

**Contributions to the knowledge of the genus *Microcerberus*
Karaman (*Crustacea Isopoda*) with a description of a
new species from the central Californian coast**

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With 5 figures in the text and 3 plates

In connection with an invitation from the Kaiser Foundation Research Institute, Oakland, I was given the opportunity to carry out some studies on the microfauna at the Pacific Marine Station, Dillon Beach, and at Hopkins Marine Station, Pacific Grove. The present paper is one of the results of these studies.

To the Kaiser Foundation Research Institute I wish to express my sincere gratitude for travelling expenses and to Statens Naturvetenskapliga Forskningsråd, Stockholm, for financial grants. I am also greatly indebted to my fellow-traveller and colleague Dr. Tor G. Karling, of Stockholm, to the director of the Pacific Marine Station, Dr. Joel Hedgpeth, and to Dr. Donald P. Abbott, of the Hopkins Marine Station.

Some notes on the morphology of *Microcerberus*

The mouth parts

In his description of *Microcerberus mexicanus* n. sp. Pennak (1958, p. 299) says *inter alia* (the italics are mine): "*Mandibles, first maxillae, second maxillae, and maxillipeds are . . . typical in structure.*" What is the meaning of this? Because of the difficulty of dissecting out the mouth parts they are described only in some few species and the different authors have figured, described, and interpreted them in quite different manners. In addition to this all the descriptions and interpretations are incorrect.

When Pennak wrote his paper 15 species had already been described. The mouth parts (or some of them) mentioned by him were examined, however, only in the species *stygius* Karaman (1940), *delamarei* Remane and Siewing (1953), *remyi* Chappuis (1953), *remanei* Chappuis and Delamare (1954), *predatoris* Gnanamuthu¹ (1954), *adriaticus* Karaman (1955), and *pauliani* Chappuis and Delamare (1956*a*). In the same year as Pennak published his paper, Chappuis and Delamare (1958) described the mouth parts in their new species *plesai*.

¹ This species Gnanamuthu (l.c.) placed in a new genus *Robostura*. As was pointed out by Delamare (1960, p. 329) this genus is a synonym of *Microcerberus*.

In the text figure 1 have been reproduced the present figures of the mandibula, maxillulae, maxillae, and labium of the above-mentioned species. From the figure of Remane and Siewing their interpretation of the mandibula in *M. delamarei* is obvious. In order to illustrate the interpretations of the other authors in a simple way, I have marked in Fig. 1 the palpus of the mandibula with P, the pars incisiva with I, the lacinia mobilis with L, the spines or setae with S, and the processus molaris with M.

Concerning the mandibula in *M. delamarei* Remane and Siewing (l.c. p. 281) state that they have a two-jointed palpus, the second joint of which is tubular. This joint is no doubt nothing but a seta. If a palpus is present in the Peracarida, it always terminates in one or more setae. In this connection it may be noted that Karaman (1933, p. 165) in his diagnosis of *Microcerberus* writes that the palpi of the mandibula are five-jointed. No doubt he has intended the palpi of the maxillipeds.

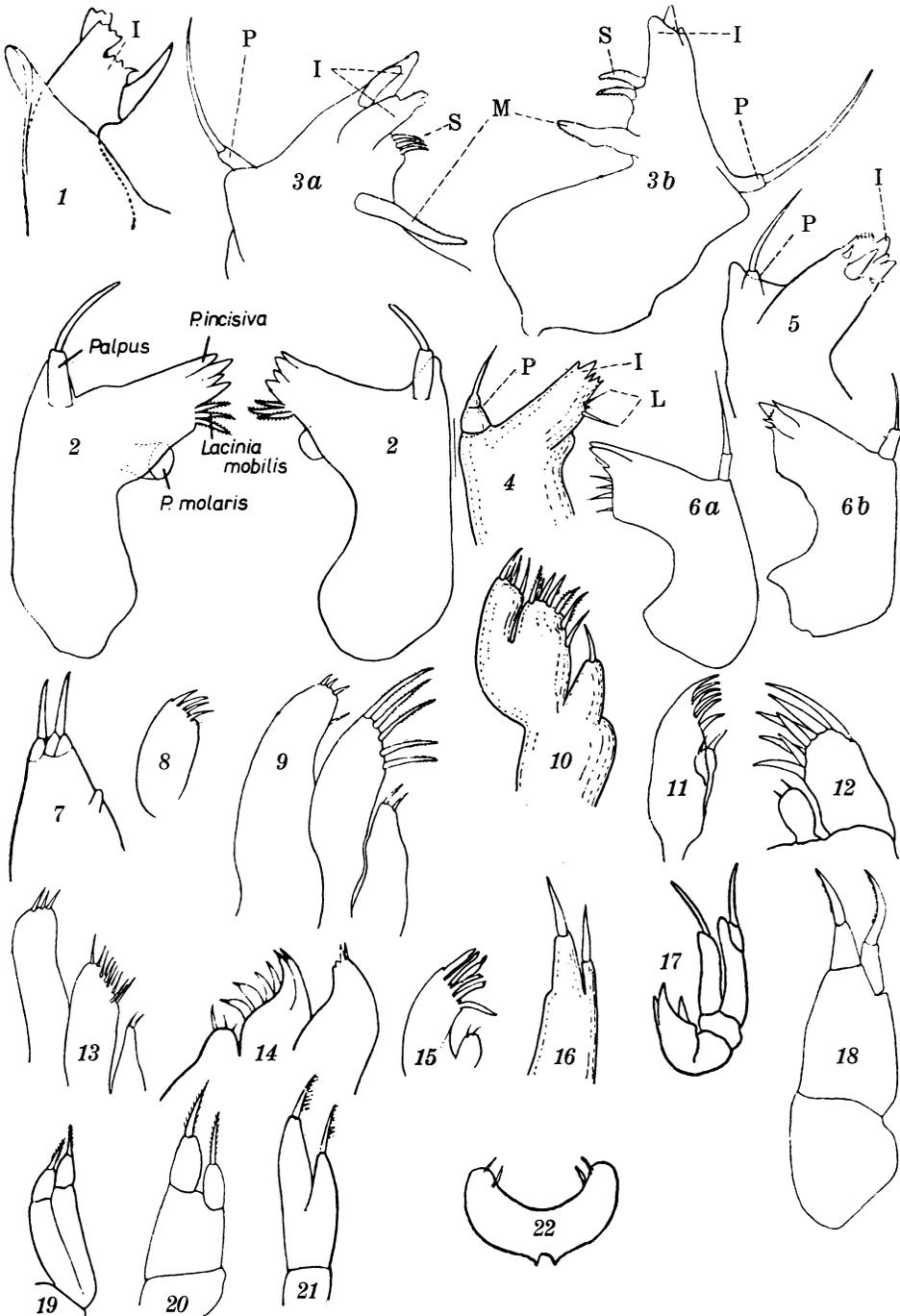
According to the figures and statements in the papers referred to, a processus molaris is present only in the species *delamarei* and *remyi*. For good reasons, however, I think that the processus molaris is present in all the species. That it has not been observed is most probably due to the fact that the authors—with the possible exception of Remane and Siewing—have not dissected out the mouth parts. Concerning these parts Chappuis and Delamare (1954, p. 132) write: "Les pièces buccales sont très difficiles à isoler. . . Elles s'insèrent au début de la seconde moitié de la tête, laissant un vide entre les mandibules et la base de l'antenne. Cette concentration . . . complique considérablement la dissection. Il est plus facile d'observer ces appendices en place après avoir éclairci la tête dans une solution de soude caustique."

It is, however, as I have convinced myself, impossible to ascertain the construction of the separate mouth parts in this manner. In such preparations the processus molaris is mostly concealed by the maxillulae. It is necessary to dissect out the mouth parts.

The mandibles of the peracarids differ most often in that the right mandible lacks, while the left mandible has, a lacinia mobilis. Immediately under the pars incisiva of the right mandible and immediately under the lacinia mobilis of the left mandible a number of spines or setae are to be found.

In *Microcerberus* the lacinia mobilis is mentioned in the species *delamarei* by Remane and Siewing (1953, p. 281, Taf. 35, Abb. 6) and in *remanei* by Chappuis and Delamare (1954, p. 133). From the figure of Remane and Siewing reproduced here (Fig. 1, 2), in which the original terminology has been retained, it appears that they interpreted the setae as the lacinia mobilis. They did not observe the lacinia mobilis in question. It lies, in fact, so close to the pars incisiva (see Fig. 3, 7), that it almost completely coincides with this, when the mandible is viewed from the posterior or anterior margin. If the mandible is placed so that the processus molaris points straight upward, the lacinia mobilis is fairly easy to observe. In this position this part can also be prepared away without great difficulty.

Fig. 1. 1-6. Mandibula of (1) *M. stygius*, (2) *M. delamarei*, (3) *M. remyi* (a = sinistrum, b = dextrum), (4) *M. remanei*, (5) *M. adriaticus*, (6) *M. plesai* (a = sinistrum, b = dextrum). 7-13. Maxillulae of (7) *M. stygius*, (8) *M. delamarei*, (9) *M. remyi*, (10) *M. remanei*, (11) *M. predatoris*, (12) *M. adriaticus*, (13) *M. plesai*. 14-21. Maxillae of (14) *M. stygius*, (15) *M. delamarei*, (16) *M. remanei*, (17) *M. predatoris*, (18) *M. remyi*, (19) *M. adriaticus*, (20) *M. plesai*, (21) *M. pauliani*. (22) Labium of *M. predatoris* (*M. stygius* after Karaman 1940, *M. delamarei* after Remane and Siewing 1953, *M. remyi* after Chappuis 1953, *M. remanei* after Chappuis and Delamare 1954, *M. predatoris* after Gnanamuthu 1954, *M. adriaticus* after Karaman 1955, *M. pauliani* after Chappuis and Delamare 1956a, *M. plesai* after Chappuis and Delamare 1958).



That Chappuis and Delamare (l.c.) also interpreted the spines as *lacinia mobilis* is shown from their statement that under the *pars incisiva* of the left mandible "s'in-sèrent 2 épines assez grosses qui représentant la *lacinia mobilis*".

Lacinia mobilis is always a dentate, strongly chitinized plate. It is most probably to be found in all species of *Microcerberus*, and can be seen on Chappuis' figure of the left mandible of *M. remyi* (Fig. 1, 3a) reproduced here, but he has clearly interpreted it as a part of the *pars incisiva*: "Entre cette épine (i.e. the *processus molaris*; my remark) et la *pars incisiva* nous trouvons à la mandibule gauche trois tiges barbelées . . ." (Chappuis 1953, p. 660).

Delamare's work "Biologie des eaux souterraines littorales et continentales", which was awaited with great expectation and was published this year, contains, *inter alia*, a monograph on the genus *Microcerberus*. The monograph consists chiefly of a literal quotation of the species described in French and a more succinct translation of the descriptions of species described in other languages. In the diagnosis of the genus in question he states (p. 329), *inter alia*: "Maxilla I à 3 endites." This, however, does not prevent him from informing the reader concerning *M. delamarei* (p. 338) that the above-mentioned maxilla is "composée d'un endite oval" and that in *M. predatoris* (p. 346) it has one "petite endite proximal . . . et un endite distal . . .".

The notion of Delamare and Chappuis that the maxillulae of *Microcerberus* have three endites, is undoubtedly owing to the fact that they have studied the mouth parts *in situ* in specimens treated with a solution of potassium. In addition they seem not to have known that the isopods, as in other crustaceans, have a labium. The outer four-spined endite figured by them is the lobe on the labium and it is also the same lobe which is figured by Remane and Siewing (compare Text-figs. 1, 9, 10 and 13 with Test-fig. 3, 11 and Pl. I, Fig. 1) as the maxillula.

The maxillulae of the free-living isopods, in which the mouth parts are not transformed for suction or perforation, always consist of two endites.

According to Gnanamuthu (1954, p. 267), each maxilla in *M. predatoris* is three-lobed and "the proximal lobe bears a claw with a spine on either side of it". I must say that, like the other investigators in this field, I have not been able to find the slightest trace of the lobe in question. As is to be seen from Figs. 1, 7 and 1, 14 Karaman has confused maxillula and maxilla.

The maxilliped of the *M. predatoris* according to Gnanamuthu (p. 268), has "a short cushion-like coxa which bears a short broad epipodite". I have not been able to find any trace of this either. My observations on this mouth part agree completely with the observations of the other authors.

Gnanamuthu is the only author who has mentioned and figured the labium (p. 266, Fig. 5 G and p. 267; see also this paper, Fig. 1, 22).

The pleon and the pleopods

Concerning the pleon and pleopods the authors agree (1) that the pleon—with the pleotelson included—consists of three segments, (2) that the males have one more pair of pleopods than the females and (3) that this pair of pleopods, which serves as a copulation apparatus, corresponds to the second pair of pleopods of the males in other isopods, in which it has the same function. In other respects the opinions are divergent.

¹ In this work the terms maxillulae and maxillae will be used instead of maxillae I and maxilla II respectively.

For tactical reasons it is most suitable to begin with the second pair of pleopods of the males.

The joint, to which the exo- and endopodite are attached, is designated by Chappuis sometimes as basis (Chappuis 1953, p. 661), sometimes as sympode (Chappuis 1954, pl 3). Chappuis and Delamare call it either sympode (see, for example, Chappuis and Delamare 1952, p. 2016; 1956a, p. 84), sympodite (see, for example, Chappuis and Delamare 1958, p. 329) or basipodite (Delamare, Chappuis and Paulian 1956, p. 68). Karaman (1940, p. 50) calls it sympode or (1955, p. 145) basis. Pennak (1958, p. 300) uses for the same joint the term protopod. Remane and Siewing (1953, p. 282) and Gnanamuthu (1954, p. 268) call it the basis. Basis is the correct term.

All authors, with the exception of Gnanamuthu, state that each pleopod of the pair of pleopods in question consists only of the above mentioned joint and of an exo- and endopodite attached to this. According to Gnanamuthu, on the contrary, both the bases in *M. predatoris* issue from a common coxal plate. From Karaman's description and figure of the pleopod in question in *M. stygius* (1940, p. 50 and p. 51, Fig. 90) and Remane and Siewing's figure of the pleon of the male of *M. delamarei* (l.c., Pl. 36, Fig. 11) it appears that a coxal plate, which is what it should be called, is present also in these species (whether the plate is formed by a fusion of the praecoxae and coxae of both legs is a question which I must leave open, since embryological investigations are completely lacking). The figures referred to are incomplete in as much as the upper margin of the plate has not been drawn. In the new species described below, only the lower and lateral parts of the coxal plate are strongly chitinized. The rest of the plate is wholly hyaline. It is almost impossible to see the plate, if it is not dissected away. On Chappuis' figure (1953, p. 662, fig. 14) of the last pleonite and pleotelson with their extremities in the male of *M. remyi* the total coxal plate is to be seen. It is obvious, however, that Chappuis did not understand what he observed. The coxal plate is figured as an independent structure with its limit quite close to the bases of the pleopods. In addition the coxal plate on Chappuis' figure is of the same length as the second pleonite and according to his description the second pleopod pair is attached at the end of the second pleonite (p. 661). *A coxal plate is present with most probability in all Microcerberus species.*

To which pleonite is the pleopod pair in question attached? For those authors who interpret the pleopod as consisting only of a basis with exo- and endopodite, it is evident that the pleopod is situated on the second pleonite. According to Gnanamuthu (p. 268), the coxal plate issues "from the hind edge of the first abdominal segment", but by comparison he finds that the pleopod pair must correspond to the second pleopod pair of other isopods. He concludes that in *Microcerberus* the first pleonite has disappeared.

Both the pleonites are so close to one another that on undissected specimens it is nearly impossible to decide if the coxal plate issues from the posterior margin of the first pleonite or from the anterior margin of the second pleonite. If, however, one bends the pleopod pair in such a way that the coxal plate and sternite are perpendicular to one another, both the pleonites are relatively easy to separate. I have done this on a couple of specimens and found that *the coxal plate is attached very near the anterior margin of the second pleonite. Consequently the first pleonite is not suppressed in Microcerberus.*

The superficiality with which the endopodites in question have been studied contrasts strongly with the decisive role which has been attributed to them in the species systematics within the genus.

Since the question concerning the systematic position of *Microcerberus* will be dealt with below, it will only be pointed out here that I, in common with other investigators, completely agree with Karaman's opinion (1940, p. 46), that the genus is most closely related to the anthurids.

On the median margin of the endopodites of the second pleopod pair there occurs in the males of the anthurids a narrow, more or less long, defined process. This process is termed by several investigators, e.g. Harger (1880, p. 404) and Barnard (1925, p. 116) "the stylet", while Zimmer (1926-27, p. 717) designates it "appendix masculina". In their descriptions of the species of *Microcerberus* Chappuis and Delamare name it "apophyse" or "endite". The most satisfactory term is the one used by Zimmer. The appendix masculina is, as I have convinced myself after studying my material, a trough-shaped structure by means of which, with all certainty, the sperm is transferred to the female just as in other isopods.

In the anthurid males the endopodites of the second pleopod pair are always one-jointed and the appendix masculina is situated on the median margin of the endopodite. In several species of *Microcerberus*, on the contrary, the endopodites have been described as two-jointed. This is the case, e.g. in *arenicola* (Delamare and Chappuis 1956*b*, p. 366; in the text it is stated that "l'article externe proximale se termine par un lobe en oreillette", but from their fig. 1*d* it appears that it is the distal joint which ends in this manner), *pauliani* (Chappuis and Delamare 1956*a*, p. 83), *ruffoi* (Chappuis 1954, p. 3) and *adriaticus* (Karaman 1955, p. 145). The endopodite in *M. remanei* is said to be "biramé, peut-être est-il composé de deux articles dont le premier a une apophyse du côté interne comme chez certains Harpacticides" (Chappuis and Delamare 1954, p. 135). This comparison with the harpacticids is from all points of view extremely unfortunately chosen.

In my material of the *Microcerberus* species described below, there are in one sample a number of males with a completely developed last peraeopod pair, but with the second pleopod pair in different stages of development.

As appears from the figures (Figs. 4, 8-9) and photographs (Pl. I, Figs. 4-5), in younger specimens each endopodite is sac-like. Through a narrow incision two lobes are formed (Pl. I, Fig. 4). Of these the median, longer lobe gives rise to the appendix masculina, which becomes defined when the organ is nearly completely developed. If the incision is very profound, the appendix masculina will be situated high up as in *M. remanei*. If the appendix masculina becomes defined right up to the lateral margin, the endopodite obtains the same appearance as in *arenicola*, *pauliani*, *ruffoi* and *adriaticus*. It is therefore more correct to say that the appendix masculina in these species extends to the lateral margin of the endopodite than to say, as some have done, that the endopodite is two-jointed.

It is obvious (see Pl. II, Fig. 2) that the males continue to moult, even after they have become sexually mature (that the male from which the photograph is taken is sexually mature is apparent because it has developed spermatozoa).

Among the *Microcerberus* species described the endopodites of *stygius* (Karaman 1940, p. 50 and 51, Fig. 90), *littoralis* (Chappuis and Delamare 1956*b*, p. 395, fig. 14*a*) and *plesai* (Chappuis and Delamare 1958, p. 329) have the same appearance as shown in Pl. I, Figs. 4-5. Consequently the specimens on which these species have been based are immature individuals. That *stygius* has been described from a manca stage is also apparent, since the last peraeopod pair is not completely developed (Karaman 1933, p. 166, Fig. 1*a* and 1940, p. 47, Fig. 74). The same seems also to be

the case with the species *renaudi*¹ (Delamare and Chappuis 1956b, p. 386, figs. 7a-7b and p. 388, fig. 9b), *monodi* (Delamare and Chappuis 1957, p. 497, fig. 2d; in the text they designate the exopodite as the endopodite) and *predatoris* (Gnanamuthu, p. 266, Fig. 5B). In any case Gnanamuthu's statement (p. 268), that the endopodite behind the subterminal process has "a deep circular cavity for the reception of sperms" is incorrect. Such a "cavity" does not exist in any isopod.

Judging from the figures, the second pleopod pair in the species *remyi* (Chappuis 1953, p. 662, fig. 14), *predatoris* (Gnanamuthu) and *mexicanus* (Pennak, p. 301, Fig. 2) has only been studied *in situ*. In such a way one cannot obtain a correct idea of the pleopod in question. To obtain this, the pleopod pair must be dissected free and studied from different sides.

I shall now proceed to the pleotelson and the remaining pleopods, which are similar in the two sexes. According to Karaman (1940, p. 49, Fig. 82, and p. 50), there rises from the posterior margin of the second pleonite in the female of *M. stygius* a semicircular plate, which covers the pleotelson. He adds, however, that because of the absence of a distinct line of demarcation, the plate seems to him to be only an extension of the first pleonite (according to his figure, it is the second pleonite). On each side of the pleotelson three pleopods, attached to a common base-joint, lie in a ventral, longitudinal groove. Into this groove the pleopods can be wholly retracted and they can also be completely extended from it. The above mentioned plate contributes to the covering of the pleopods, which also are covered by a small chitin lamella, situated at the base of the pleopods (p. 50-52).

Karaman (1955, p. 145, Fig. 18) also found the groove in the female of *M. adriaticus*, the pleotelson of which has a trapezium-shaped plate on the ventral surface as in *M. remanei*, according to Chappuis and Delamare.

Chappuis and Delamare (1952, p. 2016) interpret the plate in the last-mentioned species and also in *M. pauliani* (Chappuis and Delamare 1956a, p. 86) as the second female pair of pleopods. The plate is attached to the end of the second pleonite and covers the base of the respiratory pleopods, which lie in a marginal duplication of the pleotelson. Later Chappuis (1954, p. 3) changed this statement; the respiratory pleopods are retracted below the third, one-branched and chitinized pleopod.

This plate is also mentioned in *M. delamarei* by Remane and Siewing (1953, p. 283, Pl. 36, Fig. 12), who also state that it issues from the second pleonite, in *M. predatoris* by Gnanamuthu (p. 268, Fig. 5D), who interprets it as the fused protopod of the third pleopod, which is "attached to the hind edge of the second abdominal segment", and in *M. mexicanus* by Pennak (p. 300 and p. 301, Fig. 3), according to whom the second pleonite lacks appendages, while the pleotelson has a pair of two-branched pleopods "lying in a narrow chamber between the surface of the body and a plate-like lamella arising at the lateral margin of the pleotelson . . .".

In reality, as the figures of the pleotelson given by Chappuis and Delamare (1954, p. 135, fig. XIV:1), Remane and Siewing (l.c.) and Karaman (1955) show, there are to be found two such plates, which together form a figure resembling an hour-glass. These plates, however, are not limited to the females. In young (small) males they are distinct and likewise in the old (large) males they are sometimes completely or partly visible. In some females they appear very clear, in others hardly at all. In this connection I would like to point out that the plates gradually become invisible in glycerine.

¹ Delamare and Chappuis (1957, p. 498) refer in a foot-note to "*M. Debyseri* Del. et Ch.". In the work they refer to, however, the species is called *renaudi*.

What then is the above-mentioned plate, which is said to issue sometimes from the second pleonite, and sometimes from the pleotelson and which is interpreted in such different ways?

That it is impossible to lift up the plate or to place even the finest needle under it is perhaps not so easy to establish. However, it is easily seen that there are muscles between the posterior margin of the second pleonite and the distal corner of the plate. These muscles are a direct continuation of a segmentally arranged ventral body musculature (Fig. 5, 3).

The "plates" are nothing more than chitinous strips which serve as attachments for the muscles. In all probability they represent sternites.

As will be shown below, to the former of these are attached two pair of pleopods, of which the anterior pair is one-branched, the posterior two-branched. Since every pleonite never bears more than one pair of pleopods, we can, if we agree with this interpretation, conclude that the anterior sternite represents a fusion of the sternites of third and fourth pleonites, while the posterior sternite is a fusion of the fifth and sixth pleonites and telson. It is possible, however, that the telson has disappeared. The position of the uropods indicates that such may be the case. Only embryological investigations, however, can provide information concerning this.

As already mentioned, Karaman (1940, p. 50) considers that *M. stygius* has three pleopods, which issue from a common base. These are covered, *inter alia*, with a chitinous lamella, which Karaman interprets as a part of a pleopod. Concerning *M. adriaticus*, the same author only states (Karaman 1955, p. 145) that the third pleopod is in fact only a spiny process for the protection of the other pleopods, which seem to consist of two, partly bipartite rami. Remane and Siewing (p. 282) find in *M. delamarei* three appendages with a short common base. Of these the outer appendage is extended and bent (this apparently corresponds to the chitinous lamella of *stygius*), the other two are oval. According to these authors, there exist "demnach eine Übereinstimmung mit *M. stygius*". This assertion must depend on a misinterpretation, since, as already has been pointed out, *stygius* is said to have three pleopods in addition to the chitinous lamella.

According to Chappuis and Delamare (1954, p. 136) it is probable that *M. remanei* has only one pair of respiratory pleopods (the chitinous lamella is not mentioned). In *M. remyi* (Chappuis 1953, p. 661) and *M. ruffoi* (Chappuis 1954, p. 3) the fourth and fifth pleopods are covered by the third pleopod, which is triangular and chitinized. In the latter species (p. 3 and p. 4, Fig. 9) the fourth pleopod—Chappuis has written endopodite—is two-branched; the exopodite is very short and issues from a small basal joint which is said to be situated on the anterior (lower) surface of the endopodite. It is quite impossible that the exopodite should be situated in such a manner.

I have already discussed (see above p. 499) Gnanamuthu's interpretation of the third pleopod pair in *M. predatoris*. Here I only wish to add that, according to him, each pleopod is "single-jointed" and that this "joint", which probably corresponds to the endopodite, is smooth in the adults but has a four-dentate margin in the young specimens. The fourth pair of pleopods in this species consists of two "single-jointed" plates, "attached to the anterior region of the third segment . . . one on either side in a sessile manner, there being no protopod". Near the postero-lateral corner of the pleotelson occurs a "small fleshy papilla" with two setae, which are probably vestiges of the fifth pleopod pair.

Chappuis and Delamare's figure (1958, p. 331, fig. 2a) of the pleopods in *M.*

plesai is rather similar to Karaman's first figure (1933, p. 167, Fig. 2a) of the pleopods in *M. stygius*. On both figures, three leaf-shaped structures issue from a common, remarkable long basal joint. In *stygius* two of these are "in enger Verbindung zu einander". This statement may be interpreted to mean that Karaman considers them to be exo- and endopodite of the same pleopod. At the base of the pleopods there are, according to Karaman, vestiges of other pleopods. Concerning the pleopods in *M. plesai*, I cannot understand Chappuis and Delamare's interpretation (p. 332): "C'est le pléopode 2 qui forme un bouclier sous lequel les autres pléopodes . . . peuvent être retirés. Près de la base du pléopode 3 . . . s'insère un organe cylindrique et élastique qui peut être sorti ou retiré. Dans sa portion distale, cet organe porte trois feuilles respiratoires qui pourraient fort bien correspondre aux pléopodes 4 et 5, le 5 n'ayant, chez beaucoup d'Isopodes, qu'un endopodite."

Pennak's statement concerning the pleopods in *M. mexicanus* has already been mentioned. For other species information is lacking.

Gnanamuthu's opinion that the chitinous lamella represent the endopodite of the third pleopod is undoubtedly correct. It is a general rule that the exopodite reduces before the endopodite in the higher crustaceans. As Gnanamuthu has pointed out, the third pleopod in the young specimens is equipped with spines. In the species investigated by me the pleopod in the young specimens has five spines and in the older specimens at least the terminal spine is present. *Each pleopod has a short basis*, attached to the lower lateral margin of the anterior sternite (Fig. 5, 3). This can easily be seen if the pleopod is dissected away. One can then also see that under this pleopod there is a somewhat longer basal joint which bears two branches (Fig. 5, 3). That these branches represent the exo- and endopodite of the fourth pleopod seems self-evident to me. Together they form a typical isopod-pleopod. Chappuis' interpretation (1954, p. 3) that they represent the fourth and fifth pleopods, the bases of which have fused with one another is quite unreasonable.

The pleopods lie, as several investigators have pointed out, in a slight depression. They certainly cannot be extended and retracted in a manner such as Karaman (1940) and Chappuis and Delamare (1958) postulate. Karaman expressly states that he never observed these movements in living specimens.

What is the basis of these reports? I believe I can give an explanation. In order to study the pleotelson, I had laid one specimen in glycerine with its ventral side upward and covered it with a cover-glass. This rested on a couple of thin pieces of paper. The pleotelson came to lie obliquely downward and in order to bring it to a horizontal position I pressed slightly on the cover-glass. The pleopods then seemed to extend themselves so that they nearly reached the posterior margin of the pleotelson. The cause of this I found to be that the specimen had begun a moult, which I had not observed before. When I pressed on the cover-glass, the old cuticle of the pleopods was pushed backward (pl. II, Fig. 3).

Gnanamuthu's assumption that the setae, which are situated near the posterolateral corner of the pleotelson, are vestiges of the fifth pleopod pair, cannot be correct. Against this supposition we have the fact not only that those pleopods which are to be found completely lack setae, but also that there are setae of exactly the same appearance on all the segments.

Karaman altered his earlier statement (1933, p. 168 and p. 167, Fig. 2a) that the uropods in *M. stygius* consist of two basal joints and an exo- and endopodite in his later study (1940, p. 52, p. 49, Figs. 79, 82 and p. 51, Fig. 91). As in other *Microcerberus* species the uropods in *stygius* have only one basal joint.

The gonopores of the male

Three quite different opinions prevail concerning the location of the male gonopores. According to Karaman (1940, p. 52), the apertures are situated below the attachment of the last pair of peraeopods; according to Gnanamuthu (1954, p. 266, Fig. 5B, p. 267 and p. 272), the vasa deferentia open into a pair of sharp-pointed "penial styles" each with two spines, while Chappuis and Delamare (1954, pp. 134, 136, fig. XV:3-4) are of the opinion that a penis is absent and that "les spermatozoïdes sont assemblés dans une vésicule qui a son orifice vers l'extérieur dans un replis du tegument ventral" (see also Chappuis 1954, p. 3; Chappuis and Delamare 1956*a*, p. 84, fig. 2*a*; 1956*b*, p. 388, fig. 9*a*, and p. 389).

Only a superficial study of total specimens shows that Chappuis and Delamare have interpreted the ganglion of the last peraeonite as a vesicula. The sperm figured by them is nothing but the ganglion cells. Better still, it is evident from sections of the segment in question (Pl. III, Figs. 1-3). The "replis du tegument ventral" are the "penial styles" mentioned by Gnanamuthu.

Gnanamuthu is right. The end of each vas deferens is ampullaceous, strongly muscular, and surrounded by a strong ring of chitin (Pl. III, Fig. 4). The ampullaceous part projects ventrally and posteriorly and in the lower median part it is provided with two small spinous openings, directed obliquely backwards. As it is quite impossible that this part should serve as a penis, the term used by Gnanamuthu is inadequate. In most other crustaceans the analogous part is termed genital papilla.

How is the sperm transferred to the appendices masculinae? In order to obtain an answer to this question, the present author has bent the second pair of pleopods of *Microcerberus* straight forwards. In this position the spinous openings of the genital papillae almost meet the proximal part of the appendices masculinae. Because of this it seems to me very likely that the transmission takes place in this way. The strong musculature of the genital papillae indicates that the sperm is ejaculated with great force.

The systematic position of *Microcerberus*

In his discussion of the systematic position of *Microcerberus* Karaman (1940, pp. 44-46) concludes that the genus is to be placed either as a separate family beside the Anthuridae or as a relict of an extinct sub-order beside the Flabellifera. He chooses the first alternative. When Karaman published his paper, however, Anthuridae had long since (Monod 1922, pp. 135-136) been removed from the Flabellifera and placed in a separate sub-order, Anthuridea.

Chappuis and Delamare (1954, pp. 130-131) divide the Anthuridae into the sub-families Microcerberinae, with only the genus *Microcerberus*, and Anthurinae, comprising all the other genera of Anthuridae. Their reason for this arrangement, that *Microcerberus* differs from the Anthuridae in negative characters only, is not tenable. In the Anthuridae the mouth parts are modified for perforation and suction, the peraeopods I-II are subchelate, the carpus of the peraeopods is stunted and the almost obsolete dactylus has only a single claw. In *Microcerberus* the mouth parts are not modified; only peraeopod I is subchelate, the carpus and the dactylus of the peraeopods are well-developed and the dactylus has two claws. As regards these characters *Microcerberus* is more primitive than the Anthuridae.

Because of this and the strong modification of the second male pleopod the present

author is of the opinion that *Microcerberus* is to be placed in a reparate sub-order, Microcerberidea. This sub-order, however, is no doubt most closely related to the Anthuridea.

The distribution of the genus *Microcerberus*

Karaman (1953, p. 164) believes that the relict hypotheses concerning *Microcharon*¹ and *Microparasellus*² are untenable because of the discovery of a *Microcharon* species in the centre of the karst region of the western part of the Balkans. The small subterranean isopods "*Microcharon*, *Microcerberus*, *Microparasellus* dürften weit älter sein als die Aegeischen bzw. Pannonischen Seen und Meere, sie sind weit früher in das Grundwasser eingedrungen . . ." and they "dürften den Weg über das Meeres-Grundwasser und nachher Küsten-Grundwasser benutzt haben, um in das süsse Grundwasser einzudringen . . ." Remane (1952, p. 350) and Schultz (1954, pp. 254–255) agree with this opinion. The present author does not doubt that these and also other small marine animals are capable of entering the fresh water in this manner. This, however, by no means contradicts the hypothesis of their relict nature. The present writer shares the opinion of Delamare (1960, pp. 353–354) that *Microcerberus* is a relict, but not his opinion that the genus in question must be a Tertiary relict. The probability that the genus existed during the Cretaceous is just as possible. It may therefore be better to say that *Microcerberus* is a Tethys relict (Fig. 2). The genus is found only in subterranean water.

Microcerberus abbotti n.sp.³

Description. Male (Fig. 3, 1) colourless and transparent. Length of largest specimen from anterior margin of cephalon to posterior margin of pleotelson about 0.95 mm, greatest width about 0.09 mm. Mutual length of visible segments about 40:24:24:26:26:30:35:35:20:22:35. Cephalon with three small, simple, lateral setae and with a minute dorsal seta near the anterior part of the lateral margins. Peraeonite I in front as broad as cephalon, backwards tapering; tergite shield like, as broad as the sternite; front margin produced into an acute ventro-lateral projection; lateral margins with a small, simple seta. Tergites of peraeonites 2–4 indistinctly subdivided into two side-plates. The anterior part of the tergites is somewhat narrower than the sternites. Anterior margin with a pair of lobes on either side of the mid-dorsal line; median lobes not defined by a suture, each of them with a small, simple seta at the tip; lateral lobes defined by a distinct suture, much more prominent and acute than the median lobes, with a small tooth approximately in the middle of the median margin; lateral lobes of second peraeonite with a small simple, lateral seta on the lower third. Tergites of peraeonites 5–7 much narrower and somewhat shorter than the sternites, distinctly subdivided into two side-plates. Posterior margin of each side-plate with a triangular projection, forming the upper part of the acetabulum for the peraeopod. Approximately in the middle, each plate has a small, simple, dorsal seta near the lateral margin.

¹ See Chappuis (1944).

² See Angelier (1953).

³ Named in honour of Dr. D. P. Abbott, of the Hopkins Marine Station.

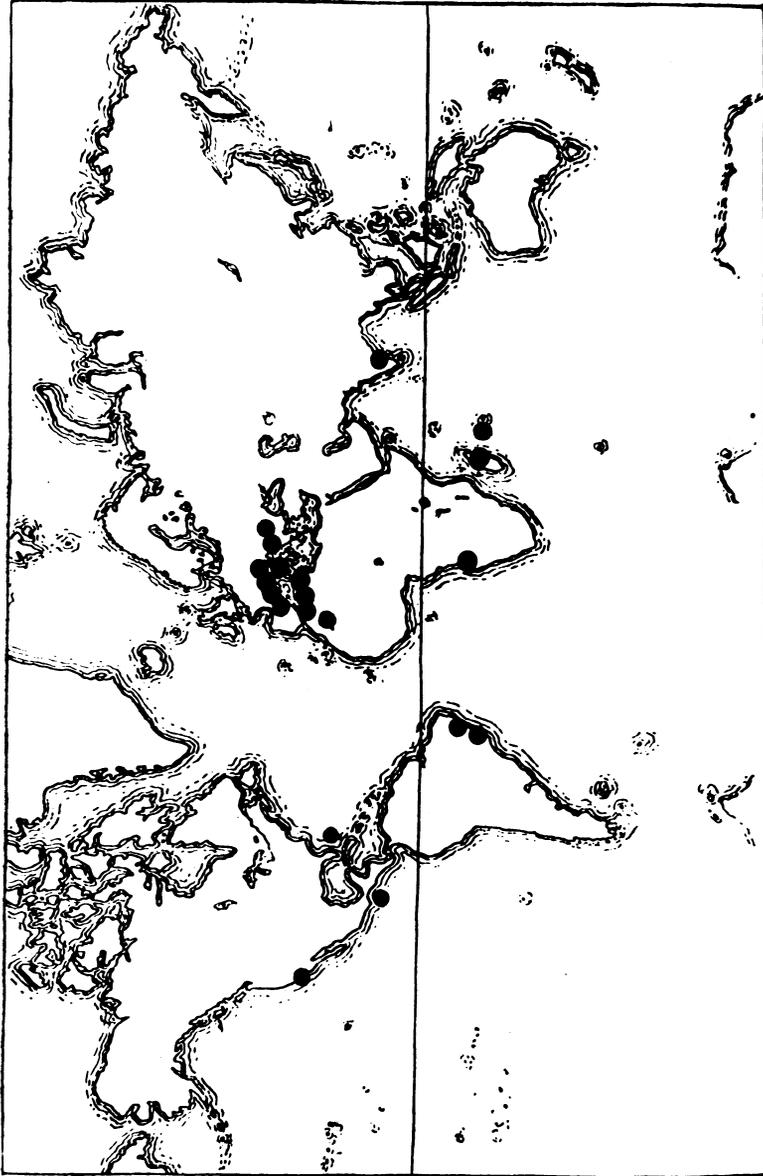


Fig. 2. The distribution of the genus *Microcerberus* (after Delamare-Deboutteville 1960—completed).

Tergites of pleonites and pleotelson shield-like, somewhat broader than the sternites. Lateral margins of each segment with a small, simple seta. Sternites of pleonites 1-2 without raised areas. The shape of the ventral side of the pleotelson has already been discussed (see above, pp. 499-500).

Antennulae (Fig. 3, 4) six-jointed; mutual length of the joints about 6:5:3:2:3.4:2.4; first and second joints considerably more robust than the other joints. First joint with one simple seta at the outer distal corner. Second joint with one long and one short, spatulate and plumose, sensory seta in the proximal part of the outer margin and in front of these with one simple seta; inner distal corner with two simple setae. Outer margin of the following joints smooth. Inner distal corner of the three following joints with simple setae; third joint with two long, fourth joint with one minute and fifth joint with one long seta; third joint moreover with one minute, simple seta on the upper fourth of its length. The last joint bears at the tip three simple setae, the one of which is more than twice as long as the others, one short, spatulate, plumose seta, and one long cylindrical aesthetasc.

Antennae (Fig. 3, 5) with six-jointed peduncle; mutual length of the joints about 3:3:9:4:7:9. First joint almost triangular, with one simple seta at the outer distal corner. Upper surface of second joint with one simple seta near the middle of the distal margin and with a dentiform process near the inner proximal corner. Third joint with a dentiform projection approximately in the proximal third of the inner margin. All the joints with simple setae of different length, sixth joint moreover with one short and one long, spatulate, plumose, sensory seta close to the outer distal corner. Flagellum six- or seven-jointed; in the last case the first joint is often indistinctly defined.

Mandibula (Fig. 3, 6-10). Corpus with a hump-shaped elevation at the base of the small, one-jointed, unisetose palpus. Processus molaris long, slender, its distal half finely ciliated and thinner than the proximal half. Pars incisiva of both mandibles brownish coloured, horny, four-dentate. Mandibulum sinistrum with a brownish, horny, three-dentate lacinia mobilis and just below this with two, finely ciliated setae. Mandibulum dextrum with only three, finely ciliated setae just below pars incisiva.

Maxillulae (Pl. I, Fig. 1 and Text-fig. 3, 11) with two endites. Outer endite in both maxillulae with eight spines on the distal margin; seen from the side these spines show a somewhat different appearance. No palpus. Inner endite much smaller than the outer one, with two short, but strong, spines at the tip.

Maxillae (Pl. I, Fig. 2 and Text-fig. 3, 12) with two-jointed protopodite ending in two lobes enlarged at the base. These lobes are distinctly delimited and to each of them muscles are attached. Because of this they should be called arthrites and not endites.

Maxillipedes (Fig. 3, 13) six-jointed. Mutual length of the joints (the joints are measured along the middle) about 8:2:4:6:5:5. Inner distal corner of first joint (most probably this joint represents coxa + basis) extended and provided with one small seta at the tip. Second joint without spines and setae. Third and fourth joints each with two minute spines and one long seta. Fifth joint with two long setae. Last joint with three long setae at the tip, and with one shorter seta on the outer margin; lower (posterior) surface with a row of five spines or small setae, upper (anterior) surface with one such spine or seta.

Fig. 3. *Microcerberus abbotti* n. sp. Mature male. (1) Dorsal view. $\times 165$. (2) Anterior margin of the tergite of the second peraeonite. $\times 550$. (3) Right lateral lobe of the second peraeonite of another male. $\times 550$. (4) Antennula. $\times 465$. (5) Antenna. $\times 465$. (6) Mandibulum sinistrum. $\times 800$. (7) Pars incisiva and lacinia mobilis of the same. $\times 1200$. (8) Lacinia mobilis of the same. $\times 1200$. (9) Pars incisiva of the same. $\times 1200$. (10) Pars incisiva of mandibulum dextrum. $\times 1200$. (11) Maxillula. $\times 800$. (12) Maxilla $\times 800$. (13) Maxilliped. $\times 750$. (14) Labium. $\times 800$. (All the figures —(1) and (3) excepted— from the same specimen. The original figures are reduced to half.)

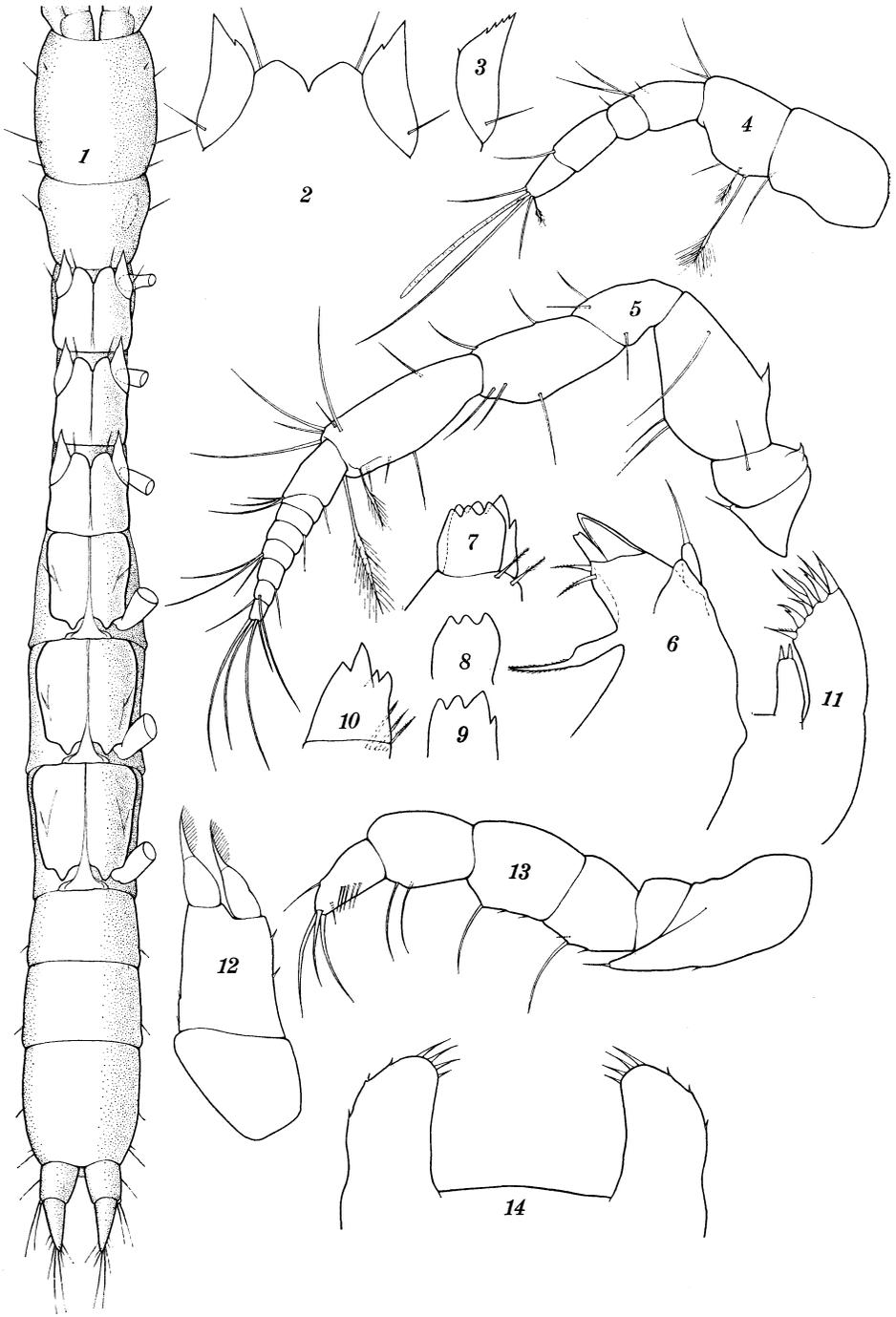


Fig. 3. Explanation of the figure on p. 505.

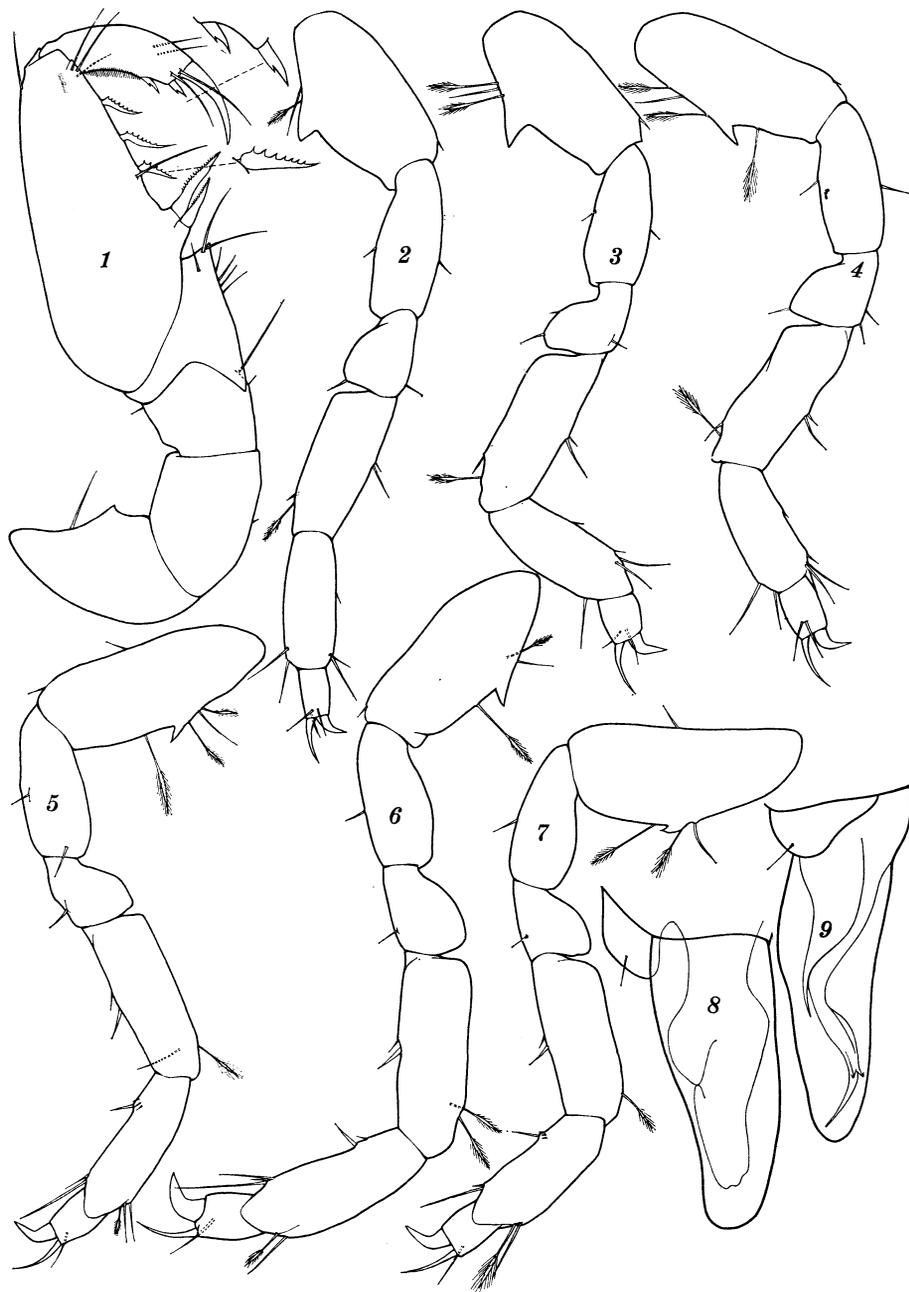


Fig. 4. *Microcerberus abboti* n.sp. 1-7. Peraeopods 1-7 from the same male as in Fig. 3. $\times 550$.
8-9. Second pleopod of young males. $\times 800$. (The original figures are reduced to half.)

Labium (Pl. I, Fig. 3 and Text-fig. 3, 14) ending in two, not delimited, lobes, each provided with four spines at the tip.

Peraeopod I subchelate (Fig. 4, 1). Basis about as long as ischium, with a simple seta and a dentiform projection on the anterior margin. Merus distinctly shorter than ischium. Posterior part of carpus produced into a fairly broad lobe. Propus almost as long as the preceding joints combined; posterior margin with five serrated spines, the two proximal of which are close to one another and more finely serrated than the three others. Dactylus with a dense row of fine cilia and with a bifid spine on the posterior margin; distal margin with a bifid spine and a long claw. The armament for the remainder of this leg is shown in the figure.

Peraeopods II-IV (Fig. 4, 2-4) directed backwards, peraeopods V-VII (Fig. 4, 5-7) forwards. Basis of peraeopods II-IV with a dentiform projection approximately in the middle of the anterior margin, that of peraeopods V-VII with a similar projection about in the middle of the posterior margin. Above the projection peraeopods II, VI, and VII have one spatulate, plumose, sensory seta and one simple seta, peraeopods III-V two spatulate, plumose, sensory setae, and between them one simple seta. Below the projection peraeopods IV-VII have one spatulate, plumose, sensory seta. Carpus of peraeopods II-IV with one seta of the same nature near the anterior, distal corner; carpus of peraeopods V and VII with one, that of peraeopod VI with two such setae near the posterior distal corner. Moreover there is one such seta close to the posterior distal corner of the propus of peraeopods V-VII. The armament of the remainder of these legs is shown in the figures.

In all the peraeopods the basis is the largest joint. Ischium of peraeopod II about as long as carpus; ischium of peraeopods III-VII distinctly shorter than carpus. Merus short, in peraeopods II-IV with the anterior margin, in peraeopods V-VII with the posterior margin expanded. Carpus of peraeopods II-IV distinctly longer than propus, carpus of peraeopods V-VII about as long as propus. Distal margin of propus of peraeopods II-IV straight, that of peraeopods V-VII coniform produced. Dactylus short, almost rectangular, with two terminal claws, the one of which is shorter, but stronger and more curved than the other.

Second pair of pleopods (Fig. 5, 1, Pl. II, Fig. 1). Coxae fused into a broad, rectangular, hyaline plate, the distal and lateral margins of which are strongly chitinous. Basis rectangular, somewhat longer than broad, with the inner distal corner running out into a small bilobated prominence. Exopodite small, slightly inwards curved, with a small, simple seta at the tip. Endopodite large with a long appendix masculina, the outer margin of which extends to the lateral margin of the ramus. The tip of the endopod is divided into a narrow, acute, outer lobe, and an inner broader lobe weakly bipartite at the tip. Proximal part of appendix masculina, i.e. the part from the base to the end of the inner lobe of the endopodite, with rows of fine cilia on the anterior surface; distal, incurvated part with two small hooks in front of the acute tip.

The following pleopods have already been treated (see pp. 500-501).

Uropods (Fig. 5, 4). Basis with fine spines on the inner, curved margin; outer margin with one simple seta about in the middle; dorsal surface with one such seta near the distal margin. Exopodite very small, at the base indistinctly defined, with two long, simple setae. Endopodite long, curved slightly inwards, with five spatulate, plumose, sensory setae.

The *female* differs from the male only by its greater length (longest female about 1.2 mm) and by the absence of the second pair of pleopods.

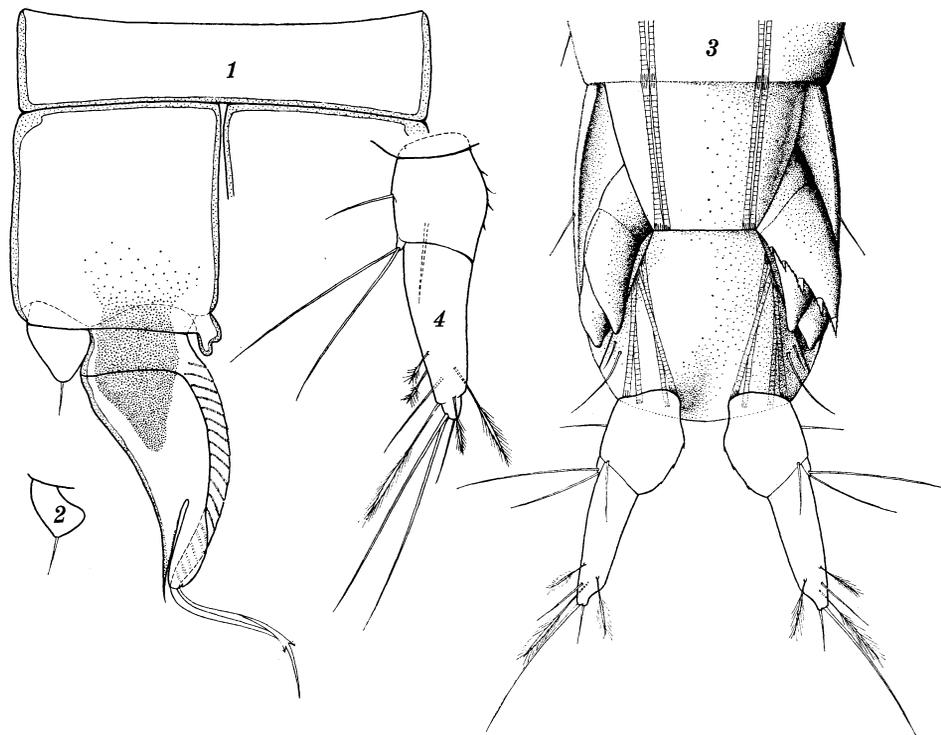


Fig. 5. *Microcerberus abbotti* n.sp. (1) Second pleopod of the same male as in Figs. 3-4. $\times 365$. (2) The exopodite of the same male in another position. $\times 365$. (3) Pleotelson and uropods of a young female. $\times 445$. (4) Uropod of the same male as in Fig. 5, 1. $\times 550$. (The original figures are reduced to half.)

Manca stages. The collected material contains two manca stages which differ from each other only by their length and by the absence (13 specimens) or presence (23 specimens) of the last pair of pereopods. In the latter specimens the pair of pereopods in question is U-shaped, backwards directed, and the dactylus is small and conical (Pl. II, Fig. 4). In both stages the pleopods of the pleotelson are developed, and the number of joints in the flagellum of the antennula is the same as in the adults. In the latter respect they differ significantly from the manca stages of *Jaera albifrons* Leach. According to Forsman (1945, pp. 25-26), this species has three manca stages; the number of joints in the above-mentioned flagellum increases from one stage to the other, and the adults always have more joints than any one of the manca stages.

Variability. The only differences found in specimens of the same length are that the left mandible may have three setae instead of two (in one of six dissected specimens), and that the median lobes of the tergites of pereonites 2-4, or in one of them, are flatter than in the species described. In one female the median margin of the right lateral lobe of the second pereonite is four-dentate (Fig. 3, 3).

Material. 91 ♀♀, 30 ♂♂, 36 manca. Hopkins Marine Station, 11.9 and 12.9 1960. Subterranean coastal water. Fine shell-sand.

Remarks. The species differs from all the other species of the genus in the shape of the second pleopod of the male.

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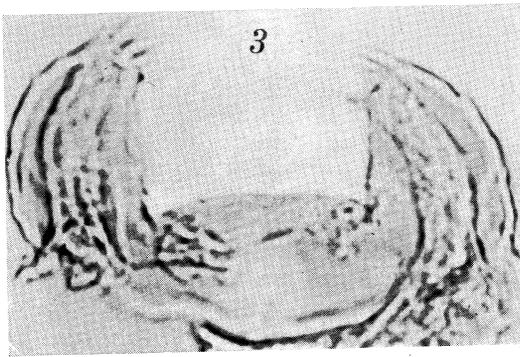
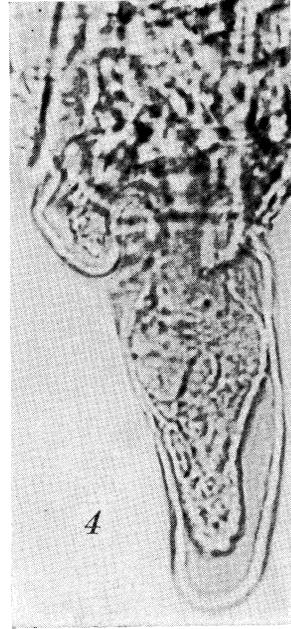


Plate I. *Microcerberus abbotti* n.sp. ♂. (The same specimen as figured in the text.) (1) Maxillula. $\times 1535$. (2) Maxilla. $\times 900$. (3) Labium. $\times 1120$. (4-5) Second pleopod of two young males.

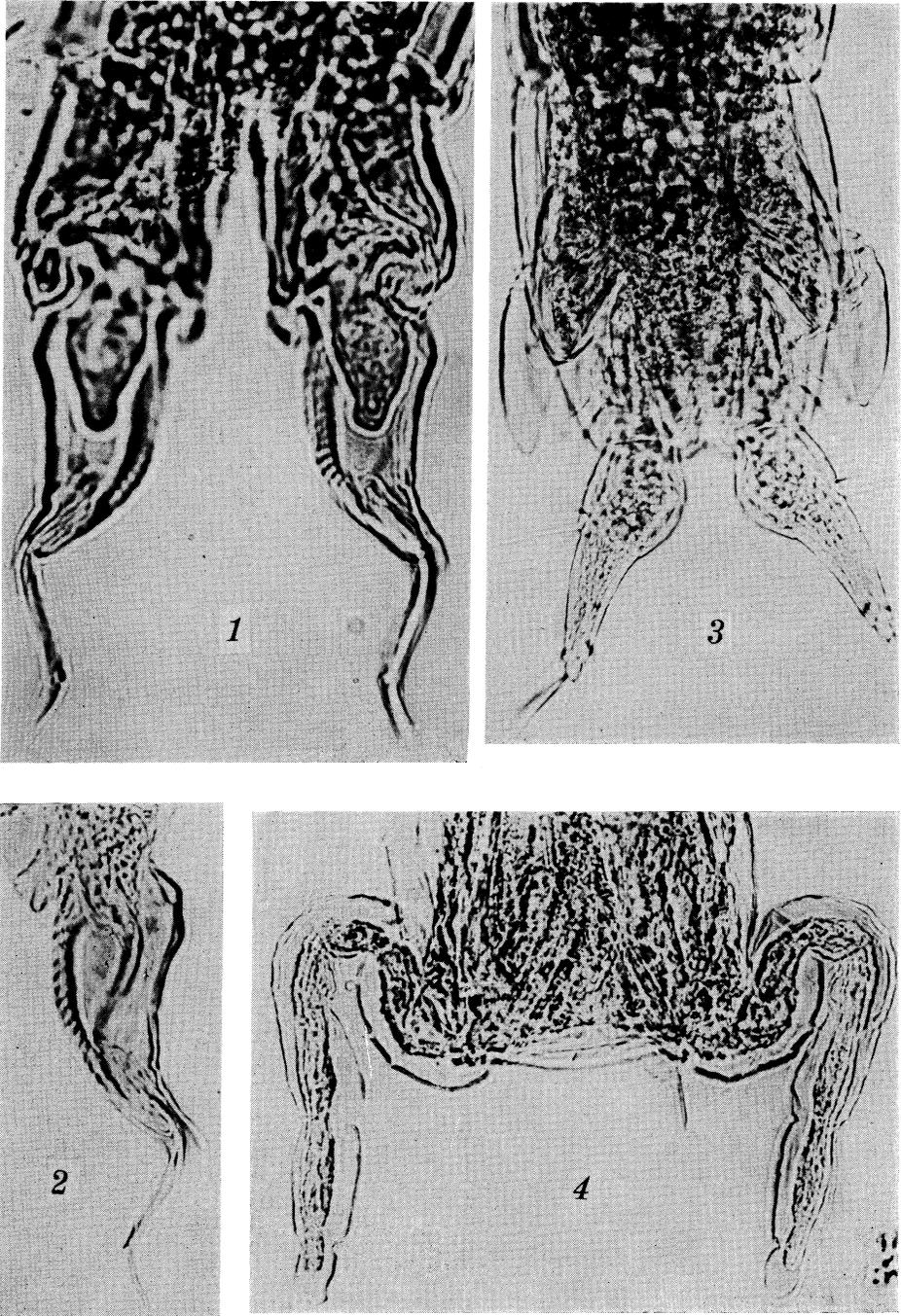


Plate II. *Microcerberus abbotti* n. sp. (1) The second pair of pleopods. $\times 800$. (The same male as in Text-fig. 5, 1 and Pl. I, Figs. 1-3.) (2) Second pleopod of a σ^7 which will soon moult. $\times 800$. (3) Pleotelson of a moulting f . $\times 420$. (4) Seventh pair of pereopods of a manca stage. $\times 600$.

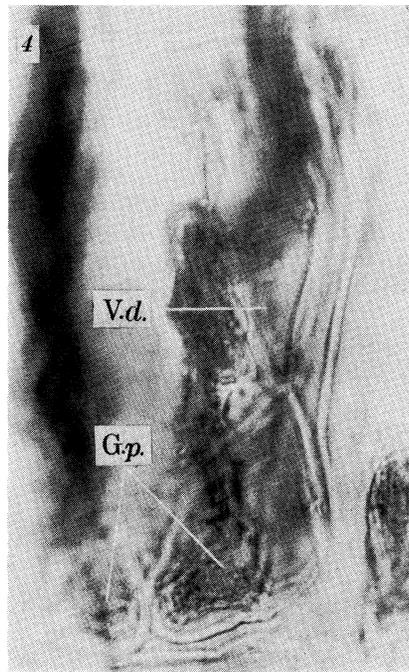
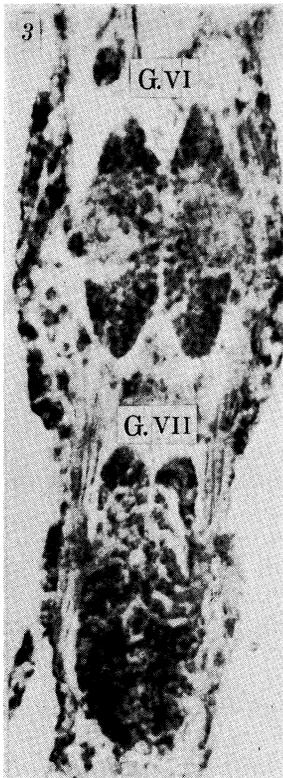
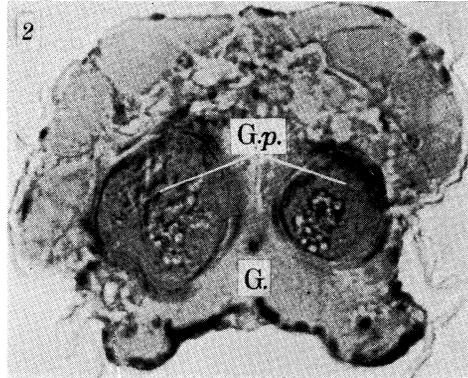
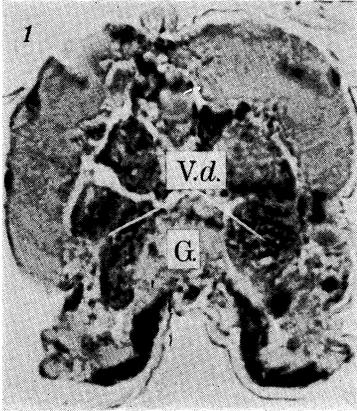


Plate III. *Microcerberus abbotti* n. sp. ♂. (1-2) Transverse sections of peraeonite VII. $\times 1120$. (3) Horizontal section of peraeonites VI-VII. $\times 720$. (4) The genital papillae (the spinous ducts are not visible on the figure). $\times 660$. Vd = vas deferens, G = ganglion, G VI and CVII = ganglion of peraeonites VI and VII, G.p. = genital papilla.