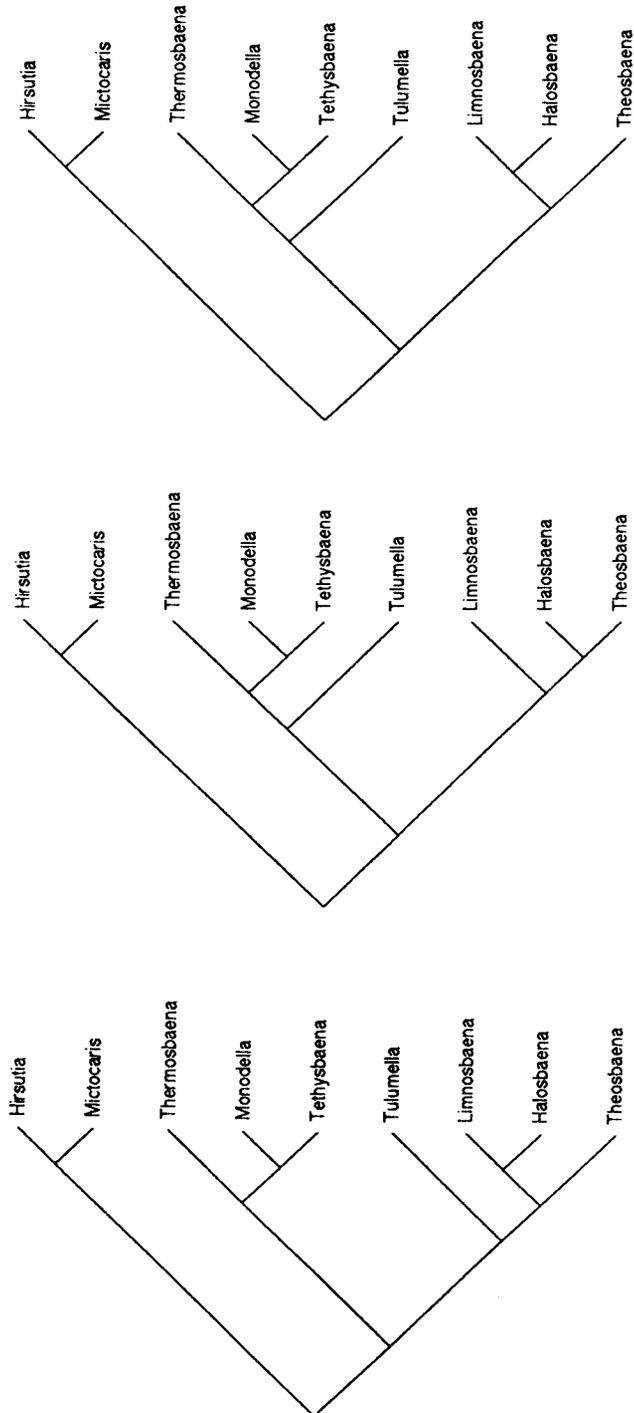
64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
1	1	1'	1'	2	1	1	0	1	0	0	0	0	1	1	1	1	2	2	0	0	0	0	0	1
1	1	1'	1'	2	1	1	0	1	0	1	1	0	1	1	1	1	0	2	1	0	0	0	0	1
0	1	0	0	0	0	0	2	0	1	0	0	0	1	1	1	1	2	2	0	2	1	1'	1	0
0	1	0	0	0	0	0	?	0	1	0	0	1	0	0	0	0	1	1	0	2	1	1	0	0
0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	2	1	1	0	0
0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	1	0	0	1	2	1	1	0	0
1	2	0	1	2	2	1	2	0	1	1	1	0	1	1	1	1	0	2	1	1	1	0	0	1
1	2	1	1	2	2	1	2	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1
1	2	1	1	2	2	1	2	0	1	1	1	0	1	1	1	1	0	1	1	2	1	0	1	0

### 5.5. Phylogeny of the species-groups of *Tethysbaena*

Of the three genera of the Thermosbaenacea that are not monotypic *Tethysbaena* is unquestionably the most prolific in numbers of species. This invites a more detailed study of its internal phylogenetic relationships. As indicated in the systematic part of this study (chapter 4), six more or less monophyletic groups (two of which monotypic) can be distinguished. Therefore, in this paragraph the phylogenetic analysis discussed concentrates on the species-groups only. An alternative method to eventually obtain an idea of the phylogenetic relationships within *Tethysbaena*, *Halosbaena* and *Tulumella* at the specific level will be discussed in the part preceding the comprehensive phylogenetic model (§ 5.6).

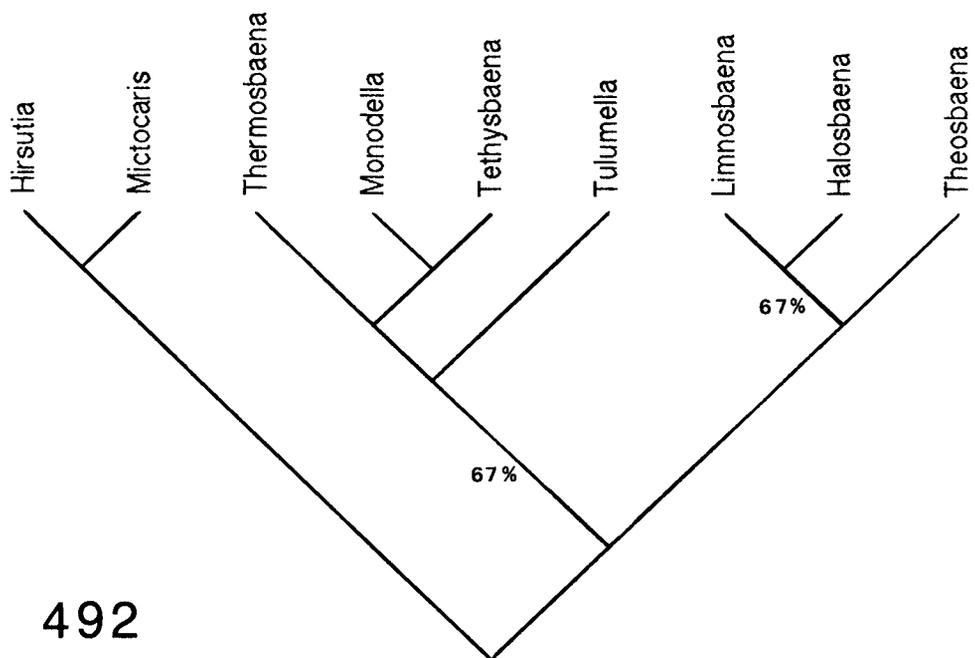
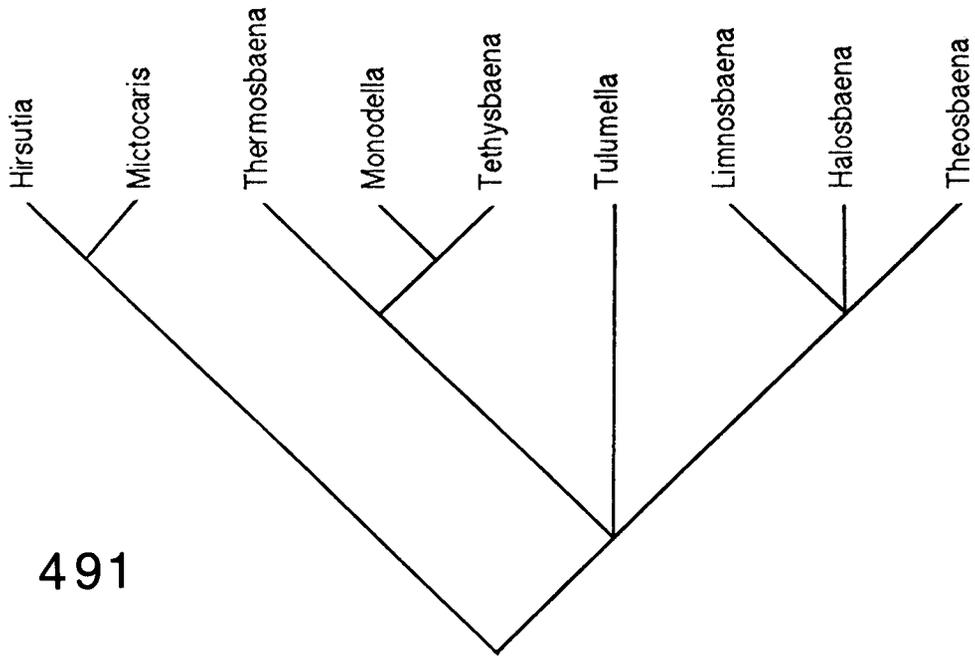
#### 5.5.1. Character analysis

In this analysis only a limited number of characters, 11 in all, were found suitable to calculate the possible phylogenetic relationships (table 10). As in the previous two analyses, the characters have been arranged in traditional morphological order of treatment. Four characters are quantitative (characters 89, 91, 93 and 98), the remaining characters are qualitative in nature. Except for the number and shape of the central protrusions of the terminal stretch of the telson (character 98) all characters could be defined binary, i.e., into two classes: plesiomorphic and (syn)apomorphic. Although it must be remarked that the classes defining the state of development of the unisetulate macroseta on palp segment 3 of maxilla 1 (character 92) are not absolute, since in the “*T. sanctaerucis*-group” (*T. juglandis*) and the “*T. argentarii*-group”, exceptions exist contradicting their present classification in the data matrix. In latter group, the presence of a well-developed unisetulate macroseta seems dependent on sex and species. The number and structure of the protrusion(s) on the central part of the terminal stretch (character 98), however, not only required the more sophisticated definition into a transformation series, but also comprises an alternative (aut)apomorphic state.



490

Fig. 490. Shortest and most parsimonious trees found for the phylogeny of the Thermosbaenacea at the generic level.



Figs. 491-492. Consensus cladograms of the Thermosbaenacea at the generic level. 491, strict consensus; 492, 50% majority-rule consensus.

Table 10. Character transformation series used in the phylogenetic analysis of *Monodella* and the *Tethysbaena* species-groups. 0 = plesiomorphous state; 1 - 2 = apomorphous states in transformation series; 1' = alternative apomorphous state.

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<p>89. <i>Antenna 1</i>: average number of segments of the main flagellum 0 : 8 or more 1 : up to 8</p>	<p>95. <i>Uropod</i>: distal margin endopodite 0 : protruding beyond first segment exopodite 1 : not protruding beyond first segment exopodite</p>
<p>90. <i>Mandible</i>: plumidenticulate macrosetae of palp segment 3 0 : not species dependent 1 : species dependent</p>	<p>96. <i>Telson</i>: 0 : longer than wide 1 : wider than long</p>
<p>91. <i>Mandible</i>: number of plumidenticulate macrosetae of palp segment 3 0 : 5 1 : 6 or more</p>	<p>97. <i>Telson</i>: terminal stretch 0 : straight to slightly convex 1 : concave, anal lobes protruding the</p>
<p>92. <i>Maxilla 1</i>: well-developed unisetulate macroseta of palp segment 3 0 : usually present 1 : usually absent</p>	<p>98. <i>Telson</i>: number of (clear) protrusions on central portion of the terminal stretch 0 : 1 1 : bump 2 : 0 1' : 3</p>
<p>93. <i>Maxilliped</i>: terminally implanted plumidenticulate macrosetae (except subterminal ones) 0 : 8 or more 1 : 5 or less</p>	<p>99. <i>Telson</i>: glandular simple macrosetae 0 : present 1 : absent</p>
<p>94. <i>Pereiopods 2 to 7</i>: number of ovate microsetae on propodus 0 : not sexually dimorphic 1 : sexually dimorphic</p>	

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### 5.5.2. Cladistic analysis

Following the results of the cladistic analysis of the Thermosbaenacea at the generic level, *Monodella* (with its only representative *M. stygicola*), was selected as the sister-group of *Tethysbaena*, and subsequently served as the out-group in the ordered analysis. The analysis resulted into seven trees with a calculated length of 22 (fig. 493). The strict consensus of these trees (fig. 494) has the very low consensus index of 0.400, and features a polytomy for almost all species-groups. Only the "*T. sanctaerucis*-group" and "*T. relicta*-group" form a clade as one of the five branches of the polytomy. Although *Tethysbaena* is clearly monophyletic, the strict consensus seems to suggest that the number of characters is not sufficient to resolve the phylogenetic tree completely. The 50% majority-rule consensus (fig. 495), however, partially solved the polytomy, leaving a trichotomy among *T. texana*, *T. vinabayesi*, and the "*T. argentarii*-group", while its consistency index reached 0.800. This solution was calculated up to a 57% majority-rule consensus.

The unordered analysis performed gave an exactly similar resolution of the rela-

Table 11. Distribution of character states in species-groups of Monodellidae. Unknown states are indicated with “?” (see table 10 for description and explanation of character numbers).

	89	90	91	92	93	94	95	96	97	98	99
<i>Monodella stygicola</i>	0	0	0	1	1	?	1	1	0	2	0
<i>T. sanctaegrucis</i> -group	1	1	1	1	0	0	0	1	1	2	1
<i>T. relict</i> a-group	1	0	1	0	1	0	0	1	1	1	1
<i>T. atlantomaroccana</i> -group	1	0	0	1	0	1	0	0	0	2	0
<i>T. texana</i>	1	0	1	0	0	1	1	0	0	0	1
<i>T. vinabayesi</i>	1	0	1	1	0	1	1	0	0	1	0
<i>T. argentarii</i> -group	0	1	1	0	0	1	0	0	0	0	0

tionships within the species-groups of *Tethysbaena* and *Monodella* (the latter now defined as in-group). The consistency indices found were equal to that of the ordered analyses as well.

#### 5.6. Phylogenetic model of the Thermosbaenacea

With the integration of the two 50% majority-rule consensus trees obtained for the Thermosbaenacea (figs. 492 and 495) already a reasonably dichotomous tree can be constructed for the order. For a further refinement, an alternative use of the PAUP computer program was made. For two species-groups of *Tethysbaena*, viz. the “*T. sanctaegrucis*-group” and the “*T. argentarii*-group”, all characters from tables 1 and 2 (see chapter 4) that were not used in the character sets of the phylogenetic analysis were defined as transformation series. This definition was made in such a manner, that always at least one set of apomorphic characters was defined, and recognized by the program as “informative”. Only exactly equal states received the same format symbol. In this way all equal character states for the species concerned were recognized and plotted by the program on the basis of similarity.

For the “*T. sanctaegrucis*-group” the format symbols varied from 0 to 9. In total 46 characters were used for the “*T. sanctaegrucis*-group”. All characters were unweighed and an in-group comparison was carried out. Only one cladogram resulted as being the most parsimonious solution (fig. 496), with a consistency index of 1.00 and no polytomies at all.

For the “*T. argentarii*-group” the method was slightly different. In this analysis two characters defining the sub-groups received double weight in order to obtain two clades (viz. *T. argentarii-halophila-aiakos* and *T. scabra-siracusae*). This concerned the presence of scales on the body, and the number of plumidenticulate macrosetae of the basipodal endite 1 of maxilla 2, as both characters represent true synapomorphies. As in the phylogenetic tree of § 5.5.2 a trichotomy occurred between *T. texana*, *T. vinabayesi*, and the “*T. argentarii*-group” the character states of the first two species are inserted in the data matrix as well. For this analysis 39 characters were used, the format symbols varying from 0 to 5. Not only an in-group analysis, but also an out-group analysis (with *T. texana* and *T. vinabayesi* serving as out-group) was carried out. In both analyses the “*T. argentarii*-group” formed a monophyletic group. Only one cladogram was constructed as being the most parsimonious solution, with a con-

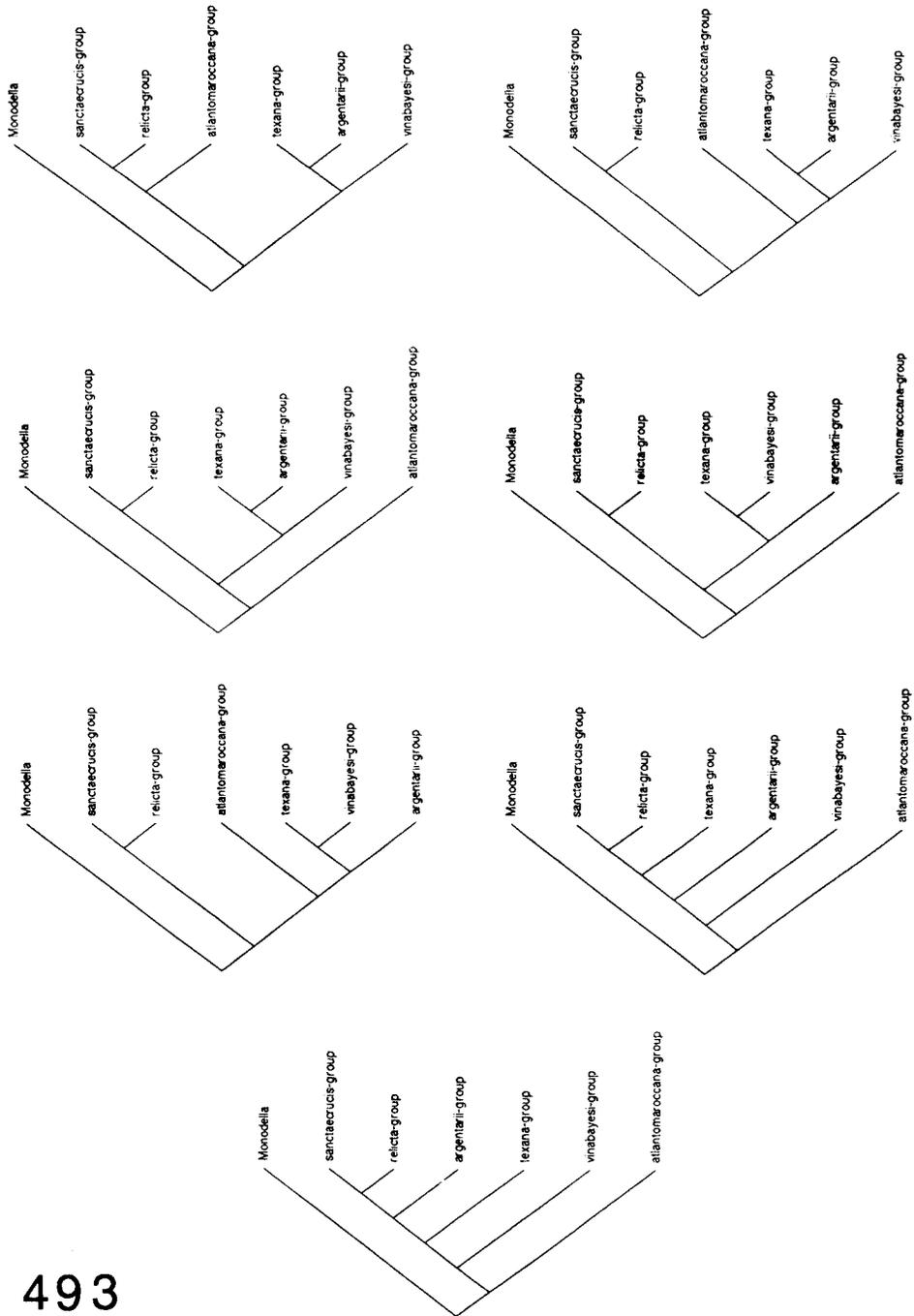
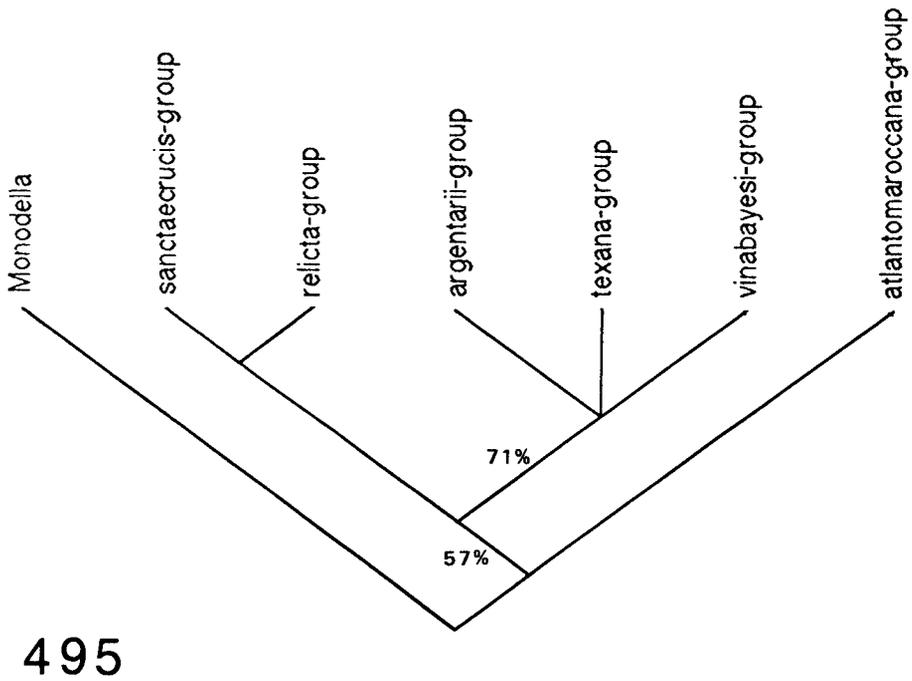
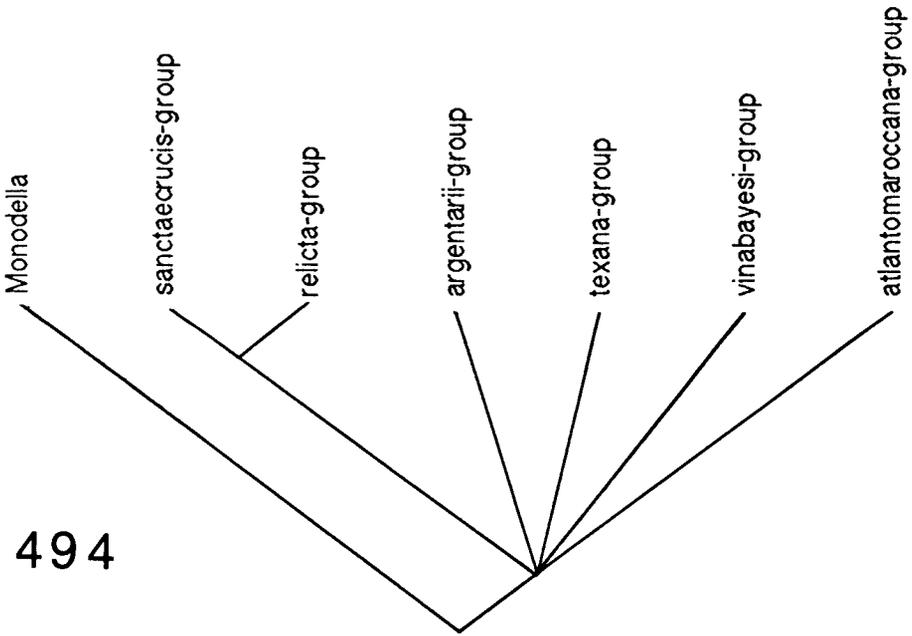
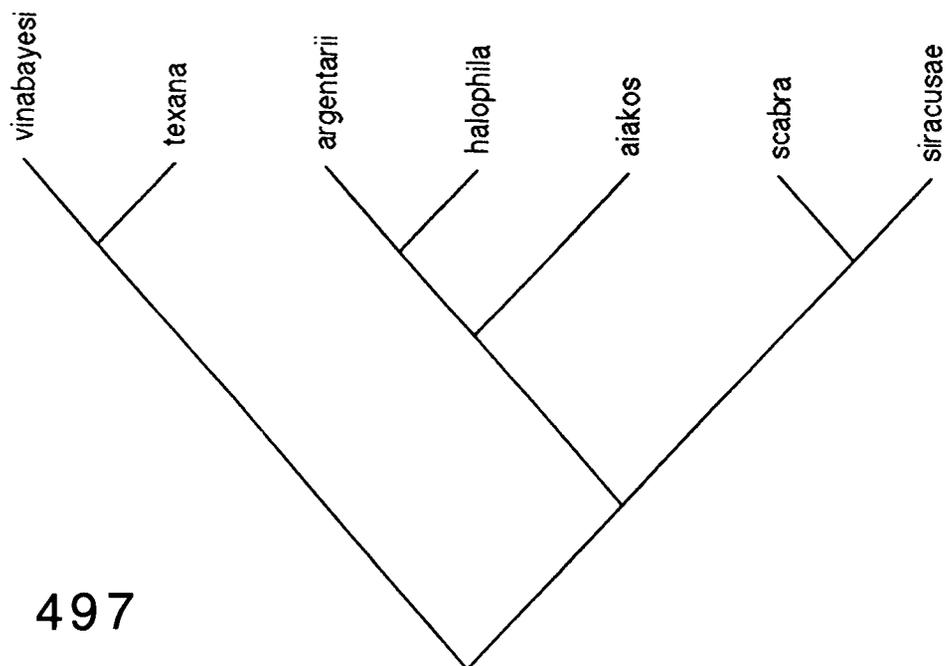
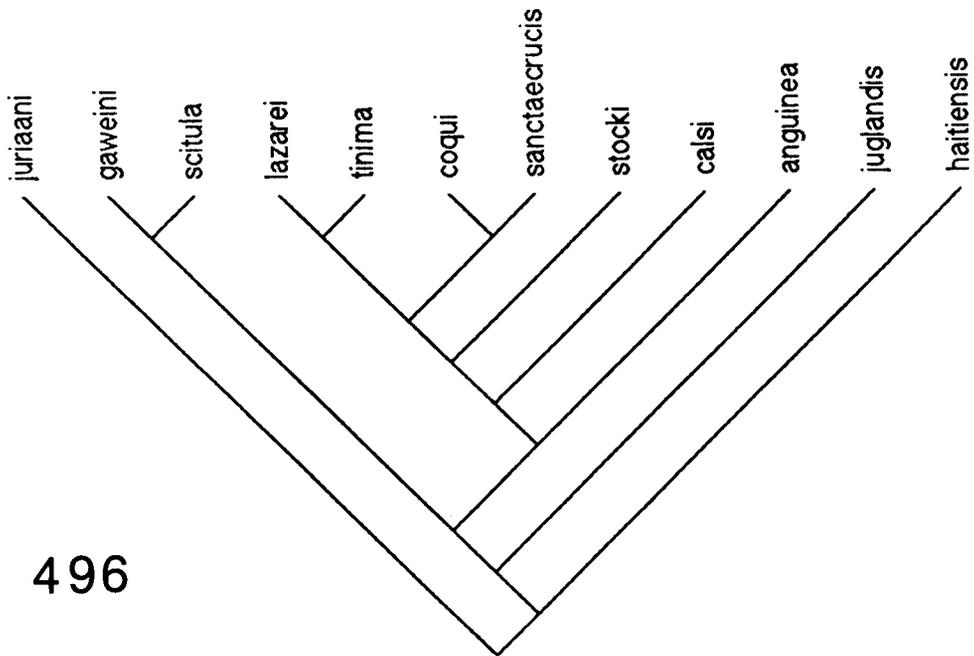


Fig. 493. Shortest and most parsimonious trees found for the phylogeny of the species groups of *Tethysbaena*.



Figs. 494-495. Consensus cladograms of the phylogeny of the species-groups of *Tethysbaena*. 494, strict consensus; 495, 50% majority-rule consensus.



Figs. 496-497. Shortest species-group trees. 496, Shortest tree found for the "*Tethysbaena sanctaetrucis*-group". 497, Shortest tree found for the "*Tethysbaena argentarii*-group", with *T. texana* and *T. vinabaysi* (as out-group).

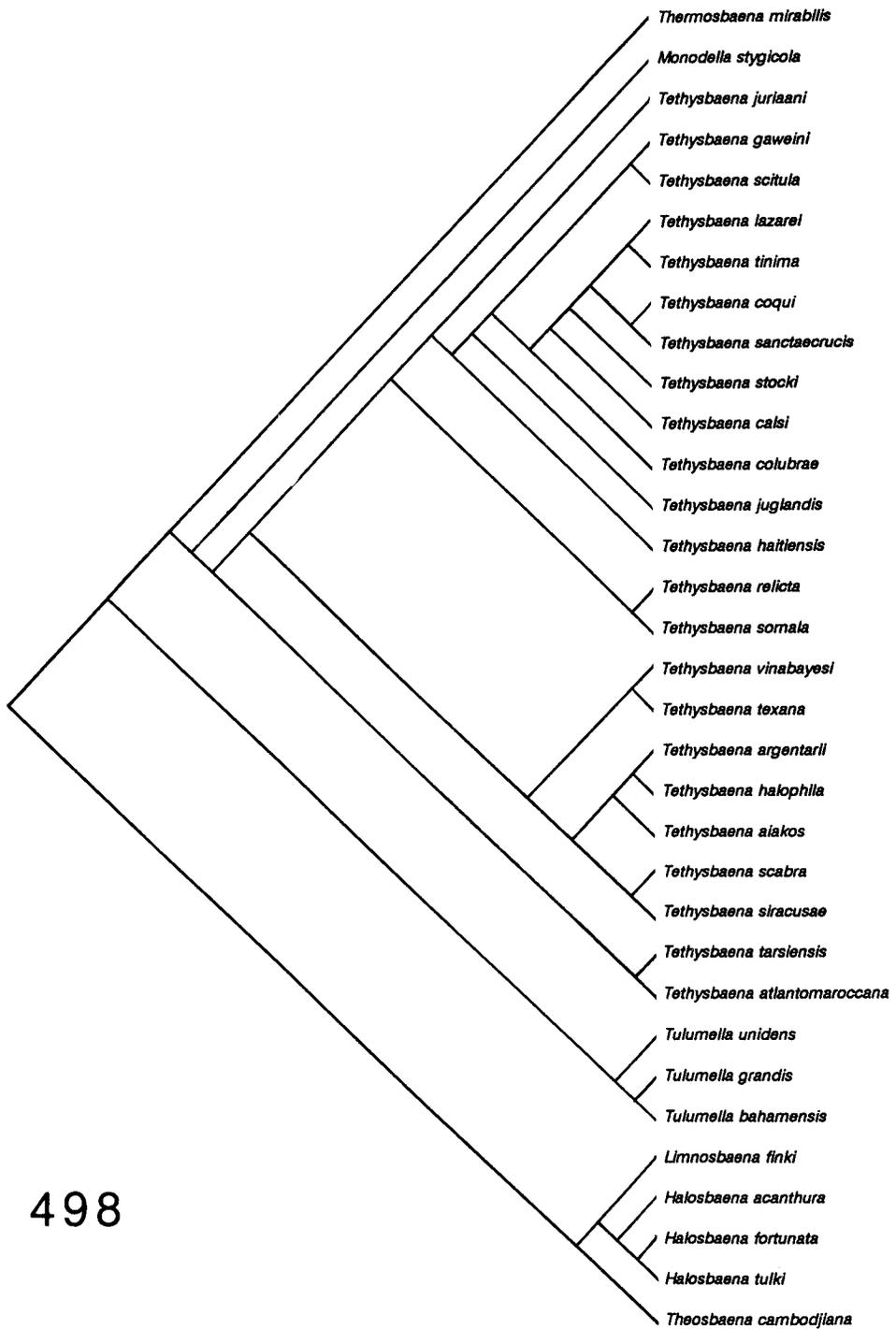


Fig. 498. Proposed phylogenetic tree of the Thermosbaenacea.

sistency index of 1.00 and no polytomies at all. The tree obtained with the out-group analysis (fig. 497) is selected here for the hypothetical, comprehensive model presented in fig. 498.

For the three species known to date of each *Halosbaena* and *Tulumella*, a similar comparison was carried out, based on the data provided in tables 3 and 5. This resulted in *Halosbaena acanthura* and *H. fortunata* sharing more characters than any of them do compared with *H. tulki*. The same holds true for *Tulumella grandis* and *T. bahamensis* in comparison with *T. unidens*.

Of course, the validity of the alternative method employed can be questioned as not truly cladistic, but at this level it is not possible to determine plesiomorphies and (syn)apomorphies satisfactorily in the present study. The advantage of the PAUP program, however, lies in the fact that it has no requirement to treat "0" automatically as the ancestral state. This means, of course, that, as an alternative to determining the plesiomorphous state a priori, either qualitatively (i.e., via considerations on the morphology) or via out-group comparison, this may be performed in a "non-supervised learning" procedure. The largest clique of characters with compatible character state distributions may thus be determined in a completely unprejudiced way, by allowing the polarity of all linear transformation series to be read in either direction until the best fit has been determined. This enabled me to carry out the alternative method described above as in-group comparison, according to "widespread equals primitive", character polarity occurred. A single tree as shortest (or most parsimonious) alternative resulted for both the "*T. sanctaerucis*-group" and the "*T. argentarii*-group", as well as solving the trichotomy found earlier for *Tethysbaena texana*, *T. vinabayesi*, and the "*T. argentarii*-group". These trees integrated in the tree already obtained by means of the "regular" method, result in the hypothetical, comprehensive tree that will function as the proposed model of the phylogeny of the Thermosbaenacea (fig. 498) as a whole. This tree will be the one tested against the zoogeographical and paleogeographical data discussed in the next chapter.

## 6. Biogeography

### 6.1. Introduction

Short after the discovery of the first thermosbaenacean(s), Bruun (1939) and Ruffo (1949b) suggested a "Tethyan" origin for the group, i.e. the present day species supposedly having been "stranded" as a result of the retreat of the Tethys Sea. S.L. Karaman (1953, 1954) considered the ancestral thermosbaenaceans of marine origin. His point of view found support from Barker (1959, 1960), who suggested that the members of this group have been interstitial animals in the bottom of the Tethys Sea. He (Barker, 1959, 1960) also discussed another theory, in which he assumed a much more recent origin, namely, during lacustrine periods in the late Pliocene or Quaternary. This second explanation was, however, quickly abandoned upon the discovery of a thermosbaenacean in the New World (Maguire, 1964, 1965). Fryer (1965) suggested these animals have a marine shallow water origin and got "stranded" by regression of the sea somewhere in between Mid-Miocene and Pliocene. Tsumamal & Pór (1971) reached similar conclusions in their study on the subterranean fauna of

the Jordan Rift Valley. Stock (1976) proposed a "Regression Model" (Stock, 1977, 1980a) to explain the presence and distribution of subterranean animals in general. He stated that the Thermosbaenacea (as well as most other stygobionts) originated from marine shallow water ancestors that got "stranded" in the interstitium or inland groundwaters during periods of marine regression. Iliffe et al. (1984) subsequently proposed an alternative hypothesis, which suggested deep sea ancestors from which (part of) the present day anchihaline stygobionts would have evolved (see also Hart et al., 1985; Iliffe, 1986; Wilkens et al., 1986). The improbability of the "deep sea" theory was discussed in detail by Stock (1986c, 1990) and Danielopol (1990). Nowadays Stock's Regression Model theory is widely accepted (many studies are referable to Regression Model evolution) and in recent years it was refined by contributions of Boutin & Coineau (1990) and Notenboom (1991). Also the distribution of the Thermosbaenacea can be explained by means of the Regression Model.

## 6.2. Biogeographic patterns

When we consider the distributional pattern of the Thermosbaenacea as a whole, it becomes obvious that their Recent distribution area falls within the limits of the ancient Tethys belt. All species known so far, are distributed in the zone once covered by the shallow Tethys Sea or its coastlines. Regressions, in successive geological periods, of the different areas resulted in "stranding" of the present biota. Various comparable patterns at taxonomic levels lower than that of the order can be observed, too, and, these will consequently be discussed below.

### 6.2.1. Biogeography of the Monodellidae and the Thermosbaenidae

As noted in earlier papers (Wagner, 1988, 1990), the distribution of the members of the Monodellidae as a rule is confined to the northern part of the general distribution of the whole order (fig. 499). Though exceptions do exist (e.g., *Tethysbaena somala* and *T. atlantomaroccana* are found on the African continent in Somalia and Morocco), at the time the putative ancestors of those species are supposed to have entered the continental ground water, Afro-European shallow-water connections were present. In total, three such connections play an important role in understanding the present-day distribution of the Monodellidae and the Thermosbaenidae. Two of these connections will be discussed later with the species-groups of *Tethysbaena*, but the third also concerns *Monodella* and *Thermosbaena*, whence it is relevant here.

As remarked above, the Thermosbaenidae can be considered a unique and strongly modified derivation of the Monodellidae for a number of reasons: (1) the chaetotaxy of *Thermosbaena* is so close to that of *Tethysbaena* that a common ancestor cannot be denied, whereas the remaining external morphology of the body is sufficiently distinct to justify separation at a familial level; (2) the fact that *Thermosbaena mirabilis* could evolve in the ground water of Tunisia not earlier than Late Pliocene to Pleistocene, i.e., later than most of the Old World *Tethysbaena* species and later than *Monodella*, points to a group much younger than the Monodellidae as a whole. The extrinsic basis for the development of such a unique taxon undoubtedly lies in the exceptional circumstances of the habitat to which *Thermosbaena* got adapted, i.e., to hot

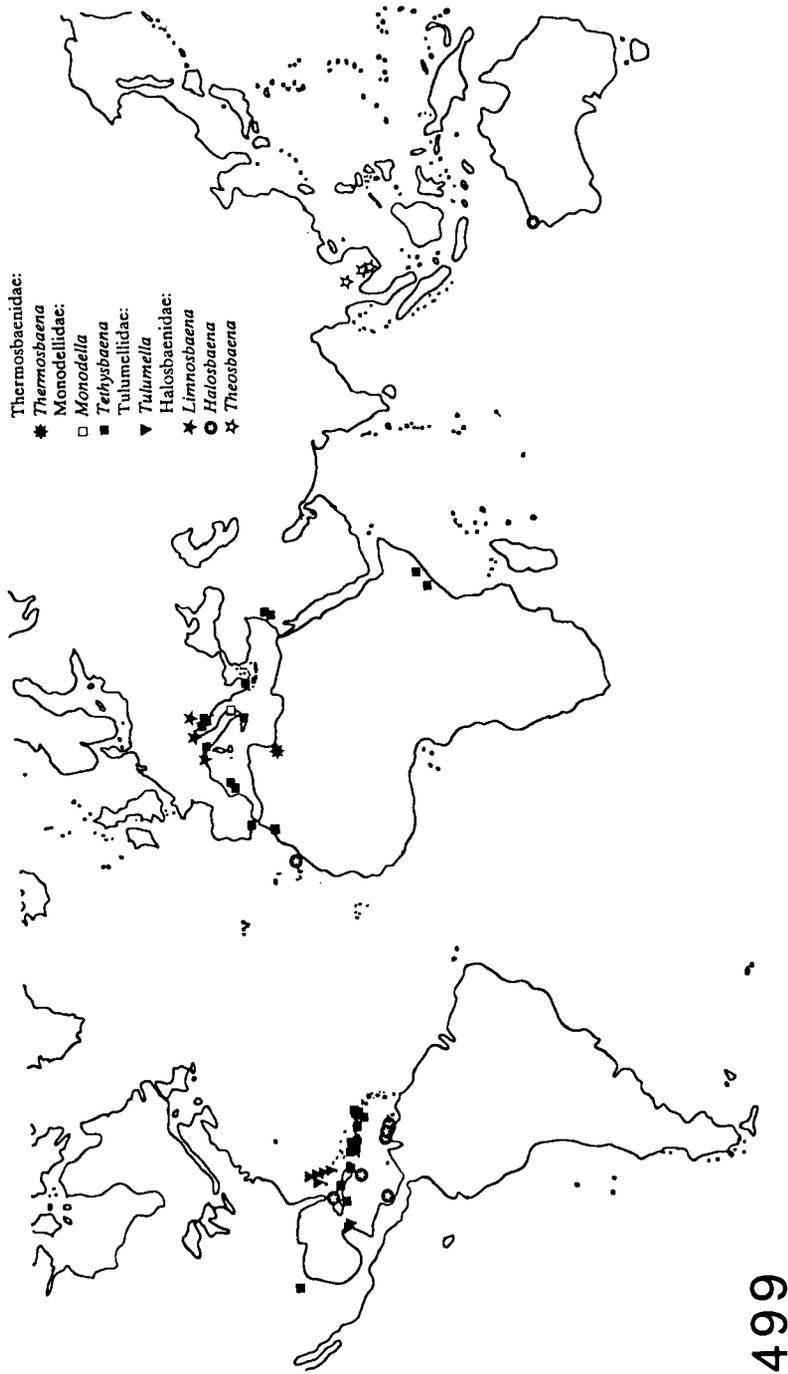


Fig. 499. Distribution of the Thermosbaenacea.

(44.5–48°C) brackish water. Actually, the scenario of *Monodella stygicola* can be seen in the same perspective. Here, as well, for some local reason a unique, species evolved after its stranding in the Pliocene. It must be emphasized, however, that for both *Thermosbaena mirabilis* and *Monodella stygicola* not much is known about the circumstances under which they have evolved. Both appear to be a one-of-a-kind experiment of nature. It is strange, indeed, that only in this area, two unique taxa originated, each with close affinities to the same wide-spread taxon that usually exhibits such a low degree of morphological differentiation.

On the biogeography and the origin of the species-groups of *Tethysbaena* more information is available; in the following each species-group will be treated separately.

The “*T. relict*a-group”: Both *T. somala* and *T. relict*a once belonged to a single ancestral stock that entered the “Great Rift system” during a transgression in the Pliocene. Herewith the easternmost Afro-European connection was established. Later on, this system got split up by a subsequent regression followed by the vicariant evolution of the ancestral form into two distinctive species (Pór, 1963).

The “*T. argentarii*-group”: All species of the “*T. argentarii*-group” occur in deposits not older than the Pliocene, but part of these were flooded by a transgression in the Pleistocene (e.g. the habitats of *T. argentarii*, *T. scabra*, and *T. aiakos*). So it is not clear if all members of this species group originated in the same period and as a result of the same regression. The two morphological subgroups (*T. argentarii-halophila-aiakos* and *T. scabra-siracusae*) were situated in the Pliocene at either side of the not submerged central part of present-day Italy. Except for *T. argentarii*, *T. aiakos*, and *T. siracusae*, which are only known from (the vicinity of) their respective type-localities, the remaining two species occur on more than one Mediterranean island. Geological data for *T. siracusae* are not available to me. Due to the fragmentary knowledge of the distribution and paleogeological background of the larger part of the taxa from this species-group, not much can be added to extend ideas about the the Mediterranean scenario in this area. Both the remarkable distributional patterns of the Halosbaeniidae in this area, and those of stygobiont amphipods (e.g., *Pseudoniphargus*) indicate to a rather complex scenario of periods of transgression and regression, as well as other kinds of geological activity (Stock, 1980a; Notenboom, 1988c). Hence, no simple satisfactory solution based on distributional data of these thermosbaenaceans can be achieved.

The “*T. atlantomaroccana*-group”: In the late Miocene (Messinian) to Pliocene period a shallow sea formed the third Afro-European “bridge” that existed between southern Spain and Morocco (Notenboom, 1988c), so the putative ancestor of *T. atlantomaroccana* and *T. tarsiensis* must have been able to disperse freely in this area. With the regression that followed the ancestral stock was vicariantly split up, and, due to the small areas occupied, the respective refugia enclosed two different genetic lineages which eventually formed the two present species.

*Tethysbaena texana* : This species actually represents a monotypic “species-group” with very close affinities to *T. vinabayesi* from Isla de Juventud, Cuba, which also holds a position as a monotypic “species-group”. Although the Edwards Aquifer region (Texas) finds its sedimentary origin back into the Cretaceous, its fauna is supposed to be distinctly younger (Kroschewsky, pers. comm.). It is not unlikely that *T.*

*texana* got "stranded" after a Pliocene regression like the situation in the Old World. As *T. texana* shows a stronger affinity in external morphology to the Old World species than it does to the members of the geographically close "*T. sanctaerucis*-group", a common stranding scenario and -period as for the Old World species might be a realistic option.

*Tethysbaena vinabayesi* : Actually, the same story holds true for *T. vinabayesi*. This species, too, may have "stranded" after a Pliocene regression. It shows a far greater similarity to the Old World species than to its other Caribbean congeners.

The "*T. sanctaerucis*-group": All members of this species-group are limited in their distribution to the Greater Antilles (Cuba, Hispaniola, Puerto Rico, and the Virgin Islands). Except for *T. juriaani*, all species have entered their present habitat not before the Pleistocene or even the Holocene. Thus, most of the species of this species-group have been "stranded" during later regressions than the members of all other species-groups. At the base of this species-group the putative ancestor of *T. juriaani* (and other derived species) holds a key position in the evolution of the "*T. sanctaerucis*-group", as it is the only species that possibly got "stranded" by a Pliocene regression. The next successive "stranding" period took place during the Pleistocene on Cuba, Puerto Rico, and the Virgin Islands; the second-next period in which species got settled took place during the Holocene on Hispaniola, during a strong orogenesis (uplift) which created in some parts of the island new barriers that led to an radiation into three species (*T. haitiensis*, *T. juglandis* and *T. gaweini*). The apparently vicariant, relict, and exclusively subterranean distribution, along with the phylogeny and the considerable number of Caribbean records, makes this species-group, together with the data provided by the Tulumellidae and Halosbaenidae, a suitable tool for testing the evolutionary scenario of the Caribbean region, which will be discussed towards the end of this chapter (see § 6.3.).

## 6.2.2. Biogeography of the Tulumellidae

The distribution of the Tulumellidae (fig. 499), as far as known at present, is limited to the Yucatan Peninsula and the off-coastal Cozumel island, both Mexico, and the Bahamas (Grand Bahama, Abaco, South Andros, Cat Island, and Long Island). Similar "tracks" have been observed for other stygofaunal elements by Holsinger (1989, 1992). He ascribes the origin of this pattern to the (vicariant) fragmentation of earlier, continuous ranges of putative ancestors, whose common areas of endemism were affected by the same isolating events. These events happened at various times during the Tertiary between 48 and 7 million years ago (Holsinger, 1992). The colonization by the present faunas took place approximately during the Pleistocene. A similar distributional pattern was observed by him for the remipede *Speleonectes*, the cirrulanid isopod *Bahalana*, the amphipod *Bahadzia*, the decapod shrimp *Agostocaris*, and the ostracod *Danielopolina*. However, some of those animals have more extensive distributions, as e.g. *Bahadzia* in southwestern Haiti (Hispaniola), *Danielopolina* in northern Cuba (this latter genus, together with *Speleonectes*, even occurs on the other side of the Atlantic Ocean on Lanzarote, Canary Islands, as well). The locality of *Danielopolina* in the Matanzas Province coincides with the occurrence of *Halosbaena* (Halosbaenidae), a genus that also occurs in the same lava tunnel on Lanzarote where

*Danielopolina* and *Speleonectes* are found. Thus, the distributional "tracks" of Holsinger must be seen and discussed in a definitely wider scope, i.e., corresponding with the synthesis of the geological history and biogeography of the Caribbean region as initiated by Rosen (1976, 1978, 1985). This aspect will be dealt with towards the end of this chapter, where also the information on all other Caribbean thermosbaenaceans will be incorporated (see § 6.3.).

### 6.2.3. Biogeography of the Halosbaenidae

Contrary to the distributional pattern of the Monodellidae, the distribution of members of the Halosbaenidae (fig. 499) is characterized by the fact that they are as a rule confined to the southern part of the general distribution of the whole order (Wagner, 1988, 1990). However, here also exceptions do exist (viz., *Limnosbaena*), but at the time the putative ancestors of these species are supposed to have entered the northern belt of the Tethys Sea an Afro-European shallow-water connection was present. This is the same shallow part that was discussed above in the treatment of the Monodellidae and Thermosbaenidae, i.e., the connection that existed between North Africa and Europe where now Italy is present. The north of present Italy was submerged at that time and the putative ancestor of the recent species of *Limnosbaena* was distributed from Bosnia-Herzegovina to southern France. With the regression of the sea (and uplift of the continent ?) during the Pleistocene, the ancestor of *Limnosbaena* survived in the ground water but got isolated at both sides of Italy and speciated into the present two species.

Not much can be said, unfortunately, about the monotypic genus *Theosbaena*, which inhabits cave lakes of Holocene age in southeast Asia, as information on the Asian stygofauna is still very scarce. This is also an exceptional taxon that does not occur on the southern part of the Tethys Sea.

The only genus with a very wide range is *Halosbaena*. Although only three species are known, their presence in northwestern Australia and at both sides of the Atlantic (Canary Islands and Caribbean) clearly indicates that the group has an ancient history that goes back into the Mesozoic. Poore & Humphreys (1992) showed that northwestern Australia is a remnant of the eastern Tethys belt. The present northwestern Australian stygofauna is supposed to have colonized the groundwater in the late Pleistocene. Both *H. fortunata* (Canary Islands) and *H. acanthura* (Antilles) thus represent descendants derived from ancestors that were distributed along the southern Tethys belt. It is suggested that *H. fortunata* colonized the Lava Tunnel and the island's interstitial realm quite recently, i.e., in the Holocene. The scenario for *H. acanthura* is a more difficult puzzle, as the coral shingle it inhabits is generally not older than the Holocene, while the «grieta» at Cuba dates back to Pliocene or Pleistocene times, and the cave lakes are formed in between the Miocene or the Pleistocene. At Curaçao, the species is even found in the interstitium at the bottom of the sea (-4 m). Most probably, this species initially entered the present groundwaters in the Pleistocene, as was suggested before by Stock (1976). The distribution may then satisfactorily be explained by assuming a later stranding at the «grieta» than its formation, and a more recent colonization of the Holocene deposits. *Halosbaena* can be incorporated into the generalized "tracks" of Holsinger (1989, 1992). This would lead

to two conclusions: (1) Both *Tulumella* and *Halosbaena* entered the present groundwater biota simultaneously, and (2) their distributions then partially overlapped, illustrated by the presence of other faunal elements (*Speleonectes*, *Danielopolina*) that got stranded approximately at the same period and co-occur to date with both thermosbaenacean taxa. Actually, if this is true, it would only be a matter of time that *Speleonectes* will be discovered in the Matanzas Province of Cuba, and in Northwest Australia. Also the presence of *Danielopolina* in Northwest Australia may then be expected.

### 6.3. Caribbean biogeography exemplified by the Thermosbaenacea

As referred to above, and stated in previous papers (Wagner, 1988, 1990), the wealth of distributional data on the Thermosbaenacea in the Caribbean provides us with a tool to assess the evolution of this area by using the phylogeny of the order. However, before entering the discussion on the biogeographic model of the Caribbean initiated by Rosen (1976, 1978, 1985), some attention must be given to the phylogenetic tree obtained in the previous chapter.

#### 6.3.1. The balance between phylogeny and biogeography

Before one turns to discussing the historical biogeography of any area, one must be sure that the synthesis of past geological events and the phylogenetic tree will accurately reflect the evolution of the studied group in terms of time and space.

As for the time argument, there is no great conflict with the phylogenetic tree of fig. 498. *Thermosbaena*, *Monodella*, and the putative ancestors of all species-groups of *Tethysbaena* were already present at least in the Pliocene, but undoubtedly find their origin further backway, in the Mesozoic. For the Tulumellidae and the Halosbaeniidae, on the other hand, no older evidence can be produced than the Pleistocene. But, do we need such evidence? Admittedly, there is no fossil record that supports any age of the groups at all. Yet, the periods mentioned above are always minimal time scales, as the animals had to be present on their Pliocene marine locations before they could get "stranded". Fossil remains of Thermosbaenacea will probably never be found, as the cuticula is too thin to survive a complete process of fossilization. The genera *Halosbaena* and *Tethysbaena* are so wide-spread that a Mesozoic origin in the former Tethys Sea is highly probable. Moreover, these genera have not changed appreciably since they entered the present groundwater biotas. The divergence process at the generic level must be very slow in the ground water, an observation that has been made earlier for other stygobionts in general (Sterr, 1973; Stock, 1977, 1980a, 1990, 1993; Notenboom, 1991; Holsinger, 1991). What about dispersal? The dispersal capacity of most groundwater animals is extremely poor: they produce very few eggs, have no free-living larval stages, are unable to compete with epigeal animals, can neither raft on driftwood, or tree-trunks, nor are they likely to get airborne. The Thermosbaenacea are no exception to this rule. It is even improbable that the freshwater species are capable of surviving contact with sea-water to migrate from one island to another. So, the present-day distribution of the Thermosbaenacea is most likely to reflect the pattern of their ancestors, expected to date back to the

Mesozoic. The present phylogenetic tree, indeed, does present a realistic picture of the geological/vicariance events in time (fig. 500), although the events evoking the branching off of *Tethysbaena*, *Monodella* and *Thermosbaena*, must have happened distinctly earlier than the Pliocene. The branches at the specific level are somewhat younger in time, up to Holocene in age.

The same phylogenetic tree can be replaced by distributional data (fig. 500). Except for the monospecific taxa (*Thermosbaena*, *Monodella* and *Theosbaena*) a reasonable tree is obtained for the distribution of *Halosbaena* and *Tulumella*. The supposedly closest related species correspond with areas that are closest to each other in space. In the tree of *Tethysbaena* this is not the case. At the species-group level, we find the "*T. relict*a-group" closer to the "*T. sancta*crucis-group" than to the other groups. Here, a problem in the phylogenetic tree is demonstrated. Actually, there are a number of quite unique characters shared by the species of the "*T. relict*a-group" (aut-apomorphies for this species-group), but the computer program's search for similarity does not value these characters as it is only comparing (apparently) similar characters which have been selected for the data-matrix. It is true, that in both the "*T. relict*a-group" and the "*T. sancta*crucis-group" the telson is somewhat concave at the terminal margin, and that anal lobes protrude, but the nature of these characters is homoplastic rather than homologous. An earlier branching off corresponding to an "older" and "more primitive place" for the "*T. relict*a-group" in the phylogenetic tree, would presumably be a better representation of the truth. At the species level, a strange picture is achieved in the "*T. sancta*crucis-group". The position in the phylogenetic tree of *T. scitula* and the four species from the Dominican Republic does not coincide with the order of the breakup of the islands of the Greater Antillean Arc, but the successive stranding of the Thermosbaenacea and breaking up of this arc does not necessarily follow a simultaneous pattern. If one accepts *T. juriaani* (southern Dominican Republic) as oldest representative of the species-group, its position in the tree is not unexpected, and certainly the position *T. gaweini* (northern Dominican Republic) is as close as possible to what can be expected since both are from the same island. The presence of both *T. juglandis* (endemic in a small area in the northwest of Haiti) and *T. haitiensis* (central and southeastern Haiti) at the opposite branch alludes to the development of other specific characters independent of those of *T. juriaani* and *T. gaweini*. As stated above in my discussion on the biogeographic patterns in the Monodellidae, it is supposed that formation of new taxa in the "*T. sancta*crucis-group" occurred more than once. The quite recent radiation of taxa in Hispaniola most probably blurs this part of the phylogenetic tree. If we consider the small random changes which occurred in the vicariantly isolated population(s) of the putative ancestor(s) of this species-group, mosaic evolution may be expected, whence an equivocal pattern is likely to result. Apart from the Hispaniolan taxa, the position represented by *T. scitula* (Virgin Gorda) is difficult to interpret, as it shows a close similarity to *T. gaweini*, which may, however, be based on convergence rather than on true relationship. So some wrinkles are bound to be present in the phylogenetic tree as here constructed. On the basis of the present information it can be concluded that the phylogenetic pattern found merely is a simplified model, and that the actual phylogenetic relationships are more complex than the model presents. Yet, bearing the above mentioned objections in mind, the present results suffice to use the larger part of the tree for a discussion on the historical biogeography of the Caribbean.



Fig. 500. Distributional and geological data of the corresponding taxa from the proposed phylogenetic tree of fig. 498.

### 6.3.2. Historical biogeography of the Caribbean region

The hypothesis on the evolution of the Caribbean region entered a new phase when Rosen (1976, 1978, 1985) proposed a biogeographic model based primarily on the "vicariance" concept. Up till then, one was inclined to explain the zoogeographic patterns found on the basis of dispersal only (Matthew, 1918; Richards, 1937; Simpson, 1956; Darlington, 1957). Rosen's model was inspired by the works of Croizat (1958, 1964), Nelson (1974) and Croizat, Nelson & Rosen (1974). As, initially, his model left only minimal space for dispersal explanations, a strong controversy between the two models followed (McDowall, 1978; Pregill, 1981; Hedges, 1982). MacFadden (1980, 1981) and Stock (1981a) pleaded in favour of a combination of dispersal and vicariance models to explain the various distributional patterns. Stock demonstrated that certain groups probably got their present distribution by vicariance, while for other groups dispersal played an important role. As noted above, distributional patterns of stygobionts, like the Thermosbaenacea, can best be explained by assuming that the ancestor of the group was distributed along the shores of the Tethys Sea before the opening of the Atlantic in the Mesozoic, and that the taxa became primarily isolated by vicariance through Mesozoic and Tertiary plate tectonics. The idea of this concept was proposed by Sterrer (1973) for interstitial sand faunas and has not yet lost any of its value today. The Regression Model of Stock (1980a) conveniently refined this idea to a detailed level. All these theories combined into one picture, not only horizontal movements (plate tectonics), but also vertical movements (sinking and uplift of land, and transgressions and regressions of the sea) occurred, this may be found reflected in the recent distribution of the Caribbean fauna. Based on Malfait & Dinkelman's (1972) geological evidence, Rosen (1976) proposed a "proto-Antillean archipelago" or "Caribbean Plate" (= Greater Antillean Arc of Malfait & Dinkelman, 1972) that drifted eastwards when the North and South American tectonic plates separated in the late Mesozoic. The "proto-Antillean archipelago" was bordered by two decoupling faults. As the relative westward drift of the North and South American plates continued a new fault zone appeared between the two decoupling faults and the "proto-Antillean archipelago" got divided into the ancestral Greater Antilles and the Lesser Antillean subregions. A change in the orientation of the northern fault isolated proto-Cuba and formed the Puerto Rican Trench. In the Late Tertiary the Aves ridge was formed and East and West Cuba united into one island. Whether Jamaica had an East-West migration (as suggested by Hedges, 1982), a West-East migration (Donnelly, 1988), or Jamaica and the southwestern peninsula of Haiti formed a part of the Caribbean Plate (Durham, 1985), remains a matter to be solved.

If we look at the patterns of the various Caribbean thermosbaenaceans we can recognize two groups, viz., one of northern Tethyan elements (*Tethysbaena*) and one representing southern (and western) Tethyan elements (*Halosbaena* and *Tulumella*). Undoubtedly the invasion and settlement of *Tethysbaena* spp. in their present refugia is the result of vicariance, as these freshwater animals have lost any ability to disperse through the marine waters of the Caribbean sea. Thus these northern Tethyan elements are true indicators for those islands that were once part of the northern Caribbean Plate (or proto-Greater Antilles). *Halosbaena*, by contrast, is an indicator for

those islands that are formed in an area of southern Tethyan origin, like Curaçao, Bonaire, Las Aves (Venezuela), and San Andres Island (Colombia). None of these islands are part of the South American Plate, but instead are considered chips of a Southern Antillean "Plate" or are younger of age. Noteworthy is the presence of *Halosbaena* in the north of western Cuba and on Jamaica. If *Halosbaena* indeed is an indicator for islands with a southern Caribbean (or Tethyan) origin, these islands (or parts of them) never formed part of the Northern Caribbean Plate or proto-Greater Antilles. Rauchenberger (1988), after an analysis of twelve groups of freshwater fishes, reached the very same conclusion: Western Cuba and Jamaica represent a southern Tethyan element. She also suggested that the southwestern peninsula of Haiti represents a part with a southern Tethyan origin. This point of view cannot be supported by evidence from the Thermosbaenacea. However, Stock (1985) discussed the close relationship of the amphipod *Bogidiella (Mexigidiella) hamatula* Stock, 1985, with the other members of its subgenus in Central America. He (Stock, pers. comm.) accepted the occurrence of this amphipod in southwestern Haiti as evidence for a possible southern Tethyan origin of its peninsula, the more so as Thermosbaenacea are absent in this part of the island.

Contrary to the results of Rauchenberger (1988), who suggested a southern origin for Isla de Juventud, the thermosbaenacean occurring there, viz., *Tethysbaena vinabayesi*, points to an origin from the northern Caribbean Plate. Here, biological evidence clearly is contradictory, whence a definitive conclusion must remain open to debate for the time being.

Species of *Tulumella* have some intermediate position in a rather broad sense. Not only have the animals intermediate characters between Monodellidae and Halosbaenidae, or northern Tethyan and southern Tethyan elements, but they also show overlap in distribution. Generally the Bahamas are considered parts that originated from the northern "plate" (although Freeland & Dietz (1972) show the Bahama platform close to the South American Plate) while Yucatan, Mexico, clearly is of southern origin. Therefore I am inclined to consider *Tulumella* primarily a western element of the Tethys Sea belt, with its northern limits in the Bahamas, its southern limits in central America. This means that it can be considered an intermediately distributed group with a closer relation to the Southern Caribbean Plate than to the Northern Caribbean Plate. This point of view is also supported by the accompanying stygofauna observed.

My conclusions thus are, that the biogeographic model of the Caribbean region as suggested by Rosen (1976, 1978, 1985) fairly well coincides with the distributional patterns of the Thermosbaenacea in that area. However, the western part of Cuba and Jamaica can never have been part of the northern Caribbean Plate, as evidenced by the distribution of *Halosbaena acanthura*. Also, the origin of Isla de Juventud (south of Cuba) is uncertain, as biological evidence (Thermosbaenacea versus freshwater fishes) is contradictory. The origin of the southwestern peninsula of Haiti cannot be established by evidence derived from the Thermosbaenacea, although the results of previous studies (Stock, 1985; Rauchenberger, 1988) seem to support a southern origin.

#### 6.4. Difference in faunal diversity between Cuba and Hispaniola

To conclude this chapter a strange phenomenon noted by Stock (1981b, 1983a, 1983b, 1985) will be discussed briefly. Stock noticed that Cuba (114.500 km<sup>2</sup>) despite its larger size showed a lower (endemic) faunal diversity than Hispaniola (77.280 km<sup>2</sup>). This cannot be explained by Hispaniola being a composite island, as the same holds true for Cuba. To consider Hispaniola as a migration route for stygofauna is also highly unlikely as most stygofauna distributional patterns are the result of vicariance. The actual reason might be, that Hispaniola shows a distinctly more complex orogenesis than Cuba. Cuba has one central mountain ridge, while in the Dominican Republic four ridges diverge from the Cordillera Central. As a result, isolation events must have been more frequent on Hispaniola than on Cuba. The larger diversity of *Tethysbaena* on Hispaniola, with four species (all vicariantly isolated by mountain ridges), as compared to Cuba, with two species (isolated by a single mountain ridge), is illustrative of this view.

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