DISTINGUISHING THE GENERA *APOMATUS* PHILIPPI, 1844 AND *PROTULA* RISSO, 1826 (POLYCHAETA: SERPULIDAE). A FURTHER PLEA FOR A METHODICAL APPROACH TO SERPULID TAXONOMY

by

HARRY A. TEN HOVE

and

FRANS J.A. PANTUS

Ten Hove, H.A. & F.J.A. Pantus: Distinguishing the genera *Apomatus* Philippi, 1844 and *Protula* Risso, 1826 (Polychaeta: Serpulidae). A further plea for a methodical approach to serpulid taxonomy.

Zool. Med. Leiden 59 (32), 31-xii-1985: 419-437, figs. 1-7. — ISSN 0024-0672.

Key words: Polychaeta; Serpulidae; *Apomatus; Protula;* taxonomy; Mediterranean.

Ventral thoracic bloodvessel-patterns were defined in a random sample of 152 living specimens of the *Apomatus/Protula*- complex. Two main patterns and a derived one could be recognized. Eight characters, often used in Serpulid taxonomy and retraceable in preserved material, were determined too: e.g. presence or absence of an operculum and pattern of thoracic setae. These parameters were correlated to the vascular patterns.

It was shown that (a) all operculate specimens possess a vascular system of one main pattern; 86% of those closely studied have "*Apomatus*-setae" at least from setiger 4 onwards; all have radioles with paired rows of compound eyespots. (b) The non-operculate specimens generally possess the other main vascular pattern; the thorax often has limbate setae throughout (56%) or "*Apomatus*- setae" in posterior segments only (31%); 70% show paired rows of simple eyespots. (c) The depths of occurrence of operculate worms differ significantly from those of non-operculate specimens. (d) The derived vascular pattern occurs in five out of seven specimens from a depth of 200 m.

Correlation of characters clarified a long existing taxonomic problem: *Apomatus* and *Protula* are distinct taxa.

Harry A. ten Hove & Frans J.A. Pantus, Laboratorium voor Zoölogische Oecologie en Taxonomie, Rijksuniversiteit Utrecht. Present address: Instituut voor Taxonomische Zoölogie, University of Amsterdam, P.O. Box 20125, 1000 HC Amsterdam, The Netherlands.

INTRODUCTION

According to the literature distinguishing the nominal taxa *Apomatus* and *Protula* is difficult or even impossible (e.g. Fauvel, 1927: 381-385; Zibrowius, 1968: 182). This is not surprising since the original diagnoses of Risso (1826) and Philippi (1844) were scanty and did not mention the setation pattern of the worms.

Philippi (1844: 189) erected *Apomatus* (Gr.: *a* = without, *poma* = lid) to contain the nominal non-operculate genera *Protula* and *Psygmobranchus* Philippi, 1844 but also for the operculate *A. ampulliferus* Philippi (1844: 197), in his opinion a doubtful species. However, many later authors confined the use of this genus name to operculate species. Mörch (1863: 363) already noted the discrepancy, but nevertheless used the generic name for Philippi's operculate species. Consequently Quatrefages (1865: 551), Marion (1874: 401) and Marion & Bobretzky (1875: 95-96) used the name *Apomatus* for operculate forms too. Ever since the presence of an operculum in *Apomatus* and absence in *Protula* was the only difference between the two nominal genera upon which authors agreed.

Subsequent descriptions of new species in the *Apomatus/Protula*-complex have all been based upon small differences in shape of collar, numbers of branchial radioles, form of setae and uncini, etc. These differences may have been caused by varying states of preservation, variation in age of the worms, a different way of figuring or interpretation by the authors, and finally by the fact that nearly all descriptions are based on one or a few specimens at most. Beckwitt (1981: 245) warned against this practice, after an elegant study of variation in *Pileolaria* spp.

Throughout the literature statements on presence or absence of "*Apomatus*- setae" in the thorax, and on the form of abdominal setae and uncini are contradictory, and we have not been able to find even a majority point of view. Some authors believed that "*Apomatus*- setae" always occur in operculate forms and not in non-operculate forms (e.g. Saint-Joseph, 1894: 263; Soulier, 1902: 49), but others emphatically attributed these setae to non-operculate forms too (Augener, 1906: 188; Fauvel, 1910: 693-695; Hartmann-Schröder, 1971: 540). Zibrowius (1968: 119) criticized the incomplete observations of authors on absence or presence of "*Apomatus*-setae", causing considerable confusion in the nominal genera *Vermilia* Lamarck, 1818, and *Vermiliopsis* Saint-Joseph, 1894.

Hanson (1948: 581-584) observed that four distinct types of patterns could be discerned in the ventral thoracic bloodvessels, correlating with the four nominal species as hesitatingly discerned by e.g. Saint-Joseph (1895: 263) and

Fauvel (1927: 381-385). This observation has largely been neglected in the later literature.

A complicating factor is that the branchial crowns of the species in both nominal genera are readily autotomized, especially when the animals are handled roughly, as done in dredging operations or scratching tubes from rocks. Moreover the operculum may get stuck in the tube, break off and be lost, when a specimen retracts deep in its tube following disturbance. In contradistinction to other operculate genera, where the operculum is commonly borne on a special smooth peduncle, it is fixed to a normal pinnule-bearing radiole in *Apomatus*. Therefore, loss of operculum is hardly traceable in this genus, and has caused many erroneous identifications.

Since apparently Hanson's results were promising, we tried to correlate anatomical observations to some characters used in the classic descriptions, by means of a statistical approach. Ten Hove (1984) and ten Hove & Jansen-Jacobs (1984) pleaded for better and more reproduceable methods in serpulid (and polychaete) taxonomy. This is a third contribution towards an analysis of morphological characters and how to make use of them. Available time and practical possibilities limited the number of parameters.

MATERIALS AND METHODS

Although the pattern of superficial bloodvessels of the ventral surface of the thorax should be visible in formalin-preserved specimens (Hanson, 1948: 581), we have not been able to find these patterns in preserved specimens. Therefore only living material was used.

The material was collected by diving (31 dives down to 55 m) and dredging (3 times, 100-200 m), on 18 different localities in and near Marseille and Banyuls (Mediterranean). During dives, cobbles with serpulid tubes were placed in containers and airlifted to the surface. Although the animals were kept in water all the time, a temperature shock of at least up to 10°C could not be avoided. The worms could be kept in the laboratory in running sea-water for at least three days, or in cooled water (at 6°C) for a week or longer, provided that sponges had been removed upon arrival. The temperature-shock had no apparent effect on the animals.

In the laboratory the worm-tubes were removed from the substrate by applying pressure with a scalpel to the convex sides of the undulating tubes. Generally the tubes then came off in a few large fragments, one or two of them still containing the worms. If the tube splintered during this process, the worms were too much damaged to be used and were discarded. Using pincers

with adjustable jaws, it was possible to break the tube from behind and force the worm forward, without damaging it.

Routinely the following parameters were determined:

a) Date of collecting and depth of occurrence.

b) Type of ventral thoracic bloodvessel-pattern. We discerned five types of patterns (fig. 1).

c) Length and width of thoracic membranes, as an indication of size. These measurements were taken with a micrometer in the stereomicroscope, with the animals lying on their dorsal side, which causes the thoracic membranes to spread.

d) Radius of operculum (if present).

e) Sex. During handling most worms shed their sexual products through pores in the body-wall. Sperm appear milky white, ova as discrete granules.

f) Colour-type of branchial crown. We discerned four patterns: 1) orange radioles with red transverse markings; 2) white radioles with red transverse markings; 3) entirely white radioles; 4) radioles with a transparent basis, a broad "granular" zone and white tips. The colour is rapidly lost in preservatives.

g) Form of the collar.

These observations being completed, the worms were fixed and preserved in formalin. Subsequently the following parameters were determined:

h) Setae of thoracic setigers nr. 1, 4, and 7, in 65 specimens. In some of those, uncini were studied too.

i) Setae of anterior, middle and posterior abdomen, in 25 specimens.

Small pieces of tissue, including setae and/or uncini were mounted in glycerin-gelatin (refraction index 149). The slides were sealed with nailpolish. Presence of four types of setae (fig. 2) was coded to enable the automatized handling of the data: 1 = limbate setae; 2 = "*Apomatus*- setae"; 3 = sickle-
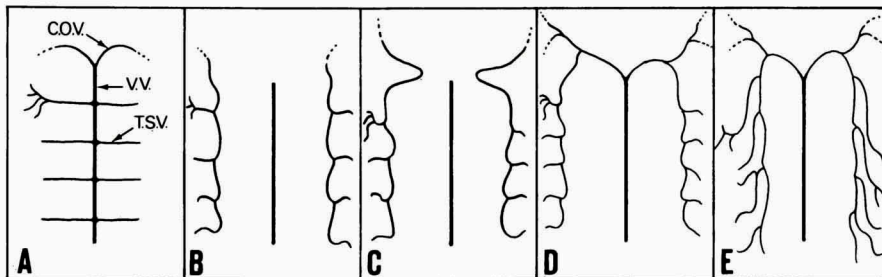

Fig. 1. Ventral thoracic bloodvessel-patterns. Essentially two types can be discerned: A, with transseptal vessels (T.S.V.), and B-E, without such vessels. C.O.V. = circum oesophageal vessel; V.V. = ventral vessel. Further explanation in text.
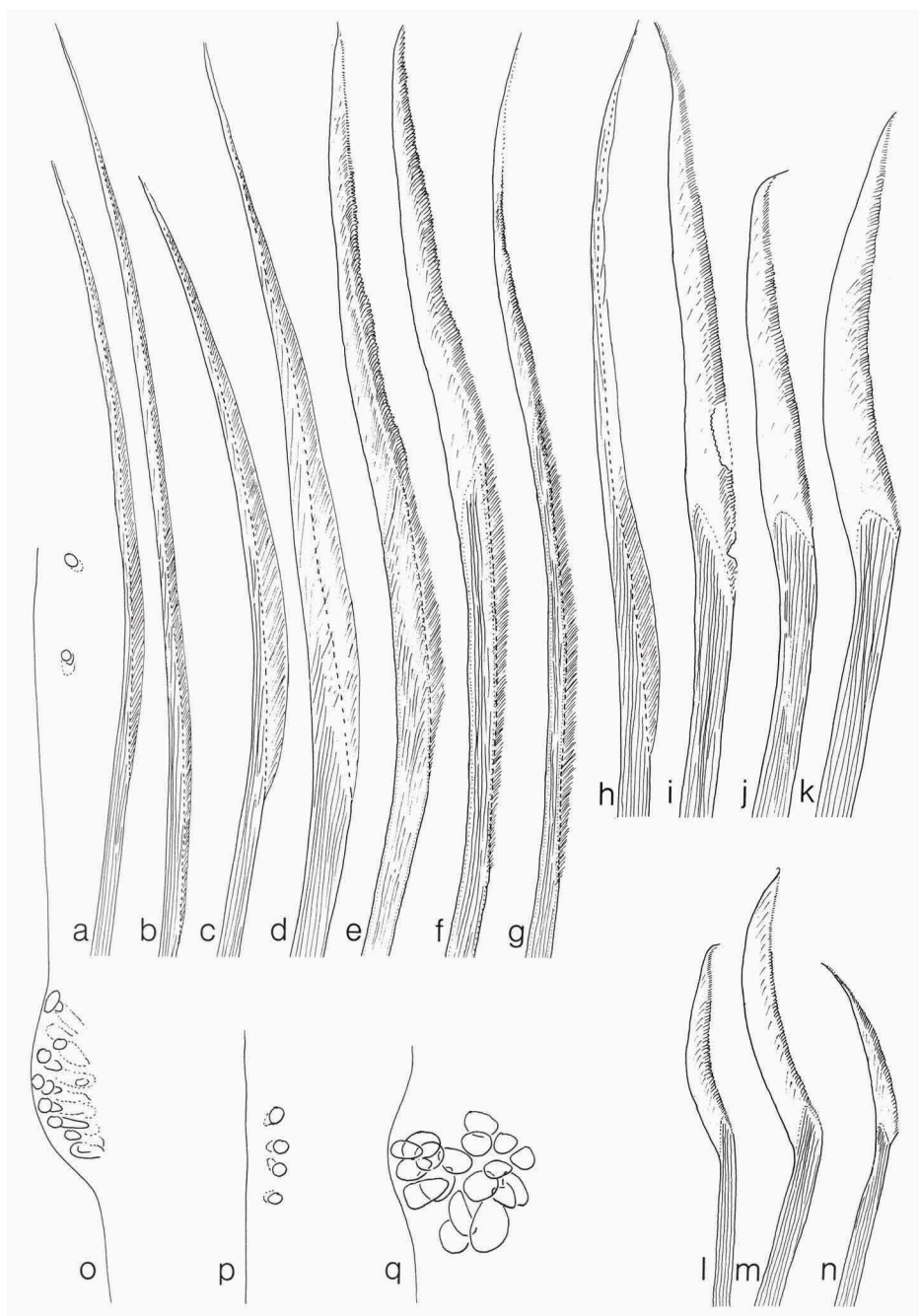
Fig. 2. Setae and eyespots, of operculate specimens (A) and non-operculate worms (P) a.-b.-capillary collar setae (P, A); c-d.-limbate collar setae (P, A); e.-g.- "*Apomatus*- setae" (A, P, P), in operculate specimen with short proximal limbate zone and long palissade of teeth distally, in non-operculate specimens this ratio is reversed; h.-thoracic seta, intermediate in form between limbate and "*Apomatus*" type (see p. 428); i-n.-abdominal setae from anterior abdomen, with the exception of k, which is from the middle abdomen (P, P, P, P, A, A). i-j, variation within one bundle. i-k, gradual differences between straight (or slightly geniculate) and sickle-shaped setae. l, seta of very small specimen. m, sickle-seta of operculate specimen from shallow water. n, geniculate seta of operculate specimen from deep water. o-q.-eyespots (P, A, A). For explanation see text.

shaped (falcate) setae; 4 = geniculate setae. The code 111 thus indicates that only limbate setae were found in 1st, 4th and 7th thoracic setiger; 122 indicated limbate setae on setiger 1, "*Apomatus*-setae" as well on setigers 4 and 7; 333 indicates sickle setae on anterior, middle and posterior abdomen. The invariably capillary setae of the posterior abdominal segments were left out of consideration.

For a better understanding of the structure of setae and uncini a few SEM micrographs were made. Small pieces of tissue with setae and uncini were airdried, covered with gold and photographed with a Philips 600 M.

j) Finally the branchiae of 44 specimens were checked for the occurrence of hyaline structures, most probably eyespots. When careful illumination under the stereomicroscope (magnification 10-60 ×) still failed to show such structures, the 3rd or 4th left or right radiole were mounted in glycerin, and examined under a high power microscope. Sometimes staining with Methyl Green facilitated the observations.

Handling the data of the 152 worms was facilitated by use of a microcomputer. Most of the material, and a copy of the original Dutch report with appendix catalogueing it, have been deposited in the Rijksmuseum van Natuurlijke Historie, Leiden. A few specimens are in the senior author's collection.

RESULTS

a) Depth of occurrence.

The depth of occurrence varies from 10-50 m, mean 23, SD 10.05 in 47 operculate worms. In 87 non-operculate worms it varies from 3-55 m, mean 12.11, SD 9.26. Compared with the Mann-Whitney test we find $U = 799$, $U' = 3290$, $Z = 5.80$. The depths of occurrence differ significantly ($p < 0.01$).

b) Type of ventral thoracic bloodvessel-pattern.

As can be seen from fig. 1, type A differs essentially from all other types (B-E), in the presence of transseptal vessels. During this study it appeared that types B and C are both expressions of type D, depending upon the depth of imbedding in tissue and/or extent of filling with blood of the circumoesophageal vessel. A type B sometimes scored type C, when observed half an hour later. Type E evidently is a modification of type D. Thus the five originally discerned patterns can be reduced to two main patterns (A and D), and a derived one (E).

Of the 140 complete specimens, 82 had a thoracic bloodvessel-pattern type A, 58 a different type. In fig. 3 patterns have been presented against the

presence or absence of an operculum. The vast majority of non-operculate worms had a type A pattern, all operculate worms had a different type. The derived pattern E occurred almost exclusively in the sample from 200 m depth (five out of six determined worms, the 6th scored pattern D). Only one specimen from 25 m depth scored a pattern E too. Comparison of our fig. 1 with that of Hanson (1948) shows that our type A is the same as the pattern ascribed to *Protula intestinum* (Lamarck, 1818) by Hanson (1948, fig. 1A). Our types D and E show a great similarity to Hanson's figures 1C and 1D, of *Apomatus similis* Marion & Bobretzky, 1875 and *A. ampulliferus* respectively. In view of our observation that our types B and C (compare fig. 1B of Hanson) are both expressions of the same type D, we question the identification of *Protula tubularia* sensu auct. by Hanson, it may have been a specimen which accidentally had lost its operculum.

We made a few observations of bloodvessel-patterns in other genera. In *Hydroides pseudouncinata* Zibrowius, 1968, *Serpula concharum* Langerhans, 1880 (sensu auct.) and *S. vermicularis* Linnaeus, 1767 (sensu auct.) we observed transseptal vessels. However, the presence of a ventro-lateral vessel, as mentioned by Hanson (1950. fig. 12, 13) could not be confirmed. Our observation of *Vermiliopsis infundibulum* (Philippi, 1844) confirms Hanson's (1950, fig. 14), except for minor details. In *Pomatoceros triqueter* (Linnaeus, 1767) we observed transseptal vessels, although Hanson gives none (1950, fig. 11). It still is too early to draw conclusions, but the results are promising.

c) Lenght and width of thoracic membranes.

In fig. 4 both parameters are presented. It is evident that width increases with increasing length. It can be computed that width = 0.89 × length. A comparison of operculate and non-operculate specimens did not show statistical differences (Mann-Whittney test).

d) Radius of operculum.

	bloodvessel-pattern	
	a	**≠a**
operculate	0	53
non-operc	82	5

Fig. 3. Distribution of bloodvessel-patterns and opercula. Specimens without branchial crowns are left out, as well as those where the type of bloodvessel-pattern could not be defined.

The results are given in a frequency diagram (fig. 5). The opercular radii do not show a normal distribution (tested with Chi-square, $p < 0.025$). The biological meaning of this is not clear.

There is a linear correlation between radius of operculum and thoracic width (fig. 6), indicating that the radius is a function of growth too.

e) Sex.

In 24 operculate worms, all with a bloodvessel-pattern type $\neq$ A, the ratio males: females was 18 : 6. In 38 non-operculate specimens this ratio was 21 : 17. Since it is not known whether males and females shed their sexual products equally easy or not, these figures do not necessarily give the sex ratio.

f) Colour-patterns.

In non-operculate specimens the colour-patterns 1 and 2 were found in more or less equal proportions (37 : 47); two showed a pattern 3. Operculate worms preponderantly showed a pattern 2, a smaller portion pattern 1 (37 : 14). White spots, persistent in formalin, occur in about 30% of the non-operculate worms only (checked in 57 specimens). The material from 200 m

Fig. 4. Correlation between width of thoracic membrane (vertical axis) and length of thorax (horizontal axis).

depth was markedly homogeneous: seven had a pattern 4, one a pattern 1.

Sometimes it was difficult to distinguish between colour patterns 1 and 2, since yellow radioles did occur. Moreover, these patterns 1 and 2 occurred commonly in both operculate and non-operculate forms, and thus cannot be used for discrimination between them. If white, persistent spots are present, the worm always is non-operculate (*Protula*), the reverse statement is not necessarily true.

g) Form of the collar.

The variability in shape proved to be great. The membrane was easily damaged, causing doubt as to whether an incision was real or represented an artefact. We had the impression that natural medial incisions did not occur. In view of these difficulties, we did not continue the observations. However, three about 10 cm long specimens, labelled *Protula intestinum* did show a medial incision (BMNH ZK 1898.5.6.84/5, Naples).

Fauvel (1909: 71) and Rioja (1923, fig. 216, 222; = 1931, pl. 145 fig. 6, 146 fig. 6) used the form of the collar for species distinction in *Protula*. In view of our observations, it is evident that if the form of the collar is to be used, the infraspecific and infrageneric variation will have to be documented better.

h) Thoracic setae and uncini.

All operculate worms from shallow depths showed limbate setae and
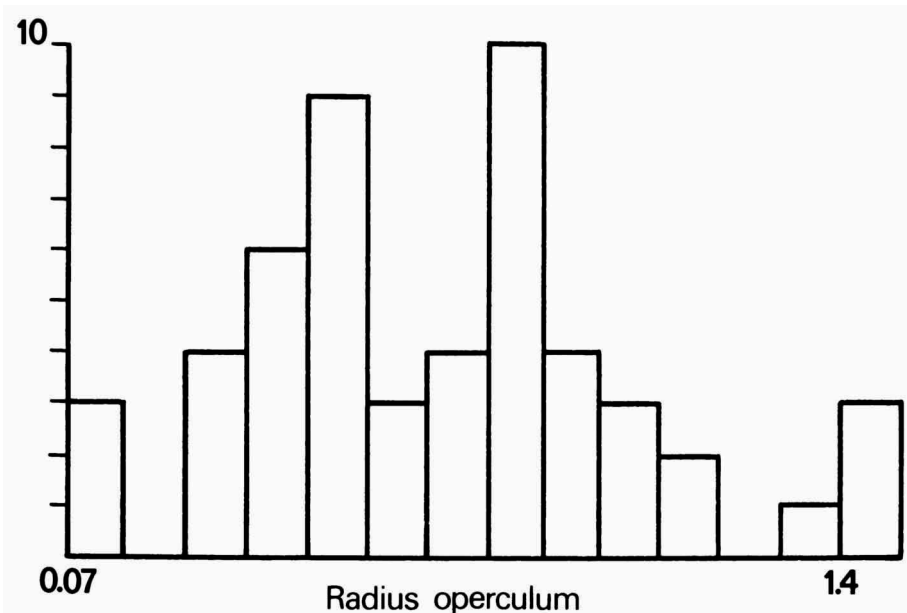

Fig. 5. Frequency (vertical axis) diagram of radius of operculum (horizontal axis).
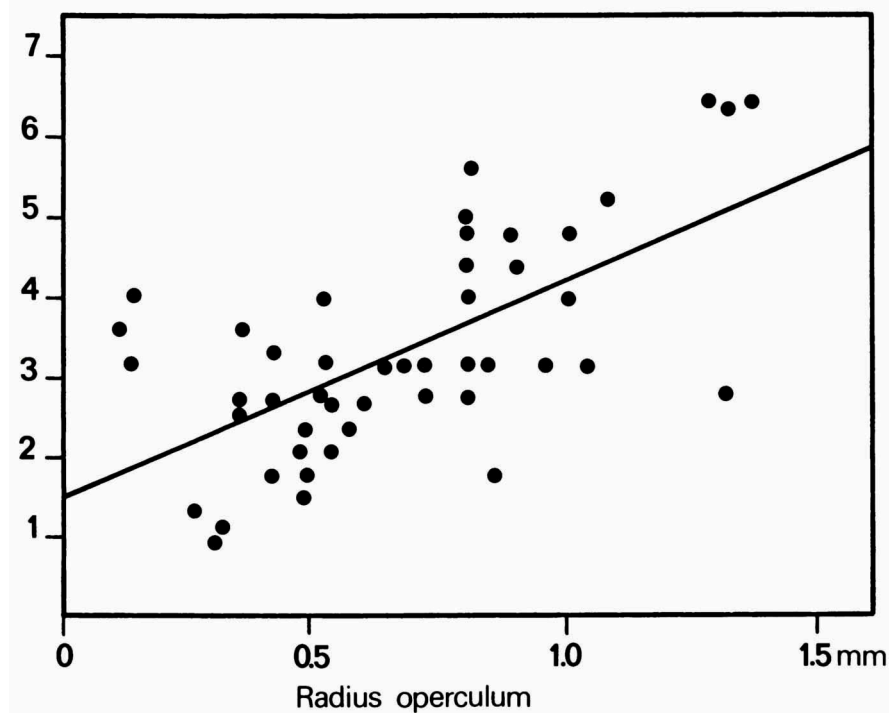
Width of thoracic membrane mm

Fig. 6. Correlation between width of thoracic membrane (vertical axis) and radius of operculum (horizontal axis).

"*Apomatus*- setae" in the 4th and 7th thoracic setigers (condition 122, n = 23). In ten whole mounts we found that "*Apomatus*- setae" in fact occur from setiger 3 onwards. In some specimens we observed doubly curved setae, without a palissade of teeth distally (fig. 2h), in anterior setigers on the place where "*Apomatus*- setae"are inserted in the more posterior setigers.

The sample from 200 m depth shows six operculate animals with conditions 112 (4 spec.) and 122 (2 spec.). The two non-operculate worms from this depth show condition 112. In the seven specimens with a bloodvessel-pattern ≠ A *(Apomatus)* these setae occur from setiger 4 or 5 onwards.

Of 34 non-operculate specimens 19 showed limbate setae only (condition 111), ten had "*Apomatus*- setae" as well in posterior segments (condition 112), whilst five had some in both the 4th and 7th thoracic setigers (122).

Apparently the question is not so much if non-operculate specimens do show "*Apomatus*- setae" or not, but as to where these setae start occurring. The character seems a simple one, but in fact is difficult to use. In large

specimens it was necessary to look twice before a positive identification of these setae could be made. Preliminary observations missed them in six out of eight slides, in which they were later seen to be present. This may explain many contradictory remarks in the literature as to whether "*Apomatus*-setae" are present or not in non-operculate worms. See conclusions too.

We could not find differences between both forms in the exact shape of the thoracic uncini. With a light microscope we observed rasp-shaped uncini in both, with 2-4 rows of teeth in operculate forms, up to six rows in non-operculate specimens. The character should be studied in more detail with electron microscopy, since our three SEM observations (fig. 7a-d) indicate that the uncini are all saw- to rasp-shaped. In view of the technical difficulties we did not continue the observations on the exact shape of the uncini.

In the past emphasis has been placed too on the occurrence of the rows of thoracic uncini (e.g. Marenzeller, 1893: 36, 38). It is not always easy to find these in large specimens. We checked 14 non-operculate worms: uncini may occur from setiger 2 onwards (5 specimens), setiger 3 (4 spec.), setiger 4 (1 spec.), setiger 6 (2 spec.) or may lack completely. We had the impression that especially in large specimens the uncini may disappear secondarily, since the spots were uncini might be expected were sometimes still marked by lamellar structures. In operculate specimens uncini occur from setiger 2 onwards (n = 5).

i) Setae of anterior, middle and posterior abdominal segments.

The form of the setae is open to various interpretations: in one specimen we observed sickle-shaped setae one day, but thought them to be geniculate the other day. Within one bundle of 12 abdominal setae of a non-operculate worm we observed straight to geniculate setae, as well as two more or less sickle-shaped ones (fig. 2i-j). In material from shallow depths there is a tendency towards sickle-shaped setae in operculate specimens, geniculate and/or sickle setae in non-operculate specimens. The four specimens checked from a depth of 200 m all showed geniculate setae (fig. 2n).

Fauvel (1927: 382, 385), Rioja (1931: 444), and Zibrowius (1968 :183) for example stated that *Protula tubularia* and *P. intestinum* can be distinguished by presence of sickle-shaped setae in the first, and geniculate setae in the second species. Our results are far from conclusive (fig. 2 i-n). More research is necessary to clarify the infraspecific and intra-individual variability, preferably with scanning microscopy, before the statement can be verified.

j) Occurrence of eyespots.

We checked 44 worms for the occurrence of eyespots. All operculate specimens (18) except one showed paired compound eyespots of 4-16 lenses each (fig. 2q). In non-operculate specimens essentially paired rows of simple
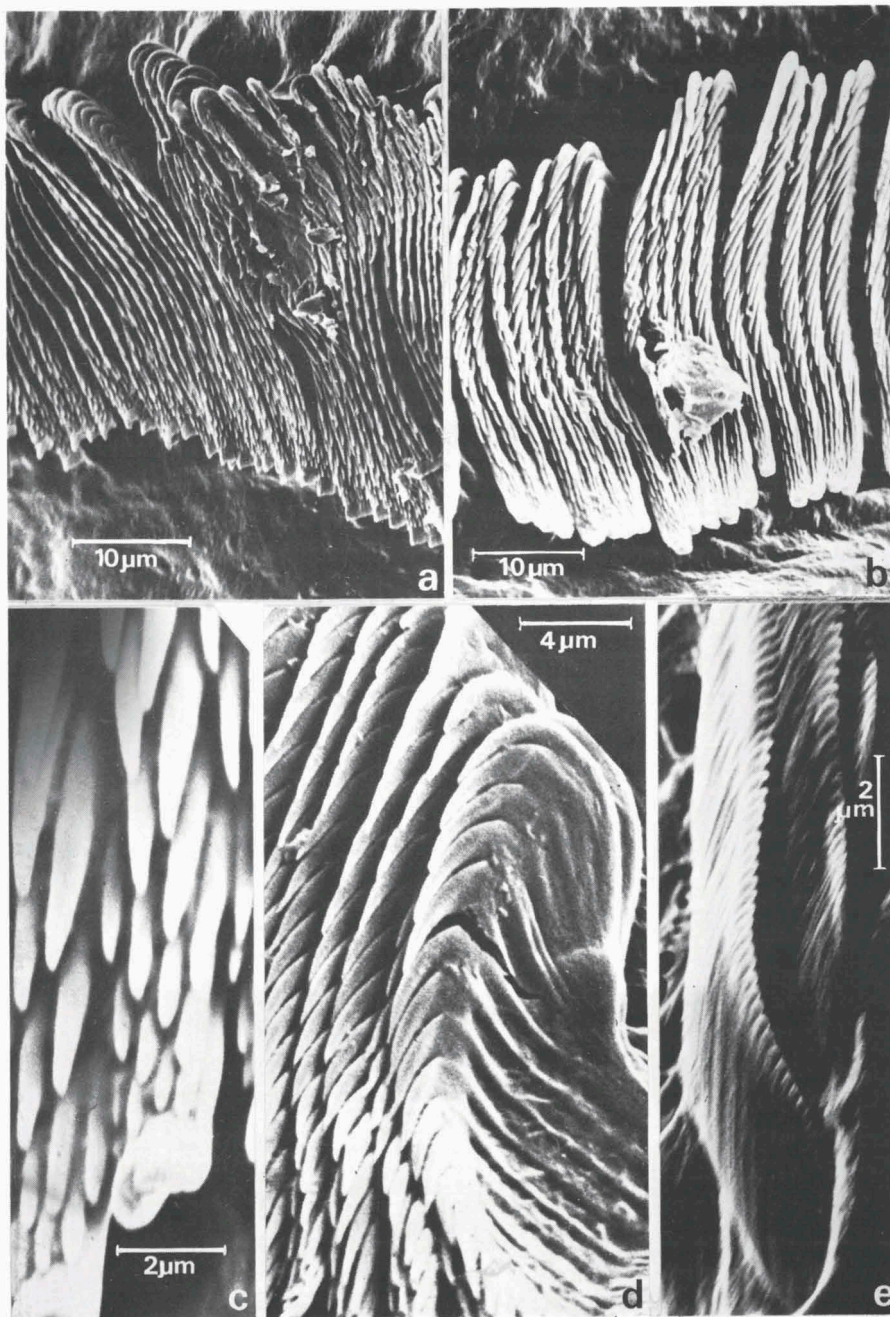
Fig. 7. Scanning electron micrographs of thoracic uncini (a-d) and abdominal seta (e). a.c.-operculate specimen, detail showing most anterior teeth. b, d.- non-operculate specimen, detail from second specimen. e.- non operculate specimen.

eyespots (fig. 2p) occurred (n = 14). In four we failed to find lenses at all, although traces of pigment could be seen; in two we found paired compound eyespots. In a few large non-operculate worms paired compound eyespots of 3-8 lenses were observed in proximal radiole-parts, followed more proximally by paired groups of 2-3 simple eyespots in line, alternating with single simple eyespots; distally only single (paired) simple eyespots were found (fig. 2o). Six specimens from a depth of 200 m all had 4-16 pairs of lateral knobs on their radioles, presumably eyespots, but in only one of them lenses (5-9 per knob) could be discerned.

Although many studies dealt with the photic behaviour of serpulid larvae (e.g. Klöckner, 1976: 62-64), and with shadow respons of adult (e.g. Rullier, 1948; Nicol, 1950 for sabellids), information on the location of this sense of light is hard to find in the taxonomic literature. Consequently reviews by Radl (1912), Hanström (1926), Beklemishev (1968) and Mill (1978) hardly mention serpulids.

This lack of interest in branchial "eyes" in serpulids is in marked contrast to the situation in the related family Sabellidae, where recently the ultrastructure of the eyespots in many species has been studied (e.g. Krasne & Lawrence, 1966; Kerneis, 1975; Ermak & Eakin, 1976). Moreover, in taxonomic literature on Sabellidae presence or absence of branchial "eyes" apparently is used in genus distinction (e.g. Fauchald, 1977; Knight-Jones, 1983). By analogy Imajima & ten Hove (1984) used the character in their emended diagnosis of the serpulid genus *Dasynema* Saint-Joseph, 1894. However, the great majority of authors in the last decennia do not even mention eyespots in their descriptions. The imbalance between these two families will be redressed with studies by Smith (1984, and in preparation), dealing with structure and presence of photoreceptors in eight species of five genera of Australian serpulids.

Mill (1978: 86-89) proposed a consistent terminology of which a short version is given here. Simple ocelli are defined as being composed of one or more simple photoreceptor cells enclosed in a common pigment cup, without a separate lens. In simple and compound eyespots each photoreceptor unit consists of a receptor cell and a lens and is surrounded by pigment cells. Eyes are all those structures in which a group of photoreceptor cells share a common pigment cup and a common lens. According to Smith (pers.comm.) the branchial eyespots in serpulids may be organized to such an extent, that they overlap Mill's distinction between eyespots and eyes proper.

In the *Apomatus/Protula* -complex branchial eyespots were mentioned in a few descriptions, and sometimes have been used for species distinction (e.g. Marion & Bobretzky, 1875; Marenzeller, 1893; Saint-Joseph, 1894; Soulier,

1902; Fauvel, 1914; Rioja, 1923, 1931; Uchida, 1978). Some records are contradictory (Fauvel, 1914 :361), doubtlessly partly caused by erroneous identifications and imperfect observations. As for *Apomatus similis* most authors agree that there are 4-18 pairs of compound eyespots in each radiole, with 8-18 (crystalline) lenses each. For *Protula tubularia* there is an apparent consensus that there are 15-24 pairs of simple eyespots. In not yet entirely studied material from the Canary Islands we (ten Hove & Aarts, in preparation) found indications that patterns may be different here, with lower numbers of lenses in the compound eyespots of operculate specimens, and clustered rows of up to nine simple eyespots in non-operculate worms. In conclusion it is not unlikely that we are dealing with two different taxa, one characterized by rows of compound eyespots and more or less in accordance with *Apomatus similis;* and one with essentially simple eyespots, like *Protula tubularia* auct. Species distinction within the genera with help of this character will have to wait until more statistical data are available.

Since lack of record of eyespots does not necessarily mean that they are absent (see Materials and methods), a complete survey is impossible. The following summary is based on a random sample of literature: Fauvel 1909, Imajima & ten Hove 1984, Iroso 1921, Langerhans 1884, Rioja 1931, Uchida 1978, Vine & Bailey-Brock 1984, Zibrowius 1968.

Photoreceptors of an undefined type are mentioned for: *Filogranula* Langerhans, 1884 (as *Omphalopoma* Mörch, 1863), *Janita* Saint-Joseph, 1894 (as *Omphalopomopsis* Saint-Joseph, 1894), *Microprotula, Paraprotis, Paraprotula* (all of Uchida, 1978).

Ocelli, most likely brain-associated ones, are found in: *Filograna* Berkeley, 1835, *Josephella* Caullery & Mesnil, 1896, *Hyalopomatus* Marenzeller, 1878, *Metavermilia multicristata* (Philippi, 1844, as *Vermiliopsis*) and *Semivermilia* ten Hove, 1975 (as *Vermiliopsis undulata* Zibrowius, 1968 and *Josephella carenata* Zibrowius, 1968).

Simple radiolar eyespots have been observed in: *Metavermilia acanthophora* (Augener, 1914), *ovata* Imajima, 1978 (ten Hove, unpubl.), and *Vermiliopsis* spp.

Compound radiolar eyespots are mentioned for *Dasynema*. Two elliptic compound eyespots at both sides of the head are mentioned for *Protula intestinum* (as *P.protula,* Radl, 1912 :246). We cannot confirm this observation (see remarks above) although three specimens from Naples showed 3-5 compound eyespots of up to ten lenses each on the dorsal radioles.

Other types of photoreceptors are mentioned for *Placostegus* Philippi, 1844, with a girdle of eyespots in the collar segment, and for *Spirobranchus* spec. (Vine & Bailey-Brock, 1984), with a field of lenses on the opercular bulb.

In the taxonomically confused *Filograna/Salmacina*- complex we found distinct ocelli in the prostomial area in 20 operculate specimens (traditionally *Filograna)* from Marseille. These were still marked in preserved material, by two rows of 4-6 pigmented cells. Contrarily we could find no trace of pigment cells in 20 non-operculate specimens, *Salmacina* sensu auct. However, McIntosh (1919) was unable to find a consistent correlation between ocelli and operculum in this complex. In *Metavermilia* Bush, 1905, too, photoreceptors may prove to be a useful character, *M. multicristata* with ocelli, *acanthophora* and *ovata* with simple radiolar eyespots and *gravitesta* Imajima, 1978, and *spicata* Imajima, 1977, apparently without (ten Hove, unpubl.). Differences in photoreceptors certainly are taxonomically useful in *Spirobranchus* Blainville, 1818. Richard Smith (pers.comm.) reports that some closely related species possess a pair of well developed compound branchial eyes, at the base of the first radiole of each branchial spire. These eyes represent the highest level of photoreceptor organisation reported for serpulids so far, both in their gross structure and the fine structure of the receptor cells. In other species paired simple eyespots are found on the radioles. We already mentioned the opercular eyespots in a new species of *Spirobranchus*.

CONCLUSIONS

Ostensibly our results are confusing, just as the literature. There is a general trend that non-operculate specimens have a thoracic bloodvessel-pattern type A, limbate thoracic setae throughout or at most *"Apomatus*- setae" as well in the posterior segments only and rows of simple eyespots in the radioles. However, many exceptions on this trend occur. *Mutatis mutandis* the same holds when viewing the single characters of the operculate specimens.

A completely different pattern, however, emerges when these four characters are reviewed simultaneously for the material up to a depth of 100 m. It then becomes evident that the nominal genus *Apomatus* not only is characterized by the presence of an operculum (mostly accompanied by a pseudo-operculum), but also by a thoracic bloodvessel-pattern unlike type A, by *"Apomatus*- setae" in abundance throughout most thoracic setigers (setal pattern 122) and by rows of compound eyespots on the branchial radioles. *Protula* is characterized by the absence of an operculum, by a thoracic bloodvessel-pattern type A, by scarce *"Apomatus*-setae" in the last thoracic setigers only if they occur at all (pattern 111 or 112, however, a single specimen from Iceland had a pattern 122) and by rows of simple eyespots on the branchial radioles.

Applying these characters simultaneously, all apparent exceptions of the rules by single characters can be explained as caused by mistaken identities. For instance six non-operculate specimens (classically *Protula)* can be identified by either a setal pattern 122, or by presence of compound eyespots and generally by both characters as belonging to *Apomatus*. Moreover, these specimens showed a thoracic bloodvessel-pattern unlike type A, a further indication of their true identity.

There is only one out of the 152 specimens, which identity remains unresolved, when applying the characters strictly. An undamaged, non-operculate specimen with a thoracic bloodvessel-pattern type A, and thus a *Protula,* showed a setal pattern 122 and conpound eyespots, both characteristic for *Apomatus*. On the hard evidence of the latter characters we now doubt if our original determination of the bloodvessel-pattern has been correct. In all probability we made either a mistake, or a false entry into the records. With four more non-operculate specimens which according to their patterns of setae, compound eyespots and bloodvessels belong to *Apomatus,* together we thus found five aberrant specimens (i.e. 8%) of *Apomatus,* without opercula. The remaining non-operculate specimen, with e.g. bloodvessel-pattern type D and thus belonging to *Apomatus,* had a damaged crown.

The single small sample from a depth of 200 m consisted of eight worms, not all studied completely. One non-operculate specimen showed a bloodvessel-pattern type A, setal pattern 112 and colour-type 1 of branchial crown. In all probability it is the same as our other *Protula* material. The remaining seven specimens all showed colour-pattern type 4, distinct from all other material; five of them had a thoracic bloodvessel-pattern type E, one a type D and one was undetermined. Most were operculate, with the exception of one undamaged specimen (bloodvessel-pattern E). Six showed paired rows of lateral knobs, presumably compound eyespots, on the radioles; one lacked a branchial crown. In all seven *"Apomatus-* setae" occurred from setiger 4 or 5 onwards. The sample is too small to draw firm conclusions, but it is not unlikely that all seven specimens belong to one essentially operculate species.

To avoid creating further confusion we propose to stick to the traditional use of *Apomatus* for operculate specimens, *Protula* for non-operculate specimens, althouth it is pointed out elsewhere (ten Hove, 1984) that both nominal genera are phylogenetically ill-defined. Following the traditional nomenclature, our shallow material of *Protula* is likely to be *Protula tubularia,* our shallow *Apomatus* should be named *A. similis,* while the operculate deep-water form might be *A. ampulliferus.* For a definite identification a full revision will be necessary, the more so since incidental observations on

material from outside the Mediterranean indicate that eyespots and setal characters may be different elsewhere.

ACKNOWLEDGEMENTS

REFERENCES

Augener, H., 1906. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea, and on the east coast of the U.S. 1877-1880, by the U.S.S. Coast Survey Steamer "Blake". XLII, Westindische Polychaeten. — Bull. Mus. Comp. Zool. Harvard 43: 91-196, 8 pls.

Beckwitt, R., 1981. The inheritance of morphological variation in Pileolaria pseudomilitaris (Polychaeta: Spirorbidae). — Zool. J. Linn. Soc. 71 (2): 237-247, 2 figs.

Beklemishev, W.N., 1968. Principles of comparative anatomy of invertebrates. 2, Organology: vii + 529 pp., 200 figs. Edinburgh.

Ermak, T.H. & R.M. Eakin, 1976. Fine structure of the cerebral and pygidial ocelli in Chone ecaudata (Polychaeta: Sabellidae). — J. Ultrastruct. Res. 54 (2): 243-260, 22 figs.

Fauchald, K., 1977. The polychaete worms. Definitions and keys to the orders, families and genera. — Nat. Hist. Mus. Los Angeles Cy, Sci. Ser. 28, 188 pp., 42 figs.

Fauvel, P., 1909. Deuxième note préliminaire sur les Polychètes provenant des campagnes de l'Hirondelle et de la Princesse-Alice, ou déposées dans la Musée Océanographique de Monaco. — Bull. Inst. océanogr. Monaco 142: 1-76, 7 figs.

Fauvel, P., 1910. Sur quelques Serpuliens de la Manche et de la Méditerranée. (Serpula vermicularis L., Protula tubularia Mont.). — C.R. Ass. franc. Avanc. Sci. Paris 38 (1909): 691-698, 4 figs.

Fauvel, P., 1914. Annélides polychètes non pélagiques provenant des campagnes de l'Hirondelle et de la Princesse-Alice (1885-1910). — Rés. Camp. Sci. Monaco 46: 1-432, 31 pls.

Fauvel, P., 1927. Polychètes Sédentaires. Addenda aux errantes, Archiannélides, Myzostomaires. — Faune de France 16, Paris: 1-494, 152 figs.

Hanson, J., 1948. The genera Apomatus and Protula (Polychaeta, Serpulidae. — J. mar. biol. Ass. U.K. 27: 581-584, 1 fig.

Hanson, J., 1950. The blood-system in the Serpulimorpha (Annelida, Polychaeta). I. The anatomy of the blood-system in the Serpulidae. — Quart. J. micr. Sci. 91 (2): 111-129, 18 figs.

Hanström, B., 1926. Eine genetische Studie über die Augen und Sehzentren von Turbellarien, Anneliden und Arthropoden (Trilobiten, Xiphosuren, Eurypteriden, Arachnoiden, Myriapoden, Crustaceen und Insecten). — Kung. svenska Vetensk. Akad. Handl. (3) 4 (1): 1-176, 80 figs.

Hartmann-Schröder, G., 1971. Annelida, Borstenwürmer, Polychaeta. — Die Tierwelt

Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise, 58: 1-594, 191 figs.

Hartman, O., 1969. Atlas of the sedentariate polychaetous annelids from California: 1-812, illustr. Allan Hancock Found., L.A., Calif.

Hove, H.A. ten, 1984. Towards a phylogeny in serpulids (Annelida; Polychaeta). — Proc. first Int. Polychaete Conf., Sydney, P.A. Hutchings (ed.): 181-196, 7 figs.

Hove, H.A. ten & M.J. Jansen-Jacobs, 1984. A revision of the genus Crucigera (Polychaeta, Serpulidae); a proposed methodical approach of serpulids, with special reference to variation in Serpula and Hydroides. — Proc. first Int. Polychaete Conf., Sydney, P.A. Hutchings (ed.): 143-180, 12 figs.

Imajima, M. & H.A. ten Hove, 1984. Serpulinae (Annelida, Polychaeta) from the Truk Islands, Ponape and Majuro Atoll, with some other new Indo-Pacific records. — Proc. Jap. Soc. syst. Zool. 27: 35-66, 6 figs., 4 maps.

Iroso, I., 1921. Revisione dei Serpulidi e Sabellidi del Golfo di Napoli. — Pubbl. Staz. Zool. Napoli 3: 47-91, pl. 3-4.

Kerneis, A., 1975. Étude comparée d'organes photorécepteurs de Sabellidae (Annélides Polychètes). — J. Ultrastruct. Res. 53: 164-179, 21 figs.

Klöckner, K., 1976. Zur Ökologie von Pomatoceros triqueter (Linné 1758) (Serpulidae, Polychaeta). — Thesis, Univ. Tübingen: 1-168, 33 figs., 24 tabs. (mimeogr.).

Knight-Jones, P., 1983. Contributions to the taxonomy of Sabellidae (Polychaeta). — Zool. J. Linn. Soc. 79: 245-295, 21 figs.

Krasne, F.B. & P.A. Lawrence, 1966. Structure of photoreceptors in the compound eyespots of Branchiomma vesiculosum. — J. Cell. Sci. 1: 239-248, 11 figs., 1 tab.

Langerhans, P., 1884. Die Wurmfauna von Madeira. IV. — Z. wiss. Zool. 40: 247-285, pl. 15-17.

Marenzeller, E. von, 1983. Polychaeten des Grundes, gesammelt 1890, 1891 und 1892. — Denkschr. Akad. Wiss. Wien (mathem. naturw. Classe) 60: 25-48, 4 pls.

Marion, A.F., 1874. Sur les Annélides du golfe de Marseille. — C.R. Acad. Sci. Paris 79: 398-401.

Marion, A.F. & N. Bobretzky, 1875. Étude des annélides du Golfe de Marseille. — Ann. Sci. Nat. Paris (6, Zool.) 2 (1): 1-106, 12 pls.

McIntosh, W.C., 1919. Notes from the Gatty Marine Laboratory, St. Andrews. No. 42. 1. Preliminary studies on Filograna. — Ann. Mag. Nat. Hist. London (9) 3: 124-162.

Mill, P.J., 1978. Physiology of annelids: i-xvi + 1-683, illustr. London, etc.

Mörch, O.A.L., 1863. Revisio Critica Serpulidarum. Et bidrag til rørormenes Naturhistorie. — Naturh. Tidsk. Henrik Krøyer, København (3) 1: 347-470, 1 pl.

Nicol, J.A.C., 1950. Responses of Branchiomma vesiculosum (Montagu) to photic stimulation. — J. mar. biol. Ass. U.K. 29, 2: 303-319, 6 figs.

Philippi, A., 1844. Einige Bemerkungen über die Gattung Serpula, nebst Aufzählung der von mir im Mittelmeer mit dem Thier beobachteten Arten. — Arch. Naturg. Berlin 10, 1: 186-198, pl. 8. (translated in: Ann. Mag. Nat. Hist. London (1) 14: 153-162).

Quatrefages, A. de, 1865. Histoire naturelle des Annelés marins et d'eau douce. Annélides et Géphyriens, 2 (2) — Libr. Encycl. de Rôret, Paris: 337-794, 20 pls.

Radl, E., 1912. Neue Lehre vom Zentralen Nervensystem: i-vii + 1-496, 100 figs. Engelmann, Leipzig.

Rioja, E., 1923. Algunas especies de anelidos poliquetos de las costas de Galicia. — Bol. R. Soc. Esp. Hist. Nat. Madrid 23: 333-345, 3 figs.

Rioja, E., 1931. Estudio de los poliquetos de la Peninsula Iberica. — Mems. Acad. Cienc. exact. fis. quim. nat. Zaragosa 2: 1-472, 151 pls.

Rullier, F., 1948. La vision et l'habitude chez Mercierella enigmatica Fauvel.-Bull. Lab. Marit. Dinard 30: 21-27, 4 figs.

Saint-Joseph, A. de, 1894. Les Annélides Polychètes des Côtes de Dinard. III. — Ann. Sci. Nat. Paris (7, zool.) 17: 1-395, pl. 1-13.

Smith, R.S., 1984. Novel organelle associations in photoreceptors of a serpulid polychaete worm. — Tissue Cell 16 (6): 951-956, 3 figs.

Soulier, A., 1902. Revision des annélides de la région de Cette. I. — Trav. Inst. Zool. Univ. Montpellier (2) 10: 1-55, 10 figs.

Uchida, H., 1978. Serpulid tube worms (Polychaeta, Sedentaria) from Japan with the systematic review of the group. — Bull. Marine Park Res. Sta. 2: 1-98, 6 figs., 19 pls.

Vine, P.J., & J.H. Bailey-Brock, 1984. Taxomony and ecology of coral reef tube worms (Serpulidae, Spirorbidae) in the Sudanese Red Sea. — Zool. J. Linn. Soc. 80: 135-156, 8 figs.

Zibrowius, H., 1968. Étude morphologique, systématique et écologique, des Serpulidae (Annelida Polychaeta) de la région de Marseille. — Rec. Trav. Sta. Mar. Endoume, Bull. 43 (59): 81-252, 14 pls.