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A PRELIMINARY REVISION OF THE PROXENETES GROUP

 \mathbf{BY}

C. DEN HARTOG

(Communicated by Dr. J. Verwey at the meeting of November 27, 1965)

SECTION II (Angustus section)

Receptaculum seminis very large, connected with the atrium genitale by a bursal canal, the latter being in some cases differentiated into a bursa copulatrix and a ductus spermaticus. Bursal appendage consisting of a ring from which arises a duct that coils once and proximally splits into two narrow, parallel ducts.

This section is rather heterogeneous and consists of several species groups, some of which may be regarded as subsections. The most homogeneous group is characterized by the shape of the stylet, this narrows distally and its proximal part bends downward. It contains 6 species: Proxenetes angustus, P. bilioi, P. trigonus, P. intermedius, P. minimus and P. segmentatus. The other 6 species of the Angustus section have a stylet which is more or less shaped like a walking stick. Among these species P. quadrispinosus and P. britannicus show an obvious relationship, and so do P. pratensis and P. cisorius. P. puccinellicola and P. inflatus have a more isolated position, showing no direct relationship to the other species of the section.

P. pratensis and P. cisorius have been placed in the Angustus section with some doubt, as these species have some characters which perhaps will justify the erection of a new section. Firstly the cuticular copulatory organ of these species does not have a closed cuticular mantle; the stylet is only partly sheathed, a character which they have in common with the genus Ceratopera. Secondly the bursal appendage is surrounded by a free cuticular ring situated well above the base.

KEY TO THE SPECIES

- 1. Stylet proximally bent downward, narrowing in distal direction.
 - 2. Bursal canal between receptaculum seminis and atrium genitale commune without any differentiation.

- 3. Bursal appendage smaller than 70 μ . Cuticular mantle of the copulatory organ sheathing at lasst $\frac{1}{2}$ of the length of the stylet. Cuticular copulatory organ consisting of less than 6 spines.
 - 4. Cuticular copulatory organ larger than 50 μ .
 - 5. Cuticular copulatory organ 60-63 μ long, consisting of 2 spines forming the cuticular mantle and 2 free spines within the mantle. Cuticular mantle sheathing ca. ³/₄ of the length of the stylet. Distal part of the stylet with a lumen 6. P. angustus
- 3. Bursal appendage 110–130 μ long. Cuticular copulatory organ 65–67 μ long, consisting of 8 spines. Cuticular mantle sheathing $\frac{3}{2}$ — $\frac{1}{2}$ of the length of the stylet 9. *P. intermedius*
- 2. Bursal canal between receptaculum seminis and atrium genitale commune differentiated into a ductus spermaticus and a bursa copulatrix.
- 1. Stylet more or less shaped like a walking stick, proximally semicircularly or even more strongly curved, distally straight, almost equal in width over its whole length.
 - 7. Distal part of the stylet sheathed by a continuous cuticular mantle; sometimes a claviform organ on the distal tip of the stylet. Bursal appendage with a basal ring.
 - 8. Proximal part of the stylet covered by a thin cuticular membrane. Free spines lining the curved part of the stylet.
 - 9. Cuticular copulatory organ 85–95 μ long. Cuticular mantle sheathing $\frac{1}{3} \frac{2}{5}$ of the length

- of the stylet. Concave side of the proximal part of the stylet lined with 4 wedge-shaped spines 12. P. quadrispinosus
- 9. Cuticular copulatory organ $64-71~\mu$ long. Cuticular mantle sheathing $\frac{1}{2}-\frac{3}{5}$ of the length of the stylet and distally connate with the thick-walled stylet. Concave side of the proximal part of the stylet with 1 wedge-shaped spine . .13. *P. britannicus*
- 8. Proximal part of the stylet not covered by a cuticula. Free spines absent along the curved part of the stylet.
 - 10. Cuticular copulatory organ distally continuing as a claviform organ with anchor-shaped apex, totally 130–180 μ long 14. P. puccinellicola
 - Cuticular copulatory organ ca. 40 μ long, without a claviform organ.
 Straight part of the stylet inflated and projecting with its distal tip out of the conspicuously inflated cuticular mantle.
 15. P. inflatus
- 7. Distal part of the stylet only sheathed at one side by a cuticular mantle. Claviform organ always absent. Bursal appendage surrounded by a free cuticular ring situated obviously above the base.
 - 11. Cuticular mantle sheathing only the inward side of the stylet for $\frac{3}{3} \frac{3}{4}$ of its length. Efferent tract of the female genital apparatus consisting of a tubular bursa seminalis. Bursal appendage very fine, forming an almost complete coil. 16. P. pratensis
 - 11. Cuticular mantle sheathing only the outward side of the stylet for $\frac{1}{2} \frac{3}{5}$ of its length. Efferent tract of the female genital apparatus differentiated into a voluminous spherical or ovoid receptaculum seminis and a small bursa copulatrix, connected by a narrow ductus spermaticus. Bursal appendage plump, shaped like a davit. 17. *P. cisorius*

Proxenetes angustus Ax, 1951

Ax, Zool. Jb. Syst. 80, 321–322, f. 24 (1951); idem, Vie et Milieu, Suppl. 5, 118–119, f. 30 (1956); idem, Zool. Jb. Syst. 87, 100 (1959). — Fig. 23.

The animals are oblong, $1-1\frac{1}{2}$ mm long, and white or grey in colour. The anterior part of the body is truncate. The pharynx lies at ca. $\frac{2}{3}$ of the body length. The cuticular copulatory organ is slender and consists of a $60-63~\mu$ long slightly curved stylet, open at its proximal end, but soon becoming closed and gradually narrowing in distal direction. The proximal end bends sharply downward, forming a large hook. Distally the stylet is for $\frac{3}{4}$ of its length surrounded by an oblique, rather close-fitting cuticular funnel, composed of two lamellar spines. At its proximal margin this funnel is connected with the extreme tip of the proximal hook of the stylet. Within the funnel two free wedge shaped spines occur.

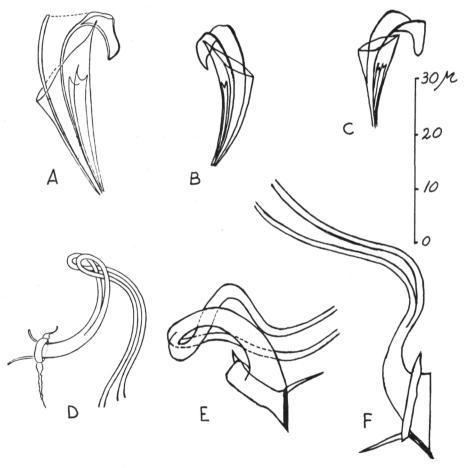


Fig. 23. Proxenetes angustus Ax, 1951: A-C. Cuticular copulatory organ; D-F. bursal appendage (A and D after AX; B, E-F after specimens from the Braakmanpolder, Zeeuws Vlaanderen; C after a specimen from the Lauwerszee, Friesland.

The scale refers to E-F only, B-C were drawn free hand).

The shape of the copulatory organ is almost identical with that of P. simplex. The bursal appendage consists of a cuticular ring which bears two diametrically opposite spines at its outer side. A rapidly narrowing duet, coiling once and dividing into two very thin cuticular duets, originates from this ring.

Geographical distribution:

Although *P. angustus* was not described before 1951 its area of distribution is very large. Ax (1951) discovered the species in Kiel Bay, where it was rather common, and found it also on some of the North Frisian Islands. Later he recorded the species from some "étangs" along the Mediterranean coast of France (Ax, 1956) and from Turkey, where it occurs along the Black Sea, the Bosporus and the Sea of Marmara (Ax, 1959). Recently the species has been found in the Netherlands, in the Waddenzee area as well as in the Deltaic area. It is probable that it will be found along the whole of the West-European coast.

Localities in the Netherlands:

Province of Friesland:

Dokkumer Nieuwe Zijlen, in the Lauwerszee, May 1961.

Province of Zeeland:

Zeeuws Vlaanderen: Salt-marsh creek west of the Braakmanpolder, June 1963.

Ecology:

Proxenetes angustus is, according to Ax (1951), an indifferent species without any preference for a special habitat; it may be found in coarse sand as well as in fine mud. In the Lauwerszee I found the species in a salt-marsh pool in soft mud at a salinity of ca. $10^{\circ}/_{00}$ Cl'. In the salt-marsh area west of the Braakmanpolder the species was found also in a pool with a rather muddy bottom. There is coexisted with Monocelis fusca (form with the long penis stylet), Ptychopera westbladi and some less numerous species.

As *P. angustus* looks very similar to *P. simplex* and the recently discovered *P. bilioi* the possibility can not be excluded that Ax in fact had to do with more than one species. According to my observations *P. simplex* is mainly an inhabitant of fine-sand biotopes, while *P. angustus* seems to be a species of muddy bottoms in still-water biotopes.

In this species proterogyny occurs. In the population from the Braakman salt-marshes I found some specimens with a well-developed female copulatory apparatus, but in which the male apparatus was not yet or only slightly cuticularized. In the receptaculum seminis of one of those specimens I found sperm.

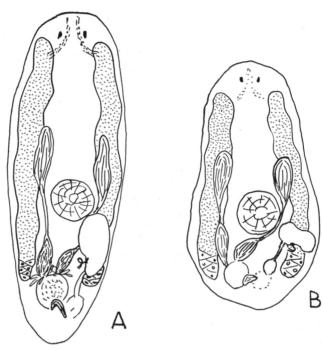


Fig. 24 A. Proxenetes bilioi nov. sp., general view. — B. P. minimus nov. sp., general view.

Proxenetes bilioi nov. sp. Fig. 24 A, 25.

The animals are oblong, 550-600 μ long, and white in colour. The anterior part of the body is truncate. Two diverging rhabdite tracks pass between the 2 eyes. The pharynx lies at $\frac{3}{5}$ of the body length. The testes are elongate and lie anteriorly to the pharynx. The vasa deferentia widen into very large spermaducal vesicles before entering the large muscular bulbus of the copulatory organ. The cuticular copulatory organ is 55–58 μ long, and has about the same shape as that of P. angustus, but its finer structure is quite different. It consists of an open stylet closing distally directly into a duct, which is surrounded by a funnel-shaped cuticular mantle. The stylet is only proximally curved, it is of equal width along its whole length apart from the distal end, which narrows into a blunt point. The stylet wall, however, increases progressively and distally in thickness, so that discharge of the sexual secretory products has to be via the side wall of the stylet as the distal tip is completely massive. When pressed under a coverslip the massive cuticular tip of the stylet breaks up into a bundle of fibres. The extreme proximal part of the stylet is bent downward forming a large hook, which is connected with the cuticular mantle. This rather wide mantle sheaths the stylet for $\frac{1}{2}$ of its length. Its upper margin is oblique and smoothly curved. The mantle itself consists of two broad, proximally coherent lamellae, each ending

distally in a blunt spine. The distal part of each lamella is strengthened by a large, wedge-shaped "free" spine, which has become completely adnate with this lamella. The vitellaria are elongate and extend from behind the eyes to the posterior part of the body, where they join the germaria. The receptaculum seminis is more or less bean-shaped and ca. 130 μ long. It is connected with the atrium genitale commune by a bursal canal. The bursal appendage consists of a double cuticular ring, from which arises a gradually narrowing duct that bends abruptly and then splits into two narrow, parallel ducts. The total length of the bursal appendage above the ring is $40{\text -}50~\mu$. The upper ring is very narrow, but at one side considerably thickened. This thickening is drawn out at each side into a $10{\text -}20~\mu$ long curved spine. The basal ring is drawn out into a triangular point, which is opposite to the thickening in the upper ring.

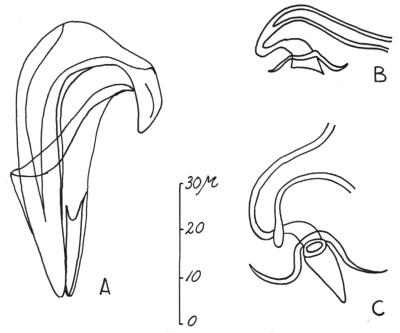


Fig. 25. Proxenetes bilioi nov. sp.: A. Cuticular copulatory organ; B-C. bursal appendage (after specimens from Bergen op Zoom).

Geographical distribution:

The species has been found in the Netherlands and along the German North Sea coast.

Locality in the Netherlands:

Province of Noord-Brabant:

Salt-marsh area south of Bergen op Zoom, October 1964, collected by BILIO (Type).

Locality in Germany:

State of Schleswig-Holstein:

Meldorfer Bucht, in salt-marsh creek, March 1964, collected by S. Lorenzen (BILIO, personal communication).

Ecology:

Three specimens of *P. bilioi* have been collected south of Bergen op Zoom in the transition belt between mud-flat and salt-marsh, where the glass-wort, *Salicornia europaea*, forms an association. The turbellarian fauna of this belt is very rich, and dominated by *Macrostomum balticum* Luther and *Psittorhynchus verweyi* nov. gen. nov. sp.¹).

Proxenetes trigonus Ax, 1960

Ax, Z. wiss. Zool. 163, 225–227, f. 20–23 (1960). – Fig. 26; Pl. VI, fig. A–E.

The animals are small, 0.4-0.6 mm long, and white in colour. The pharynx lies just behind the middle of the body. The testes are elongate and lie anteriorly to the pharynx. The vasa deferentia widen into very large spermaducal vesicles before entering the relatively small muscular bulbus of the copulatory organ. The cuticular copulatory organ is 40–50 μ long (own measurements 43–48 μ) and of a simple construction. It consists of a slightly curved stylet, of which the proximal end is bent downward and somewhat pennant-shaped. The stylet is open at its proximal end but soon closes into a duct. The distal tip of the stylet is often slightly incurved. The distal part of the stylet is surrounded by a wide, oblique, funnel-shaped cuticular mantle. The proximal margin of this mantle reaches almost to the extreme proximal end of the stylet but is not connected to it. The wall of the cuticular mantle shows 2 very obvious folds at each side of the stylet. When pressed under a coverslip the cuticular mantle is ruptured into 2 large spines, which follow the cuticular folds, and a very small spine the nature of which is not yet clear to me. A part of the cuticular mantle seems to be coherent with the stylet. The elongate vitellaria lie dorsolaterally and extend from just behind the eyes to far posterior of the pharynx. They continue at their caudal end into the germaria. The receptaculum seminis is very large and beanshaped. It is connected with the atrium genitale commune by a narrow bursal canal. The bursal appendage consists of a double ring from which a gradually narrowing duct arises. This duct coils and divides into two very narrow cuticular ducts. The total length of the appendage above the ring is ca. 70 μ . The basal part of the double ring is obliquely funnelshaped, has a thickened wall and is drawn out into a triangular point; the upper part is thickened at one side and this thickening is drawn out into two diametrically opposite spines of considerable size.

¹⁾ A description of this taxon will be published in the near future.

C. DEN HARTOG: A preliminary revision of the Proxenetes group (Trigonostomidae, Turbellaria). VI

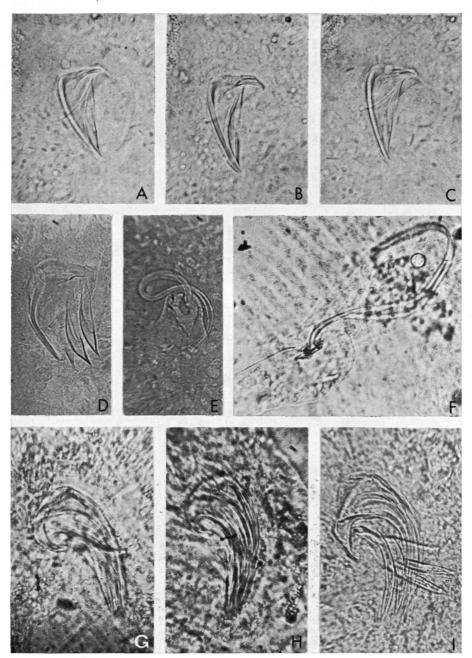


PLATE VI. Proxenetes trigonus Ax, 1960.

 $\mbox{A-C.}$ Cuticular copulatory organ, D. Cuticular copulatory organ, strongly squashed, so that the 2 large spines and the small spine have become clearly visible. E. Bursal appendage.

Proxenetes intermedius nov. sp.

F. Bursal appendage, placed on the receptaculum seminis. G–H. Cuticular copulatory organ. I. Cuticular copulatory organ showing the characteristic arrangement of the spines after squashing. (A–H after specimens from Kattendijke, Zuid-Beveland; I after a specimen from Bergen op Zoom).

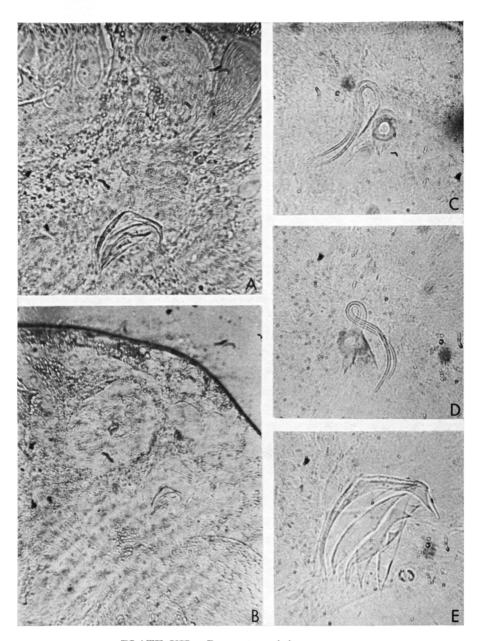


PLATE VII. Proxenetes minimus nov. sp.

A. Cuticular copulatory organ, muscular bulbus and the two spermaducal vesicles. B. Part of the genital system; to the right the cuticular copulatory organ, the muscular bulbus and the spermaducal vesicles are visible; to the left the receptaculum seminis with the bursal appendage, the ductus spermaticus and the bursa copulatrix.

Proxenetes segmentatus nov. sp.

C-D. Bursal appendage. E. Cuticular copulatory organ, strongly squashed. (A-B after a specimen from Oudenhoorn, Voorne-Putten; C-E after specimens from Bergen op Zoom).

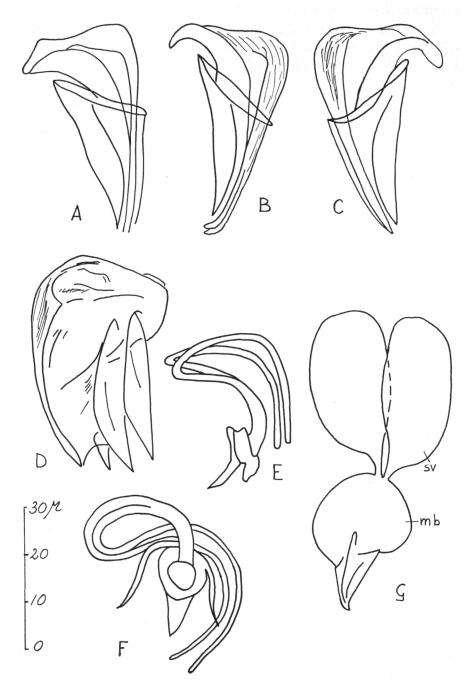


Fig. 26. Proxenetes trigonus Ax, 1960: A-C. Cuticular copulatory organ; Dr cuticular copulatory organ, strongly squashed; E-F. bursal appendage; G. cuticula. copulatory organ with muscular bulbus (mb) and the two spermaducal vesicles (sv) (after specimens from Kattendijke, Zuid-Beveland. The scale refers to A-F).

Geographical distribution:

P. trigonus has been found, according to Ax (l.c.), on the Westhever Sand along the German North Sea coast and in two localities in Kiel Bay. Recently it has been discovered in the south-western part of the Netherlands.

Locality in the Netherlands:

Province of Zeeland:

Zuid-Beveland: Kattendijke, intertidal sand flats, October and November 1964.

Ecology:

Along the German North Sea coast P. trigonus has been recorded from an intertidal sand-flat with Arenicola marina (Ax, l.c.). In Kattendijke the species occurs in a similar habitat. There it has been found as a scarce but constant species in detritus-rich fine sand with Arenicola marina in the vegetation of Zostera noltii. It inhabits the small elevations, on which the sea-grass is rooting, as well as the slight depressions between these elevations which at low tide are water-logged and covered with a thin film of water. In these depressions a rich turbellarian fauna occurs, of which Monocelis fusca (form with the long penis stylet) and Mecynostomum auritum are the dominant species. In the elevations, which at low tide are somewhat better drained, the turbellarian fauna is poor and without a dominant species. Higher on the sand-flat, where it borders on the last remains of a salt-marsh, P. trigonus was found in a muddy depression which at low tide was covered with a layer of $\frac{1}{2}-1$ cm water. This depression contained a rich turbellarian fauna completely dominated by representatives of the genus Promesostoma, of which P. rostratum was the most numerous species.

In Kiel Bay *Proxenetes trigonus* occurs sublittorally at 2–6 m depth in coarse and in fine sand (Ax l.c.); in the latter biotope it coexisted with *Arenicola marina*. In the same area it has been found once on a salt-marsh in the *Puccinellietum maritimae*, but this occurrence must be regarded as accidental (Billo, 1962, 1965).

It seems from these data that *Proxenetes trigonus* shows a preference for the more or less detritus-rich fine-sand bottoms with *Arenicola marina*.

The species is very active and likes to swim freely above the substrate. When the animals are contracted they show sometimes a slight segmentation, but this feature is not so pronounced in *P. trigonus* as in the related *P. segmentatus*. In the intestines of one specimen I found the remains of a copepod.

Proxenetes intermedius nov. sp.

Fig. 27-28; Pl. VI, fig. F-I.

The animals are oblong, 350–600 μ long, and white in colour. The anterior part of the body is truncate and contains the 2 eyes. The pharynx

lies at 3 of the body length. The testes are elongate and lie anteriorly to the pharynx. The vasa deferentia widen into large spermaducal vesicles before entering the muscular bulbus of the copulatory organ. The cuticular copulatory organ is 65-67 μ long and has a very characteristic shape (fig. 27 A). It consists of a very wide, open stylet, that distally closes into a duct surrounded by a funnel-shaped cuticular mantle. The stylet is curved over its whole length and narrows gradually. It shows several longitudinal folds. Its extreme proximal part is bent downward, forming a large hook. At its concave side it is accompanied by a narrower open duct, situated also within the cuticular mantle and showing the same curvature as the stylet. The cuticular mantle sheaths $\frac{3}{7} - \frac{1}{9}$ of the length of the stylet. Its upper margin is oblique and slightly curved and just connected with the extreme proximal hook of the stylet. The structure of the cuticular mantle is difficult to ascertain. By pressure on the coverslip it splits up into 8 spines, 4 of them remaining parallel with the distal part of the stylet, while the 4 other spines show the reverse curvature. Their position is comparable with the position that the tusks of an elephant have with respect to the trunk (fig. 27 B). The secondary duct splits probably into two longitudinal spines. The vitellaria are elongate and extend from behind the eyes to the posterior part of the body, where they join the germaria. The elongate to saccate receptaculum seminis is connected with the atrium genitale commune by a bursal canal. The bursal appendage consists of a double basal ring from which arises a

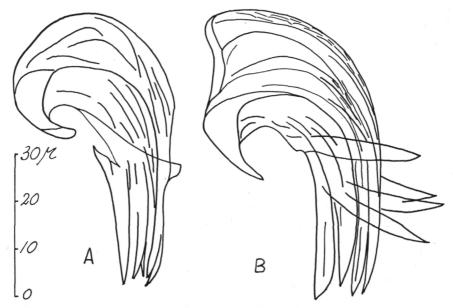


Fig. 27. Proxenetes intermedius nov. sp.: A. Cuticular copulatory organ. B. cuticular copulatory organ showing the characteristic arrangement of the spines after squashing (A after a specimen from Kattendijke, Zuid-Beveland, B after a specimen from Bergen op Zoom).

narrow duct that almost directly splits into two parallel ducts; these show a complete coil and then bend in a wide curve in proximal direction. The total length of the bursal appendage above the ring is 110–130 μ . The upper ring is thickened at one side and this thickening is drawn out into 2 diametrically opposite spines. The basal ring is drawn out into a triangular point.

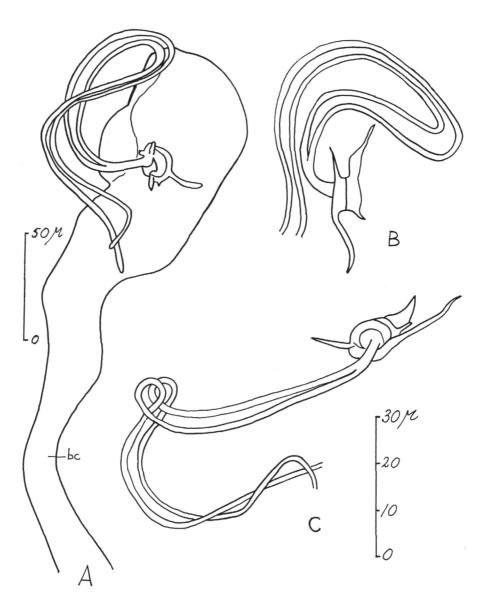


Fig. 28. Proxenetes intermedius nov. sp.: A. Bursal appendage placed on the receptaculum seminis; bc = bursal canal; B-C. bursal appendage (A and C after specimens from Bergen op Zoom, B after a specimen from Kattendijke, Zuid-Beveland. The smaller scale refers to A, the larger scale to B-C).

Geographical distribution:

The species has been found along the German North Sea coast and in the south-western part of the Netherlands.

Localities in the Netherlands:

Province of Zeeland:

Zuid-Beveland: 1. Kattendijke, sandy mud-flat, October and November 1964 (Type).

Province of Noord-Brabant:

2. Salt-marsh area south of Bergen op Zoom, October 1964, collected by BILIO.

Locality in Germany:

State of Schleswig-Holstein:

Meldorfer Bucht, upper part of intertidal belt, March 1964, collected by S. Lorenzen (BILIO, personal communication).

Ecology:

Proxenetes intermedius has been obtained from several samples and seems to be a characteristic species for the sandy mud-flats of the upper part of the intertidal belt. I found the species on the intertidal flats of Kattendijke in detritus-rich fine sand in the Zostera noltii association. It occurred there only in the slight depressions, where the bottom is covered by a thin layer of water during the time of exposure. Higher on the flat, at the transition with the remains of an old salt-marsh, I found the species also in a depression covered by 1 cm of water at low tide. There the bottom consisted of detritus-rich mud, with a low content of sand. In both cases it was accompanied by P. trigonus. Near Bergen op Zoom Bilio found the species also in the transition area between mud-flat and salt-marsh, in the association Salicornietum strictae and in a shallow muddy salt-marsh pool without vegetation. In all cases only one or a few specimens were obtained. The species does not seem to penetrate into the salt-marsh vegetation.

Both localities are situated in the euhaline part of the Deltaic area.

Proxenetes minimus nov. sp.

Fig. 24 B, 29-30; Pl. VII, fig. A-B.

The animals are oblong, $350-650~\mu$ long, and white in colour. The anterior part of the body is truncate and contains the 2 eyes. The pharynx lies in the posterior part of the body, at $\frac{3}{5}-\frac{2}{3}$ of the body length. The testes are elongate and situated anteriorly to the pharynx. The vasa deferentia widen into large spermaducal vesicles before entering the spherical muscular bulbus of the copulatory organ. The cuticular copulatory organ is plump, $32-37~\mu$ long, and its general shape is more or less

triangular. It consists of a wide, open stylet, that distally closes directly into a duct, surrounded by a funnel-shaped cuticular mantle. The stylet is curved over its whole length and becomes distally gradually narrower. The proximal end of the stylet is provided with a large recurved hook, of which the extreme tip is connected with the cuticular mantle. The upper margin of the cuticular mantle is obliquely placed and shows a slight curve. The mantle itself shows several folds and consists of 4 spiny lamellae, which are proximally coherent. Within the mantle 4 wedgeshaped, free spines occur as well. A very characteristic feature is the small bulge in the upper part of the concave side of the cuticular mantle. The mantle sheaths only $\frac{3}{7} - \frac{4}{7}$ of the length of the stylet. Its lower margin is oblique and the blunt distal tip of the stylet projects just outside the mantle. The vitellaria are elongate sacs which extend from behind the eyes to the posterior part of the body, where they join the germaria. The efferent tract of the female genital apparatus is differentiated into a bursa copulatrix and a receptaculum seminis connected to each other by a ductus spermaticus. The bursa copulatrix is ovoid, 60 μ long and 43 μ wide. The receptaculum seminis is more or less bean-shaped, 110–115 μ long and 50-55 μ wide. The narrow ductus spermaticus measures 40-45 μ . The bursal appendage consists of a double cuticular ring, from which arises a gradually narrowing duct, that coils once and splits into two short narrow, parallel ducts. The total length of the bursal appendage above the ring is only 30-35 μ . The upper ring is at one side provided with a long inflexed spine. Just below that spine the basal ring is drawn out into a triangular point.

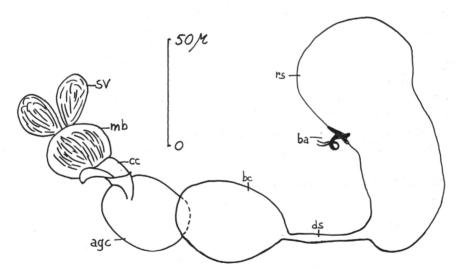


Fig. 29. Proxenetes minimus nov. sp.: Genital organs; bc = bursa copulatrix, ds = ductus spermaticus, rs = receptaculum seminis, ba = bursal appendage, agc = atrium genitale commune, cc = cuticular copulatory organ, mb = muscular bulbus, sv = spermaducal vesicle.

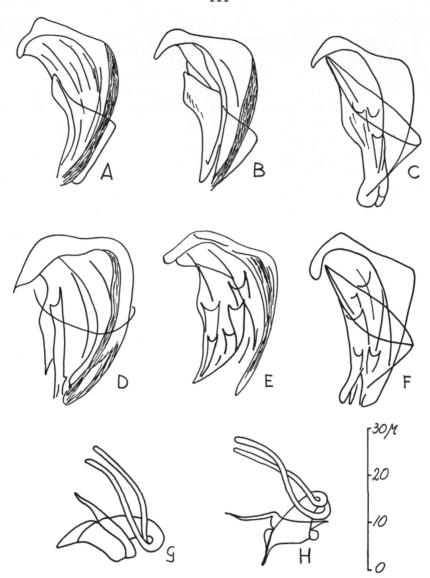


Fig. 30. Proxenetes minimus nov. sp.: A-F. Cuticular copulatory organ; G-H. bursal appendage (A, D-E after specimens from Bergen op Zoom, B after a specimen from Oudenhoorn, Voorne-Putten, C and F-H after specimens from Ossendrecht.

Noord-Brabant).

Geographical distribution:

The species has been found so far only in the south-western part of the Netherlands.

Localities in the Netherlands:

Province of Zuid-Holland:

Voorne-Putten: 1. Salt-marsh south of Oudenhoorn, November 1964.

Province of Noord-Brabant:

- 2. Salt-marsh south of Bergen op Zoom, October 1964, collected by BILIO.
- 3. Ossendrecht, salt-marsh, October 1964, collected by BILIO (Type).

Ecology:

Proxenetes minimus seems to be a characteristic species of the salt-marshes, as it has been found only in low grass vegetations dominated by Puccinellia maritima. Its distribution in the Deltaic area characterizes the species as very euryhaline. Bergen op Zoom is situated in the euhaline section, Ossendrecht in the border area between poly- and mesohalinicum, while the salt-marsh near Oudenhoorn is in the mesohalinicum; the average salinity in the latter locality amounts to ca. $2~0/_{00}$ Cl'.

(to be continuea)

A PRELIMINARY REVISION OF THE PROXENETES GROUP (TRIGONOSTOMIDAE, TURBELLARIA). VII

BY

C. DEN HARTOG

(Communicated by Dr. J. Verwey at the meeting of November 27, 1965)

Proxenetes segmentatus nov. sp.

Fig. 31-33; Pl. VII, fig. C-E.

The animals are oblong, 0.6-1.2 mm long, and white to yellowish brown in colour. When contracted the body has an obvious segmented appearance. The anterior part of the body is truncate and contains the two eyes; in a few cases, however, no eye-pigment could be found. The pharynx lies just behind the middle of the body. The testes are elongate and situated laterally to the pharynx. The vasa deferentia widen into large spermaducal vesicles before entering the muscular bulbus of the copulatory organ. The cuticular copulatory organ is plump and 57-60 μ long. Its general shape is more or less the same as that of P. minimus but its finer structure is different and more complicated and its size almost twice as much. It consists of a wide, open stylet, that distally closes directly into a duct surrounded by a funnel-shaped cuticular mantle. The stylet is faintly curved over its whole length and becomes distally gradually narrower. The proximal end of the stylet is bent downward, forming a large hook of which the ultimate tip is connected with the cuticular mantle. The cuticular mantle sheaths $\frac{3}{5}$ of the length of the stylet. The upper margin of the cuticular mantle is obliquely placed and slightly curved. The structure of the mantle itself is rather obscure. It consists of at least 6 spiny lamellae, which show ridges and folds. Within the mantle 6-8 rather complicate free spines occur. Some of these spines are wedge-shaped, others show triangular lateral processes or are partly untraceable in the tangle of spines. The vitellaria are elongate and extend from behind the eyes to the posterior part of the body where they join the germaria. The efferent tract of the female genital apparatus is differentiated into a small bursa copulatrix and a receptaculum seminis, which are connected by a wide, somewhat twisted ductus spermaticus. The latter is 100-140 μ long. The bursa copulatrix is a 30-35 μ long bulge with a wide opening in the atrium genitale commune. The receptaculum seminis is rather variable in shape and may be bean-shaped to elongate saccate. It is 70–120 μ long and 30–45 μ wide. The bursal appendage consists of a

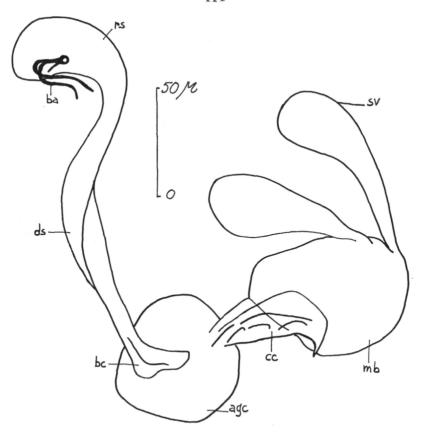


Fig. 31. Proxenetes segmentatus nov. sp.: Genital organs, bc = bursa copulatrix, ds = ductus spermaticus, rs = receptaculum seminis, ba = bursal appendage, agc = atrium genitale commune, cc = cuticular copulatory organ, mb = muscular bulbus, sv = spermaducal vesicle.

double cuticular ring, from which arises a duct that splits almost immediately above the ring into two parallel narrow ducts. These ducts coil once. The total length of the bursal appendage above the ring is ca. 60 μ . The upper ring is at one side provided with a thickening which at only one side is drawn out into a 30–35 μ long spine. The basal ring is drawn out into a triangular point.

Geographical distribution:

The species has been found in one locality in the Netherlands.

Locality in the Netherlands:

Province of Noord-Brabant:

Salt-marsh area south of Bergen op Zoom, October 1964, collected by BILIO (Type).

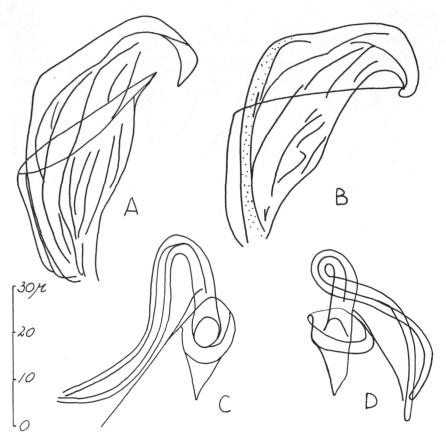


Fig. 32. Proxenetes segmentatus nov. sp.: A-B. Cuticular copulatory organ; C-D. bursal appendage (after specimens from Bergen op Zoom).

Ecology:

In the transition belt between mud-flat and salt-marsh, where the glass-wort, Salicornia europaea, is the only phanerogam, P. segmentatus is probably not uncommon. The sample of Dr. Bilio contained 19 mature and 6 juvenile specimens. The turbellarian fauna of this belt is dominated by Macrostomum balticum and Psittorhynchus verweyi. P. segmentatus has been collected also in a shallow, muddy salt-marsh pool.

The animals are very sluggish. When contracted they show a great number of rings, giving them a segmented appearance. I have noticed this feature in a lesser extent also in *P. trigonus*. Among the 25 specimens which I had at my disposal two lacked eye pigment. *P. segmentatus* is the only species of the genus, of which I have seen blind specimens.

The species is proterogynic, as among the juvenile specimens there was one that had a well-developed female genital apparatus but no trace of a cuticular copulatory organ. It could be easily identified by the characteristic structure of the efferent tract of the female genital apparatus and its segmented appearance.

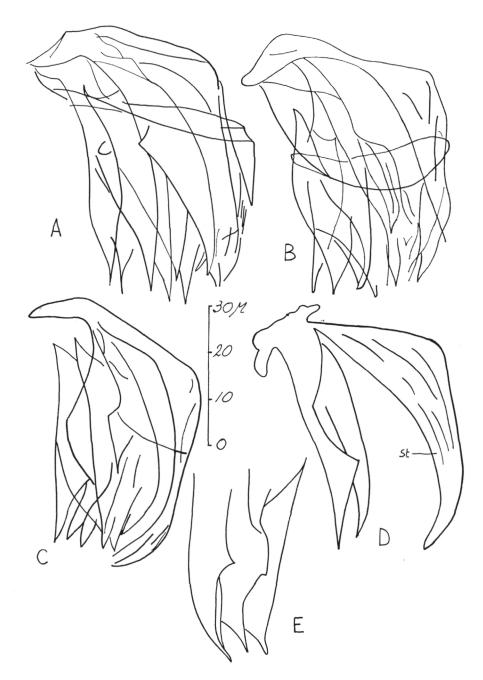


Fig. 33. Proxenetes segmentatus nov. sp.: A–C. Cuticular copulatory organs of three specimens, strongly squashed so that the individual spines have become visible; D–E. Some spines and the stylet (st) after preparation (after specimens from Bergen op Zoom).

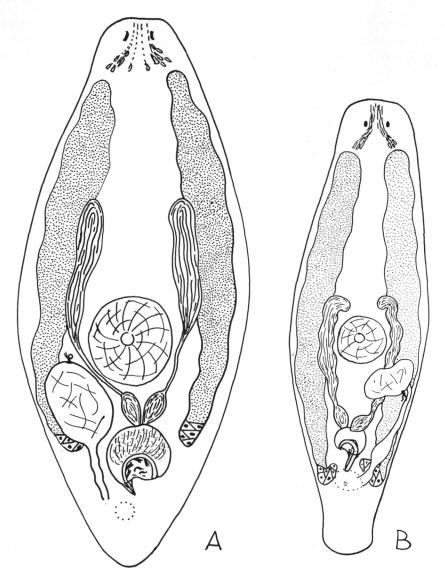


Fig. 34 A. Proxenetes quadrispinosus nov. sp., general view. — B. Proxenetes britannicus nov. sp., general view.

Proxenetes quadrispinosus nov. sp.

Fig. 34 A, 35; Pl. VIII-IX.

The animals are quite plump, 1–1.3 mm long, and grey in colour. The anterior part of the body is truncate and contains 4 well-developed rhabdite tracks, which pass between the 2 very frontally placed eyes. The pharynx lies at $\frac{2}{3}$ of the body length. The testes are elongate and situated for the larger part anteriorly to the pharynx. The vasa deferentia widen into very large spermaducal vesicles before they enter the large

muscular bulbus of the copulatory organ. The cuticular copulatory organ is 85–95 μ long and very complicated in structure. It consists of a stylet that receives sperm as well as the granular secretion of the prostatic glands. The proximal part of the stylet is semicircularly curved, the

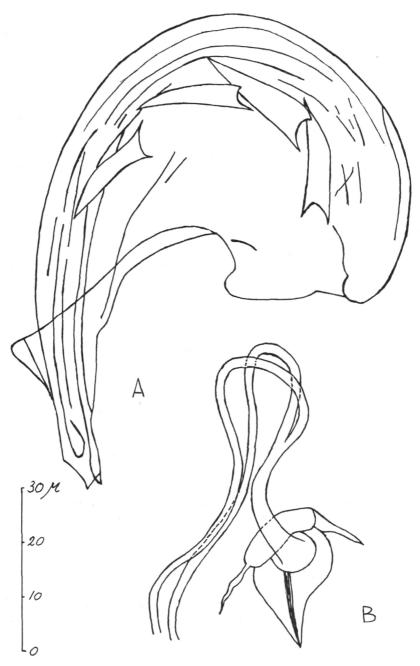


Fig. 35. Proxenetes quadrispinosus nov. sp.: A. Cuticular copulatory organ;
 B. bursal appendage (after specimens from Stavenisse, Tholen).

C. DEN HARTOG: A preliminary revision of the Proxenetes group (Trigonostomidae^c Turbellaria). VII

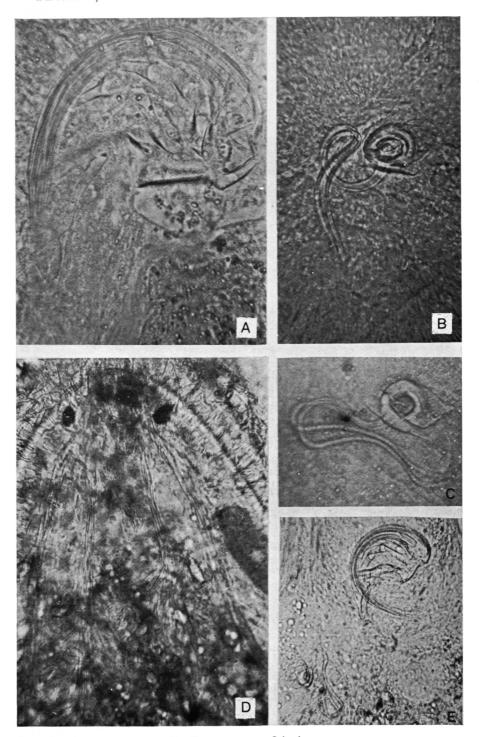
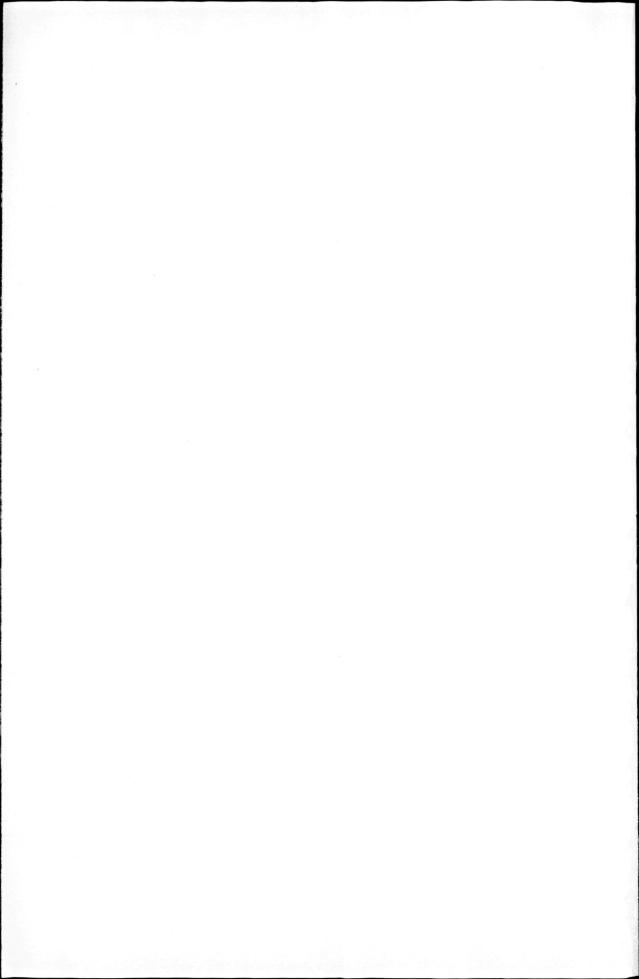


PLATE VIII. Proxenetes quadrispinosus nov. sp.

A. Cuticular copulatory organ. B-C. Bursal appendage. D. Anterior part of a squashed specimen showing the position of the eyes and the tracts of rhabdites; to the right a parasitic gregarine is visible. E. Cuticular copulatory organ (slightly damaged) and bursal appendage. (After specimens from Stavenisse, Tholen).



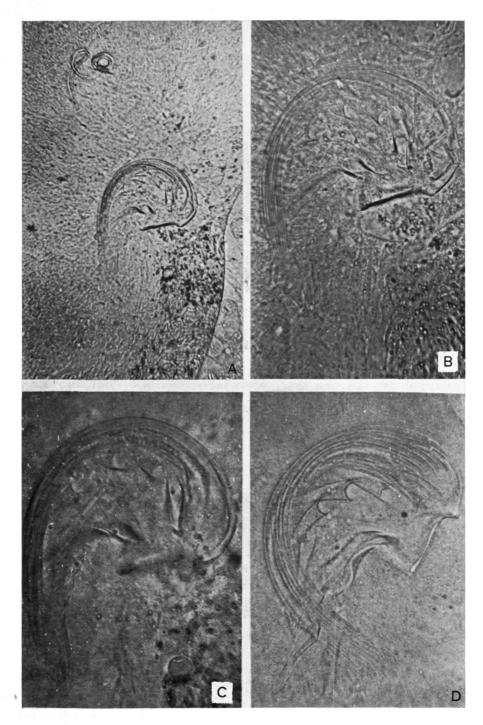


PLATE IX. Proxenetes quadrispinosus nov. sp.

A. Cuticular copulatory organ and bursal appendage. B-D. Cuticular copulatory organ, in D. slightly damaged. (After specimens from Stavenisse, Tholen).

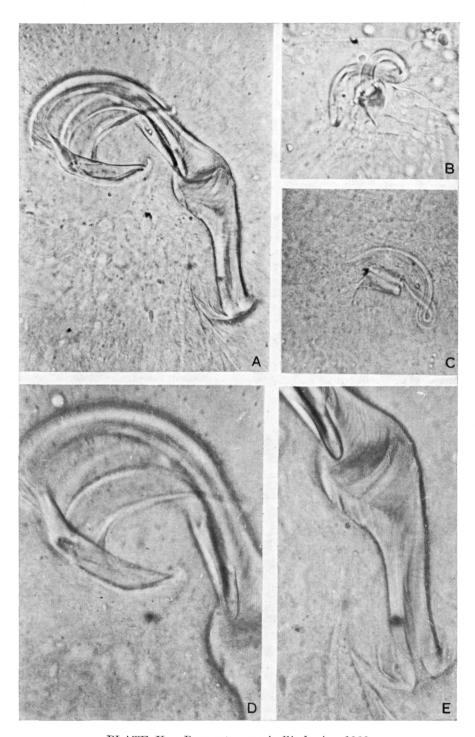


PLATE X. Proxenetes puccinellicola Ax, 1960.

A. Cuticular copulatory organ and claviform organ. B—C. Bursal appendage. D. Cuticular copulatory organ. E. Distal part of the cuticular copulatory organ and the claviform organ. (After specimens from Stavenisse, Tholen).

straight distal end is short, viz. $\frac{1}{3}$ of the total length of the copulatory organ. The straight part of the stylet is surrounded by a funnel-shaped mantle, which consists of 4 broad lamellae, distally ending in blunt spines, and two probably free spines. This funnel is connected with the distally directed proximal end of the stylet. The proximal arc of the copulatory organ is covered also by the stiffened atrial membrane. The concave side of the stylet is lined with 4 very characteristic, wedge-shaped spines, which are distally acute and proximally bicuspidate. The stylet itself consists of longitudinal fibres, which in squash preparations become loosened by strong pressure on the coverslip. The vitellaria lie dorsolaterally and are elongate, reaching from just behind the eyes. The germaria are situated just posterior to the pharynx. The receptaculum seminis is very large, bean-shaped and connected with the atrium genitale commune by a narrow bursal canal. The bursal appendage consists of a double ring, from which arises a gradually narrowing duct coiling once and splitting into 2 long, narrow, parallel curved ducts. The basal ring is obliquely funnel-shaped and drawn out into a triangular point. The upper ring is thickened on one side and this thickening is drawn out into two opposite spines.

Geographical distribution:

The species has been found so far only in one locality in the Netherlands.

Locality in the Netherlands:

Province of Zeeland:

Tholen: Stavenisse, salt-marsh creek, April and November 1963 (Type).

TABLE 2
The turbellarian fauna of the salt-marsh creek of Stavenisse (Tholen)

Proxenetes quadrispinosus nov. sp.	3	2
Still-water species:		
Provortex balticus (Schultze)	7	7
Monocelis fusca Oersted (form with short penis)	1	11
Proxenetes flabellifer Jensen	1	1
Ptychopera westbladi (Luther)	5	***************************************
$Promesostoma\ rostratum\ { m Ax}$	2	
Promonotus schultzei Meixner	1	-
Fine-sand species:		
Provortex tubiferus Luther	16	9
Proxenetes simplex Luther	5	1
Pogaina suecica (Luther)	. 2	
Eurytope species:		
Promesostoma marmoratum (Schultze)	2	7
Archilopsis unipunctata (Fabricius)	2	4
Pseudostomum quadrioculatum (Leuckart)		29
Both samples taken on April 23, 1963.		

Ecology:

In the creek which runs through the salt-marsh of Stavenisse $P.\ quadrispinosus$ has been found in several samples taken from the muddy sand bottom. It seems to be a member of the still-water association of detritusrich fine sand. This can be seen from Table 2, in which the quantitative composition of 2 samples of turbellarians from the type locality of Proxenetes quadrispinosus is given.

The average salinity of the flood water, which at every tidal period fills the salt-marsh creek of Stavenisse, is ca. $16.5\,^{0}/_{00}$ Cl'. In spring and in late autumn lower salinities (down to $14\,^{0}/_{00}$ Cl') sometimes occur. The species seems to feed mainly on diatoms. In several specimens I found the intestinal tract completely filled with diatom valves and found only a few remains of nematodes or oligochaetes. Once I found a specimen that was parasitized by a gregarine.

Proxenetes britannicus nov. sp.

Fig. 34 B, 36.

The animals are slender, 500–850 μ long, and greyish white in colour. The anterior part of the body is truncate and contains the 2 eyes. The pharynx lies just behind the middle of the body. Near the caudal end the body is slightly constricted, so that a somewhat spatulate rear end is formed. The testes are sausage-shaped and anteriorly curved. They are situated in the posterior part of the body, dorsolateral to the pharynx. At their anterior end they are strongly swollen, becoming gradually narrower in caudal direction and showing no marked transition to the vasa deferentia. The vasa deferentia widen abruptly into large spermaducal vesicles before they enter the large muscular bulbus of the copulatory organ. The cuticular copulatory organ is 64–71 μ long and consists of a stylet, which is proximally semicircular. The extreme proximal end of the stylet is an inwardly directed hook. There the stylet is open, but it closes into a duct at the middle of the semicircular arc. The straight and extremely thick-walled distal half of the stylet is sheathed by a slightly oblique, funnel-shaped cuticular mantle. The proximal margin of the funnel is connected with the proximal hook of the stylet. The funnel is $\frac{1}{2} - \frac{3}{5}$ the length of the cuticular copulatory organ. Its distal part closely adheres to the distal part of the stylet. The proximal arc of the stylet is covered also by a stiffened, finely striated atrial membrane. At the concave side of the stylet one small wedge-shaped spine occurs. This spine is difficult to find when the cuticular copulatory organ is intact but it becomes visible by pressing hard on the coverslip. The distal part of this spine is just sheathed by the cuticular mantle. The granular secretion as well as the sperm are discharged through the stylet. The vitellaria are elongate and extend from just behind the eyes to far posterior of the harynx. They continue at their caudal end into the germaria. The

receptaculum seminis is bean-shaped to saccate and communicates with the atrium genitale commune by a markedly differentiated bursal canal. The latter shows a deep constriction in its proximal part and is at its distal end widened into a bursa-like sac, which is at right angles to the bursal canal. The bursal appendage consists of a double ring from which arises one cuticular duct, showing a sharp bend and then splitting into two short narrower ducts. These narrow ducts are of the same length as the undivided proximal duct. The total length above the ring is ca. 40 μ . The basal ring is thick and at one point drawn out into a long strong spine. The upper ring is delicate and is provided with one long, thin spine, which is situated just above the spine of the basal ring. The upper margin of the upper ring is often crenulate.

Between *P. britannicus and P. quadrispinosus* a close systematic relationship exists. The shape of the cuticular copulatory organ differs somewhat in both species, but it is much more important that they are the only species in the genus which have the proximal part of the stylet covered by a stiffened atrial membrane and which have spines lining the proximal arc of the stylet.

Geographical distribution:

The species has been found in England and Scotland, and recently also in the Netherlands.

Locality in the Netherlands:

Province of Noord-Brabant:

Salt-marsh area south of Bergen op Zoom, October 1964, collected by BILIO.

Locality in England:

County of Devon:

Salt-marsh along the river Tamar, opposite Cargreen (in the Plymouth area), July 1964 (Type).

Locality in Scotland:

County of East Lothian:

Aberlady Bay local nature reserve, salt-marsh, ca. $30~\mathrm{km}$ east of Edinburgh, August 1964.

Ecology:

Proxenetes britannicus has been found only in samples from salt-marshes. I collected several specimens in the Puccinellietum maritimae on a salt-marsh along the river Tamar. They lived in a humose, clayish bottom with crumbly texture together with Uteriporus vulgaris and Monocelis lineata. On the salt-marsh along Aberlady Bay the species was numerous

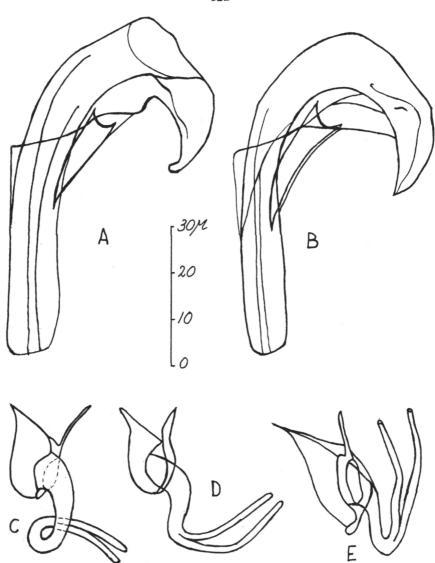


Fig. 36. Proxenetes britannicus nov. sp.: A-B. Cuticular copulatory organ; C-E. bursal appendage (A and E after specimens from Aberlady Bay near Edinburgh, B-D after specimens from the Tamar estuary near Plymouth).

in an initial stage of the *Puccinellietum maritimae* on sandy clay. There it was accompanied by *Monocelis lineata*, *M. fusca* (form with the long penis stylet), *Proxenetes deltoides*, *Provortex karlingi* and a few other species. Bilio also recorded the species from the *Puccinellietum maritimae* in the salt-marsh area south of Bergen op Zoom.

Although the salt-marsh along the river Tamar is situated rather far upstream, its flora and fauna suggest that it belongs yet to the polyhaline section of the estuary. Aberlady Bay is an euhaline station, which may

be subjected to a temporary decrease in salinity due to discharge of fresh water.

In the intestinal tract of several specimens I found the remains of oligochaetes.

In *P. britannicus* of the sample collected near Bergen op Zoom proterogyny has been observed. In some specimens the female genital tract was well-developed, while the male apparatus was not yet cuticularized or could not be traced at all.

Proxenetes puccinellicola Ax, 1960

Ax, Z. wiss. Zool. 163, 222-223, f. 9-12 (1960). - Fig. 37-38; Pl. X.

The animals are slender, $1-1\frac{1}{2}$ mm long, and grey or milky white in colour. The pharynx is small and lies at ca. ²/₃ of the body length. The cuticular structures in this species are very characteristic. The cuticular copulatory apparatus is 130-180 μ long. It consists of a semicircularly curved stylet through which the sperm and granular secretion are discharged and has an oblong opening at its proximal end, from where a large hook extends distally. This hook is connected with some cuticular lamellae, which together surround the proximal part of the stylet like a sheath. The distal part of the stylet continues through a strong claviform organ, which is at its proximal part considerably swollen. At the tip of this organ the ductus ejaculatorius widens and from the wall of the tip two proximally directed projections originate, thus giving the tip an anchor-shaped appearance. According to Ax (l.c.) these two projections probably form the optical cross-section of a recurved edge of the cuticular wall, surrounding the distal end of the claviform organ like a cuff. In my preparations I did not find the slightest indication that such a cuff really exists. The surface of the claviform organ is finely striate, due to two perpendicular systems of spirally coiled fibrous bundles, which are distally fixed to the two distal projections of the claviform organ. By strong pressure on the coverslip these projections disintegrate and at the same time the fibrous bundles straighten. The receptaculum seminis is $100-130~\mu$ long and more or less bean-shaped, with a very characteristic oblong bulge near its distal end. The bursal appendage consists of a double ring from which a gradually but slightly narrowing duct arises. This coils once and divides into two very narrow cuticular ducts. The basal part of the double ring is obliquely funnel-shaped and has an extremely thick wall, the other part is drawn out into two diametrically opposite spines.

Geographical distribution:

The species was known only from two localities, Nordstrand and Meldorfer Bucht along the German North Sea coast (Ax, l.c.). Recently the species has been discovered also in several localities in the southwestern part of the Netherlands.

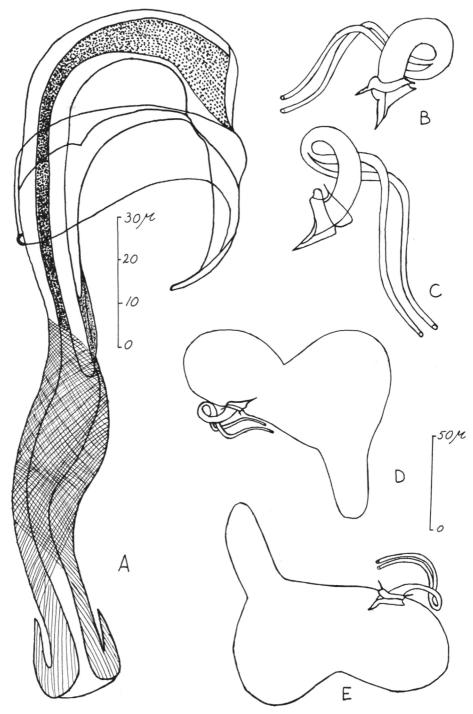


Fig. 37. Proxenetes puccinellicola Ax, 1960: A. Cuticular copulatory organ; B–C. bursal appendage; D–E. receptaculum seminis with bursal appendage (A–D after specimens from "het Zwin", Zeeuws Vlaanderen, E after a specimen from Stavenisse, Tholen. The larger scale refers to A–C, the smaller scale to D–E).

Localities in the Netherlands:

Province of Zeeland:

Tholen: 1. Stavenisse, salt-marsh, November 1963.

Zeeuws Vlaanderen: 2. International nature reserve "het Zwin", in the Dutch part, April 1962, November 1964; 3. Verdronken Zwarte Polder near Cadzand, November 1964.

Province of Noord-Brabant:

4. Salt-marsh area south of Bergen op Zoom, October 1964 (BILIO, personal communication).

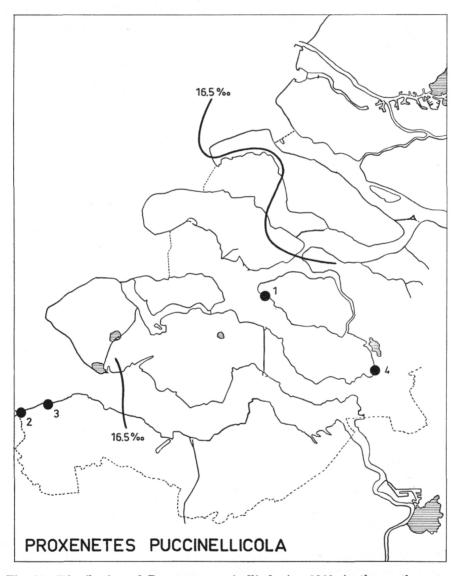


Fig. 38 Distribution of *Proxenetes puccinellicola* Ax, 1960, in the south-western part of the Netherlands. The average annual isohaline of $16.5~^{0}/_{00}$ Cl $^{\prime}$ at high tide is given.

Ecology:

Ax (l.c.) and Billo (1962, 1965) recorded P. puccinellicola from the lower part of the Puccinellietum maritimae on acrescent salt-marshes. On the salt-marshes in the Deltaic area the species was found on rather sandy detritus-rich soil in the same plant association. Along "het Zwin", the sea-inlet at the frontier between the Netherlands and Belgium, the Puccinellietum locally forms a narrow belt, which seems rather stable there, as the deposit of silt in the vegetation is hardly of importance and as no features of abrasion could be noticed. The two specimens of P. puccinellicola, obtained from a mud sample of this vegetation in April 1962, were associated with several specimens of Baicalellia brevituba (Luther). No other flatworms were found in this sample. In November 1964 the species was found in a similar station, but with a high siltcontent. There it was accompanied by a rich turbellarian fauna, which is listed in Table 3. In the same locality P. puccinellicola was collected in the Halimionetum portulacoidis of the outerside of the levees at a slightly higher level than the Puccinellietum maritimae (Billo, personal communication).

In the Verdronken Zwarte Polder near Cadzand both Billo and I obtained P. puccinellicola from the Puccinellictum maritimae.

On the salt-marsh of Stavenisse the Puccinellietum maritimae occurs only in the rather extended, shallow depressions, called "kommen", which are surrounded by the levees of the small tidal creeks. They are flooded only when the floods are high and the water flows over the levees. When the water falls again, discharge from the depressions is hampered, so that the water stagnates and flows off only slowly. The bottom of these depressions is always very wet. A small clump of Puccinellia maritima with the earth between the roots was taken and put in a glass-jar with purified sea water. This sample contained altogether 14 species of Turbellaria, of which Proxenetes puccinellicola, Monocelis lineata and Vejdovskya halileimonia were abundant. The other species were represented by a single or a few specimens. The composition of this sample is given also in Table 3.

Bilio (personal communication) found *P. puccinellicola* on the salt-marsh south of Bergen op Zoom only in the *Puccinellietum maritimae*. So far the species has been recorded only from the *Puccinellietum maritimae* and once from the adjacent *Halimionetum portulacoidis*.

Although the distribution of the species in the Deltaic area is imperfectly known it may be mentioned that all localities are situated in the euhalinicum, where the average salinity is $16.5~^{0}/_{00}$ Cl' or higher, and lower salinities occur only for short periods in spring and late autumn.

P. puccinellicola is omnivorous and apparently very voracious. In the intestinal tract I found valves of diatoms, nematodes and oligochaetes and also remains of animals of other groups. Sometimes I found 2 or 3 complete worms together in the intestines of one animal. In the bodies I noticed sometimes the occurrence of parasitic gregarines.

TABLE 3

The turbellarian fauna of the Puccinellietum maritimae on the salt-marshes of Stavenisse (Tholen) and "het Zwin" (Zeeuws Vlaanderen).

Salt-marsh species:	Stavenisse ¹)	Zwin²)
Proxenetes puccinellicola Ax	20	5
Vejdovskya halileimonia Ax	15	3
Coelogynopora schulzii Meixner	1	2
Proxenetes deltoides nov. sp.	2	
Ptychopera tuberculata (Von Graff)	1	
Macrostomum spirale Ax		17
Macrostomum balticum Luther		3
Proxenetes pratensis Ax		2
Still-water species:		
Monocelis lineata (O. F. Müller)	30	11
Monocelis fusca Oersted (form with the long penis stylet)	4	
Proxenetes karlingi Luther	· 1	
Maehrenthalia dubia Ax	1	
Provortex balticus (Schultze)	1	
Mecynostomum auritum (Schultze)	1	3
Fine-sand species:		
Provortex tubiferus Luther	2	
Macrostomum pusillum Ax	1	
Other species:		
Microstomum sp.		2
Unidentified	1	1

¹⁾ Surveyed on November 20, 1963. 2) Surveyed on November 2, 1964.

In an aquarium the animals swim sometimes freely around. Strong light stimulates their activity. I did not notice that they were attracted to the light source, as was the case with *Vejdovskya halileimonia*, nor that they shunned the light.

In P. puccinellicola proterogyny occurs. The specimen that I collected in the Verdronken Zwarte Polder had a well-developed female tract but the male copulatory organ had been hardly cuticularized. Its contours could be distinguished already quite well, in particular the stylet and some parts of the cuticular mantle. The claviform distal extension of the copulatory organ, however, did not show any differentiation except for some longitudinal striation.

(To be continued)

A PRELIMINARY REVISION OF THE PROXENETES GROUP (TRIGONOSTOMIDAE, TURBELLARIA). VIII

 \mathbf{BY}

C. DEN HARTOG

(Communicated by Dr. J. Verwey at the meeting of November 27, 1965)

Proxenetes inflatus nov. sp.

Proxenetes nov. spec. II

Riedl, Thalassia Jugosl. 1, 150, 151, 154, 155 (1956). - Fig. 39.

The animal is slender, 0.7-0.9 mm long, and milky white in colour. The anterior part of the body is truncate, with the 2 eyes in the extreme front. The pharynx lies at $\frac{2}{3}$ of the body length. The testes are elongate and lie behind the middle of the body. The vasa deferentia widen into spermaducal vesicles before they enter the very large muscular bulbus of the copulatory organ. The cuticular copulatory organ is ca. 40 μ long and consists of a stylet surrounded by a cuticular mantle. The stylet is proximally semicircular and open; distally it closes into a straight, wide, somewhat inflated duct. The cuticular mantle sheaths almost completely the straight part of the stylet; only the ultimate tip projects out of the mantle. The cuticular mantle is strongly inflated and gives the copulatory organ a saccate appearance. The proximal margin of the cuticular sheath is connected with the proximal end of the stylet. The vitellaria extend from close behind the eyes to $\frac{5}{6}$ of the body length, where they bend suddenly in proximal direction and join the germaria. The receptaculum seminis is bean-shaped. The bursal appendage consists of a cuticular ring, placed on a slight elevation of the receptaculum seminis. A sharply narrowing duct, coiling once and dividing into 2 narrower cuticular ducts, originates from this ring.

$Geographical\ distribution:$

This species has been discovered by Dr. R. Riedl along the Swedish west coast.

Locality in Sweden:

Province of Bohuslän:

Kristineberg, Gullmar Fjord, channel between the island of Rödskär and Grötö, September 1951 (Type; RIEDL, personal communication; see also RIEDL, 1956).

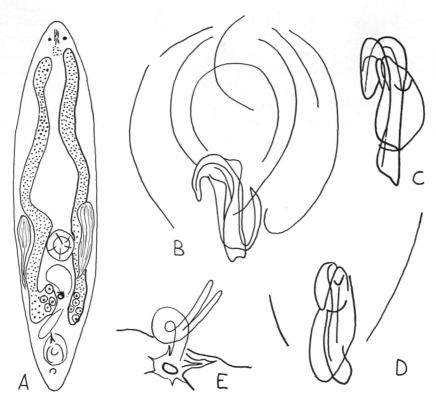


Fig. 39. Proxenetes inflatus nov. sp.: A. General view; B-D. copulatory organ; E. bursal appendage (after unpublished sketches of Dr. R. Riedl).

Ecology:

Dr. Riedl found only one specimen of this peculiar species in a sample, taken from a soft muddy loam bottom at 40 m depth. The accompanying turbellarian fauna consisted mostly of Acoela, among which *Paraphanostoma submaculatum* Westblad and *Haploposthia viridis* (An der Lan) were the most numerous. *Proxenetes inflatus* is probably characteristic for this deep-water community. It does not show close affinity to any of the other known representatives of the *Angustus* section.

In the intestinal tract a partly digested nemertine was found.

Proxenetes pratensis Ax, 1960

Ax, Z. wiss. Zool. 163, 223-225, f. 13-19 (1960). - Fig. 40-41.

The animals are slender, 0.3–0.6 mm long, white in colour and with a slight constriction near their caudal end, so that a somewhat spatulate rear end is formed. The anterior part of the body is truncate and contains the 2 eyes. The pharynx lies usually in the middle of the body but can be situated slightly more anterior. The testes are ovoid and lie on both sides of the pharynx or slightly more posterior. The vasa deferentia

widen into relatively small spermaducal vesicles before entering the muscular bulbus of the copulatory organ. The cuticular copulatory organ is $52-55 \mu$ long. The stylet is at its proximal end narrowly bow-shaped, so that the funnel-shaped proximal opening is in fact distally directed. Except for its ultimate proximal part the width of the stylet is equal over the whole of its length. The cuticular mantle sheaths the stylet only at the transition between the curved and the straight part. An obtuse linear lamella originates from this "cuff" at an acute angle. This lamella lies close to the inward side of the straight part of the stylet but does not reach to the distal tip of the latter. The upper margin of the cuticular "cuff" is connected with the ultimate proximal tip of the stylet. The elongate vitellaria extend from behind the eyes over $\frac{3}{4}$ of the body length before they join the germaria. The efferent tract of the female genital apparatus does not show a differentiation into a receptaculum seminis and a bursal canal, it consists merely of a large tubular bursa seminalis, which gradually narrows to its distal end. At the transition to the atrium genitale commune an ovoid, 18 μ long lump of secretory products occurs. This lump has been drawn also by Ax (l.c. fig. 14), although it has not been mentioned in the text of his paper. The bursal appendage is placed on the proximal end of the bursa seminalis and

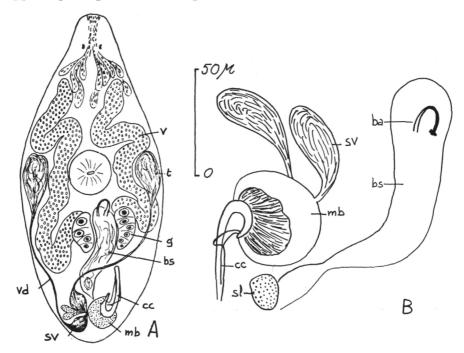


Fig. 40. Proxenetes pratensis Ax, 1960: A. General view. B. genital organs; v = vitellarium, g = germarium, t = testis, cc = cuticular copulatory organ, mb = muscular bulbus, sv = spermaducal vesicle, vd = vas deferens, bs = bursa seminalis, ba = bursal appendage, sl = lump of secretory products (A after Ax, B after a specimen from "het Zwin", Zeeuws Vlaanderen).

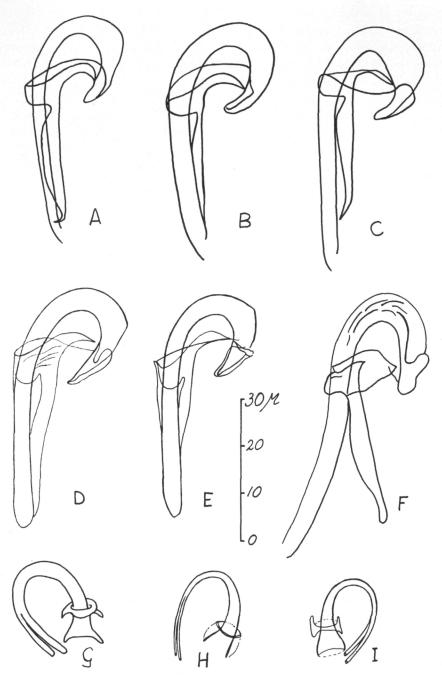


Fig. 41. Proxenetes pratensis Ax, 1960: A–E. Cuticular copulatory organ; F. cuticular copulatory organ, strongly squashed; G I. bursal appendage. (A–C, F–G after specimens from "het Zwin", Zeeuws Vlaanderen; D–E, H–I after Ax. The scale refers only to A–C and F–G).

consists of a duct that is funnel-shaped at its base, but soon becomes narrower. It curves semicircularly and splits into 2 short, very narrow, almost straight cuticular ducts. A short distance above its funnel-shaped base the duct is surrounded by a cuticular ring, which is armed with 2 very small, reflexed spines.

The species has a very isolated position in the genus. Certainly it is related to *P. cisorius*, with which it has in common, that the cuticular mantle sheaths the stylet only partly and that the ring surrounding the bursal appendage is situated above the base. However, the affinity is not very close, as the species differ in the differentiation of the efferent tract of the female genital apparatus, which is in *P. pratensis* a tubular sac but in *P. cisorius* consists of a well-developed receptaculum seminis and a bursa copulatrix connected by a narrow ductus spermaticus. Other differences exist in the position of the pharynx, the shape of the bursal appendage and the structure of the cuticular copulatory apparatus.

Geographical distribution:

P. pratensis has been found along the German North Sea coast on the "Grüne Insel" near the mouth of the river Eider, and in two localities in Kiel Bay (Ax, l.c.; Billo, 1962, 1965). Recently, it has been discovered also in one locality in the south-western part of the Netherlands.

Locality in the Netherlands:

Province of Zeeland:

Zeeuws Vlaanderen: International nature reserve "het Zwin", in the Dutch part, November 1964.

Ecology:

According to Bilio (1962, 1965) Proxenetes pratensis is a faithful species for the grassy salt-marsh vegetations, in particular for the Puccinellietum maritimae. In "het Zwin" the species has been found in the same plant association in the clayey mud between the roots of Puccinellia maritima, together with several characteristic salt-marsh species, such as Proxenetes puccinellicola, Coelogynopora schulzii, Macrostomum spirale, M. balticum and Vejdovskya halileimonia (Table 3). Although its Dutch locality is an euhaline habitat the occurrence of P. pratensis on the salt-marshes of Kiel Bay indicates that it must be a rather euryhaline species.

Proxenetes cisorius nov. sp.

Fig. 42–44; Pl. XI.

The animals are rather plump, 560–930 μ long, and white in colour. The truncate anterior end contains the two eyes. The posterior part of the

C. DEN HARTOG: A preliminary revision of the Proxenetes group (Trigonostomidae Turbellaria). VIII

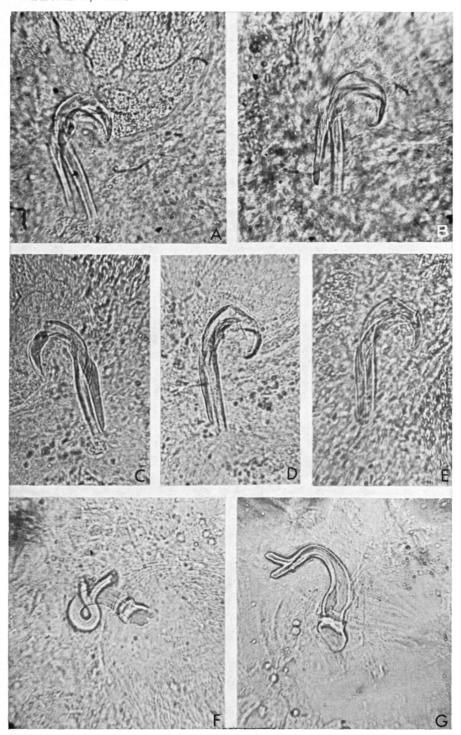
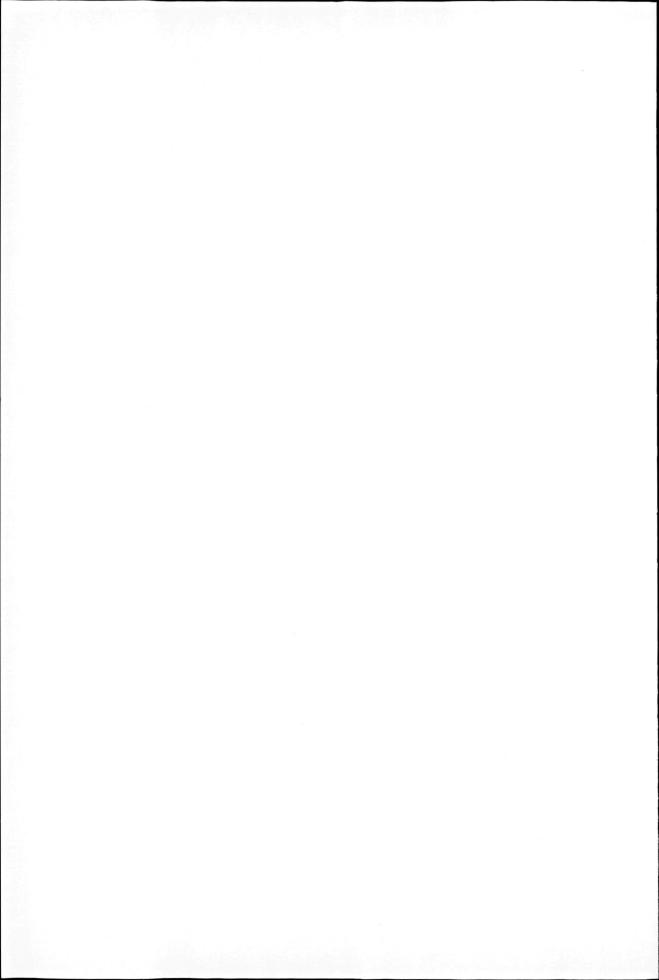


PLATE XI. Proxenetes cisorius nov. sp.

A. Cuticular copulatory organ and muscular bulbus; stylet and cuticular sheath placed at an acute angle. B. Cuticular copulatory organ; stylet and cuticular sheath placed at an acute angle. C–E. Cuticular copulatory organ; stylet and culticular sheath close together. F–G. Bursal appendage. (After specimens from the Verdronken Zwarte Polder near Cadzand, Zeeuws Vlaanderen).



body is rounded. The widest part of the body lies behind the middle. The pharynx is situated at $\frac{1}{2} - \frac{3}{5}$ of the body length. The testes are oblong and lie anterior to the pharynx. The vasa deferentia widen into large spermaducal vesicles before entering the muscular bulbus of the copulatory organ. The muscular bulbus is spherical; its diameter is $70-100~\mu$. The cuticular copulatory organ is $52-55~\mu$ long. The semicircularly curved proximal part of the stylet is wide open but directly closes to a duct. The distal part of the stylet is almost straight. Its wall consists of two systems of spiralling fibre bundles, which are placed at right angles. The cuticular mantle sheaths the stylet only at the transition between the curved and the almost straight part. It consists of a wedge-shaped, very slightly curved, acute lamella, which lies close to the outward side of the straight part of the stylet and has the same length. The curvature of stylet and lamella is opposite. They are jointly capable of a restricted

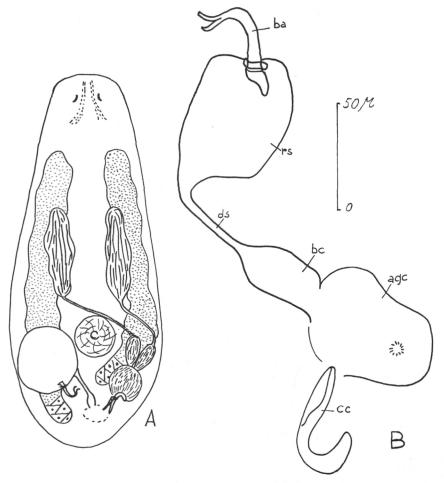


Fig. 42. Proxenetes cisorius nov. sp.: A. General view; B. genital organs; cc=cut. cular copulatory organ, age = atrium genitale commune, bc = bursa copulatrix, ds = ductus spernaticus, rs = receptaculum seminis, ba = bursal appendagei

scissor-like movement. The cuticular mantle is proximally connected with the concave side of the semicircular part of the stylet. At the inward side of the stylet only a small spine occurs. When strongly pressed under a coverslip an other spine becomes visible between the stylet and the large lamella. In my opinion this must be an artefact caused by breaking the sheathing part of the cuticular mantle. It is, however, a consistent feature, as I observed this "spine" in all specimens that were heavily squashed.

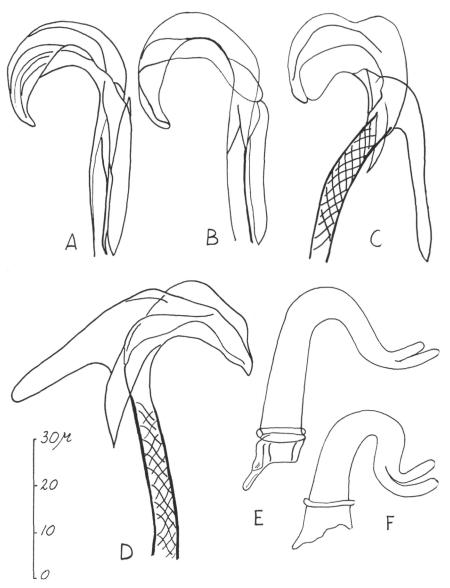


Fig. 43. Proxenetes cisorius nov. sp.: A-B. Cuticular copulatory organ; C-D. cuticular copulatory organ, strongly squashed; E-F. bursal appendage. (After specimens from the Verdronken Zwarte Polder, Zeeuws Vlaanderen).

The vitellaria are elongate and extend from the middle part of the anterior half of the body far into the posterior part, where they join the germaria. The efferent tract of the female genital organ is differentiated into a large receptaculum seminis and a small bursa copulatrix connected by a ductus spermaticus. The receptaculum seminis is spherical or ovoid and has a diameter or greatest length of 70–130 μ . The ductus spermaticus is narrow and ca. 40 μ long. The bursa copulatrix is 40 μ long and 20 μ wide and connects by a wide opening with the atrium genitale commune. The bursal appendage is a coarse cuticular duct, consisting of longitudinally arranged fibrous strands, bending sharply at $\frac{1}{2}-\frac{2}{3}$ of its length and then splitting into 2 narrower ducts, which curve in the opposite direction, giving the organ the appearance of a davit. Sometimes, however, the distal part of the bursal appendage is coiled. It is surrounded by an unarmed cuticular ring, which lies well above the base.

Geographical distribution:

P. cisorius has been found so far in several places in the south-western part of the Netherlands.

Localities in the Netherlands:

Province of Zuid-Holland:

Voorne-Putten: 1. Oostvoorne, Groene Strand, salt-marsh, October 1964 (BILIO, personal communication).

Province of Noord-Brabant:

2. Salt-marsh area south of Bergen op Zoom, October 1964 (BILIO, personal communication).

Province of Zeeland:

Zuid-Beveland: 3. Kattendijke, intertidal flat, November 1964. Zeeuws Vlaanderen: 4. Verdronken Zwarte Polder near Cadzand, salt-marsh, March and November 1964. 5. International nature reserve "het Zwin", in the Dutch part, salt-marsh, November 1964 (BILIO, personal communication).

Ecology:

Proxenetes cisorius has been found on well-differentiated salt-marshes where a gradual transition to a dune landscape occurs. The species inhabits in particular slight depressions in the higher parts of the salt-marshes, which are reached by the flood water only at high spring tides or during stormy weather, but which are only exceptionally flooded in summer, and where after the floods the water stagnates for some time. Such places have mostly a vegetation belonging to the Puccinellietum maritimae or the Halimionetum portulacoidis.

In the Verdronken Zwarte Polder the species appeared to find optimal conditions in a small area with a dense vegetation of *Puccinellia maritima*, surrounded by higher situated fields of *Halimione portulacoides* and *Festuca*

rubra. The bottom consisted of compact clay, mixed with large quantities of humus and only a little sand. It was covered by a 3–5 cm thick layer of litter mixed with silt. The bottom was wet, probably as a result of its bad permeability. The litter layer was well-aerated as a consequence of its loose texture. The fauna consisted mainly of terrestrial animals, such as enchytraeids and collemboles. The amphibious, estuarine, brackishwater snail Assiminea grayana Fleming was present and the aquatic fauna was represented by a few rotifers and copepods. The turbellarian fauna was poor in species, although the number of individuals was relatively

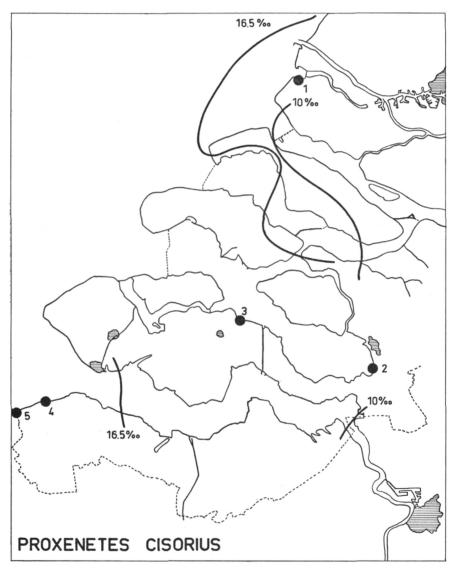


Fig. 44. Distribution of *Proxenetes cisorius* nov. sp. in the south-western part of the Netherlands. The average annual isohalines of $10~^{0}/_{00}$ Cl' and $16.5~^{0}/_{00}$ Cl', both at high tide, are given.

high. This appears from the following list of Turbellarians obtained from ca. 150 cm³ of soil:

Proxenetes cisorius nov. sp. 27 Vejdovskya halileimonia Ax 26 Not identified 1

The behaviour of *Proxenetes cisorius* differs much from that of the coexisting species *Vejdovskya halileimonia*. When the sample was placed in a jar and covered with sea water *V. halileimonia* left its shelter and begun to swim freely around. This species is attracted to the light source and swims only in the daytime. On the contrary, *P. cisorius* shuns the light and swims only when the light intensity is low or when it is dark. When exposed to the light of a lamp the animals immediately disappear into the mud.

In other places, situated somewhat lower than those described above, as well dominated by the grass Puccinellia maritima and where the bottom consists of a mixture of clay and fine sand covered by a thin layer of litter, Proxenetes cisorius has been found also, but there it seems rather an infrequent invader than a resident. In these stations the bottom has a better permeability as a consequence of the higher sand-content, but inundation by flood water takes place more frequently. The snail Hydrobia ulvae (Penn.) is the most conspicuous animal in such places. The turbellarian fauna is very different from the one just mentioned, being dominated by either Macrostomum spirale or Monocelis lineata or by both species together, while Proxenetes deltoides and Mecynostomum auritum are constant companion species. I found this combination of species not only in the Verdronken Zwarte Polder, but also in other localities.

In the international nature reserve "het Zwin" *P. cisorius* has been found in the *Halimionetum portulacoidis* of a depression reached by the sea only in the winter half-year, and in the same plant association along the creek side of a levee (Bilio, personal communication). In the adjacent *Puccinellietum maritimae* along the same creek *P. cisorius* was absent and *Vejdovskya halileimonia* was represented by a few specimens (cf. Table 3).

The one specimen of *P. cisorius* that I found in the *Zostera noltii* vegetation on the sandy mud-flat of Kattendijke must be regarded as an accidental find, the animal probably having been washed from a saltmarsh during a recent gale.

The species has been found in the euhaline and the polyhaline section of the Deltaic area. It inhabits the higher parts of dune-bordered salt-marshes, where salinity is subjected to considerable fluctuations caused by precipitation, evaporation and the fresh ground-water from the dunes. Thus *P. cisorius* may be expected to occur even in the mesohalinicum (cf. *Proxenetes unidentatus* in part V of this paper). It is remarkable that a species of the transition area between salt-marshes and sand-dunes does

not occur in sandy bottoms. It seems to be confined to litter-covered humose clay with a very low sand-content. Therefore, I think that the transport of fresh dune water in seaward direction is an essential factor for the species. The continual flow of this dune water, combined with the impermeable clay bottom, results in these biotopes being rather moist in summer, so that the animals or their egg-capsules are safeguarded against desiccation.

In the intestinal tract of *P. cisorius* I found several times half-digested nematodes and oligochaetes.

(to be continued)

A PRELIMINARY REVISION OF THE PROXENETES GROUP (TRIGONOSTOMIDAE, TURBELLARIA). IX

BY

C. DEN HARTOG

(Communicated by Dr. J. Verwey at the meeting of November 27, 1965)

SECTION III (Karlingi section)

Receptaculum seminis and bursa copulatrix well-developed, separated by a deep constriction. Bursal appendage consisting of a ring and a long winding duct which distally splits into two very narrow parallel ducts or is only notched at its tip.

KEY TO THE SPECIES

- 1. Distal part of the bursal appendage split into two thin ducts.

Proxenetes karlingi Luther, 1943

LUTHER, Act. Zool. Fenn. 38, 66-69, f. 7, 20, 53-61, Pl. 1, f. 2-3, Pl. 3, Pl. 5, f. 1-2 (1943); idem, Faun. Fenn. 12, 53-54, f. 21 (1962).

Proxenetes filum Meixner, 1938

Meixner in Grimpe-Wagler, Tierw. Nord-Ostsee 33 IV b, 115, 129 (1938), nomen nudum. - Fig. 45, 46 A–D, 47; Pl. XII.

The animals are elongate, $1-1\frac{1}{2}$ mm long, and white in colour. The anterior end is truncate. The pharynx lies at $\frac{2}{3}-\frac{3}{4}$ of the body length. The cuticular copulatory organ is 55–60 μ long and triangular in shape. It consists of a wide funnel-shaped stylet, proximally open and ending in a recurved hook. Sperm and granular secretion are discharged through the stylet. Sperm is also discharged via the obliquely placed, funnel-

shaped cuticular mantle, which surrounds the stylet rather tightly and consists of 4 spiny lamellae. Within the cuticular mantle 4–6 free spines occur. The proximal margin of the mantle is connected with the proximal hook of the stylet. The bursa copulatrix is large and completely separated from the enormous receptaculum seminis, although their walls have grown together. Luther (l.c.) supposed that during the copulation the "common wall" is perforated by the male cuticular copulatory organ and that the wound heals soon afterwards. The bursal appendage consists of a basal ring from which a long winding duct arises. This duct distally splits into two narrower ducts. The distal ends of these ducts are slightly widened. The length amounts to $200-250~\mu$.

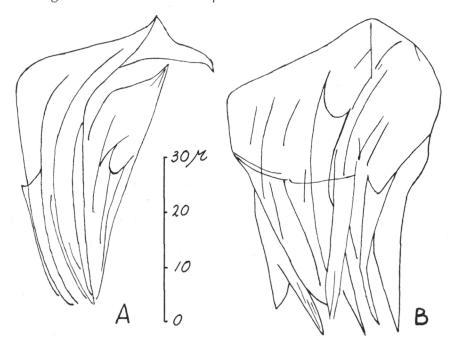
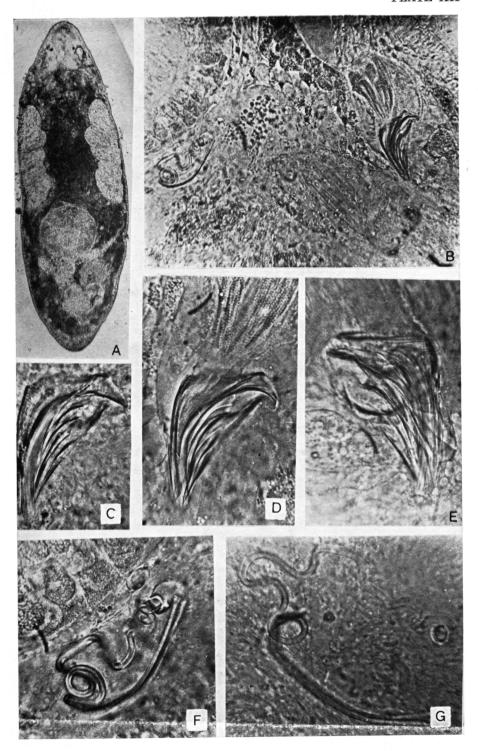


Fig. 45. Proxenetes karlingi Luther, 1943: A–B. Cuticular copulatory organ. (A after a specimen from Oude Doel, Belgium, B after a specimen from Den Bommel, Goeree-Overflakkee).

PLATE XII. Proxenetes karlingi Luther, 1943.

A. General view of a squashed specimen in which are visible the eyes, the pharynx, the germovitellaria, the muscular bulbus, the cuticular copulatory organ, the two spermaducal vesicles, the bursa copulatrix, the receptaculum seminis and the bursal appendage. B. Cuticular and muscular copulatory organ (in the latter the prostatic glands are visible), one of the spermaducal vesicles, bursa copulatrix, receptaculum seminis and bursal appendage. C. Cuticular copulatory organ. D. idem, but a part of the muscular bulbus is visible. E. Cuticular copulatory organ, strongly squashed, so that at least 4 spines have become visible. F-G. Bursal appendage. (A-D and F after specimens from Oude Doel, Belgium, E and G after specimens from Den Bommel, Goeree-Overflakkee).

PLATE XII



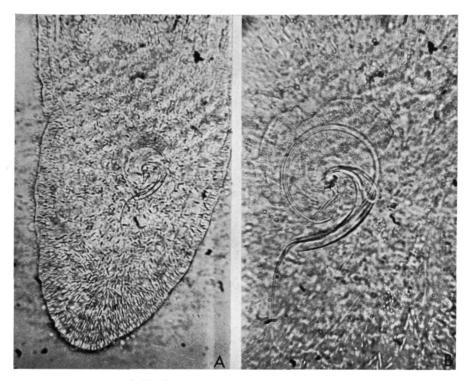


PLATE XIII. Messoplana elegans (Luther, 1948).

A. Posterior part of a squashed specimen showing the cuticular copulatory organ and the muscular bulbus. B. Cuticular copulatory organ, consisting of a long and thin stylet and a funnel-shaped additional duct. (After a specimen from Kattendijke, Zuid-Beveland).

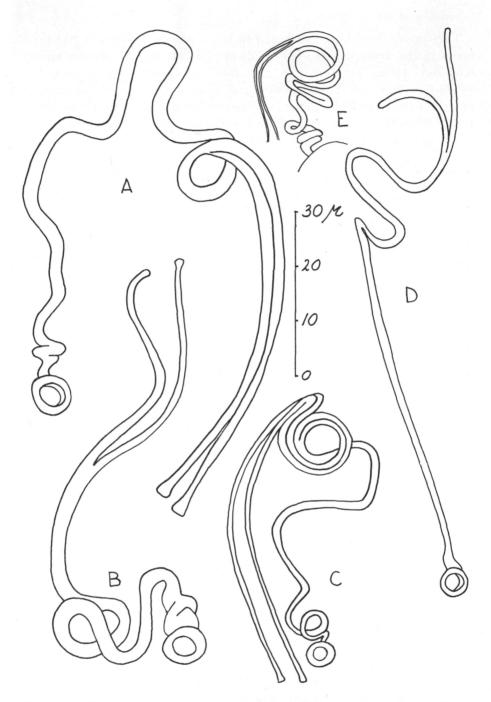


Fig. 46. A–D. *Proxenetes karlingi* Luther, 1943: Bursal appendages (A after a specimen from Den Bommel, Goeree-Overflakkee, B–C after specimens from Oude Doel, Belgium, D after a specimen from Stavenisse, Tholen) — E. *P. lutheri* nov. nom.: bursal appendage (after Luther).

Geographical distribution:

The species is widely distributed in the Baltic Sea, where it has been found in the western part of the Gulf of Finland, near Stockholm and in Kiel Bay. It has been recorded also from the Gullmar Fjord along the Swedish west coast (Riedl., 1956) and from the "Grüne Insel" in the mouth of the river Eider along the German North Sea coast (Billo, 1962, 1965). Recently I have found it in the Deltaic area of the rivers Rhine, Meuse and Scheldt (fig. 45).

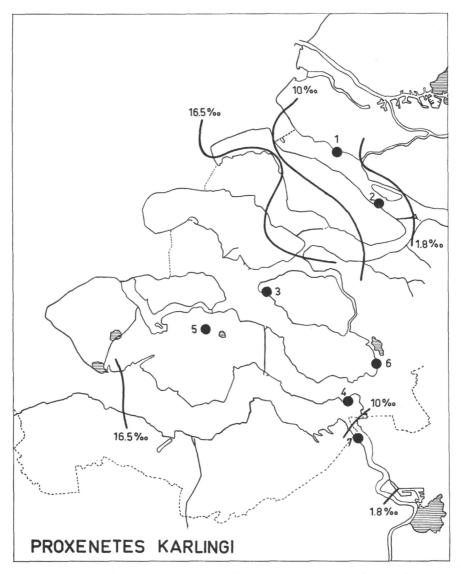


Fig. 47. Distribution of *Proxenetes karlingi* Luther, 1943 in the south-western part of the Netherlands. The average annual isohalines of $10~^{\circ}/_{00}$ Cl' and $16.5~^{\circ}/_{00}$ Cl', both at high tide, are given.

Localities in the Netherlands:

Province of Zuid-Holland:

Voorne-Putten: 1. Salt-marsh south of Oudenhoorn, November 1964. Goeree-Overflakkee: 2. Den Bommel, salt-marsh pool, May 1963.

Province of Zeeland:

Tholen: 3. Stavenisse, salt-marsh, November 1963. Zuid-Beveland: 4. Bath, salt-marsh, May 1963; 5. Terluchtse Weel, west of Goes, brackish inland water, September 1964.

Province of Noord-Brabant:

6. Salt-marsh south of the town of Bergen op Zoom, October 1964, collected by BILIO.

Locality in Belgium:

Province of Oost-Vlaanderen:

7. Oude Doel, salt-marsh along the river Scheldt, May 1963.

Ecology:

Proxenetes karlingi occurs, according to Luther (1943, 1962), in the Gulf of Finland on sandy bottoms at a depth of 1-5 m. According to Ax (1951) it is an inhabitant of the still-water biotopes, living in mud and Vaucheria cushions, Billio (1962, 1965) has recorded the species from the salt-marsh vegetation along the North Sea coast. My observations in the Deltaic area agree very well with those of Ax and Billio. Near Den Bommel, Bath and Oude Doel P. karlingi has been found in shallow, often dried out, salt-marsh pools, in mud and between algae. The specimens from Den Bommel were obtained from a Vaucheria cushion. On the brackish salt-marsh of Oudenhoorn and on the marine salt-marsh of Stavenisse the species has been collected in the Puccinellietum maritimae. Billo found near Bergen op Zoom several specimens in the Salicornietum strictae at the transition between mud-flat and salt-marsh. The most remarkable locality of the species is the Terluchtse Weel, a coastal inland pool, which has been isolated from the sea since 1831. There it lives near the water-edge in the Puccinellia maritima vegetation together with Proxenetes deltoides.

 $P.\ karlingi$ is known as a brackish-water species, but it is probably more justified to regard it as an euryhaline species. Its salinity range is extremely wide, covering the mesohaline, polyhaline and euhaline sections of the Deltaic area. With $P.\ minimus$ it is the most euryhaline species of the genus. At Oudenhoorn and Den Bommel the species occurs at an average salinity at high tide of ca. $2^{0}/_{00}$ and $3.7^{0}/_{00}$ Cl' respectively, while the fluctuations of the salinity in the course of the year amount to at least $12^{0}/_{00}$ Cl'. The localities in the river Scheldt are situated in the transition area between meso- and polyhalinicum, where the salinity fluctuations are also considerable. The salt-marshes of Stavenisse and

Bergen op Zoom are euhaline habitats. In the Terluchtse Weel the salinity fluctuates over a wide range (cf. *Proxenetes deltoides* in Part IV of this paper).

It is noteworthy that *P. karlingi* occurs in the euhalinicum in the salt-marsh vegetation, while at lower salinities it is almost always submerged or living at the water-edge. This may be an indication for brackish-water submergence of the species. The occurrence of *P. karlingi* at a depth of 1–5 m in the Gulf of Finland (Luther, l.c.) also supports this line of thought. More observations are needed, however, for a decisive conclusion on this point.

The food consists, according to Luther (1943), of free-living nematodes.

Proxenetes lutheri nov. nom.

Proxenetes cochlear (non Von Graff) Luther, 1948 Luther, Act. Zool. Fenn. 55, 64-67, f. 87-89 (1948). — Fig. 46 E.

The animal is ½ mm long; its pharynx lies just behind the middle of the body. The male cuticular copulatory organ is triangular in shape and consists of a wide funnel-shaped, slightly curved stylet, open at its proximal end, and a funnel-shaped cuticular mantle, containing two spines. The efferent tract of the female copulatory organ consists of a wide bursa copulatrix and a voluminous receptaculum seminis, separated by a deep constriction. The narrowing between the two organs is called ductus spermaticus by Luther, but this is not homologous with the ductus spermaticus of Ptychopera and Beklemischeviella. The bursal appendage is a long, winding duct, splitting into two narrow ducts at its distal end. Luther did not find a basal cuticular ring, and the extreme distal ends of the two ductlets do not seem to have the slight widenings which are so characteristic in P. karlingi. Luther gave no measurements of the cuticular structures.

LUTHER identified his specimen with some doubt as P. cochlear. This identification is indeed incorrect. In the first place his species has a large bursa copulatrix, while Von Graff (1882) drew P. cochlear as having a rather wide bursal canal. Moreover, the bursal appendage of LUTHER's species coils 5-6 times, is split into 2 narrow ducts at its distal end and does not seem to have a basal ring. On the contrary, in Von Graff's figure of P. cochlear the bursal appendage coils only twice, is not split at its distal end and is at its base surrounded by a ring. Although the figure of Von Graff is inaccurate where it concerns the cuticular copulatory organ, and perhaps inaccurate where it concerns the bursal appendage, I do not think that he made mistakes when drawing the bursal canal and the coils in the bursal appendage, as they are already easily visible in squash preparations at low magnification. Luther's species belongs to section III, while Von Graff's P. cochlear is according to me probably a representative of the Angustus section. Therefore, LUTHER's species had to be renamed.

Geographical distribution:

The species has been described from one specimen, collected at Fiskebäckskil in the Gullmar Fjord along the Swedish west coast.

Ecology:

The species had been taken from sublittoral mud.

Proxenetes monotubulus nov. sp. Fig. 48.

The animal is elongate, $1\frac{1}{4}$ mm long, and white in colour. The anterior end is truncate. The pharynx lies at $\frac{2}{3}$ of the body length. The cuticular copulatory organ is 47 μ long and triangular in shape. Its structure has been investigated only incompletely. The stylet is widely funnel-shaped and slightly curved over its whole length. It is proximally open but soon closes into a duct which narrows gradually in distal direction. The cuticular mantle is obliquely placed and connected with the recurved proximal hook of the stylet. It sheaths $\frac{3}{5}$ of the length of the stylet, leaving free its proximal part and its extreme distal tip. I have not made notes on the number of spiny lamellae and free spines within the mantle. The efferent tract of the female genital circuit is differentiated into a receptaculum seminis and a bursa copulatrix connected by a very short ductus spermaticus. The receptaculum seminis is ovoid with a deep lateral notch, it is 75 μ long and 50 μ wide. The ductus spermaticus is 18 μ long and slightly twisted. The bursa copulatrix is spherical, with a diameter of 55 u. The bursal appendage consists of a double ring, from which arises a curved, thin, 85 μ long, single duct; this has distally two openings separated by a small notch. A very fine longitudinal line is visible on the duct. The basal ring is drawn out into a triangular point and the upper ring is provided with a short process.

The fact that the bursal appendage was not split, as is usually the case in *Proxenetes*, made me think at first that this organ was deformed, and I am still not convinced that this is not the case. It appeared further that the combination of the other characters of the animal did not match any species of the genus hitherto known.

The dubious *P. cochlear*, which has been described and depicted by Von Graff (1882: p. 279, Pl. 8, f. 1–4) as having an undivided, twice coiled, bursal appendage, differs from the above specimen, as it has a long, rather wide, slightly constricted bursal canal instead of a bursa copulatrix.

The shape and the size of the cuticular copulatory organ of the specimen are very similar to that of P. deltoides, but that species does not have a bursa copulatrix either. Instead it has a long bursal canal with a distal widening containing a large spine apparatus.

The specimen differs from P. karlingi by the smaller size of the cuticular

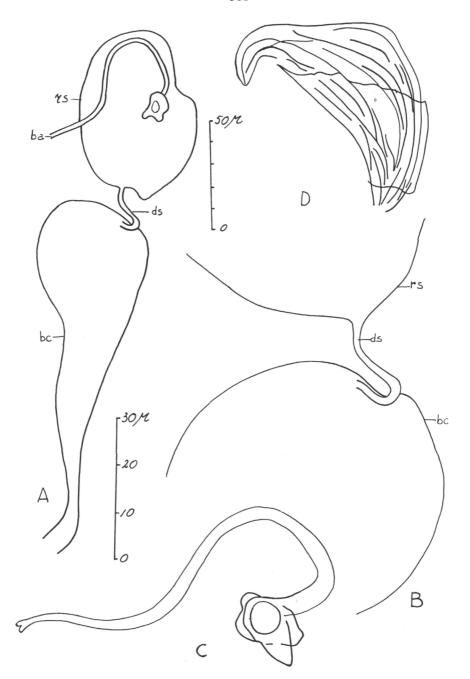


Fig. 48. Proxenetes monotubulus nov. sp.: A. Efferent tract of the female genital system; be = bursa copulatrix, ds = ductus spermaticus, rs = receptaculum seminis, ba = bursal appendage; B. ductus spermaticus (ds) and its connection with bursa copulatrix (bc) and receptaculum seminis (rs); C. bursal appendage; D. cuticular copulatory organ. (After a specimen from the Verdronken Zwarte Polder, Zeeuws Vlaanderen. The small scale refers to fig. A, the larger one to B-D).

copulatory organ and the connection between receptaculum seminis and bursa copulatrix.

Therefore, although the finer structure of its cuticular copulatory organ is insufficiently known, I have described the specimen as a new species, and provisionally placed it in section III, as its bursa copulatrix and receptaculum seminis are very similar to the corresponding organs in *P. karlingi* and *P. lutheri*. Further, the distally notched bursal appendage may be considered a special case of the distally split bursal appendage of *P. karlingi* and *P. lutheri*. The shape of the ring of the bursal appendage shows, however, more similarity with that of species belonging to section II.

Geographical distribution:

Proxenetes monotubulus has been discovered by Dr. M. Billio in the south-western part of the Netherlands (see below).

Locality in the Netherlands:

Province of Zeeland:

Zeeuws Vlaanderen: Verdronken Zwarte Polder near Cadzand, salt-marsh, November 1964 (Type).

Ecology:

Only one specimen of *P. monotubulus* has been collected and that was in the *Puccinellietum maritimae*.

5 MESSOPLANA nov. gen.

Pharynx posterior. Efferent tract of the female genital apparatus consisting of a receptaculum seminis and a bursal canal. Bursal appendage consisting of a cuticular ring in the wall of the receptaculum seminis and two very short, delicate cuticular ducts which project partly into the receptaculum seminis. Male cuticular copulatory organ consisting of a stylet and an additional duct, connected to each other only by their proximal ends.

Type: Proxenetes falcatus Ax

The bursal appendage of the genus *Messoplana* seems to me to be the most primitive stage of the corresponding structure occurring in the species of the "Coronatum" group of Trigonostomum. The very peculiar cuticular copulatory organ, consisting of two only proximally connected ducts, could have been derived from Ceratopera, as the cuticular mantle in that genus sometimes is transformed into an additional duct. However, in the latter genus it is always connected with the straight distal part of the stylet. In some species of Proxenetes a secondary duct occurs beside the stylet, within the cuticular mantle, e.g. in P. flabellifer; this duct arises at the proximal end of the copulatory organ.

KEY TO THE SPECIES

- 1. Stylet and additional duct differently shaped.
 - 2. Stylet shaped like a walking stick, fibrous, stiff, 80–95 μ long. Additional duct shorter with a falcate distal part . . 1. M. falcata

Messoplana falcata (Ax, 1953)

Proxenetes falcatus Ax, 1953

Ax, Kieler Meeresf. 9, 238–239, Pl. 22 (1953); idem, Zool. Jb. Syst. 87, 100 (1959). — Fig. 49.

The animals are slender and 1.3-1.5 mm long. The anterior end is obtuse or truncate. The caudal end shows a slight constriction, so that a just conspicuous rear end is formed. The pharynx lies at ca. $\frac{2}{3}$ of the body length. The cuticular copulatory organ is 80-95 μ long and consists of two ducts, which are proximally connected. The main duct, which is the stylet, is semicircularly curved at its proximal end and proceeds in distal direction as a straight duct, the distal end of which is widened and composed of more or less fibrous strands. The additional duct, which is almost as long as the stylet, is connected to it by a duct-like branch near the proximal opening. The distal part of the additional duct is sickle-shaped. This duct is derived from the transformed cuticular mantle. The bursal appendage consists of a cuticular ring and 2 short ducts. The ring is drawn out into two diametrically opposite spines and bears, moreover, 2 small upwardly directed processes. The ducts are 24 μ long and project with the S-shaped and pointed proximal parts deep into the receptaculum seminis. The distal parts are straight, parallel or somewhat divergent.

Geographical distribution:

Messoplana falcata has been found in a few localities in Kiel Bay, on Amrum along the German North Sea coast, along the southern coast of Sicily, in the Sea of Marmara and near Sile along the Black Sea (Ax, 1953, 1959).

Ecology:

Messoplana falcata seems to inhabit only pure sand biotopes in the sublittoral.

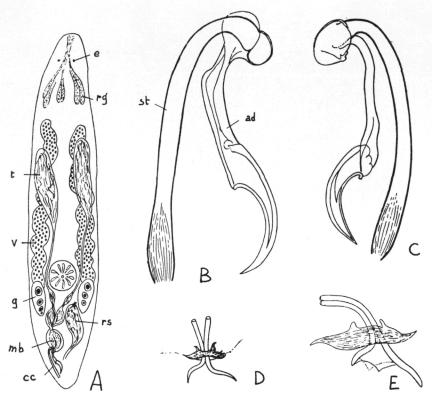


Fig. 49. Messoplana falcata (Ax, 1953): A. General view; e = eye, rg = rhabdite glands, t = testis, v = vitellarium, g = germarium, mb = muscular bulbus, cc = cuticular copulatory organ, rs = receptaculum seminis; B-C. cuticular copulatory organ, st = stylet, ad = additional duct; D-E. bursal appendage. (After AX).

Messoplana elegans (Luther, 1948)

Proxenetes elegans Luther, 1948

Luther, Act. Zool. Fenn. 55, 76–81, f. 106–109 (1948). - Fig. 50–51; Pl. XIII.

The animals are linear, 0.5–1 mm long, and white in colour. The anterior part of the body is truncate. The pharynx lies at ca. $\frac{2}{3}$ of the body length. The testes are elongate and lie laterally to the pharynx. The vasa deferentia swell up into rather large spermaducal vesicles before entering the muscular bulbus. The muscular bulbus is somewhat curved and measures 70–80 by 35–40 μ . The stylet is S-shaped, extremely thin and flexible and ca. 300 μ long. Its extreme proximal end is a small, but wide, open canal that soon closes into a very narrow duct. This duct makes an almost complete coil, then it proceeds parallel with the additional duct, and finally it curves in the opposite direction. The whole proximal part of the stylet is completely embedded in the muscular bulbus. The funnel-shaped additional duct is 45–50 μ long. Its distal tip is bifid and incurved.

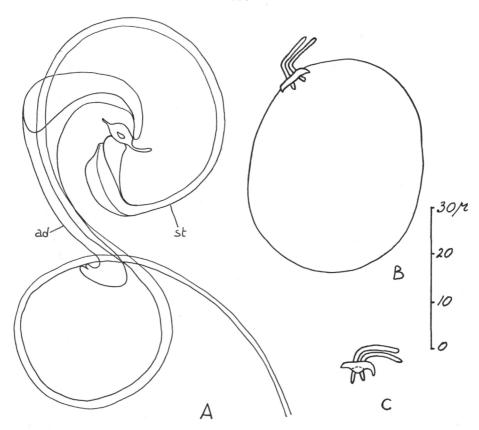


Fig. 50. Messoplana elegans (Luther, 1948): A. Cuticular copulatory organ;
 st = stylet, ad = additional duct; B. receptaculum seminis with bursal appendage;
 C. bursal appendage (After a specimen from Bergen op Zoom).

Proximally the funnel is drawn out to one side, forming a recurved hook. This hook is connected with the extreme proximal end of the stylet by a falcate, perforated process. The receptaculum seminis is ovoid and measures 45 by 35 μ . The very inconspicuous bursal appendage consists of a cuticular ring and two, very short, delicate cuticular duets, which project with the smaller part into the receptaculum seminis. The duets are at most 15 μ long and only project for $\frac{2}{3}$ of their length above the ring.

LUTHER (l.c.) expressed some doubt as to whether some of the dissected specimens which he investigated really belonged to his *Proxenetes elegans*, because the structure of their female genital apparatus did not match very well with that of another specimen in which he traced the filiform "Chitin-anhang" of the copulatory organ. I think that his figures 110–115 of "P. elegans?" have indeed nothing to do with that species. According to the structure of the efferent tract of the female genital apparatus, of the bursal appendage, and of the cuticular copulatory organ, they represent a true *Proxenetes* species.

In figures 107 and 108a of LUTHER's paper, which have been drawn

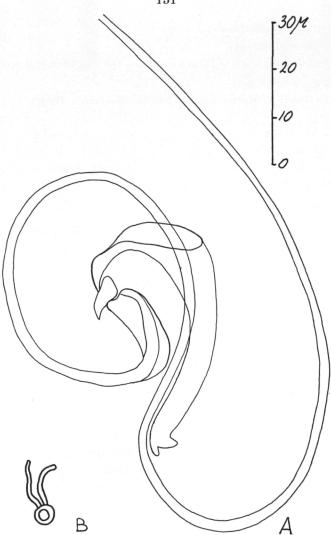


Fig. 51. Messoplana elegans (Luther, 1948): A. Cuticular copulatory organ; B. bursal appendage. (After a specimen from Kattendijke).

by Westblad, a cuticular spine apparatus is illustrated. In the specimens which I had at my disposal I have not seen such a structure at all. I have not hesitated, however, to identify my material with Luther's *P. elegans*, as the extremely characteristic shape of the cuticular copulatory organ excludes every doubt.

Geographical distribution:

Messoplana elegans has been described from specimens collected in the surroundings of Kristineberg along the Swedish west coast (LUTHER, l.c.), where it was found again by RIEDL (1956). Ax (1953) recorded the species from Kiel Bay. Recently, it has been found along the German North Sea coast and in the south-western part of the Netherlands.

Localities in the Netherlands:

Province of Noord-Brabant:

 $1.\ {\rm Salt\text{-}marsh}$ are a south of Bergen op Zoom, October 1964, collected by BILIO.

Province of Zeeland:

Zuid-Beveland: 2. Kattendijke, tidal flat, November 1964.

Locality in Germany:

State of Schleswig-Holstein:

Meldorfer Bucht, salt-marsh creek, March 1964, collected by S. Lorenzen (BILIO, personal communication).

Ecology:

The original specimens of *Messoplana elegans* were collected in muddy sand at depths between 5 and 20 m at two stations in the Gullmar Fjord (Luther, l.c.). Ax (1953) recorded the species from the sublittoral of Kiel Bay, where it inhabits greyish-black muddy sand at 9–10 m depth. Riedle (1956: p. 148–150, sample G 3) discovered *M. elegans* in the Gullmar Fjord in very shallow water in a mixture of mud with fine shell-grit and coarse detritus. There it occurs in small quantities in a community dominated by *Pogaina suecica* and *Provortex tubiferus*. This community is more or less identical with the association of detritus-rich fine sand of Ax (1951).

In the Deltaic area the species occurs in small numbers on the tidal flats. Near Kattendijke it has been collected in the Zostera noltii association in the detritus-rich fine sand of shallow depressions which are covered with a thin film of water during the exposure period. The dominant animals of this biotope are Arenicola marina and juvenile Cardium edule, while among the Turbellarians Monocelis fusca (form with the long penis stylet) and Mecynostomum auritum are the most numerous species. Among the accompanying species of Messoplana elegans in this habitat Proxenetes trigonus, P. intermedius, Ptychopera westbladi and M. geminata may be mentioned. Billio (personal communication) found M. elegans in the saltmarsh area south of Bergen op Zoom in a shallow salt-marsh pool with a soft mud bottom and in the Salicornietum strictae. In the latter association, which is characteristic for the transition between the tidal flat and the salt-marsh on an accrescent coast, the turbellarian fauna was dominated by Macrostomum balticum and Psittorhynchus verweyi, while among the companion species beside Messoplana elegans many other representatives of the Proxenetes group were found, viz. Ptychopera westbladi, Proxenetes segmentatus, P. karlingi, P. bilioi, P. intermedius and P. deltoides.

Bilio (personal communication) found M. elegans in a sample from a salt-marsh creek in the Meldorfer Bucht.

As *M. elegans* has not been found in the salt-marsh vegetation I think that it is a characteristic species for the tidal flats, inhabiting detritusrich fine sand as well as the muddier still-water biotopes.

In the Deltaic area the species has been found only in the euhaline section of the estuary. Its occurrence in Kiel Bay indicates that it must be tolerant to some dilution of the sea water.

In the intestinal tract of several specimens I found half-digested oligochaetes and unicellular chlorophyceae.

Messoplana geminata nov. sp. Fig. 52.

The animal here described is elongate, 450 μ long, and white in colour. Its anterior end is obtusely truncate and contains 2 semilunar eyes. The pharynx lies at $\frac{2}{3}$ of the body length. The cuticular copulatory organ is 43 μ long and consists of a stylet and an additional duct of the same size. The stylet is proximally open but soon closes into a duct. Its proximal part is markedly curved, while its distal part is almost straight. The proximal part of the additional duct runs parallel with the stylet and shows the same curvature. The straight distal part of that duct is obliquely placed with regard to its proximal part. The distal tips of the stylet and the additional duct are both provided with a convex, ring-shaped cuticular thickening. Both ducts are proximally connected. I am, however, not sure whether the connection is direct or whether an intermediate, perforated cuticular link connects the two ducts. I could not study the efferent tract of the female genital apparatus.

Although the structure of its female genital apparatus is unknown the species can be easily recognized by the shape of its cuticular copulatory organ.

Geographical distribution:

So far the species has been found only once in the south-western part of the Netherlands.

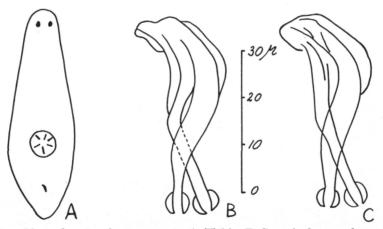


Fig. 52. Messoplana geminata nov. sp.: A. Habit; B–C. cuticular copulatory organ after slight and strong pressure respectively. (After a specimen from Kattendijke.

The scale refers to B and C only).

Locality in the Netherlands:

Province of Zeeland:

Zuid-Beveland: Kattendijke, tidal flat, November 1964 (Type).

Ecology:

The ecological demands of Messoplana geminata are yet unknown. I have collected only one specimen in the Zostera noltii vegetation, in the detritusrich fine sand of a slight depression which during the time of exposure is covered with a thin layer of water. The rich turbellarian fauna of this spot was dominated by Monocelis fusca (form with the long penis stylet) and Mecynostomum auritum, while the Proxenetes group, beside by Messoplana geminata, was represented by P. trigonus, P. intermedius, Ptychopera westbladi and Messoplana elegans.

(To be continued)

A PRELIMINARY REVISION OF THE PROXENETES GROUP (TRIGONOSTOMIDAE, TURBELLARIA). X

BY

C. DEN HARTOG

(Communicated by Dr. J. Verwey at the meeting of November 27, 1965)

DUBIOUS SPECIES

Proxenetes arenarius Meixner, 1938

MEIXNER in GRIMPE-WAGLER, Tierw. Nord-Ostsee 33, IVb, 115 (1938), nomen nudum.

This species has been recorded from sand in the Belt Sea, probably from Kiel Bay.

Proxenetes cochlear Von Graff, 1882

Von Graff, Monogr. Turbell. 1, 279, Pl. 8, f. 1–4 (1882); idem, Z. wiss. Zool. 83, 85 (1905); idem, Tierreich 35, 189, f. 175 (1913).

The animal is slender, 1 mm long, and white in colour. Its anterior end is truncate. The pharynx lies just behind the middle of the body. The characters which are used nowadays to distinguish the species of Proxenetes from each other have been insufficiently described for this species. The cuticular copulatory organ is considerably smaller than that of P. flabellifer and, according to Von Graff, of simpler structure. It consists "im Wesentlichen aus drei löffelartigen Platten". This must be a wrong interpretation of his observation, as it is very unlikely that the copulatory organ consists of spoon-shaped cuticular plates only, without a stylet. From the figures (1882: Pl. 8, f. 4a-b) it appears that the organ is triangular in shape, and that it distally ends with 3 spines, one of which probably representing the distal tip of the stylet. The receptaculum seminis is large and more or less bean-shaped. It is connected with the atrium genitale commune by a long, rather wide bursal canal, which is slightly constricted in the middle and has no spine apparatus in its distal end. According to Von Graff there occur instead numerous "Chitinhöckerchen". It is doubtful whether they have any relation to the spine apparatus that occurs in the typical section of the genus, as they are not localized in one special place but are spread all over the inner wall of the distal part of the bursal canal. The bursal appendage is a "spiralig gedrehten Schwänzchen, das mit einer feinen Spitze in die Leibeshöhle hineinsieht". The figure (1882: Pl. 8, f. 1) shows an undivided, twice coiled duct, that at its base is surrounded by an oblique, thickened ring. The structure of the vitellaria and germaria, the testes and the two spermaducal vesicles show the normal features of the genus.

The undivided bursal appendage—if this organ is drawn correctly by Von Graff—is similar to that of P. monotubulus. This species, which I placed provisionally in section III, differs, however, by the presence of a bursa copulatrix. The occurrence of a bursal canal in P. cochlear instead of a bursa copulatrix and the absence of a spine apparatus or muscular lump in its bursal canal point to section II of Proxenetes. When the single bursal appendage is regarded as a deformation, viz. a fasciation of two ducts, P. cochlear fits even better in section II. Among the 12 species described in that section there is not one that can be identified with P. cochlear.

Von Graff described *P. cochlear* from a littoral pool at Millport in Scotland.

Proxenetes? echinatus (Uljanin, 1870)

Von Graff, Monogr. Turbell. 1, 283 (1882).

Mesostomum echinatum Uljanin, 1870

ULJANIN, Trudy otd. zool. anat. physiol. Moscow 2, 15, Pl. 5, f. 4 (1870); Leuckart, Arch. Nat.gesch. 37, no. 2, 482 (1871); Von Graff, Tierreich 35, 200 (1913).

The animal is 0.57 mm long and colourless. The anterior and the posterior end of the body are widely obtuse. The eyes lie very close to each other, at $\frac{1}{5}$ of the body length. The pharynx lies at $\frac{2}{5}$ of the body length. The lateral, elongate germovitellaria extend from the pharynx in caudal direction. The small, oblong testes lie at $\frac{2}{3}$ of the body length. The cuticular copulatory organ is a hook-shaped funnel, which is placed with its wide proximal part on the muscular bulbus. The species was described from one specimen, collected in shallow water in the Bay of Sebastopol.

ULJANIN misinterpreted the function of the genital organs. The "testes" in his figure in fact represent the germovitellaria and the "ovaria" the testes.

According to Von Graff (1882) the species is very similar to *Proxenetes tuberculatus*. I do not think that *Proxenetes echinatus* is identical with *Ptychopera tuberculata*, as in that case Uljanin could not have failed to see the very conspicuous bursa copulatrix the latter possesses. As the genital organs of *Proxenetes echinatus* have been recorded very imperfectly by Uljanin a certain identification of the species seems impossible.

Proxenetes sensitivus (Uljanin, 1870)

Von Graff, Monogr. Turbell. 1, 282–283 (1882); idem, Tierreich 35, 182–183 (1913).

Mesostomum sensitivum Uljanin, 1870

ULJANIN, Trudy otd. zool. anat. physiol. Moscow. 2, 14–15, Pl. 5, f. 2 (1870); LEUCKART, Arch. Nat.gesch. 37, no. 2, 482 (1871).

The animal is 1 mm long and colourless. It is pear-shaped; the anterior part of the body is rather slender but the posterior part is plump. The eyes lie close together, at $\frac{1}{6}$ of the body length. The pharynx lies at $\frac{2}{5}$ of the body length. The lateral, elongate germovitellaria, called "testes" by Uljanin and Von Graff, extend from just behind the eyes in caudal direction. Just behind the pharynx lie two spherical organs, called ovaries ("Keimstöcke") by Uljanin and Von Graff; they are probably the testes. According to Von Graff (1882) the cuticular copulatory organ has roughly the same shape as that of *Proxenetes gracilis*, except that its tip is acute. It is placed on a large muscular bulbus. In the figure of Uljanin a small, elongate, transversely striped vesicula occurs. This is probably the receptaculum seminis, or the transition between that organ and the bursal canal.

ULJANIN's figure is difficult to interpret as some ducts are connected incorrectly to some organs. Nevertheless, this figure to me resembles the figure of *Proxenetes flabellifer* in the work of Pereyaslawzewa (1892, f. 26). The latter is a *Ceratopera* species. As the specimens of ULJANIN and those of Pereyaslawzewa both originated from the Bay of Sebastopol it is very probable that they belong to the same species. The differences in shape of the specimens figured may be ascribed to different stages of contraction of the animals. Von Graff (1882) thought he had found this species near Messina.

Proxenetes? striatus (Uljanin, 1870)

Von Graff, Monogr. Turbell. 1, 283 (1882).

Mesostomum striatum Uljanin, 1870

ULJANIN, Trudy otd. zool. anat. physiol. Moscow. 2, 12, Pl. 5, f. 3, 3a (1870); Leuckart, Arch. Nat.gesch. 37, no. 2, 482 (1871); Von Graff, Tierreich 35, 200 (1913).

The animals are 0.56-0.74 mm long and pale yellow in colour. The anterior part of the body is truncate, the posterior part obtusely rounded. The eyes are widely spaced and lie at $\frac{1}{4}$ of the body length. The pharynx lies at $\frac{2}{5}$ of the body length. The germovitellaria, called "testes" in the works of Uljanin and Von Graff, extend from the eyes in caudal direction. The testes, called "ovaria" by Uljanin and Von Graff, lie posterior of the pharynx. The male copulatory organ consists of a spherical muscular bulbus and a cuticular organ. According to Uljanin's figure the latter is funnel-shaped, its proximal part is longitudinally striped due to parallel secretion strands, and its distal part forms an obtuse angle with the proximal part. The oblong, longitudinally striped bursa copulatrix

is connected with a smaller receptaculum seminis by a ductus spermaticus.

Although the figure of Uljanin is incorrect in several respects, e.g. in that the germovitellaria are connected with the muscular bulbus, while the testes are connected with the bursa copulatrix, it certainly illustrates a species of Ptychopera. According to Uljanin the species is not uncommon between the algae in the Bay of Sebastopol. The one species of Ptychopera known to occur in the Black Sea is P. plebeia. I am, however, not certain that Ulianin's species is identical with P. plebeia. In P. plebeia the eyes are closer to each other and more anteriorly placed than in P. striata. The pharynx also is more anterior. Further the elongate testes of P. plebeia extend from the pharynx and lie in the anterior part of the body, while in P. striata the testes are more elliptic and lie just behind the middle of the body. The receptaculum seminis of P. striata is half the size of the bursa copulatrix, in P. plebeia the ratio is 1/6-1/10. The drawing of the copulatory organ of P. striata is insufficiently detailed for a comparison with that of P. plebeia, P. plebeia is slightly smaller than P. striata and is brown, while the latter is pale yellow. How far these differences are real or have to be ascribed to inaccurate recording by Ulianin can not be decided here.

EXCLUDED SPECIES

Proxenetes affinis (Jensen, 1878)

RIEDL, Thalassia Jugosl. 1, 150, 159 (1956).

Vortex affinis Jensen, 1878

JENSEN, Turbell. Norvegiae 43-44, Pl. 3, f. 11-13 (1878).

In the work of Riedl the name *Proxenetes affinis* is twice used instead of *Provortex affinis* (Jensen, 1878).

Proxenetes? chlorosticus (O. Schmidt, 1857)

Von Graff, Monogr. Turbell. 1, 283 (1882).

Mesostomum? chlorosticum O. Schmidt, 1857

O. Schmidt, Sitzber. kais. Ak. Wiss. Wien 23, 354–355, Pl. 2, f. 6 (1857); Von Graff, Tierreich 35, 353–354 (1913).

According to the habitus figure of this very inadequately described species it certainly is not a *Proxenetes*. I think it must be related to the Pseudostomidae but owing to lack of detailed data—even the pharynx was not seen by Schmidt—a correct identification is impossible. Schmidt found this species near Naples.

Proxenetes lictor Beklemischev, 1927

Beklemischev, Bull. Inst. rech. biol. Perm. 5, 190-191, 203-204, Pl.1, f. 8-9 (1927).

According to Ax (1959, p. 98–99) this species is identical with *Trigonostomum mirabile* (Pereyaslawzewa, 1892).

Proxenetes rosaceus Von Graff, 1882

Von Graff, Monogr. Turbell. 1, 282, Pl. 7, f. 28 (1882); idem, Tierreich 35, 182 (1913); Riedl, Thalassia Jugosl. 1, 152, 158 (1956).

This species, which has been described from Madeira, does not belong to the *Proxenetes* group. Its germaria are not the caudal continuations but lateral extensions of the vitellaria. The copulatory organ is hardly known, as is apparent from Von Graff's description: "Wir erkennen in diesem (the penis) die runde Samenblase und den nach Langerhans' Notizen mit "glänzendem Rand" versehenen Ausführungsgang derselben. Wahrscheinlich stellt letzterer ein chitinöses Copulationsorgan von vielleicht compliciterem Bau dar." The species is perhaps a representative of the subfamily Brinkmanniellinae. RIEDL (1956) claims to have found it in the Skagerrak.

GENERAL REMARKS

It is with hesitation that I make the following remarks on the geographical distribution and the ecology of the *Proxenetes* group, because the data are very limited.

1. Our knowledge of the distribution of the *Proxenetes* group shows so many gaps that it does not seem possible to give a definite opinion about it. With the exception of one record from North America and one from Greenland all data are from Europe and the adjacent part of Asia (Caspian Sea, Aral Sea). The first-mentioned records make it likely, however, that the group has not only a wide distribution along the European coasts but also along the American side of the Atlantic. The areas of distribution of the species are not or hardly known. Some species up till now are known from one locality only, viz. *Beklemischeviella brevistyla*, *Ceratopera steinboecki*, *C. reisingeri*, *C. levinseni*, *C. paradoxa*, *Proxenetes quadrispinosus*, *P. segmentatus*, *P. inflatus*, *P. lutheri*, *P. monotubulus* and *Messoplana geminata*. Other species seem to have a very extensive area of distribution, although the number of certain records is small, viz. *Ptychopera westbladi*, *Proxenetes flabellifer*, *P. angustus* and *Messoplana talcata*.

The available data are sufficient, however, to delimitate the centres of distribution of the various genera.

Beklemischeviella seems to be a boreal brackish-water genus, the distribution of which has a relict character. It is known from the Baltic, the Caspian and the Aral Sea and from southern England.

Ptychopera is widely distributed in boreal and warm-temperate marine and brackish waters. It occurs in the Atlantic as well as in the Mediterranean coastal waters.

Ceratopera is a marine, warm-temperate genus, distributed in the Mediterranean and along the Lusitanian coast. There is one outlying record from Greenland, C. levinseni.

Proxenetes s.s. is a boreal genus, distributed in marine and brackish waters along both sides of the Atlantic. Only one species, *P. angustus*, is known to occur also in the Mediterranean coastal waters.

Messoplana is widely distributed in boreal and warm-temperate marine waters. It has been recorded from the Atlantic and from the Mediterranean.

With the exception of a few short notes nothing has been published on the ecology of the *Proxenetes* group. From the available data it is clear, however, that most representatives of this group occur by preference in shallow waters along sheltered coasts. They inhabit detritus-rich sandy and muddy bottoms of shallow coastal waters, intertidal flats, coastal inland waters and salt-marshes. Several of the species are stenobiontic and limited to very special biotopes. Proxenetes puccinellicola, P. pratensis, P. cisorius, P. britannicus, P. minimus and Ptychopera tuberculata are characteristic inhabitants of the salt-marsh vegetation. Proxenetes trigonus, P. bilioi, P. intermedius and Messoplana elegans inhabit the mud- and sand-flats of the intertidal belt and shallow still-water biotopes. Proxenetes flabelliter and P. quadrispinosus seem to be characteristic for salt-marsh creeks. Other species may be found in several of these biotopes, e.g. Ptychopera westbladi, Proxenetes deltoides and P. karlingi. The species of the genus Ceratopera seem to occur in the algal vegetation of the upper part of the sublittoral. Only a few species are found at depths below 5 m.

The exceptions to the rule that the *Proxenetes* group is characteristic for shallow waters are few. *Proxenetes inflatus* and *Ceratopera levinseni* have been taken from deep water only. *Ceratopera steinboecki* and *C. reisingeri* are known from submarine caves. *Messoplana falcata* has been found in sublittoral sand bottoms only.

3. I have paid special attention to the distribution of the representatives of the *Proxenetes* group with relation to salinity. As the group as a whole is almost completely limited to habitats in shallow coastal waters it is obvious that all species are more or less euryhaline. Some of the *Ceratopera* species of the Mediterranean, which live in the sublittoral between algae and in caves, are perhaps stenohaline.

Although the *Proxenetes* group is obviously of marine origin several of its representatives penetrate far into the brackish water or are even bound to it. The tendency to invade waters of lower salinity is not equally shown by all genera of the group; the number of brackish-water species is preponderant in the primitive genera, while in the higher developed

genera brackish-water species are absent or largely outnumbered by the euryhaline marine species.

Beklemischeviella has been found so far in brackish water only.

In *Ptychopera* the situation is different. *P. westbladi* occurs mainly in euhaline and polyhaline waters, *P. plebeia* in poly- and mesohaline waters and *P. tuberculata* in euhaline and mesohaline waters. The recently discovered *P. spinifera* nov. sp.¹) inhabits meso- and oligohaline brackish waters and penetrates even into habitats with an average salinity below $0.3 \, ^{0}$ /₀₀ Cl'; it is the only species of the group reaching into the fresh water.

The representatives of *Ceratopera* occur in the euhalinicum and the polyhalinicum.

The genus Proxenetes is mainly euryhaline marine. Most species penetrate for some distance into the brackish waters, but they do not exceed the $10^{-0}/_{00}$ Cl' isohaline. P. unidentatus, P. minimus and P. karlingi appear to be the most euryhaline species as they inhabit also the whole mesohaline range.

Messoplana species occur in euhaline and polyhaline waters.

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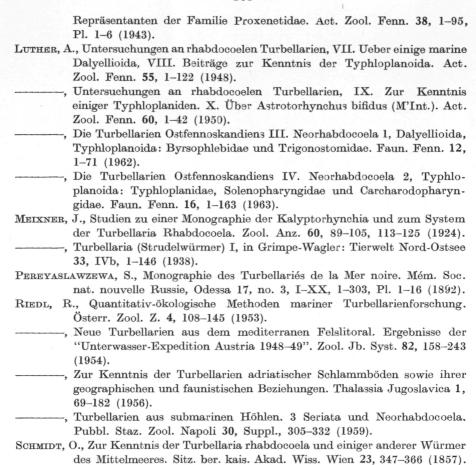
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¹⁾ This new species will be described in a supplement to the present revision.

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