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UITGEGEVEN DOOR HET

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REMARKS ON THE SUBCLASS UDONELLIDA (MONOGENEA), WITH DESCRIPTION OF A NEW SPECIES

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With 29 text-figures

Introduction

Flatworms living as commensals on parasitic copepods from marine fishes were known already as early as 1835, when Johnston described *Udonella caligorum* from *Caligus* spec., a parasite of *Hippoglossus hippoglossus* (L.). Since then a number of similar genera and species have been described, but none of these is clearly different from *Udonella caligorum*, as far as can be judged from the descriptions. Therefore only one valid species is recognized by most modern authors (Price, 1938; Sproston, 1946; Ivanov, 1952b). *Calinella ophiodontis* Kay, 1945, a species not listed by these authors, probably is another synonym to be added to the long list, but Kay's material should be re-examined before a final decision can be made. In Yamaguti's compilation (1963) the genus *Calinella* Monticelli, 1910, is still maintained, based on the incorrect assumption that this genus should differ from *Udonella* in having the intestine fenestrated.

In the present paper a new species is described, which is provisionally included in the genus *Udonella*. Material of *Udonella caligorum* could also be studied.

Udonella papillifera n. sp. (fig. 1-22)

Material. — Dr. W. Vervoort found 12 specimens of this new species loose in a vial with about 30 specimens of *Ceratocolax euthynni* Vervoort (Copepoda, Cyclopoida), which were collected from the nasal fossae of *Euthynnus alleteratus* (Rafinesque) from the Gulf of Guinea, off Abidjan, Ivory Coast (Vervoort, 1965). From a few to more than 40 eggs of *Udonella* were attached to the carapax, the genital segments and the egg strings of nearly

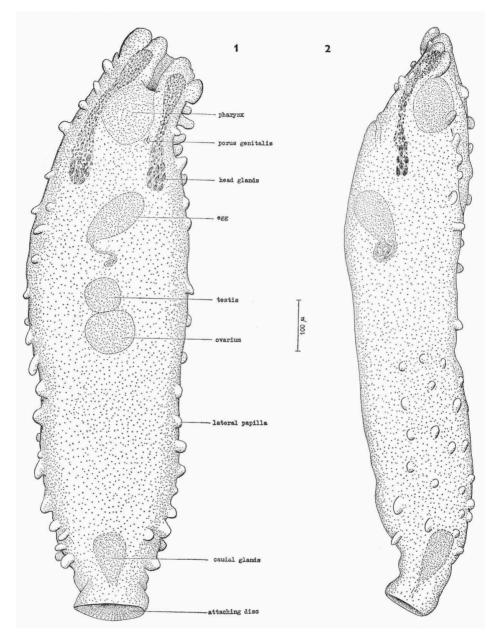
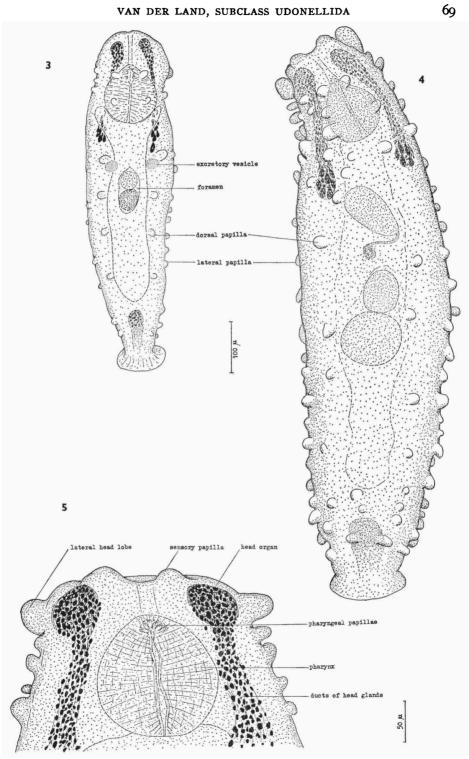


Fig. 1-2. Udonella papillifera n. sp. 1, habitus, ventral view; 2, habitus, lateral view.

Correction: transpose "testis" and "ovarium".

Fig. 3-5. Udonella papillifera n. sp. 3, habitus of young specimen, dorsal view; 4, habitus, dorsal view; 5, head, slightly flattened, dorsal view.



all host copepods. It is not known whether the copepods were collected from one fish host or from more fishes. Other samples of the same copepod species contained smaller numbers of *Ceratocolax* and only a few eggs of *Udonella*.

Part of the material was carmine stained and prepared as balsam mounts. As this procedure resulted in some distortion, the remaining specimens were prepared as glycerine mounts (method Seinhorst, 1959), with much better results. As the internal anatomy can only successfully be studied from sections, two specimens were serially sectioned and stained. It is to be regretted that apparently some autolysis had taken place before fixation, so that only the gross anatomy could be studied and histological studies could not satisfactorily be undertaken.

Holotype: whole mount no. 5807. Paratypes: whole mounts nos. 5808-5815, 5818, eggs nos. 5816-5817, cross-sections no. 5819, longitudinal sections no. 5804. All specimens are in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden.

Description. — Body elongate, subcylindrical, length up to 2 mm, maximum width, at the utero-ovarian level, up to 0.45 mm. The cuticle seems to be very finely striated, which is caused by the strong longitudinal muscle fibers (fig. 8); on the head, where the ring-muscles are strongest, the striation is transverse. The lateral and dorsal sides of the body bear numerous papillae of unequal proportions. The lateral papillae are irregularly distributed and most numerous in the anterior and posterior parts of the body. The dorsal papillae are arranged in two symmetrical rows in young individuals but later these rows tend to become irregular.

The adhesive disc is circular in outline and directed slightly ventrally. Its maximum diameter is considerably smaller than the maximum body width. One group of adhesive gland cells is present, their tiny ducts opening separately to the outside all over the central part of the disc; large collecting ducts were not observed.

The head is dorso-ventrally flattened, with pairs of lateral head lobes, sensory papillae and head organs (fig. 5). The lateral head lobes are inconspicuous in the young, but large, up to 50 μ high, in mature individuals. The broad, conical sensory papillae, up to 25 μ high, are situated on the frontal margin between the head organs. Nerve fibers are inconspicuous. The head organs consist of a cavity with a frontal opening, and a subglobular, protrusable adhesive organ, diameter up to 45 μ , which receives the ducts from the head glands (fig. 7). The irregular clusters of head glands extend on either side of the body from the posterior part of the pharynx to the level of the oötype. The opening of the head organ is not surrounded

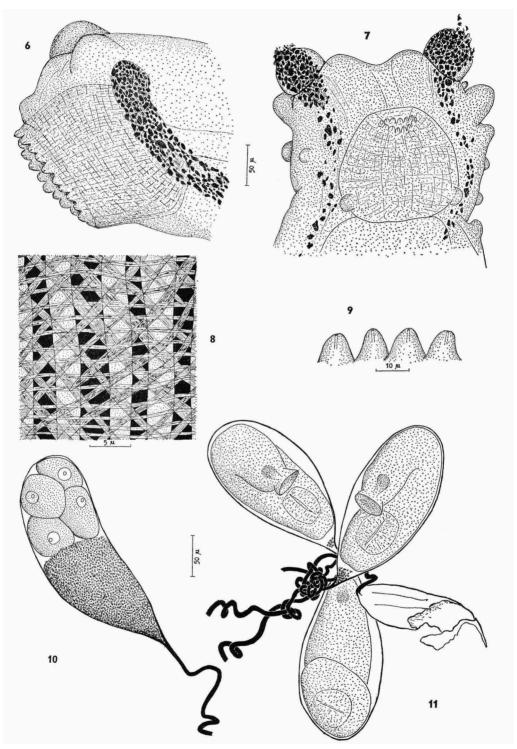


Fig. 6-11. Udonella papillifera n. sp. 6, head, pharynx protruded, lateral view; 7, head, head organs protruded, dorsal view; 8, detail of dermal musculature; 9, pharyngeal papillae; 10, egg in early stage of development; 11, cluster of eggs with young individuals

by papillae. The mouth is subterminal; the oral margin, which becomes visible when the pharynx is protruded, is not denticulated.

The large, doliiform pharynx is partially protrusable (fig. 6); its length is from 15% of the body length in young specimens to 10% of the body length in mature individuals. The anterior opening is much widened when the pharynx is protruded to the outside. Its margin is provided with about 20 papillae, 8 to 10 μ high, with a diameter of 11 to 15 μ at their base (fig. 9). On top of each papilla one duct of a pharyngeal gland opens to the outside. The pharynx is attached to the ventral body wall in its anterior part (fig. 13) and to the dorsal body wall in its posterior part.

The oesophagus is lacking. The single, sac-like intestine extends into the posterior third of the body, and is provided with a foramen in the region of ovarium and testis.

The two primary excretory pores are located dorsally, on the level of the oötype (one represented in fig. 19). The large terminal vesicles can only be observed in young specimens (fig. 3). The condition of the material did not allow further studies of the excretory system. The nervous system could not be observed either.

The single, subglobular testis is situated in the middle of the body. Its diameter ranges from 6 % of the body length in young individuals to more than 10 % of the body length in mature individuals. The vas deferens originates from the left part of the testis and runs forward dorsal to ovarium and uterus; its terminal part is widened to serve as a false vesicula seminalis. The vesicula prostatica is situated between the vesicula seminalis and the terminal portion of the uterus. The seminal and prostatic vesicles both open into a short ejaculatory duct, which has a dilation, but does not show any other differentiation. The small atrium genitale opens to the outside ventral to the posterior part of the pharynx, to the left of the median line (fig. 15).

The subglobular ovary lies immediately anterior to the testis. Its diameter is 5 to 8% of the body length. It is always smaller than the testis. The short, broad germiduct arises from the left ventral surface of the ovarium, in its anterior part, and proceeds backward to about the middle of the ovarium. A large receptaculum seminis is situated ventral to the posterior part of the ovary and the anterior part of the testis. The oviduct receives at short intervals the narrow duct of the receptaculum seminis, the germiduct, which has a narrow opening (fig. 21), and the vitelloduct. Vagina or genito-intestinal duct are absent. The rather short, wide oviduct proceeds forward to enter the oötype at the level of the anterior part of the ovarium. The structure of the large oötype could not exactly be determined. Part of the shell glands is situated outside the compact mass of the other glands of the

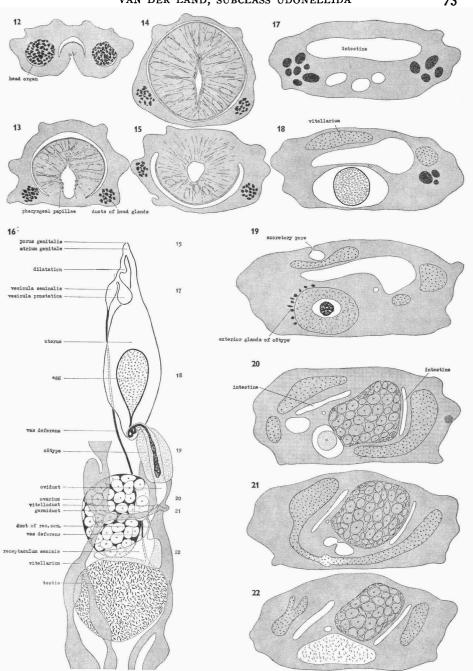


Fig. 12-22. Udonella papillifera n. sp. 12-15, cross-sections through pharynx; 16, reproductive organs, ventral view, semi-diagrammatic reconstruction from cross-sections (the numbers refer to the cross-sections); 17-22, cross-sections through reproductive organs, semi-diagrammatic.

oötype (fig. 19). The uterus is a large, fusiform sac-like organ, containing one egg at a time. Eggs were present only in the three largest specimens, which were 1.3 mm, 1.7 mm and 2 mm long. Two branched and lobed vitellaria extend along the whole length of the intestine on either side of the body (fig. 16, 18-22). The two transverse yolk ducts join together near the ventral body wall to form a very short common vitelloduct (fig. 21).

The eggs (fig. 10) are piriform, large, 200-250 μ long and about 100 μ wide, without operculum, provided with a long, winding caudal filament with an attaching disc. The eggs are strongly glued to the body or the egg strings of the copepod host and are often laid in clusters (fig. 11). The young in the egg (200-300 μ long) resembles the adult in all aspects, so there is no larval stage.

Udonella caligorum Johnston, 1835 (fig. 23-29)

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Udonella caligorum Johnston, 1835: 495-498; Price, 1938: 194-197; Sproston, 1946: 264-269; Delamare Deboutteville, 1950: 362-363; Ivanov, 1952a: 175-178; Ivanov, 1952b: 112-163; Poljanskii, 1955: 44, 114, 129, tab. 22; Caballero y C., et al., 1956: 181; Dawes, 1956: 120-122; Yamaguti, 1958: 61-62; Causey, 1961: 314-318; Yamaguti, 1963: 164-165.

Calinella craneola Monticelli, 1910: 1-9; Guiart, 1938: 52-53; Yamaguti, 1963: 165.

Calinella myliobati Guberlet, 1936: 958-961; Yamaguti, 1963: 166.

?Calinella ophiodontis Kay, 1945: 111-114.

Udonella ophiodontis Yamaguti, 1963: 165.

Older synonyms: vide Sproston, 1946.
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Material. — Many specimens of all stages of this species were found attached to the edge of the carapace and to the genital segments of a female specimen without egg strings of the parasitic copepod Caligus curtus O. F. Müller. The specimen of Caligus was found on Gadus morrhua L. from the Trondheimsfjord, Norway (63° 37′ N 9° 46′ E), during an excursion of students of the Leiden University in August 1961. Numerous eggs of Udonella were attached to the copepod.

The collection studied consists of: 3 carmine stained balsam mounts (nos. 5820-5822), 14 glycerine mounts with 21 specimens, and a number of eggs (nos. 5799, 5828-5840), longitudinal sections of 2 specimens (nos. 5826-5827), cross-sections of 2 specimens (nos. 5824-5825), a number of eggs and young specimens attached to the host (no. 5823), all in the Rijksmuseum van Natuurlijke Historie, Leiden.

Description. — Since this species is well kown and has often been described (vide Sproston, 1946; Ivanov, 1952b; Dawes, 1956; Yamaguti, 1958) no extensive description is given here. Attention is given mainly to characters in which it differs from *U. papillifera*,

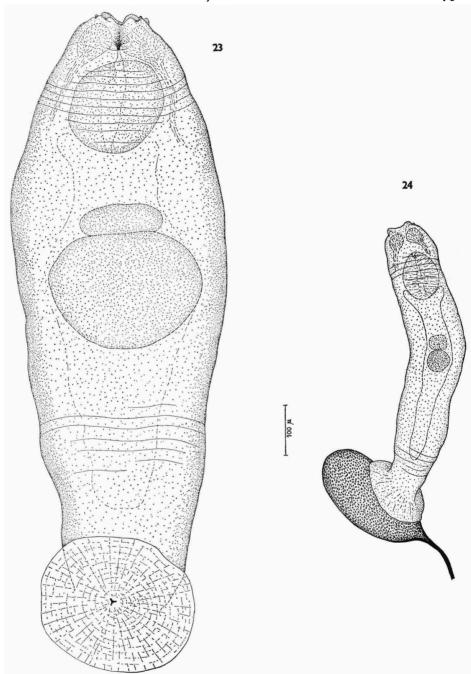


Fig. 23-24. *Udonella caligorum* Johnston. 23, mature individual, slightly flattened, ventral view; 24, young individual, attached to egg, dorsal view.

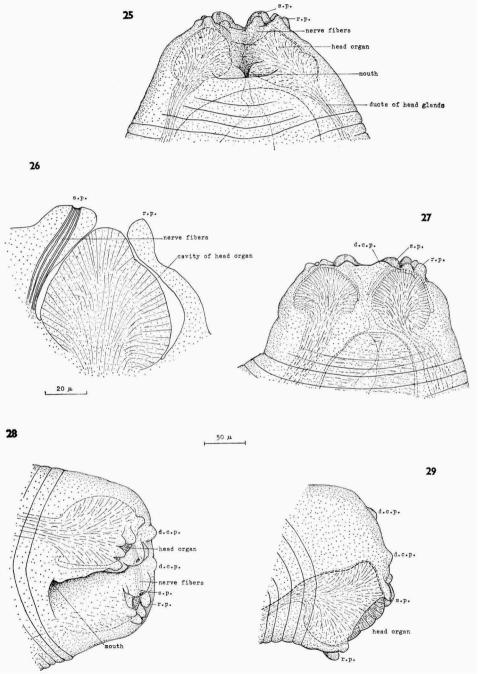


Fig. 25-29. Udonella caligorum Johnston. 25, head, slightly flattened, ventral view; 26, optical section through head organ; 27, head, dorsal view; 28, head, ventro-lateral view; 29, head, head organ partly protruded, dorso-lateral view. Abbreviations: d.c.p. = dorsal cephalic papilla, r.p. = ring papilla, s.p. = sensory papilla.

Body elongate, cylindrical, length up to 4 mm, maximum width, at the utero-ovarian level, up to 0.5 mm. Body papillae lacking. Two zones with a faint annulation, an anterior and a posterior (not to be confused with annulation due to contraction). The maximum diameter of the attaching disc is equal to the maximum width of the body or only slightly larger (especially in young individuals) or smaller. Ducts from the single group of caudal gland cells open separately to the outside, but in addition a larger collecting duct opens to the outside in the centre of the disc (fig. 23).

The head is provided with sensory papillae, head organs, ring papillae, and dorsal cephalic papillae. The conical sensory papillae are innervated by about 6 nerve fibers. The nerve endings lie in a shallow pit on top of the papilla (fig. 26). The frontal apertures of the head organs are surrounded by a ring of prominent papillae; each aperture with a sensory papilla and five or six "ring papillae", which are placed close together when the head organ is inactive, but wide apart when the adhesive organ is protruded (fig. 29). The two dorsal cephalic papillae are situated dorsal to the sensory papillae. The oral margin could not be observed, the pharynx not being protruded in any of the specimens. The pharyngeal papillae are of the same type as those of *U. papillifera*, but their number could not be determined.

The eggs are 200 to 250 μ long and 105 to 135 μ wide, and are for the greater part laid in large clusters.

Discussion

It is remarkable that both species, although differing very much in their external characters, have a similar internal structure, for which reason the new species is provisionally included in the genus *Udonella*. The sections of the two species also differ considerably in appearance, but this may be due to the fact that the material of *U. papillifera* was fixed too late.

In the present material of both species, the ovarium is smaller than the testis. Sproston (1946) observed that the ovarium outgrows the maximum size of the testis when the worms have reached about three-quarters of their maximum length. If this is always true, our specimens are not yet full grown. In the material of *U. caligorum* no eggs are present in the uterus, so that it is quite well possible that they had not yet reached the egg producing stage which means that they may become considerably longer than 4 mm. From the fact that an egg was present in the uterus of a specimen of 1.3 mm length of *U. papillifera*, we may conclude that this species probably remains much smaller than *U. caligorum*, although its eggs are of the same size. The anatomy of the material of *U. caligorum* in general agrees very well with the published descriptions (Guberlet, 1936; Price, 1938; Kay, 1945;

Sproston, 1946; Ivanov, 1952b; Yamaguti, 1958). Discrepancies between the various descriptions are partly due to differences in interpretations and methods, but some aspects deserve special attention.

Some investigators observed only one group of caudal glands (Kay, Sproston, Ivanov), like in the present material, whereas others (Price, Yamaguti) stated the presence of two lateral groups of gland cells. Yamaguti in addition stated that two strongly winding collecting ducts are present, joining together in the median line to form a common duct, which proceeds toward the center of the attaching disc.

Kay (1945) did not observe a prostatic vesicle, but according to him "the ejaculatory duct is ensheathed by a cluster of cells which may function as a prostate gland". This may be attributable to a faulty interpretation, since Kay did not make serial sections, and confirmation is necessary.

In Kay's figure of an egg the shell has a rugose appearance. He did not mention this character in the text of his paper, and it may be due to fixation. The eggs found by Price (1938) were "considerably wrinkled", which this author attributed to fixation.

Causey (1961) stated that "Udonella caligorum tends to select the egg strings of the host copepod as a site of attachment in European waters, and the body of the copepod in American waters". However, he refers to two European writers only: Van Beneden (1858) and Dawes (1946). Other authors do not confirm his statement: Sproston (1946), Delamare Deboutteville (1950), Euzet & Baer in Grassé (1961). The first author even stated that she never found eggs on the egg strings of the copepods. The present material was also attached to the body of the host.

THE SYSTEMATIC POSITION OF UDONELLA

Udonella has since long been included in the class Monogenea, in which it was recognized to occupy an isolated position. The group was first given the status of a family, later that of a superfamily or an order.

Ivanov (1952a, b) thoroughly studied the anatomy of *Udonella* and concluded that it differs so much from the other Monogenea, that he proposed the new class Udonelloidea, which was accepted by Bychowsky (1961), who did not treat *Udonella* in his monograph of the Monogenea. Indeed *Udonella* differs from the other Monogenea in a number of characters, the most important of which are: the absence of posterior hooks, the absence of a ciliated larval stage, the most peculiar excretory system and some characteristics of the sex organs. Other characters mentioned by Ivanov, are of minor importance. The fact that *Udonella* lives as a commensal on parasitic copepods is not important either, since it feeds on mucous and

epithelial cells of fishes just like many other Monogenea. *Udonella* just has a special location on the fish host. Moreover some genuine Monogenea live similarly on parasitic isopods.

If we should agree to Ivanov's proposal, some other groups of flatworms, e.g., Aspidocotylea, Gyrocotylida, and Gnathostomulida, would also have to be given the rank of a class, which action would be altogether justified. It is the present authors opinion that nothing is gained by an excessive splitting of the highest categories of flatworms. It is a much more practical method to keep the small aberrant groups in the same class as the large groups with which they are most closely related. The erection of subclasses is a much better solution. Consequently we may recognize the class Monogenea, with three subclasses: Udonellida, Monogenea s. str. and Gyrocotylida (vide Llewellyn, 1965).

Conclusion

As a result of the present study, the following differential diagnoses of the relevant taxa may be given:

Subclassis Udonellida Ivanov, 1952

Monogenea, without cercomere; attaching disc simple, with adhesive glands only. Head organs with adhesive glands; oral suckers absent. Pharynx dolliform. Intestine simple, sac-like. Excretory system intricate, with giant paranephrocytes in pseudometameric arrangement, numerous small flame cells, and with a physiologically separated secondary system of canals and pores, in addition to the normal, primary system.

One testis; no copulatory organ. Ventral porus genitalis communis in anterior part of the body. Genito-intestinal duct and vagina absent. Eggs large, with caudal filament, without operculum. Development direct, without larval stage.

Udonella Johnston, 1835

Body elongate, subcylindrical. Adhesive disc circular in outline. Two sensory papillae on the frontal margin of the head. Head organs consisting of a cavity with a protrusable adhesive organ. Clusters of head glands on either side of the body between pharynx and ootype. Mouth subterminal. Pharynx partially protrusable; its anterior margin provided with papillae. Oesophagus lacking. Intestine fenestrated in the region of ovarium and testis.

Testis subglobular, in the middle part of the body. False vesicula seminalis, and vesicula prostatica present. Ductus ejaculatorius not differentiated. Atrium genitale and porus genitalis ventral to pharynx. Ovarium subglobular, immediately pretesticular. Receptaculum seminis ventral to ovarium and testis. Oötype large, differentiated. Uterus sac-like, containing one egg at a time. Two branched and lobed vitellaria extending along the intestine on either side of the body. Eggs large, piriform, with a long, winding filament, which is provided with an attaching disc.

Commensals on parasitic copepods of marine fishes.

Type species: Udonella caligorum Johnston, 1835.

Udonella caligorum Johnston, 1835

Length up to 4 mm, probably more. Body partially annulated, without papillac. Diameter of attaching disc about equal to the maximum body width. Caudal glands with collecting duct. Head tapering, not flattened, with two dorsal cephalic papillae, without lateral head lobes. Head organs with 5 or 6 ring papillae. Oral margin denticulated.

Commensals on many species of Copepoda on many species of fish. Cosmopolitan.

Udonella papillifera n. sp.

Length up to 2 mm. Body not annulated, provided with numerous lateral papillae and two irregular rows of dorsal papillae. Diameter of attaching disc considerably smaller than maximum body width. Caudal glands without collecting duct. Head broad, dorsoventrally flattened, without dorsal cephalic papillae, with two lateral head lobes. Ring papillae lacking. Oral margin not denticulated.

Commensals of Ceratocolax euthynni Vervoort, a parasitic Copepod of the fish Euthynnus alleteratus (Rafinesque). Gulf of Guinea.

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^{*} The papers marked with an asterisk were not available to me.