

HYDROBIOLOGY

AN ANALYSIS OF THE GNATHORHYNCHIDAE
(NEORHABDOCOELA, TURBELLARIA) AND THE POSITION OF
PSITTACORHYNCHUS VERWEYI nov. gen. nov. sp.

IN THIS FAMILY

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Mededeling no. 66
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YERSEKE - Nederland

(Communicated by Prof. H. BOSCHMA at the meeting of May 25, 1968)

The family of the Gnathorhynchidae was erected by MEIXNER in 1929 to accomodate 3 species belonging to the genera *Gnathorhynchus* and *Prognathorhynchus*. Since then several other representatives of this family have been described by KARLING (1947, 1952, 1956b), Ax (1952, 1953) and L'HARDY (1963, 1964, 1966), by which the number of genera increased to 7 together containing 16 species. I can now add another gnathorhynchid belonging to a hitherto undescribed genus, *Psittacorhynchus verweyi* nov. gen. nov. sp.

Generic characters of the Gnathorhynchidae:

From a study of the diagnoses of the gnathorhynchid genera it became obvious that the following characters are supposed to have diagnostic value:

1. the muscular structure of the proboscis and its motory musculature
2. the structure of the proboscis hooks
3. the position of the pharynx in the body
4. the position of the testis in the body
5. the course of the ductus ejaculatorius in relation to the prostatic vesicle and the place where sperma and prostatic secretory products are mixed
6. the presence or absence of a cuticular stylet
7. the presence or absence of a spermaducal vesicle
8. the presence or absence of a bursa copulatrix
9. the presence or absence of a ductus utero-communis
10. the position of the genital pore
11. the presence or absence of eye-pigment.

Comments will be made upon these characters with the sole purpose of establishing their significance for the taxonomy within the family. One is referred to the works of MEIXNER (1929), KARLING (1947, 1956a) and L'HARDY (1963) for detailed treatments of the anatomy and histology of the various genera.

1. The muscular structure of the proboscis and its motory musculature

The structure of the proboscis shows a remarkable variation within the family but seems to be constant within each genus. Four different types can be recognized. The first type occurs in *Ancistrorhynchus*, *Drepanorhynchides* and *Gnathorhynchus*, here one finds in the proboscis 2 cylindrical muscular "pads" (German: "Muskelwülste"; French: "bourrelets musculaires") completely surrounded by a membrane. In the second type the proboscis contains two compressed, disc-shaped muscular "pads", this type occurs in *Prognathorhynchus*, *Odontorhynchus* and *Psittacorhynchus*. In *Neognathorhynchus* the proboscis possesses 2 compressed, muscular "pads", which are distally connected by a series of muscular lamellae (U-shaped). In the proboscis of *Uncinorhynchus* in place of the muscular "pads" there is a strong ring musculature. The terminal cone of the proboscis is very short in most of the genera, in *Uncinorhynchus* it is almost non-existent, in contrast in *Ancistrorhynchus* it is almost as large as the basal part of the proboscis.

The motory musculature of the proboscis shows even more variation. Each genus seems to have a fixed number of proboscis retractors and in some genera there are tegumentary retractors as well. However, this character has to be treated with care, as in most cases the musculature of the genus was studied by means of only one species from it. In *Ancistrorhynchus* there are 4 pairs of short proboscis retractors and no tegumentary retractors. In *Gnathorhynchus* and *Drepanorhynchides* also tegumentary retractors are absent, but here 6 pairs of short proboscis retractors occur. The proboscis of *Neognathorhynchus* has 4 pairs of short retractor muscles and only weakly developed tegumentary retractors. *Prognathorhynchus* and *Uncinorhynchus* both have 4 pairs of long proboscis retractors and tegumentary retractors as well, but the places of attachment of these muscles differ considerably in the two genera. *Odontorhynchus* has tegumentary retractors and only 1 pair of long proboscis retractors. The proboscis musculature in *Psittacorhynchus* has not been studied.

2. The structure of the proboscis hooks

The structure of the proboscis hooks seems to be a very distinctive character for the genera of the Gnathorhynchidae, so far 5 different types have been described. In *Ancistrorhynchus* and *Gnathorhynchus* each hook is laterally winged and has a basal plate with the appearance of a webfoot. In *Drepanorhynchides* each proboscis hook consists of a horseshoe-shaped basal plate on which 2 or 3 unequal sized teeth are inserted. In *Neognathorhynchus* the hooks have an obtuse axial outgrowth and 2 lateral wings. The proboscis hooks of *Uncinorhynchus* have each a horseshoe-shaped basal plate, the apices of which touch those of the opposite hook, and a central inwardly curved tooth. In *Odontorhynchus* the proboscis hooks have a roundish to square, not always very distinct, basal plate, on which 1 straight hook is inserted, sometimes also 2 very small lateral teeth.

In *Prognathorhynchus* and *Psittacorhynchus* the proboscis hooks are very similar in structure to those of *Odontorhynchus* but are usually better developed; the basal plate is round and somewhat arched, while the tooth is usually curved; sometimes 2 very small lateral teeth can be found at the base of the large tooth.

3. The position of the pharynx in the body

The position of the pharynx varies. In *Ancistrorhynchus*, *Drepanorhynchides* and *Gnathorhynchus* it is situated in the posterior part, in *Odontorhynchus*, *Prognathorhynchus*¹⁾ and *Uncinorhynchus* in the anterior part and in *Neognathorhynchus* and *Psittacorhynchus* in the middle part of the body.

4. The position of the testis in the body

The testis is single and is usually dorsal, but in *Prognathorhynchus* and *Drepanorhynchides* it is ventral, and in *Neognathorhynchus* it is distinctly lateral. In *Ancistrorhynchus* and *Drepanorhynchides* the testis lies in front of the pharynx, and in *Prognathorhynchus*, *Neognathorhynchus* and *Odontorhynchus* it is posterior to it. In *Gnathorhynchus*, *Uncinorhynchus* and *Psittacorhynchus* the testis extends from in front of the pharynx to far behind this organ.

However, L'HARDY (1963) noticed that in *Ancistrorhynchus* the testis sometimes lies in another position. I noticed the same in *Psittacorhynchus*. In that genus the testis is generally dorsal median, but is sometimes oblique, or postpharyngeal.

5. The course of the ductus ejaculatorius in relation to the prostatic vesicle and the place where sperma and prostatic secretory products are mixed

In 6 genera the ductus ejaculatorius traverses axially the prostatic vesicle, but in *Prognathorhynchus* and *Ancistrorhynchus* it is situated at the outer side of the prostatic vesicle within the muscular sheath of the granular bulb.

Usually the mixing of sperma and the prostatic secretory products of the prostatic glands takes place outside the granular bulb, in the proximal part of the stylet (*Drepanorhynchides*, *Prognathorhynchus*, *Psittacorhynchus*, *Uncinorhynchus*) or in the distal part of the ductus ejaculatorius (*Ancistrorhynchus*, *Gnathorhynchus*). In the genera *Odontorhynchus* and *Neognathorhynchus* sperma and prostatic secretions are mixed already within the prostatic vesicle.

6. The presence or absence of a cuticular stylet

There are only two genera in which the male genital tract is not terminated by a cuticular stylet, viz. *Gnathorhynchus* and *Ancistrorhynchus*.

¹⁾ In *Prognathorhynchus typhlus* L'Hardy, 1964 the pharynx is situated rather close to the middle of the body.

7. The presence or absence of a spermaducal vesicle

The occurrence of a spermaducal vesicle has been recorded in all previously described genera. In *Uncinorhynchus* this organ can become very voluminous and reach $\frac{1}{3}$ of the body length. In the genus *Psittacorhynchus* this organ is completely absent. I did not find even the slightest widening of the vas deferens before it enters the granular vesicle, although I examined carefully many specimens in all stages of maturity.

8. The presence or absence of a bursa copulatrix

Odontorhynchus has a bursa copulatrix; this organ is absent in all other Gnathorhynchidae.

9. The presence or absence of a ductus utero-communis

In the genera *Drepanorhynchides*, *Gnathorhynchus*, *Odontorhynchus*, and *Uncinorhynchus* the uterus opens directly into the atrium genitale commune and not via the female genital canal. In *Neognathorhynchus* and *Ancistrorhynchus* the uterus is connected with the female genital canal and thus one can speak of a ductus utero-communis. With respect to this character the genus *Prognathorhynchus* is not homogeneous. In the species *P. dubius* Meixner, 1929 and *P. campylostylus* Karling, 1947 there is definitely a ductus utero-communis, but in *P. canaliculatus* Karling 1947 and *P. typhlus* L'Hardy, 1964 the uterus opens directly into the atrium genitale commune. In *Psittacorhynchus* I could not see the terminal part of the uterus duct, but from the general position of the uterus it seems likely that it opens into the atrium.

10. The position of the genital pore

The genital pore is terminal in *Drepanorhynchides*, *Neognathorhynchus* and *Prognathorhynchus*. It is ventral, subterminal in *Ancistrorhynchus*, *Gnathorhynchus*, *Odontorhynchus*, *Psittacorhynchus* and *Uncinorhynchus*.

11. The presence or absence of eye-pigment

The presence or absence of eye-pigment has already been rejected by KARLING (1947) as a generic character. In the taxonomy of the Gnathorhynchida it can, however, be applied as a character at species level. The species of *Ancistrorhynchus*, *Gnathorhynchus*, *Neognathorhynchus* and *Psittacorhynchus* have eyes, while in species of *Odontorhynchus* and *Uncinorhynchus* eye-pigment is absent. In *Prognathorhynchus* four of the five species have eye-pigment, while *Drepanorhynchides* has one blind species and one with eye-spots.

From the above it is apparent that the various diagnostic characters are not of equal importance. The character of eye-pigment is of little value, being only applicable at species level, and the pigment itself is usually lost when a species adapts itself to life in the ground water. Characters concerning the position of certain organs in the body (e.g.

that of the pharynx and the testis) are more liable to vary than characters concerning very complicated structures (such as the proboscis and the male genital apparatus). A considerable variation in the position of the testis has been reported for *Ancistrorhynchus* and *Psittacorhynchus*. The character whether the uterus is connected with the ovovitelloduct or directly with the atrium genitale commune is also of a topographical nature. The characters based on complex structures, such as the proboscis and the male copulatory organ, must be preferred in taxonomic considerations to topographical or metric characters.

Further there appears to be no mutual association between the characters of proboscis and male genital apparatus within the Gnathorhynchidae. Genera in which the structure of the proboscis and proboscis hooks is very similar, and which thus show an obvious relationship, may have very different male genital organs, e.g. *Prognathorhynchus* and *Psittacorhynchus*. In the same way, genera showing an obvious similarity in the structure of their male genital organs may have a very different proboscis apparatus, e.g. *Drepanorhynchides* and *Psittacorhynchus*. The "reticulate" relationships within the Gnathorhynchidae make it difficult to elaborate a natural arrangement of the genera. The same is true for the preparation of a key to the genera. There is a great deal of arbitrariness in the choice of characters to be used for the first division of a key. I chose the characters of the proboscis for practical reasons, because they are conspicuous and occur also in juvenile specimens. Had I chosen the structure of the male genital apparatus as the first character for division the key would have shown quite another grouping of the genera.

KEY TO THE GENERA

1. Pharynx posterior. Proboscis with 2 cylindrical muscular "pads", completely surrounded by a membrane. Cuticular stylet present or absent.
 2. Cuticular stylet present. Proboscis hooks with horseshoe-shaped basal plate *Drepanorhynchides* L'Hardy, 1964
 2. Cuticular stylet absent. Proboscis hooks with wing-shaped lateral lobes.
 3. Ductus ejaculatorius axially traversing the prostatic vesicle *Gnathorhynchus* Meixner, 1929
 3. Ductus ejaculatorius beside the prostatic vesicle *Ancistrorhynchus* L'Hardy, 1963
1. Pharynx anterior or in the middle of the body. Proboscis of another structure. Cuticular stylet present.
 4. Proboscis with 2 disc-shaped muscular "pads". Proboscis hooks with a curved basal plate and one central spine, sometimes with two smaller lateral ones.

5. Pharynx anterior; spermaducal vesicle present.
 6. Ductus ejaculatorius axially traversing the prostatic vesicle. Bursa copulatrix present . *Odontorhynchus* Karling, 1947
 6. Ductus ejaculatorius beside the prostatic vesicle. Bursa copulatrix absent . . *Prognathorhynchus* Meixner, 1929
5. Pharynx in the middle of the body. Spermaducal vesicle absent. Ductus ejaculatorius axially traversing the prostatic vesicle *Psittacorhynchus* nov. gen.
4. Proboscis and proboscis hooks of another structure.
 7. Proboscis with 2 distally connected muscular "pads". Proboscis hooks with an obtuse basal plate and wing-shaped lateral lobes. Pharynx in the middle of the body. Sperma and granular secretion mixing in the prostatic vesicle *Neognathorhynchus* Karling, 1956
 7. Proboscis without muscular "pads". Proboscis hooks consisting of a horseshoe-shaped basal plate with a curved central spine. Pharynx anterior. Sperma and granular secretion mixing in the proximal part of the stylet . *Uncinorhynchus* Karling, 1947

PSITTACORHYNCHUS nov. gen.

Proboscis with 2 disc-shaped muscular "pads" and a very short terminal cone. Proboscis hooks with a round, arched basal plate on which 1 large tooth is inserted, sometimes also 2 very small, additional teeth. Pharynx in the middle of the body. Testis elongate, dorsal and median, extending from in front of the pharynx to far behind this organ, sometimes showing a lateral deviation in the pharyngeal area. No spermaducal vesicle. Ductus ejaculatorius axially traversing the prostatic vesicle; prostatic secretions and sperma discharging separately into the funnel-shaped proximal part of the cuticular stylet, where mixing takes place. Genital pore ventral, subterminal. No bursa copulatrix.

Type: *Psittacorhynchus verweyi* nov. sp.

With respect to the structure of its proboscis and proboscis hooks *Psittacorhynchus* is closely related to *Prognathorhynchus* and *Odontorhynchus*. The male genital apparatus of *Psittacorhynchus* is, however, very different from that of *Prognathorhynchus*, and, although there seems to be some similarity with that of *Odontorhynchus*, it should be noted that mixing of sperma and prostatic secretions in *Psittacorhynchus* takes place in the proximal part of the stylet, while in *Odontorhynchus* mixing occurs already within the prostatic vesicle. The general structure of the male genital apparatus of *Psittacorhynchus* is rather similar to that *Drepanorhynchides*. The position of the pharynx in the middle of the body is a character that

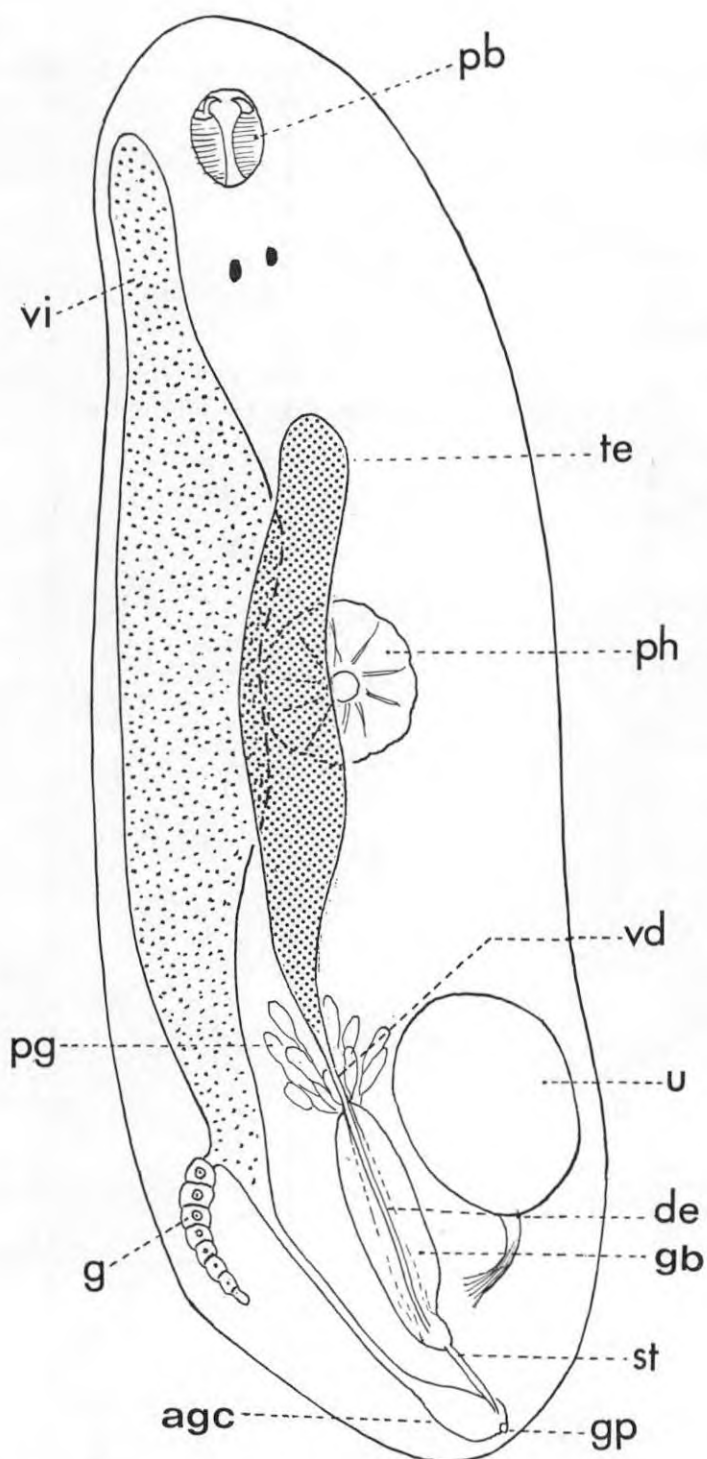


Fig. 1. *Psittacorchynchus verweyi* nov. sp. General view. agc=atrium genitale commune; de=ductus ejaculatorius; g=germarium; gb=granular bulbus; gp=genital pore; pb=proboscis; pg=prostatic glands; ph=pharynx; st=stylet; te=testis; u=uterus; vd=vas deferens; vi=vitellarium.

Psittacorhynchus has in common with *Neognathorhynchus*. In the complete absence of a spermaducal vesicle *Psittacorhynchus* differs from all other Gnathorhynchidae so far described.

***Psittacorhynchus verweyi* nov. sp.**

Psittacorhynchus verweyi Den Hartog, 1966.

DEN HARTOG, Proc. Kon. Ned. Ak. Wet. C. 69, 104, 115, 152 (1966), nomen nudum. — Fig. 1-3; Pl. I-III.

The animals are oblong, 750-1350 μ long and white in colour. The anterior part is truncate, the posterior part broadly obtuse. The widest

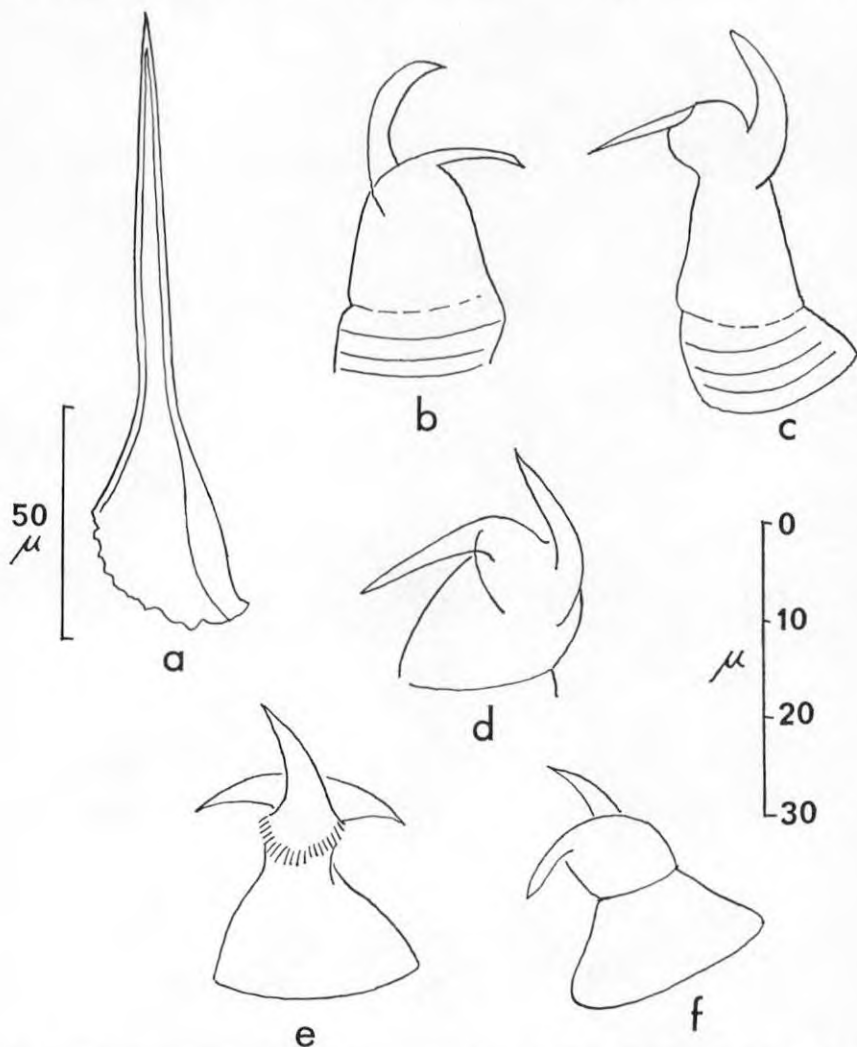


Fig. 2. *Psittacorhynchus verweyi* nov. sp. A. Stylet; B-F. Proboscis hooks. (A-D drawn from specimens from Stellendam; E-F drawn from specimens from Bergen op Zoom.)

part of the body lies behind the middle. Proboscis 70–90 μ long with 2 disc-shaped, compressed, dorso-ventrally placed muscular "pads", consisting of a series of muscular lamellae, and a very short terminal cone. Proboscis glands large. Proboscis hooks 24–28 μ long, consisting of a round, arched basal plate, which often is incompletely cuticularized, an inwardly directed lateral extension and a distinctly curved terminal tooth. The basal part of this tooth is at least partly longitudinally grooved, sometimes with 2 very small additional teeth. Eyes 2, just behind the proboscis, ca. 20 μ . Pharynx rosulatus situated in the middle of the body, ca 130 μ in diameter. Testis elongate, sausage-shaped, 400–500 μ long,

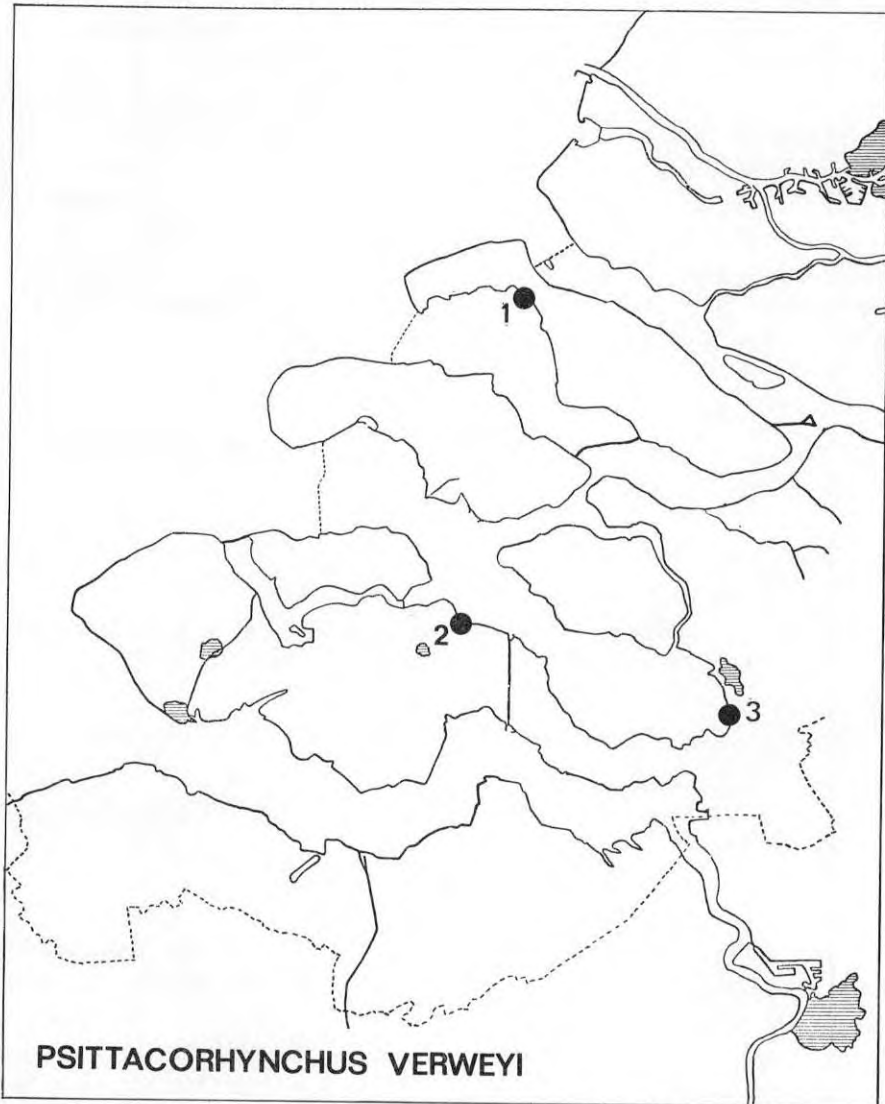


Fig. 3. Distribution of *Psittacorhynchus verweyi* nov. sp. in the south-western part of the Netherlands.

dorsal and median, extending in caudal direction from in front of the pharynx, sometimes showing a lateral deviation in the pharyngeal area; exceptionally it is oblique or post-pharyngeal. The vas deferens is a long and narrow duct penetrating the granular bulbus, without intervention of a spermaducal vesicle, proceeding axially through the prostatic vesicle as an independent, thin-walled ductus ejaculatorius. Granular bulbus thick-walled, 180–200 μ long, traversed by 2 granular strands. Prostatic glands discharging proximally in the granular bulbus. Ductus ejaculatorius somewhat widened in the distal half of the prostatic vesicle, and filled with secretory balls. Stylet obliquely funnel-shaped at its proximal end, proceeding distally as a straight, gradually narrowing, hollow, acute spine, 105–140 μ long; near its base sometimes curved; proximal margin rather indistinct. Prostatic secretory products and sperma mixing in the proximal part of the stylet. Germarium unpaired, ca 150 μ long; age difference of the oocytes rather distinct. Vitellarium large, situated at the left side. Atrium genitale commune more or less spherical, ca 50 μ ; stylet entering it from the right. Genital pore subterminal and ventral. Although the uterus is well developed, it was not possible to trace whether it connects with the female genital tract or directly with the atrium genitale commune. Egg-capsule 230 by 160 μ , without a stalk, with a hyaline, mucose drop at its base, orange-brown.

Geographical distribution:

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

Localities in the Netherlands:

Province of Zuid-Holland:

Goeree-Overflakkee: 1. Stellendam, on sandy tidal flat in front of the salt-marsh, along the Grevelingen, May 1963 (type locality).

Province of Zeeland:

Zuid-Beveland: 2. Kattendijke, intertidal sand-flat, November 1964.

Province of Noord-Brabant:

3. Salt-marsh area south of Bergen op Zoom, October 1964 (collected by Dr. M. Bilio).

Ecology:

Psittacorchynchus verweyi seems to be restricted to the high-littoral, muddy sand-flats in the euhaline section of the Deltaic region. In the salt-marsh area south of Bergen op Zoom, in the transition belt between the mud-flat and the salt-marsh, where *Salicornia europaea* forms an open but uniform vegetation, *Psittacorchynchus verweyi* and *Macrostomum bal-ticum* Luther together dominate a rich turbellarian fauna. Near Stellingdam a specimen of *Psittacorchynchus verweyi* was found at the lower limit

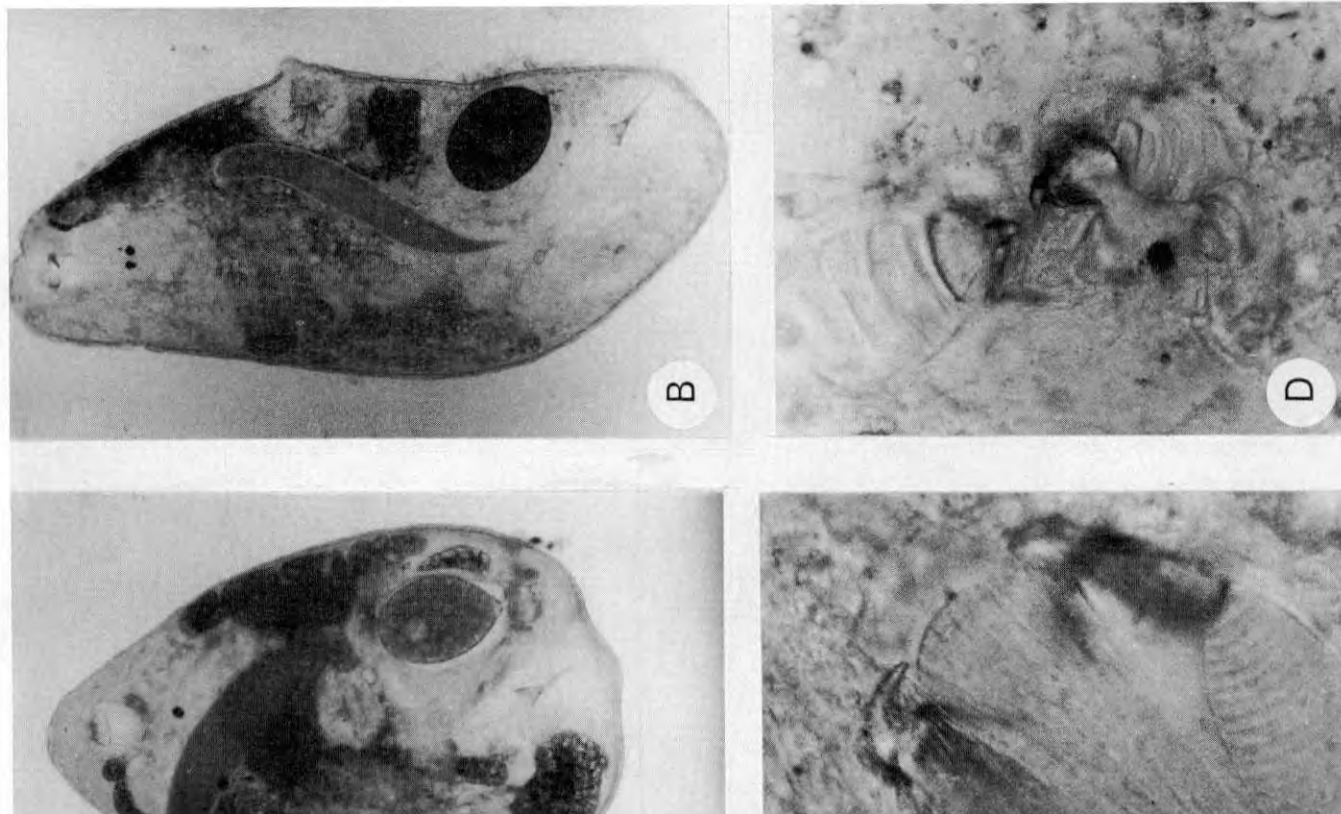


PLATE I. *Psittacorhynchus verveyi* nov. sp.
Dorsal view of squashed specimens in which are visible the eyes, the proboscis

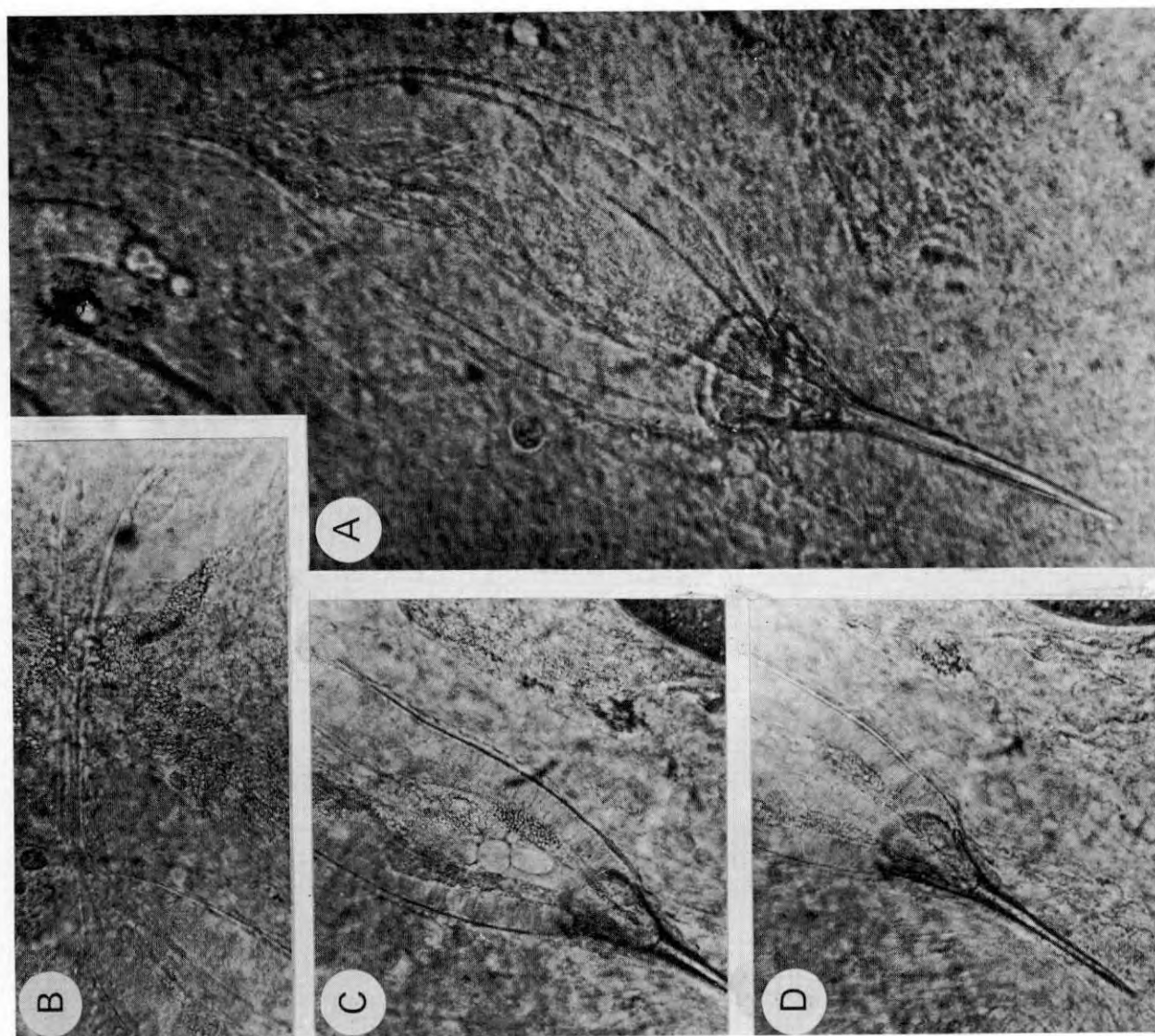


PLATE II. *Psittacorhynchus verveyi* nov. sp.

A. Cuticular stylet and granular bulbus (after a specimen from Kattendijke). E-D. The male genital tract (after a specimen from Stellendam). B. Distal part of the testis (to the right), gradually narrowing into the ductus ejaculatorius, which in its turn enters the proximal part of the granular bulbus (to the left). C. The ductus ejaculatorius traverses axially the granular bulbus, opening in the basal part of the stylet, where mixing of sperma and granular prostatic secretory products takes

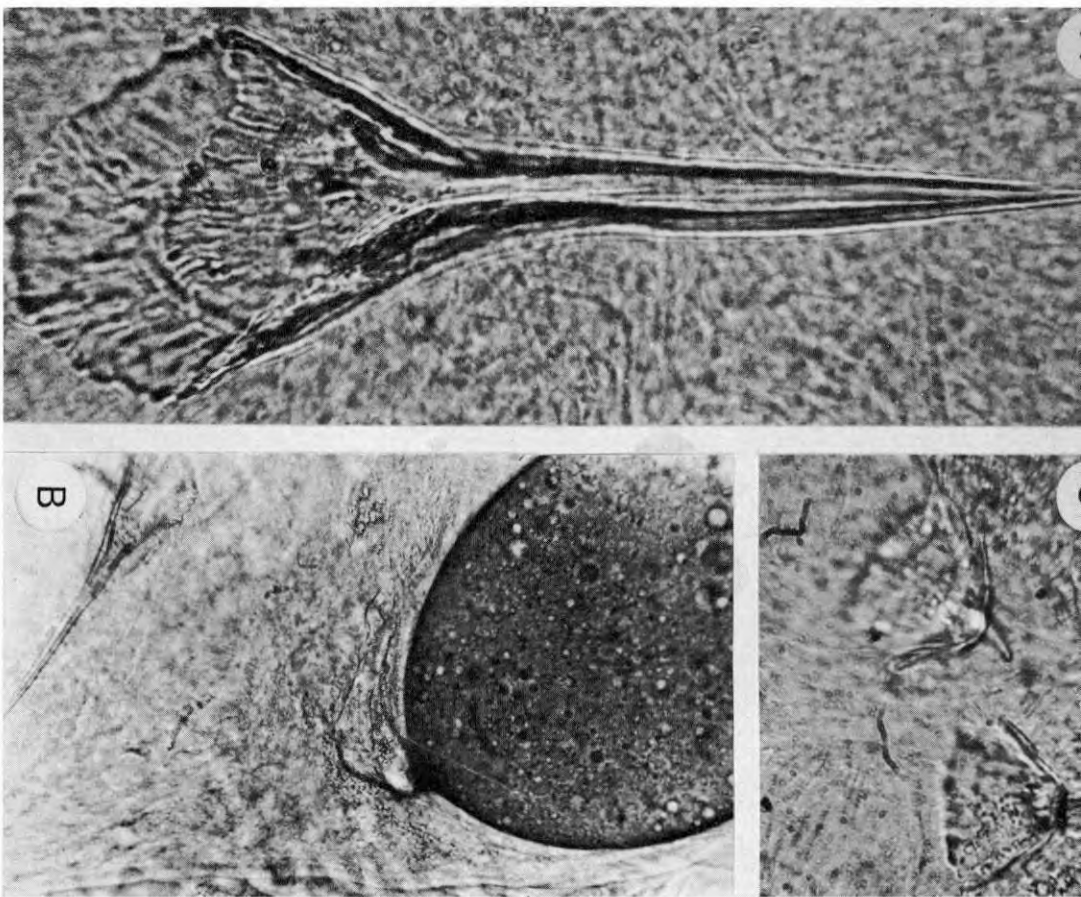


PLATE III. *Psittacophrynechus verweyi* nov. sp.

A. Cuticular stylet (after a specimen from Bergen op Zoom). B. Part of the uterus with egg-cocoon and basal mucus drop (after a specimen from Stellendam). C. Proboscis hooks (after a specimen from Kattendijke).

of the *Spartina townsendii*-vegetation, in detritus-rich fine sand, where *Arenicola marina* (L.) is the most conspicuous animal and the surface is spotted by brownish diatom colonies. The predominant turbellaria in this locality were *Monocelis fusca* Oersted (form with long penis stylet), *Promesostoma marmoratum* (Schultze) and *P. rostratum* Ax. In a small creek in the same area another specimen was found amongst numerous *Pseudograffilla arenicola* Meixner.

Finally 3 specimens of *Psittacorhynchus* were found in the *Zostera noltii*-association on the tidal flat of Kattendijke, in detritus-rich fine sand, in a shallow depression, where during low tide the sand is covered by a thin film of water. The predominant turbellaria in this locality were *Monocelis fusca* (form with long penis stylet) and *Mecynostomum auritum* (Schultze).

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