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CHORDEUMA OBESUM, A NEW PARASITIC COPEPOD ENDOPARASITIC IN *ASTERONYX LOVENI* M. TR.

BY

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THE new Parasitic Copepod I am going to describe[1]) was originally found by Dr. TH. MORTENSEN who kindly called my attention to the parasite he had observed when working on the structure of the Ophiuroid *Asteronyx loveni* M. Tr. In his treatise on the latter, published 1912 (14 p. 283), he mentions this parasite as follows: "Beim Öffnen einiger Exemplare von *Asteronyx* wurde eine andere interessante Beobachtung gemacht. Es zeigte sich, dass in den Geschlechtsorganen eine sehr eigentümliche schmarotzende Copepode lebt. Auf dem ziemlich grossen, 3 mm langen Weibchen wurde das viel kleinere, nur 1,5 mm lange und viel weniger umgebildete Männchen gefunden. Die Geschlechtsorgane werden vom Schmarotzer gänzlich zerstört, aber nur diejenigen, die bewohnt sind. In einem Exemplare habe ich zwar sämtliche Geschlechtsorgane von Schmarotzern erfüllt gefunden, in einem andern Exemplar waren aber nur wenige der Ovarien von Schmarotzern bewohnt, die andern waren normal ausgebildet. Vollständige Kastration wird somit jedenfalls nicht immer vom Schmarotzer veranlasst.

Nur ein ähnlicher Fall von Parasitismus wurde bisher unter den Ophiuren gefunden, und zwar bei der allbekannten *Amphiura squamata.* Zuerst von FEWKES beobachtet, wurde der Schmarotzer später von HÉROUARD genauer beschrieben und *Philichthys amphiurae* genannt. Der Schmarotzer von *Asteronyx* ist von *Philichthys amphiurae* sehr verschieden und wird kaum zu derselben Gattung hingeführt werden können. Auf eine Beschreibung davon werde ich doch nicht eingehen können; sie wird gelegentlich von einem hiesigen Kollegen gegeben werden".

That Dr. MORTENSEN was somewhat mistaken as to the exact seat of the parasite inside the host, I discovered, when I took up the closer investigation of the animal by means of the large material of *Asteronyx* which Dr. MORTENSEN had put into my hands. This material belongs to the collections of that division of our Museum which is under the charge of my colleague G. M. R. LEVINSEN. To both gentlemen I am greatly indebted for the opportunity of examining the rich material of *Asteronyx* collected in the Skagerak partly in 1897, partly 1904, 1906 and 1911. All the specimens of *Asteronyx* were found clinging to *Funiculina quadrangularis*; as Dr. MORTENSEN has pointed out

[1]) An abstract of this paper (13) was read at the Meeting of the British Association at Dundee, Septbr. 1912.

(l. c. p. 265) this Ophiuroid never occurs on *Kophobelemnon stelliferum*; but outside the Skagerrak it has been found on *Halipteris christii*; in fact our Museum possesses two specimens of the latter sea-pen, resp. from Finmarken and from the Faeroes, each carrying an *Asteronyx*.

The Parasitic Copepod in question is apparently a very common parasite in the interior of *Asteronyx loveni*, at any rate in the Skagerrak; with very few exceptions I found it present in every specimen of *Asteronyx* examined. Some hosts only contained a few or about a dozen of the parasite, but some were so immensely infested that their whole interior looked very much like a mass of parasites, and in such cases the gonads of the host seem not to develop [1]). In most cases ripe and unripe specimens of both sexes occur in the same host, and in the strongly infested hosts every gradation as to size and age may be found. It is a true endoparasite, every specimen being enclosed in the tissues of the host inside the body wall of the latter; only quite exceptionally — in two cases — I found the parasite visible externally. It is enclosed in a thin membranous capsule, a kind of "gall" formed by the tissues of the host, and these galls may be found in every part of the tissues lining the bursal pouches: on the outer (bursal) walls of the intestinal tract, among the genital sacs, upon the latter, in the dorsal body-wall; practically in every part of the interior, except inside the gonads and inside the digestive cavity. In the two cases alluded to above, the gall was seated so superficially in the dorsal body-wall that its greater part protruded externally.

The membranous capsule fits tightly round the parasite which generally is distinctly seen through the transparent membrane. Each gall contains a single parasite in all cases, where immature specimens are concerned. Very often also the mature male is found in a gall of its own, whereas galls with a mature female generally also contain its egg-mass, strongly distending the one end of the sac, and in most cases the largest galls, containing a ripe female with its brood, also enclose a ripe male (seldom two males), completely imbedded in the egg-mass, and sometimes empty spermatophores as well.

The eggs do not form "ovisacs" but are only loosely cemented together into one large mass distending that part of the gall which lodges the posterior end of the mother. Not only the embryonic development but almost the whole post-embryonic metamorphosis is performed inside the gall, as will be more fully described below sub II.

I. Description of the developed (imaginal) stages of *Chordeuma obesum* n. g., n. sp.

The adult female (Pl. I, Fig. 2, 3; 10, 13) is 4—5,3 mm in length, sausage-shaped and clumsy — hence the name I propose for the new genus and species:

[1]) In some hosts a parasitic Nematode — resembling a small *Ascaris* — was found together with the Crustacean.

Chordeuma obesum. The body is composed of a head (ce, cephalon), four thoracic segments (th_1—th_4) and an unsegmented abdomen (g, ap) (postabdomen). The head-region carries three pairs of appendages: antennules (a_1), antennæ (a_2) and maxillæ (mx); every trace of mandibles and maxillulæ as well of eyes is wanting. That my explanation of the appendages present is the correct one will be proved by the developmental stages described below sub II.

The antennules (a_1) are situated in front and somewhat ventrally on the rounded head; they are short, clumsy and unsegmented, ovoid with two blunt terminal processes and a smaller ventro-lateral spine nearer the base. On the ventral side of the head, far behind the antennules, immediately in front of the upper lip of the mouth (ul), and close together, are a pair of slender papilliform appendages (a_2), also unsegmented; the development shows that they are the antennæ; and besides there seem to be rudiments of an antennal gland present at the base (if functional appears doubtful, as I have not been able to find an excretory pore). The distal slender, finger-like part of the antenna is clad with delicate adpressed hairs (at all events in unripe specimens). The mouth-opening is protected in front by a small rounded upper lip (ul), and close behind the mouth are the maxillæ (mx), proportionally strong and with their bases almost meeting in the ventral middle line. These are the largest and the only segmented appendages of the whole body, consisting of three segments, the terminal one forming a curved claw. The inner side of the large basal and middle segments, and the front side of the latter and of the claw are provided with similar spines and bristles as in the male (comp. the description of the latter and Fig. 12); the concave ventral side of the claw also carries a single large bristle.

Each of the four thoracic segments (th_1—th_4) has a pair of short, conical, unsegmented feet, (p_1—p_4) looking almost like parapodia and set rather far apart; distally they often are curved like a (weak) claw, and in unripe individuals this terminal part is sparsely beset with short hairs (Pl. II, Fig. 25). The anterior pair are somewhat smaller and weaker than the rest, the posterior generally largest and strongest. Each foot represents the stem and outer branch of the typical Copepod-swimming-foot, as shown by the larva, and by the fact that often — and quite regularly in young immature specimens — a papilliform rudiment of an inner branch (i) may be seen on the second, third or fourth pair (Pl. I, Figs. 3, 6 i and Pl. II, Fig. 25 i).

The two posterior thoracic segments (th_2, th_3) are shorter and narrower than the anterior, from which they are divided by a deep constriction, the latter as it were more joining the head, the former the abdomen. In this constriction fits tightly the membranous wall of the gall; thus two compartments of the capsule are formed, the posterior containing the hinder part of the female and its egg-mass, and in most cases a male.

The anterior part of the abdomen is broad and swollen, intimately joined to the hindmost thoracic segment. The whole abdomen represents three segments, but these are not distinctly marked out. By far the greater part is the genital segment (g); laterally this sends out a large, rounded, terminally somewhat deepened process (l), ventrally it carries the two genital openings (go); the latter are close together, semilunar, almost in contact with their convex sides; in front of them is often, but by no means always found an unpaired rounded prominence or hunch [1]). The posterior part of the genital segment is somewhat tapering; from a deepening in this part the rest of the abdomen (representing two segments) protrudes as a short and narrow appendix (ap), dorsally at its base sending out a blunt process and terminating with two bifurcated claws. There is no anus, and no trace of an intestine is contained in the abdomen.

Young females (Pl. I, Figs. 5, 6, 7) differ in general shape and several details a good deal from the ripe. The smallest females found after metamorphosis are 0,832—0,912 mm in length; probably their form is essentially the same as that possessed immediately after emerging from the larval cuticle; but while I have found a great many young males together with the cast larval skin, I never succeeded in finding with certainty the same case for the young females. The outer shape of the smallest females is very nearly that of the somewhat larger, ca. 1 mm in length, represented on Pl. I Figs. 5—7.

The body is less clumsy than in the mature female, more cylindrical, without constriction between the second and third thoracic segments; the genital segment (g) is less prominent, its lateral processes (l) conical and directed backwards; all appendages are proportionally larger, the thoracic feet on second, third and often also the fourth pair provided with very distinct rudiments of an inner branch (i). The modifications leading to the final shape and maturity are performed simply during growth, without any moultings. I have particularly directed my attention to the question of moulting, but I never saw anything indicating the formation of a new cuticle below the older one, and I am quite sure that after the casting of the larval envelope no further moulting takes place [2]).

[1]) In one case the left side of the genital segment had behind the lateral process l a short, sausage-shaped outgrowth.

[2]) The same, as far as I can see, holds good for *Lernaea*, *Pennella*, *Lernæenicus*, *Sarcotretes* — in short all members of the family *Lernaeidae* —; having reached the copulatory stage (Claus, 9, Tab. III, Figs. 3, 4) neither male nor female undergo any further moultings; but after copulation the body of the fertilized female — especially the genital segment — grows enormously and alters considerably in shape; outgrowths (f. ex. the three "horns" in *Lernaea*) are developed etc., while the appendages — antennæ, swimming feet etc. — generally preserve the form and size of the young copulatory stage. Against the general rule, therefore, part of the chitinous cuticle in these cases must be subjected not only to simple expansion but also in some way or other to "growth".

In the living or fresh animals probably a great deal of the inner structure may be observed directly through the transparent cuticle. In adult females preserved in spirit only part of the genital organs is distinctly seen as a broad stripe of densely packed eggs on each side, reaching almost from the front end of the head to the posterior limit of the third thoracic segment; generally more than the middle third part of the whole breadth of this region of the body is taken up by the egg-stripe. The foremost rounded end of the latter contains the ovary, the rest is part of the oviduct, distended by eggs, still unfertilized and without membrane. Specimens stained and cleared in glycerine, or better in xylol, reveal considerably more of inner structures. Especially if young, unripe females are used, a fairly complete view of the inner organisation may be obtained. For sake of control and for further examination microtome-sections, after imbedding with parafin, have been made. The cuticle, thick and leathery as it seems to be, is no real obstacle; the tissues are easily stained, imbibition with parafin and the cutting into sections are performed without difficulty; in many cases complete series of very thin sections have been obtained. In the same way males and larval stages have been studied.

Genital organs. (Pl. I, Figs. 8, 9). There are two ovaries (ov), situated in the head. Each is a lenticular body sending out from its medial margin a short and narrow transverse branch to connect with the corresponding branch from the opposite side, thus forming a bridge dorsally across the stomach (if the branches really are completely fused at their meeting point or a dividing membrane is left here, I have not made out with certainty). The anterior and medial margins with the bridge contain small genital cells; the remaining part of the ovary is taken up by considerably larger egg-cells. From the lateral and posterior part passes out the oviduct (od), the greater part of which runs straight to the third thoracic segment and is laterally somewhat compressed; distended with eggs, as in ripe females, its transverse section is ovoid; when empty, as in unripe females, the shape is more rounded. The epithelium of this part is almost cubic. In the ripe females the eggs contained in the oviduct increase in size from before backwards; near the ovary they are only somewhat larger than those of the ovary; from here and through the head they may be arranged in two strata, in the thorax according to their size they are arranged in a single stratum, but in several rows and so densely crammed that their shape is more or less angular. In the third thoracic segment the oviduct suddenly narrows for immediately again to expand into a sausage-shaped terminal part, the epithelium of which is high and secreting. In the interior of this part I never found any eggs but more or less of a secretion, staining deeply with hæmatoxyline, carmine (hæmalum) etc.; the piling up of eggs always ceases at the constriction. Probably the eggs on being laid pass rapidly through the terminal part, the epithelium of the latter yielding

the matter by which the eggs after extrusion loosely cohere, and corresponding to the substance secreted in other Copepoda by the same part of the oviduct and generally forming the "ovisacs".

The distal end of the oviduct suddenly narrows into a very small pore opening in the short vagina (Fig. 8, vg); the latter has a chitinous lining continuous with the outer genital slit. Like this the vagina in transverse section is crescent-shaped, the lateral wall or outer lip being strongly thickened, completely filling out the concavity of the half-moon (Fig. 10); a strong muscle, serving as dilatator (dil, Fig. 10), is inserted in the outer lip. Just at the same spot where the oviduct opens in the vagina, debouches also a narrow and short duct from a large, unpaired receptaculum seminis (Fig. 8, rs). The latter is rounded or pear-shaped, with one pole imbedded between the distal ends of the oviducts, the other projecting backwards into the genital segment; its front end and the distal ends of the oviducts are surrounded by a mass of large unicellular glands. In females with eggs in the oviduct the receptacle and its ducts always have been found filled with sperma; in young, unripe, females with empty oviducts no sperma have been found, only a secretion, which seems not capable of staining (produced by the unicellular glands?).

Thus in the Parasitic Copepod before us the following features may be pointed out as unusual: 1) an unpaired receptaculum seminis with paired outlets, one to each opening of the oviduct in the vagina; 2) absence of separate copulatory pores.

Separate copulatory pores (or a single pore) are generally supposed to be typical in Parasitic Copepoda, although their existence in many cases has not been proved (GIESBRECHT 10, p. 190—191 throws some doubt upon their occurrence in certain *Asterocheridae*).

In *Chordeuma* the same slits, through which the eggs are laid, undoubtedly also serve for copulation. I have examined the region in question very carefully, and besides I have seen in some specimens spermatophores fastened into the genital (or vaginal) slits (comp. Pl. I fig. 13 spf).

Alimentary canal. (Pl. I Fig. 8). Behind the rounded upper lip (ul) the narrow mouth-opening leads into a short, slit-like pharynx, lined with a continuation of the outer cuticle. Muscles pass obliquely behind the root of the upper lip and are inserted into the roof of the pharynx; a little further back other muscles are inserted in its floor, taking their origin laterally and from behind; both sets act as dilatators, antagonistically counteracted by the elasticity of the chitinous lining of the pharynx; thus a sucking process may be brought about. The pharynx is continued into a short and slender, cylindrical oesophagus (oe), passing through the central nervous system (nv) and opening in the ventral side of the stomach (in). The epithelial wall of the oesophagus consists of comparatively high cells, arranged in a single layer round

an extremely narrow space. The stomach (in) is a capacious, pear-shaped sac, tapering backward and ending blindly in the last thoracic segment; it has a single layer of rather flat epithelial cells. It always contains an ovoid body, concentrically composed of layers, probably indigestible matters deposited as a kind of "stone", as there is no practicable way to get rid of any faeces. In some cases this "stone" may be large enough to be seen with the naked eye.

Nervous System. (Fig. 8). The brain (cb) is situated dorsally to the antennæ, close in front of the oesophagus; it is rounded and provided with a coating of ganglionic cells; a short, rather broad commissure on each side of the oesophagus connects with the ventral nerve-mass (nv.); the structure of the latter is the same as that of the brain; it lies dorsally to the maxillæ and tapers into a thread coated with nerve-cells and reaching at least through the first and second thoracic segments. From each side of the brain a long nerve is seen going to the antennules; from the broad anterior part of the ventral mass other nerves are going to the maxillæ, but the greater part of the peripheral nerves I have not been able to make out.

Muscles. (Fig. 8). The muscles of the body form quite narrow ribbons, isolated from each other by considerable interspaces. The longitudinal muscles are made up of four dorsal and two ventral ribbons. The former — one pair of dorsal (md), and one of latero-dorsal (mdl) muscles — take their origin from the inner concave surface of the head in the region of the ovary and stop at the last thoracic segment, being divided for each segment by an insertion in its front margin. The latero-dorsal pair are a little stronger than the dorsal. The ventral pair (mv) take their origin inside the head near the middle of the base of the maxillæ; from here they diverge feebly in the head and first thoracic segment, are almost parallel in the second and converge evenly through the third and fourth, almost meeting at the same point of insertion in the front margin of the genital segment. Thus the abdomen has no longitudinal muscles of its own but is acted upon by means of those of the trunk, the flexors acting directly, the extensors indirectly.

There are several pairs of transverse and oblique muscles originating dorsally or dorso-laterally in the head and thorax and inserted at the base of the appendages; some of them seem to be fastened rather to the body-wall near the limbs than directly into the latter, and it is not quite clear to me, how they may act on the appendages. Most of these muscles belong to the head and first thoracic segment, and here they run obliquely in different directions (cf. Fig. 8), some of them more superficially than others and therefore more easily seen. In each of the three last thoracic segments only one pair of strictly transverse muscles is found, running deeply on each side, between the stomach and the oviduct.

In the abdomen a set of deep strong muscles is observed, the paired nature of

which is obscured by the close opposition of its members; this apparently unpaired muscle runs in the middle line obliquely from the ventral base of the caudal appendix, over the receptaculum seminis, between the distal ends of the oviducts to the front margin of the genital segment, where it is inserted at the posterior ends of the longitudinal ventral muscles. Very feeble muscular strands, traversing the posterior part of the genital segment, and inserted at the dorsal base of the appendix, seem to act antagonistically to the great oblique muscle. On the ventral side of the genital segment the fanshaped dilatator for the vulva, mentioned above, originates laterally in the body-wall and is inserted in the thickened outer lip of the vaginal slit.

All the appendages are provided with intrinsic muscles; those of the antennæ and thoracic limbs are feeble, those of the antennules stronger, and those of the maxillæ very strong.

The whole muscular equipment apparently allows a certain amount of mobility which hardly would be expected in an animal like this, confined inside a tightly fitting capsule.

The adult male (Pl. I, Fig. 1, 4, 11, 12) is considerably smaller than the ripe female, reaching at most a length of 2 mm. At first sight it seems very unlike the female, slender, almost cylindrical, curved, and resembling an insect-maggot, but closer inspection reveals fundamentally the same structure. The head takes up between the third and fourth part of the total length; a carapace is distinctly marked off, and trace of a rostrum may be seen between the antennules; the four thoracic segments are very evident, the posterior one somewhat shorter than the three anterior; taken together they make up the greater part, more than half the total length. The body tapers evenly towards the abdomen. The latter is short, unsegmented (but also here representing three segments, as shown by the larva). The part representing the genital segment also in the male is by far the greatest and sends out on each side a large outgrowth (l), conical, firmly chitinized and directed backwards, reaching (almost) as far as the end of the tail; it corresponds to the clumsy lateral outgrowth in the ripe females, and resembles — to a certain degree — that of the youngest unripe females, as upon the whole the general likeness with the latter is more conspicuous. Ventrally the genital segment carries genital openings (Fig. 11, go); they form large crescent-shaped slits, arched over by the lateral opercular lips into which a special levator muscle (Fig. 4 dil) is inserted. Towards the medial margin of the opercle short rows of small hairs are found, at the posterior corner generally a larger spine or bristle (largest in young individuals). The posterior end of the tail (ap), corresponding to the "appendix" of the female, and representing two segments, forms a short narrow part, terminating in two bifurcated claws; the outer one of each of these is generally somewhat larger, the inner one provided ventrally with small hairs or bristles. In

some cases I have found only one simple claw on each side, probably the inner one not having been developed.

The same appendages as in the female are present, and likewise the mandibles, maxillulæ and eyes absent. The antennules (a_1) are proportionally larger, somewhat less clumsy than in the female, their terminal processes a little longer, generally curved upwards and basally provided with a small spine; the lower and outer is a little larger than the upper and inner one; a similar spine to that found in the female is present on the middle of the ventral aspect of the antennule. The antennæ (a_2) are like those of the female; the maxillæ (mx) are both proportionally and absolutely larger than in the female. The basal joint (Fig. 12, 1) carries on the inner side two patches of small spines and a group of similar spines arranged more sparsely around a central larger one; the second joint (2) has short, oblique, arched groups of spinelets on the inner side, on the outer side scattered bristles, pointing towards the terminal claw; the latter (3) is on the concave side provided with a large bristle and on the convex side with a few smaller ones.

The thoracic feet (Fig. 1, p_1—p_4) are unsegmented, slender, almost threadlike, and pointed; they may all be simple, but often a rudiment of the inner branch (i) is present on the members of second, third or fourth pair in the shape of a slender papilla; it is always found in young specimens, largest shortly after their emerging from the larval cuticle (Pl. II, Fig. 26, i); at that age it is present also on the first pair of limbs. Hairs seem never to develop on the terminal part of the feet in the male.

The smallest males found (Pl. II, Fig. 26) measure 0,36—0,48 mm, that is about half the length of that of the smallest females observed. In the case of these small males I am able to state with certainty that they quite recently have undergone metamorphosis: all of them have been found together with the cast larval skin, in many cases with the tip of the tail still enclosed inside the latter. As they, however, are much larger than the ruptured cuticle — generally more than twice its size — they must have grown considerably after emerging from it. In no case has any other cuticle than that of the larva been found together with these males, and no more than in the female have later stages shown any signs of further moultings. The newly hatched males differ in several respects from their final shape: the body is hardly curved, the head proportionally larger, the tail with two simple claws; the appendages are proportionally larger, and all the thoracic limbs with distinctly developed inner branch; furthermore in the antennules the lower and outer terminal process is almost as long as the remaining part; as far as I have seen, it represents the greater part of the long antennule in the larva, while only the first or the two first basal joints of the latter are transformed into the clumsy antennule of the adult.

The inner organisation of the male (Fig. 4) is much the same as that of the female. Regarding the genital organs we find two ovoid testes (te) in the head, connected, as is the case with the ovary, by means of a narrow transverse bridge. The spermaduct (vd) corresponds in shape and course to the oviduct; near the testis it is a little narrowed but widens soon, keeping the same width to the third thoracic segment; here it suddenly narrows for again to expand into a sausage-shaped terminal part, opening with a pore into a space corresponding to the female vagina, lined with cuticle and covered by the genital opercle.

The peripheral part of the testis contains genital cells, the central part spermatozoa. The epithelium of the spermaduct is made up of columnar cells with large nuclei, leaving a narrow lumen; in the terminal part the cavity is wider. In each duct a spermatophore is formed, consisting of a long thread-like neck, reaching from the testis till past the constriction, and a sausage-shaped expansion or "receiver", almost filling the terminal part. Thus, during copulation, two spermatophores are discharged at the same time; as already mentioned they may be found adhering to the genital slits of the female.

The stomach (in) seems more elliptical, the front end as well as the posterior being narrower than in the female; otherwise the alimentary canal agrees in both sexes, also as regards the presence of a "stone". The nervous and the muscular systems are also alike; only the muscles are stronger and therefore more easily seen. In the abdomen, however, the median transverse muscles differ considerably: they are fanshaped, originating widely spread dorsally but inserted as in the female at the junction of the ventral longitudinal muscles. The paired nature is clearly shown only by the proximal bundle, and only at their origin.

The stronger development of the muscular system in the male and the more strongly marked segmentation of its body suggest a greater agility than in the case of the female; probably it has to leave its own capsule and work its way into that of the female, with which it wants to copulate and afterwards to stay.

How far the living *Chordeuma obesum* possesses any colour, I am unable to tell, as I have only seen specimens preserved for years in spirit. At all events no dark pigment is found, and the preserved specimens are colourless. As the eggs sometimes show traces of pink colour, I think they may be more intensely red in the fresh state and may give a certain amount of colour to the transparent body of the female.

II. The development.

The eggs of the egg-mass contained in the gall are spherical and provided with a thin shell. Before cleavage their diameter is 0,160—0,184 mm, when containing an

embryo somewhat larger, 0,192—0,208 mm. In the same gall may be found newly laid eggs, eggs in cleavage (the cleavage is total and — at any rate at commencement — equal) and eggs with embryos in different stages of metamorphosis up to the Cyclopid, described below. The egg-mass, therefore, probably must be formed of eggs fertilized and extruded at intervals. Quite generally eggs and free Nauplii will be found together, whereas I only in single cases have besides found the later stages; that these cases, however, are quite normal, I do not doubt, and I take it for granted, that the regular methamorphosis is intracapsular and always will show the series a—e described below.

a. The Nauplius (Pl. II, Fig. 14) is ovoid, 0,20—0,21 mm in length, 0,13—0,14 mm in breadth, with the typical three pairs of appendages and two furcal setæ (c), but without eyes. The absence of eyes characterizes as well all the following stages.

The antennules (a_1) are three-jointed, the basal joint short, the terminal one long (the segmentation is, however, very feebly pronounced, and the number of joints rather difficult to settle). Terminally the antennulæ have three setæ, one short, two longer and stronger; the middle joint has, ventrally, one long seta, the basal joint one, somewhat shorter and feebler. The antennæ (a_2) possess two indistinctly jointed branches; the shaft is probably composed of two joints (without "masticatory process"); the outer branch is the longer and stronger and seems to be many-jointed; distally it carries five strong setæ (each probably marking a joint); the inner branch seems two- or three-jointed, has terminally three setæ, one short and two long and strong ones. The mandibles (md) have almost the same structure, only the outer branch has (generally) but four setæ. There are no plumules on the setæ nor on the caudal setæ.

Through the arched dorsal body-wall the large brain is distinctly seen, as are the strong muscles going to the appendages. On the ventral side — or better in profile — is seen a prominent hunch on which — later — the mouth-opening is found.

Inside the nauplial cuticle the differentiation of several organs takes place. From the ectoderm the ventral nervous system originates together with the rudiments of four postoral pairs of limbs. The cuticle is cast, and b) the first Metanauplius-stage (Fig. 15) ensues. It resembles the Nauplius, only the body is a little more lengthened; the size is about the same, ca. 0,208—0,224 mm in length, 0,136 mm in breadth; but in addition to the three pairs of appendages one pair of free limbs has heen added: the maxillulæ (mx^1); the remaining limb-rudiments are still only cell-groups, condensed along the ventral side, below the new cuticle and behind the prominent mouth. The nauplial appendages are as before, only the antennules are directed more forwards, the antennæ and mandibles somewhat ventrally curved.

The dorsal part of the body is more transparent, only one or a few large drops of oil being present in the embryonic entoderm, while the Nauplius-stage had many small and dispersed drops. The maxillulæ consist each of a large seta terminating a

very small cylindrical prominence. In all the specimens seen the body inside the cuticle had contracted and left a space in which always some characteristic small, drop-like, deeply stained bodies were found; in moulting they are left in the cast cuticle.

The next stage c) is a second Metanauplius, ca. 0,23—0,24 mm in length (Fig. 16—17); the appendages of the former stage are preserved, and in addition maxillæ (mx), two anterior pairs of swimming feet (p_1, p_2) and a rudiment of the posterior (p_3) have appeared. The maxillulæ are as in the first Metanauplius, only the "shaft" a little larger and — as seen in sections — provided with extremely feeble muscles. The maxillæ are large, directed backwards, as are the swimming feet. The first and second pair of the latter show distinctly a basal part and two clumsy branches, the outer considerably larger than the inner and provided with a few short bristles. The third and fourth pairs are simple conical rudiments. The swimming feet are set wider apart from each other than the maxillæ, and the thoracic segments, especially the anterior are distinguishable. The central nervous system forms a dark mass easily seen in profile against the transparent back; in sections the composing ganglionic elements are quite distinct. Muscles to the fully developed appendages as well as rudiments of the longitudinal body-muscles and of those of the developing limbs are observable. The body is somewhat pear-shaped, the back arched, the ventral side more flat but with a prominent mouthpart, now carrying an opening. In sections the rudiment of an oesophagus is seen, passing between the brain and the foremost ventral ganglia and abutting on the embryonic entoderm, not yet forming a hollow stomach. An antennal gland is distinct, also a shell-gland (maxillary-gland). Thus, both these glands here are found together, while generally in Copepoda the antennal gland is said to occur in the larva, and the shell-gland to appear later.

The next moulting produces d) a third Metanauplius (Fig. 18—19). The size has not altered much, the length being ca. 0,248—0,280 mm, and the shape of the body is almost the same, only the mouth is less prominent, and the segmentation more distinctly marked, corresponding to the greater development of the thoracic limbs. Most interesting are the appendages. The outer ramus of the antennæ (a_2) at first sight seems lost; closer examination shows, that on its place is an empty cuticular case, without any setæ, while the inner ramus has the same shape as in former stages. The mandibles (md) are still more reduced: both rami and almost the whole shaft form empty and naked sheaths, only at the very base of the shaft enclosing a minute papilla of tissue. The maxillulæ — from the first appearance rather rudimentary — are now completely lost. The maxillæ (mx), on the other hand, are further developed, large and removed from the swimming feet, and directed forwards; they have now distinctly three segments, the terminal one rounded and carrying a hooked spine.

The three anterior pairs of swimming feet are bifurcate, the outer ramus with short bristles; the fourth pair is still undivided and small. The ventral crest joining the members of each pair of swimming feet in the Copepoda is already distinctly seen. Antennal-and shell-glands are present as before, the latter now the greater.

e). The following, fifth, stage (Figs. 20, 21), is 0,288—0,312 mm in length; it is to be called a Cyclopid (or Copepodid), as the shape now resembles that of a *Cyclops* in so far, as the abdomen is fully developed, consisting of three distinct segments, and all the swimming feet are biramous, although those of the last pair still are smaller. The antennules (a_1) often are held laterally outstretched, the antennæ (a_2) pointing forwards. The latter now are slender, unbranched, the last trace of the outer branch having fully disappeared; they are indistinctly three-jointed, the last joint with two terminal setæ. The mandibles are completely lost. The maxillæ are strong, three-segmented, with claw-shaped terminal joint. The anterior three pairs of swimming feet have the outer ramus longer and narrower than in the preceding stage, and the setæ better developed; also the inner branch has grown but is much smaller than the outer, and its setæ are quite small. Fourth pair is short and clumsy, directed backwards and upwards, the rami broad and rounded, the setæ very small. The segmentation of the body and the short tail is distinct; the telson of the latter is flat, and carries in most specimens the two caudal setæ found in all the preceding stages; in some of the oldest specimens two additional small setæ may be seen. The intestine is filled with a large oil-drop, and ends blindly in the thorax without reaching the abdomen. The ventral nervous system now does not show any distinct ganglia; it is condensed into a mass, broad behind the mouth, pointed backwards between the first pair of thoracic feet. Antennal-and shell-gland are as in the preceding stage.

The cyclopid stage is the last stage of metamorphosis which I have found enclosed in the maternal gall; in some specimens, however, I have seen inside the cuticle of its antennules a new antennule resembling very much that of the larval stage, found outside the gall; it seems therefore pretty certain, that the Cyclopid will change into the sixth stage, f) the Cyclops-larva (Figs. 22—24). This stage has been found either attached to the walls of the bursal pouches in *Asteronyx* or loosely imbedded in the connective tissue of these walls. Probably the moulting, which produces this larva, takes place inside the maternal gall; soon after emerging the larvæ then leave the gall — in which way I am not able to state; there is no regular previously formed opening on the capsule, fit for escaping, and no structure in the larva seems specially adapted for boring through any tissues. Once escaped from the gall the larvæ probably either settle again in the same host, in which they were raised, or they make their way out, seeking to infest other individuals of *Asteronyx*. In the first case they add to the stock of parasites already present; thus we easily might explain, why some

hosts are provided with an enormous number of this parasite, and why these are to be found of very different age and size. In the latter case the larvæ might most easily make their way out through the bursal slits, and in spite of their lack of eyes they may find without great difficulty new *Asteronyx*, as these animals cling to the often densely congregated sea-pens. The way leading to the interior of the new hosts, I think again would be the bursal slits. In both cases the larva is supposed to attach itself by means of its hooked maxillæ, either among the genital sacs of the host, or on that face of its intestinal wall, which looks towards the bursal pouch, or on the inner dorsal body-wall, and the stimulation due to this fixation may cause the tissues to produce a gall. Quite exceptionally the larva may fix itself on the outer surface of an *Asteronyx*; this is shown by the few cases of external galls mentioned before. That the larvæ should be able to make their way to the interior of the host by active working through its body wall (f. ex. through the dorsal wall, the inside of which is often studded with parasites), seems to me most improbable. How far the course of things here set forth will prove to be the right one, I hope will be tested some day by others, who may have the luck of investigating the living animals in their mutual relations.

The Cyclops-larva (Fig. 22—23) has a length of 0,304—0,320 mm from the front to the end of the telson (of this the tail takes up only ca. 0,072 mm; the furcal setæ have about the length of the tail). The general shape is that of a *Cyclops*; the trunk is ovoid, somewhat compressed laterally; the short and slender abdomen is often directed obliquely upwards. The head has a carapace distinctly marked off, with a short, rounded rostrum, curved down between the antennules; the thoracic segments, especially the three last ones, are sharply defined; the belly is arched; hence the body, seen in profile, is rather high. The antennules are strong and — as far as I have made out — composed of seven joints, the outermost one long and transversely cut at the end; each joint is provided on its front side with a seta, some of the basal joints with two setæ; the terminal joints have besides setæ on their back; the ultimate, penultimate and the fourth (from the tip) carry each a large "aesthetasc" (ae) [1]).

The antennæ (a_2) are short, slender, three-jointed (the outer branch of course is absent); the last joint with two terminal setæ. Mandibles, maxillulæ and eyes are absent. The maxillæ (mx) are very strong, composed of three segments, the terminal a hooked claw. Each of the four thoracic swimming feet (Fig. 24) has a well developed basal stem (b) and two rami (y and i) of unequal length; as usual in Copepoda

[1]) It may be possible that all the larvæ, I have found, are male individuals, although I have found and examined a good many specimens. When I have not been able to make a full statement regarding the number of joints in the antennules, their number of setæ and the arrangement and length of the latter, the reason is that the segmentation is very feebly pronounced, and that particles of the tissues of the host, obscuring the structures, could not be cleared completely away.

the stems of the members of the same pair are connected by a transverse crest, projecting from the ventral side of the segment in question. The rami are flat, oblong, each made up of one segment; the outer ramus (y) is considerably larger than the inner (i) and on the distal part of its inner arched margin beset with four long and stiff bristles (in a single case I found five on the third pair); at the end of the straight or feebly concave outer margin a fifth short bristle is present. The short and narrow inner ramus (i) is terminally provided with three bristles, of which two belong to the inner, one to the outer margin. The bristles have no plumules, while plumules are present on the two pairs of furcal setæ, of which the inner ones are the longest. There are no furcal appendages, the setæ originating directly from the posterior margin of the telson.

As the tissues of these larvæ were rather badly preserved, I have not been able to make out inner structural details of any amount, in spite of my transverse and longitudinal sections being quite successful. Distinctly discernible are: the narrow oesophagus leading into the wide intestine (mid-gut), closed behind in the thorax, about at the level of the third pair of swimming feet; and the central nervous system, consisting of the large brain and the ventral ganglionic mass, narrowing towards the first pair of thoracic feet; further back I have not been able to trace it. The presence of antennal or shell-glands as well as of rudiments of genital organs I cannot state with certainty.

The Cyclops-larva moults and changes into the seventh stage, the parasitic form described sub I. This is sufficiently proved in the case of the male by the fact, already stated, that quite a number of extremely small males — like that represented Pl. II, Fig. 26 — have been found together with the ruptured cuticle of the Cyclops-larva, in some cases with the tail still lodged inside the latter; and in a single case a very small female was found near an empty larval cuticle. In all cases observed the formation of a gall was indicated as a condensing of the connective tissue surrounding the young parasite and the cast larval cuticle. After the moulting through which the parasitic form ensues, no further moultings take place, but the Copepod and its gall continue for a while to grow considerably; during the growth the parasite undergoes some slighter modifications in shape of body and appendages, as shown above sub I, and develops its inner structures; finally it attains full size and sexual maturity.

Concluding remarks.

In spite of the fact that I have had at my disposal only specimens of *Asteronyx* collected for other purposes and preserved for years in spirit, I have been successful enough to find out every step — so I venture to think at least — of the meta-

morphosis and the later development of its parasite. Very few indeed — if any at all — of the Parasitic Copepods have been followed up more completely. I therefore feel somewhat abashed in being unable to settle the systematic position of the new genus. I have tried in vain, by going through the vast and dispersed literature concerning Parasitic Copepods, to find any close allies to the *Chordeuma*. None of the established families seem to me fit for its reception; evidently therefore it represents a new family. The obvious idea, that some of the Parasitic Copepods known to infest Echinoderms might be related to the genus in question, I soon abandoned. The ectoparasitic *Asterocheridae* (10) seem widely different; the *Pionodesmotes phormosomae* Bonnier (1, 15), producing galls inside the shell of *Phormosoma uranus* W. Th., and by its author regarded as the type of a family of its own, does not show any near affinity, and the same is the case with the "*Philichthys amphiurae*" Hérouard (12), hitherto the only Parasitic Copepod found endoparasitic in any Ophiuroid. Neither seems the structure of *Chordeuma* to allow an admission into the extremely varied family *Ascidicolidae* (2, 3, 4, 5—8), of which at least one member infests an Echinoderm, the *Enterognathus comatulae* Giesbr., living in the intestine of *Antedon rosaceus* (11). Although some of the most degraded members of this family (f. ex. *Enterocola*, *Enteropsis*, *Aplostoma*, *Ophioseides*, *Mychophilus*) may — the one or the other — show certain features analogous to those found in *Chordeuma* f. ex. reduction of antennules, reduction or loss of the outer branch of the antenna, of the mandibles or maxillulæ, reduction of the thoracic feet, which may become uniramous, of the abdomen etc., most of these features only occur in the more or less sessile female, while the male is adapted to lead a more or less free life; and all the resemblances are certainly superficial, only due to convergence, while the fundamental structure as well as the development are very different.

The fundamental conformity of both sexes in *Chordeuma*, of the body as well as the appendages — the latter all being uniramous and, except the maxillæ, unsegmented —, the absence in both sexes of every trace of buccal appendages (mandibles, maxillulæ), the blindly closed intestinal tract, without any abdominal part, the absence of eyes in every stage of development, the absence of furcal appendages, and of segmentation of the rami of the swimming feet in the Cyclops-larva etc. are features which, as far as I know, do not occur combined in any other Parasitic Copepod.

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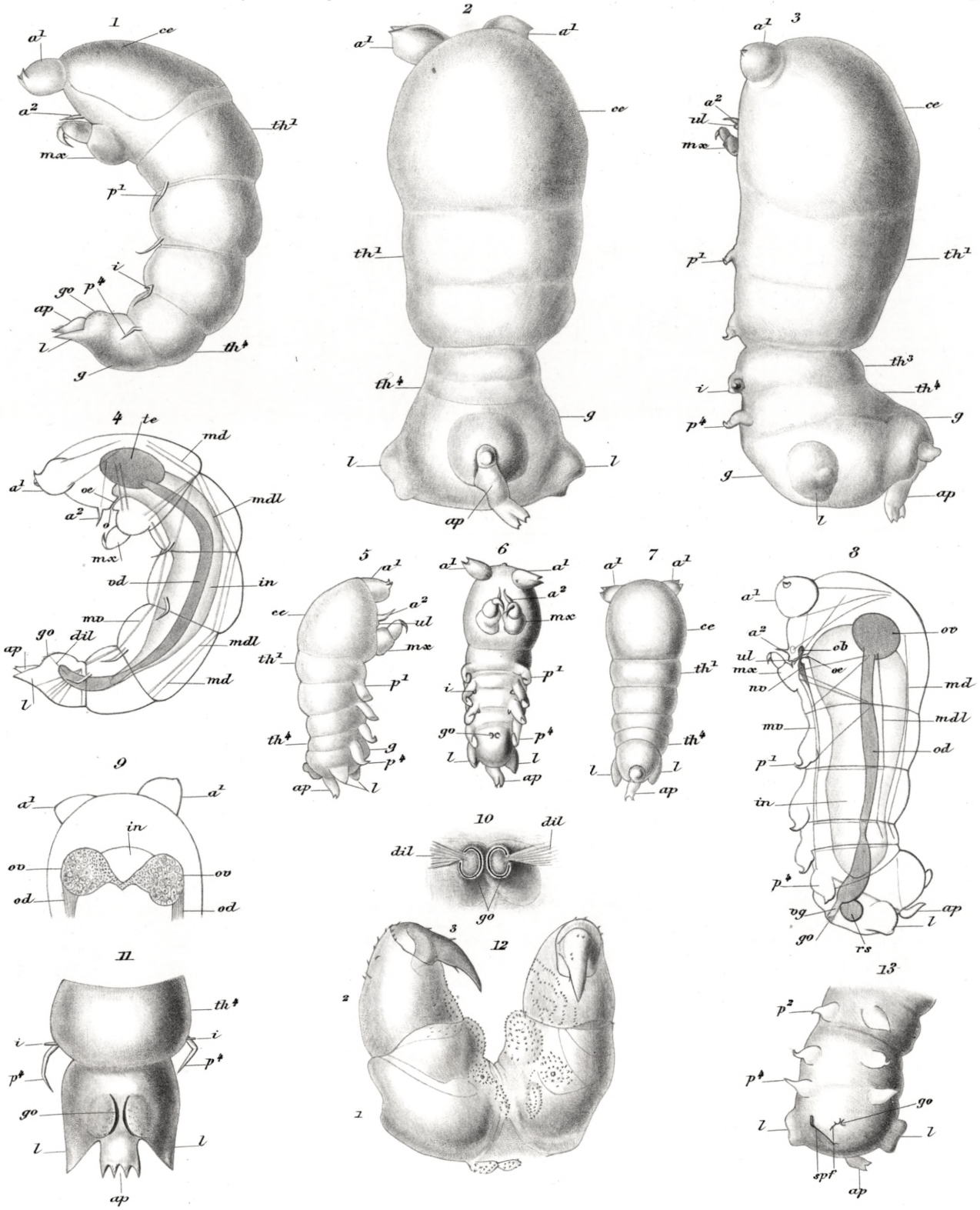
EXPLANATION OF THE PLATES

Reference letters.

a_1 = antennule.
a_2 = antenna.
ae (Pl. II) = aesthetasc.
ap = posterior part of abdomen.
b (Pl. II) = basal segment of thoracic feet.
c (Pl. II) = furcal setæ.
ce = head (cephalon).
dil = dilatator muscle.
g = genital segment.
go = genital opening.
i = inner ramus of thoracic feet.
in = intestine (mid-gut).
l = lateral outgrowth from genital segment.
md (Pl. II) = mandible.
md (Pl. I) = longitudinal dorsal muscle.
mdl = longit. dorso-lateral muscle.
mv = longit. ventral muscle.
mx = maxilla.
mx_1 = maxillula.
nv = ventral ganglionic mass.
o = month-opening.
od = oviduct.
oe = oesophagus.
ov = ovary.
p_1—p_4 = thoracic feet.
rs = receptaculum seminis.
spf = spermatophore.
te = testis.
th_1—th_4 = thoracic segments.
ul = upper lip.
vd = vas deferens.
vg = vagina.
y = outer ramus of thoracic feet.

Plate I.

Fig. 1. *Chordeuma obesum* n. g., n. sp., adult male. Zeiss Comp. Oc. 4, Apochr. 16.
— 2. Adult female, dorsal view. Zeiss Oc. 1, Obj. A A.
— 3. The same, from left side. Zeiss Oc. 1, Obj. A A.
— 4. Adult male, from left side. × as Fig. 1.
— 5—7. Young, unripe female, from right, ventral and dorsal side. Z. Oc. 1, Obj. A A.
— 8. Female, not fully ripe, from left side. × as Figs. 2—3, 5—7.
— 9. Female, not ripe, front part of head; dorsal view. × as Fig. 8.
— 10. Female, region of genital openings (the figure is somewhat misleading, in so far as the muscles, dil, and the deeper parts naturally ought to be represented as seen through the cuticle). × Zeiss Comp. Oc. 6, Apochr. 8.
— 11. Adult male, posterior part from ventral side. × Zeiss Comp. Oc. 6, Apochr. 16.
— 12. Adult male, maxillæ, ventral aspect. 1 : basal, 2 : middle, 3 : terminal joint. Zeiss Comp. Oc. 6, Apochr. 8.
— 13. Adult female, posterior part, ventral view. A. spermatophore, spf, is fastened into the vulvar slit, but its neck is broken. Zeiss Comp. Oc. 1, Apochr. 16.



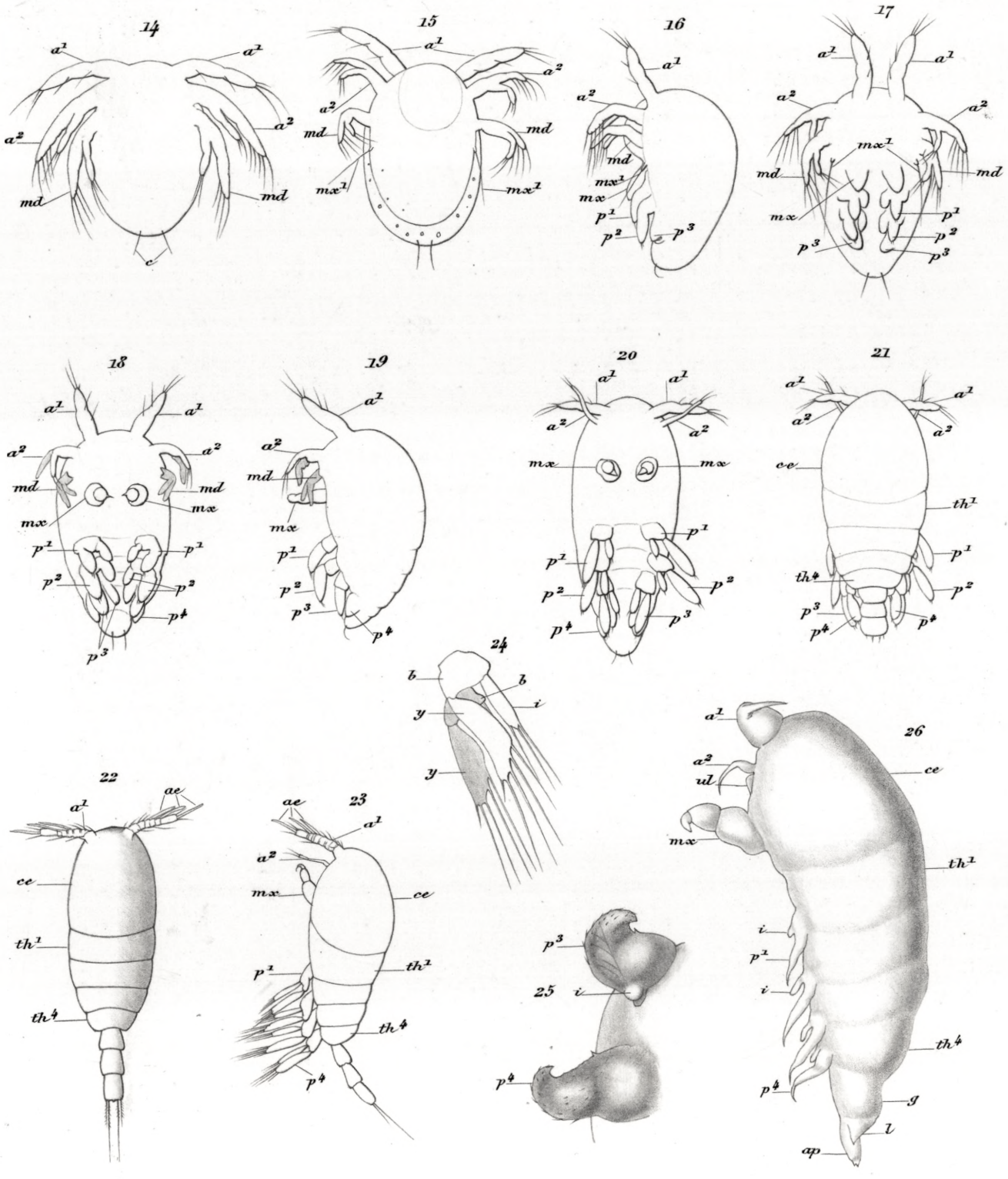
Autor del.

Chordeuma obesum n. g., n. sp.

T.N. Möller sc.

Plate II.

Fig. 14. Nauplius, dorsal view. Zeiss Comp. Oc. 6, Apochr. 8.
— 15. First Metanauplius, ventral view. × as Fig. 14.
— 16—17. Second Metanauplius, left side and ventral view. × as Figs. 14–15.
— 18—19. Third Metanauplius, ventral and left side view. × as Figs. 14—17.
— 20—21. Cyclopid (Copepodid) stage, fifth step, ventral and dorsal view (two different specimens). × as Figs. 14—19.
— 22—23. Cyclops-larva (sixth stage), dorsal and left side view. × as Figs. 14—21.
— 24. Cyclops larva, swimming feet of third and fourth pairs, ventral aspect. Zeiss. Comp. Oc. 12, Apochr. 8.
— 25. Unripe female, right thoracic feet of third and fourth pairs. Z. Comp. Oc. 6, Apochr. 8.
— 26. Young male, newly escaped from the cast cuticle of the Cyclops-larva. Zeiss Comp. Oc. 6. Apochr. 8.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Chordeuma obesum n.g., n.sp.