Bijdragen tot de Dierkunde, 50 (2): 375-386 — 1980

AMSTERDAM EXPEDITIONS TO THE WEST INDIAN ISLANDS, REPORT 8 *)

A NEW CAVE AMPHIPOD (CRUSTACEA) FROM CURAÇAO: *PSAMMOGAMMARUS CAESICOLUS* N. SP.

by

JAN H. STOCK

Institute of Taxonomic Zoology, University of Amsterdam, P.O. Box 20125,
1000 HC Amsterdam, The Netherlands

ABSTRACT

A new species of Amphipoda, *Psammogammarus caesicolus,* is described from interstitial, anchihaline waters in Blauwbaai cave, Curaçao, Netherlands Antilles. By the morphology of the third uropod, the new species links the somewhat aberrant *Ps. longiramus* from the Red Sea with the type-species of the genus, *Ps. coecus,* from the Mediterranean.

The classification of the *Eriopisa* complex, to which *Psammogammarus* belongs, is reviewed, resulting in a stricter delimitation of, presumably monophyletic, genera, and the creation of three new genera: *Madapisella* (type-species *Eriopisa madagascarensis* Ledoyer, 1968), *Nippopisella* (type-species *Eriopisella nagatai* Gurjanova, 1965), and *Tunisopisa* (type-species *Eriopisa seurati* Gauthier, 1936). The distribution of the known species over the various genera is revised as well.

1. INTRODUCTION

The amphipod described in the present paper has been known to me for a good number of years. It is not uncommon in the cave of Blauwbaai, on the southern coast of Curaçao, where it inhabits a rather special habitat, viz. the interstitia of the sand, coral debris and rubble on the cave bottom (and not the "open" water of the small pool at the end of the cave, which is the habitat of another hypogean amphipod, *Metaniphargus curasavicus orientis* Stock, 1977). Single specimens of the species described here as new have also been found accidentally in the interstitia, always in coral debris, of two other localities in Curaçao, although this type of habitat is mainly characterized by another amphipod, *Saliweckelia emarginata* Stock, 1977.

All specimens found so far were devoid of their third uropods, and so the study of the material has been postponed for several years. During our stygobiological explorations in the West Indies (see station list, Stock, 1979), a special trip was made to Blauwbaai cave, and this time entirely intact specimens were caught, on which the present description is based.

The material belongs to the genus *Psammogammarus,* as recently redefined by G. Karaman & Barnard (1979). The morphology of its third uropod links the somewhat aberrant *Ps. longiramus* (Stock & Nijssen, 1965), from a salty subterranean habitat in Entedebir, a Red Sea island, with the generotype of *Psammogammarus, Ps. coecus* S. Karaman, 1955, from the Mediterranean.

2. **Psammogammarus caesicolus** n. sp.

2.1. Material examined. — CURAÇAO: 1 ♂ (holotype), 12 paratypes (both sexes), sta. 78-309, Blauwbaai cave (12°08'20" N 68°59'05" W), in interstitia of cave bottom (rubble, sand, loam); anchihaline habitat, chlorinity at the moment of collection 9400 mg/l; May 20, 1978 (Zoölogisch Museum Amsterdam, coll. no. ZMA Amph. 106, 583).

Six specimens, sta. 73-17, same locality, pumped with phreatobiological pump in gravel near the cave entrance, occasional marine splash; chlorinity 17820 mg/l; December 28, 1973 (ZMA Amph. 106, 586).

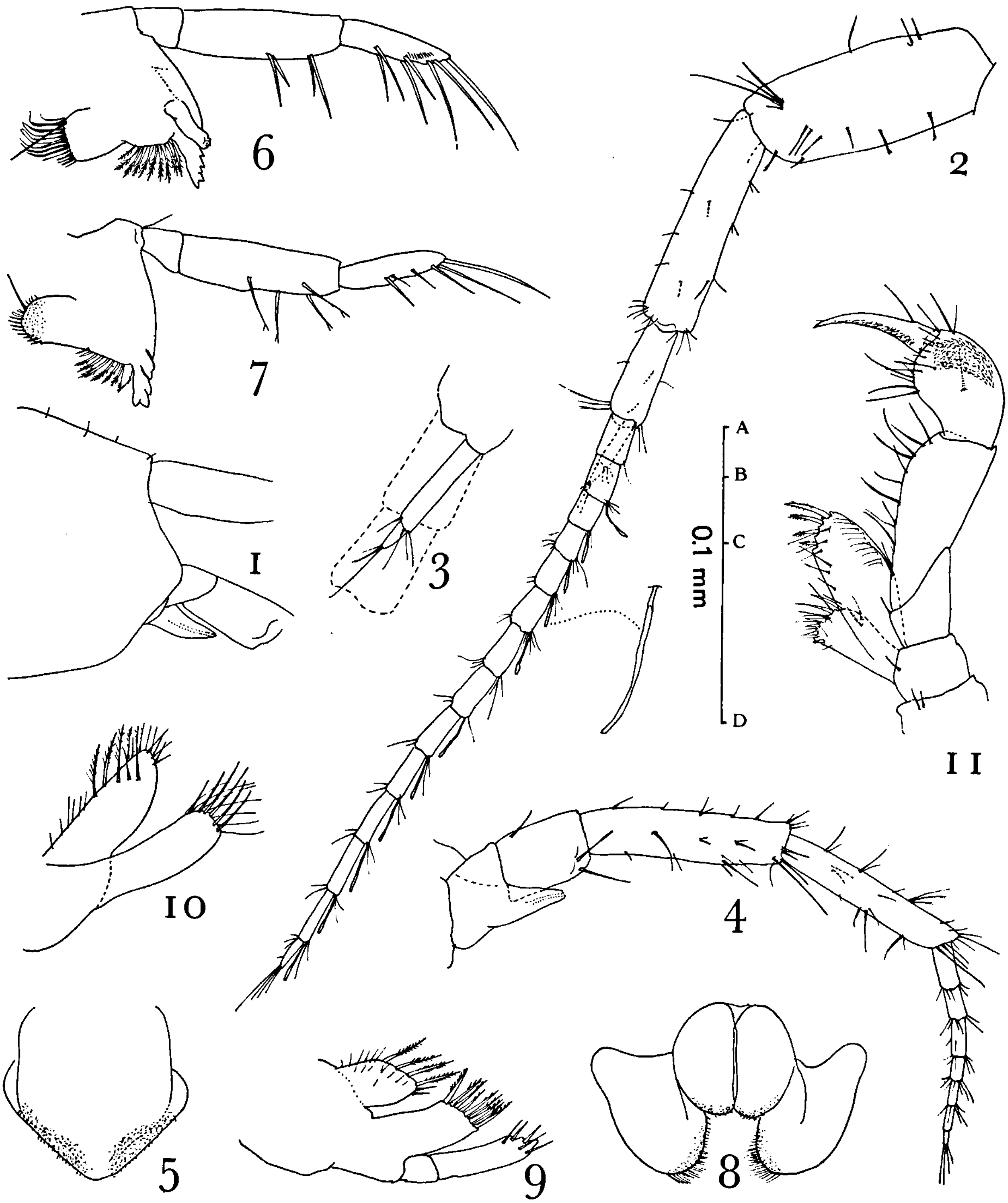
One ♀, sta. 73-19, St. Michiel (12°09'05" N 68°59'49" W), in coral debris of a bar between the saltpit and the sea; chlorinity 33858 mg/l; December 30, 1973 (ZMA Amph. 106, 585).

One ovigerous ♀, Hummelinck sta. 1619, Salinja Jan Thiel, seepage of sea water behind wall of coral debris, chlorinity < 50 000 mg/l, October 28, 1967 (ZMA Amph. 106, 584). (See Hummelinck, 1977: 8 and 60.)

2.2. Derivatio nominis. — The proposed specific name, *caesicolus,* is composed of the Latin words *caesius* (= blue) and *incolere* (= to inhabit), in allusion to the Blauwbaai (= Blue Bay) cave.

---

*) Report no. 7 appeared in Stud. Fauna Curaçao, no. 190: 61-65 (1980).



Figs. 1-11. *Psammogammarus caesicolus* n. sp. (♂ holotype, ♀ paratype): 1, head, ♂, from the right (scale AB); 2, first antenna, ♂ (AB), one of the aesthetes more strongly magnified; 3, accessory flagellum, ♂ (AC); 4, second antenna, ♂ (AB); 5, labrum, ♀ (AC); 6, left mandible, ♀ (AC); 7, right mandible, ♀ (AC); 8, labium, ♀ (AC); 9, first maxilla, ♀ (AC); 10, second maxilla, ♀ (AC); 11, maxilliped, ♀ (AC).

2.3. Description. — Unpigmented. Blind. Entire animal very similar in aspect to *Eriopisa longiramus* (see Stock & Nijssen, 1965, fig. 3a). Females with only few (1 or 2) large eggs. Body length (head to base of telson) up to 3.2 mm. First antenna of largest specimens 2.43 mm long, third uropod 1.36 mm. Body smooth, except for scattered minute setules on its dorsal surface.

Head (fig. 1) without antennal sinus.

First antenna (fig. 2): 1st segment 470 μm, 2nd segment 451 μm, 3rd segment 203 μm. Flagellum 14-segmented, all segments but the first with a slender aesthete. Accessory flagellum (fig. 3) 2-segmented, slightly longer than the 1st flagellum segment. Setosity sparse.

Second antenna (fig. 4) slightly more than half as long as the first antenna: gland cone tapering, straight, rather long; peduncle segments 4 and 5 subequal, slender; flagellum longer than peduncle segment 5, 7-segmented. Setosity sparse.

Labrum (fig. 5) triangular.

Mandibles slightly asymmetric. Left mandible (fig. 6): pars incisiva with 2, finely toothed, blades and 10 barbed setae; pars molaris with 13 + 1 long setae. Right mandible (fig. 7): pars molaris with 2 coarsely toothed blades, a lacinia mobilis and 8, partly barbed, setae; pars molaris with numerous short and 1 long setae. Both mandibles have a 3-segmented palp, of which segment 2 is by far the longest; segment 1 is naked, segment 2 bears 4 setae, segment 3 bears 3 terminal and 3 or 4 ventral setae, the latter not arranged in a regular row.

Labium (fig. 8) with fleshy inner lobes, outer lobes well-separated.

First maxilla (fig. 9): palp 2-segmented, symmetrical, armed with 2 + 3 stiff setae; outer lobe with 9 distal spines; the outer spines with 2, 3 or 4 medial teeth, the innermost spine with 7 such teeth; inner lobe widened, with 2 small, naked, and 4 to 5 longer, plumose setae.

Second maxilla (fig. 10): outer lobe with 6 to 7 setae; inner lobe with 3 + 7 distal setae, an oblique row of 5 plumose setae and some medial cilia.

Maxilliped (fig. 11): distal palp segment swollen; claw slender, long. Outer lobe with 4 distal spines; inner lobe with 6 spines and some setae.

First gnathopod (fig. 12): coxal plate as long as wide, rounded-rectangular; carpus much shorter than propodus, triangular; propodus longer than wide, palm convex, moderately oblique; 3 palmar angle spines; palmar margin with a row of minute spinules and 2 mid-palmar setae; claw slender, external seta beyond 1/3 of the length of the claw.

Coxal gills on second to sixth legs.

Second gnathopod (fig. 13): coxal plate slightly longer than wide; carpus short, triangular, without free lobe. Propodus sexually dimorphous. In the male (fig. 14), there are 4 palmar angle spines placed at a slight distance from the palmar corner; the latter is indicated by a triangular process; the palmar margin is proximally convex, distally it shows a marked rounded excavation; the palmar margin is armed with bifid spinules (fig. 14, detail) and 6 setae. In the female (fig. 15) there are 3 palmar angle spines and the palmar margin is regularly convex over its entire length. In both sexes, the outer dactylar seta is situated beyond 1/3 of the length of the claw.

Oöstegites narrow, linear, armed with 5 setae (fig. 17).

Third and fourth pereiopods (figs. 16, 18) similar; coxal plates trapezoidal, slightly longer than wide; distal segments poorly setose. Propodus with about 6 sole spines.

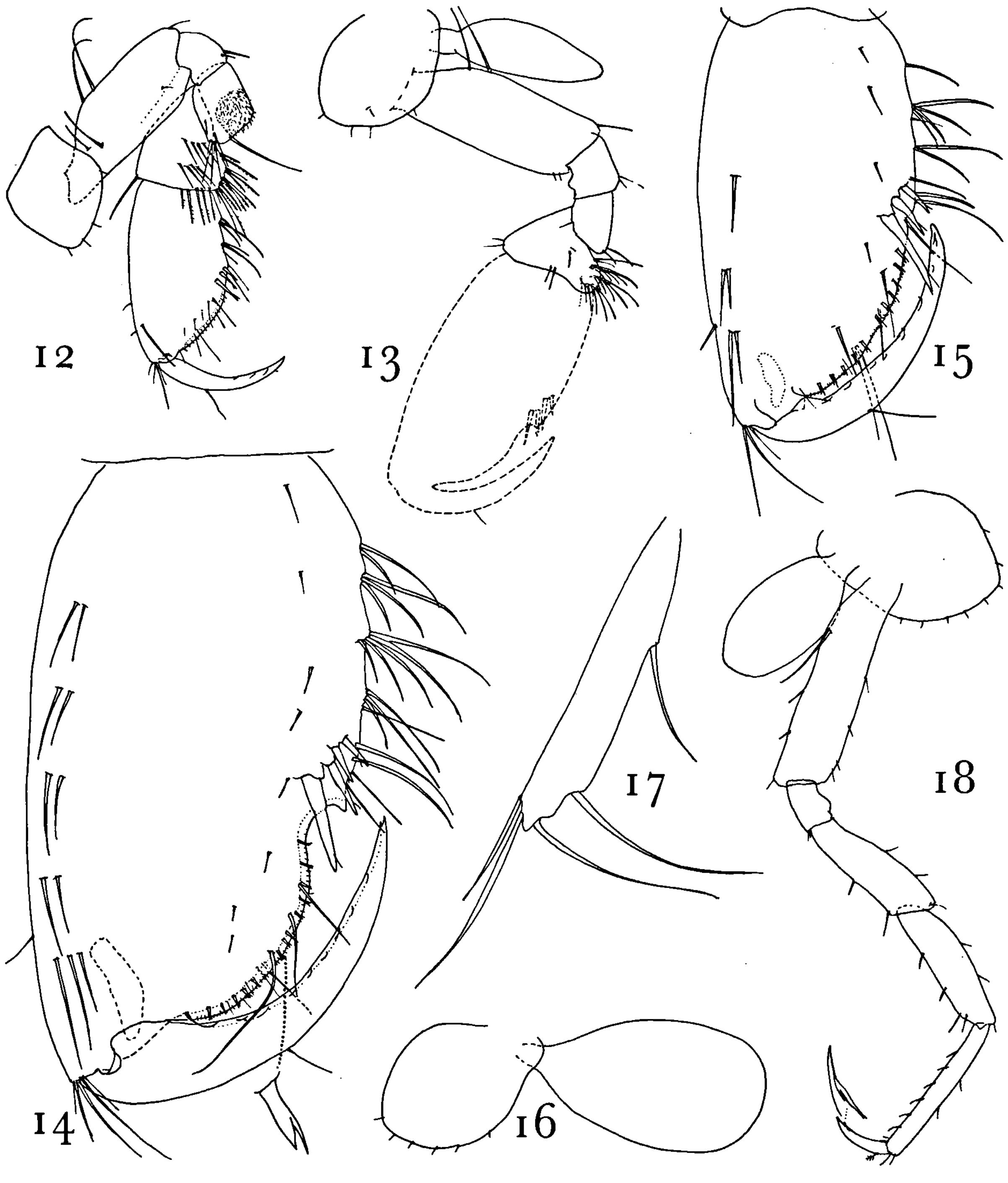
Fifth pereiopod (fig. 19) shorter than the sixth; coxal plate with larger anterior and smaller posterior lobe; basis slightly tapering, almost rectangular; posterior margin of basis almost straight, armed with some 10 spinules; posterior corner not lobate. Long segments moderately spinose.

Sixth pereiopod (fig. 20) shorter than the seventh; coxal plate with 2 lobes of equal size; basis about as in P5. Long segments moderately spinose.

Seventh pereiopod (fig. 21): coxal plate practically not lobate; basis slightly tapering, posterior margin slightly curved, armed with 9 or 10 setules, almost not lobate.

Pleopods biramous, normally segmented, not transformed; 2 retinacula (fig. 22) per pleopod, hook-shaped.

Epimeral plates subrectangular (fig. 23); inferior margin with 0 (plate I) or 1 (plates II and III) spinule; posterior margin with 1 setule.



Figs. 12-18. *Psammogammarus caesicolus* n. sp. (♂ holotype, ♀ paratype): 12, first gnathopod, ♂ (scale AB); 13, second gnathopod, ♂ (AB); 14, distal part of second gnathopod, ♂ (AC), one of the bifid spinules on palmar margin more strongly magnified; 15, distal part of second gnathopod, ♀ (AC); 16, coxal plate and coxal gill of third pereiopod, ♂ (AB); 17, oöstegite of third pereiopod, ♀ (AC); 18, fourth pereiopod, ♂ (AB).

Uropod 1 (fig. 24) with 2 or 3 basofacial spines; exopodite shorter than endopodite, both rami with marginal spines.

Uropod 2 (fig. 25): pedunculus with distal row of 4 spines; exopodite shorter than endopodite.

Uropod 3 (fig. 26): pedunculus short. Exopodite 2-segmented, strongly elongated, segment 1 slightly longer than segment 2; margins of segment 1 with several groups of spines. Endopodite tapering, about 3/4 as long as exopodite segment 1; both margins with several spines.

Telson (fig. 27) completely cleft; medial slit narrow; each lobe widest near the base; the length/width ratio of each lobe is about 3; armature, even of contralateral lobes, variable to some degree; fundamentally, 1 pair of mediolateral spines is present, 1 or 2 lateral, subdistal spines, 1 distal spine, 2 long sensory setae and a varying number of shorter spinules and setules.

2.4. Distinction. — Of the four species classified in this paper with *Psammogammarus,* two, *garthi* (J. Barnard, 1952) and *gracilis* (Ruffo & Schiecke, 1976) have short (parviramus type) endopodites on uropod 3. The other two, viz. *longiramus* (Stock & Nijssen, 1965) and *coecus* S. Karaman, 1955, have longer (variiramus) endopodites, a condition shared with the present species.

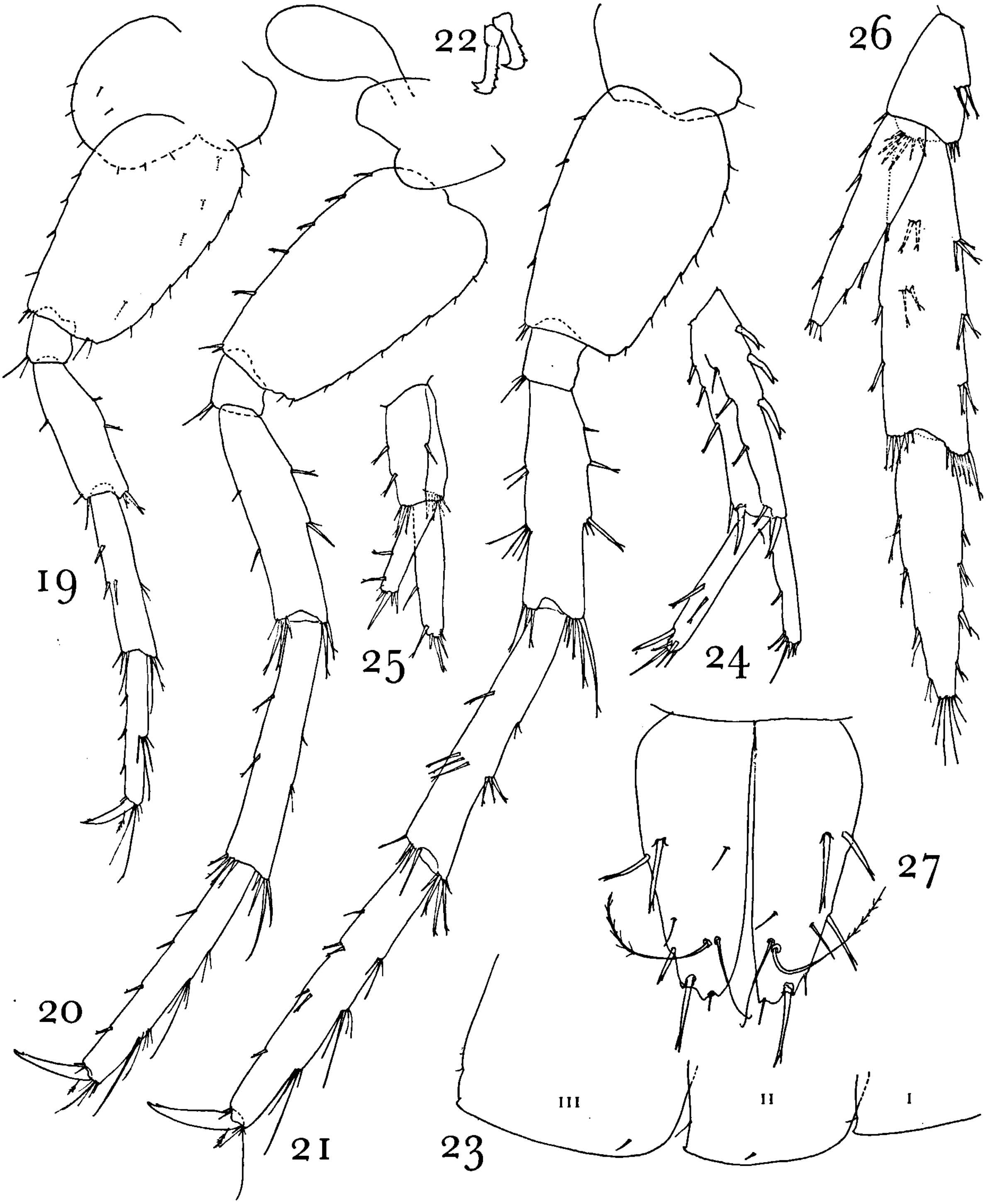
As point of fact, the length of the endopodite of the new species (3/4 of exopodite segment 1) is intermediate between that of *longiramus* (as long as exopodite segment 1) and *coecus* (½). The new species deviates from *longiramus* in the lower number of setae on the inner lobe of maxilla 1 (at most 7 versus 15), and the lower number of setae in the oblique row on the inner lobe of maxilla 2 (5 versus 12). In these respects, it resembles *Ps. coecus* more closely.

There are, however, many differences, be it of rather subtle nature, between *Ps. coecus* and the new species: (1) second segment of accessory flagellum of *coecus* is larger; (2) A2 gland of *coecus* is shorter; (3) coxal plates 1 to 4 of *coecus* are wider than long; (4) the outer dactylar seta of Gn. 1 and 2 is placed in a much more proximal position in *coecus;* (5) the propodus of Gn. 1 of *coecus* is less rectangular and more triangular; (6) gnathopod 2 of *coecus* has only 2 palmar angle spines in both sexes; (7) the propodus of P3 and P4 of *coecus* has fewer (2 or 3) sole spines; (8) the basis of P5 to P7 is not tapering in *coecus,* and the number of setules on the posterior margin is lower; (9) merus and carpus of P5 of P7 bear fewer spines in *coecus;* (10) epimeral plate III of *coecus* is distinctly more pointed; (11) uropod 1 of *coecus* lacks marginal spines on the exopodite; (12) uropod 2 of *coecus* lacks a distal row of spines on the pedunculus; (13) uropod 3 has a shorter endopodite in *coecus,* whereas the spinose armature, both on the endopodite and the first exopodite segment, is less developed; (14) the telson lobes of *coecus* are less slender, about 2½ times as long as wide.

2.5. The type-locality. — Blauwbaai cave was discovered (at least as a profitable stygobiont habitat) during the 1973 fieldwork in Curaçao. The cave has three entrances; the lower one, almost at sea level, is completely blocked by rubble and boulders. There is a small pool near this lower entrance, inhabited mainly by marine animals (Polychaeta, Harpacticoida...). Two other openings, higher in the steep cliff, give access to a single, semi-dark, low chamber which descends gradually to a small pool. The water in this pool is of fluctuating salinity; in rainy periods, it is fresher than during periods of drought. Moreover, the water level moves with the tides. The lowest chlorinity observed (on November 25, 1973) was 8910 mg/l, the highest was well over 22000 mg/l (April 16, 1974). The pool itself is inhabited by *Metaniphargus curasavicus orientis* Stock (Amphipoda), *Cyathura* sp. (Isopoda), Polychaeta and Collembola. When a hole is dug in the rubble of the cave floor, one reaches soon the groundwater which contains the *Psammogammarus* described in this paper, as well as *Halosbaena* (Thermosbaenacea), *Cyathura* (Isopoda), Cyclopoida, Harpacticoida, Polychaeta, and Oligochaeta.

3. THE STATUS OF *ERIOPISA LONGIRAMUS* STOCK & NIJSSEN, 1965

J. Barnard (1976: 424) and Zimmerman & Barnard (1977: 567) are of the opinion that *E. longi-*



Figs. 19-27. *Psammogammarus caesicolus* n. sp. (♂ holotype): 19, fifth pereiopod (scale AB); 20, sixth pereiopod (AB); 21, seventh pereiopod (AB); 22, retinacula of third pleopod (AD); 23, epimeres I-III, from the right (AB); 24, first uropod (AB); 25, second uropod (AB); 26, third uropod (AB); 27, telson (AC).

ramus is "requiring a distinct genus", as it is "to be distinguished ... by variramus uropod 3". This argument is weakened by the large variation in the length of the endopodite of uropod 3 shown in other gammarid genera (e.g. in *Metaniphargus,* cf. Stock, 1977), even on infraspecific level (e.g. in *Rhipidogammarus variicauda,* cf. Stock, 1978). Moreover, the uropodal endopodite of *Psammogammarus caesicolus* n. sp. is just intermediate in length between the so-called aberrant *Ps. longiramus* and the generotype *Ps. coecus.* Bousfield (1977) reckons *E. longiramus* among the genus *Eriopisa* (he does not mention the taxon *longiramus,* but quotes its type-locality, "sink-holes ... Red Sea Region" under *Eriopisa*), whereas G. Karaman & Barnard (1979: 149) classify it with *Psammogammarus.*

Stock & Nijssen (1965) advocated the synonymy of *Psammogammarus* with *Eriopisa.* The main reason for keeping *Psammogammarus* apart, is for J. Barnard (1976: 424), the "loss of sexual dimorphism on gnathopod 2", and for Zimmerman & Barnard (1977: 567) "the apparent loss of sexual dimorphism in gnathopod 2" and "the evenly but minutely spinose palm of gnathopod 2". In the most recent paper (G. Karaman & Barnard, 1979: 149) two entirely new distinctions are brought forward, and the previous ones are dropped: "Differing from *Eriopisa* in the lack of diversity on article 2 of pereiopods 5-7 and the shorter article 3 of the mandible palp, which in *Eriopisa* is much longer than article 2 and which in *Psammogammarus* is shorter than article 2".

As the shift in discriminating features indicates already, the distinction between *Eriopisa* and *Psammogammarus,* if any, is subtle. Certain characters mentioned by J. Barnard and his co-authors are subject to doubt. Certain is, after the elucidating paper of Ruffo & Schiecke, 1976, that the type-species of *Psammogammarus* (by them placed in *Eriopisa),* certainly has not lost sexual dimorphism in gnathopod 2, but that material described as *Eriopisa peresi* Ledoyer, 1968b, actually is the male of the females known as *Psammogammarus coecus* S. Karaman, 1955.

As to the length of article 3 of the mandible palp, I feel that this character is unsuitable for distinctions on generic level (however useful it may be on specific level). At least one species attributable on the basis of all its other characters to *Eriopisa* has a mandible palp characteristic of *Psammogammarus,* i.e. *E. philippensis* (Chilton, 1921). Even within *Psammogammarus* s.str. a trend towards reduction in length of the 3rd mandibular palp article is visible (Ruffo & Schiecke, 1976: 433). This reduction affects at the end also the armature of the palp, as can be seen in *Eriopisella* and its allies.

Reconsidering the matter with the knowledge acquired about the morphological expressions exhibited by the species known in 1980, it appears to me that *Eriopisa* and *Psammogammarus* have an exceedingly similar morphology, but that separation (perhaps not on generic but on subgeneric level?) is possible on the basis of the following characters:

(1) *Eriopisa* has a mid-palmar spine on gnathopod 2 (♂), *Psammogammarus* has not.

(2) *Eriopisa* has a widened, lobate basis on pereiopod 7 (this segment is dissimilar to the homologous segment in pereiopods 5 and 6), whereas in *Psammogammarus* the basal segments of P5 to P7 are similar: elongate and scarcely lobate.

(3) The coxa of gnathopod 1 is sharply pointed anteriorly in *Eriopisa,* rounded in *Psammogammarus.*

(4) In *Eriopisa* P5 is shorter than P6 but P6 is subequal to P7, whereas in *Psammogammarus* $P5 \leqslant P6 < P7$.

Within *Psammogammarus* thus delimited, a mouthpart reduction trend, present in the entire *Eriopisa-Eriopisella*-hadziid group, is also visible (Ruffo & Schiecke, 1976): the number of setae on the inner lobe of maxilla 1 decreases, palp segment 3 shortens and the number of setae of the oblique row on the inner lobe of maxilla 2 decreases.

The most plesiomorphic state, both by its mouthparts and by its third uropod, is shown by *Ps. longiramus.*

We have to await the discovery of other forms before we can make out with certainty whether the four differences mentioned above will be sufficient to delimit *Psammogammarus* from *Eriopisa.* For the moment, I have adhered the line developed in

G. Karaman & Barnard's (1979) elegant attempt to diagnose the various genera more sharply. However, I am worried about the fact that the restricted genera, although morphologically apparently coherent, are not ecologically coherent (members of each still occur all over the transect marine-freshwater), whereas the zoogeographic evolution within each genus is still entirely misty.

4. THE TAXA OF THE *ERIOPISA-ERIOPISELLA* GROUP

The two oldest genera of this group, *Eriopisa* and *Eriopisella,* represent two lines from which a number of other genera can be derived. In essence, these two lines can be distinguished as shown in table I.

Clearly, the *Eriopisa* line is the more plesiomorphic one, closely related to the plesiomorphic members of the hadziid group. In addition to the characters mentioned in table I, the members of the *Eriopisa* line usually have a strongly elongated third uropod, more in particular the 2nd exopodite segment shows a tendency towards elongation (exception: *Tunisopisa*). The *Eriopisella* line usually has a wide, V-shaped telson cleft (exception *Madapisella*), and a shortened mandible palp with strongly reduced armature (exception *Nippopisella*).

A number of apomorphs of the *Eriopisa-Eriopisella* group, characterized by complete suppression of the second segment in the third uropod (such as *Anchialella* J. Barnard, 1979 and *Galapsiellus* J. Barnard, 1976) are not treated in this paper.

4.1. The *Eriopisa* line. — To this line belong the following genera: *Eriopisa* Stebbing, 1890 (s. str., = approximately sensu G. Karaman & Barnard, 1979), *Psammogammarus* S. Karaman, 1955 (approximately sensu G. Karaman & Barnard, 1979, but see section 3 of this paper), *Tunisopisa* n. gen., and *Victoriopisa* G. Karaman & Barnard, 1979.

These four genera can be distinguished with the aid of the following key:

1a. Flagellum segment 1 of A2 elongated, composed of several fused segments. Inner lobes of labium obsolescent. Ischium of P7 dilated . . . *Victoriopisa*
b. Flagellum segment 1 of A2 short, no flagellum segments fused. Inner lobes of labium prominent, fleshy. Ischium of P7 narrow 2
2a. Propodus of Gn. 1 subchelate, carpus linear. Exopodite segment 2 of Ur. 3 short, small. . . . *Tunisopisa*
b. Propodus of Gn. 1 "normal", carpus triangular. Exopodite segment 2 of Ur. 3 elongated 3
3a. Coxal plate 1 sharply pointed anteriorly. Palma of Gn. 2 with mid-palmar spine(s). P6 and P7 subequal in length. Basis of P7 expanded, strongly lobate. *Eriopisa*
b. Coxal plate 1 blunt anteriorly. Palma of Gn. 2 without mid-palmar spines. P6 shorter than P7. Basis of P7 almost linear, hardly lobate . . . *Psammogammarus*

4.2. Diagnoses of the genera of the *Eriopisa* line. — The differential diagnoses of the four genera of the *Eriopisa* line, and the species attributed to these genera, are as follows (for extended characterizations of the majority of the generic units, the reader is referred to the excellent paper of G. Karaman & Barnard, 1979):

Eriopisa Stebbing, 1890
A2 flagellum short, all articles free.
Labium, inner lobes fleshy.
Gn. 1, coxal plate sharply pointed anteriorly; propodus "normal", carpus triangular, palma transverse.
Gn. 1 < Gn. 2.

TABLE I
Salient differences between the *Eriopisa* and *Eriopisella* lines.

Eriopisa line	*Eriopisella* line
— Corpus mandibulae with row of spines between the pars incisiva and the pars molaris	— Without such a row of spines
— First maxilla, inner lobe widened, armed with 4 or more setae	— Inner lobe narrow, with 1 to 3 setae
— Second maxilla, inner lobe with oblique row of setae and/or median setae	— Both oblique row and median setae absent
— Gnathopod 2 homoiochronous (i.e., propodus Gn 1 < Gn. 2)	— Gnathopod 2 heterochronous (i.e., propodus Gn 1 = Gn. 2)

Gn. 2, palma oblique; with mid-palmar spine.
P5 < P6, P6 and P7 subequal.
P7, basis expanded, lobate; ischium narrow.
Ur. 3, exopodite elongated, 2nd segment long.

Type-species (by original designation): *E. elongata* (Bruzelius, 1859) (as *Eriopis,* preoccupied).

Other species: *E. philippensis* (Chilton, 1921b) (as *Niphargus*) and *E. incisa* McKinney et al., 1978.

Habitat: Marine (sublittoral) and fresh water.

Distribution: North Atlantic, Mediterranean, Gulf of Mexico, North Pacific, Philippines.

Psammogammarus S. Karaman, 1955
A2 flagellum short, completely segmented.
Labium, inner lobes fleshy.
Gn. 1, coxal plate blunt anteriorly; propodus "normal", carpus triangular, palma almost transverse.
Gn. 1 < Gn. 2.
Gn. 2, palma moderately oblique; mid-palmar spines absent.
P5 < P6 < P7.
P7, basis almost linear, hardly lobate; ischium narrow.
Ur. 3, exopodite elongated, 2nd segment long.

Type-species (by original designation): *Ps. coecus* S. Karaman, 1955.**)

Other species: *Ps. longiramus* (Stock & Nijssen, 1965) (as *Eriopisa*), *Ps. gracilis* (Ruffo & Schiecke, 1976) (as *Eriopisa*), *Ps. garthi* (J. Barnard, 1952) (as *Eriopisa*), *Ps. caesicolus* n. sp.

Habitat: Marine (sublittoral and littoral) and anchihaline inland waters.

Distribution: Mediterranean, California, West Indies, Red Sea.

Tunisopisa n. gen.
As *Psammogammarus* but:
Gn. 1, propodus very small, subchelate ("parachelate"); carpus linear.
Gn. 1 ⩽ Gn. 2.
Gn. 2 (♀♂), palma very long, very oblique; with mid-palmar spines.
P5 < P6, P6 and P7 subequal.
P7, basis ovate, feebly lobate.

Type-species (by monotypy): *T. seurati* (Gauthier, 1936) (as *Eriopisa*).

Habitat: Slightly brackish well.

Distribution: Tunisia.

Victoriopisa G. Karaman & Barnard, 1979
A2 flagellum, segment 1 elongated, consisting of several fused segments.
Labium, inner lobes obsolescent.
Gn. 1, coxal plate more or less produced anteriorly; propodus "normal", carpus triangular, palma transverse.
Gn. 1 ⩽ Gn. 2.
Gn. 2, palma very oblique, long; mid-palmar spines absent.
P5 to P7 subequal.
P7, basis broadly rounded, lobate; ischium dilated.
Ur. 3, exopodite segment 2 strongly elongated.

Type-species (by original designation): *V. chilkensis* (Chilton, 1921a) (as *Niphargus*).

Other species: *V. australiensis* (Chilton, 1923) (as *Niphargus*), *V. epistomata* (Griffiths, 1974) (as *Eriopisa*).

Habitat: Marine (sublittoral), brackish and fresh (subterranean) inland waters.

Distribution: South Africa, India, Australia.

4.3. The *Eriopisella* line. — To this line belong the following genera: *Eriopisella* Chevreux, 1920, *Madapisella* n. gen., and *Nippopisella* n. gen.

These three genera can be distinguished with the aid of the following key:

1a. Coxal plate 1 blunt anteriorly. Carpus and propodus of Gn. 2 linear, carpus non-lobate. Flagellum of A2 > pedunculus. Telson cleft narrow, slit-like. Rami of Ur. 1 without lateral spines. Rami of Ur. 2 abbreviated . . . . *Madapisella*
b. Coxal plate 1 pointed anteriorly. Carpus of Gn. 2 triangular, lobate; propodus "normal". Flagellum of A2 < or ⩽ pedunculus. Telson cleft wide, V-shaped. Rami of Ur. 1 with lateral spines. Rami of Ur. 2 elongate. 2
2a. Basis of P7 strongly lobate. Md. palp long, segments 2 and 3 each with several (>5) setae. Palm of Gn. 1 and of Gn. 2 long, very oblique . . *Nippopisella*
b. Basis of P7 non-lobate. Md. palp short, segments 2 and 3 with few (<4) setae. Palm of Gn. 1 and of Gn. 2 short, transverse . . . . *Eriopisella*

**) The statement in G. Karaman & Barnard, 1979: 148, that *Ps. coecus* has coxal gills on P3 to P6 is based on a lapsus calami in the text of Ruffo & Schiecke, 1976: 420; their text-fig. III-3 shows correctly the presence of a coxal gill on P2 as well.

4.4. Diagnoses of the genera of the *Eriopisella* line. — The differential diagnoses of the three genera belonging to this line, and the species attributed to each genus, are as follows:

Eriopisella Chevreux, 1920
Flagellum A2 < pedunculus.
Md. palp, segment 2 with 0-1 seta, segment 3 with 2-3 setae, all terminal.
Coxal plate 1 sharply produced anteriorly.
Palma Gn. 1 and Gn. 2 short, transverse.
Gn. 2, carpus triangular, lobate posteriorly; propodus "normal".
P7, basis non-lobate, elongated-oval.
Ur. 1, rami with lateral spines.
Ur. 2, rami and pedunculus slender.
Telson with wide, V-shaped cleft.

Type-species (by monotypy): *E. pusilla* Chevreux, 1920.

Other species: *E. sechellensis* (Chevreux, 1901) (as *Eriopisa*), *E. upolu* J. Barnard, 1970 (as subspecies of *E. sechellensis;* raised to specific rank by G. Karaman & J. Barnard, 1979), *E. capensis* (K. Barnard, 1916) (as *Eriopisa*), *E. epimera* Griffiths, 1974.

Habitat: Marine (0-285 m).

Distribution: France, South Africa, Indo-West Pacific region.

Madapisella n. gen.
Flagellum A2 > pedunculus.
Md. palp as in *Eriopisella.*
Coxal plate 1 rounded anteriorly.
Palma Gn. 1 and Gn. 2 short, transverse.
Gn. 2, carpus and propodus linear; carpus non-lobate.
P7, basis non-lobate, broadly oval.
Ur. 1, rami without lateral spines.
Ur. 2, rami and pedunculus abbreviated.
Telson cleft narrow, slit-like.

Type-species (monotypic): *M. madagascarensis* (Ledoyer, 1968a) (as *Eriopisella*).

Habitat: Marine (shallow).

Distribution: Madagascar.

Nippopisella n. gen.
Flagellum A2 very short, < peduncle segment 5.
Md. palp long; segment 2 with 5, segment 3 with about 10 setae, both ventral and terminal.
Coxal plate 1 as in *Eriopisella.*
Palma of Gn. 1 and Gn. 2 long, very oblique.
Gn. 2, carpus triangular, lobate posteriorly; propodus "normal".
P7, basis strongly lobate, circular.
Ur. 1 and Ur. 2 as in *Eriopisella.*
Telson as in *Eriopisella.*

Type-species (monotypic): *N. nagatai* (Gurjanova, 1965) (as *Eriopisella*).

Habitat: Marine (30-50 m).

Distribution: Japan.

4.5. Species transferred to other genera, once classified with the *Eriopisa-Eriopisella* group. —
Eriopisa(?) hamakua J. Barnard, 1970 → *Dulzura* J. Barnard, 1969 (see: Zimmerman & Barnard, 1977).
Eriopisa laakona J. Barnard, 1970 → *Metaniphargus* Stephensen, 1933 (new combination).
Eriopisa melitaformis Ledoyer, 1979 *Dulzura* J. Barnard, 1969 (new combination).
Eriopisa schoenerae Fox, 1973 → *Protohadzia* Zimmerman & Barnard, 1977 (see Zimmerman & Barnard, 1977).
Eriopisa sp. (not described, mentioned only, by Matsumoto, 1976) must remain unclassified.
Eriopisa peresi Ledoyer, 1968b = male of *Psammogammarus coecus* S. Karaman, 1955 (see Ruffo & Schiecke, 1976).

5. AFFINITIES OF THE ERIOPISID GAMMARIDS

There is no doubt in my mind that the *Eriopisa-Eriopisella* group is very closely related to the hadziid group within the Gammaridae s.l. The best proof of such an affinity comes from a rather unexpected side: J. L. Barnard, who presumes (1970: 138) a relationship between the *E.-E.* group and the *Melita-Netamelita* group, described in the same paper two species as *Eriopisa (hamakua* and *laakona*), which he decided later (Zimmerman & Barnard, 1977) to transfer to the hadziid genera *Dulzura* and *Hadzia.*

It must be admitted that the distinction between

Hadziidae and Melitidae (see J. Barnard, 1976: 424; Zimmerman & Barnard, 1977) appears to be based on two characters only: (1) the obsolescent palm of the second female gnathopod, provided with setae, in the hadziids; and (2) the lacking inner labium lobe in the hadziids. As to the first of these characters, I wish to bring forward that in certain hadziids (e.g. *Dulzura* J. Barnard, 1969, *Protohadzia* Zimmerman & Barnard, 1977) the palm of Gn. 2 ♀ certainly may be called nondescript, and setose. In other hadziids, however, (e.g. *Metaniphargus,* especially *M. beattyi* Shoemaker, 1942) the palm of Gn. 2 ♀ is spinose and well-delimited. This character then does not seem fit to distinguish between the two groups. Also the second character, the presence or absence of inner labium lobes, does not appear to be watertight. In the revision of the West Indian hadziids, Stock (1977) has shown the presence of weak inner labium lobes in several hadziid genera, including the type-genus *Hadzia.* Moreover, the recently described genus *Victoriopisa* G. Karaman & Barnard, 1979, belonging to the eriopisid/melitid group according to its authors, has "obsolescent" inner lobes.

The members of the *E.-E.* group of genera differ from the less transformed hadziids in a reduced ornamentation of the ventral margin of mandible palp segment 3, lacking a regular row of D-setae. Both the *E.-E.* genera and the hadziids show a tendency of simplification of the structures in the oral area (gradual reduction of the inner lobes of the labium, reduction of the number of spines on the masticatory part of the mandible, reduction of the armature and of the number of segments of the mandible palp, and simplification of the armature of the inner lobes of the maxillae 1 and 2).

Both the *E.-E.* group and the hadziids have similar ecological preferences: they populate the interstitial and phreatic habitat, ranging from littoral interstitia of mobile substrates to inland, mostly hypogean, waters. Associated with this trend is first a reduction and later loss of eye pigment and eyes.

ACKNOWLEDGEMENTS

The fieldwork of our West Indian program has been supported by grants of the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), The Hague (WR 87-79 and 87-144), The Treub-Maatschappij, Utrecht, and the Beyerinck-Popping Fonds, Amsterdam.

I am indebted to the staff of the Caribbean Marine Biological Institute, Curaçao, for hospitality during the fieldwork, and to Dr. Steven Weinberg and Mrs. Francisca Weinberg, who participated in the 1978 fieldwork.

REFERENCES

BARNARD, J. L., 1952. A new species of amphipod from Lower California (genus Eriopisa). Pacif. Sci., **6**: 295-299.

——, 1969. Gammaridean Amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. Bull. U.S. natn. Mus., **258**: i-x, 1-230.

——, 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands. Smithson. Contr. Zool., **34**: i-vi, 1-286.

——, 1976. Affinities of Paraniphargus lelouparum Monod, a blind anchihaline amphipod (Crustacea) from the Galápagos Islands. Proc. biol. Soc. Wash., **89** (36): 421-432.

——, 1979. Littoral Gammaridean Amphipoda from the Gulf of California and the Galápagos Islands. Smithson. Contr. Zool., **271**: i-vi, 1-149.

BARNARD, K. H., 1916. Contributions to the crustacean fauna of South Africa. Ann. S. Afr. Mus., **15** (3): 105-302, pls. XXVI-XXVIII.

——, 1935. Report on some Amphipoda, Isopoda and Tanaidacea in the collections of the Indian Museum. Rec. Indian Mus., **37** (3): 279-319.

BOUSFIELD, E. L., 1977. A new look at the systematics of gammaridean amphipods of the world. Crustaceana, Suppl. **4**: 282-316.

BRUZELIUS, R. M., 1859. Bidrag till kännedomen om skandinaviens Amphipoda Gammaridea. K. svenska Vetensk. Akad. Handl., **3** (1): 1-104, pls. I-IV.

CHEVREUX, E., 1901. Mission scientifique de M. Ch. Alluaud aux Iles Séchelles, Crustacés Amphipodes. Mém. Soc. zool. Fr., **14**: 388-438.

——, 1920. Sur quelques Amphipodes nouveaux ou peu connus provenant des côtes de Bretagne. Bull. Soc. zool. Fr., **45**: 75-87.

CHEVREUX, E. & L. FAGE, 1925. Amphipodes. Faune de France, **9**: 1-488 (Lechevalier, Paris).

CHILTON, C., 1921a. Fauna of the Chilka Lake. Amphipoda. Mem. Indian Mus., **5**: 519-558.

——, 1921b. Niphargus philippensis, a new species of amphipod from the underground waters of the Philippine Islands. Philipp. J. Sci., **17** (5): 516-523, pls. I-III.

——, 1923. Occasional notes on Australian Amphipoda. Rec. Aust. Mus., **14** (2): 79-100.

FOX, R. S., 1973. Ceradocus shoemakeri and Eriopisa schoenerae, new amphipods (Crustacea: Gammaridea) from the Bahama Islands. J. Elisha Mitchell scient. Soc., **89**: 147-159.

GAUTHIER, H., 1936. Eriopisa seurati, nouvel Amphipode du Sud-tunisien. Bull. Soc. Hist. nat. Afr. Nord, **27**: 133-143.

GRIFFITHS, C. L., 1974. The Amphipoda of southern Africa, 4. The Gammaridea and Caprellidea of the Cape Province east of Cape Agulhas. Ann. S. Afr. Mus., **65** (9): 251-336.

GURJAVONA, E. F., 1965 [Concerning the systematics and relationships of the genera Eriopisa, Eriopisella and Niphargus (fam. Gammaridae, Crustacea-Amphipoda)] (in Russian). Trudy zool. Inst. Leningr., **35**: 216-231.

HUMMELINCK, P. WAGENAAR, 1977. Marine localities. Stud. Fauna Curaçao, **51**: 1-68.

KARAMAN, G. S. & J. L. BARNARD, 1979. Classificatory revisions in gammaridean Amphipoda (Crustacea), 1. Proc. biol. Soc. Wash., **92** (1): 106-165.

KARAMAN, S. L., 1955. Ueber einige Amphipoden des Grundwassers der Jugoslavischen Meeresküste. Acta Mus. maced. Sci. nat., **2** (11/22): 223-242.

LEDOYER, M., 1968a. Amphipodes Gammariens de quelques biotopes de substrat meuble de la région de Tuléar (République Malgache). Annls. Univ. Madagascar, **6**: i, 17-62.

——, 1968b. Ecologie de la faune vagile des biotopes méditerranéens accessibles en scaphandre autonome, IV. Synthèse de l'étude écologique. Recl. Trav. Stn. mar. Endoume, **60**: 125-295.

——, 1979. Les Gammariens de la pente externe du Grand Récif de Tuléar (Madagascar) (Crustacea, Amphipoda). Memorie Mus. civ. Stor. nat. Verona, (2) **2**: 1-150.

McKINNEY, L. D., R. D. KALKE & J. S. HOLLAND, 1978. New species of amphipods from the western Gulf of Mexico. Contr. mar. Sci., **21**: 133-159.

MATSUMOTO, K., 1976. An introduction to the Japanese groundwater animals with reference to their ecology and hygienic significance. Int. J. Speleol., **8**: 141-155.

RUFFO, S., 1959. Contributo alla conoscenza degli Anfipodi del Mar Rosso. Bull. Sea Fish. Res. Stn. Haifa, **20**: 1-26.

RUFFO, S. & U. SCHIECKE, 1976. Descrizione di Eriopisa gracilis n.sp. (Amphipoda, Gammaridae) delle coste di Malta e ridescrizione di E. coeca (S. Karaman, 1955) (= E. peresi M. Ledoyer, 1968). Boll. Mus. civ. Stor. nat. Verona, **2**: 415-438.

SARS, G. O., 1894. An account of the Crustacea of Norway, **1** (22/23): 514-516, pl. CLXXXI fig. 2 (Cammermeyer, Christiania).

SHOEMAKER, C. R., 1942. Notes on some American freshwater amphipod crustaceans and descriptions of a new genus and two new species. Smithson. misc. Collns., **101** (9): 1-31.

SIVAPRAKASAM, T. E., 1967. Notes on some amphipods from the South East coast of India. J. mar. biol. Ass. India, **9** (2): 372-383.

STEBBING, T. R. R., 1890. The right generic names of some Amphipoda. Ann. Mag. nat. Hist., (6) **5**: 192-194.

STEPHENSEN, K., 1933. Fresh- and brackish-water Amphipoda from Bonaire, Curaçao and Aruba. Zool. Jb. (Syst.), **64**: 415-436.

STOCK, J. H., 1977. The taxonomy and zoogeography of the hadziid Amphipoda with emphasis on the West Indian taxa. Stud. Fauna Curaçao, **55**: 1-130.

——, 1978. A remarkably variable phreatic amphipod from Mallorca, Rhipidogammarus variicauda n. sp., in which the third uropod can assume the "parviramus" or the "variiramus" condition. Bijdr. Dierk., **48** (1): 89-95.

——, 1979. Amsterdam Expeditions to the West Indian Islands, Report 4. Station list. Versl. techn. Gegevens I.T.Z., **20**: 1-78.

STOCK, J. H. & H. NIJSSEN, 1965. Eriopisa longiramus n. sp. a new subterranean amphipod from a Red Sea island. Bull. Sea Fish. Res. Stn. Haifa, **38**: 28-39.

ZIMMERMAN, R. J. & J. L. BARNARD, 1977. A new genus of primitive marine hadziid (Amphipoda) from Bimini and Puerto Rico. Proc. biol. Soc. Wash., **89** (50): 565-580.

Received: 3 June 1980