

THE HYPOGEAN PARANTHURIDAE *CRUREGENS* CHILTON AND *CURASSANTHURA* KENSLEY (CRUSTACEA, ISOPODA), WITH REMARKS ON THEIR MORPHOLOGY AND ADAPTATIONS

by

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ABSTRACT

The morphology of the only two known hypogean Paranthuridae (*Cruregens fontanus* Chilton, 1881; *Curassanthura halma* Kensley, 1981) is described. *Curassanthura* has no closely related marine relatives and must be placed at the base of the more specialized Paranthuridae; *Cruregens* is closely related to the specialized genus *Colanthura*, which lives in the upper littoral. Comparing the hypogean paranthurids with *Colanthura*, several analogies can be found in the hypogean species (body slender, only P 1 with stout subchela, P 4-6 slender, P 7 missing, uropods slender or short and bearing long setae), which can be explained from the way of living of the Paranthuridae.

ZUSAMMENFASSUNG

Die Morphologie der einzigen bekannten hypogäischen Paranthuriden (*Cruregens fontanus* Chilton, 1881; *Curassanthura halma* Kensley, 1981) wird beschrieben. *Curassanthura* hat keine nahen marinen Verwandten und steht an der Basis der spezialisierten Paranthuridae; *Cruregens* dagegen ist nah mit der abgeleiteten Flachwassergattung *Colanthura* verwandt. Im Vergleich mit *Colanthura* zeigen sich bei den hypogäischen Paranthuriden mehrere analoge Anpassungen (schlanker Körper, nur P 1 kräftig subchelat, P 4-6 schlank, P 7 fehlend, Uropoden schmal oder kurz und lang beborstet), die sich aus der Lebensweise der Paranthuriden erklären.

INTRODUCTION

The Paranthuridae are a highly evolved group of marine Isopoda living mainly in upper littoral biotopes, where they feed on arthropods. In the present study the morphological and functional adaptations of the only two hypogean Paranthuridae (*Cruregens fontanus* Chilton, 1881 and *Curassanthura halma* Kensley, 1981) are compared and some new details on their morphology are presented.

LIST OF ABBREVIATIONS

A 1	antenna 1	Mxp	maxilliped
A 2	antenna 2	P 1-7	pereopod 1-7
Hy	hypopharynx	Plp 1-5	pleopod 1-5
La	labrum	Tel	telson
Md	mandible	Urp	uropod
Mx	maxilla 1		

Curassanthura halma Kensley, 1981

Another three specimens of this interesting species were found on Curaçao (West Indies). This very recently described species (Kensley, 1981) belongs to a monotypic genus that must be placed at the base of the "higher Paranthuridae" (see Wägele, 1981) and has no marine sister genus. In the following some hitherto unknown features are presented and the phylogenetic position of the genus is discussed.

Material. — Two non-reproductive adult specimens (2 mm, 2.3 mm), Amsterdam Expeditions to the West Indian Islands, sta. 78/308. Curaçao: Blauwbaai, below the entrance of Blauwbaai cave (12°08'20" N 68°59'05" W), gravel and rock, 3 m from the sea, chlorinity 18840 mg/l, Bou-Rouch phreato-biological pump, 20 May 1978, J. H. Stock coll.

One non-reproductive adult (2.2 mm), sta. 78/314. Curaçao, Jan Thiel, just E. of swimming pool (12°04'40" N 68°52'40" W), interstitia in coral rubble, just above the edge of the surf, fully marine, Bou-Rouch phreato-biological pump, 21 May 1978, J. H. Stock & S. Weinberg coll.

The description of Kensley (1981) can be completed with the following observations on an older specimen (sta. 78/308) (figs. 1-3):

Relative length of pereonites: 1 < 2 = 3 = 4 > 5 > 6 > 7. Pereonite 7 very short. Pleonites 1-5 together shorter than pereonite 6, pleonite 6 fused with telson. Mouthparts forming a piercing and sucking cone (fig. 1). Palp of Mxp 5-segmented. P 2 and P 3 not subchelate, very slender, carpus triangular in lateral view. Carpi and propodi of P 4-P 7 slender and cylindrical (fig. 2), P 7 lacking. Exopod of Plp 1 with 9, endopod with 3 swimming setae. Exopod of Plp 2 with 4, endopod with 3 swimming setae. Tail-fan see fig. 3.

Remarks. — The Paranthuridae sensu Wägele (1981) comprise genera with "normal", i.e. not piercing mouthparts, as well as genera with a very specialized piercing and sucking cone (= Paran-

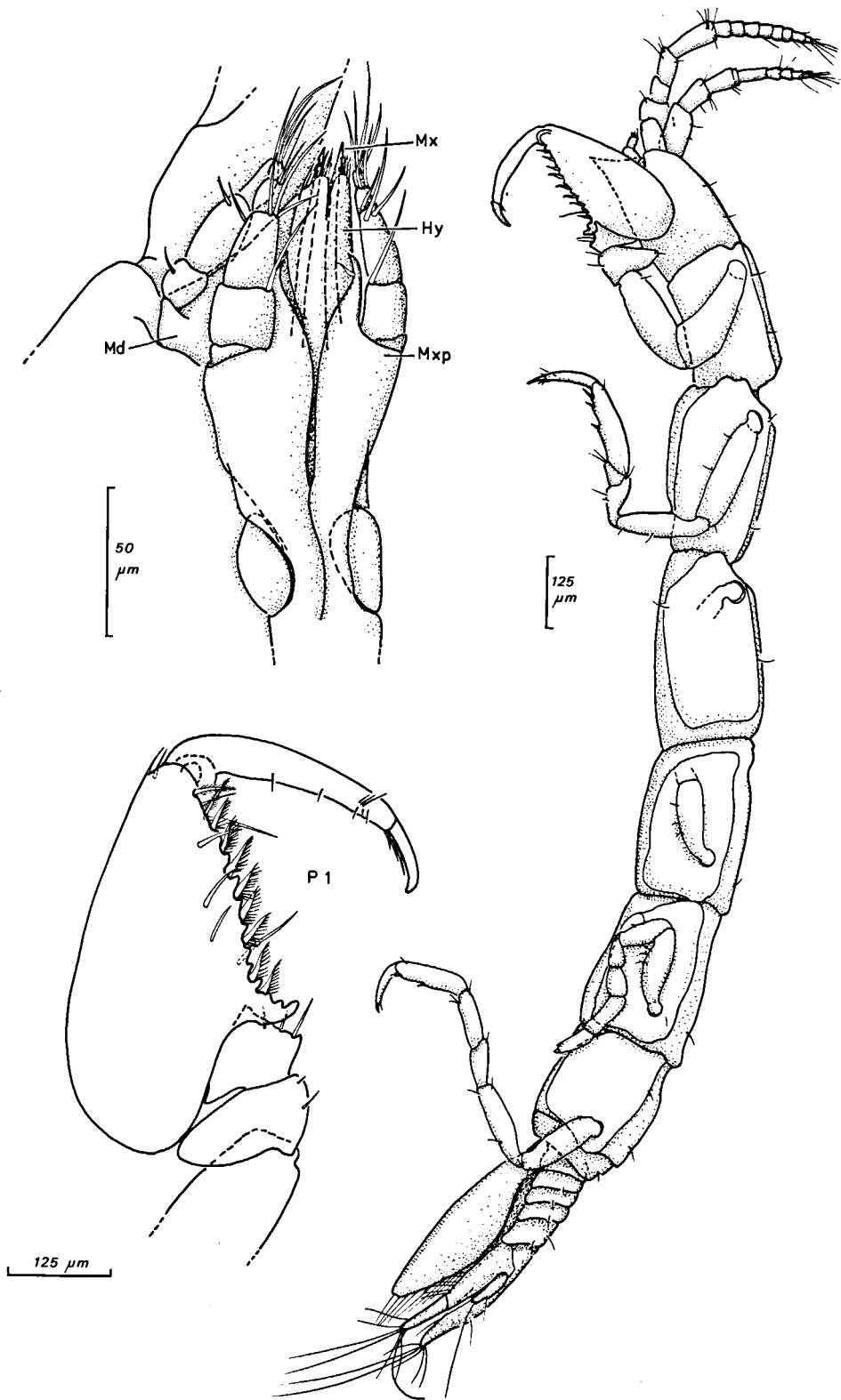


Fig. 1. *Curassanthura halma* Kensley, 1981 (immature adult). For symbols consult list of abbreviations.

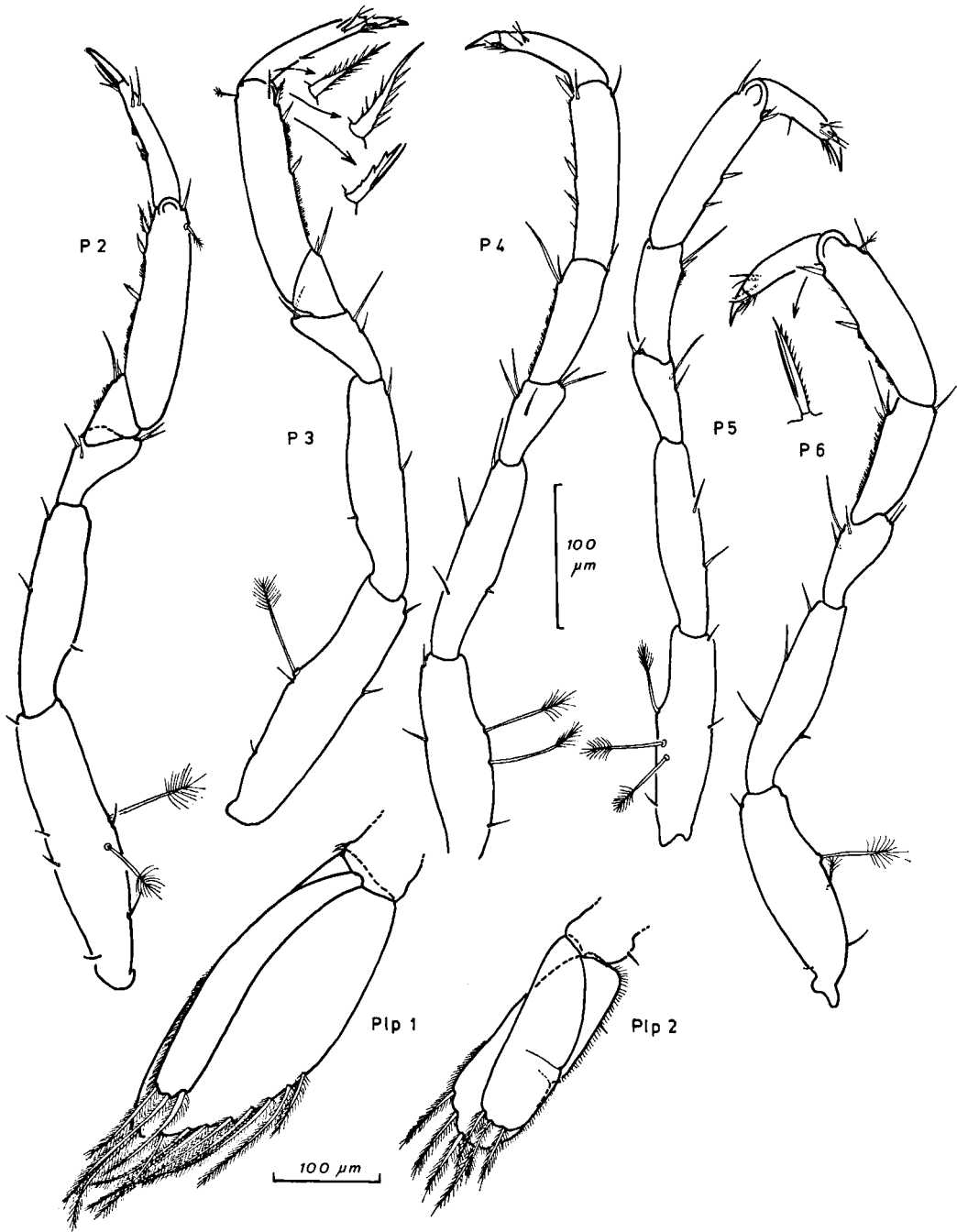


Fig. 2. *Curassanthura halma* Kensley, 1981 (immature adult).

thuridae sensu Menzies & Glynn, 1968). Between both groups of genera some intermediate forms exist, as demonstrated by the genera *Panathura* Barnard, 1925, *Expanathura* Wägele, 1981 and *Natalanthura* Kensley, 1978. Morphologically, between *Natalanthura* and the basic group of the "Paranthuridae sensu Menzies & Glynn" there is a gap. In this basic group the Md has already an acute pars incisiva, the lateral endite of the Mx has its distal teeth reduced, and the palp of the Mxp is short, slender and the number of articles is reduced to three. *Curassanthura* appears to fill this gap. The mouthparts of *Curassanthura* are more evolved than in *Natalanthura*, but primitive in comparison with *Accalathura*/*Calathura*. The acute cone of the mouthparts is already formed, the Mxp is slender and has a long basipodite, but the palp still has 5 articles. In contrast to the "higher Paranthuridae" the pereopods 2 and 3 are slender, not subchelate. On the other hand, *Curassanthura* has a basal projection on the palm of the propodus of P 1 and several serrated spines on the propodi of P 2-P 6, features very common among the "Paranthuridae sensu Menzies & Glynn". The antennae are primitive in having a long flagellum; the last article of the A 1 bears no aesthetascs.

***Cruregens fontanus* Chilton, 1881**

Since 1894, the date of the more detailed description of *C. fontanus* by Chilton, no new data have been published on this singular freshwater paranthurid. The following descriptions are based on a collection of *C. fontanus* in possession of Professor H. K. Schminke, who sampled them in different localities in New Zealand in 1967/68. Chilton (1894) had not found sexually mature male specimens in his material. In the following mature males are described for the first time, proving that *Cruregens* really reaches maturity in the manca stage. Chilton's description can be completed with some detailed drawings.

Material. — Several specimens with a length between 4 and 8.5 mm. Localities (fig. 2 in Schminke, 1973): New Zealand, North Island, sample No. 63 (South Hinaki Stream, North Branch, gravel at riverside, 5.7.1967, NZMS: N 157/975/614), No. 85 (Makareta River, at the bridge of the Takapau Rd., gravel, depth 40 cm, 28.7.1967, NZMS: N 145/802/772), sample from Carrington (Wairarapa) leg.

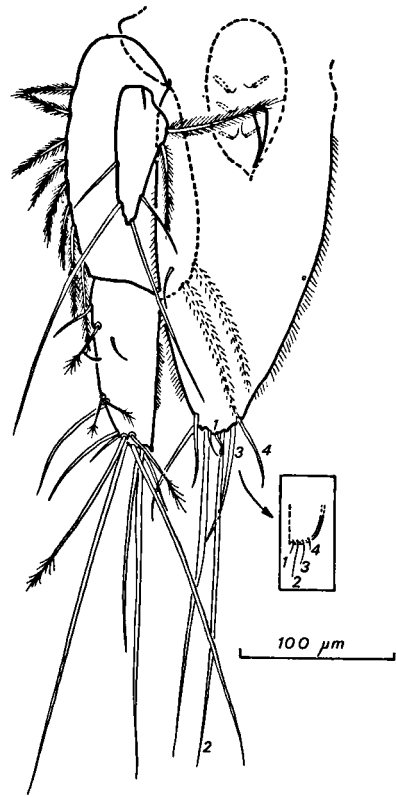


Fig. 3. *Curassanthura balma* Kensley, 1981 (immature adult).

C. L. Hopkins; South Island: sample No. 121 (Ashley River, fine gravel with stones, 8.85 m from riverside, depth 95 cm, 3.11.1967, NZMS: S 67/588/939), No. 158 (Leader River, gravel, 7.10 m from riverside, depth 65 cm, 18.1.1968, NZMS: S 55-56/589/599).

Description of a male (8.5 mm) from Wairarapa (figs. 4-7: M₁). — Cephalothorax longer than wide, eyes lacking; without chromatophores; relative length of pereonites: 1 < 2 = 3 = 4 = 5 > 6 > 7. Pleon shorter than pereonite 6, pleonites 1-5 not fused; pleonite 1 longest, pleonite 6 fused with telson.

A 1 with 5-segmented flagellum; first article of flagellum small, with 1 feather-like bristle, second and third article longest, third article with 4 distal aesthetascs and 3 setae; fourth and fifth article very short, each with 1 aesthetasc, last article with 4 long setae. A 2 with rudimentary flagellum (fig. 5).

Mouthparts covered dorsally by labrum. Md without palp, immovably fused with cephalothorax, pars incisiva not acute. Mx lancet-like as in all higher paranthurids, apex serrated laterally.

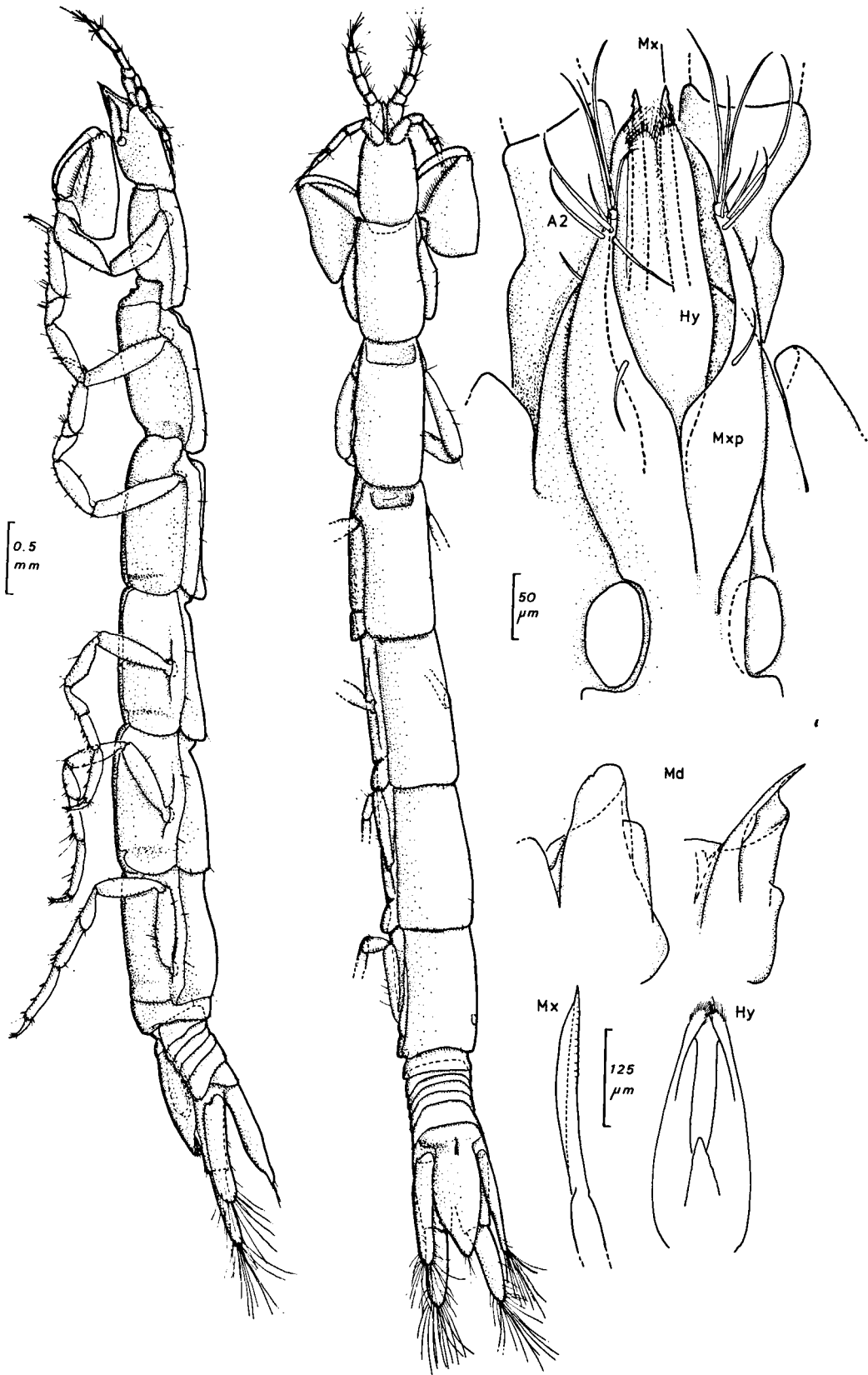


Fig. 4. *Cruregens fontanus* Chilton, 1881 (male from Wairarapa, New Zealand). Mandible (Md) from two different views.

Hypopharynx with long lateral lobes, fringed distally; medial lobes shorter, fused medially. Left and right Mxp fused medially at the base, with only 1 tiny distal article, reduced endite; dorsal side of Mxp concave, covering mouthparts ventrally (fig. 4).

P 1 very stout, propodus broadening proximally, palm with basal projection and a row of about 40 simple setae and a second row of 16 pectinate spines and one simple seta (fig. 5). Lateral side of propodus with distal row of 5 simple setae. P 2 and P 3 with slender propodus, palm with 6 sensory spines. P 4-P 6 with long, cylindrical articles, carpus and propodus each with 3 sensory spines.

Exopod of Plp 1 operculiform, with 9 short swimming setae, endopod slender and shorter, with 8 short swimming setae. Exopod of Plp 2 with 5 swimming setae, endopod without setae. Appendix masculina stiletto-like (fig. 7), not surpassing endopod. Plp 3, see fig. 7.

Telson dorsally convex, without statocysts, apex bearing 3 pairs of setae (see scheme for M_3 , fig. 7).

Uropods long and slender. Sympod somewhat shorter than endopod; endopod less wide than sympod, surpassing telson, with distal tuft of long setae. Exopod longer and nearly as wide as endopod, with distal tuft of long setae.

Variations. — In figs. 5-7 some features of males (M_{1-3}) and of a non-reproductive adult

(A) can be compared. The investigation proves that the specimens from the North Island of New Zealand have the same variability as those from the South Island. Most of the variations are due to differences of age and size (see table I).

Males are discernible by features of the A 1 and the appendix masculina. The appendix masculina of mature males (fig. 7: Plp 2) surpasses the branches of the pleopod. The flagellum of A 1 has 5 instead of 3 articles (fig. 5) and bears more aesthetascs than the undifferentiated adult. The immature male (fig. 5: M_1) has no aesthetascs on the second segment of the flagellum, whereas the mature males (M_2 , M_3) have 3 aesthetascs, altogether 7-10 aesthetascs on the A 1. It can occur that the two distal articles fuse (fig. 5: M_3). Some variations of the setation, probably due to injuries, could be observed comparing left and right extremities of one animal and the telsonic apex of different animals.

Remarks. — Mature females were not present in the samples studied. Perhaps females of *Cru-regens* have their oöstegites reduced. In such case females would not differ in their morphology from the undifferentiated adult.

The specimen drawn by Chilton (1894) seems to have been a male (aesthetascs on A 1!), but it had three tiny distal segments on the A 1 instead of 2. Chilton's specimen also had a richer setation than the animals of the present study, probably due to its large size (table I). The struc-

TABLE I
Variations of the setation of *Cru-regens fontanus* in relation to body length.

Sample	No. 121	Wairarapa	No. 158	No. 63	No. 85	Wairarapa	Chilton, 1894
length (mm)	5	4.5	5.5 (♂)	6.5	7 (♂)	8.5 (♂)	12
spines on propodus of P 2/P 3	3	4	4	4	6	6	8
spines on carpus/propodus P 4	1/2	2/2	2/2	2/3	2/3	3/3	3/5
spines on carpus/propodus P 5	2/2	2/2	2/3	2/2	?*)	3/3	?*)
spines on carpus/propodus P 6	2/2	2/2	2/2	2/3	?*)	3/3	?*)

*) No. 85 had incomplete P 5/P 6; Chilton omitted descriptions of P 5 and P 6.

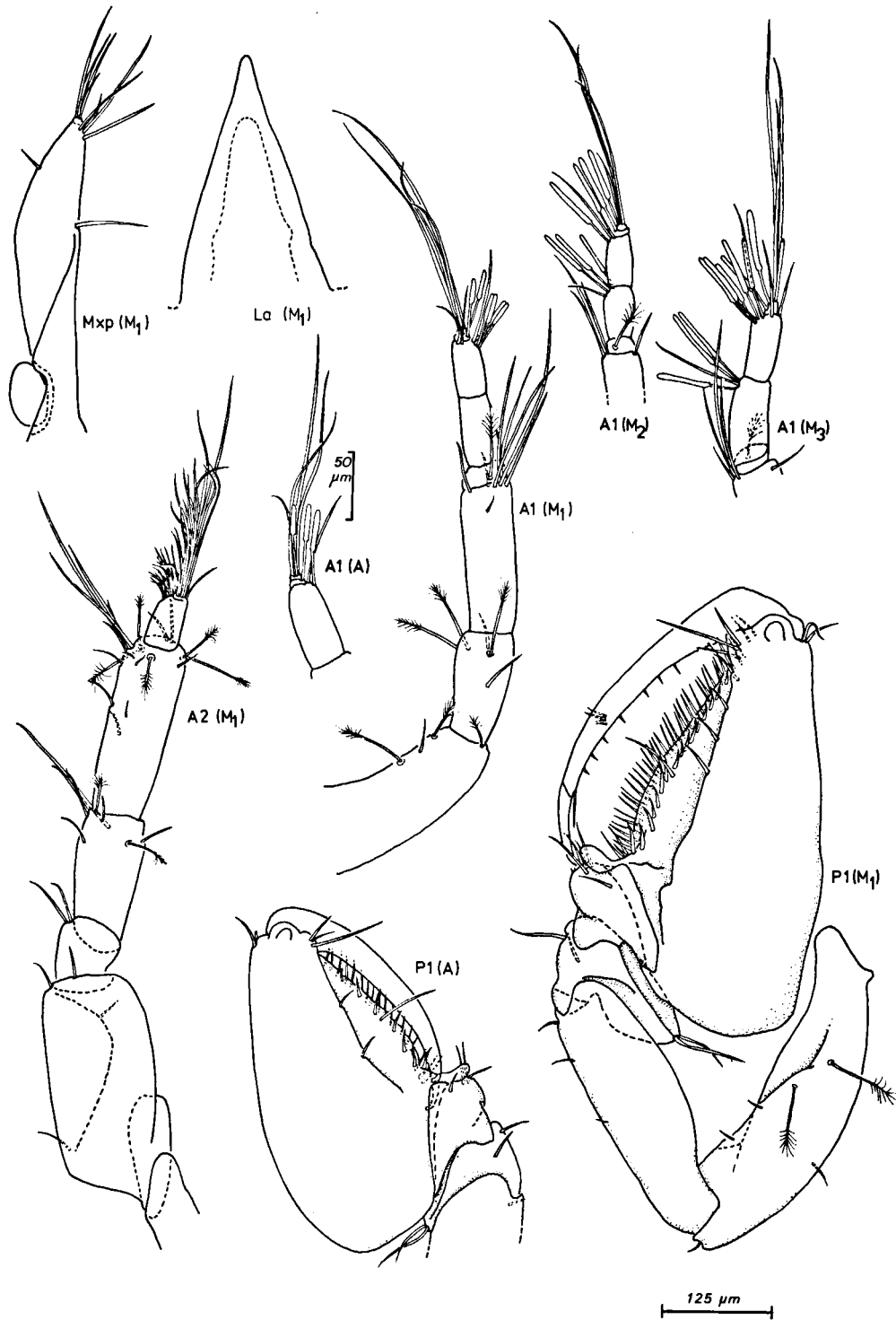


Fig. 5. *Cyuregens fontanus* Chilton, 1881. M₁ = male from Wairarapa; M₂ = male from sample No. 158; M₃ = male from sample No. 85; A = immature adult from Wairarapa.

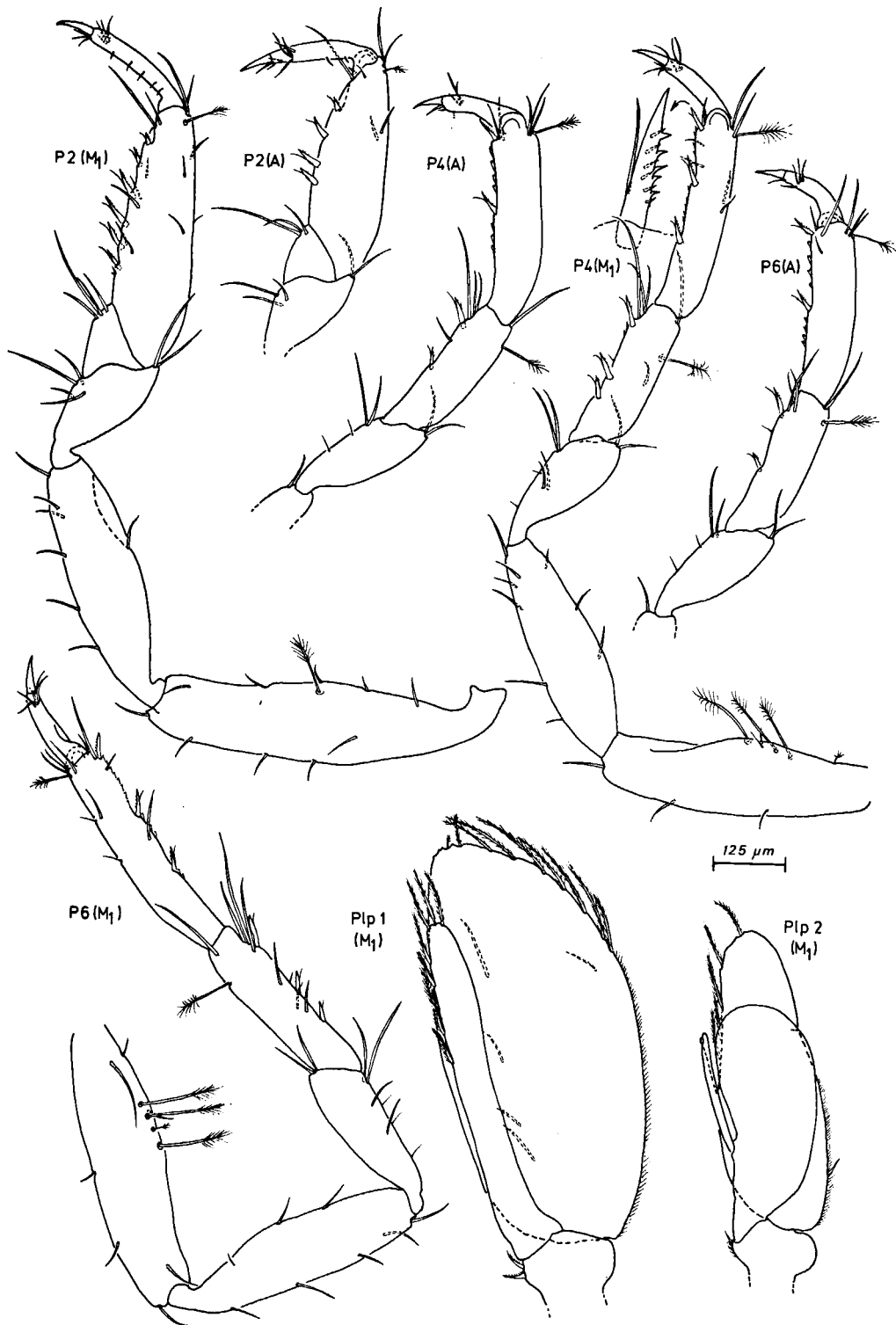


Fig. 6. *Cruregens fontanus* Chilton, 1881. Male (M₁) and immature adult (A) from Wairarapa.

ture of the mouthparts of *Cruregens* is no enigma anymore, the parts can be homologized with other paranthurid mouthparts. The hypopharynx of the Paranthuridae is not fused with the Mx 2 (as suspected by Dohrn, 1869, and Chilton, 1894) as the Anthuridea have no Mx 2. This is reduced during the development of the embryo (Wägele, 1979a). Chilton's description of the Md is correct. His statement "the telson is distinctly separated from the sixth segment" (Chilton, 1894: 217), often repeated in literature for several Anthuridea, is not exact; the authors have been misled by a dorsal ridge on the anterior part of the pleotelson which is taken for an articulation: telson and pleonite 6 are fused.

As far as our present knowledge goes, *Cruregens* must be placed within a young, specialized group of the Paranthuridae being closely related to the genus *Colanthura* (features of A 2, Mxp, Md; absence of P 7 and statocyst: Wägele, 1981). Species of *Colanthura* live in upper littoral biotopes and often have dark chromatophores, but there are also blind and colourless species (*C. caeca* Mezhov, 1976) resembling *Cruregens* in these features. The Md of *Colanthura* has been described in few species but it has the same characteristics as in *Cruregens*. The palp is lacking, the pars incisiva is not prolonged to a stiletto-like structure (Menzies, 1951; Nunomura, 1975; Mezhov, 1976) and it seems that the Md is fused with the cephalothorax. *Cruregens* differs from *Colanthura* by the shorter flagellum of A 1, which bears short aesthetascs; by the slender propodi of P 2, P 3 and the longer carpi of P 4-P 7; the propodus of P 1 of the male has no proximal group of short setae; the narrow uropods of *Cruregens* are longer than the telson and bear a tuft of very long setae; the pereon is less wide in the hypogean species; the endopods of the pleopods 2-5 have no swimming setae.

ADAPTATIONS TO HYPOGEAN LIFE

Most of the features in which *Cruregens* differs from *Colanthura* probably are adaptations to hypogean life. It is evident that such species have to be slender (Delamare Deboutteville, 1960: 105), the delicate aesthetascs cannot be long, oöstegites

of females might be reduced (Vandel, 1964: 417) as in isopods burrowing in sand (*Excirolana*, *Paragnathia*; Klapov, 1970) or in the tube-dwelling *Eisothistos* (Wägele, 1979b). As these animals probably do not swim they do not need long swimming setae on the pleopods. The modifications of P 1-P 3 are understandable if one considers the nutrition of the Paranthuridae (Wägele, 1981): With the help of the modified mouthparts, including the immovable Md, *Cruregens* is only able to puncture a prey with the Mx and to suck it by oesophageal peristaltics. For this purpose the prey must be seized and held in front of the mouthparts with the stout P 1. In the narrow spaces of the interstitial system the subchelae of P 2 and P 3 cannot take part in this task and therefore are more slender than in other Paranthuridae.

Knowing the function of the uropods in anthurid isopods (Wägele, 1981) the special structure of these extremities in *Cruregens* can be explained: Species living in sand and mud burrow backwards by opening the tail-fan and widening the passage with the broad exopod of the uropods. The tail-fan of non-burrowing Anthuridea is modified having a tiny exopod of the uropod or an operculiform tail-fan to close worm-tubes *Eisothistos*, *Anthura*; some species of *Paranthura*; possibly also *Pseudanthura*, *Xenanthura*). Burrowing is not necessary for animals living in interstitial spaces. Another important function of the tail-fan is the palpation of the surrounding space for the orientation during backward movement or retreat. From this point of view it is understandable that the exopod of the uropods of *Curassanthura* and *Cruregens* is slender or short, bearing long setae.

The functional interpretation of the morphological adaptations is supported by the analogies found in *Cruregens* and *Curassanthura*. *Curassanthura* is not closely related with *Cruregens*. The obvious analogies are the stout P 1, the slender P 2 and P 3, the cylindrical articles of P 4-P 6, the reduction of the P 7 (an indication for a process of fetalization). The uropods are not used for tube-building and bear long setae.

The mechanism by which the paranthurids conquered the marine-interstitial and the freshwater-phreatic biotas is not known. *Curassanthura* could

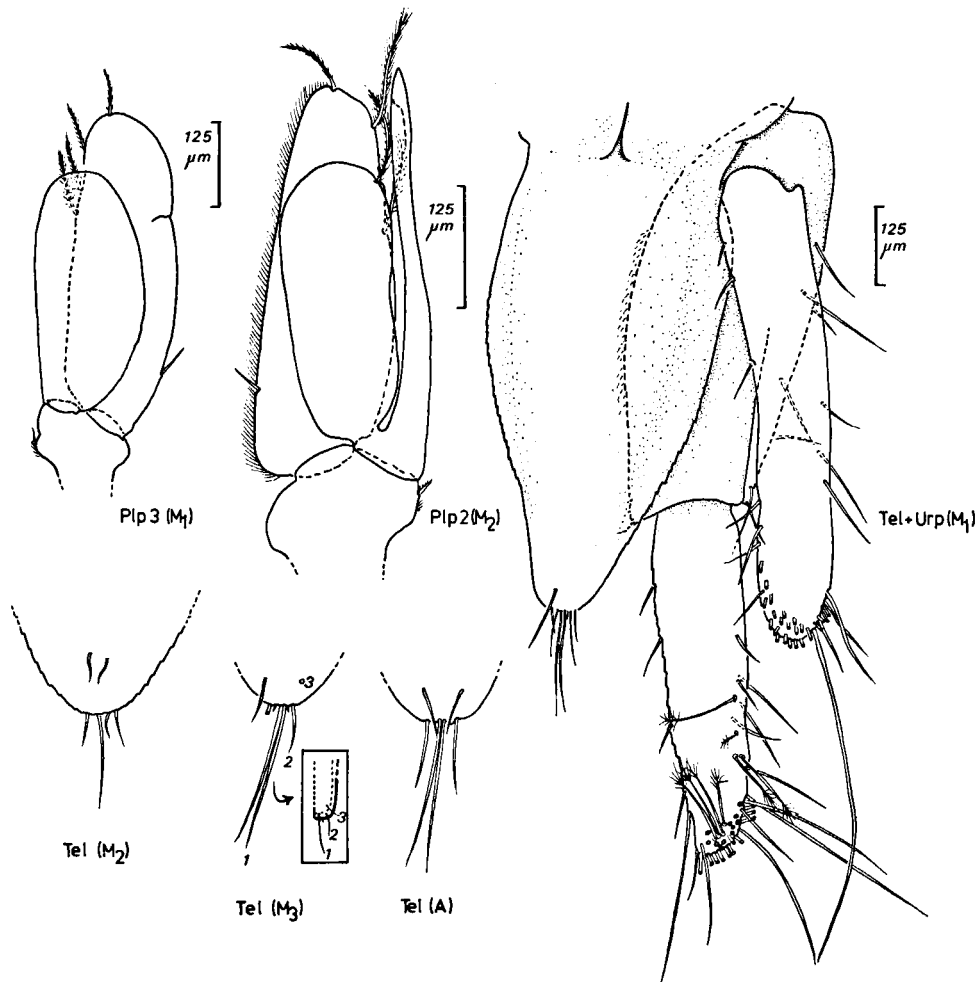


Fig. 7. *Cruregens fontanus* Chilton, 1881. For symbols see legend of fig. 5. Tail-fan of M_1 in dorsal view, most of the long setae of the uropods cut off.

have evolved by direct migration from the sea into the marine-interstitial habitat (Kensley, 1981), but possibly at a very early time, as no marine relative is known. It is interesting to note that other stygobiont paranthurids very similar to *Curassanthura* live in the marine-interstitial on the distant isle of Cuba (Coineau & Botosaneanu, 1973: photo XIII, p. 221) suggesting a long history of these hypogean paranthurid populations in the Caribbean (for models of evolution see Stock, 1981). In the case of *Cruregens* the marine relatives belong to a specialized genus (*Colanthura*) of shallow water; after overcoming the salinity barrier the adapted species spread over the freshwater phreatic biotas of New Zealand.

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