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

BY

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In the years 1962 and 1963 I made a survey of the Turbellarian fauna of some intertidal still-water biotopes in the south-western part of the Netherlands. My samples were mainly taken from salt-marsh creeks, salt-marsh pools and sandy mud-flats. A few samples from salt-marsh vegetations were also investigated. The Turbellaria which were found belonged for the larger part to the Seriata, which were dealt with earlier (DEN HARTOG, 1963, 1964) and to the Neorhabdocoela. Representatives of several families of the Neorhabdocoela were found, but the Trigonostomidae and the Provorticidae are certainly the most characteristic families for the investigated habitats, where the bulk of the individuals is composed of quite a number of species from the two families. The Trigonostomidae are represented by 3 genera of the *Proxenetes* group with together 16 species. Several of them appeared to be undescribed. This made a survey of the literature on this group necessary, and as I had at my disposal such rich material I thought it would be useful to summarize my results in the form of a preliminary revision of the group.

In the following sections the subdivision of the Trigonostomidae and the taxonomical relationships within the *Proxenetes* group will be treated according to morphological criteria. A chapter on the anatomy of the group has not been added, as this was treated extensively by LUTHER (1943, 1948), and I have little to add to his admirable works. The descriptions of the Dutch species were made from living specimens, while the other descriptions have been compiled from the literature. For practical reasons they have been kept as short as possible, and give mainly the data which are necessary for identification, e.g. the cuticular structures. My ecological observations on some of the species have been included in this work.

I am well aware that this revision is in fact only a review of the present state of the taxonomy of the *Proxenetes* group. In 1948 only 14 species were known with certainty, since that time 14 new species have been recognized. As a consequence of study in other regions and other biotopes it can be expected that the number of species will become even greater.

The taxonomical subdivision of the Trigonostomidae

In 1924 MEIXNER published a thorough treatise of the Trigonostomidae, a family which at that time consisted of one genus, *Trigonostomum*. This family had been placed by VON GRAFF (1913) in the suborder Kalyptorhynchia on the ground of the occurrence of a small anterior proboscis. According to MEIXNER (l.c.) the anatomical structure as well as the ontogenetic development of the proboscis of the Kalyptorhynchia and of the Trigonostomidae are completely different. The Kalyptorhynchia have a so-called "Scheidenrüssel", i.e. a proboscis consisting of an anterior muscle cone, which is separated from the remaining mesenchyma by a membranous muscle septum and which (at rest) is sheathed distally by a well-differentiated integumental invagination. On the contrary, the proboscis of the Trigonostomidae consists only of a subanterior, ventral, eversible integumental invagination. Consequently the muscular mechanism of the proboscis differs greatly in both groups. In the Kalyptorhynchia it consists of a complicated system of retractor, protractor, fixator and dilator muscles, while in the Trigonostomidae only retractor and dilator muscles are involved. MEIXNER, therefore, considered the Trigonostomidae to be a family of the suborder Typhloplanoida and repeatedly pointed out its relationship to the family Proxenetidae. Indeed the similarity between the two families is striking, especially where the genital organs are concerned, but also in many other characters. MEIXNER (l.c.) kept, nevertheless, the two families apart. It appears from his classification scheme that this separation is based on the fact that the Trigonostomidae have a proboscis and an anteriorly placed pharynx. The Proxenetidae, in contrast, do not have a proboscis. The proboscis of *Astrotorhynchus*—which genus was placed by MEIXNER (l.c.) in the Proxenetidae—has quite a different structure and represents in fact the anterior point of the body, which can be drawn in by retractor muscles. The proboscis of the Trigonostomidae and that of *Astrotorhynchus* are thus independent and incomparable structures. It is apparent, however, that in the Proxenetidae a tendency also exists to form a specialized proboscoid organ that can be used for catching prey. It is a question of personal approach, whether one wants to stress the few differences or the many similarities. In this case MEIXNER had chosen the first solution, but the relationship between the two families was not denied: "Die rüsselartig verstülpbare Integument-einsenkung zusammen mit den charakteristischen Bau- und Lageverhältnissen des Pharynx rechtfertigen die Beibehaltung der Familie Trigonostomidae, hindern jedoch nicht, an der im Bau der Geschlechtsorgane gut begründeten Verwandtschaft mit den Proxenetidae festzuhalten" (l.c. p. 105).

The same point of view is maintained in the system published by BRESSLAU (1933).

In 1943 LUTHER proposed a new taxonomical arrangement within the

family Proxenetidae. He distinguished 3 subfamilies, the Proxenetinae, the Promesostominae and the Paramesostominae, according to the structure of the vitellaria and their connection with the germaria and the length of the male genital canal. This subdivision was not very satisfactory as the subfamily Proxenetinae is certainly more closely related to the Trigonostomidae than to the two other subfamilies. LUTHER was well aware of this aesthetic fault, and in a second revision of this group he (LUTHER, 1948) amended and extended his subdivision considerably. In the first place he no longer kept separate the Proxenetidae and the Trigonostomidae, but joined both families under the older name Trigonostomidae. Further, the subfamily Proxenetinae was split into the Proxenetinae sensu stricto and the Brinkmanniellinae, on the grounds of the occurrence of separate efferent and deferent tracts between the germovitel-laria and the atrium genitale in the first subfamily, while in the latter only one connection exists between these organs. The genus *Astrotorhynchus*, placed by VON GRAFF (1913) in a separate monogeneric family, was now classed as a special subfamily of the Trigonostomidae. The subdivision of the Trigonostomidae, according to LUTHER, is summarized in table 1.

TABLE 1

Classification of the Trigonostomidae according to LUTHER (1948)

Subfamily:	Genus:
1. Brinkmanniellinae	Brinkmanniella, Westbladiella,
	Tvaerminnea, Coronhelimis, Einarella
2. Proxenetinae	Proxenetes, Beklemischeviella
3. Trigonostominae	Trigonostomum
4. Promesostominae	Promesostoma
5. Paramesostominae	Paramesostoma
6. Astrotorhynchinae	Astrotorhynchus

In a later paper LUTHER (1962) did not alter this system, but he remarked that *Coronhelimis* and *Tvaerminnea* both probably represent separate monogeneric subfamilies.

In my opinion the family Trigonostomidae in the sense of LUTHER is a heterogeneous assemblage of groups with some characters in common, viz. the existence of only one genital pore in combination with paired germaria or germovitel-laria. In three of LUTHER's subfamilies, the Proxenetinae, the Trigonostominae and the Astrotorhynchinae, a double connection occurs between the germovitel-laria and the genital atrium. Fertilization of the eggs takes place in a fecundatorium. Sperm is transported to it through an efferent tract, which in the diverse genera shows a varying differentiation. The fertilized eggs are transported to the atrium genitale through a deferent tract, the female genital canal (fig. 1). In the Paramesostominae also an efferent and a deferent tract occur; however, the entrance to the efferent tract lies not in the atrium genitale commune,

but is a pore in front of the genital opening. On the contrary, the Brinkmanniellinae and the Promesostominae have only one connection between the female gonads and the exterior and this has an efferent as well as a deferent function. For this reason I prefer to exclude the Promesostominae and the Brinkmanniellinae from the Trigonostomidae and to regard them as subfamilies of a new family Promesostomidae.

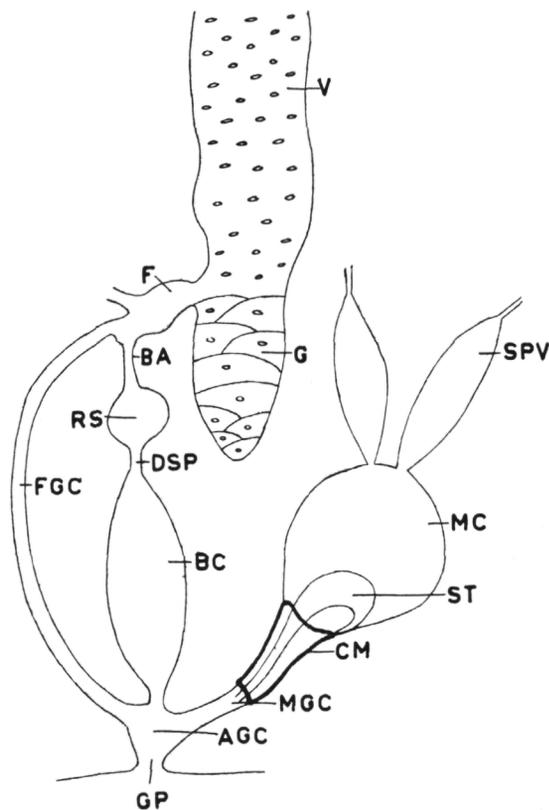


Fig. 1. Schematical outline of the genital apparatus in the subfamily Trigonostominae. V= vitellarium; G=germarium; F=fecundatorium; FGC=female genital canal; GP=genital porus; AGC=atrium genitale commune; BC=bursa copulatrix; DSP=ductus spermaticus; RS=receptaculum seminis; BA=bursal appendage; MGC=male genital canal; CM=cuticular mantle; ST=stylet; MC=muscular copulatory organ; SPV=spermaducal vesicle.

The Trigonostominae and the Proxenetinae differ slightly in that the first-mentioned subfamily has a small anterior proboscis and the second not. Their genital organs have a very similar structure. These subfamilies form a natural group, of which the Proxenetinae represent the more primitive stages and the Trigonostominae the higher stages of development. On these grounds I prefer to combine them and to regard them as one subfamily, the Trigonostominae (*sensu lato*). I will deal more extensively with the relationships within this subfamily in the next section.

The remaining two monogeneric subfamilies, the Paramesostominae and the Astrotorhynchinae of LUTHER's classification, have also a closer relationship to each other than to his other 4 subfamilies. Both are characterized by reticulate anastomosing vitellaria, which are separated from the germaria, and by the existence of an unpaired spermaducal vesicle, while the margin of the pharynx in both groups is ciliate. They differ, however, as *Astrotorhynchus* has developed a proboscoïd organ, and such an organ is missing in *Paramesostoma*. Other differences are the presence of an uterus in *Astrotorhynchus* and the position of the entrance of the bursa copulatrix, in front of the genital pore, in *Paramesostoma* (LUTHER, 1950). Nevertheless, I think it justified to unite these subfamilies under the name Paramesostominae (sensu lato).

Some reference must be made to the monotypic genus *Marinellia*, which has been described by RIEDL (1954) and placed in the Trigonostominae. This genus is in some respects intermediate between the Trigonostominae and the Paramesostominae. The female genital apparatus shows the typical circuit of an efferent and a deferent tract between the fecundatorium and the atrium genitale commune, and it is provided with a cuticular bursal appendage (in German: "Bursaanhang, Bursamundstück, Mundstück des Receptaculum seminis"). The two vitellaria are lobate and very close to each other, without forming visible anastomoses. The vitellaria continue caudodorsally each into a small germarium. The proboscis is of a more advanced type than that of *Trigonostomum setigerum* and is tongue-shaped. These characters justify classification into the Trigonostominae. However, the vasa deferentia unite into one spermaducal vesicle and the margin of the pharynx is ciliate. These situations are typical for the Paramesostominae.

I will conclude this section with a summary of the proposed subdivision and the new or amended definitions of the higher taxa.

Promesostomidae nov. fam.

Typhloplanoida with one genital porus and paired male and female gonads. Testes solid, ventral to the vitellaria. One connection between the female gonads and the exterior.

subfam. *Brinkmanniellinae*

Germaria and vitellaria closely joined. Male genital canal very short.

subfam. *Promesostominae*

Germaria and vitellaria almost completely separated, only connected by a very narrow duct. Male genital canal long, forming a copulatory atrium. Cuticular stylet a very long duct.

Trigonostomidae

Typhloplanoida with one genital porus and paired male and female gonads. Testes solid, ventral to the vitellaria. Female gonads connected with the exterior by a deferent and an efferent tract.

Subfam. *Trigonostominae*

Vitellaria caudally continuing into the germaria. Efferent and deferent tracts of the female copulatory organ connecting the fecundatorium and the atrium genitale commune. Efferent tract always provided with a cuticular bursal appendage. Vasa deferentia widened into two spermaducal vesicles, before they enter the muscular part of the copulatory organ (except in *Marinellia*, where only 1 spermaducal vesicle occurs). Male cuticular copulatory organ consisting of the penis stylet and mostly also of the stiffened wall of the male genital atrium (except in *Beklemischeviella*). Margin of the pharynx without ciliae (except in *Marinellia*).

Subfam. *Paramesostominae*

Vitellaria reticulate and anastomosing, separate from the germaria. The short vitellogerms and germoducts unite into one oviduct. Efferent and deferent tracts of the female copulatory organ connecting the fecundatorium with the atrium genitale commune in *Astrotorhynchus*, but in *Paramesostoma* the efferent tract has a special opening in front of the genital porus. Cuticular bursal appendage absent. Male cuticular copulatory organ consisting of a penis stylet. Margin of the pharynx ciliate. Vasa deferentia uniting into one spermaducal vesicle before entering the muscular part of the copulatory organ.

Taxonomical relationships within the subfamily Trigonostominae

According to LUTHER's classification (1943) the subfamily Proxenetinae consists of two genera, *Proxenetes* and *Beklemischeviella*. The latter genus was erected by LUTHER in 1943 for a species differing from *Proxenetes* in the shape of its male cuticular copulatory apparatus, which is hooked at its distal end, and in the structure of its bursal appendage, which consists of a single slightly or not at all cuticularized duct. The cuticular copulatory organ of *Proxenetes* is not hooked, but consists of a complicated apparatus, formed by the stylet and the stiffened wall of the male genital atrium. The bursal appendage in this genus consists, according to LUTHER (l.c.), of a basal cuticular ring and two cuticularized ducts, which may be proximally joined together.

In a later publication LUTHER (1948) revised his description of *Beklemischeviella* in comparison with *Proxenetes*. He stressed again the differences in the male copulatory organs of the two genera and he recorded that the muscular bulb of this organ is round in *Beklemischeviella*, but retort-shaped in *Proxenetes*. The structure of the bursal appendage was not given any longer as a distinguishing character. This was certainly justified, as the genus *Proxenetes* in the sense of LUTHER shows a lot of variation in the structure of this organ.

After the separation of *Beklemischeviella* from *Proxenetes* the latter genus remained, however, a rather heterogeneous assemblage of species.

I have been able to distinguish in this genus six rather homogeneous units, which are more or less closely allied to each other or show clear affinities to certain species groups of the genus *Trigonostomum*. Three of these units have been regarded by me as separate genera, viz. *Ptychopera*, *Ceratopera* and *Messoplana*. The other three units, which show much closer mutual affinities, are considered to represent sections of the genus *Proxenetes* sensu stricto.

For this subdivision I used the following criteria:

1. Morphological differentiation of the efferent tract of the female genital apparatus.
2. Structure of the bursal appendage.
3. Situation of the pharynx.
4. Structure of the male cuticular copulatory organ.
5. Presence or absence of secondary cuticular structures in a widening of the distal part of the bursal canal.

1. The differentiation of the efferent tract of the female genital apparatus shows in the various units of the *Proxenetes* group a quite different development. This tract consists in the genera *Beklemischeviella* and *Ptychopera* of a very large, longitudinally folded bursa copulatrix and a very small receptaculum seminis, connected by a ductus spermaticus. A differentiation into a large bursa copulatrix and a receptaculum seminis exists also in the *karlingi* section of *Proxenetes*. In this case the bursa copulatrix and the receptaculum seminis are more or less of the same size. They are, however, not connected by a ductus spermaticus, but are merely separated by a deep constriction, which in *Proxenetes karlingi* seems to be complete (LUTHER, 1943). It is doubtful whether the bursa copulatrix and the receptaculum seminis in this section are homologous with the corresponding organs in *Beklemischeviella* and *Ptychopera*.

In the typical section of *Proxenetes* the receptaculum seminis is very large and connected with the atrium genitale commune by a long, rather wide bursal canal, which is homologous with the bursa copulatrix of the *karlingi* section. A similar differentiation of the efferent female genital tract occurs also in the *angustus* section of *Proxenetes*, in *Ceratopera* and in *Messoplana*. In *Ceratopera* the bursal canal is sometimes extremely long and narrow and its receptaculum seminis is often provided with cuticularized longitudinal folds. Moreover, in some species of *Ceratopera* the transition between bursal canal and receptaculum seminis may be cuticularized.

In the related *Trigonostomum* group the mostly very voluminous receptaculum seminis is connected with the atrium genitale commune also by a bursal canal, which may be rather wide, as in *Proxenetes*, or very long and narrow, as in *Ceratopera*. Moreover, in some *Trigonostomum* species the transition from the bursal canal to the receptaculum seminis may be cuticularized (MEIXNER, 1924).

2. The structure of the bursal appendage within the *Proxenetes* group shows also a wide range of variation, but the different types which can be distinguished are highly characteristic and constant for each genus. In the primitive genera *Beklemischeviella* and *Ptychopera* the bursal appendage consists only of one long, narrow, not or slightly cuticularized duct. In the proximal part of the bursal ducts in *P. plebeia* (cf. BEKLEMISCHEV, 1927, Pl. 1, f. 11) and *P. tuberculata* a longitudinal ridge occurs. This may be considered to be the precursor of the more evolved paired ducts in the higher organized genera of the Trigonostominae.

The bursal appendage of *Ceratopera* consists also of one duct, but this is strongly cuticularized and from its base many short cuticular ridges radiate on the outer wall of the receptaculum seminis. In distal direction the duct becomes gradually narrower, coils inward and becomes in the most extreme case contorted. According to LEVINSEN (1879) the duct is distally split in *C. levinseni*.

In the genus *Proxenetes* the structure of the bursal appendage is considerably more complicated. It consists of a cuticular ring in the wall of the receptaculum seminis, and from this ring originate two narrow cuticular ducts. In most cases the ring is double, and it is mostly armed with spines. In the typical section of the genus the two ducts are completely separate, but may have a common wall within the ring ("Doppeltrichter"). In the *angustus* section only one duct arises from the ring, but it very shortly splits into two very narrow ones. In the *karlingi* section the splitting into two takes place only at the very distal end of the duct. In this genus the ducts pass through the ring, but do not penetrate into the receptaculum seminis itself.

The bursal appendage of *Messoplana* also consists of a cuticular ring through which two very short ducts pass, but these ducts project obviously within the receptaculum seminis, and they are always completely separated.

Some of the structures of the bursal appendage in the *Proxenetes* group occur also in the *Trigonostomum* group and show there even a further differentiation. The bursal appendage of the species of the "*setigerum*" group of the genus *Trigonostomum* (MEIXNER, 1924) and of *Marinellia* (RIEDL, 1954) is very similar to that of the typical section of *Proxenetes*. If one accepts that in the course of evolution the numerous cuticular ridges which radiate from the bursal duct of *Ceratopera* have developed into free, but closely packed cuticular strands together forming a cylindrical sheath, a phenomenon characteristic of *T. penicillatum* and some allied species, then the bursal appendage of *Ceratopera* may be considered to represent the basic type of this organ in the "*penicillatum*" group of *Trigonostomum*. The bursal appendage of *Messoplana* may be regarded as the most primitive stage of the structure which occurs in the species of the "*coronatum*" group of *Trigonostomum*. Thus the structure of the

bursal appendage of the different species groups of the genus *Trigonostomum* seems to have been derived from different genera of the *Proxenetes* group. Therefore, I can not see *Trigonostomum* as a homogeneous natural genus, but consider it to be an artificial group of species with several roots in the *Proxenetes* group and agreeing mainly in their common possession of a subanterior proboscis. The three species groups of *Trigonostomum* represent certainly independent genera.

3. The pharynx in the majority of the species is placed in the posterior part of the body. This is true for *Proxenetes*, *Beklemischeviella* and *Messoplana*. In *P. pratensis* the pharynx lies in the middle of the body. In the genus *Ptychopera* the pharynx is situated anteriorly, and in *Ceratopera* it is situated at ca. $1/3-2/5$ of the body length. In the *Trigonostomum* group the pharynx lies always in the anterior part of the body.

4. The male copulatory organ shows some characters which are of more than specific importance. The cuticular part of the copulatory organ consists in *Beklemischeviella* of a stylet only, which, moreover, is strongly hooked. In the other genera of the *Proxenetes* group stiffenings in the wall of the male genital atrium are involved also in the cuticular apparatus, giving it a more or less complicated structure. The ground pattern of the copulatory apparatus is largely the same. The stylet¹⁾ is surrounded by an open or funnel-shaped sheath, composed of the stiffenings in the wall of the male genital atrium. This sheath shows the tendency to become independent of the stylet and is in some cases transformed into a duct parallel to the stylet.

The stiffened wall of the male genital atrium forms a closed funnel-shaped sheath around the stylet in *Ptychopera* and *Proxenetes*. In *Ceratopera* the stiffenings of the atrial wall form an open cuticular mantle surrounding only partly the straight part of the stylet. In *C. axi* and *C. steinboeckii* this mantle is transformed into a closed duct, which at its proximal and distal ends is connected with the stylet. In *Messoplana* species the separation of stylet and atrial duct is almost completed, as both ducts are only proximally connected.

Differences in the curvature of the stylet, folds in the cuticular sheath,

¹⁾ In the works of several authors (VON GRAFF, MEIXNER, STEINBÖCK, RIEDL) the stylet is often indicated as the discharging duct for the granular secretion of the prostatic glands, while the sperm is said to be discharged through the cuticular sheath. LUTHER (1943) recorded that in *Proxenetes flabellifer* sperm as well as granular secretion are discharged through the stylet, and that granular secretion was found also in an additional duct within the cuticular sheath. In *P. karlingi* I found granular secretion and sperm in the stylet, but sperm also within the cuticular sheath. In *P. quadrispinosus* sperm and granular secretion were found in the stylet only. Apparently, there is on this point a considerable variation, and, therefore, such functional terms as "Kornsekretrohr" and "Samenrohr" should be avoided.

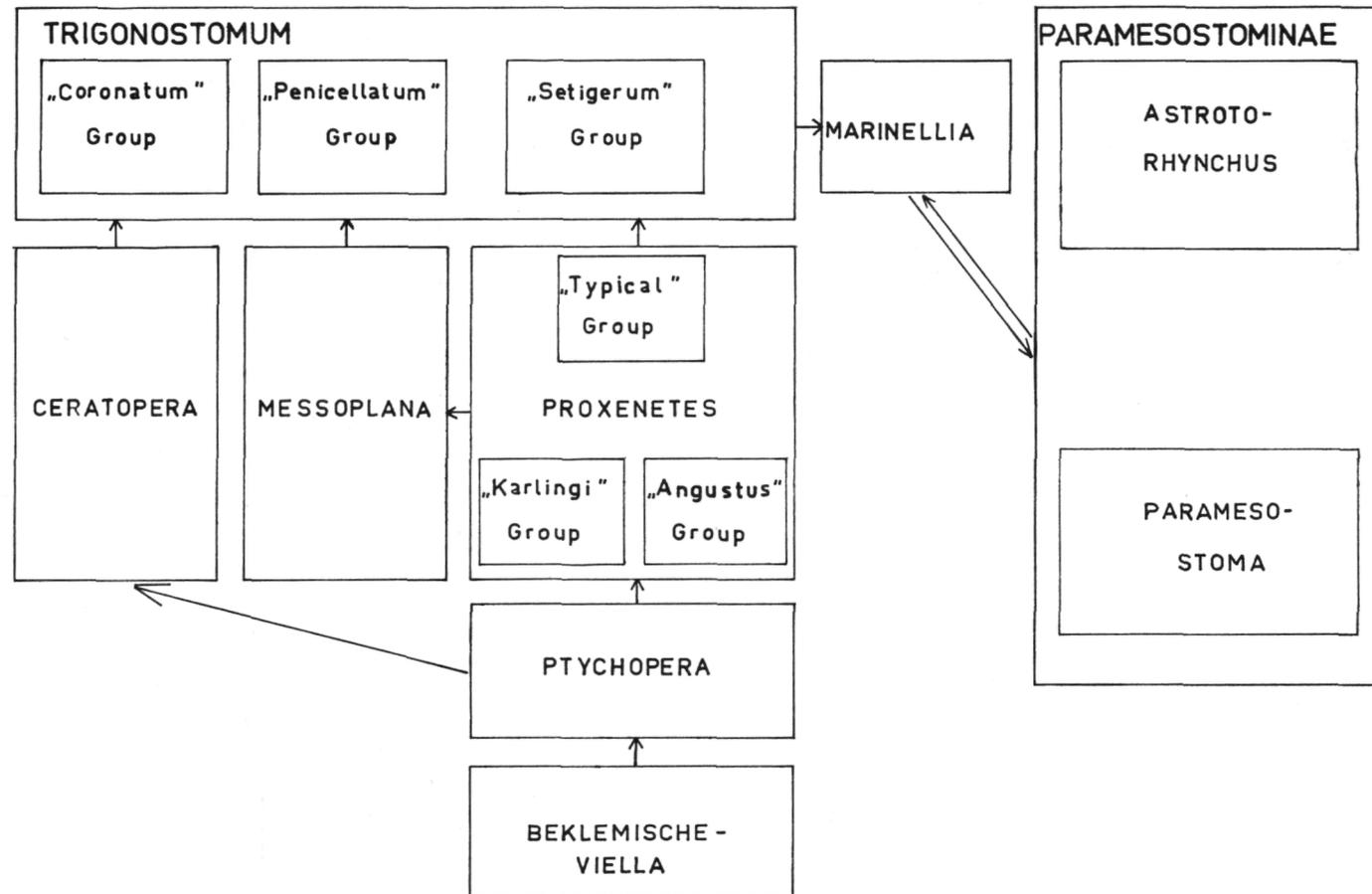


Fig. 2. The taxonomic relationship within the family Trigonostomidae.

absence or presence of spines, and the presence of highly specific additional structures (e.g. the club-shaped distal organ in *P. puccinellicola*) are characters indispensable for specific identification. Although the shape of the copulatory organs is thus apparently in a high measure characteristic for the species, there are, nevertheless, some cases in which the copulatory organs of different species show a striking similarity in structure (e.g. *Proxenetes simplex* and *P. angustus*).

5. Secondary cuticular structures in a widening of the distal part of the bursal canal have been found only in the species of the typical section of *Proxenetes*. These, with the exception of *P. simplex* have a comb-like spine apparatus, of which the number of teeth is variable within certain limits. In *P. simplex* a muscular lump occurs and this is covered with a thin papillose cuticula.

The relationship within the family Trigonostomidae is given in fig. 2.

KEY TO THE GENERA OF THE PROXENETES GROUP

1. Efferent tract of the female genital apparatus differentiated into a large bursa copulatrix and a small receptaculum seminis connected by a narrow ductus spermaticus. Bursal appendage consisting of only one very narrow, hardly cuticularized duct.
 2. Male cuticular copulatory organ consisting of a distally hooked, longitudinally striped penis stylet. Male genital atrium without cuticular stiffenings. Pharynx posterior. . . 1. *Beklemischeviella*
 2. Male cuticular copulatory organ consisting of a funnel-shaped penis stylet sheathed by the stiffened wall of the male genital atrium. Pharynx anterior. 2. *Ptychopera*
1. Efferent tract of the female genital apparatus differentiated by constriction into a bursa copulatrix and a receptaculum seminis (thus without a ductus spermaticus) or consisting of a receptaculum seminis and a narrow bursal canal (representing the reduced bursa copulatrix).
 3. Bursal appendage consisting of an involute, strongly cuticularized tapering duct, from which base often many small cuticular ridges radiate on the outer wall of the receptaculum seminis. Male cuticular copulatory organ consisting of a stylet, which is distally surrounded by an open cuticular mantle. The latter may be transformed into an additional duct beside the stylet, but is always connected with the stylet. . . . 3. *Ceratopera*
 3. Bursal appendage consisting of a cuticular ring in the wall of the receptaculum seminis and two delicate, parallel, cuticular ducts, which are completely separated or partly united.

Male cuticular copulatory organ consisting of a stylet surrounded by a closed cuticular mantle or consisting of two proximally connected ducts.

- 4. Male cuticular copulatory organ consisting of a penis stylet surrounded by a funnel-shaped cuticular sheath. Ducts of the bursal appendage rather long, coiled, completely separated or partly united, not projecting into the receptaculum seminis. 4. *Proxenetes*
- 4. Male cuticular copulatory organ consisting of a stylet and an additional duct which are connected at their proximal ends only. Ducts of the bursal appendage very short, separated, partly projecting into the receptaculum seminis. 5. *Messoplana*

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BY

C. DEN HARTOG

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1. BEKLEMISCHEVIELLA

LUTHER, Act. Zool. Fenn. 38, 71-73 (1943).

Pharynx posterior. Efferent tract of the female genital apparatus differentiated into a large bursa copulatrix and a small receptaculum seminis connected by a narrow ductus spermaticus. Bursal appendage consisting of a short, delicate, hardly cuticularized duct. Wall of the bursa copulatrix with more or less conspicuous longitudinal folds. Male cuticular copulatory organ consisting only of a distally hooked penis stylet with a longitudinal lamellate structure. The male genital atrium is without cuticular structures.

Type: *Proxenetes contortus* Beklemishev

The genus *Beklemischiella* differs from the other genera of the *Proxenetes* group by the fact that its cuticular copulatory organ consists of the stylet only. This stylet is strongly hooked. The differentiation of the efferent tract of the female genital apparatus is very similar to that of *Ptychopera*. The position of the pharynx, however, is posterior in *Beklemischiella* and anterior in *Ptychopera*.

KEY TO THE SPECIES

1. Proximal part of the stylet widely funnel-shaped, becoming abruptly narrower.
 2. Narrow part of the stylet so strongly hooked that its distal tip reaches to the proximal funnel. 1. *B. contorta*
 2. Narrow part of the stylet curved so that its distal tip is proximally directed, but not reaching as far as the proximal funnel. 2. *B. brevistyla*
1. Stylet becoming gradually narrower. 3. *B. angustior*

Beklemischiella contorta (Beklemishev, 1927)

LUTHER, Act. Zool. Fenn. 38, 73-75, f. 9, 17, 71-79, Pl. 1, f. 4, 5, 8, Pl. 4 (1943); BEKLEMISCHEV, Bull. Soc. Nat. Moscow (Biol.) 58, 35-36, f. 1

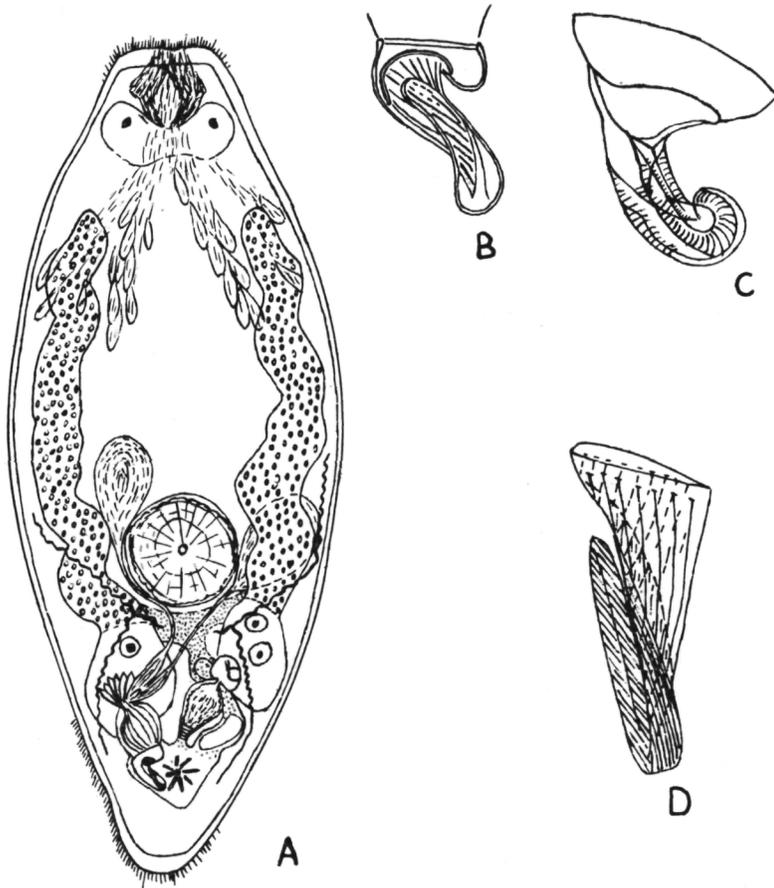


Fig. 3. A-B, *Beklemisheviella contorta* (Beklemishev, 1927); A, general view; B, penis stylet; C, *B. brevistyla* Beklemishev, 1953, penis stylet; D, *B. angustiro* Luther, 1943, penis stylet. (A-B and D after LUTHER, C after BEKLEMISHEV).

(1953); LUTHER, Faun. Fenn. 12, 55-56, f. 22 (1962); idem, Faun. Fenn. 16, 149 (1963). — Fig. 3 A, B.

Proxenetes contortus Beklemishev, 1927

BEKLEMISHEV, Zool. Jb. Syst. 54, 101-102, f. 3a-b (1927).

The animals are oblong to linear, 0.6-1.0 mm long, and white in colour. The anterior part is truncate or obtusely rounded. The pharynx lies in the posterior part at ca. 2/3 of the body length. The cuticular copulatory organ consists of a short, but wide proximal funnel, which suddenly becomes narrower (Fig. 3 B). The narrow part of the stylet is so strongly hooked that its distal tip reaches to the proximal funnel. It is striate, due to fine lamellation of the cuticula. The length of the stylet is 30-36 μ .

Geographical distribution:

B. contorta has been described by BEKLEMISCHEV (l.c.) from the Aral Sea from only one specimen. Later it was found in the Baltic Sea, where it is widely distributed from Kiel (AX, 1951) and Malmö to the Gulf of Finland (LUTHER, 1962).

Although some minor differences exist between the Baltic specimens and the specimen from the Aral Sea no decision can be made as to the taxonomical status of the two forms before new material from the Aral Sea has become available (BEKLEMISCHEV, 1953; AX, 1959).

Ecology:

B. contorta was collected in the mesohaline Aral Sea at a depth of 3 m in a vegetation of *Naias marina*. In the Baltic it is almost completely limited to the mesohaliniticum. It inhabits there sandy as well as muddy bottoms, but it occurs also between algae and water plants or between mussels at a greater depth. According to LUTHER (1962) it occurs often under algae which have been washed ashore.

Beklemischeviella brevistyla Beklemishev, 1953

BEKLEMISCHEV, Bull. Soc. Nat. Moscow (Biol.) 58, 36-37, f. 2-3. — Fig. 3 C.

The animals are elliptic, less than 1 mm long and colourless. The pharynx lies at 2/3 of the length of the body. The cuticular copulatory organ consists of a short, but wide, oblique proximal funnel, which suddenly becomes narrower (Fig. 3 C). The narrow part of the stylet is curved, so that its distal tip is proximally directed; the latter is short and does not reach to the proximal funnel. The narrow part of the stylet is transversely striped, due to fine lamellation of the cuticula. According to BEKLEMISCHEV (l.c.) the stylet of this species is shorter and more compact than that of *B. contorta*. The length of the stylet is, however, not given.

Geographical distribution:

The species has been found in the Caspian Sea near Lenkoran.

Ecology:

BEKLEMISCHEV l.c. found the species in small numbers between algae and bryozoa on poles.

Beklemischeviella angustior Luther, 1943

LUTHER, Act. Zool. Fenn. 38, 75-77, f. 80-83, Pl. 1, f. 7 (1943); idem Act. Zool. Fenn. 55, 81-83, f. 116-120 (1948); idem, Faun. Fenn. 12 57-58, f. 23 (1962). — Fig. 3 D.

The animals are oblong, 0.6-1.2 mm long, and white or colourless

The anterior as well as the posterior part of the body is obtusely rounded. The pharynx is situated at ca. $2/3$ of the length of the body. The cuticular copulatory organ consists of a stylet gradually narrowing in distal direction (Fig. 3 D). The distal part of the stylet is hooked back, so that the tip reaches to the proximal part. The stylet shows a conspicuous torsion; it is striate due to lamellation of its cuticula. The length of the stylet, from its proximal end to the angle of the hook, is, according to LUTHER (1962, f. 23 D), 57μ .

Geographical distribution:

The species has been found in the Baltic Sea, viz. at the entrance of the Gulf of Finland and near Stockholm.

Ecology:

The species has been found in fine and coarse sand as well as in gravel, mixed with fine, detritus-rich mud. It occurs also in the coastal ground water of salt-marshes and the vegetation along the water edge. All records are from the summer.

2. PTYCHOPERA nov. gen.

Pharynx anterior, at $1/5$ – $1/3$ of the body length. Efferent tract of the female genital apparatus differentiated into a large bursa copulatrix and a small receptaculum seminis connected by a narrow ductus spermaticus. Bursal appendage consisting of a rather long, delicate, hardly cuticularized duct. Wall of the bursa copulatrix with many longitudinal, more or less cuticularized folds. Male cuticular copulatory organ consisting of a funnel-shaped penis stylet and of the stiffened wall of the male genital atrium.

Type: *Proxenetes westbladi* Luther.

This genus is closely allied to *Beklemischeviella*, as the structure of the efferent tract of the female genital apparatus is essentially similar in both genera. The structure of the male cuticular copulatory organ is, however, much more complicated than in *Beklemischeviella*, as the cuticularized wall of the male genital atrium is also part of it. The male copulatory organs of *Ptychopera* and *Proxenetes* agree in many respects. The anterior position of the pharynx is unusual in the *Proxenetes* group and is somewhat similar to the situation that exists in the *Trigonostomum* group. *Ptychopera* shows also a relationship with *Ceratopera*, as both genera have a bursal appendage consisting of one duct and an anteriorly placed pharynx. The bursal appendage of the latter genus is, however, heavily cuticularized and more complicated than in *Ptychopera*.

KEY TO THE SPECIES

1. Bursa copulatrix ellipsoid, without interior cuticular structures. Cuticular copulatory organ larger than 50 μ , not ending in a distal knob and not barbed.
2. Cuticular copulatory organ 60–65 μ long. From its cuticular mantle an obliquely placed, linear projection extends to the obtuse distal tip of the stylet. Bursal appendage and ductus spermaticus inserted beside each other on the receptaculum seminis. Pharynx at 1/5 of the body length. Testes far caudal to the pharynx. Germaria anterior to the copulatory organ. 1. *P. westbladi*
2. Cuticular copulatory organ 80 μ long. The stylet narrows suddenly in distal direction and proceeds on the one side as a linear process with obtusely rounded tip, while on the other side it forms a wide lateral bulge. Bursal appendage and ductus spermaticus inserted diametrically opposite on the receptaculum seminis. Pharynx at 1/3 of the body length. Testes extending from just behind the pharynx. Germaria lateral to the copulatory organ.
. 2. *P. plebeia*
1. Bursa copulatrix bell-shaped, containing two cuticular bars, which project with their hooked distal parts into the atrium genitale commune. Cuticular copulatory organ 44–46 μ , ending in a small distal knob (or hook). Convex side of the cuticular mantle barbed, due to a number of small spines. 3. *P. tuberculata*

Ptychopera westbladi (Luther, 1943)*Proxenetes westbladi* Luther, 1943

LUTHER, Act. Zool. Fenn. 38, 69–71, f. 1a–b, 8, 18, 62–70 (1943); Ax Vie et Milieu, Suppl. 5, 116–118, f. 29 (1956). — Fig. 4–7, Pl. 1 A–B

The animals are oblong, at most 0.5–0.7 mm long and indigo-blue in colour. The anterior part of the body is more or less truncate. Close behind the eyes lies the pharynx, at ca. 1/5 of the body length. The testes lie in the middle part of the body far behind the pharynx. The vitellaria extend from just behind the pharynx. The germaria are always anterior to the male copulatory organ. The cuticular copulatory organ is 60–65 μ long, and is proximally embedded in the muscular bulb (Fig. 5–6). It consists of a funnel-shaped stylet, which becomes distally slightly curved and has an obtuse distal tip. Beside the stylet lies a short second funnel, that narrows in distal direction and unites with the distal part of the stylet. The distal part of the stylet is surrounded by a cuticular mantle composed of the stiffened wall of the male genital atrium. As a consequence of folds in its surface several spines and ridges occur along the inner surface of the mantle. Very characteristic is an obliquely placed,

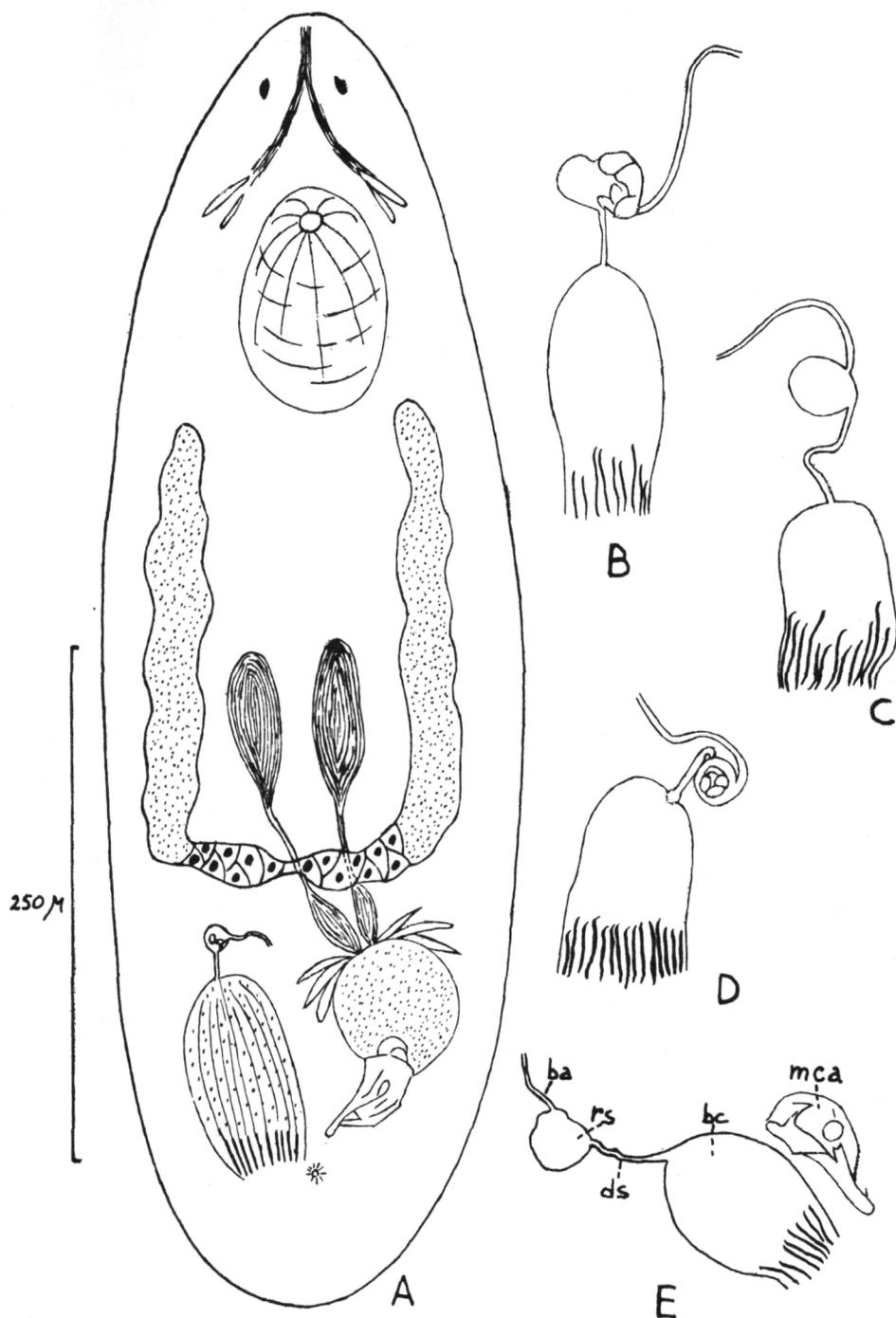


Fig. 4. *Ptychopera westbladi* (Luther, 1943); A, general view, B-E, differentiation of the efferent tract of the female genital apparatus. bc=bursa copulatrix; ds=ductus spermaticus; rs=receptaculum seminis; ba=bursal appendage; mca= male cuticular copulatory apparatus. (Original after specimens from the Deltaic area).

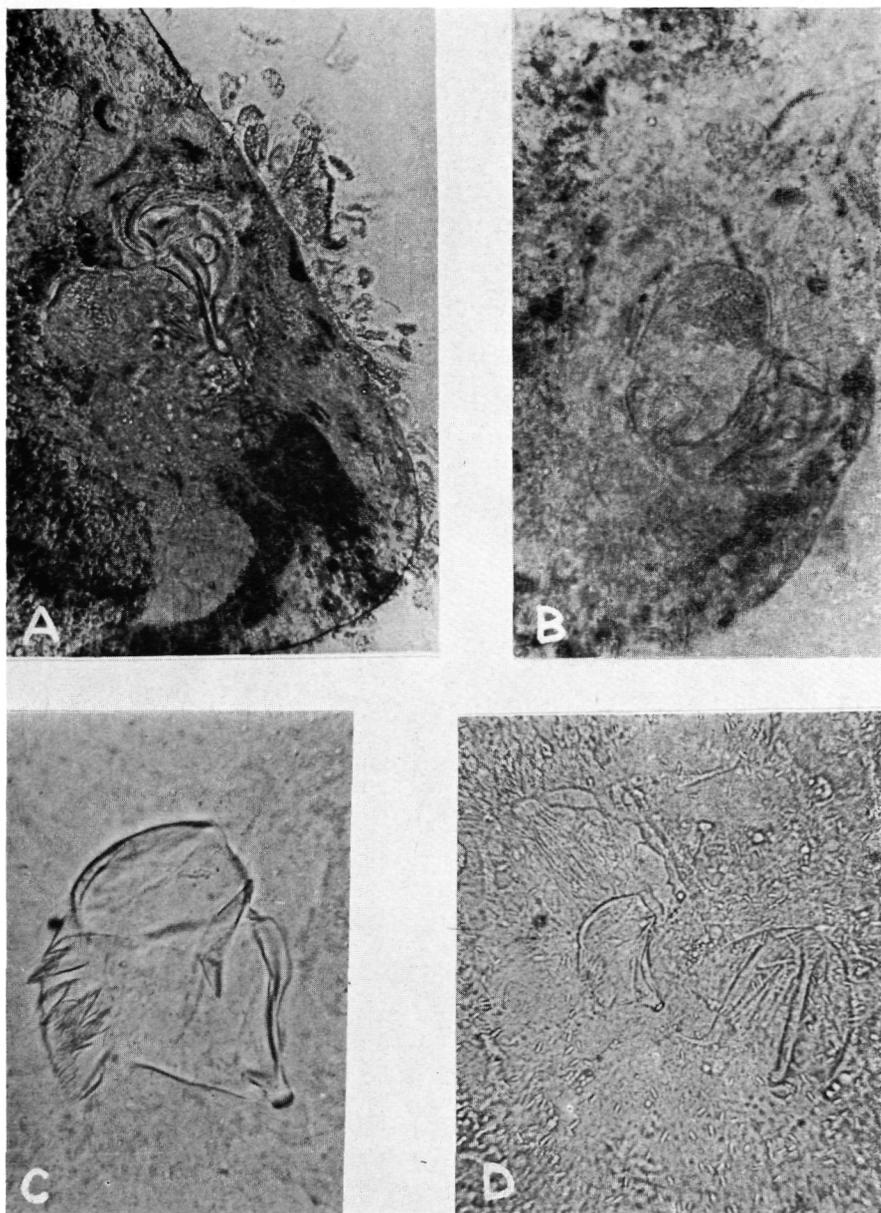


PLATE I

A-B, *Ptychopera westbladi* (Luther, 1943);

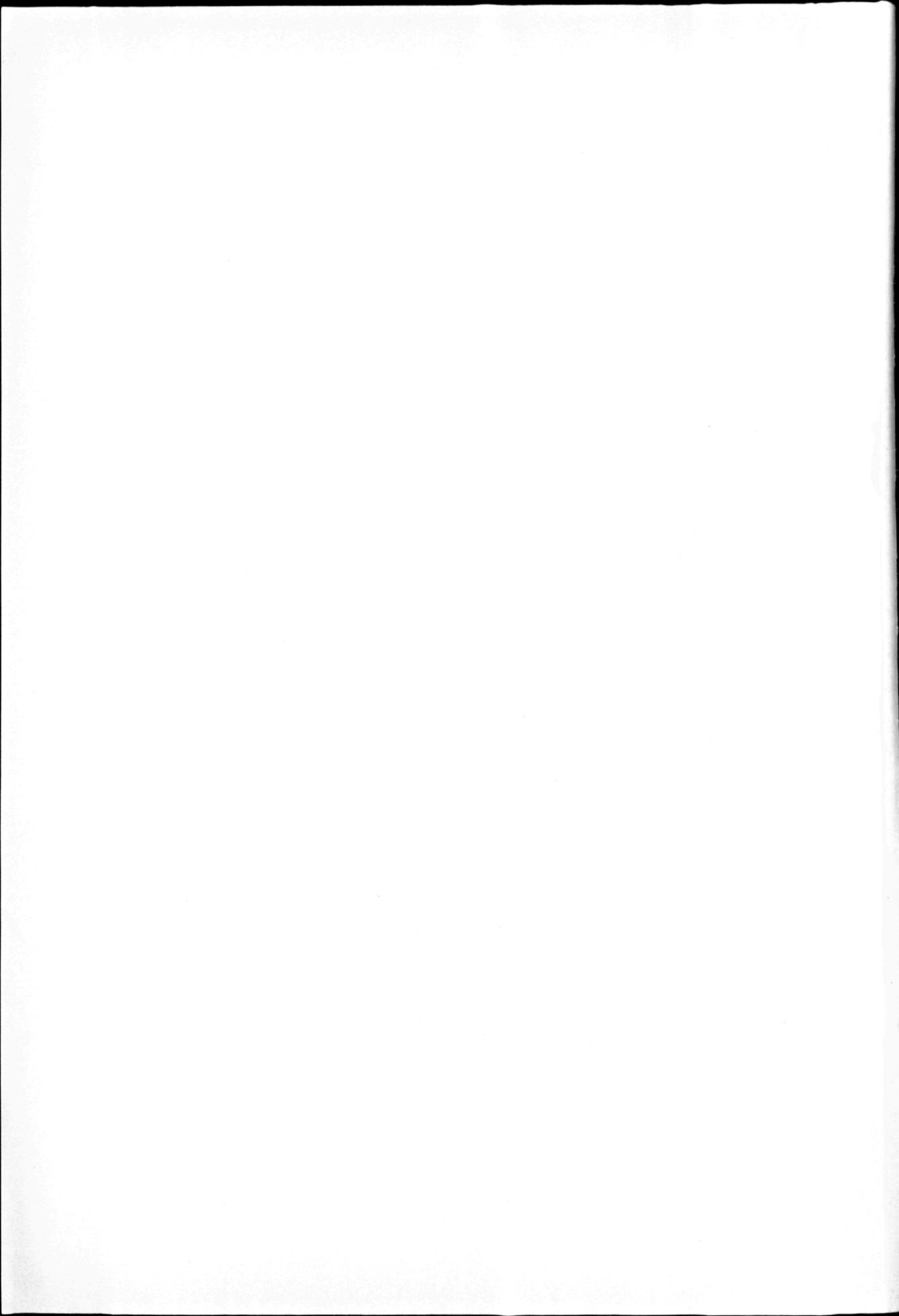
A, Cuticular copulatory organ and bursa copulatrix;

B, idem, but the receptaculum seminis, the ductus spermaticus and the bursal appendage also visible;

C-D, *P. tuberculata* (Von Graff, 1882);

C, Cuticular copulatory organ after strong pressure;

D, the genital organs, to the left the muscular and cuticular copulatory organ, at the top the two spermaducal vesicles, and to the right the bursa copulatrix containing two cuticular bars.



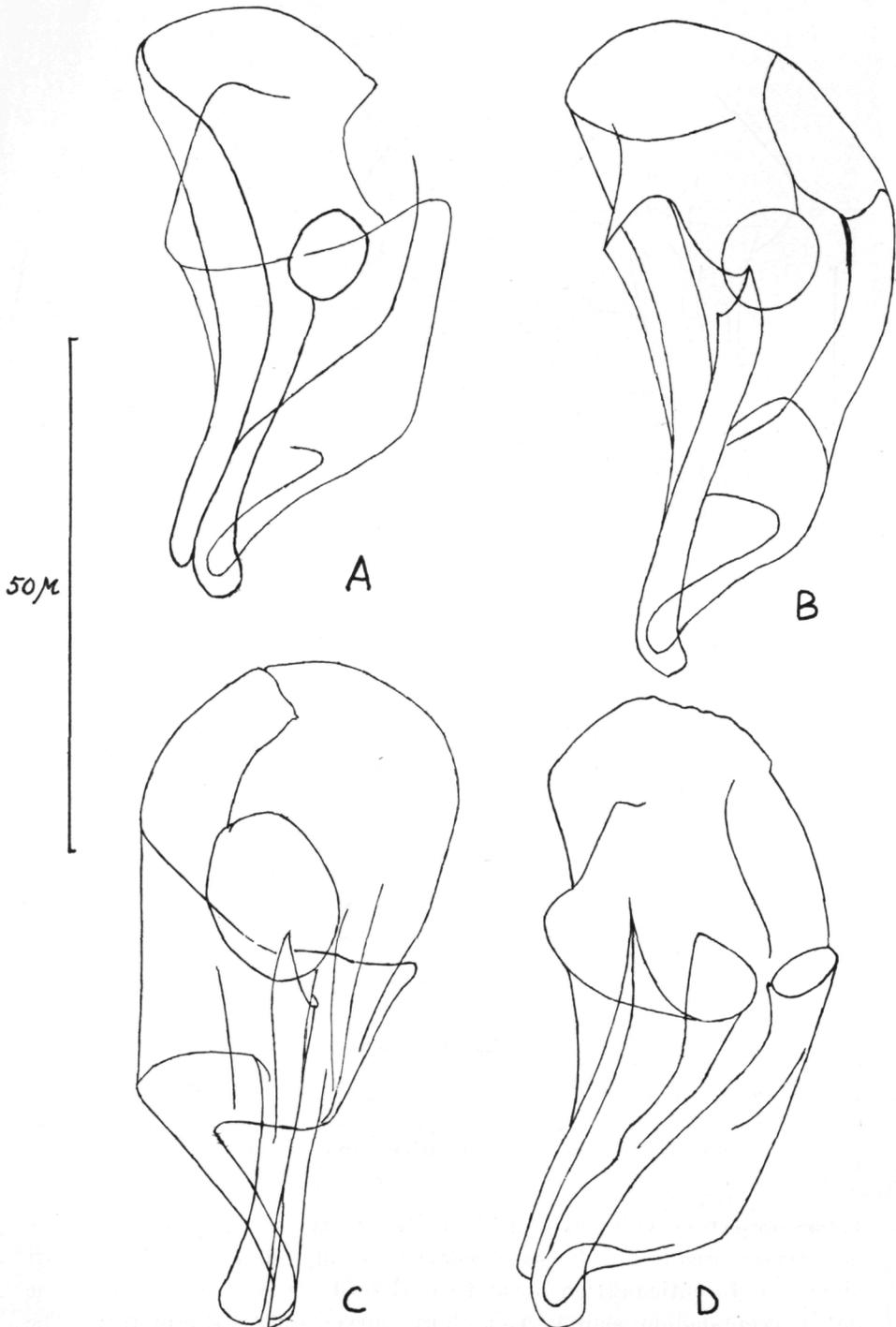


Fig. 5. *Ptychopera westbladi* (Luther, 1943), A-D, cuticular copulatory apparatus. (Original after specimens from the Deltaic area).

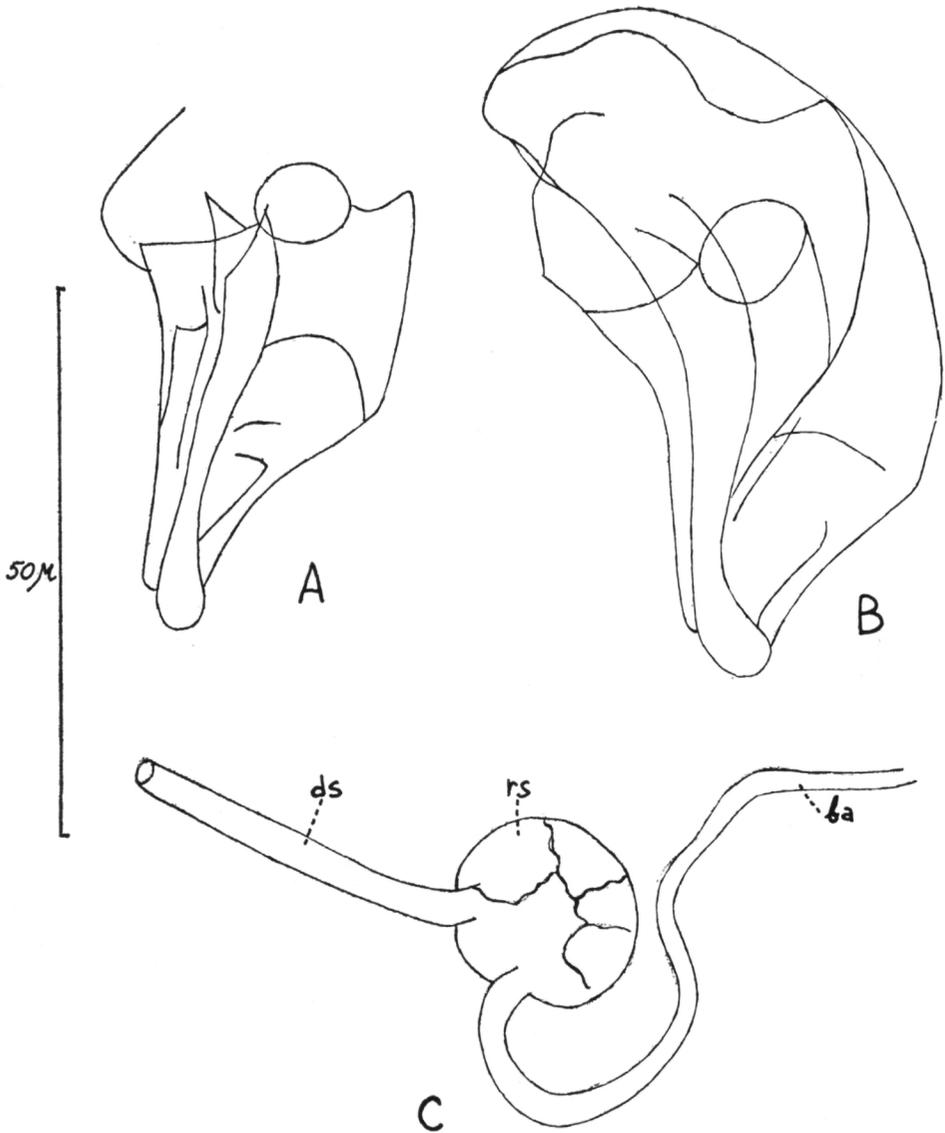


Fig. 6. *Ptychopera westbladi* (Luther, 1943); A-B, cuticular copulatory apparatus; C, receptaculum seminis (rs) with the bursal appendage (ba) and the ductus spermaticus (ds). (Original after specimens from the Deltaic area).

linear projection which extends from the mantle to the distal tip of the copulatory organ. The bursa copulatrix is ellipsoid and its distal part shows ca. 15 cuticularized linear folds (Fig. 4). It is connected with the small receptaculum seminis by a short, curved ductus spermaticus. The wall of the receptaculum seminis shows a few cuticular lines. The bursal appendage is long and hardly cuticularized. It originates from the receptaculum seminis just beside the ductus spermaticus (Fig. 6 C).

LUTHER (l.c. p. 40, 42) recorded that the bursal appendage of *P. westbladi* consists of two very narrow ducts. However, in the ca. 300 specimens seen by me I found always one duct. LUTHER was probably misled by the fact that the ductus spermaticus and the bursal appendage are inserted close beside each other. Consequently he could not find the connection between the ductus spermaticus and the receptaculum seminis. As the ductus spermaticus curves strongly before it enters the receptaculum seminis its course is often difficult to trace, especially in sectioned material. LUTHER unfortunately had only sectioned animals at his disposal. I made many squash preparations and from these could follow quite clearly the course of the bursal appendage and the ductus spermaticus. A double receptaculum seminis, as is mentioned by LUTHER, I have never seen.

Geographical distribution:

P. westbladi has been described from Kristineberg along the Swedish west coast. AX (1951) recorded the species from the German Baltic coast and from the North Frisian island Amrum. Later he found it also in the "étangs" along the French Mediterranean (AX, 1956). In the Deltaic area of the rivers Rhine, Meuse and Scheldt it is a very common species (fig. 7).

Localities in the Netherlands:

Province of Zuid-Holland:

- Goeree-Overflakkee: 1. Springersgors near Ouddorp, in salt-marsh creeks, May 1963; 2. Stellendam, salt-marsh along the Grevelingen, May 1963; 3. Oude Tonge, embanked salt-marsh, May 1963.

Province of Zeeland:

- Schouwen-Duiveland: 4. Oosterland, salt-marsh creek, April 1963.
St. Philipsland: 5. Salt-marsh north of the village of St. Philipsland, May 1963.
Tholen: 6. Stavenisse, salt-marsh creeks, April 1963; 7. Salt-marsh called Karnemelkspot along the Eendracht north of the town of Tholen, June 1962.
Zuid-Beveland: 8. 's-Gravenpolder, salt-marsh, May 1963; 9. Borssele, salt-marsh creeks and pools near the large breakwater, May 1963.
Zeeuws-Vlaanderen: 10. International nature reserve "het Zwin", in the Dutch part, small creeks, June 1963; 11. Nummeréén, salt-marshes, June 1963; 12. Salt-marshes in front of the Braakmanpolder, June 1963; 13. Hontenisse, mud-flat, June 1963; 14. De Paal, salt-marshes, May 1963.

Ecology:

According to AX (1951) the species occurs in Kiel Bay in quiet water on detritus-rich fine sand. The type material was collected by WESTBLAD also from fine sand (LUTHER, 1943). In the Deltaic area of the rivers Rhine, Meuse and Scheldt the species is also characteristic for still-water biotopes, where it has been taken from sandy mud and detritus-rich fine sand, but also from floating algae. The species has been found to be most numerous in the tidal creeks which run through the salt-marshes, and

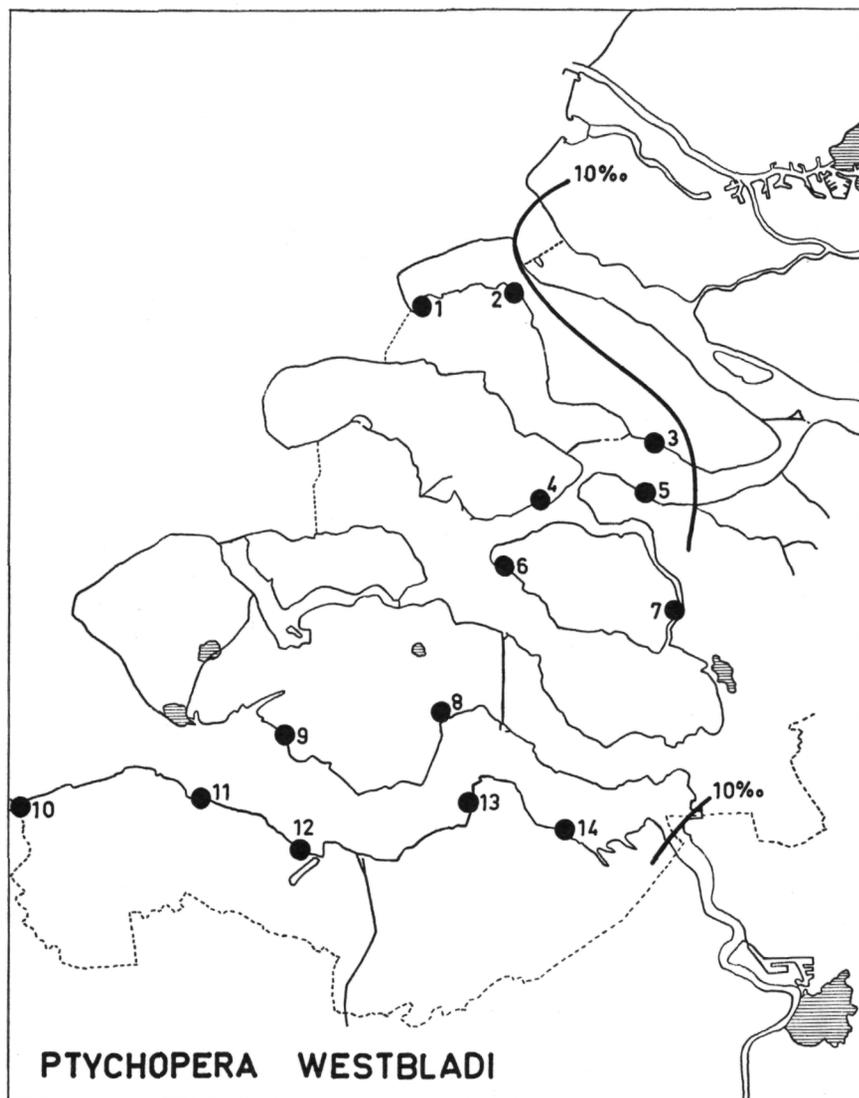


Fig. 7. Distribution of *Ptychopera westbladi* (Luther, 1943) in the south-western part of the Netherlands. The average annual isohaline of 10‰ Cl⁻ at high tide is given.

where at low tide a thin layer of water is left. In the slopes of the levees of these creeks many specimens were also found between *Vaucheria* patches and in the soft mud. In quiet places in the creeks, where floating algae, in particular *Ulva* and *Enteromorpha*, are driven together, *P. westbladi* is most abundant and associated with *Promesostoma marmoratum* (Schultze), *P. rostratum* Ax, *Provortex affinis* (Jensen), *P. balticus* (Schultze), *P. tubiferus* Luther and *Pseudostomum quadrioculatum* (Leuckart). The tidal flats form an other habitat of *P. westbladi*. The species is not numerous there, but rather often found, especially in places which are continually

covered with a film of water. On the sandy flats it occurs together with *Pseudograffilla arenicola* Meixner. In pools on the salt-marshes, particularly those in which floating *Ulva* and *Enteromorpha* form a secondary vegetation by vegetative propagation, the species may be extremely abundant. In the salt-marsh vegetation itself the species is rare and its occurrence there may be considered accidental. Specimens found there have probably got lost or became caught between the grass when the water was falling. I found *P. westbladi* once in the *Puccinellietum maritimae* and once in the *Spartinetum townsendii*.

In the Deltaic area the species inhabits the euhalinicum and the polyhalinicum, reaching its lower salinity limit at the isohaline of 10–11 ‰ Cl' at high tide. At low tide the species is subjected to a lower average salinity. The salinity limit reached by the species in the Baltic Sea with its relative stable salinity is about the same. The great salinity fluctuations in the Dutch estuaries do not seem to be a barrier to *P. westbladi*, but other ecological factors must be involved in the limitation of its area.

In glass-jars the animals like to swim freely in the water and move by preference to the light. They are easily recognized by their indigo-blue colour in spite of their small size. I have several times found half-digested nematodes in the intestinal tract of *P. westbladi*, and these obviously form at least part of its food. Once I found a specimen that was infected by parasitic gregarines.

The species has been found only in the months of April, May and June. In the summer months the biotope of *P. westbladi* was not investigated. The species was not found in October and November, when samples were taken in several salt-marsh creeks where it was present in spring.

***Ptychopera plebeia* (Beklemishev, 1927)**

Proxenetes plebeius Beklemishev, 1927

BEKLEMISCHEV, Bull. Inst. rech. biol. Perm. 5, 188–190, 203, Pl. 1, f. 11–12 (1927); AX, Vie et Milieu, Suppl. 5, 114–116, f. 28 (1956); idem, Zool. Jb. Syst. 87, 100 (1959). — Fig. 8.

The animals are at most 0.5 mm long and brown in colour. The pharynx lies at 1/3 of the body length. The testes are situated in the middle of the body; they reach to the pharynx. The vitellaria extend posteriorly from the eyes. The germaria lie in the caudal part of the body, by the side of the copulatory organ. The cuticular copulatory organ is 80 μ long and as complicated as in the related *P. westbladi* (Fig. 8 B-C). It consists of a wide funnel-shaped stylet, which narrows suddenly in distal direction, one side of it proceeding as a linear process with obtusely rounded distal tip, the other becoming a wide lateral bulge. It is surrounded by at least two large cuticular plates, composed of stiffenings in the wall of the male genital atrium, and several complicated ridges due to folds in the cuticular

atrial wall. The efferent tract of the female genital apparatus shows the typical features of the genus. The ductus spermaticus, according to the drawings of BEKLEMISCHEV (l.c.) and AX (1956), seems to enter the receptaculum seminis diametrically opposite the insertion of the bursal appendage. This is in contrast with the situation in *P. westbladi*. In BEKLEMISCHEV's drawing of the bursal appendage a line parallel to the walls of the duct is given, but in the German text of the description the existence of this line, probably a cuticular ridge, is not recorded.

Geographical distribution:

BEKLEMISCHEV (l.c.) discovered the species in the Black Sea near Odessa. It has since been found in some "étangs" along the French Mediterranean (AX, 1956) and in the Sea of Marmara (AX, 1959).

Ecology:

It seems that *P. plebeia* is an euryhaline brackish-water species. BEKLEMISCHEV (l.c.) recorded it from the coast near Odessa in water with an average salinity of 8.5 ‰ Cl' and where it is subjected to fluctuations from 1.8 to 11.3 ‰ Cl'. In the Sea of Marmara it lives at a salinity of ca. 13 ‰ Cl' (AX, 1959), while it has been found in the French "étangs"

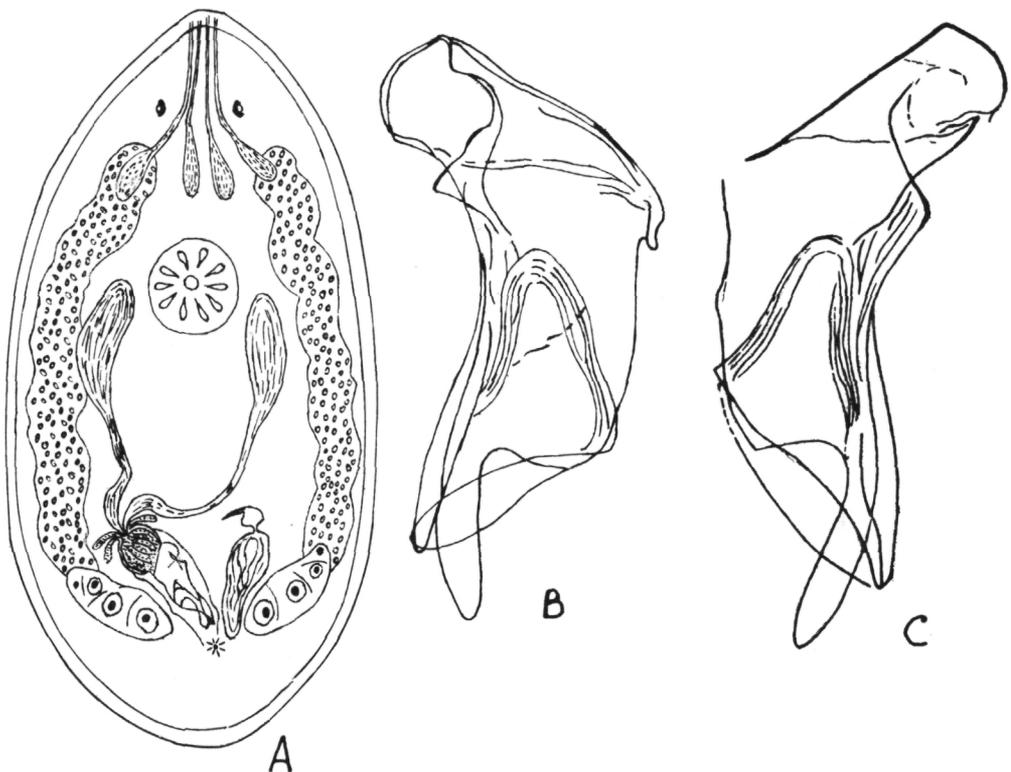


Fig. 8. *Ptychopera plebeia* (Beklemishev, 1927); A, general view, B-C, cuticular copulatory apparatus. (After Ax).

of Salses and Canet at salinities between 6 and 10 ‰ Cl'. The various localities of *P. plebeia* agree, however, in this respect, that they all may be regarded as "still-water biotopes".

***Ptychopera tuberculata* (Von Graff, 1882)**

Proxenetes tuberculatus Von Graff, 1882

VON GRAFF, Monogr. Turbell. 1, 281-282, Pl. 7, f. 21-27 (1882); idem, Tierreich 35, 183-184, f. 168 (1913). — Fig. 9-10, Pl. 1 C-D.

The animal is slender, 0.6 mm long and brown in colour. The anterior part of the body is truncate. The pharynx is small and lies at 1/3 of the body length. The vitellaria are elongated sacs which extend from just behind the eyes in caudal direction. They join the germaria which lie just in front of the copulatory organ at ca. 2/3 of the body length. The testes are small, subspherical in shape, and lie just behind the pharynx. The vasa deferentia are rather long ducts, and just before entering the muscular bulbus of the copulatory organ they swell conspicuously and become the spermaducal vesicles. In the muscular bulbus the secretory glands are grouped in a roundish mass. The cuticular copulatory organ is proximally embedded in the muscular bulbus (Fig. 10). It is 44 μ long. It consists of a wide funnel-shaped stylet, which shows a slight curve and ends distally in a knob. The stylet is surrounded by a cuticular mantle composed of the stiffened wall of the male genital atrium. This mantle is composed of 2 or 3 plates, which on the concave side of the copulatory organ seem to be united or at least very closely pressed to the wall of the stylet. On the convex side the mantle has a barbed appearance, due to the occurrence of 7 or 8 spines and a number of small papillae. These normally lie flat on the cuticula, but by strong pressure they become erect. The bursa copulatrix is bell-shaped and ca. 60 μ long (Fig. 9). Its wall shows several longitudinal, more or less cuticularized folds. The bursa copulatrix contains two cuticular bars which project with their hooked distal parts into the atrium genitale commune. They are fixed by their somewhat widened proximal ends to the proximal wall of the bursa. The bursa copulatrix is connected with the very small receptaculum seminis by a very short and narrow ductus spermaticus. The bursal appendage lies beside the entrance of the ductus spermaticus in the receptaculum seminis. It consists of a short and very narrow duct and only its basal part is slightly cuticularized; in that part of the duct a short longitudinal ridge occurs.

Although there are several differences between the specimens of *Proxenetes tuberculatus* described by VON GRAFF and the specimen described here I have identified my specimen with VON GRAFF's species as the points of agreement seem too obvious.

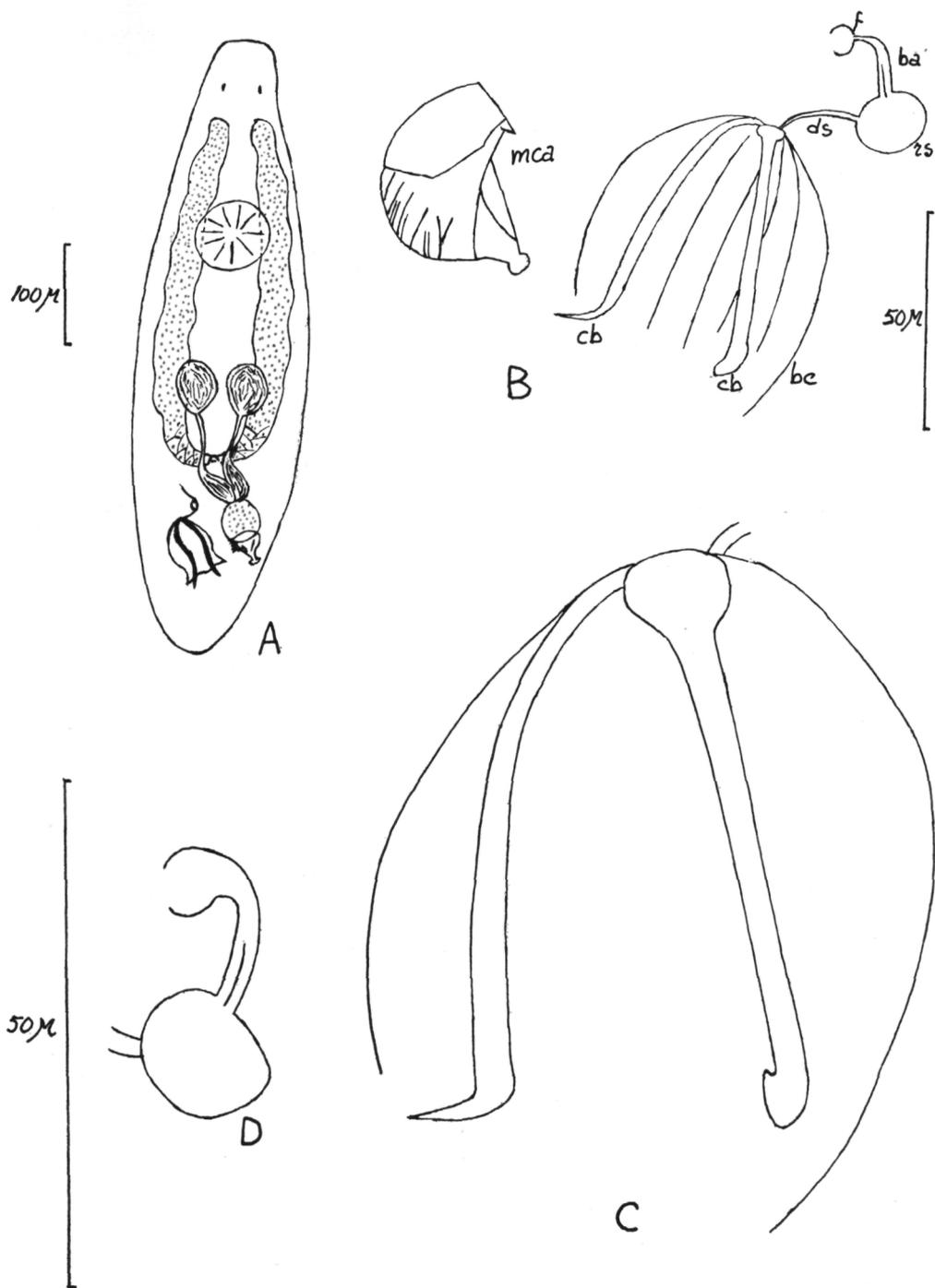


Fig. 9. *Ptychopera tuberculata* (VON GRAFF, 1882); A, general view, B, male cuticular copulatory organ (mca) and efferent tract of female genital apparatus (bc=bursa copulatrix; ds=ductus spermaticus; rs=receptaculum seminis; ba=bursal appendage; f=fecundatorium; cb=cuticular bar); C, bursa copulatrix; D, receptaculum seminis, bursal appendage (ba) and fecundatorium (f). (Original after a specimen from Stavenisse).

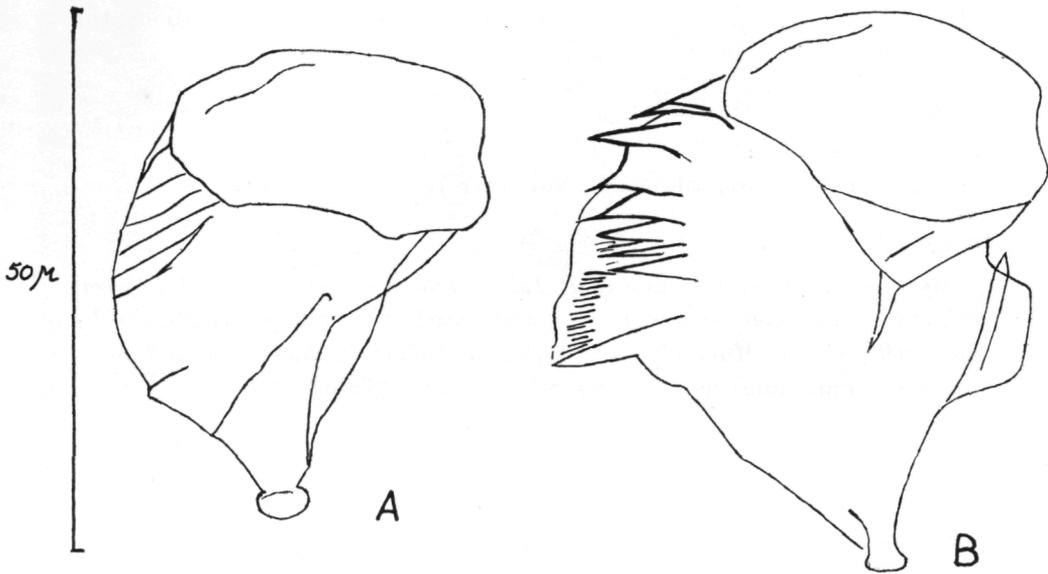


Fig. 10. *Ptychopera tuberculata* (Von Graff, 1882); A, cuticular copulatory organ; B, the same after strong pressure. (Original after a specimen from Stavenisse).

VON GRAFF recorded that the anterior and the posterior end of the body were set with 20 obtuse, more or less short papillae. I did not notice these papillae in my specimen. Probably it was squashed too much by the pressure of the coverslip. According to VON GRAFF the vitellaria extend posteriorly from just behind the pharynx, while in my specimen they extended from just behind the eyes. The form of the testes was given by VON GRAFF as being oblong, while in my specimen they were subspherical. More important, however, is the agreement in some characters of the cuticular copulatory organ. The size of this organ was in my specimen 44μ and in those of VON GRAFF 46μ . In his drawings (l.c. Pl. 7, f. 23-24) the barbed convex side is given and in the text mentioned as "zahlreiche verstärkte Längsleisten". VON GRAFF had not discovered the spiny nature of these "Längsleisten". The distal end of the copulatory organ has according to VON GRAFF a small right-angled acute point, or even two such points. In my specimen I found only a knob. In the bursa copulatrix VON GRAFF found the two cuticular bars connected by a cuticular cross-bar. In my specimen I did not find the slightest indication of such a cross-bar and I think that VON GRAFF did in fact see the distal margin of the bursa copulatrix. It is, however, clear from his figures that he did not find the ductus spermaticus, the receptaculum seminis and the bursal appendage.

Geographical distribution:

The distribution of the species is unknown. VON GRAFF (l.c.) described it from an aquarium in Frankfurt and supposed it to be an inhabitant

of the North Sea. My specimen from the Netherlands seems to be the first one that has been collected in a natural habitat.

Locality in the Netherlands:

Province of Zeeland:

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

Ecology:

My one and only specimen of *P. tuberculata* was collected in the *Puccinellietum maritimae*, where it was associated with numerous *Proxenetes puccinellicola* Ax, *Monocelis lineata* (O. F. Müller) *Vejdovskya halileimonia* Ax and small numbers of some other species (Table 3).

Addendum

After submitting this paper for publication, I discovered one specimen of *Beklemischeviella contorta* (Beklemischev) in a sample taken in September 1964 near Aveton Gifford (Devonshire) along the south coast of England in a narrow side creek of the river Avon estuary. The bottom of this creek consists of fine, detritus-rich, muddy sand, and during low tide fresh water continually flows over it. The accompanying fauna, mainly consisting of the turbellarians *Archilopsis unipunctata* (Fabricius) and *Baical-ellia brevituba* (Luther), the isopod *Sphaeroma rugicauda* Leach the amphipod *Corophium multisetosum* Stock and the gastropod *Pseudamnicola confusa* (Frauenfeld), indicates that the station can be regarded as oligo- to mesohaline.

The specimen agreed completely with the specimens described by LUTHER (1943) from the Baltic.

The genus *Beklemischeviella* was known so far only from brackish waters in the Baltic, the Caspian Sea and the Aral Sea. Ax (1959, p. 171-173) considered the genus by reason of this distribution a glacial-marine relict, and thought that its origin had to be sought in the brackish coastal waters of the Arctic Ocean. Many brackish-water species have indeed their origin in the Arctic waters and have migrated to southern regions during the Pleistocene. This may explain that the Baltic, the Aral and the Caspian Sea have a number of brackish-water species in common, but it does not prove their exclusiveness to these areas. The occurrence of *B. contorta* in brackish water in the southern part of England is an indication that this species migrated along the Atlantic coast as well.

HYDROBIOLOGY

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

BY

C. DEN HARTOG

(Communicated by Dr. J. VERWEY at the meeting of September 26, 1964)

3. CERATOPERA nov. gen.

Pharynx lying just before the middle of the body. Efferent tract of the female genital apparatus consisting of a large receptaculum seminis and a very narrow, elongate bursal canal. Bursal appendage consisting of a curved or coiled, strongly cuticularized duct, from which base often a number of cuticular ridges radiate over the external surface of the receptaculum seminis. Male copulatory organ consisting of a stylet, distally sheathed by an open cuticular mantle. Stylet proximally bow-shaped or semicircularly curved and distally straight. Mantle composed of one or more lamellae, which are stiffenings in the wall of the male genital atrium and may be transformed into a separate duct, but in that case it is proximally connected with and distally sheathing the straight part of the stylet.

Type: *Proxenetes gracilis* Von Graff

The genus *Ceratopera* is well defined by the following three characters: the shape of the bursal appendage, the structure of the copulatory organ and the anterior position of the pharynx.

KEY TO THE SPECIES

1. Cuticular mantle open, not transformed into an additional duct, partially sheathing the stylet.
2. Cuticular mantle consisting of one lamella, which proximally sheaths the straight part of the stylet and continues along its inward side. 1. *C. gracilis*
2. Cuticular mantle consisting of two lamellae, which may be free or connected.
3. Lamellae proximally connected and sheathing the straight distal part of the stylet.
4. One lamella proximally surrounding the straight part of the stylet and proceeding as a duct, closely pressed to the stylet. The other lamella curving strongly inward and sheathing with its distal end the stylet and the tubular lamella. 2. *C. sellai*

4. The larger lamella narrowing in distal direction and ending in a transversely placed spine. The other lamella widening in distal direction and ending obtusely. . . . 3. *C. levinseni*
3. Lamellae free but touching distally. The shorter lamella sheathing the inward side of the stylet; the longer lamella proximally extending above the stylet and sheathing the outward side. 4. *C. reisingeri*
1. Cuticular mantle transformed into an additional duct, which is proximally and distally connected with the straight distal part of the stylet.
 5. Duct proximally with a short but wide collar; a lateral extension of the collar just sheathing the stylet. 5. *C. steinboeckii*
 5. Duct proximally funnel-shaped, one side of the funnel surrounding proximally the stylet.
 6. Distal part of the duct almost perpendicular to its proximal part and surrounding the stylet above its distal tip. Proximal funnel with a lateral hook. 6. *C. paradoxa*
 6. Distal part of the duct obliquely placed, its acute distal part sheathing the distal end of the stylet. Proximal funnel without lateral extensions. 7. *C. axi*.

***Ceratopera gracilis* (Von Graff, 1882)**

Proxenetes gracilis Von Graff, 1882

VON GRAFF, Monogr. Turbell. 1, 280–281, Pl. 8, f. 6–14 (1882); idem, Tierreich 35, 184–186, f. 169–170 (1913). — Fig. 11 A–B.

The animals are very slender, 1.5–2 mm long and transparent. The anterior end is truncate. The eyes lie at ca. 1/8 of the body length. Two tracts of rhabdites pass between the eyes. In rostral direction they each divide into three diverging lines. In caudal direction also the two rhabdite tracts split, but these divisions are less conspicuous. The pharynx is situated at 2/5 of the body length. The testes are ellipsoid. The vasa deferentia widen and form large spermaducal vesicles before entering the muscular bulbus of the copulatory organ. The cuticular copulatory organ is inserted on the muscular bulbus (Fig. 11 B). Its length is not given in the literature. It consists of a stylet, the proximal part of which is semicircularly curved; its straight distal part is for the greater part surrounded by a cuticular sheath. Near the extreme proximal tip of the stylet an opening occurs in its convex side, where the granular secretion enters. The cuticular mantle, which is composed of the stiffened part of the wall of the male genital atrium, surrounds proximally the straight part of the stylet, but more distalward the mantle extends only along the

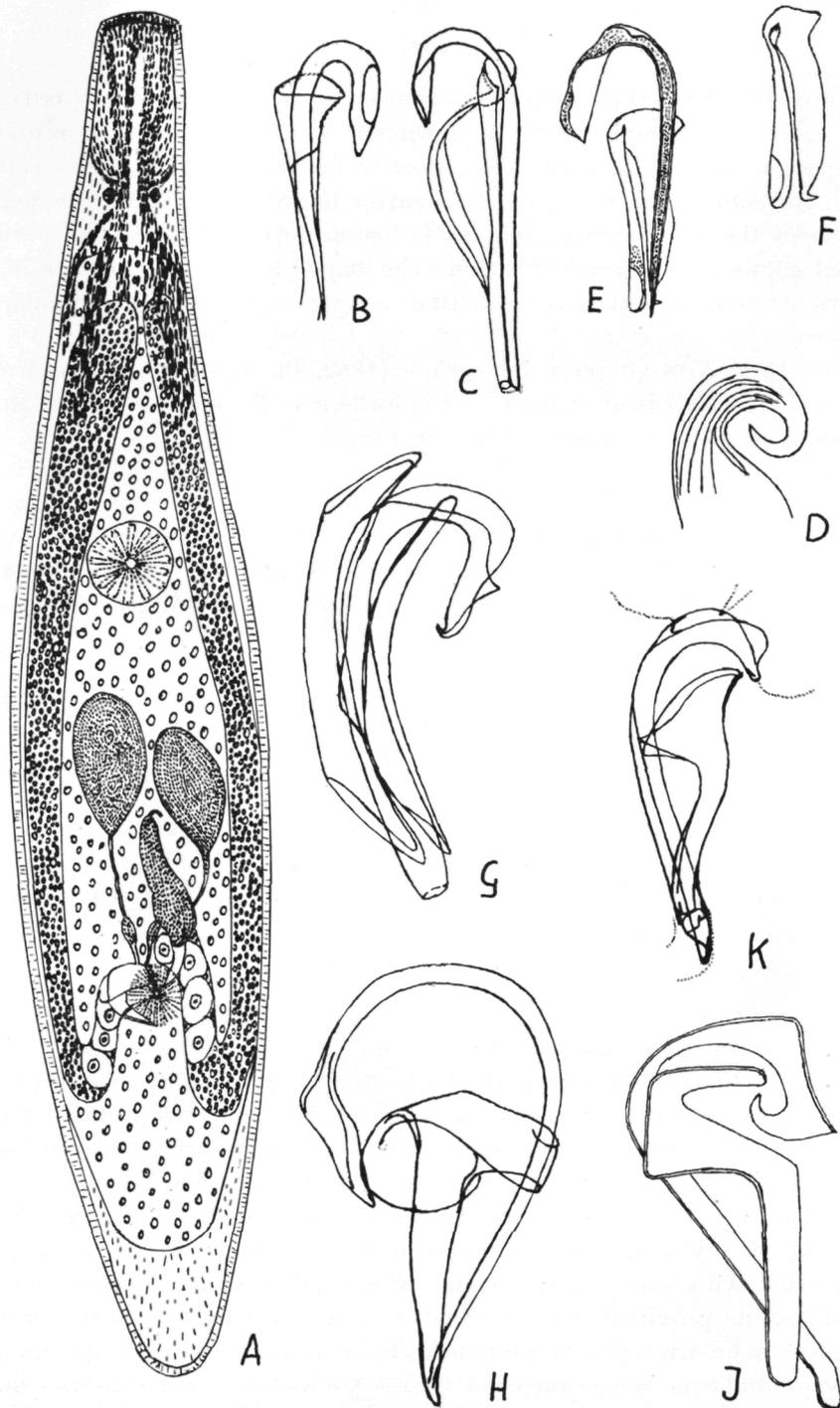


Fig. 11. A-B, *Ceratopera gracilis* (Von Graff, 1882); A, general view; B, cunicular copulatory organ; C-D, *C. sellai* (Steinböck, 1933), C, cunicular copulatory organ; D, bursal appendage; E-F, *C. levinseni* Den Hartog nov. nom., E, cunicular copulatory organ; F, cunicular mantle consisting of two lamellae; G, *C. reisingeri* (Riedl, 1959); cunicular copulatory organ; H, *C. steinboeckii* (Riedl, 1959), cunicular copulatory organ; J, *C. paradoxa* (Pereyaslawzewa, 1892), cunicular copulatory organ; K, *C. axi* (Riedl, 1954), cunicular copulatory organ. (A-B, after VON GRAFF, C-D after STEINBÖCK, E-F after LEVINSEN, G-H and K after RIEDL and J after PEREYAS-LAWZEWA).

inward side of the stylet, ending in a distal point. The elongate vitellaria are caudally connected with the germaria. The receptaculum seminis is an elongate sac, which may show one or two constrictions. It is connected with the genital atrium by a short, narrow bursal canal. The inner membrane of the receptaculum seminis is longitudinally striped. The bursal canal shows a transverse striation. The bursal appendage consists of a short, strongly cuticularized duct, that near its distal end is semicircularly curved.

Fig. 13 in VON GRAFF's monograph (1882, Pl. 8) is so different from his fig. 12, which is given here and elsewhere as *Proxenetes gracilis*, that I doubt as to the correctness of the former.

Geographical distribution:

The species is probably widely distributed in the Mediterranean and according to VON GRAFF (1913) it occurs also in the warm-temperate waters of the Atlantic. A type locality is not indicated.

Ecology:

The species is an inhabitant of the algal vegetation of the upper part of the sublittoral belt.

Ceratopera sellai (Steinböck, 1933)

Proxenetes sellai Steinböck, 1933

STEINBÖCK, *Thalassia* 1, no. 5, 11-12, f. 2-5 (1933). — Fig. 11 C-D.

According to STEINBÖCK (l.c.) this species is externally very similar to *C. gracilis*.

The cuticular copulatory organ consists of a proximally bow-shaped stylet and an open cuticular mantle (Fig. 11C). The stylet is open at its proximal end. The straight part of the stylet is proximally at one point only surrounded by a cuticular lamella, transformed into a closed duct and running parallel to the stylet; their distal parts are closely pressed together. From the proximal end of the lamella a second lamella arises, which is strongly curved inward and sheaths with its distal end the distal ends of the stylet and the tubular lamella. The receptaculum seminis is connected with the genital atrium by a very long and narrow bursal canal. At its proximal end the canal is surrounded by 4 cuticular rings. STEINBÖCK l.c. wrongly interpreted this canal as a second bursal appendage "der in ähnlicher Weise auch bei *Proxenetes modestus* und *flabellifer* auftritt." The bursal appendage becomes distally gradually narrower and shows an almost complete coil (Fig. 11 D). A number of cuticular ridges radiate from its base over the external wall of the receptaculum seminis.

In the work of PEREYASLAWZEWA (1892) a species from the Bay of Sebastopol, described and figured under the name *Proxenetes flabellifer*

(p. 259, f. 26), is certainly a *Ceratopera* species. It has a bursal appendage consisting of one duct which is terminally placed on the large constricted receptaculum seminis. The bursal canal is long and narrow and at the transition to the receptaculum seminis it is surrounded by a series of cuticular rings. The pharynx is placed at $1/3-2/5$ of the body length. Regrettably the shape of the cuticular copulatory organ is inaccurately drawn by PEREYASLAWZEWA.

The occurrence of cuticular rings at the proximal end of the bursal canal is reported in the genus *Ceratopera* only from *C. sellai*, and it is quite well possible that the *Proxenetes flabellifer* of PEREYASLAWZEWA is in fact the same species. However, as long as the cuticular copulatory organ of the latter is not better known this point has to remain undecided.

Geographical distribution:

The species has been described from Rovinj (Rovigno) in the northern part of the Adriatic Sea.

Ecology:

It occurs between coarse sand and empty shells in the sublittoral.

***Ceratopera levinseni* nov. nom.**

Mesostomum flabelliferum Levinsen, 1879

LEVINSEN, Vidensk. Meddel. naturh. Foren. Kjøbenh. 1879-80, 175-177, Pl. 3, f. 6-10 (1879). — Fig. 11 E-F.

The name *Mesostomum flabelliferum* Levinsen is based on *Proxenetes flabellifer* Jensen. It has appeared that LEVINSEN'S species is not identical with that of JENSEN (1878). Therefore, the epithet *flabellifer* has to be used for JENSEN'S species, according to the rule of priority, and thus for LEVINSEN'S species an other name has been chosen.

The animals are very slender, 2 mm in length, and white in colour. The anterior end of the body is truncate. The eyes lie rather far from the frontal margin. The pharynx lies in or just before the middle of the body. The structure of the "soft parts" of these animals is practically unknown, as LEVINSEN drew only the outline of the two spermaducal vesicles and the spherical muscular bulbus of the copulatory organ. The cuticular copulatory organ consists of a stylet of which the distal part is sheathed by an open cuticular mantle (Fig. 11 E-F). The proximal part of the stylet is open and semicircularly curved. Its distally directed proximal end is rather conspicuous. The distal part of the stylet is straight and ends acutely. According to LEVINSEN the stylet seems to be an open canal over its whole length. The cuticular mantle consists of two broad lamellae, proximally connected by a narrow link. The larger of the two lamellae

narrows in distal direction and ends in a spine which is perpendicular to the axis of the copulatory organ. The other lamella becomes wider in distal direction and is obtusely rounded at its end. One side of this lamella is incurved near its distal end and sheaths the distal part of the stylet and the subterminal part of the other lamella. The receptaculum seminis is elongate to pear-shaped. The bursal appendage is a cuticularized duct wound up in 6 decreasing coils. According to LEVINSSEN the duct near its distal end is split into two very narrow ducts. LEVINSSEN claimed also that he had seen some radially arranged, dentate ridges or fine tubes in the vicinity of the bursal appendage, but he gave no precise information as to their exact position.

Geographical distribution:

The species has been described by LEVINSSEN from Egedesminde along the west coast of Greenland. About its ecology nothing is known.

***Ceratopera reisingeri* (Riedl, 1959)**

Proxenetes reisingeri Riedl, 1959

RIEDL, Publ. Staz. Zool. Napoli 30, Suppl., 308-309, f. 2. — Fig. 11 G.

The animal is slender, 1 mm in length, and white in colour. The anterior end is truncate. The eyes are situated at $\frac{1}{7}$ of the body length. The pharynx lies just before the middle of the body. The testes are elongate and lie caudal of the pharynx. The vasa deferentia widen into large spermaducal vesicles before they enter the muscular bulbus of the copulatory organ. The cuticular copulatory organ is 75μ long and consists of a proximally bow-shaped stylet, surrounded by an open cuticular mantle (Fig. 11 G). The proximal part of the stylet is open and ends with a distally directed hook. The distal part of the stylet is a closed straight duct. The cuticular mantle consists of two somewhat bow-shaped lamellae which partially surround the stylet. The shorter lamella sheaths the inward side and extends proximally up to the bow-shaped part of the stylet. The larger lamella sheaths the outward side and proximally projects above the stylet. The two lamellae touch each other distally, surrounding the stylet completely for a short distance. The blunt tip of the stylet projects between the acute distal ends of the lamellae. The germovitellaria are elongate and extend in caudal direction along the lateral sides, from before the pharynx. The bean-shaped, transversely placed sac, which by RIEDL is regarded as the "bursa", probably represents the receptaculum seminis. The structure of the efferent tract of the female genital apparatus is not known, nor is the shape of the bursal appendage.

I have provisionally placed this species in the genus *Ceratopera* because the pharynx is anteriorly situated and because the cuticular mantle of the male copulatory organ does not form a closed sheath around the stylet.

It is regrettable that the shape of the bursal appendage, which is a decisive generic character, is not known.

Geographical distribution:

RIEDL (1959) found only one specimen of this species near Capo di Sorrenti in the surroundings of Naples.

Ecology:

The specimen was found in a *Balanus-Halichondria* coenosis in a submarine cavern, at 1.20 m depth.

Ceratopera steinboeckii (Riedl, 1959)

Proxenetes steinboeckii Riedl, 1959

RIEDL, Pubbl. Staz. Zool. Napoli 30, Suppl. 310-312, f. 3. — Fig. 11 H.

The animals are very slender and almost linear in shape. The length is 0.7-0.8 mm. The greatest width is in front of the middle and amounts to 1/8 of the length. The anterior part is truncate; the posterior part narrows very gradually and is not conical as are most species of the *Proxenetes* group. The eyes lie at 1/5 of the body length and the pharynx lies just anterior to the middle of the body. The testes are elongate and extend caudally from the side of the pharynx. The cuticular copulatory organ is ca. 80 μ long and consists of a proximally semicircularly curved stylet and an open cuticular mantle, which has been transformed into an additional duct beside the stylet (Fig. 11 H). The stylet is very slender and only open at its distally directed, extreme proximal end, which has the shape of a pennant. The 50 μ long, additional duct is funnel-shaped and narrows gradually in distal direction. Its distal tip lies close against the slightly curved distal tip of the stylet. Proximally the duct is provided with a short but wide collar. This collar shows a lateral extension, which barely surrounds the stylet for a short distance. The germovitellaria are elongate and extend caudally from far before the pharynx. The structure of the efferent tract of the female genital apparatus is not known. RIEDL mentioned only a "bursa", which probably is the receptaculum seminis.

Although the shape of the bursal appendage is not known I have not hesitated to transfer the species from *Proxenetes* to *Ceratopera*. The shape of the cuticular copulatory organ shows largely the same general structure as that of *C. axi* and *C. paradoxa*. The anterior position of the pharynx is another indication that the species belongs to *Ceratopera*.

Geographical distribution:

The species is only known from Capo di Sorrenti in the surroundings of Naples.

Ecology:

RIEDL (1959) collected twice a specimen of *C. steinboeckii* in sublittoral vegetations dominated by the alga *Peyssonnelia* and shaded by overhanging masses of rock.

Ceratopera paradoxa (Pereyaslawzewa, 1892)

Proxenetes paradoxus Pereyaslawzewa, 1892

PEREYASLAWZEWA, Mém. Soc. Nat. nouvelle Russie, Odessa 17, no. 3, 259–261, Pl. 4, f. 25 (1892); VON GRAFF, Tierreich 35, 184 (1913).— Fig. 11 J.

The slender animals are colourless and opaque. The anterior end is truncate and the eyes lie at ca. 1/8 of the body length. The pharynx lies at 2/5 of the body length. The male copulatory organ consists of two elements, the stylet and the open cuticular mantle which has been transformed into a duct beside the stylet (Fig. 11 J). The stylet is a duct of which the proximal part is semicircularly curved and ends in a distally directed hook. Its distal part is straight, except for the extreme tip, that bends outward. The second duct is shorter. Its proximal part is funnel-shaped. One side of the funnel surrounds proximally the straight part of the stylet. The other side of the funnel is drawn out into a distally directed hook. The distal part of the duct is almost perpendicular to its proximal part and surrounds the stylet above its distal tip. The elongate receptaculum seminis is connected by a narrow bursal canal with the atrium genitale commune and is crowned by a very large, heavily cuticularized bursal appendage which is an almost complete coil.

Regrettably PEREYASLAWZEWA has not given any measurements. The species is closely related to *C. axi*. As the figure of PEREYASLAWZEWA, on which this description is based, is not very accurate a new investigation of *C. paradoxa* is desirable.

Geographical distribution:

The species has been described from the Bay of Sebastopol, where it is very common (PEREYASLAWZEWA, 1892). About its ecology nothing is known.

Ceratopera axi (Riedl, 1954)

Proxenetes axi Riedl, 1954

RIEDL, Österr. Zool. Z. 4, 133, 137 (1953) nomen nudum; idem, Zool. Jb. Syst. 82, 217–220, f. 26–27 (1954). — Fig. 11 K.

The animals are slender, 0.6–1.5 mm long, and transparent. The anterior part of the body is truncate. The eyes lie at 1/4–1/6 of the body length, while the pharynx is situated just before the middle of the body. The

male copulatory organ consists of two elements: a proximally bow-shaped stylet, which seems to be open all along its convex side, and a shorter duct derived from the open cuticular mantle (Fig. 11 K). The shorter duct is proximally funnel-shaped. One side of the funnel surrounds proximally the straight distal part of the stylet. The distal part of the duct is obliquely placed, ends acutely and sheaths the distal end of the stylet. The receptaculum seminis is a large, elongate sac, which is connected with the atrium genitale commune by a long and very narrow bursal canal. The bursal appendage is very wide at its base. Distally it becomes gradually narrower and makes an almost complete coil. From its base radiate a number of cuticular ridges over the external wall of the receptaculum seminis. The length of the copulatory organ is not given.

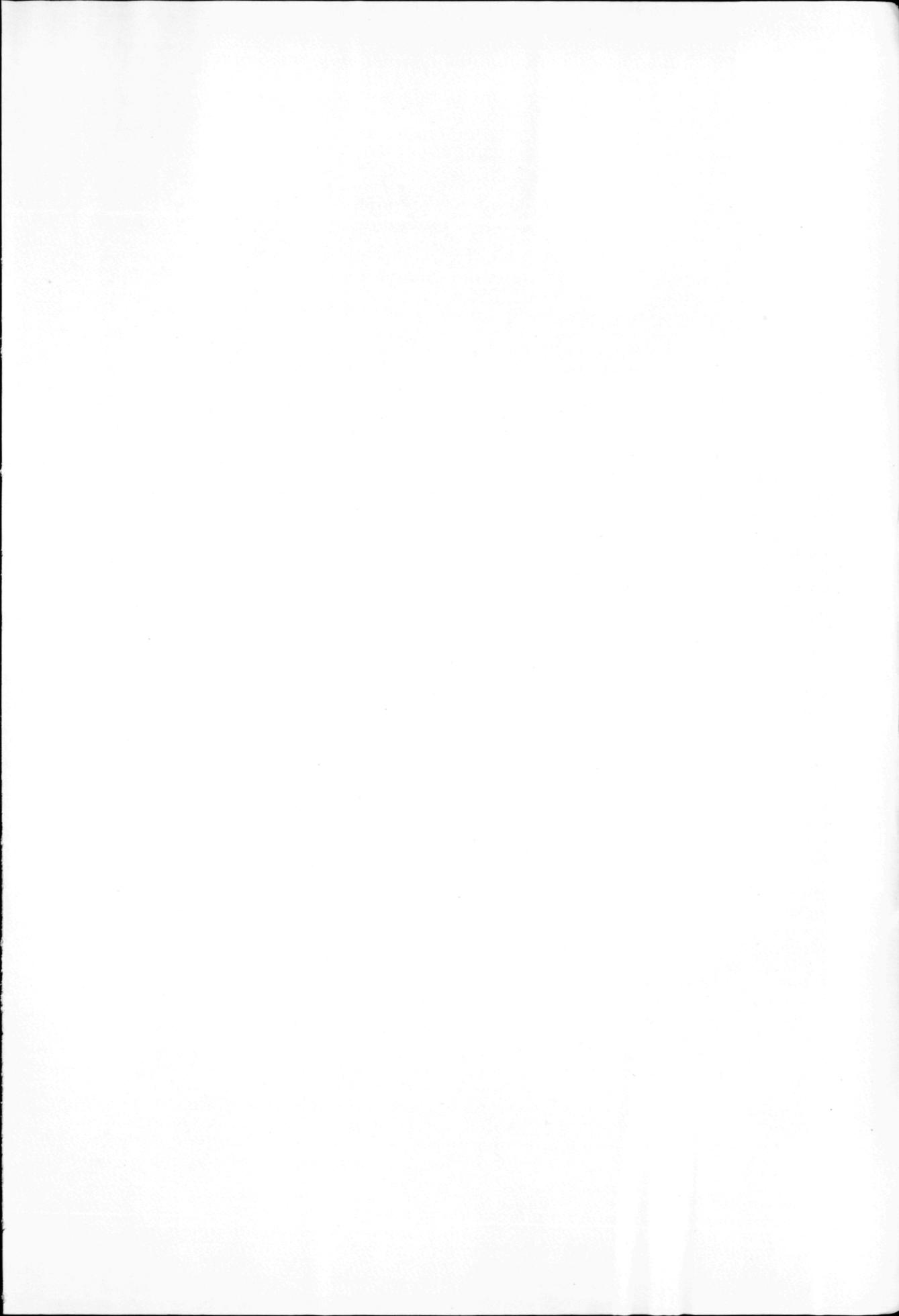
Geographical distribution:

C. axi has been found by RIEDL (1954) at Capo di Sorrento in the surroundings of Naples, and at Sampieri on Sicily.

Ecology:

The species occurs in shallow still-water biotopes, where it may be rather numerous between algae. According to RIEDL the species does not show any preference for a special association. It occurs also in the intertidal belt and in tidal pools.

(to be continued)



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