Allocation of the Mantridae Leigh-Sharpe to the Cyclopoida (Crustacea: Copepoda) with notes on *Nearchinotodelphys* Ummerkutty*

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Abstract

Mantra speciosa Leigh-Sharpe, 1934 (*ex* Poecilostomatoida), collected during the Siboga Expedition is redescribed on the basis of the holotype female. The 15-segmented antennule and the gnathostomous nature of the mouthparts exclude the Mantridae from the Poecilostomatoida and point to a relationship with the tunicate-infesting families Ascidicolidae, Notodelphyidae and Archinotodelphyidae (Cyclopoida). *Nearchinotodelphys indicus* Ummerkutty, 1960 (*ex* Archinotodelphyidae) is transferred to the Mantridae. It is suggested that the bivalve-inhabiting mantrids have diverged from the ascidicolous lineage leading to the Notodelphyidae and Ascidicolidae.

Résumé

Mantra speciosa Leigh-Sharpe, 1934 (*ex* Poecilostomatoida) est redécrite à partir de l'holotype femelle récoltée lors de l'Expédition Siboga. L'antenne antérieure de quinze articles et la nature gnathostome des pièces buccales excluent la famille des Mantridae de l'ordre des Poecilostomatoida, et indiquent une affinité aux familles ascidicoles des Ascidicolidae, Notodelphyidae et Archinotodelphyidae (Cyclopoida). *Nearchinotodelphys indicus* Ummerkutty, 1960 (*ex* Archinotodelphyidae) est transférée dans la famille des Mantridae. On suggère que la famille des Mantridae, infestant des Bivalves, a divergée de la lignée ascidicole comprenant les Notodelphyidae et les Ascidicolidae.

Introduction

Among the commensal and parasitic Copepoda obtained during the Dutch Siboga Expedition conducted in the East Indies in 1899–1900, a remarkable copepod was discovered in the bivalve *Chama* sp. for which Leigh-Sharpe (1934) coined the name *Mantra speciosa*. Leigh-Sharpe also created a new family Mantridae to accommodate *Mantra* and referred it to the suborder Cyclopiformes without discussing the possible relationships except for pointing out that the antenna recalls that of the Clausidiidae Embleton, 1901.

In spite of its doubtful position, the family Mantridae was generally not considered in later reviews of copepods associated with marine invertebrates (e.g. Lang, 1948; Gotto, 1979). This is probably due to the very inadequate and fragmentary description provided by Leigh-Sharpe. In recent literature the Mantridae are often listed as a family of the Poecilostomatoida (Bowman & Abele, 1982; Schram, 1986). This view was discounted by Humes (1987) when he described *Erebonaster protentipes* from deep-sea hydrothermal vents and subsequently discussed other poecilostomatoids showing an allegedly vestigal mandibular palp. Referring to an earlier re-examination of the holotype of *Mantra speciosa*, Humes (1987) concluded that no Poecilostomatoida are concerned and *Mantra* might instead be allocated to the Cyclopinidae Sars, 1913 within the Cyclopoida. This conclusion is based on the gnathostomous nature of the mouthparts and the armature and/or segmentation of leg 1 and leg 5. In fact, Leigh-Sharpe's (1934) illustration of

the 11-segmented antennules raises grave doubts as to the taxonomic position of the species because Poecilostomatoida have at most 7 segments in this appendage.

In order to reveal the relationships of *M. speciosa*, a redescription is given on the basis of the holotype female preserved in the Zoölogisch Museum of Amsterdam.

Material and methods

Leigh-Sharpe (1934) pointed out the bad condition of most of the Siboga material because of the 34 years gap between the collection and the examination. The holotype of *M. speciosa* (ZMA Co. 102.604) consisted of a whole mount in euparal. Dissolving of the embedding medium in acetone however, revealed the specimen to be in a nearly perfect condition. After dissection in lactic acid the dissected parts were placed in polyvinyl lactophenol mounting medium on 13 slides. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd., Poole, England). All drawings have been prepared using a camera lucida on a Leitz Dialux 20 interference microscope. The setae of the caudal rami are named and numbered as proposed by Huys (1988). Abbreviations used in the text are: P1–P6, first to sixth thoracopods; exp., exopod; enp., endopod; exp(enp)-1(-2, -3), to denote the proximal (middle, distal) segment of a ramus. The segmental composition of the mandible and maxilliped are followed according to Boxshall (1985: 341–345).

Taxonomy

Order CYCLOPOIDA Burmeister, 1834

Family MANTRIDAE Leigh-Sharpe, 1934

Diagnosis. – Cyclopoida. Genital and first abdominal somites fused in female. Anal operculum vestigial. Caudal rami with 6 setae. Sexual dimorphism in antennule, maxilliped (unconfirmed in *Mantra*), P5, P6, and in genital segmentation.

Rostrum well developed, recurved, fused at base. Antennules without aesthetascs, 15-segmented in female, 14-segmented and unigeniculate (geniculation between segments XII and XIII) in male. Antenna without abexopodal seta on basis and enp-1 (or allobasis); exp. represented by 2 long setae; enp-2 with 5 setae; enp-3 with 7 elements, innermost one forming extremely large claw, following two also long and typically bent. Labrum simple,

with spinous processes and spinules. Mandible with well developed gnathobase; palp biramous: basis with 1 seta, enp. 2-segmented (enp-1 with 4–5, enp-2 with 9 setae), exp. 4-segmented (exp-[1–3] with 1, exp-4 with 2 setae). Paragnaths weakly developed, not fused medially. Maxillula with well developed arthrite; coxa and basis fused; coxal endite unisetose, epipodite with 1–2 setae; basal endites represented by 2 and 4 setae, respectively; exp. quadrisetose; enp. unisegmented, with 9 setae. Maxillary syncoxa with 4 endites (4, 1, 2 and 3 setae); basis produced into claw-like endite; enp. 3-segmented. Maxilliped 3-segmented; synxoca with 3 endites (1, 3, 2 setae); basis with 1 seta; enp. with 5–6 setae.

P1 to P4 biramous with 3-segmented rami; seta- and spine formulae of rami as follows:

	exopod	endopod
P1	I-1; I-1; III,I1,3	0–1; 0–2; I,2,3
P2 & P3	I-1; I-1; III,I1,4	0–1; 0–2; I,2,3
P4	I-1; I-1; II,I1,4	0–1; 0–2; I,2,2

Coxa of P1–P4 with inner seta; basis P1 with inner spine.

P5 laterally displaced; 2-segmented; distal segment with 4 setae in both sexes.

Genital pores laterally displaced in female, covered by vestigial P6 with 2–3 spinules. Seminal receptacles laterally located, connected with midventral, unpaired copulatory pore via transverse copulatory ducts. Male P6 symmetrical, ventrally located; with 3 setae each.

Living in mantle-cavity of bivalved molluscs.

Type genus. – *Mantra* Leigh-Sharpe, 1934.
Other genus. – *Nearchinotodelphys* Ummerkutty, 1960.

Genus *Mantra* Leigh-Sharpe, 1934.

Diagnosis. – Cf. Table I.
Type species. – *Mantra speciosa* Leigh-Sharpe, 1934 (by monotypy).

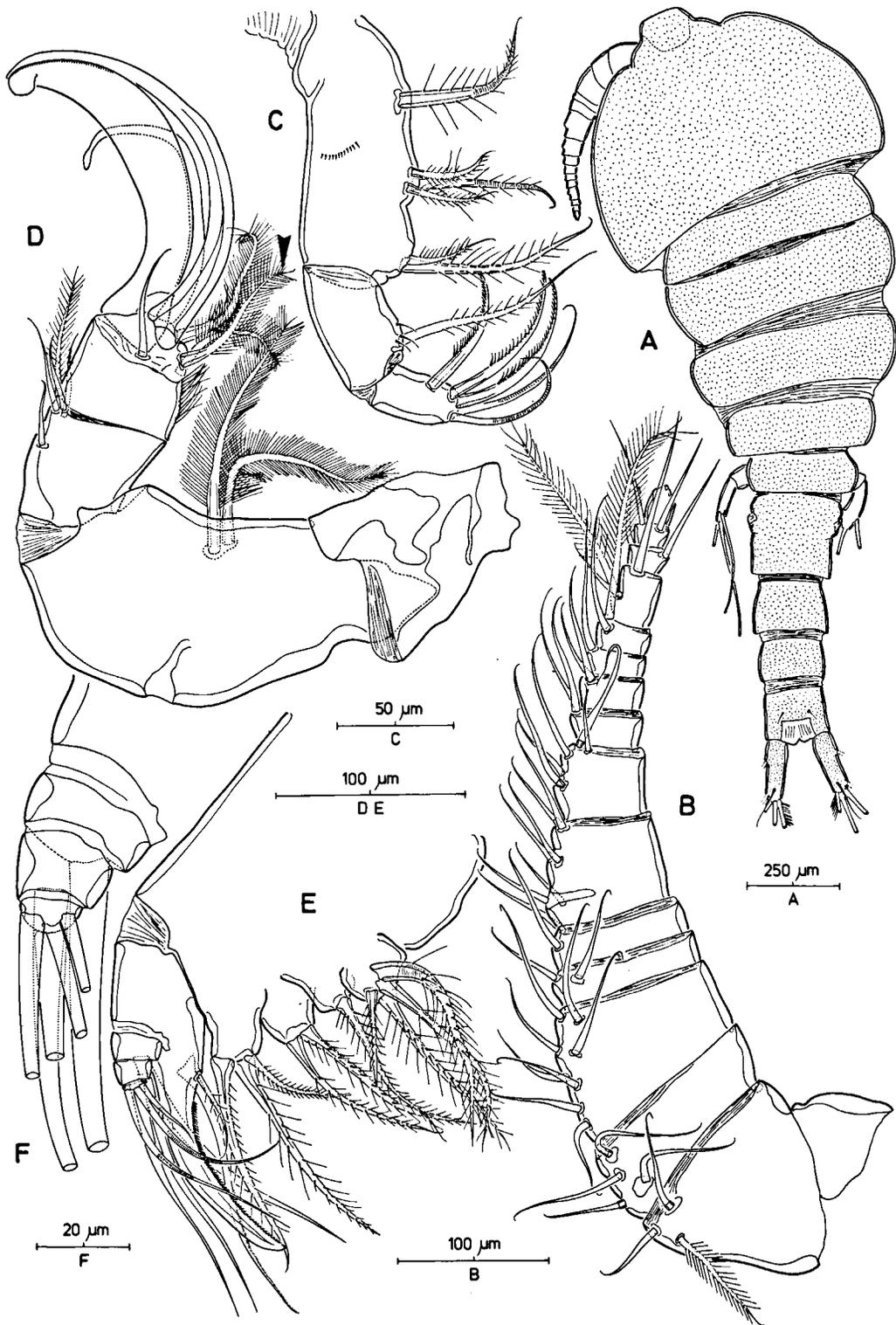**Mantra speciosa** Leigh-Sharpe, 1934.
(Figs. 1A–F; 2A–G; 3A–E)

Fig. 1. Mantra speciosa Leigh-Sharpe, 1934. Female: A, habitus, dorsal view; B, antennula; C, maxilliped; D, antenna; E, maxilla; F, maxillary endopod.

Redescription

Female:

Body length about 2.05 mm, measured from the tip of the rostrum to the posterior margin of the anal somite. Body (Fig. 1A) gradually tapering posteriorly. Maximum width measured at posterior third of cephalosome (800 μm). First pedigerous somite free, partly concealed underneath hind margin of cephalosome. Pleurotergites of thoracic somites with rounded margins, not laterally expanded. Urosome consisting of P5-bearing somite, genital double-somite and 3 equally long abdominal somites. Caudal rami (Fig. 2G) 2.7 times as long as maximum width, furnished with 6 setae of which the terminal ones (IV, V, VI) are distinctly longer than the ramus, dorsal seta (VII) bi-articulated at base.

Rostrum (Fig. 1A) ventrally directed, recurved; fused at base; without sensillae. Antennules (Fig. 1B) 15-segmented, shorter than cephalosome. Segment VI showing trace of subdivision. No aesthetascs. Armature as follows: I-[1 plumose + 2]; II-4; III-8; IV-2; V-2; VI-6; VII-5; VIII-2; IX-2; X-1; XI-[1 plumose + 1]; XII-[1 plumose + 2]; XIII-2; XIV-2; XV-? (armature of XIII–XIV is possibly incomplete). Antenna (Fig. 1D) 4-segmented; coxa-allobasis joint complex; allobasis with trace of original subdivision, without abexopodal setae; exp. represented by 2 long plumose setae; enp. 2-segmented, enp-1 with 5 setae, enp-3 with immense, blunt claw at the inner distal corner, 2 curved strong spines and 4 setae (3 plumose, 1 naked). Labrum (Figs. 2D–E) a broad, simple lobe; with spinous process on either lateral corner; anterior face armed with long spinules and 2 smaller spinous processes. Mandible with richly ornamented gnathobase (Fig. 2C); palp biramous (Fig. 2B); basis with 1 plumose seta; exp. 4-segmented with 1 seta on exp-1 [1–3] and 2 setae on exp-4; enp. 2-segmented, with 5 setae on enp-1 and 9 setae on enp-2. Paragnaths weakly developed, completely separate lobes with numerous small spinules at the outer surface (Fig. 2E). Maxillula (Fig. 2A) with 9 spines/setae on precoxal arthrite; coxa and basis fused but enp. and exp. defined at base; coxo-

endite a small unisetose process; epipodite (coxo-exite) with 1 short and 1 long seta; basal endites vestigial, represented by 2 and 4 setae, respectively; enp. unisegmented, with 5 lateral and 4 terminal setae; exp. quadrisetose. Maxilla (Fig. 1E) with 4 lobate endites on syncoxa, bearing 4, 1, 2, and 3 setae, respectively; basis largely produced into claw-like endite with 2 setae at the base; enp. 3-segmented (Fig. 1F), enp-1 with 1, enp-2 with 1 and enp-3 with 4 setae. Maxilliped (Fig. 1C) with precoxa and coxa fused into syncoxa bearing 3 vestigial endites bearing 1, 3 and 2 setae, respectively; basis with 1 seta; enp. 1-segmented, with 3 pinnate spines and 2 geniculate setae.

P1 to P4 (Figs. 3A–C) with seta- and spine formulae typical of the family. Basis without outer seta. Precoxa (Fig. 3C) represented by triangular sclerite. Coxa and basis with few minute spinules at anterior surface. Exopodal spines of P1 (Fig. 3A) with terminal flagella. Intercoxal sclerites unarmed (Fig. 3A).

P5 (Fig. 2F) 2-segmented with area of hyaline membrane between the segments; laterally displaced (Fig. 1A); basal segment without setae; distal segment with 3 setae in the present material but a scar indicates a total number of 4.

P6 (Fig. 3D) vestigial, represented by small oval plate closing off lateral gonopores and armed with 2 spinous processes (setae). Seminal receptacles laterally located near the genital antra; connected with midventral copulatory pore via transverse sclerotized spermathecal ducts. Copulatory pore (Fig. 3E) minute, located in midventral, thin-walled depression near the anterior margin of the genital double-somite, and flanked by 2 secretory pores.

Male: Unknown.

Remark. – The middle and distal endites of the maxillipedal syncoxa can have either 2 or 3 setae.

Type locality. – Siboga Expedition, Station unknown (Indonesia).

Discussion
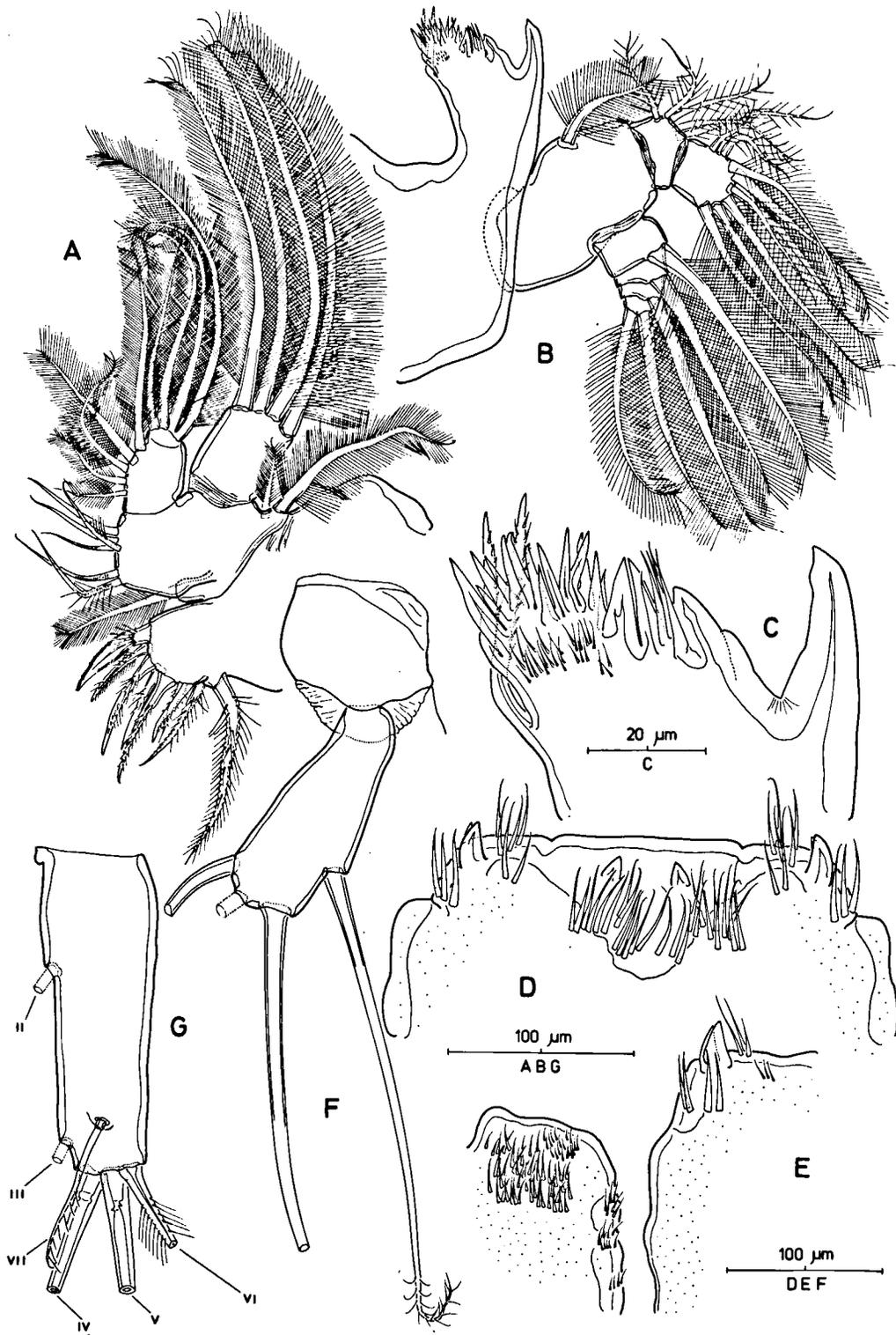
The present redescription justifies Humes' (1987)

Fig. 2. Mantra speciosa Leigh-Sharpe, 1934. Female: A, maxillula; B, mandible; C, gnathobase of mandible; D, labrum, anterior view; E, labrum and right paragnath, lateral view; F, P5; G, caudal ramus, dorsal view.
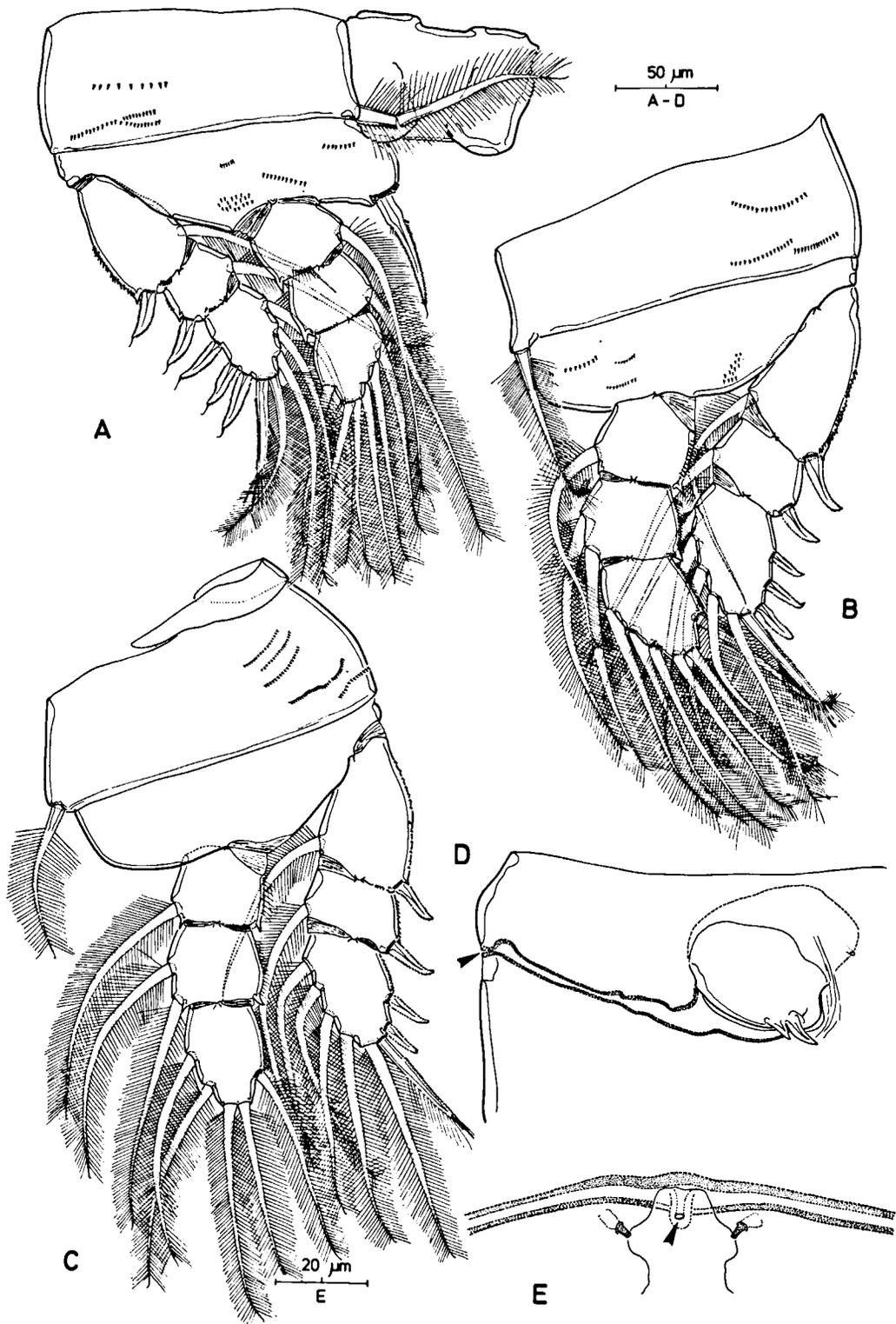
Fig. 3. *Mantra speciosa* Leigh-Sharpe, 1934. Female: A, P1, anterior view; B, P2, anterior view; C, P4, anterior view; D, genital pore with P6 and copulatory duct, lateral view; E, area around copulatory pore. Arrows in Figs. D and E indicating copulatory pore.

suggestion to place *M. speciosa* in the Cyclopoida. The 15-segmented antennule and the primitive design of the mouthparts exclude the species from the poecilostomatoids. It is also impossible to assign *M. speciosa* to the Siphonostomatoida because of the absence of a distinct siphon or mouth cone (cf. paragnaths not fused). In his phylogenetic analysis of the cyclopoid families, Ho (1986) revealed that the Lernaeidae, Ascidicolidae, Archinotodelphyidae and Notodelphyidae are separated from the free-living families by one synapomorphy, being possession of a terminal claw on the antenna. This claw is homologous with the innermost terminal seta of the distal enp. segment in the Oithonidae, Cyclopinidae and Cyclopidae. This structure is extremely developed in *Mantra speciosa*, suggesting a relationship of the Mantridae with the cluster of parasitic families within the Cyclopoida as defined by Ho (1986).

The boundaries of the Cyclopinidae, Notodelphyidae and Archinotodelphyidae have been discussed meticulously by Illg (1955) and Dudley (1966), but despite a certain deal of overlap in the respective diagnoses both authors believed that the separate status of the families should be maintained. Lang (1949) created the Archinotodelphyidae to accommodate the newly described *Archinotodelphys typicus* Lang, 1949 and *Cyclopina phallusiae* Hansen, 1934 which was placed in a second genus *Pararchinotodelphys* Lang. Since then only a few other archinotodelphyids have been described (Illg, 1955; Monniot, 1968; 1988). These ascidicolous copepods lack the dorsal incubatory pouch which presents a diagnostic apomorphy for the Notodelphyidae since it is not homologous with structures serving the incubatory purposes in the Ascidicolidae in general (pediform projections), or in the Buprorinae in particular (internal incubatory cavity) (Illg & Dudley, 1980). The latter family represents the final stage in the evolution of the ascidicolous cyclopoids and it shows such a reduction in number of segments and armature elements that it does not merit being discussed in this context.

Conversely, the Mantridae might be closely related to the Archinotodelphyidae and this is best exemplified by *Nearchinotodelphys indicus* Ummerkutty, 1960. This species does not only differ from

the other archinotodelphyids in being an associate of the boring bivalve *Lithophaga straminea* (Reeve, 1857) but also in having an enormous claw on the antenna. These differences led Monniot (1968, 1988) to suggest that *N. indicus* should be excluded from the family but no alternative was proposed as to its taxonomic position. The new information on *Mantra* clearly corroborates Monniot's opinion. A comparison of the cephalothoracic appendages leaves no doubt that *Nearchinotodelphys* belongs to the hitherto monotypic Mantridae. The diagnostic characters of the two genera are summarized in Table I.

Over 200 species of copepods − the vast majority belonging to the Poecilostomatoida and Siphonostomatoida − are known to live in various degrees of association with molluscs (Humes, 1985). Within the Cyclopoida however, most associates are known as endoparasites of ascidians or as parasites of freshwater fish. The Mantridae are the only cyclopoids known from bivalve hosts and until the very recent discovery of the Ozmanidae (Ho & Thatcher, 1989) they also constituted the only cyclopoid associates of the entire phylum. The latter family was proposed to accommodate the interesting endoparasite *Ozmana haemophila* Ho & Thatcher, recovered from the hemocoel of the freshwater opisthobranch snail *Pomacea maculata* Perry, 1810 collected near Manaus, Brazil.

The position of the Ozmanidae within the Cyclopoida is somewhat problematic. Ho & Thatcher (1989) placed the family in the parasitic clade because of the presence of terminal claws on the antenna. The strongest claw present on the antennary endopod of *O. haemophila* is not homologous with the terminal hook of the Mantridae, Lernaeidae or ascidicolous families, but is a positional homologue of the second outermost seta found in these families (and arrowed in Fig. 1D). Conversely, the homologue of the terminal claw in these families is the smallest element in the Ozmanidae, and the presence of additional claws both apically and along the abexopodal margin might indicate that the claw-like shape of this element is due to parallel evolution.

In their cladogram of the cyclopoid families, Ho & Thatcher (1989) defined the Notodelphyidae/

Table I. Diagnostic features of *Mantra* Leigh-Sharpe and *Nearchinotodelphys* Ummerkutty.

Mantra Leigh-Sharpe	*Nearchinotodelphys* Ummerkutty
– P1-bearing somite free	– P1-bearing somite fused to cephalosome
– Pleurotergites not laterally expanded	– Pleurotergites (P2–P4) laterally expanded
– Antenna with allobasis; enp-3 with 3 claws and 4 shorter setae	– Antenna with basis; enp-3 with 1 claw, 2 curved, strong setae and 4 shorter setae
– Mandible with 5 setae on enp-1	– Mandible with 4 setae on enp-1
– Maxillula with 2 setae on epipodite	– Maxillula with 1 seta on epipodite
– Maxilliped with 5 setae/spines on enp.	– Maxilliped with 6 setae/spines on enp.
– Basis of P1–P4 without outer seta	– Basis of P1–P4 with outer seta
– P5 without seta on basal segment	– P5 with seta on basal segment
– Caudal rami with long terminal setae	– Caudal rami with short terminal setae (longest seta little longer than half the length of the ramus)
– Host: *Chama* sp.	– Host: *Lithophaga straminea*

Ascidicolidae/Lernaeidae/Ozmanidae grouping on the basis of the 3-segmented antenna, an argument applied in much the same way by Lang (1949) but refuted by Dudley (1966) who pointed out the tetramerous condition in *Doropygopsis longicauda* (Aurivillius, 1882). The Lernaeidae and Ozmanidae were regarded as sister groups on the basis of the loss of the palp in the mandible and the maxillula. It is questionable whether these negative characters reflect real relationships in a case like this, involving two groups with an otherwise totally different morphology and biology. In lernaeids the maxillule is entirely absent, however, whether this condition has been preceded by an evolutionary loss of the palp is speculative. On the other hand, the Ozmanidae have retained the digeniculate antennules in the male. This character is also found in the Oithonidae, Cyclopidae and Cyclopinidae and probably it represents a character retained from the ancestral cyclopoid stock. At least the proximal geniculation is lost in the other families, indicating that the Ozmanidae might have diverged at an earlier stage.

The Mantridae are tentatively regarded as the sister group of the Notodelphyidae/Ascidicolidae-clade on the basis of (1) the 15-segmented antennules, (2) the 3-segmented maxilliped, (3) the reduced setation on the female P5 (maximum 4 setae). The Archinotodelphyidae are likely to be the outgroup of this cluster because of the female genital complex involving the lateral migration of the gonopores *and* the seminal receptacles which are connected with the midventral copulatory pore via

sclerotized transverse copulatory ducts. It follows that the bivalve-associated Mantridae have probably originated from a tunicate-infesting ancestral stock, rather than that the association with tunicates evolved convergently in the Archinotodelphyidae and in the Notodelphyidae/Ascidicolidae-lineage. A similar phenomenon has happened in the Notodelphyidae where some species have secondarily invaded octocorals (Stock & Humes, 1970) and (accidentally?) crinoids (Barel & Kramers, 1977), and in the Ascidicolidae where the Enterognathinae parasitize crinoids and pterobranch hemichordates (Illg & Dudley, 1980). The Lernaeidae are regarded as the sister group of this "ascidicolous" clade because of the terminal claw on the antenna and the loss of the proximal geniculation in the male antennules.

Acknowledgements

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