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CALABOZOIDEA, A NEW SUBORDER OF STYGOBIONT ISOPODA, DISCOVERED IN VENEZUELA

by

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SUMMARY

A new type of stygobiont Isopoda has been collected from wells in the "llanos" of Venezuela, near Calabozo, and in the hyporheal of a river in the Aragua State. On account of its body segmentation, and structure of uropods and pleopods, it must be considered as representing a new suborder. A diagnosis of the new suborder, new family and new genus, and a description of the type-species, are provided. Finally, a morphologic comparison with some of the already known suborders is made.

RÉSUMÉ

Un type nouveau d'Isopodes stygobies a été découvert dans les puits du «llanos» du Vénézuéla, près de Calabozo, et une fois dans l'hyporhéal d'une rivière dans l'État d'Aragua. Compte tenu de la segmentation du corps, et de la structure des uropodes et des pléopodes, on le considère comme représentant d'un sous-ordre nouveau. On donne la description du sous-ordre, de la famille, du genre nouveau et de l'espèce-type. Finalement, une comparaison du sous-ordre nouveau avec plusieurs sous-ordres déjà connus est donnée.

INTRODUCTION

In addition to a sampling program in islands on and off the shelf of Venezuela, the 1982 Amsterdam Expedition to the West Indian Islands also did some comparative collecting on the mainland of this country. In wells in the neighbourhood of the village of Calabozo, in the Guárico State, and in the hyporheal of the Rio Zuata, in the Aragua State, a species of aquatic isopod was encountered in great numbers. This species not only belongs to a new genus (*Calabozoa*), but it shows so many original characters that it must be considered the type of a new family, and even a new suborder, of Isopoda.

The specimens have been deposited in the Isopoda collection of the Zoological Museum, University of Amsterdam (ZMA).

Suborder CALABOZOIDEA nov.
Diagnosis. — Pleonites 1 and 2 very small, reduced to sternal part, pleonites 3, 4, 5 free, pleotelson large, composed of pleonite 6 and telson. Pleopods 1 and 2 present in both sexes, modified, non-branchial. Pleopods 3, 4, 5 branchial. Uropods lateral, their rami reduced.

Family CALABOZOIDAE nov.
Diagnosis. — Body dorsoventrally depressed, consisting of the cephalon and (dorsally) 10 free somites: the 7 anterior somites correspond with the pereionites 2 to 8, the 3 posterior somites with the pleonites 3 to 5. The pleotelson comprises only the 6th pleonite and the telson.

Mandibles without palp. Seven pairs of pereiopods present, none subchelate, pereiopods 2-7 mutually similar in shape. Pleopods 1 and 2 present in both sexes, modified for copulatory purposes in the male. Pleopods 3 to 5 mutually similar, biramous, with respiratory function.

Type-genus. — *Calabozoa* nov., with the characters of the family Calabozoidae.

Type-species. — *Calabozoa pellucida* n. sp.

*) Report 26 is published in the same issue of this journal.

Derivatio nominis. — The generic name is derived from the type-locality (Calabozo), with a clear allusion to the Greek word ζῷον "zoön"; gender feminine. The specific name is derived from the Latin *pellucidus*, meaning transparent.

Calabozoa pellucida n. sp. (figs. 1-5)

Material. — One ♂ (holotype), one ♀ (allotype), seventeen dissected paratypes and numerous undissected paratypes. Amsterdam Expeditions to the West Indian Islands, sta. 82/565: Venezuela, Calabozo, open well along the road to Paso de Caballo (08°54'00" N 67°25'23" W), water level at 5 m, water depth 3.5 m, temperature 28.8°C, chlorinity 74 mg/l, 10 March 1982 (ZMA Is. 105.207 and 208A, B, C).

Some dissected and numerous undissected specimens, sta. 82/563: Calabozo, town centre, Calleron no. 1, open well, water level at 6.5 m, water depth 1 m, temperature 28.9°C, chlorinity 35 mg/l, 10 March 1982 (ZMA Is. 105.209).

Two specimens, sta. 82/548; well near Orituco, on the road from Calabozo to Paso de Caballo (4.4 km from Estación Biologica de la Sociedad venezolana de Ciencias) (08°46'26" N 67°18'22" W), water level at 3.2 m, water depth 0.8 m, temperature 29.6°C, chlorinity <1 mg/l, 9 March 1982 (ZMA Is. 105.210).

Many specimens, sta. 82/556: Calabozo, quarter Misión (08°55'05" N 67°26'44" W), water level at 3 m, water depth 1.5 m, temperature 30.0°C, chlorinity 42 mg/l, 10 March 1982 (ZMA Is. 105.221).

Many specimens, sta. 82/557: Calabozo, quarter Misión, ca. 400 m W. of sta. 82/556, well of Nancy de Venega family (08°55'17" N 67°27'00" W), water level at 2.5 m, water depth 0.6 m, temperature 29.5°C, chlorinity 49 mg/l, 10 March 1982 (ZMA Is. 105.222).

Many specimens, sta. 82/558: Calabozo, Los Desemparados, 1 km from the road Calabozo — Corozo Pando, well of Rodriguez family, water level at 3.5 m, water depth 0.5 m, temperature 30.0°C, chlorinity 34 mg/l, 10 March 1982 (this station is near sta. 82/557) (ZMA Is. 105.213).

Many specimens, sta. 82/562: Calabozo, well along the road to Paso de Caballo (08°54'00" N 67°25'23" W), water level at 4.5 m, water depth 2 m, temperature 28.6°C, chlorinity 13.6 mg/l, 10 March 1982 (ZMA Is. 105.214).

Many specimens, sta. 82/564, house no. 7 near sta. 82/563, covered well, water level at 6.5 m, water depth 1.5 m, temperature 28.9°C, chlorinity 84 mg/l, 10 March 1982 (ZMA Is. 105.215).

Several specimens, sta. 82/566: Calabozo, N.W. part of town, Calle 5, carrera 16 (08°55'53" N 67°25'23" W), partly covered well, water level at 5 m, water depth 0.5 m, temperature 28.3°C, chlorinity 45 mg/l, 10 March 1982 (ZMA Is. 105.216).

Some specimens, sta. 82/567: Calabozo, Barrio Caya de Aqua, calle 6 final (= slightly N. of sta. 82/566), open well, water level at 4.5 m, water depth 1.5 m, temperature 27.5°C, chlorinity 52 mg/l, 10 March 1982 (ZMA Is. 105.217).

One specimen, sta. 82/568: Palo Secco, centre (09°03'31" N 67°13'46" W), open well, water level at 5.5 m, water depth 4 m, temperature 28.4°C, chlorinity 140 mg/l, 10 March 1982 (ZMA Is. 105.218).

One specimen, sta. 82/569: Palo Secco, North (estimated position 08°55'05" N 67°25'23" W), covered well of Casa Mi Refugio, Luis F. Davilav family, water level at 6 m, water depth 3.5 m, temperature 29.3°C, chlorinity 196 mg/l, 10 March 1982 (ZMA Is. 105.219).

One specimen, sta. 82/573: 2 km N. of San Casimiro (Aragua State), estimated position 10°N 67°W, hyporheal of the river Zuata, ca. 1 m from the river bank, temperature 24.1°C, chlorinity 19.2 mg/l, 10 March 1982 (ZMA Is. 105.220).

The accompanying fauna consisted of Oligochaeta (in 9 stations), *Bogidiella neotropica* Ruffo (Amphipoda) (in 4 stations), larvae of Culicidae (in 4 stations), larvae of Chironomidae (in 3 stations), Ostracoda (in 3 stations), Copepoda Cyclopidae (in 2 stations), Heteroptera (in 2 stations), Harpacticoidea (in 2 stations), larvae of Coleoptera (in 2 stations), Collembola (in 2 stations), and Nematoda (in 1 station).

The type-region. — One of the wells in the town of Calabozo has been chosen as type-locality (viz. sta. 82/565). All other wells in Calabozo can be considered belonging to the same phreatic system; the two wells of Palo Secco (stations 568 and 569) are some 36 km N.E. of Calabozo. Station 32/573 is the hyporheal of the upper part of the river Zuata, in an area with an altitude ranging from 200 to 500 m. The locality is at some 130 km N.N.E. (in direct line) from Calabozo.

The walls of the wells in Calabozo disclose several alluvial deposits, according to the literature (Goosen, 1964) of Quaternary origin. These deposits are composed of gravel of different particle size and conglomerats of gravel and sand; the sand is coloured red-brown by a large amount of iron.

The climate in the Calabozo region is characterized by the alternation of a wet, 7 months', and a dry, 5 months', season (Blanck, 1979). The landscape consists of flat, sandy savannahs with here and there a few trees. The mean annual temperature is 27.5°C. The water temperatures in our observations fluctuated between 24.1°C (in the hyporheal sample) and 30.0°C, and the chlorinities from less than 1 to 196 mg/l.

Description

Body (figs. 1A-B):

Oblong-oval, transparent whitish; unable to roll up completely into a ball. Body surface

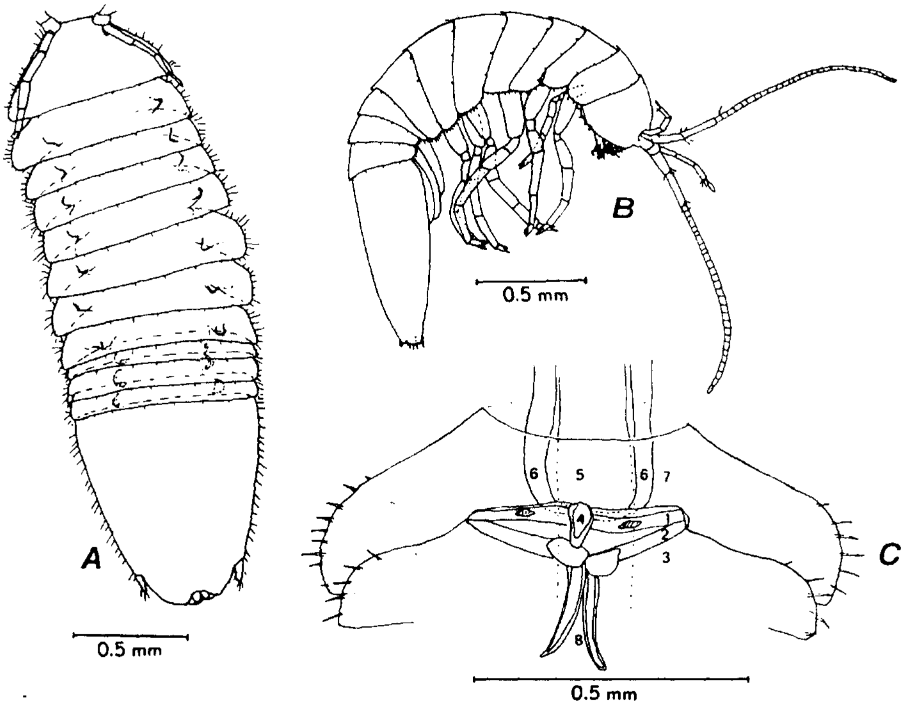

Fig. 1. *Calabozoa pellucida* n. gen., n. sp.: A, ♀, dorsal, paratype; B, immature ♂, lateral, paratype; C, ventral view of central part of the body of immature ♂ paratype (1, 1st pleonite; 2, 2nd pleonite; 3, 3rd pleonite; 4, genital papilla; 5, gut; 6, vas deferens; 7, 7th pereionite; 8, not fullgrown 2nd pleopods).

seemingly smooth, but covered with numerous setules (figs. 5C, F). Spines present only at the edges of the epimera (fig. 5F) and the pleotelson. Epimera large, present on all somites, no suture lines visible. Cephalon (figs. 2B, 5C) subtrapezoidal; eyes absent.

Body length 2-3 times the thorax width; pleonites slightly smaller than pereionites in length and width. Adult males ranging in size from 2.5 mm to 3.2 mm, females up to 3.4 mm.

Antenna 1 (figs. 2C, 5C):
Implanted posteriad to antenna 2 in a furrow. Peduncle of 3 articles, flagellum of 2 articles, the last article small. The first article of the flagellum carries an aesthetask of variable length, usually about 3/4 of this article. In the adult male the aesthetask can be up to 1 1/2 times the length of this article. The first antenna without the aesthetask is as long as the peduncle of the second antenna.

Antenna 2 (fig. 2A):
Peduncle of 5 articles, flagellum of many articles, up to 32. (Most adults have flagella of at least 26 articles, but one adult male was found with only 20 articles, and some juveniles were found with even more than 26 articles).

Mandibles (figs. 2D-F):
Without palp. The right mandible has a pars incisiva in two parts with 4 and 3 teeth, respectively. The pars molaris is obsolete, without any triturating surface, replaced by one smaller and one larger brush-like element. The left mandible is similar to the right mandible, except for the presence of a lacinia mobilis between the pars incisiva and the pars molaris. The lacinia mobilis has a denticulated apex.

Adult males have completely worn-out mandibles, in which all elements have disappeared. Possibly males, once mature, do not moult anymore.

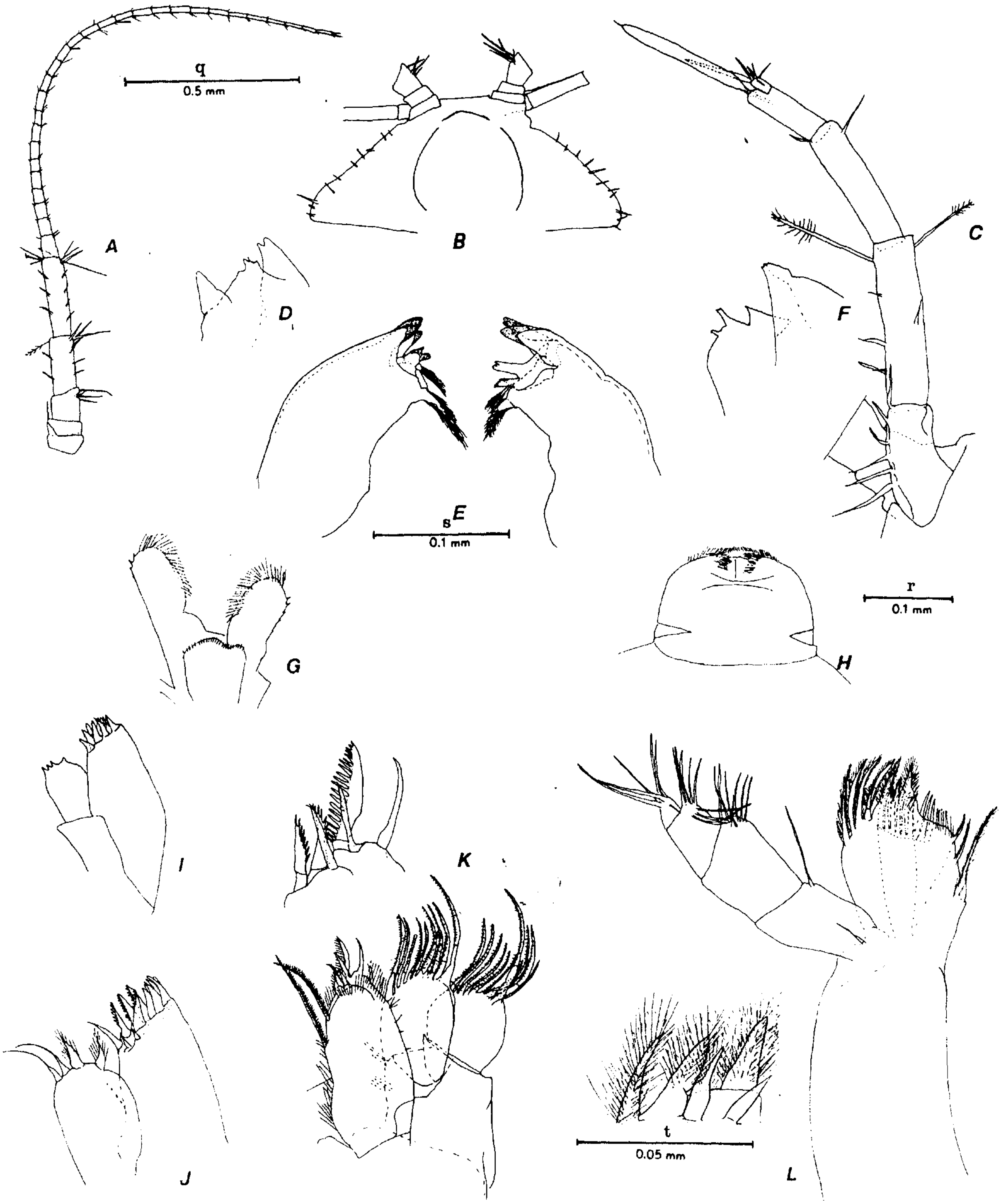

Fig. 2. *Calabozoa pellucida* n. gen., n. sp.: A, 2nd antenna, ♂ holotype (scale q); B, cephalon ventral, ♂ holotype (q); C, 1st antenna, ♂ holotype (r); D, F, right and left mandible, ♂ holotype (t); E, right and left mandible, immature ♂ paratype (s); G, H, lower and upper lip, immature ♂ paratype (r); I, 1st maxilla, ♂ holotype (r); J, 1st maxilla, ♀ paratype (s); K, 2nd maxilla (s), with apex of inner endite magnified (t), ♀ paratype; L, maxilliped (s), with apex of outer lobe magnified (t), ♀ paratype.

Maxilla 1 (figs. 2I-J):
Composed of an outer and an inner endite. Outer endite with 10 or 11 sclerotized elements. From lateral to medial 5 (or 6) simple elements, 4 serrate elements, and 1 element with a median denticule can be recognized. One or two more small, simple setae present at the inner basis of the row of setae. The inner endite typically with 2 broad, pappose elements and 2 broad, but plumed elements. Pseudochaetae present on the inner margin of the external endite and on the outer margin of the internal endite.

Maxilla 2 (fig. 2K):
Composed of an inner endite and a cleft outer endite (Gruner, 1965, 1966). The internal endite carries from lateral to medial 2 or 3 sclerotized plumose setae, 3 or 4 serrate setae and 2 or 3 simple setae; pseudochaetae are also present. The inner lobe of the outer endite with 11-13 serrate setae, the three outermost somewhat longer. The outer lobe of the outer endite with 11-14 serrate setae, likewise with 3 longer outer setae.

Maxilliped (figs. 2L, 5A-B):
Consisting of a complex endite and a palp. The endite is basically composed of two lobes. The smaller inner lobe is fused with the outer lobe on both margins, and pulls the larger outer lobe in a perpendicular position. The apex of the inner lobe is furnished with 8-11 simple setae. The outer lobe bears on the inner margin 3 or 4 plumose, sharply pointed setae, on the apex two broad, pappose elements, and on the outer margin 4 plumose setae. Another 3 pappose elements, smaller than the first two, are found at the outer side of the outer lobe, medio-posterior to the apex. The inner margin of the outer lobe is also furnished with a row of pseudochaetae.

The palp is basically composed of 5 articles, but the first article is fused with the basal part of the maxilliped. Except for several plumose setae at the tip of each article, there is one characteristic seta present at the basis of the palp.

Pereiopods (figs. 3A-G):
First pereiopod with a very short carpus and a slightly widened propodus; not subchelate. Pereiopods 2-7 mutually similar in appearance, increasing in length. Four different types of setae present: supposedly the more sensitive are at the ends of the articles and on the inner side of the propodus of the first pereiopod, the less sensitive on the inner side of the merus and carpus and the least sensitive at the outer side and on the ischium and basis (figs. 3H-J).

Pleopods (figs. 4B-L):
Female. — Pleopod 1 (fig. 4I): Protopodite nearly square, slightly longer than wide. Endopodite narrow, elongate, approximately as long as the protopodite and less than half as wide; one long plumose seta on the tip, reaching to the apex of the exopodite. Exopodite lamellar, flat, oval, at its base 2½ times wider than at its tip; usually with 3 long plumose setae around the apex and about 5 at the inner margin.

Pleopod 2 (fig. 4J): Protopodite slightly larger than that of pleopod 1, similar in shape. Endopodite like that of pleopod 1, but longer, 1½ times longer than the protopodite and half as wide. Exopodite lamellar, larger and more rounded-oval than that of pleopod 1. Normally with two long plumose setae at the apex and 5-6 smaller, plumose setae at the outer margin.

Pleopods 3-5 of female like those of male.

Male. — Pleopod 1 (fig. 4D): Protopodite nearly square, slightly longer than wide. Exopodite consisting of two parts, pediform, the posterior end bent outward. A small endopodite (fig. 4C) is implanted halfway in the first part, standing at the beginning of a furrow that is present through the entire exopodite at the inner side.

Pleopod 2 (fig. 4E): Protopodite nearly as large as the protopodites of pleopods 3, 4 and 5. Endopodite elongate, tapering from the middle to the tip and enclosing an open furrow. Endopodite 2-3 times as long as the protopodite, length of the entire pleopod equals the length of pleopod 1. Exopodite similar in shape to that of

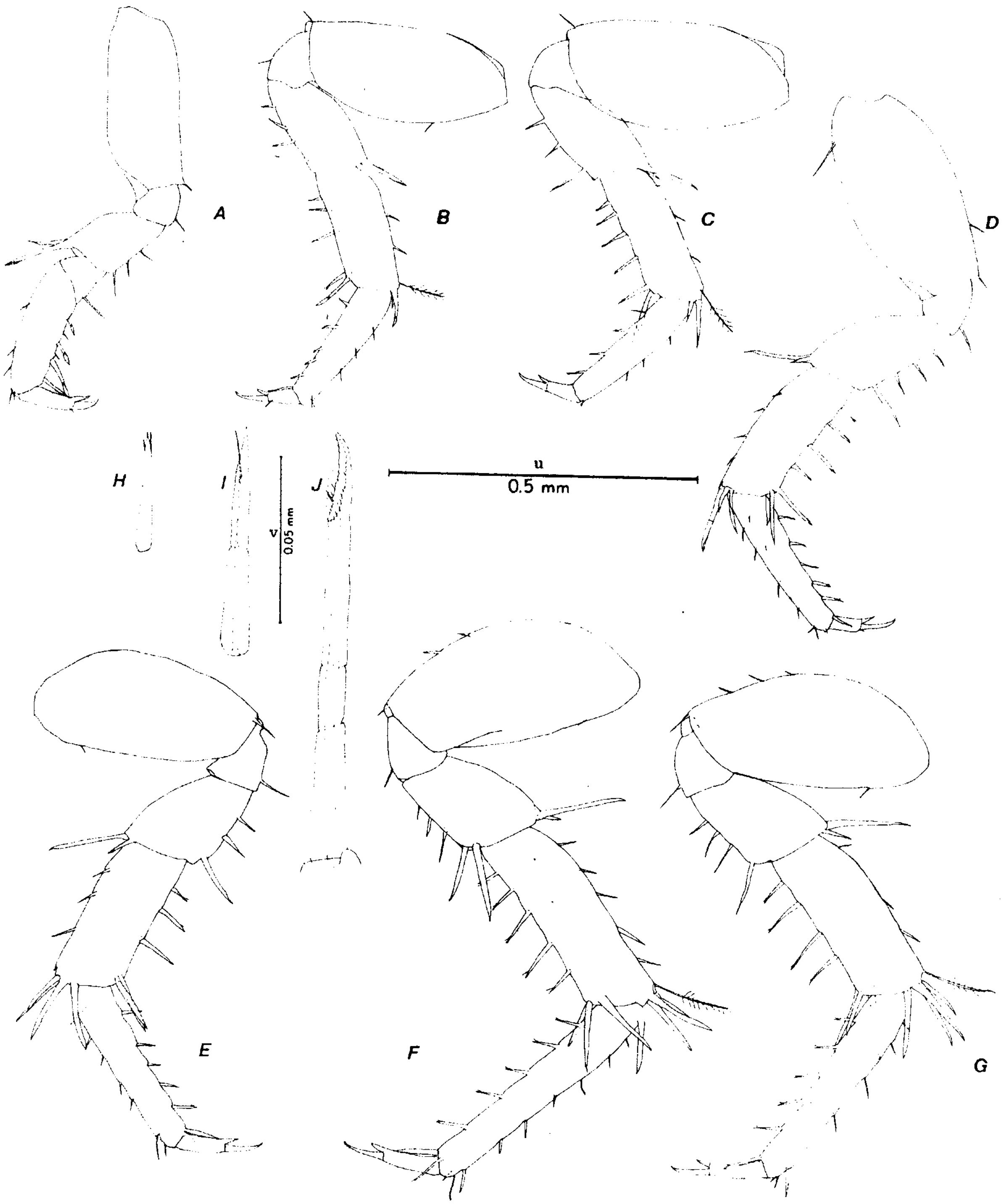

Fig. 3. *Calabozoa pellucida* n. gen., n. sp.: A-G, pereiopods 1-7, immature ♂ paratype (scale u); H-J, different types of setae, supposedly of increasing sensitivity, immature ♂ paratype (v).

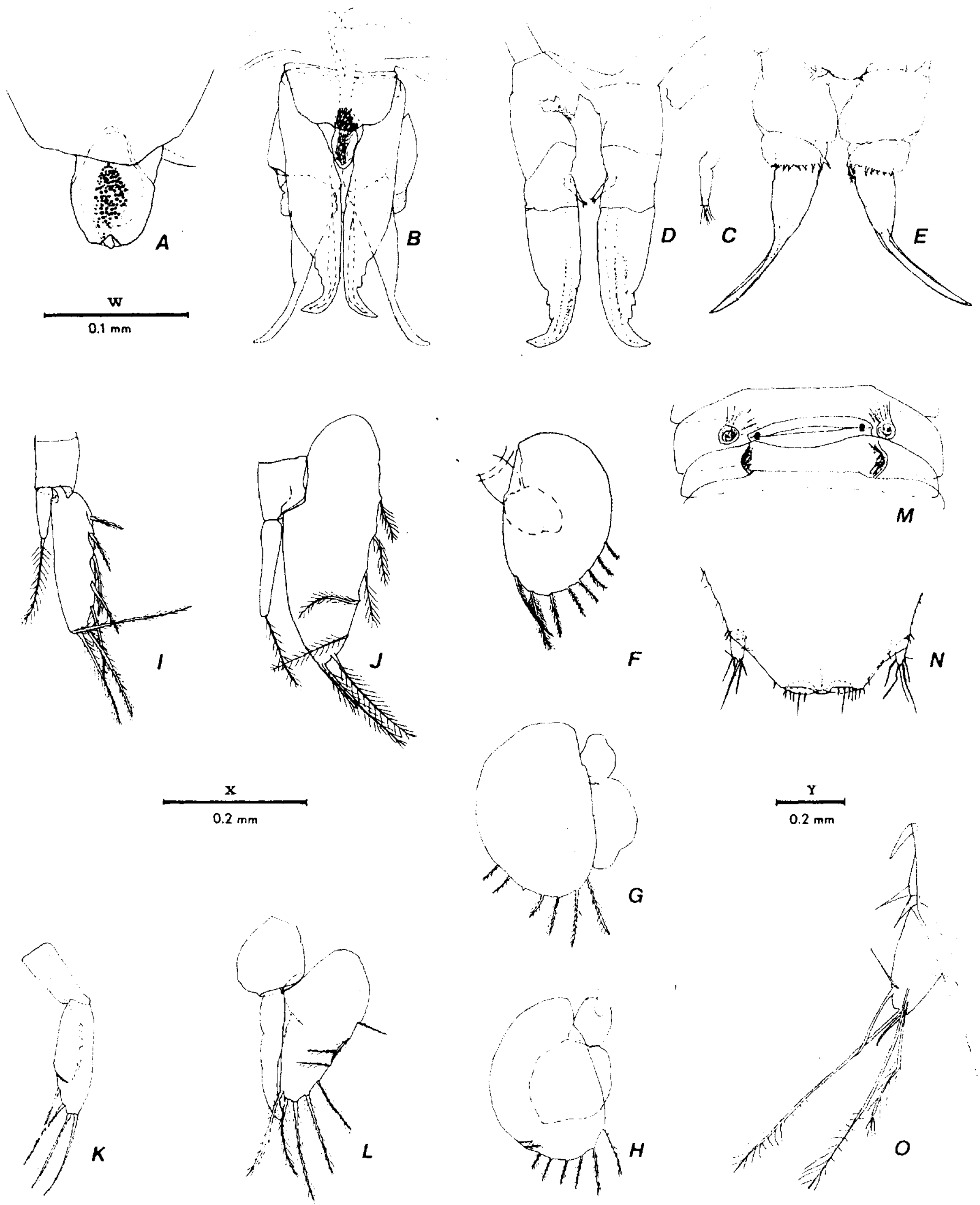

Fig. 4. *Calabozoa pellucida* n. gen., n. sp.: A, genital papilla, ♂ holotype (scale w); B, genital papilla, 1st and 2nd pleopod, ♂ paratype (simplified) (x); C, endopodite of 1st pleopod, ♂ holotype (w); D, E, pleopods 1 & 2, ♂ holotype (y); F-H, pleopods 3-5, ♂ holotype (x); I, J, pleopods 1 & 2, ♀ paratype (x); K, L, pleopods 1 & 2, immature ♂ paratype (x); M, 1st and 2nd pleonite, ♀ paratype (semidiagrammatic) (y); N, part of pleotelson, ♂ holotype (y); O, uropod, ♂ holotype (w).

the female, but approximately 4 times as small; about 9 plumose setae present.

Pleopods 3-5 (figs. 4F-H): mutually similar. Endopodites respiratory, bladder-shaped, 1/3 to 1/2 as small as the respective exopodites. Exopodites protective, with possibly a swimming function, lamellar, much larger and rounder than exopodite of pleopod 2 in female, armed with 7-10 plumose setae at the posterior and outer margins.

Pleopods 1 and 2 of juvenile males (figs. 4K, L) resemble those in adult and juvenile females, except for a more elongated endopodite in pleopod 2, which lacks a plumose seta on its apex, though there is one small plumose seta at its base. However, one exceptionally large animal was found with male juvenile pleopods. It seems that the mature male pleopods are developed only at the last moult, and that the genital papilla is only weakly developed until the last two or three stages before maturation and therefore hardly recognizable in young male specimens.

Sexual characters (♂: figs. 4A-E; ♀: figs. 4I-J):

Adult male. — A well-developed genital papilla, implanted on and protected by a lamellar expansion of the 7th pereionite, is directed posteriad. The two vasa deferentia are united at the entrance of the expansion. Exopodites of 1st and endopodites of 2nd pleopods modified into a copulatory organ, both with a furrow that may conduct the semen into the female's gonopore.

Adult female. — First and second pleopods present, but modified (see description above). Gonopores on the 5th pereionite (6th somite). Ovocytes at both sides of the gut. Incubatory pouch consisting of 10 oöstegites, arising from the coxa of the 1st to 5th pereionites.

Pleotelson (fig. 4N):

The pleotelson is composed of the 6th pleonite and the telson. It is very large, comprising almost 1/3 of the body length and it has nearly the same width. In normal position the epimeres fold somewhat over the lateral and ventral sides of the body and the individuals seem to have the same width all over.

Uropods (figs. 4-O, 5D-E):

The uropods are small and laterally inserted. The exo- and endopodites are still recognizable, but strongly reduced and fused to each other and the protopodite. The endopodite as well as the exopodite are armed with simple and plumose setae. Two short, simple elements are present at the lateral sides of the basis of the uropod. The uropods can be partly incorporated in the pleotelson, due to an excavation in the latter.

COMPARATIVE MORPHOLOGY

In table I the similarities or differences of several characters of the Calabozoidea and some of the other isopod suborders are listed.

The Calabozoidea show a mixture of plesiomorphous and apomorphous characters, as can be seen in the preceding description.

Plesiomorphous characters:

1. Pereiopods all ambulatory; monomorphic but for the slightly transformed 1st pair.
2. Pleopods 3-5 natatory and respiratory, the exopodites also protective but not operculate.
3. Pleotelson composed of 6th pleonite and telson.

Apomorphous characters:

4. Pleonites 1 and 2 reduced to sternal parts.
5. Pleopods 1 and 2 large and modified for copulatory purposes in males.
6. Pleopods 1 and 2 small and modified in females.
7. Pleotelson, though only composed of 6th pleonite and telson, very large.
8. Uropods laterally inserted on the pleotelson, and partly incorporated in it.
9. Epimeres perfectly coalescent (Racovitza, 1912).
10. Mandibles without palp and with a reduced pars molaris.
11. Eyes absent.

(ad 1) Monomorphic pereiopods are only found in the Oniscoidea. In all other suborders

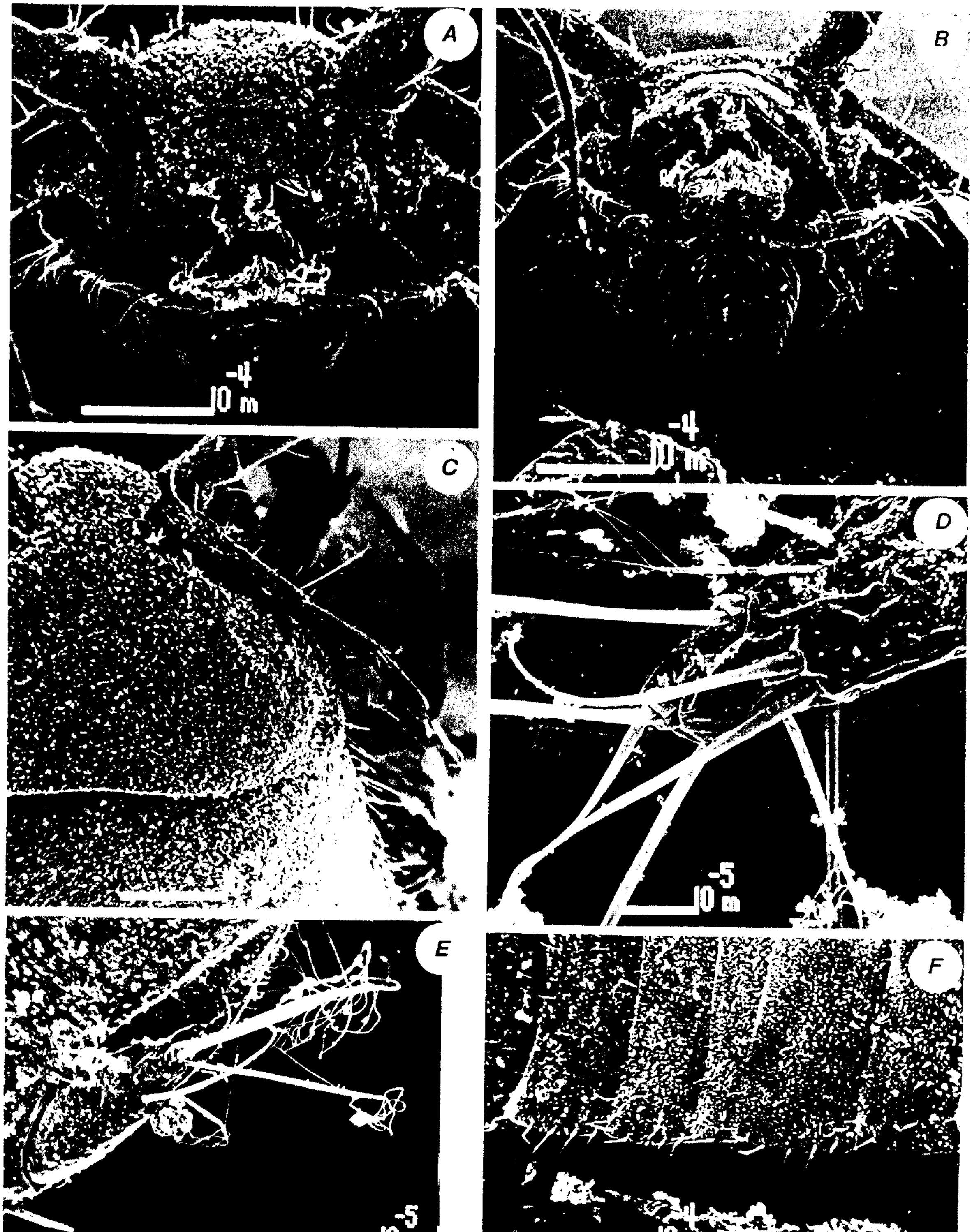

Fig. 5. *Calabozoa pellucida* n. gen., n. sp.: A, B, front and ventral view, respectively, of mouthparts; C, insertion antennae 1 and 2 in cephalon; D, detail of uropod; E, insertion of uropod in pleotelson; F, lateral view of pereionites 6 & 7 and pleonites 3, 4 & 5. (Photographs made by Mr. M. P. Schoonoord.)

most taxa have undergone a more or less obvious specialization of the first and sometimes the second or other pereiopods. In the Calabozoidea a slight transformation of the carpus and propodus on the 1st pereiopod occurs, but it is still ambulatory.

(ad 2) The most plesiomorphous state is the mutual similarity of all pleopods, as occurs in the Flabellifera. With the specialization of the 1st and 2nd pleopods, the Calabozoidea have only retained part of this plesiomorphous state.

(ad 3) The most plesiomorphous state is 6 free pleonites and the telson. Only some of the Oniscoidea and most of the Anthuridea have retained this character. All other isopod suborders, even the Flabellifera, have the 6th pleonite fused with the telson.

(ad 4) There is a general tendency in the Isopoda to reduce the number of pleonites. Usually the posteriormost pleonites are involved in a fusion complex with the telson (Sphaeromatidae, Idoteidae, Asellota), but in the Oniscoidea and some of the Asellota there is a tendency to reduce the 1st and 2nd pleonite. In for example *Asellus*, *Proasellus*, and *Lirceus* this reduction is almost complete. In the Oniscoidea the two anterior segments as a rule are smaller than the middle ones (Sars, 1899), and in the Buddelundiellidae this reduction of the 1st and 2nd pleonite has advanced considerably.

(ad 5) In the Isopoda there is a trend from a relatively simple stylet on the endopodite of the second pleopod (in the Flabellifera and the Valvifera) towards a rather complex ♂ copulatory organ, which involves the entire endopodite which consequently looses its original swimming and breathing function. This development is accomplished in the Asellota, the Calabozoidea and the Oniscoidea. In these taxa the first pleopod generally also evolves into a new kind of structure, which can protect the copulatory organ (e.g. the exopodite of pleopod 1 in *Jaera*) or might take part in the copulation itself (e.g. the endopodite of pleopod 1 in the Armadillidiidae). In the Calabozoidea it is the specialized ramus of the first pleopod that is homologous with the exopodite. However, this pleopod is not, or not only, protective, considering that it only partly covers the second pleopod, and that it bears a furrow on the inner side. This furrow is not fit for holding the second pleopod, but might serve to conduct the semen to the second pleopod.

(ad 6) The 1st and 2nd ♀ pleopods are also modified, but for no clear purposes: they probably evolved along with the ♂ pleopod specialization. The pleopods are small, the endopodites even very small, compared to the original situation in the Flabellifera, and they have lost their swimming and breathing function (which the Flabellifera have retained). There is no development into an opercular plate, as in the Asellota.

(ad 7) The pleotelson is large in the Calabozoidea, approximately 1/3 of the body size. A pleotelson of this size is very rare in Isopoda (*Sphaeroma* has a large pleotelson), and might have taxonomic value. On the other hand, this character can be an adaptation to ecological circumstances, as Monod (1932) supposed.

(ad 8) An important taxonomic character in the Isopoda is the structure of the uropods. In contradistinction to the tailfan of the Flabellifera, the valve-like uropods of the Valvifera and the terminal, most styliform uropods of the Asellota and the Oniscoidea, the Calabozoidea have laterally inserted, atrophied uropods with reduced rami. The uropods can be sheltered in an excavation of the pleotelson; the lateral body outline then is nearly continuous.

The lateral insertion is different from the lateral insertion in the Flabellifera and the Valvifera, in that they have no connection left with the 6th pleonite. It is therefore considered an apomorphous character. The advanced reduction of the two rami and the possibility of lodging the uropods in the pleotelson can well be an adaptation to life in interstitia or a life style as described by Monod, 1932 (see below).

(ad 9) The epimera in the Calabozoidea are large and completely fused with the tergites. Racovitza (1912) considers large epimera with a more or less clear suture line as a plesiomorphous character. Reduced epimera or completely coalescent epimera (with no suture line left) are considered as apomorphous characters. Monod (1932) has pointed out that a development of "marginal zones" together with a general flattening of the body, a tendency to incorporate appendages (like the uropods) in the body and a tendency towards a continuous body line are the characteristics of a life style in which the isopods cling to the substrate (stones, kelp). As the well-developed natatory pleopods do already suggest, the Calabozoidea are quite capable of swimming and running. In the present case the epimeres might have developed further in this direction, but it must be borne in mind that they represent primarily an apomorphic, commonly shared character (Flabellifera

TABLE I

Characters of the Calabozoidea in comparison with some other isopod suborders. (Partially according to McLaughlin, 1980)

	Flabellifera	Valvifera	Asellota	Calabozoidea	Oniscoidea
1. Pereiopods	ambulatory and/or prehensile	ambulatory or prehensile, occasionally reduced in number	1st often subchelate; sometimes reduced in number	all ambulatory, 2-7 monomorphous	all ambulatory and monomorphous
2. Pleopods	first 2 or 3 often natatory; posterior pairs branchial	biramous, branchial, covered by the operculate uropods	2nd or 3rd pairs operculate; last 3 pairs branchial and enclosed	1st & 2nd modified; remainder branchial, protective, natatory	endopodites respiratory, exopodites protective with pseudotracheae
3. Telson	fused with variable number of pleonites	fused with pleonites 4-6	fused with at least 4 pleonites	fused with 6th pleonite only	occasionally not fused with 6th pleonite
4. Pleonites 1 and 2	occasionally fused with other pleonites	epimeres reduced only	sometimes reduced to sternal parts	reduced to sternal parts	in general smaller; occasionally reduced
5. Male sexual pleopods	stylet on endopodite of 2nd pleopod	stylet on endopodite of 2nd pleopod	2nd pleopod (endopodite) modified; 1st pleopod (exopodite) occasionally operculate	1st (exopodite) and 2nd (endopodite) pleopod entirely modified	2nd (endopodite) and often also 1st (endopodite) pleopod modified
6. Female 1st and 2nd pleopod	normally developed; natatory and respiratory	normally developed; natatory	usually 1st pleopod wanting; 2nd pleopod can form an operculum	small, original functions lost	endopodites often reduced or wanting
7. Pleotelson	occasionally large	relatively large, because several pleonites involved	large, due to fusion with at least 4 pleonites	large, with only 6th pleonite involved	small
8. Uropods	lateral, forming a caudal fan	lateral, valve-like	terminal, mostly styliform	lateral, atrophied	terminal, mostly styliform
9. Epimera	large, at least suture line visible	large, at least suture line visible	small and obsolete	large, no suture lines visible	large, suture line hardly visible
10. Mandibles	usually with palp	usually without palp	usually with palp	without palp	without palp

and Valvifera) and only secondarily an adjustment to ecological factors, if any. *Proasellus remyi* as described by Monod (1932) on the contrary, has secondary developed pereionites and coxal lobes, after complete loss of the epimera.

(ad 10) Mandibles are structures which can show a large flexibility among higher taxa, in addition to the different feeding types. However, in most groups a general basic form can be deduced. The mandibles of the Calabozoidea resemble those of the Oniscoidae mostly, especially because of the molar process which Sars (1899) describes as "... obsolete, without any triturating surface, it being replaced by a brush-like recurved seta". This description fits the molar process of the Calabozoidea perfectly.

In *Calabozoa pellucida* the mandible palp is wanting, like in most Valvifera and all Oniscoidea. In the Asellota the mandible palp can be present or absent, and, if present, it can be composed of a varying number of articles.

(ad 11) The absence of eyes is an adaptation to the dark surroundings groundwater animals live in. It has no value in higher taxonomy.

DISCUSSION

In the above sections it has become obvious that the Calabozoidea represent a new suborder. It might be interesting though, to speculate on its possible relationships with other suborders.

As the Flabellifera are considered representing the most ancient Isopoda, the characters that the Calabozoidea and the Flabellifera have in common should be plesiomorphous and homologous (homologous in the sense of Simpson, 1961).

The apomorphous characters can be divided in two kinds:

a. The characters that are unique for the Calabozoidea, as there are the large pleotelson and the reduced, atrophied uropods.
b. The characters that are well-developed expressions of a common trend, as there are the reduced 1st and 2nd pleonite and the modified 1st and 2nd male pleopods.

(ad a) Though these characters are very typical and unusual, and constitute together with the characters mentioned under b a clear separation from the other suborders, they may well represent merely adaptations to ecological factors in the subterranean habitat.

(ad b) These apomorphous characters are more interesting for speculation. They represent parallelism sensu Simpson, 1961.

In this respect it must be stressed that characters that have evolved from a relatively simple form to a more complex structure as the 1st and 2nd male pleopods, are more important than characters that have undergone a reduction (as the pleonites 1 and 2). Even more important than the shape into which the male pleopods have evolved, is the origin of this neogenetic character. Mayr (1969: 82) declares that phenomena of parallelism always reveal a hidden genetic potential derived from a common ancestor. In this context this neogenetic character as it occurs in some of the Isopoda, is more easy to understand. Only some of the Asellota, Oniscoidea and the Calabozoidea have a development of the 1st male pleopod (together with a completely modified endopodite of the 2nd pleopod) into a copulatory structure. Whether the structure has a protective function or actually plays a role in copulation, is of no importance here; neither is the shape of the structure (which is mostly correlated with the function). The only significance of these structures in revealing a possible relationship on this level, is their origin.

In the Asellota with a modified 1st male pleopod (e.g. *Jaera*) this copulatory structure is homologous with the exopodite of the 1st pleopod. In the Oniscoidea (e.g. *Porcellio*, *Armadillidium*) it is the endopodite of the 1st pleopod that has evolved. The neogenetic characters in these taxa are therefore not homologous. The well-developed 1st pleopod of *Calabozoa pellucida* is of exopodal origin. This points to a closer relationship of the Calabozoidea to the Asellota than to any other suborder, notwithstanding the fact that the shape of the 1st male pleopod, and probably also its function, has more similarities with the

1st male pleopod of the Armadillidiidae (Oniscoidea).

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