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Zulialana coalescens gen. et spec. nov., a stygobitic cirolanid (Isopoda, Cirolanidae) from a cave in north-western Venezuela

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Abstract

A new genus and species of cirolanid isopod are described from a stream in a cave in north-western Venezuela. The depigmented and anophtalmous cirolanid is very large, able to roll into a ball, and has a number of remarkable morphological characters, such as the almost complete coalescence of pleonal segments and telson and the strong morpho-physiological reduction of the uropods. A detailed comparison is made with the only other cirolanid genera sharing such characters : *Faucheria* from southern France, *Sphaerolana* from Mexico, and *Skotobaena* from East Africa, the conclusion being that no real affinities exist between the 4 genera. Observations in the natural habitat and in aquaria show that the animal is unable to swim, but that it is rather active, moderately gregarious, and quite voracious (guanophagous).
Key words : Isopoda, cave fauna, Venezuela.

Resumen

Basado en material abundante, se describe en detalle un nuevo género y especie de isópodos cirolánidos (*Zulialana coalescens*) procedente de una corriente subterránea en una cueva de la Sierra de Perijá, noroeste de Venezuela. El cirolánido, despigmentado y anoftalmo es muy grande (cerca de 3 cm), capaz de enrollarse como una esfera casi perfecta, y con numerosos caracteres morfológicos distintivos, siendo los más conspícuos la coalescencia casi total del telson y los segmentos pleonales, y la acentuada reducción morfo-fisiológica de los urópodos. Se hace una comparación detallada con los únicos otros géneros de cirolánidos que comparten tales caracteres : *Faucheria* del sur de Francia, *Sphaerolana* de Mexico, y *Skotobaena* del este de Africa, y se concluye que no existen afinidades reales entre los cuatro géneros; los caracteres mencionados se presentan en muy diferentes estados y probablemente han sido adquiridos de manera independiente durante una prolongada evolución en el medio dulceacuícola hipogeo. Las observaciones de los animales vivos tanto en su habitat natural como en acuarios, muestran que *Zulialana coalescens* es un animal incapaz de nadar, bastante activo, moderamente gregario y muy voraz (guanófago).
Palabras clave : Isopoda, fauna de cueva, Venezuela.

Introduction

Cirolanidae is one of the two families of order Isopoda, suborder Cymothoidea represented in non-marine, subterranean water, mainly in karstic freshwater environments. Although the overwhelming majority of the cirolanids are marine (or brackish water) animals, 18 genera with some 56 described species are presently known as inhabitants of the aquatic subterranean realm. The vast majority of these genera and species are completely adapted to subterranean life. Only a few genera have marine as well as subterranean species, which constitutes possible evidence for recent colonization of subterranean water, and only a few species can be considered merely as stygophiles – not stygobionts. There is also one group of genera (gr. *Faucheria*) which is entirely adapted to subterranean life. This group includes the monospecific *Faucheria* from southern France, *Skotobaena* with two species from East Africa, and *Sphaerolana* with two species from Mexico. All of them are strikingly characterized by at least three important characters never found in marine cirolanids : the ability of the body to roll into a ball, the rather advanced coalescence of the pleonites with the telson, and the variously reduced and ankylosed uropods.

The giant stygobiont cirolanid (one of the two largest known) recently discovered from a cave of north-western Venezuela, sharing with the above mentioned genera these three characters, and described as a new genus and species below, adds a new dimension to the exciting problem of hypogean adaptation and evolution in the Cirolanidae.

Little is known about biology, ecology, and behaviour of subterranean Cirolanidae. It is thus fortunate that various observations could be performed on *Zulialana coalescens* gen. n. sp. n., not only in its natural habitat, but also in captivity.

Taxonomic descriptions

Zulialana gen. n.

TYPE SPECIES (here designated) :

Zulialana coalescens sp. n.

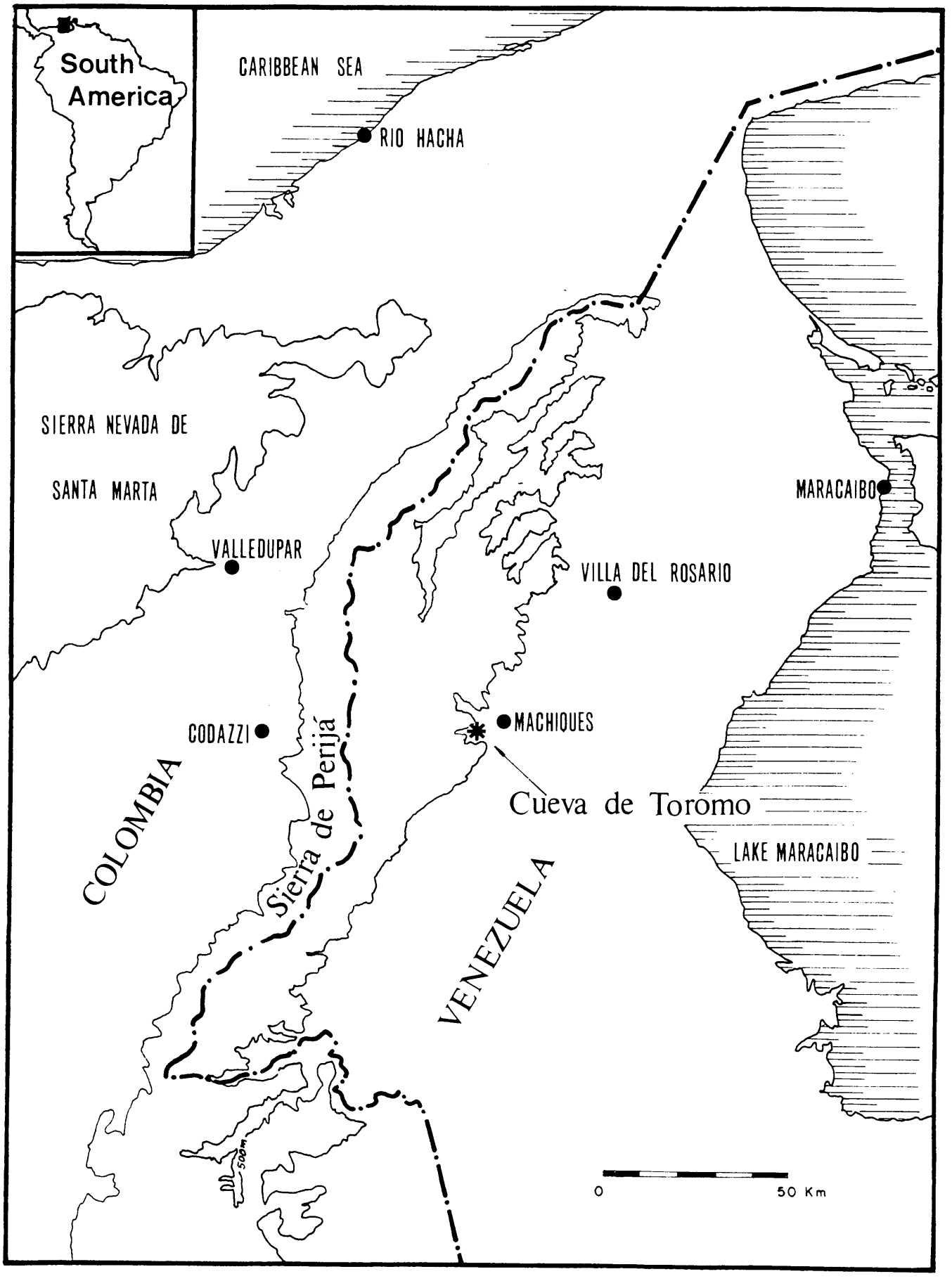


Fig. 1. – *Location of Cueva de Toromo.*

DIAGNOSIS

Very large (up to 3 cm), anophtalmous and depigmented Cirolanids, able to roll almost perfectly into a ball. Well developed tomentum on AII peduncle and all pereiopods. AI with multiarticulate flagellum with numerous aesthetascs. AII flagellum with numerous articles. Internal blade of maxilla I with five setae. Maxilla II with the three lobes extremely similar in size, shape, and length of setae. Maxilliped with epipodite, main body of sympodite clearly biarticulate. Pereiopods I-II subchelate (prehensile), III of an intermediate type, IV-VII ambulatory; I-III with poor armature of spines on the propodi, but with strongly developed dactylian organs. Oostegites developing from pereionites I-V. Pleopods : exopodites never bipartite, all with marginal setae; endopodites glabrous, III-V with annex lobe; short appendix masculina. Pleotelson wider than long, broadly rounded posteriorly, without long setae, with very advanced coalescence of pleonal segments with telson : only pleonites I-III still separated by extremely short lateral sutures. Uropods very short, ankylosed, exo- and endopodite present, but especially exp. very small.

ETYMOLOGY

From (Estado) Zulia; 'lana' is a suffix often used in naming Cirolanid genera.

Zulialana coalescens nov. spec.
(Figs. 2-28)

TYPE LOCALITY

North-western Venezuela : Cueva de Toromo, near hacienda (estate) Medellin, Sierra de Perijá, municipio Machiques de Perijá, Estado Zulia (Fig. 1). 72°40'00" W, 10°03'20" N; altitude 400 m. a.s.l.

TYPE MATERIAL

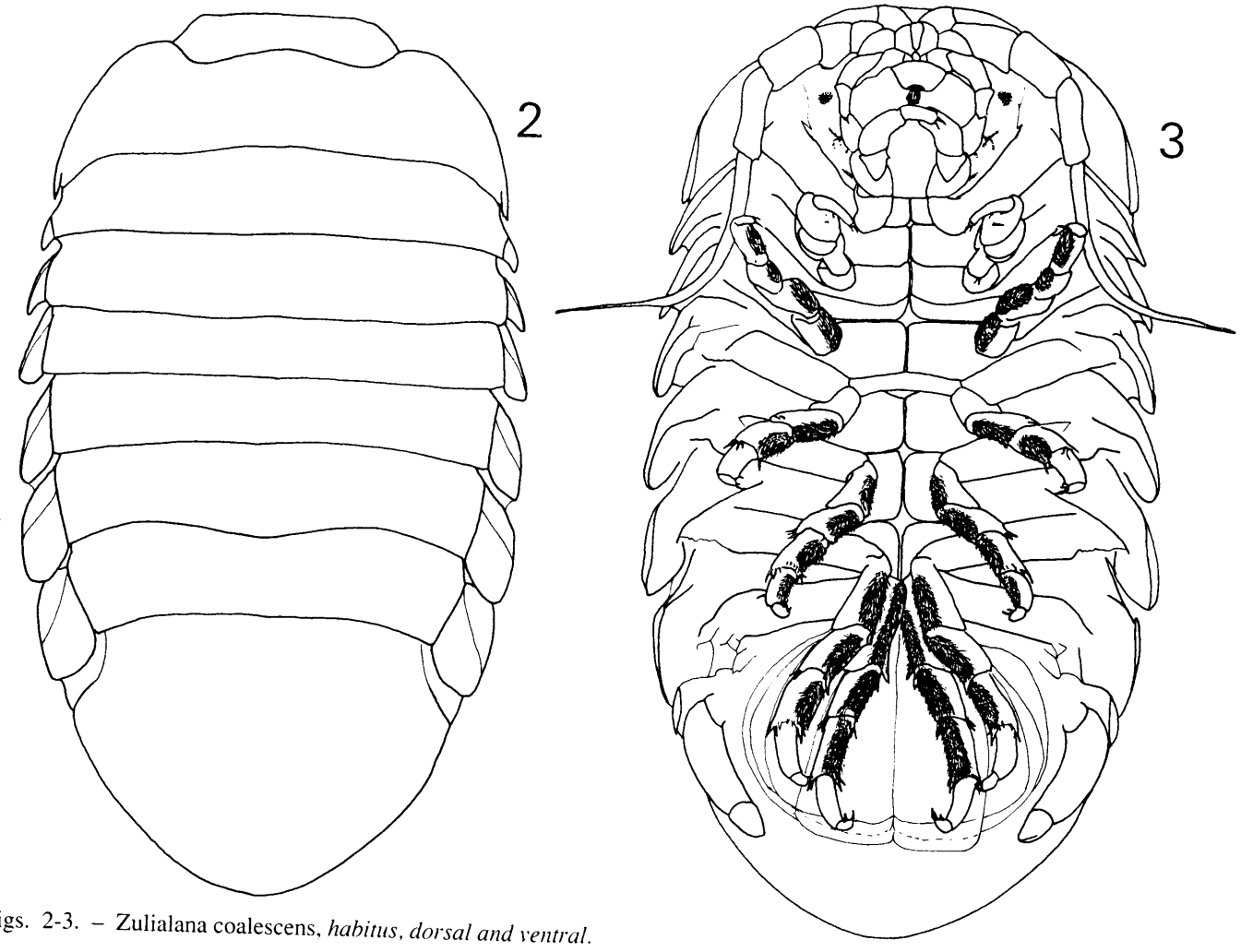
27 specimens collected on 26 March 1992 by A. VILORIA, C. GALÁN and F. HERRERA and kept in 70 % alcohol are designated as types : holotype male, 9 male paratypes, allotype female, 2 female paratypes, deposited in the Museo de Biologia, Universidad del Zulia, Maracaibo (M.B.L.U.Z., Colección de tipos; coll. nos. T-014, holotype; T-015, allotype; T-016, paratypes. 10 male paratypes, 4 female paratypes, deposited in the Zoölogisch Museum, Universiteit van Amsterdam (Z.M.A., coll. Is. 200247 and 200246). All from Cueva de Toromo (Sierra de Perijá, municipio Machiques de Perijá, Estado Zulia, Venezuela). Six paratypes collected later in the type locality, deposited in the collections of the Royal Belgian Institute of Natural Sciences, Brussels, Belgium.
Additional specimens, collected on 21 November 1992 in the type locality were not designated as types; some of them are currently kept alive for various observations in a laboratory of the University of Zulia; these additional specimens will be kept in the M.B.L.U.Z.

ETYMOLOGY

The name *coalescens* alludes to the highly characteristic, almost complete coalescence of the pleonal segments of this species.

DESCRIPTION OF MALE

This description is mainly based on the male holotype; additional information is from other type specimens.
Holotype length 3 cm, maximal width 1.5cm (the length of the ♂ paratypes, all certainly mature, varies between 1.25 and 3 cm). Anophtalmous. Depigmented, but with the following black parts : postero-median zone of labrum, acies of the two mandibles, spines of the external blade of MxI, double unguis of all pereiopods; many spines of the pereiopods are brown; in most specimens there are important anterior zones on articles 2-5 of the antennal peduncle, and internal zones on ischium, merus, carpus, and propodus of all pereiopods, stained in brownish by fine detritus accumulating at base of the tomentum covering these zones.
Body oval (Figs. 2, 3) convex, coriaceous, without conspicuous ornamentation (posterior margin of pleotelson not perfectly smooth but apparently delicately festooned, mainly because of minute spherical submarginal protuberances).
Cephalon (Fig. 4) short, with convex anterior margin (no rostrum), slightly concave posterior margin, salient antero-lateral angles; incompletely embraced by the shoulders of the first pereionite; laterally with deep furrows in which the shoulders of the first pereionite may penetrate (this coaptation allowing the animal to roll into a ball is present in all pereionites : the shoulders of each pereionite may penetrate into deep furrows on the ventral face of the preceeding pereionite).
Clypeo-labral complex (Fig. 5) : lamina frontalis stout, slightly wider at base than at apex, slightly sinuous laterally, bluntly ending; clypeus short medially (with deep antero-median sinus) but with strongly widened lateral wings with distal emargination; labrum distally slightly trilobed.
Measured on their median line, all pereionites subequal in length. Epimeres finely setose. First epimere (Fig. 6) not separated from the pereion, without diagonal ridge, and forming an obtuse point; all remaining epimeres clearly separated by sutural lines from the respective pereionites, and with faint diagonal ridge; epimeres II-IV apically rounded, epimeres V-VII considerably



Figs. 2-3. – Zulialana coalescens, *habitus, dorsal and ventral.*

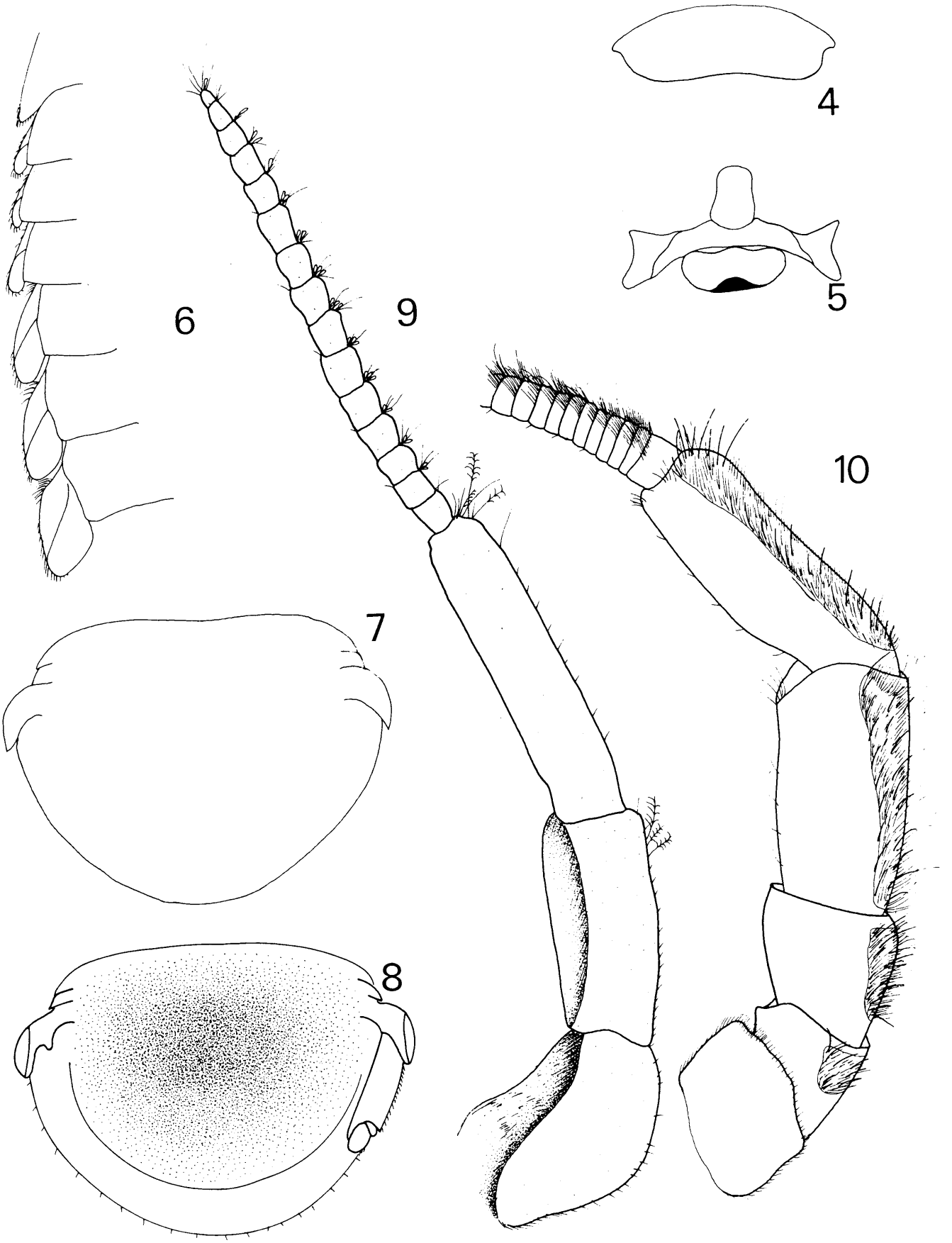
larger - VIIth being the largest; all epimeres with distinct sternal extensions; normally the epimeres of the last pereionite completely covering the pleonal epimeres.

Posteriorly broadly rounded pleotelson (Figs. 7, 8) representing a deep respiratory cup protecting the pleopods. Coalescence of the pleonal segments with the telson almost complete : only the first three pleonites (only quite laterally - dorsally as well as ventrally) being indicated by extremely short sutures; epimeres of these 3 pleonites not separated from the segments, epimeres III much stronger than I and II, and curved (uropods rooted in the axilla of epimeres III). Only few scattered, short and fine setae on the pleotelson's posterior margin.

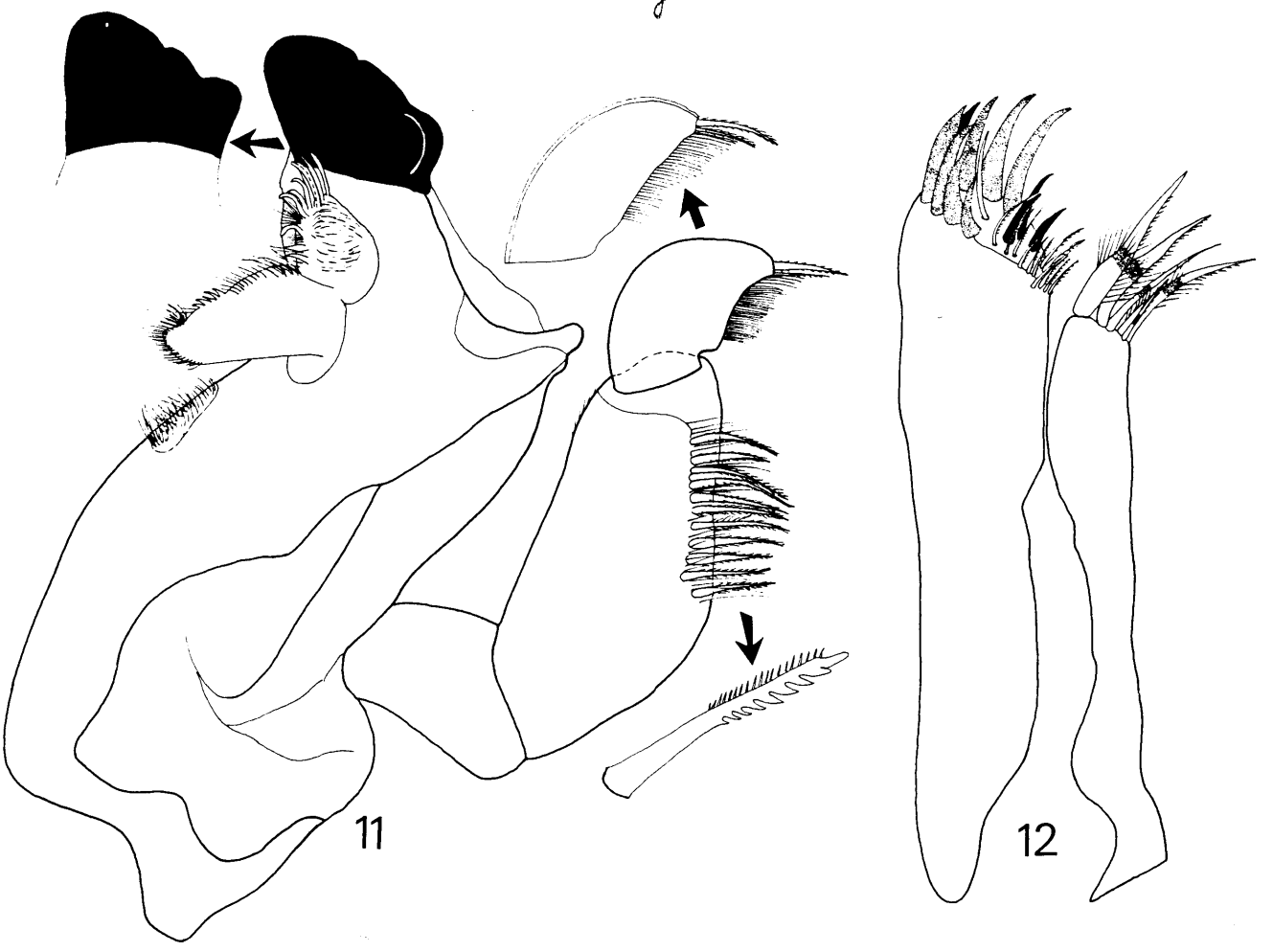
Antenna I (Fig. 9) much shorter than AII : tip of its flagellum reaching at most to the tip of AII peduncle. First two articles of peduncle prismatical, article 3 cylindrical and much longer; flagellum with 14 and respectively 15 articles in the holotype (13 and respectively 16 in a paratype of 3cm.); numerous aesthetascs present, exact number variable; holotype with the following situation : right AI : 1(0), 2(2), 3(2), 4(2), 5(3), 6(3), 7(3), 8(3), 9(2), 10(2), 11(1 or 2), 12(2), 13(1 or 2), 14(0), 15(1); left AI : 1(0), 2(2), 3(2), 4(3), 5(2), 6(2), 7(2), 8(2), 9(2), 10(2), 11(0), 12(1), 13(3), 14(2 or 3).

Antenna II (Fig. 10). Important anterior surfaces of articles 2-5 of the peduncle covered with a tomentum (extremely dense and fine, rather long, woolly setae, retaining detritus); with some normal setae scattered between them. Flagellum of the largest paratype (3 cm) with 42 articles on the right side, and 35 on the left side (in the holotype the articles are broken); articles setose.

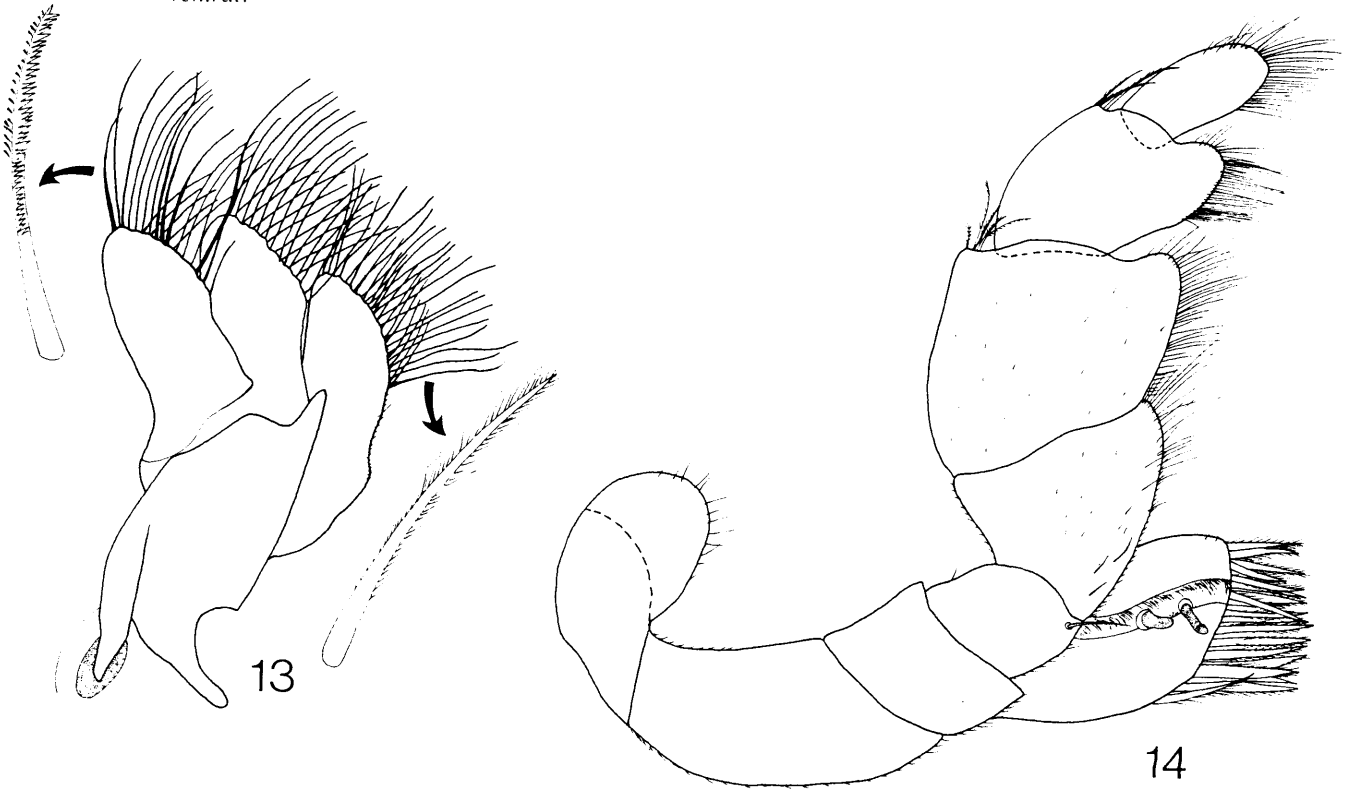
Very robust mandibles (Fig. 11). In right mandible masticatory part (acies) with three obtuse teeth – the median one being the largest; in left mandible shape slightly different : in dorsal view only 2 large teeth visible, but in ventral view shape differing only slightly from that represented in Fig. 11. Very strong anterior condylus, devoid of an auxiliary condylus. Lacinia mobilis soft, flattened, on internal margin with a row of ca. 10 spines (slender, smooth, generally slightly curved: distalmost spines being the longest; the proximal spines accompanied by fine setae). Pars molaris



Figs. 4-10. – Zulialana coalescens, *male.* - *4. Cephalon, dorsal.* - *5. Clypeo-labral complex.* - *6. Left half of pereion, dorsal.* - *7. Pleotelson, dorsal.* - *8. Pleotelson, ventral, with left uropod.* - *9. Right AI, ventral.* - *10. Right AII, ventral, only with basal part of flagellum.*



Figs. 11-12. – Zulialana coalescens, *male*. - *11. Right Mdb., dorsal (arrows pointing to more correct aspects of acies and terminal palp article, and to a strongly enlarged seta on lateral margin of 2nd palp article).* - *12. Right MxI, ventral.*



Figs. 13-14. – Zulialana coalescens, *male*. - *13. Right MxII, ventral (arrows pointing to more strongly enlarged setae; left : seta from ventral row of external lobe; right : seta from dorsal row of internal lobe).* - *14. Right Mxp., ventral.*

movable, distally and proximally with tufts of extremely fine setae, the latter shortly pennate; between these two tufts, about 5 short spines ventrally inserted. On the mandibular body, proximad from pars molaris, a rather large tuft of very fine setae. Palp : on distal half of the lateral margin of article 2 (which is much longer and wider than articles 1 and 3) a compact row of strong, characteristically serrate setae, and, slightly more dorsally, numerous other setae (finer, but still serrate); all setae of article 3 finely pennate.

Paragnath (Hypopharynx) with pair of round, fleshy lobes with tufts of extremely fine setae on their median margin.

Maxilla I (Fig. 12). No bridge connecting the two blades was found. External blade with apico-lateral crown of eight very strong, dark, slightly curved, smooth spines; one seta (dark, not pennate) in middle of this crown; towards the median angle 3 shorter dark spines, and, more ventrally inserted, about 12 finely pennate setae with dark base. Internal blade apically with five setae, the two lateralmost and the medianmost much stronger than the remaining two (one short, one long), all dark in their middle, the three strongest with long cilia in their middle and shorter cilia towards the tip; of the remaining two setae, the longer smooth, the shorter finely pennate.

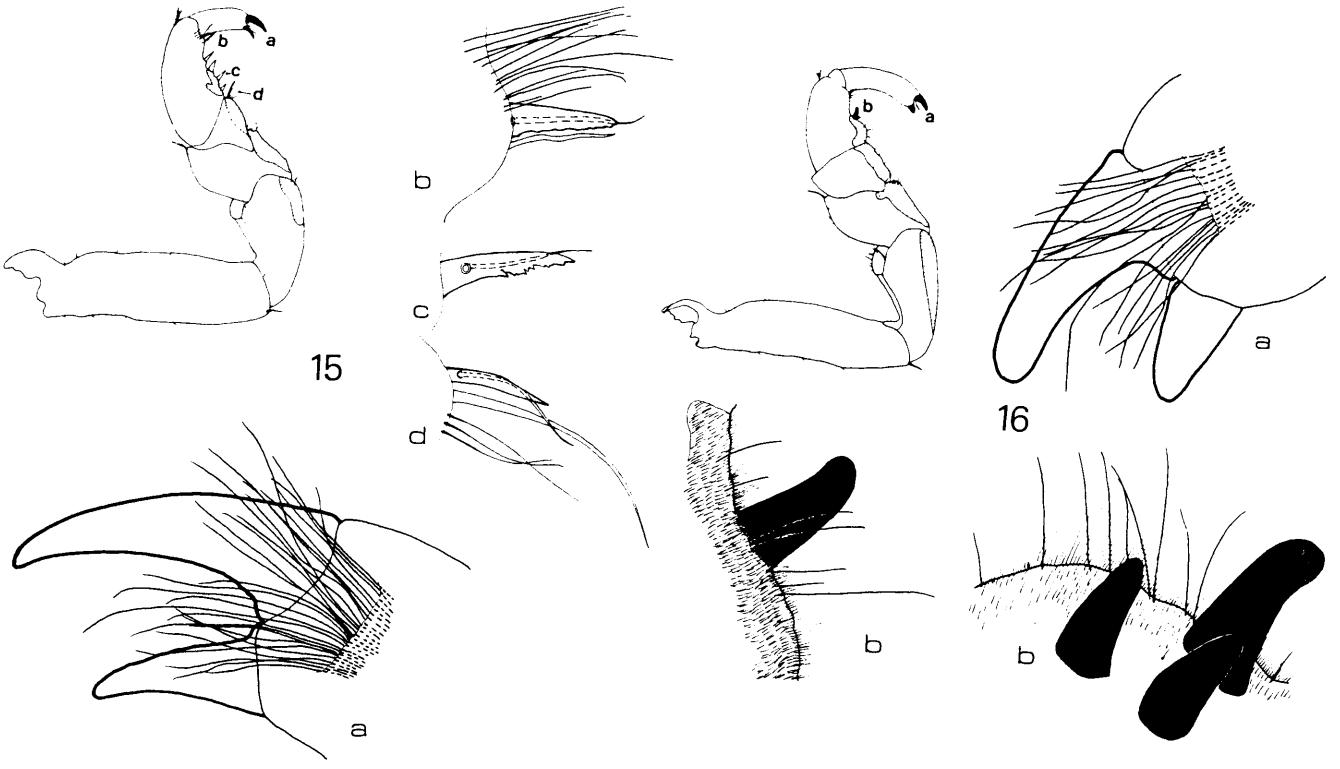
Maxilla II (Fig. 13) with the three lobes of similar size and shape, all ogival distally. All three lobes with two apical rows of more or less long setae; all long (ventral row) setae of external and median lobe finely serrate; all long (dorsal row) setae of internal lobe with dense, rather long, fine cilia (some of the shorter – ventral row – setae of internal lobe are finely serrate).

Maxilliped (Fig. 14). Oval epipodite with a few fine, smooth apical setae. Sympodite basally without heel, very distinctly divided into two large articles (it was not possible to clearly distinguish also rudiments of one or two basal articles : see also description of the ♀ maxilliped). Masticatory lobe distinctly separated by a structural limit (visible dorsally) from the terminal article of the sympodite; it has the shape of a triangular prisma and forms a 60° angle with the palp; a strong ventral ridge separating two faces of the prisma enables insertion to two retinacula; apically with a compact group of about 18 strong, densely pennate setae. All internal setae on palp smooth; the five setae in the disto-external angle of article 3, and the three setae in the disto-external angle of article 4 shortly pennate.

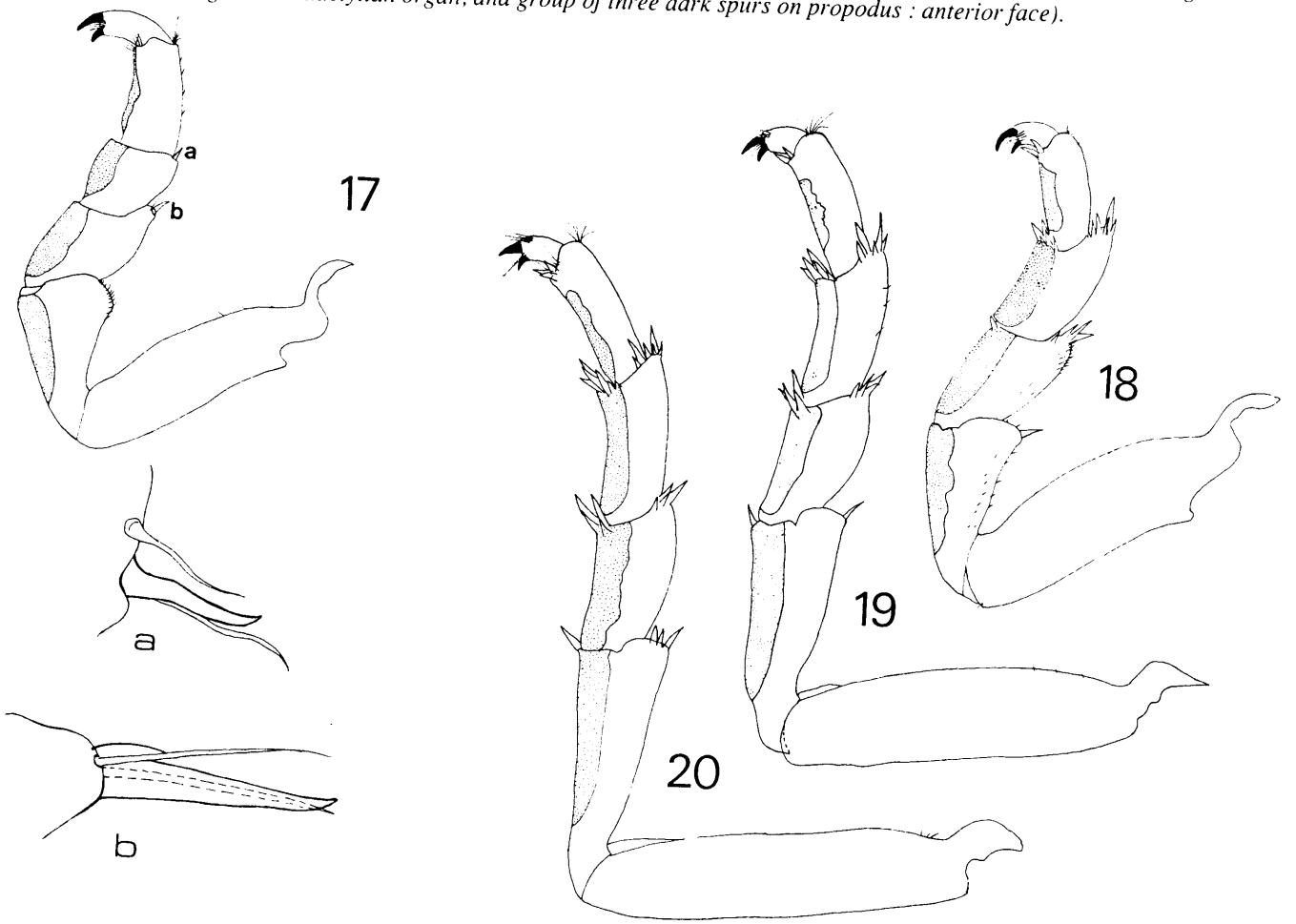
Pereiopods (Figs. 15-20). Pereiopods I-III relatively short, I-II only slightly subchelate, and with a poor armature of distal spines on the various articles. Per. IV-VII gradually longer, with more numerous distal spines. In several respects Per. III intermediary between I-II and IV-VII. Ischium, merus, carpus, and propodus of all pereiopods with internal zones of tomentum retaining detritus (starting with Per. III these zones are more strongly developed on the anterior than on the posterior face). No propodial organs. Propodus of Per. II with strong swelling of palmar margin. Dactylus relatively long in Per. I and III, longest in Per. II, short in the remaining pereiopods. All pereiopods with double, black unguis. Per. I : dactylian organ (Fig. 15a) extremely developed, consisting of at least 28-30 setae; on propodus one apico-internal spine with additional seta (Fig. 15b), and four other spines with additional setae along internal margin, these spines having a very irregularly serrate margin (Fig. 15c); apico-internally on merus a slender spine with additional seta (Fig. 15d). Per. II : dactylian organ (Fig. 16a) consisting of about 17 setae; internally and on the anterior face of propodus, three (only two in the largest paratype) stout, blunt, and dark spurs (Fig. 16b) stronger than all other pereiopodal spines. Per. III (in all repects distinct from I-II as well as from IV-VII) : dactylian organ consisting of about 14-15 setae; apico-externally on carpus and merus one spine (sometimes two on carpus) with additional seta (Fig. 17 a, b). Pereiopods IV-VII with dactylian organ consisting of 4 setae only; number of distal spines on their various articles certainly variable, spines in one group of very different sizes, and many with an annex seta; number of spines (as found in the holotype and the largest paratype) : Per. IV, ischium external angle 1, merus external angle 6-7, internal angle 2-5, carpus ext. 4-7, int. 6-8, propodus int. 2-3; Per. V, ischium ext. 1, merus ext. 7-8, int. 3-5, carpus ext. 6, int. 5-9, propodus int. 3; Per. VI, ischium ext. 1-2, int. 1, merus ext. 6-8, int. 6, carpus ext. 6-7, int. 8-9, propodus int. 3; Per. VII, ischium ext. 4-6, int. 1-2, merus ext. 8-13, int. 6-9, carpus ext. 7-10, int. 9-10, propodus int. 3-5.

Genital papillae (penes) well separated, situated on posterior limit of the sternal face of the last pereionite : Fig. 21.

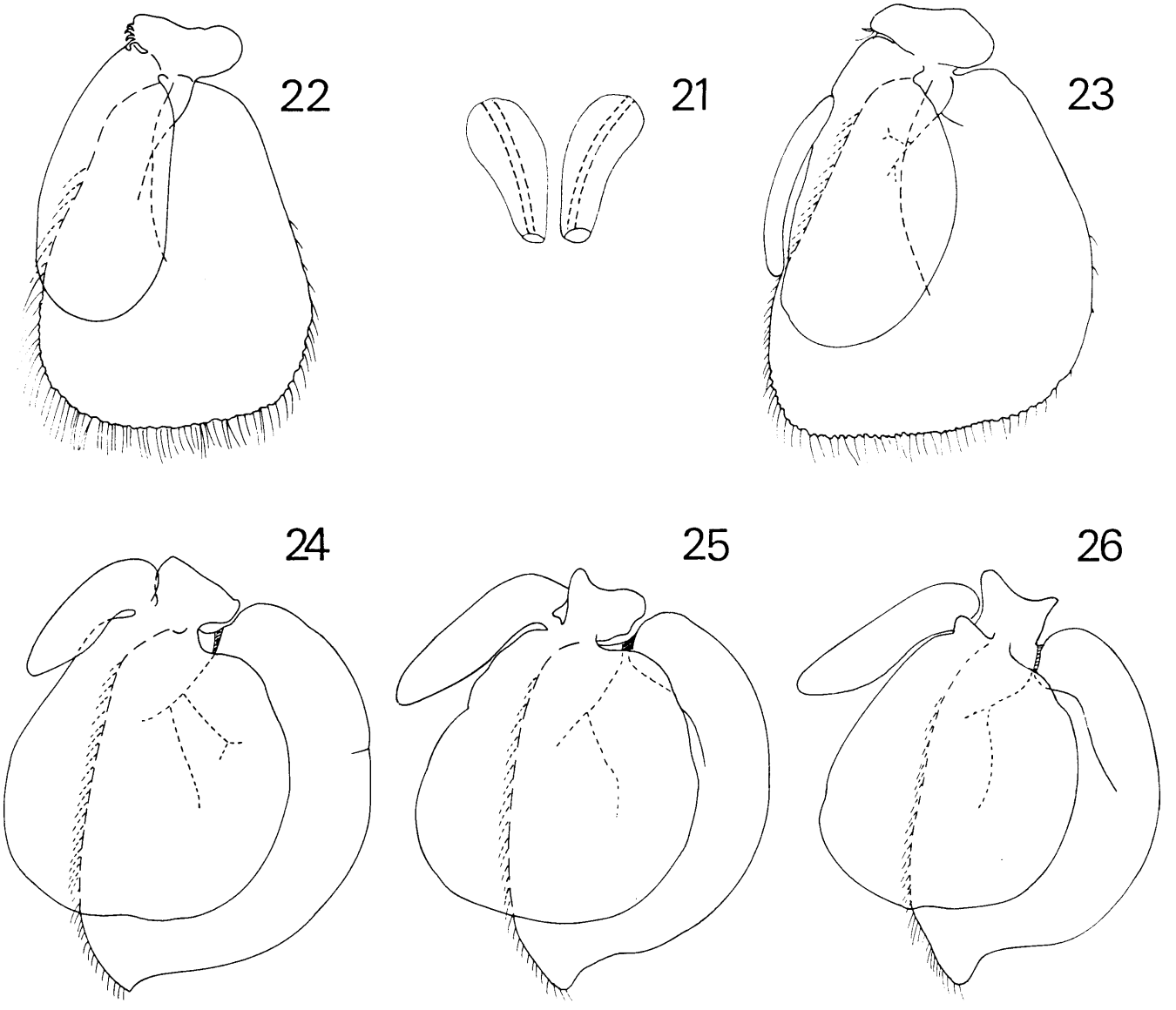
Pleopods (Figs. 22-26) rather large, all respiratory (all with distinct blood vessels in the exopodites). Exopodites never bipartite (the quite incipient bipartition in Fig. 24 is certainly irrelevant). In Pl. I-II sympodites with, in the internal angle, 4 coupling hooks and, respectively, 1 coupling hook + 3 setae; exopodites pyriform with dense pennate setae along the posterior and internal margins (these setae, often stained in brown by detritus and mud, are short but nevertheless longer than those on the following pleopods); endopodites proportionally small, oval. Sympodites in Pl. III-V without coupling hooks or setae; exopodites foliaceous with distinct apical point and with very short pennate setae along their internal margins only; endopodites proportionally larger, roughly round, with well developed annex lobes hanging from their disto-internal angles. Appendix masculina of the 2nd pleopod (Fig. 23) short, by far not reaching endopodite's apex, slightly curved, with blunt tip, rooted distally on the proximal 1/3 of the internal margin of the endopodite.



Figs. 15-16. – Zulialana coalescens, *male*. - *15. Right pereiopod I, posterior face, with four strongly enlarged details (unguis with dactylian organ : anterior face).* - *16. Right pereiopod II, posterior face, with two strongly enlarged details (unguis with dactylian organ, and group of three dark spurs on propodus : anterior face).*



Figs. 17-20. – Zulialana coalescens, *male*. - *17. Right pereiopod III, anterior face, with two strongly enlarged details.* - *18-20. Right pereiopods IV, VI, and VII, anterior face.*



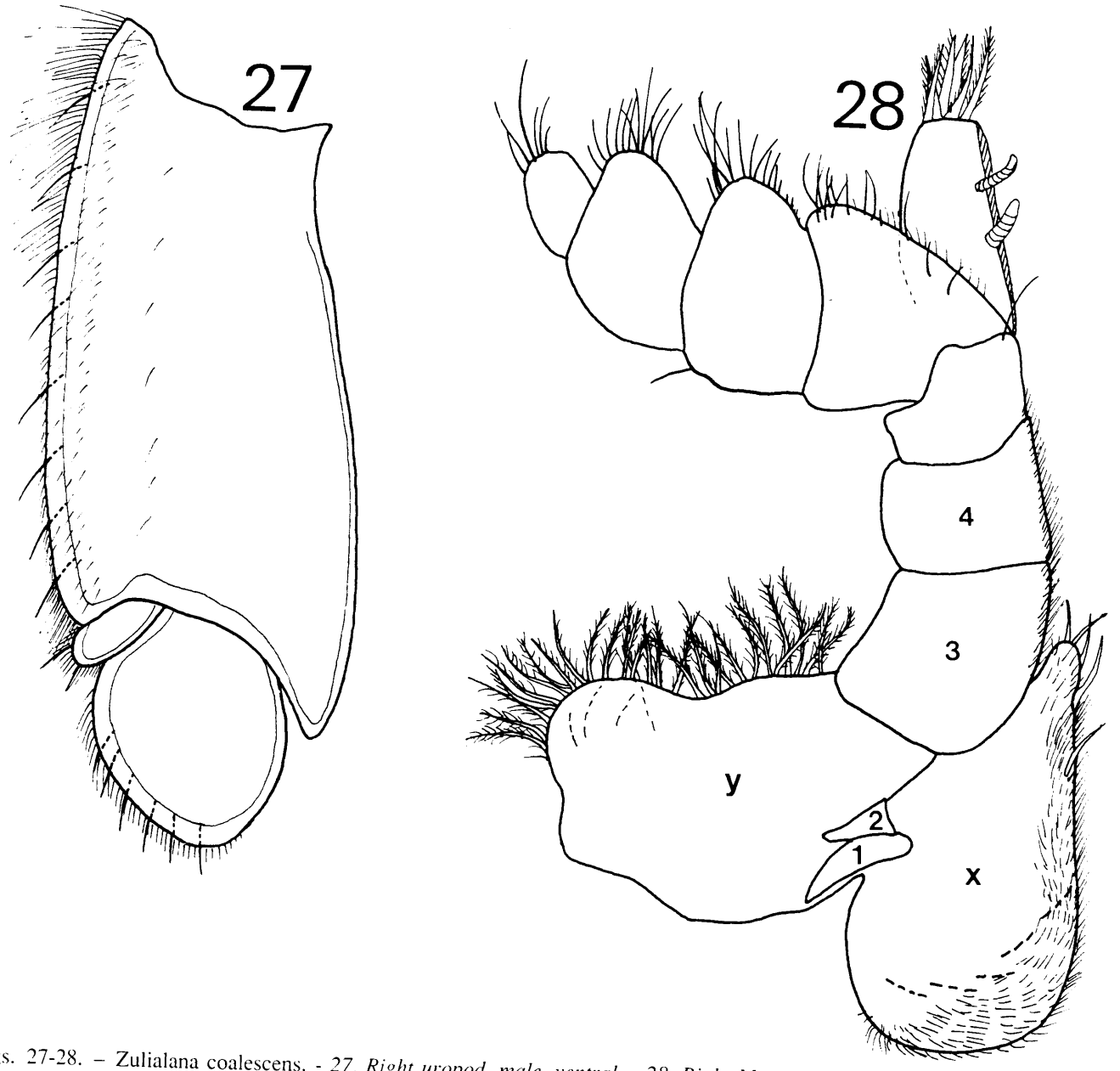
Figs. 21-26. – Zulialana coalescens, *male. - 21. Penes. - 22-26. Right pleopods I-V, dorsal.*

Uropods (Figs. 3, 8, 27) remarkably small (about 2.4 times shorter than the pleotelson and by far not reaching its tip), rooted quite proximally and latero-ventrally in the axilla of the 3d pleonal epimeres; they are hard, almost completely ankylosed (this being valid also for endo- and exopodite), ventrally convex, dorsally flat. Endopodite shortly oval, with pair of pennate setae on its dorsal face near baso-external angle. Exopodite extremely reduced.

DESCRIPTION OF FEMALE

Allotype (= the only female found with oostegites) length 1.6 cm. (length of the ♀ paratypes, all certainly mature but without oostegites : 1.5-1.9 cm.).
Flagellum of AI with 8-9 articles, of AII with 28-29 articles (numbers very different from those found in the males !).

Mxp. of female with oostegites (Fig. 28) strongly modified for anterior closing of the incubatory cavity (see discussion in RACOVITZA, 1912 : 290-294, fig. V). Main body of sympodite with quite distinct division in two large articles, as also seen in the male (3 and 4 in Fig. 28) but also with two small triangular sclerites more basally placed (1 and 2 in Fig. 28), this probably indicating a quadriarticulate sympodite. Proximad from sympodite, two large membranous expansions (functionally homologous with the oostegites); one (y in Fig. 28) forming a right angle with the sympodite and being probably developed on the expense of the epipodite; a clear bipartition of this expansion not distinguishable, anterior margin with at least 30 pennate setae; 2nd expansion (x in Fig. 28) continuing the sympodite's longitudinal axis and furnished proximally and internally with extremely fine and dense setae (a few stronger setae are inserted basally on the dorsal face, as well as in



Figs. 27-28. – Zulialana coalescens. - *27. Right uropod, male, ventral.* - *28. Right Mxp., female with oostegites, ventral (for explanation of letters and numerals : see text).*

the disto-internal angle of the expansion). Palp articles with far less setae than in the male, both on the internal and on the external edges. Strong, pennate setae of the masticatory lobe less numerous than in the male.

Oostegites, all with pattern of transparent and opaque zones, present on the pereionites I-V. Oostegites I-III much smaller than IV-V. No eggs found in the incubatory cavity. It should be noted that this is one of the very few known cases of subterranean cirolanids where specimens with oostegites were found (to the best of our knowledge the only already known case being that of *Skotobaena*).

Pleopod II, of course, without appendix masculina. Pennate setae on the posterior margin of the exopodite less dense than in the male.

AFFINITIES

The most striking characters of the new genus are the very advanced pleotelsonal coalescence, the uropod reduction, and the capacity of the animal to roll into a ball. It is thus logical to compare it to the only other Cirolanid genera (all entirely freshwater subterranean) sharing these characters. These are : *Faucheria* DOLLFUS & VIRÉ, 1905, with one species : *F. faucheri* (DOLLFUS & VIRÉ, 1900), from karst habitats in southern France : Gard, Hérault, and maybe Aude Départements (detailed description : RACOVITZA, 1912); *Sphaerolana* COLE & MINCKLEY, 1970, with two species : *S. affinis* COLE & MINCKLEY, 1970, and *S. interstitialis* COLE & MINCKLEY, 1970 – both from

thermal springs and their outflows in Mexico (Coahuila), but *affinis* also from a flooded mine in Nuevo León (Mexico); and *Skotobaena* FERRARA & MONOD, 1972, with two species, one from a cave in Ethiopia (*S. mortoni* MONOD, 1972), a second one from shallow wells in southern Somalia (*S. monodi* FERRARA & LANZA, 1978).

A detailed comparison (Table I), sometimes rendered rather difficult because of characters not very clearly described and/or illustrated in *Sphaerolana*, shows mainly numerous important differences between genera. This is especially true for *Faucheria*, whereas there is apparently some similarity between *Zulialana* and the two other genera : large size; presence (in *Skotobaena mortoni*) of a well developed tomentum; AI flagellum with numerous articles, these (*Skotobaena*) with numerous aesthetascs; AII with numerous flagellar articles; MxI internal blade with 5 setae (*Sphaerolana*); pereiopods not strongly different in the three genera, I-III with poor propodial spinulation. None of these similarities seems to be really relevant for ascertaining affinity. On the other hand, the type of reduction of the free pleonites, and the uropod shape, are strongly different in the 3 genera (uropod of *Zulialana* anyway more of the *Skotobaena* than of the *Sphaerolana* or *Faucheria* type).

BOWMAN (1975) lists the different patterns of pleonal segmentation found in the Cirolanidae and assumes that the reduction of pleonites is a derived condition. This idea seems perfectly plausible. There is no known marine Cirolanid with an advanced degree of coalescence of the pleonites with the telson, or with the ability to roll into a ball. This indicates that the freshwater and subterranean evolution of the four genera must have been a long-term phenomenon, and that we know nothing about their putative marine ancestor(s).

Table I clearly shows that no real affinities exist between the four genera. Even such striking characters as pleotelson coalescence and morpho-physiological uropod atrophy have very different states (the free pleonites reduction is most complete in *Zulialana*, whereas the uropod – and particularly exopodite – reduction is most advanced in *Sphaerolana* and *Faucheria*); such characters have been probably independently acquired as a result of independent evolution (they converge, nevertheless, towards realization of a morphology allowing more or less complete rolling into a ball). A similar view was expressed by COLE & MINCKLEY (1970 : 76-77) when comparing *Sphaerolana* with *Faucheria* (and with *Creaseriella* RIOJA, 1953 – a stygobiont genus very remote from those treated here, but also able to roll into a ball). MONOD (1972 : 215-216) warns against "... tenir pour signe de parenté directe ce qui ne relèvera que de la convergence adaptative" in his detailed discussion of the affinities of *Skotobaena*; he finds some similarity between this and another stygobiont genus, *Sphaeromides* DOLLFUS, 1898, but shows how difficult it is to weight the value of the shared characters.

It is probable that the morphological convergences in this case are responses to similar selection pressures in the subterranean freshwater realm of widely distant zones of the Northern Hemisphere.

In our opinion the *Faucheria*-group (sensu BOTOSANEANU *et al.*, 1986) is very probably a polyphyletic grouping which may, nevertheless, be maintained for practical reasons. This does not mean that the possibility of a remote common marine ancestor for the 4 genera (or for some of them, as well as for other, extinct genera) should be completely eliminated.

It is probable that a fundamentalist – cladistic analysis would reach different conclusions. Pleotelsonal coalescence, uropod reduction, rolling into a ball, would be considered as synapomorphies for the 4 genera, and these would be without hesitation used in a cladogram – but probably in different ways by different authors !

Observations on habitat and association, biology and behaviour

Cueva de Toromo, whose unique entrance opens in a rather low hillock at about 40 km from the shores of the "Lake" of Maracaibo, and about 150 km from those of the Caribbean Sea, is essentially (Fig. 29) a sinuous gallery (total length of the accessible part : 1120 m.; difference in height from a terminal syphon to the entrance : 52 m.) through which a stream flows. A description of the cave is in press (ANONYMOUS, 1993).

The origin of the stream is unknown. During dry periods the stream carries clear water, current and depth are feeble, the flow is reduced, and the stream has no epigean reach. During wet periods the water is rather turbid, flow, current, and depth are considerably increased, and – starting from a resurgence situated downstream the cave's entrance - the stream has an epigean reach, being a tributary of Rio Negro. The subterranean stream carries perfectly fresh water; in November the water temperature was 22.5°C (air temperature in the cave : 24°C); pH = 8.34; dissolved 0_2 = 7.2 mg./l. The bottom of the subterranean stream is partly covered by sand or silt, and there are several sandy beaches along its banks.

Few large animals, apart from *Zulialana*, inhabit the stream of Cueva de Toromo. From a Pseudotelphusid crab considered as stygophile, *Chaceus motiloni* RODRIGUEZ, 1980, only an exoskeleton was found in the cave. Two fish species inhabit the stream : *Trichomycterus* sp. (fam. Trichomycteridae) is maybe an undescribed species, depigmented and with a tendency towards eye reduction (microphtalmous and anophtalmous specimens are found); *Chaetostoma machiquensis* FERNANDEZ & MARTIN, 1953 (Loricariidae) is a

Table I. – *Comparison between four genera of stygobitic Cirolanids.*

	Zulialana	Sphaerolana	Skotobaena	Faucheria
Eyes, tegumental pigmentation.	Absent.	Absent.	Absent.	Absent.
Size (max.).	3 cm.	1.7 cm or 2.2 cm.	1.7 cm or 2.2 cm.	3.5 mm.
Tomentum.	Well developed on A2 peduncle and all pereiopods.	Apparently absent.	*mortoni* : on many parts of body and appendages.	Absent.
Body shape.	Rather short and broad, oval.	Rather elongate, parallel-sided.	Rather elongate, parallel-sided.	Rather elongate, parallel-sided.
Rolling into a ball.	Almost perfectly.	Perfectly.	Almost perfectly.	Perfectly.
Cephalon.	Much wider than long, without rostrum, anterior angles produced.	Trapezoidal, only slightly wider than long, with rostrum.	Trapezoidal, without rostrum (*monodi* : much wider than long; *mortoni* : slightly wider than long).	Much wider than long, with rostrum.
Lamina frontalis.	Short (stout), basally broader than at distal blunt end.	"Stout and bluntly pointed" (ogival ?).	Parallel sided, with rather strong relief ("saillie antérieure, saillie postérieure", subtriangular apex.	Like a tennis racket.
Clypeus.	Medially short, laterally strongly widened and terminally emarginated.	Very short and wide, terminally curved posteriad.	"Très courte bandelette transversale … à chaque extrémité latérale un peu dilaté et arrondi".	Triangular.
Length of pereionites.	Subequal.	?	Per. I longer than the following, which are subequal.	Per. I & V longer than the remaining.
Pereional epimeres.	Important differences between I, II-IV, V-VII.	? apparently all subequal and "conspicuous".	I ? II-VII subequal and large.	Important differences between I, II-III, IV-VII.
Pleon and telson.	Very advanced coalescence of pleonal segments with telson : only I-III still separated by extremely short dorso- and ventrolateral sutures. Epimeres I-II very small, III much longer, curved. Pleotelson wider than long, broadly rounded posteriorly, without long setae.	Pleonites I-II free, perfectly limited dorsally (II shorter than I). Epimeres : described only for I. Pleotelson almost as wide as long (*interstitialis*) or longer than wide (*affinis*), bluntly rounded posteriorly, without long setae.	Pleonites, I, II, III free. Only I and II with epimeres. Pleotelson longer than broad, U-shaped (in *monodi* maybe ? shorter), without long setae.	4 pleonites can be recognized, dorsally (especially I-II) with very incomplete limits (only laterally seen), ventrally with apparently complete limits. Epimeres I-II much smaller than III-IV, which are curved. Pleotelson slightly wider than long, very bluntly rounded posteriorly, without long setae.
A I	Much shorter than A II. Flagellum with many articles in the ♂ (13-16), much less in the ♀ (8-9), with numerous aesthetascs.	Slightly shorter than A II. Flagellum with many (10-17) articles, each usually with an aesthetasc.	Short. Flagellum with many articles (ca. 15, or 15-17), with numerous aesthetascs.	Slightly shorter than A II. Flagellum with only 5 articles (♂, ♀) with very few aesthetascs.
A II	Flagellum with numerous (more than 30) setose articles.	Flagellum with up to 15-16 articles.	Flagellum with numerous (ca. 30) extremely setose articles.	Flagellum (♂, ♀) with 7-8 articles
Mdb	Lacinia mob. : ca. 10 longer, slightly curved spines. Pars. mol. : small central group of short spines, proximally and distally from it only fine setulae.	Generally resembling *Zulialana*. Lacinia mob. : 9-16 longer, curved spines. Pars. mol. : long row of short spines.	Generall rather resembling *Zulialana*. Lacinia mob. : a few small, more or less recurved spines. Pars mol. : relatively long row of relatively long spines, and many setulae.	In all parts, more or less important differences from *Zulialana* (e.g. : palp setation). Lacinia mob. : 6 short, not curved spines. Pars mol. : 9-10 straight spines, no setulae.

Mx I	Armature of ext. and int. blades : see description. Internal blade with 5 setae.	Armature of ext. and int. blades apparently (?) similar to that to *Zulialana*.	Ext. blade : number of smooth spines rather similar to that in *Zulialana*, but only one pennate seta toward internal angle. Int. blade : like in *Zulialana* but one seta (the smooth one) absent.	Ext. blade : very strong differences in armature from *Zulialana*. Int. blade : different from all other, with three strong setae (and one very small seta near apico-external angle).
Mx II	The three lobes extremely similar in size and shape, all with equally long setae (but structure of the setae different in ext. + med. lobes versus int. lobe).	Internal lobe much wider than each of the remaining two which are similar and opposite to it. Structure of setae ?	Internal lobe much wider than each of the remaining two which are opposite to it. In *mortoni* much less setae on the three lobes than in *Zulialana* (but in *monodi* int. lobe with many setae). Structure of setae like in *Zulialana*.	Internal lobe much wider than each of the remaining two which are opposite to it. Setation of the three lobes much poorer than in *Zulialana* (some differences, too, in distribution of the two types of setae).
Mxp	Epipodite present. Main body of sympodite clearly biarticulate. On masticatory lobe some 18 terminal setae, and 2 retinacula.	Epipodite ? Main body of sympodite uniarticulate. On masticatory lobe some 7-10 terminal setae, and 2 retinacula.	Epipodite ? Main body of sympodite uniarticulate. On masticatory lobe only 3-4 terminal setae, and 2 retinacula.	Epipodite absent. Main body of sympodite uniarticulate. On masticatory lobe only 2 setae, and 1 retinaculum.
Pereiopods : shape.	I-II subchelate, III of intermediate type, IV-VII ambulatory and similar. Double unguis.	I-III subchelate (I less so than II-III), IV-VII ambulatory and similar. Single unguis (?).	I-III subchelate, IV-VII ambulatory. Double unguis.	I-III subchelate (slightly less strong from I to III), IV-VII ambulatory. Single unguis.
Pereiopods : armature of spines on propodus Per. I-III.	Poor : I (5), II (2-3), III (0). Spines normal, only those on Per. II strong (but not pluridentate).	Very poor : I (0-1), II-III (2). Spines normal.	Slightly more developed : I (ca. 5-6), II (ca. 4), III (3). Spines normal.	I-III with continuous row of "combs" on palmar margin. Spines not numerous, of special type : massive, 2- to 5-dentate.
Pereiopods : dactylian organ.	Very high number of setae on I (28-30), II (17), III (14-15); on IV-VII only 4.	?	On I-III (7-9), on IV-VII (4-5).	Very small number of setae : I (4), II (3), III-V (2), VI-VII (1).
Pleopods : sympodite.	I : 4 coupling hooks; II : 1 c.h. + 3 setae; III-V : nothing.	I : 2-6 c.h. (sometimes + 1 seta); II : 2-4 c.h. + 1-5 setae; III : up to 5 setae; IV-V : nothing.	I : ca. 7 (or 10) c.h.; II : 3 (or 4) c.h.; III-V : nothing.	I : 2 c.h.; II : 2 c.h. (or 1 +1 seta); III-IV : 1 c.h.; V : nothing.
Pleopods : exopodite.	I-II very different from III-V. Never bipartite. I-V with marginal setae.	All similar. IV-V incompletely bipartite (V maybe completely). Only I-II with marginal setae.	I-II and III-V rather dissimilar. Never bipartite. I-V with peculiar, extremely short setae adpressed to margin.	Very dissimilar (all different). III-V completely bipartite. All with very long marginal setae.
Pleopods : endopodite.	Very dissimilar : I-II smaller, ovoid; III-V larger, round, with annex lobe. All glabrous.	Relatively similar, without annex lobe. All glabrous.	Very dissimilar : I-II long; III-V small, with annex lobe. All glabrous.	Extremely dissimilar : I completely different from II - which is reduced - and from III-V. I-II (pauci) setose.
Appendix masculina.	Short, rooted at end of proximal 1/3 of enp., bluntly ending.	Rather long, rather basally rooted, "lanceolate".	Very long, basally rooted, acuminate.	Very long, apically rooted on the reduced enp., lanceolate ending.
Oostegites.	I - V	?	I - IV	?
Uropods.	Very short; sympodite straight, ankylosed; exp. and enp. present (exp. very small).	Sympodite rather large, broad, probably ankylosed; uropodite represented by one or two really minute lobes within a shallow notch on sympodite edge.	Sympodite long, curved, ankylosed. Exp. and enp. present, not particularly small (exp. smaller).	Sympodite rather large, ankylosed. Uropodite with only one article (exp. disappeared).

stygoxene species maybe endemic for Sierra de Perijá (1).

Cirolanids are mostly found on sand or silt (the places where most of them were observed are marked with arrows on Fig. 29). In their natural habitat, the animals are often solitary, but aggregations were observed in places with important accumulations of detritus. No specimens were observed in the epigean stream. *Zulialana* is unable to swim; the animals walk on sand or silt, and are frequently seen near the sandy banks; they may leave the water to crawl on sand or wet rocks from one pool to another. They clearly avoid places with strong current. When touched, or when the water is disturbed by man, they either rapidly run over the bottom to escape, or roll into an almost perfect ball; they may remain so for several minutes, depending on the disturbance. They are permanently searching for food, which they find especially towards the stream's banks; the food essentially consists of bat guano dropping into the water and accumulating towards the banks (several bat species are present in the cave; a large colony apparently exists, but could not yet be discovered). *Zulialana* is a voracious crustacean : the specimens collected were all gorged. The gut content of a large specimen was examined, most of it being represented by finely particulated dark matter containing a large amount of chitinous fragments from various terrestrial arthropods – mostly insects, mostly certainly from the guano of insectivorous bats.

Some observations could be performed on specimens kept in aquaria. Here a clear tendency towards aggregation is evident; the crustaceans prefer resting motionless on sand, near the edges of the aquarium, with their dorsal part protruding above water. Collision ('pushing aside') between large individuals was observed, especially in larger aggregations. There is some avoidance of light : the reaction to light is never violent, but, if refuges protected from direct light are available, the isopods little by little settle down there. During the night, or in complete darkness, the animals are quite active and may leave the water : one specimen which had escaped from the aquarium was found next morning rolled into a ball and apparently completely dry; yet it resumed its normal activities when replaced in water (apparently some moisture may be retained in the pleotelsonal cavity). Even when motionless, the animals maintain a permanent flux of water in this cavity, the pleopods being in permanent motion. Some individuals were observed ploughing and (incompletely) burrowing into the substrate (partly burrowed individuals could be observed in the natural habitat, too). When dying, the Cirolanids roll into a ball.

(1) It should be added that no Isopod was ever found either in the epigean stream flowing from Cueva de Toromo, or in other freshwaters of Sierra de Perijà.

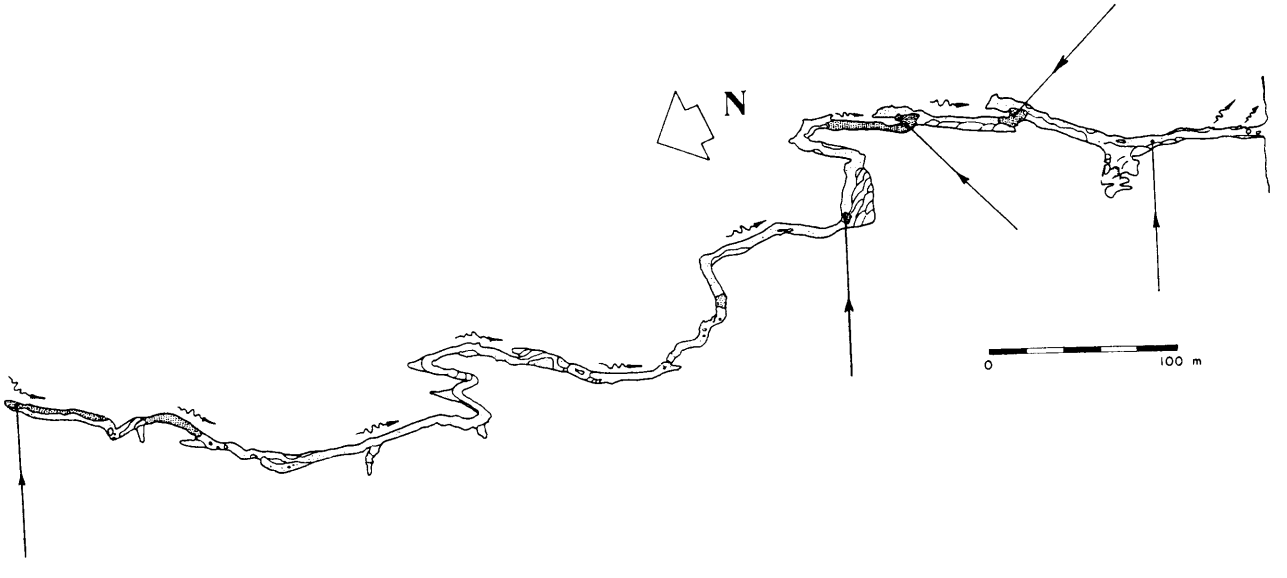


Fig. 29. – *Plan of Cueva de Toromo (Sociedad Venezolana de Espeleologia); long arrows pointing to places where* Zulialana *was observed in larger numbers.*

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