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MORPHOLOGICAL RUDIMENTATION AND NOVELTIES IN STYGOBITIC CIROLANIDAE (ISOPODA, CYMOTHOIDEA)¹

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ISOPODA CIROLANIDAE
STYGOBITIC/MARINE SPECIES
RUDIMENTATION ("REGRESSION")
EVOLUTIONARY NOVELTIES
HYPOGEAN LIFE ADAPTATION

ABSTRACT. – The diversity of cirolanid isopods, all of marine origin, in subterranean aquatic habitats, is remarkably high, 68 species being presently recognized (in 19 genera). These stygobites display, in clear contrast with the marine (i.e., non-subterranean) cirolanids numerous cases of rudimentation ("regression") but also a number of remarkable morphological and other evolutionary novelties, some of them unique in Isopoda, or even in Crustacea. Rudimentation and novelties are the two components of troglomorphy, sometimes the limit between them being not sharp. These cases are examined under the following headings: body shape; depigmentation and tegumental smoothness; absence of "molariform spines"; anophthalmy; elongation and slenderness of appendages; development of tactile (mechanoreceptory) equipment; development of chemosensors ("olfactory organs"); rudimentation and novelty in uropods; rudimentation and novelty in pleopods; some particular structures in hypogean species; the propodial organs; volvation; paedomorphy; facts related to "K-strategy". Study of this array of facts contributes to a better understanding of adaptation to hypogean life. In the introductory notes are briefly expressed the author's opinions about mechanisms considered as underlying rudimentation and novelties respectively as responses to hypogean life, and about preadaptation considered as an essential notion for understanding colonization of the Stygal, this being well exemplified by Cirolanidae. The remarkable diversity of morphological and other adaptive traits of stygobitic Cirolanidae could be explained by the fact that the hypogean aquatic environment is much more complex than seen by traditional biospeology, animals displaying a great variety of adaptive responses in order to cope with the constraints of this complex, rigorous environment.

ISOPODA CIROLANIDAE
ESPÈCES STYGOBIES / MARINES
RUDIMENTATION ("RÉGRESSION")
NOUVEAUTÉS ÉVOLUTIVES
ADAPTATION À LA VIE HYPOGÉE

RÉSUMÉ. – La diversité des Isopodes Cirolanides – tous d'origine marine – dans les eaux souterraines est remarquablement grande, 68 espèces stygobies appartenant à 19 genres étant actuellement connues. Ces espèces montrent – contrairement aux Cirolanides marins, épigés – de nombreux cas de rudimentation ("regression") mais aussi un nombre de remarquables nouveautés évolutives (morphologiques ou autres) parfois uniques chez les Crustacés. Rudimentation et nouveautés sont les deux aspects de la troglomorphie, la limite entre ceux-ci étant parfois peu distincte. Ces cas sont examinés aux titres suivants: habitus; dépigmentation et absence d'ornementation tégumentaire; absence d'"épines molariformes"; anophthalmie; allongement et gracilité des appendices; développement des phanères tactiles (mécanorécepteurs); développement des organes chémorécepteurs, ou "olfactifs"; rudimentation et nouveautés dans la morphologie des uropodes; rudimentation et nouveautés dans celle des pléopodes; autres structures particulières propres aux espèces hypogées; organes propodiaux; volvation; paedomorphose; certains faits en relation avec la "stratégie K". L'examen de tous ces faits peut contribuer à une meilleure compréhension du phénomène de l'adaptation au milieu souterrain. Dans l'introduction sont brièvement exprimées les opinions de l'auteur sur les mécanismes considérés comme pouvant déterminer rudimentation et nouveautés en tant que résultat de la vie hypogée, ainsi que sur la préadaptation considérée comme notion essentielle pour comprendre la colonisation du Stygal (ceci étant bien illustré par le cas des Cirolanides). La remarquable diversité des particularités adaptatives – morphologiques et autres – des Cirolanides stygobies pourrait être expliquée par le fait que le domaine aquatique souterrain est beaucoup plus complexe qu'il l'a été longtemps considéré par la biospéologie, les stygobies faisant montre d'une grande variété de réponses adaptatives afin de faire face aux contraintes de ce milieu complexe et rigoureux.

¹ Concerning use of the suborder name Cymothoidea Dana, 1852 instead of the widely used Flabellifera: see, i.a., Racovitza, 1912: 213-215, and Wägele, 1989: 162-163.

INTRODUCTION

The problem of adaptation to hypogean life has been addressed in numerous publications; but the aim of the present paper is definitely not a review of published information on this topic. Being neither a geneticist, nor a science philosopher, I shall tackle the problem from the point of view of a taxonomist and biospeologist. Nevertheless, I feel compelled to briefly express my views on a few general aspects.

Despite the fact that Cirolanidae are a group of isopod crustaceans having much to tell in this respect, they have not received the deserved attention. Presently some 360-370 species of marine (not subterranean) Cirolanidae are described. From subterranean aquatic habitats presently not less than 68 validly recognized species are described in 19 validly recognized genera, plus five subspecies of three of the species. These stygobitic genera will be here listed: *Antrolana* Bowman, *Arubolana* Botosaneanu & Stock, *Bahalana* Carpenter, *Cirolana* Leach (sg. *Cirolana* and sg. *Anopsilana* Paulian & Delamare Deboutteville), *Cirolanides* Benedict, *Creaseriella* Rioja, *Faucheria* Dollfus & Viré, *Haptolana* Bowman, *Marocolana* Boutin, *Metacirolana* Nierstrasz, *Mexilana* Bowman, *Skotobaena* Ferrara & Monod, *Speocirolana* Bolivar y Pieltain, *Sphaerolana* Cole & Minckley, *Sphaeromides* Dollfus, *Turcolana* Argano & Pesce, *Typhlocirolana* Racovitza, *Yucatalana* Botosaneanu & Iliffe, *Zulialana* Botosaneanu & Vilorina. All their species are fully troglomorphic, adapted to the hypogean mode of life, whereas quite a few (3 species in the genera *Annina* Budde – Lund and *Saharolana* Monod) are stygophiles possibly on route to colonizing the subterranean realm. The ratio hypogean/marine species is thus remarkably high in this group of isopods.

The stygobites, belonging to rather diverse lineages, are unanimously considered as derived from marine ancestors, but almost nothing is known about the possible ancestors. They inhabit a vast array of subterranean aquatic habitats (Botosaneanu *et al.* 1986).

For the present paper the main information sources on marine Cirolanidae were the comprehensive publications by Bruce (1986), Kensley & Schotte (1989), and Brusca *et al.* (1995). In order to avoid tedious repetition, etc., the genera of marine species which will be quoted in the text are here listed: *Annina* Budde-Lund, *Bathynomus* Milne Edwards, *Booralana* Bruce, *Cartetolana* Bruce, *Cirolana* Leach (sg. *Cirolana* and sg. *Anopsilana* Paulian & Delamare Deboutteville), *Conilera* Leach, *Dolicholana* Bruce, *Eurydice* Leach, *Exciorolana* Richardson, *Limicolana* Bruce, *Metacirolana* Nierstrasz, *Natatolana* Bruce,

Neocirolana Hall, *Oncilorpheus* Paul & Menzies, *Orphelana* Bruce, *Parabathynomus* Barnard, *Politolana* Bruce, *Pseudolana* Bruce, *Seychellana* Kensley & Schotte, *Xylolana* Kensley.

I prefer “rudimentation” to “regression”, “reduction”, or “degeneration” used in the literature; and “novelties” to “acquisitions” or “elaborated features”. Obviously, rudimentation and novelties are the two components of troglomorphy (troglomorphy). In publications, much more attention has been paid to “regressions” than to “acquisitions”, which is definitely an error (Botosaneanu & Holsinger 1991), and one aim of the present paper is to demonstrate how numerous and conspicuous the evolutionary novelties displayed by stygobitic animals can be. In fact, the limit between the two aspects is not sharp: rudimentation is, too, evolutionary novelty, and it has a possible adaptive significance – something postulated in several publications. Of course, troglomorphy has reached quite different degrees and modes of expression in various taxa.

Rather much has been published on the mechanisms on which rudimentation and novelties – as responses to hypogean life – depend (one example: the special issue of the NSS Bulletin – J Caves and Karst Studies 47 (2) 1995). Several authors (e.g. Kosswig 1965, Wilkens 1973) have stressed the role of genetic drift and accumulation of neutral mutations, or that of pleiotropy, in the induction of “regression”, a role for natural selection being retained only for “acquisitions”. Others (e.g. Heuts 1953) have – in my opinion rightly – stressed the role of natural selection even for “regression”. Whereas some (Hobbs III, 1998: 895) argue that the question simply cannot be at present answered. Various interesting ideas have been formulated in this context: adaptive value of the “reduction” processes; competitive success of “reduced” phenotypes in the hypogean environment, possibly caused by accompanying physiological improvement not morphologically detectable; the “energy economy hypothesis” stressing the importance of quantity and quality of energetical resources of the environment in induction and degree of rudimentation.

I believe that the antagonism between the two main opinion streams (*v. supra*) is unjustified: clearly, development of any organ – and in any direction – is genetically governed; and, clearly, animals are selected for life in the quite special subterranean realm. I cannot refrain from quoting a graduate student of my late colleague J.H. Stock (Van den Bosch 1988) who, after thoroughly reviewing – with a fresh mind – the literature devoted to meaning and mechanisms of eye regression, concluded that the discussion could be explained rather by “riding one’s hobby” than by factual difference.

I consider preadaptation an essential notion for understanding the colonization by animals of subterranean habitats. In terms like "exaptation" or "adoption" I see a good deal of tautology. Botosaneanu & Holsinger (1991) have criticised in some detail underestimation of the importance of preadaptation for subterranean biology. The term "preadaptation" was created by L. Cuénot and refined by him during the 1st half of past century (Guyon 1995); in 1951, Cuénot defined it as "selection of preadapted animals", a telling formula. But his idea that, once a species is adapted, it cannot "go towards more adaptation" is wrong, in my opinion: it certainly can, by accentuating characters already present in the preadapted species, and by creating novelties in accordance with the characteristic features of the colonized habitat of the (quite heterogeneous) Stygal. According to Simpson (1944) preadaptation cannot achieve much in the absence of further refining of characters by selection; commenting on this, Guyon (1995) writes: "La préadaptation est donc pour Simpson étroitement encadrée en amont et en aval par la sélection naturelle".

For understanding something about Cirolanidae preadapted for hypogean life, there is nothing more instructive than reading paragraphs devoted to habitats in publications on marine cirolanids, where these are very often described as burrowing in sand, in mangrove mud, in coral reef sediments, or living under rocks, in algal turfs or in kelp holdfasts, in the chamber of sponges or in vacant burrows of various animals, in crevices of coral rock, dead wood bored by *Sphaeroma* or *Teredo*, dead mangrove roots, or in dense mussel or barnacle beds. Not only life in such cryptic habitats and burrowing behaviour, but sometimes also anophthalmy or eye rudimentation, a smooth cuticula, and various degrees of depigmentation, characterize subterranean-preadapted marine cirolanids in genera like *Cirolana*, *Eurydice*, *Metacirolana*, *Natatolana*, *Orphelana*, *Pseudolana*. But it should be stressed that only quite seldomly morphological novelties found in stygobitic Cirolanidae have been found in marine species characterized as preadapted by their habitat, behaviour, eye rudimentation, or depigmentation.

FACTS, AND TENTATIVE EXPLANATIONS

Body shape

No generalization is possible about body shape of the stygobitic cirolanids beyond stating that species inhabiting groundwater in porous habitats are

definitely more slender than some of those living in subterranean water in karstic environments. Nevertheless, it is a fact that a series of stygobitic species, belonging to genera like *Antrolana*, *Cirolanides*, *Mexilana*, *Turcolana*, *Typhlocirolana*, or *Speocirolana* (Fig. 1-2) are more slender than most marine species with their stout, strongly domed, often strongly widened body. Even in the rare marine species with body much longer than the greatest width (some *Eurydice*, species of the small genera *Conilera*, *Oncilorpheus*, or *Xylolana*), the somewhat "clumsy" shape is striking. Clearly, the difference fades when very large cave species like *Speocirolana bolivari* (Rioja, 1953) or *Zulialana coalescens* Botosaneanu & Vilorio, 1993, are considered. Racovitza (1912: 247) observes, about body lengthening in *Typhlocirolana*, that it is possible that this character "... ne soit pas dû à la vie cavernicole et qu'il ait été hérité de l'ancêtre lucicole. Beaucoup de Cirolanides épigés le possèdent également. Peut-être est-ce un caractère de lignée qui s'est seulement exacerbé depuis la colonisation souterraine".

Depigmentation, tegument smoothness

All stygobitic cirolanid species are entirely depigmented (cuticula devoid of chromatophores) in contrast with the marine species where practically always at least some chromatophores are present even if the body is described as "white" or "whitish" (quite a few exceptions are mentioned for species of *Natatolana* like *N. bowmani* Bruce, 1986, or *N. thurar* Bruce, 1986; but in such cases conservation in formalin could be the explanation). Some integumental pigment is retained in stygophile species: *Saharolana seurati* Monod, 1930, or *Annina lacustris* Budde - Lund, 1908 (situation unknown for *A. fustis* Bowman & Iliffe, 1991).

All stygobitic species have the cuticula of cephalon, pereion, pleon, and pleotelson smooth, and often thin; in some cases it is so thin as to become translucent, allowing easy observation of pleopods and of most of the internal anatomy (this peculiarity is particularly impressive in species of *Bahalana*). In contrast, in marine species very often a relief ornamentation (tubercles, ridges...) is present, and sometimes strongly developed: species of *Cirolana* (*Anopsilana*), *C. (Cirolana)*, *Metacirolana*; whereas species of *Oncilorpheus* are characterized by a negative sculpture on the pereion dorsum. A well developed relief ornamentation characterizes also the stygophile *Annina lacustris*; this is much reduced in the equally stygophilic *A. fustis* which has probably reached a more advanced degree of subterranean adaptation.

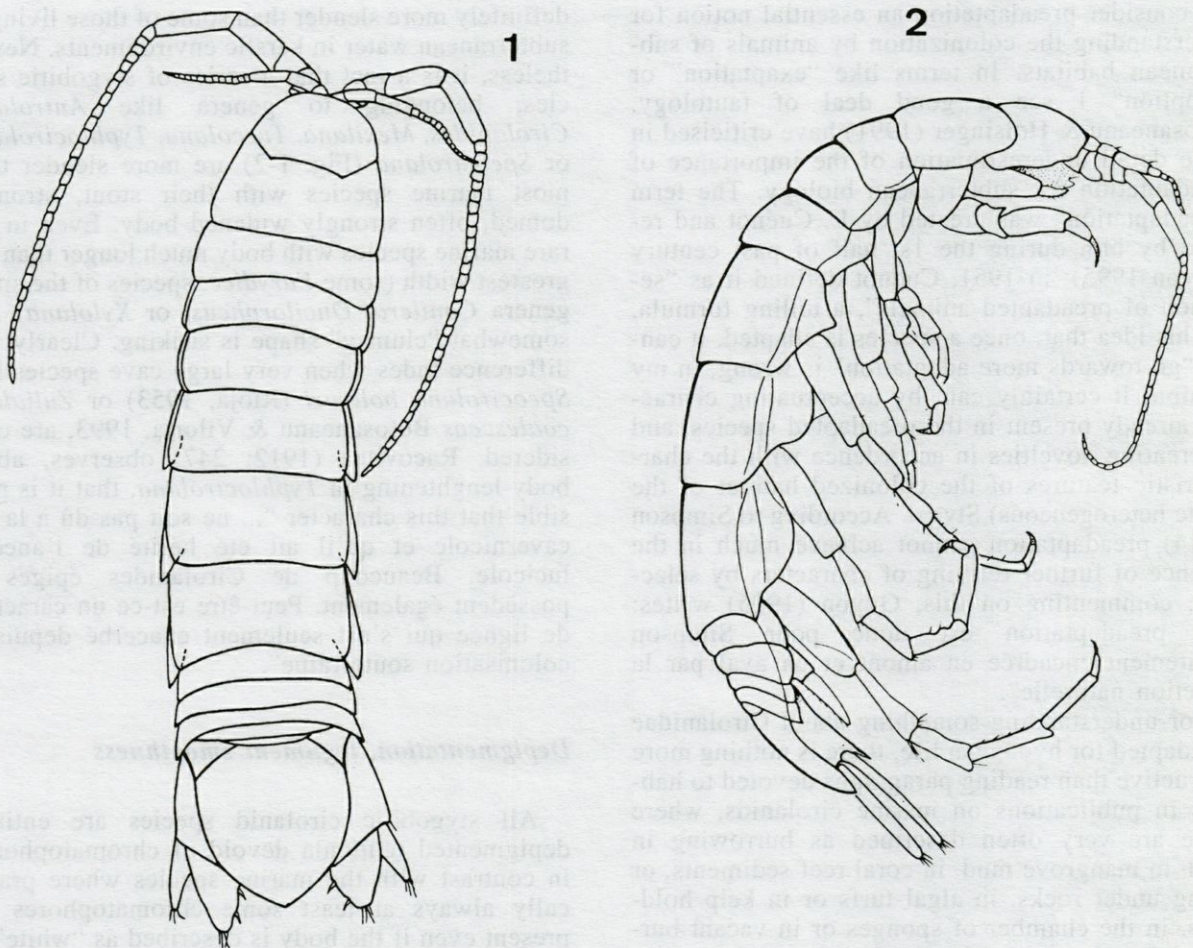


Fig. 1. – *Speocirolana thermydronis* Cole & Minckley, 1966, habitus (from Botosaneanu *et al.* 1998). – Fig. 2. – *Typhlocirolana leptura* Botosaneanu *et al.*, 1985, habitus (from the original description).

Rarity of “molariform spines”

A difference between stygobitic and marine species seems to be the absence, in most of the first, of “molariform spines” (i.e. strongly shortened and thickened phanerae essentially on the palmar margin of pereopods I-III and especially of the gnathopods) sometimes found in marine species in several genera. Of course, there is extreme diversity in shape of spines on the pereopods of stygobitic cirolanids, but they practically always conserve the “spiniform” aspect lost in the “molariform spines” (an exception is represented by the “blunt tubercles” on the gnathopod merus of species in the lineage *Typhlocirolana* – *Turcolana* – *Marocolana*). Genus *Anopsilana*, including both stygobitic and epigeal species, is particularly demonstrative in this respect, all marine species having molariform spines which are absent in all stygobitic species.

Anophtalmy

Practically all stygobitic species are anophtalmous, without any trace of ommatidia or eye pigment. An exception is the interstitial micro-oculate *Arubolana parvioculata* Notenboom, 1984. Micro-oculate is, too, the stygophile *Saharolana seurati*, whereas in *Anopsilana conditoria* Bruce & Iliffe, 1992, mention is made of presence of “indistinct cuticular traces of ocelli”. It may be added that in species of *Annina* the eyes have “a non-faceted gap separating dorsal and ventral parts” (Bowman & Iliffe 1991). About marine genera with species displaying various degrees of eye rudimentation: see Introduction.

Elongation and slenderness of appendages

Rightly considered as a compensatory element for sight loss, appendage elongation and slender-

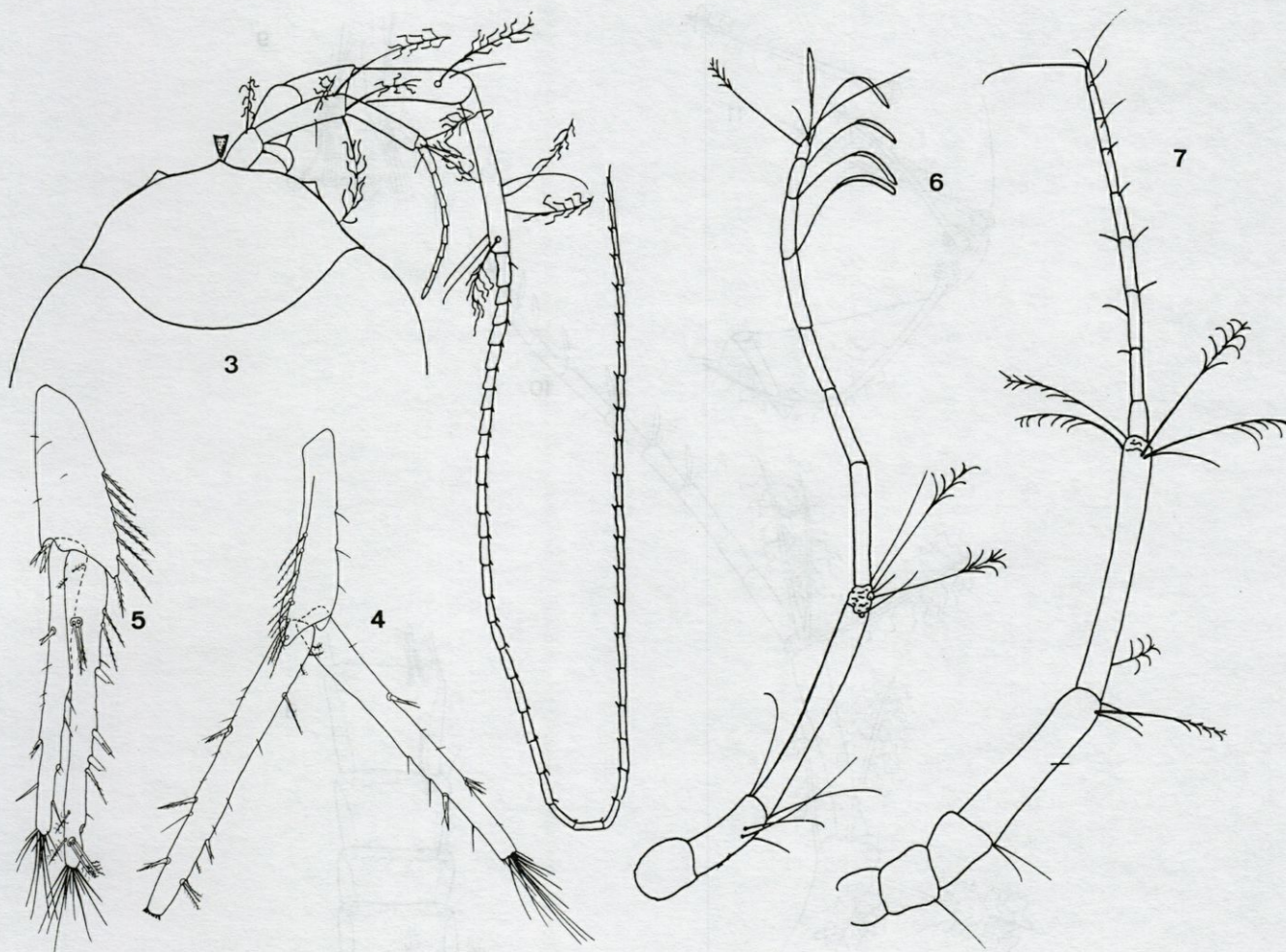


Fig. 3. – *Speocirolana disparicornis* Botosaneanu & Iliffe, 1999, cephalon with A I and A II (from the original description). – Fig. 4-5. – *Typhlocirolana leptura* Botosaneanu *et al.*, 1985, right uropod of ♀ and left uropod of ♂ (from the original description). – Fig. 6-7. – *Yucatalana robustispina* Botosaneanu & Iliffe, 1999, left A I and A II (from the original description).

ness is very often exemplified in biospeological publications. It is frequently found in appendages of stygobitic Cirolanidae, and here I give only a small selection of examples.

The extraordinary slender and elongate uropod rami in both sexes of the phreatic species *Typhlocirolana leptura* Botosaneanu *et al.*, 1985, from Morocco (Fig. 4-5) is unequalled in marine or stygobitic Cirolanidae – although uropods with slender rami are present in other *Typhlocirolana*. *Speocirolana disparicornis* Botosaneanu & Iliffe, 1999, from a Mexican karstic spring and cave, is characterized by extremely long AII almost reaching to the end of the pleotelson (Fig. 3). In *Yucatalana robustispina* Botosaneanu & Iliffe, 1999, from cenotes in Yucatan, both subequal AI and AII (Fig. 6-7) are, although not very long, extremely slender, of a type possibly never present in marine species.

Generally speaking, there are often striking differences between the development of antennulae

and antennae in hypogean and marine species, the most impressive ones being displayed by AI. Quite frequently, marine species have strongly shortened, mostly plump antennulae with sometimes strongly compressed flagellar articles, of a type clearly unknown in any subterranean species. In some marine species also the antennae are strongly shortened (as in species of *Cartetolana*, *Booralana*, *Cirolana* (*Cirolana*), *Conilera*, *Natatolana*; the most impressive case being, maybe, that of *Orphelana perplexa* Bruce, 1981); in some others, only AI belongs to this type whereas AII are not strongly shortened (*Dolicholana*, or some *Natatolana*), being sometimes even very long (*Eurydice*, some *Natatolana*).

Development of tactile (mechanoreceptory) equipment

In some stygobitic species impressive bundles of simple setae from adjacent alveolae are inserted on peduncular and flagellar articles of AII. This was

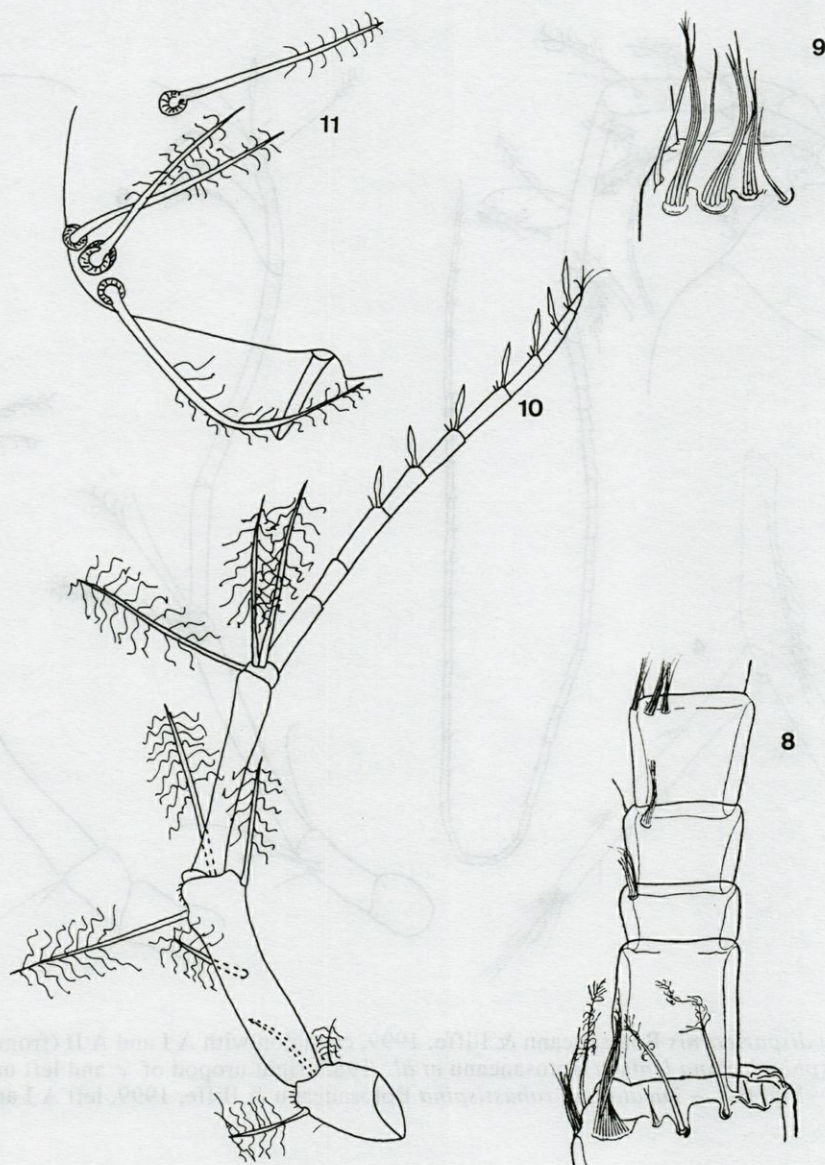


Fig. 8-9. – *Sphaeromides bureschi* Strouhal, 1963, left A II, distal part of article 5 of peduncle and flagellum articles 1-4; and distal part of 7th flagellum article (from the original description). – Fig. 10-11. – *Speocirolana disparicornis* Botosaneanu & Iliffe, 1999, left A I, and apex of uropod endopodite, dorsal view (from the original description).

well illustrated, i.a., for *Sphaeromides bureschi* Strouhal, 1963 (Fig. 8-9), as well as for species as diverse as *Anopsilana cubensis* (Hay, 1903), *Haptolana somala* Messina & Chelazzi, 1984, *Marocolana delamarei* Boutin, 1993, *Skotobaena monodi* Ferrara & Lanza, 1978, *S. mortoni* Monod, 1972, *Turcolana ruffoi* Argano, 1996, or *Zulialana coalescens*. It is a tempting idea that such formations are tactile novelties compensatory for sight loss; however, they have been, too, illustrated for various marine species, such as – to quote two extreme cases – *Exciorolana mayana* (Ives, 1891) – where the AII of adults are described (Brusca *et al.* 1995) as “brushlike antennae” – or *Oncilorpheus jerrybarnardi* Brusca *et al.*, 1995.

On the other hand it seems certain that the equipment of plumose and palmate setae – certainly the most efficient type of mechanoreceptory setal equipment – is better developed in subterranean than in epigean Cirolanidae. This is valid, at least in many cases, for AI and AII peduncles (Fig. 10: AI of *Speocirolana disparicornis* is instructive in this respect). But even more striking is the fact that the equipment of plumose and palmate setae of the uropods is by far richer in the stygobites (although it cannot be excluded that some details were not always adequately described or illustrated in the marine taxa). One thing is particularly impressive: on the dorsal face of the uropod endopodite of most – or all – stygobites

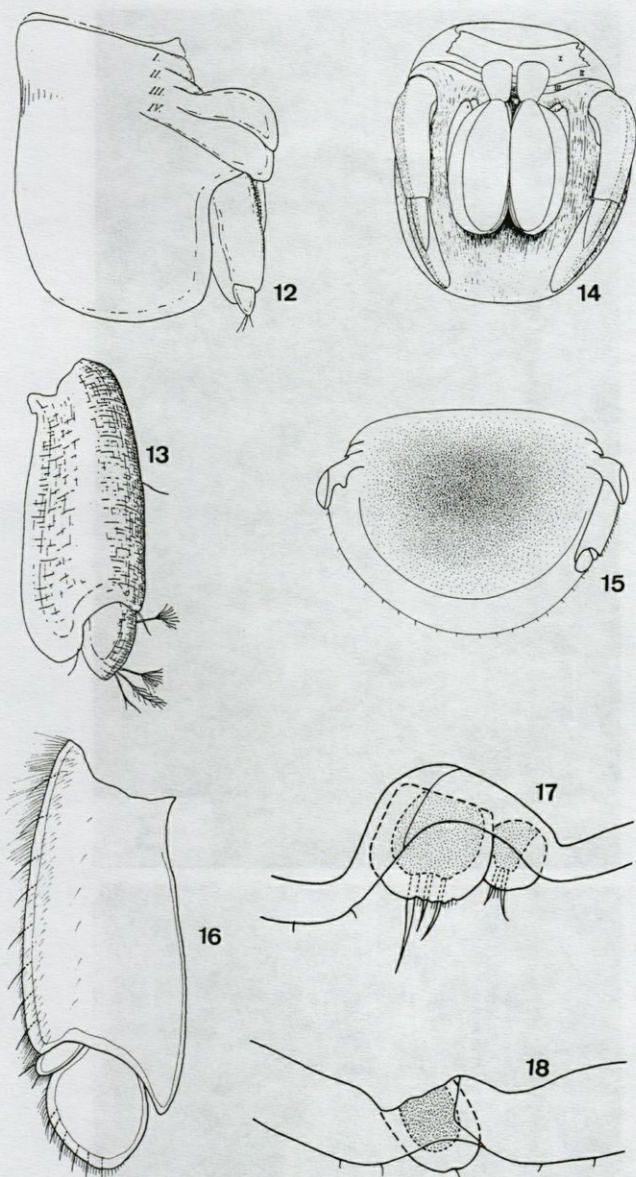


Fig. 12-13. – *Faucheria faucheri* (Dollfus & Viré, 1900), pleon and pleotelson with uropod, lateral view; and right uropod, dorsal view (from Racovitza 1912). – Fig. 14. *Skotobaena mortoni* Monod, 1972, pleon and pleotelson with the uropods, ventral view (from the original description). – Fig. 15-16. – *Zulialana coalescens* Botosaneanu & Vilorio, 1993, pleon and pleotelson with left uropod, ventral view; and right uropod, ventral view (from the original description). – Fig. 17-18. – *Sphaerolana affinis* Cole & Minckley, 1970, and, respectively *S. interstitialis* Cole & Minckley, 1970, distal parts of uropod, strongly magnified (from Botosaneanu *et al.* 1998).

there is at least one, but there are often two or several swinging palmate setae (sometimes called “tiges acoustiques”) in 1 to 4 groups, sometimes inserted on what was probably rightly described as well delimited “sensory patches”. Their presence was ascertained, for instance, in *Arubolana*, *Cirolana* (*C.*) *troglaxuma* Botosaneanu & Iliffe,

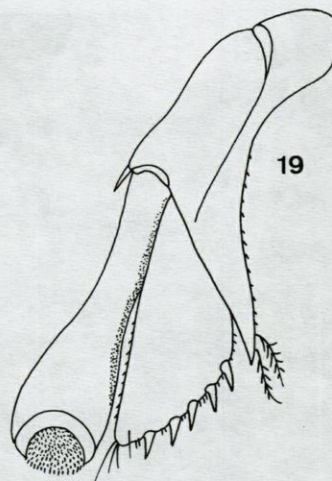


Fig. 19. – *Speocirolana fustiura* Botosaneanu & Iliffe, 1999, left uropod (from the original description).

1997, *C. (C.) pleoscissa* Botosaneanu & Iliffe, 1997, *Haptolana*, *Marocolana*, *Speocirolana*, *Sphaeromides*, *Turcolana*, *Typhlocirolana*, *Yucatalana*, *Zulialana*. Fig. 11 represents the powerful dorsal equipment of swinging palmate setae from strong alveolae near the endopodite apex of the uropod of *Speocirolana disparicornis*.

Development of chemosensors (“olfactory organs”)

It could be supposed that the equipment of chemoreceptor organites will prove to be richer in the stygobites than in the marine species (something having been advocated, for instance, for Decapoda). Actually, the reverse seems to be true (like for instance in some Ostracoda). They are, indeed, rather well or even well developed on the flagellum of AI and AII of many subterranean – adapted species; and some marine species were illustrated (correctly?) with a poor equipment of chemoreceptors. However, in a very large number of marine species – the genera relevant in this respect being *Cartetolana*, *Cirolana* (*Anopsilana*), *C. (Cirolana)*, *Eurydice*, *Exciorolana*, *Metacirolana*, *Natatolana*, *Neocirolana*, *Pseudolana* – this equipment is remarkably rich on the flagellum of AI and often on that of AII, sometimes in many or all species of a genus; and sometimes they form true rows on various articles, something only in exceptional cases seen in a subterranean cirolanid (*Haptolana trichostoma* Bowman, 1966). Generally speaking, it seems that for marine Cirolanidae more powerful chemoreceptor systems are necessary than for the fresh- or brackish water subterranean species. But it should be kept in mind that there exists published evidence (discussion in Wägele 1992: 592-593) that the chemoreceptors on AI and AII have differ-

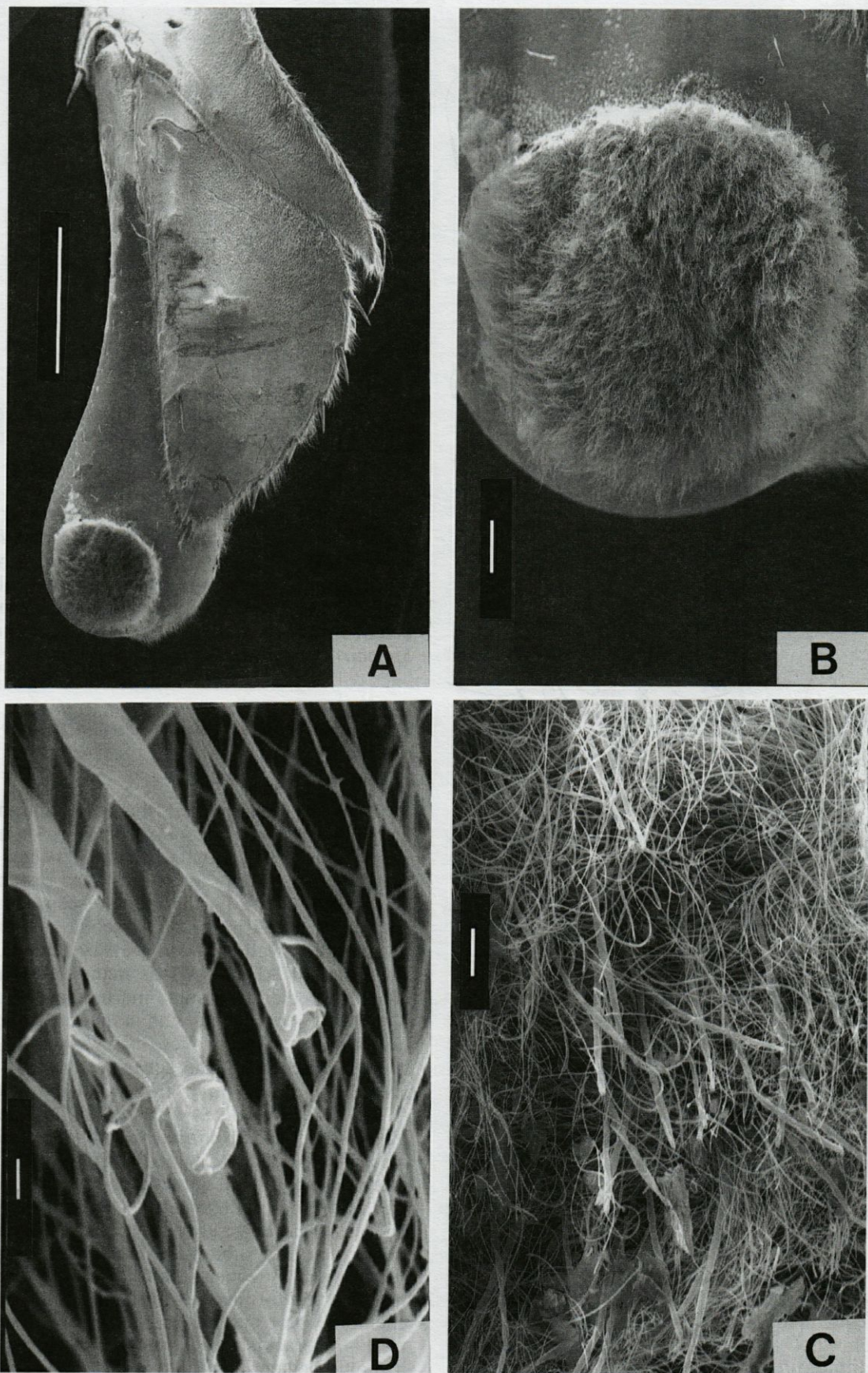


Fig. 20. – *Speocirolana fustiura* Botosaneanu & Iliffe, 1999, SEM photographs of uropod (all by A Jørgensen). A, overview (scale bar = 1 mm); B, closer view of endopodite apex (scale bar = 100 µm); C, close up of “tomentum”, showing among the dense, fine setulae, thicker “setae” abruptly ending (scale bar = 10 µm); D, close up with two blunt, hollow, probably chemosensory phanerae (scale bar = 1 µm).

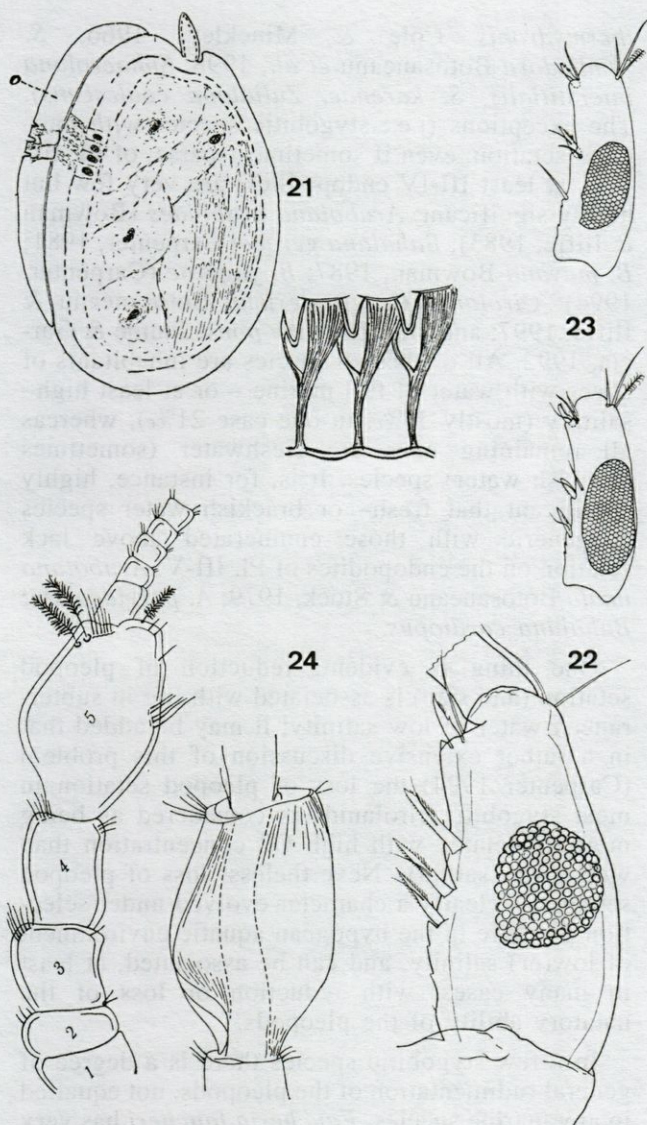


Fig. 21. – *Typhlocirolana buxtoni* Racovitza, 1912, transverse section through the propodus of PII; O = the propodial organ; small appended figure: more strongly magnified detail from section through propodial organ (from the original description). – Fig. 22. – *Turcolana steinitzi* (Strouhal, 1960), propodus of PII, ♂, with propodial organ (from the original description). – Fig. 23. – *Turcolana adaliae* Botosaneanu & Notenboom, 1989, ♂, propodus of PII (below) and of PIII (above), with propodial organs (from the original description). – Fig. 24. – *Sphaeromides polateni* Angelov, 1968, male A II peduncle with first articles of flagellum, and ventral view of article 5 of peduncle (from the original description).

ent origins and functions, only those on AI being long-distance chemoreceptors (aesthetascs), whereas the sensilla on AII are “contact chemoreceptors” sensitive to chemical and mechanical stimuli. It should also be added that in some stygobitic species (*Yucatalana robustispina*: Fig. 6; *Cirolana (Anopsilana) yucatanana* Botosaneanu & Iliffe, 2000) there are very long aesthetascs on the last flagellar

articles of A1, and that this remarkable length (and, thus, surface) may represent a counterpoise for the low number of aesthetascs.

Rudimentation and novelty in uropods

In practically all marine cirolanids the uropods are functional, movable, steering appendages normally developed in all their parts (in species of *Exciorlana* – see, i.a., Brusca *et al.* 1995: Fig. 48, etc. – the short uropod endopodite has a curious notch – or “pit” – on its lateral margin, but I do not believe that this can be considered as incipient rudimentation).

In contrast, in several hypogean genera and species belonging to quite different lineages (discussion in Botosaneanu & Vilorio 1993) various modes and degrees of uropod rudimentation are found, representing some of the most impressive morphological characteristic features induced by hypogean life. Only cases of advanced rudimentation will be mentioned here, but it should be kept in mind that in a series of other stygobitic Cirolanidae the uropods, although “normal” looking, are hard, calcified appendages capable only of restricted motion.

In *Skotobaena mortoni* from caves in Ethiopia, the hard, almost ankylosed uropods almost devoid of setation (Fig. 14) follow the lateral margins of the pleotelson, being at the same time twisted towards the median line in such a manner that the strongly reduced and hollowed exopodites acquire a ventral position; the uropods are in such a way placed as to form with the pleotelson a deep ventral chamber for the small pleopods, and they cannot be observed dorsally. The situation is practically identical in *S. monodi* from wells in southern Somalia (Ferrara & Lanza 1978); in *Faucheria faucheri* (Dollfus & Viré, 1900) from karstic habitats in southern France, the situation is similar in several respects, but here only one small branch (the endopodite?) is appended to the very strong, certainly ankylosed sympodite (Fig. 12-13). In *Zulialana coalescens* from a cave in NW Venezuela, the completely ankylosed uropods rooted in the axilla of the 3d pleonal epimeres, are extremely small (2.4 times shorter than the pleotelson), but both rami are still distinct, although the exopodite is extremely reduced (Fig. 15-16). The fact deserves mention that also in *Speocirolana disparicornis* the uropods (Botosaneanu & Iliffe 1999: Fig. 49, 68) are completely concealed under the strongly vaulted pleotelson; but they are well developed and seemingly freely movable, although probably not very efficient steering appendages. Finally, an extreme degree of modification and rudimentation is displayed by all 3 species (all Mexican) described in *Sphaerolana*: *S. affinis* Cole & Minckley, 1970; *S. interstitialis* Cole &

Minckley, 1970 (for these 2 species see also Botosaneanu *et al.* 1998); and *S. karenae* Rodriguez-Alm. & Bowman, 1995. In all three the sympodite is relatively very large, with exceedingly small rami in *S. affinis* and *S. karenae*, and with one of them (which?) having disappeared in *S. interstitialis* (Fig. 17-18).

A most extraordinary situation is that found in a species discovered in small pools at the bottom of a deep Mexican cave: *Speocirolana fustiura* Botosaneanu & Iliffe, 1999. Here, sympodite and endopodite of the ankylosed uropods have no very peculiar shape, whereas the exopodite is transformed in a way completely unknown in Cirolanidae, being a long, hard, club-shaped appendage with a round apical zone completely covered by what can be superficially described as a dense tomentum (Fig. 19; there is tomentum also along the median face of the exopodite). Thanks to the kindness of R.M. Kristensen and to the ability of A. Jørgensen, SEM photographs can be presented (Fig. 20) revealing a significant feature: at high magnifications (Fig. 20 C,D) among the very dense, thin setulae covering the round apical zone (and, in fact, each composed of about 3 even thinner, plaited filaments which unwind finally), some much thicker ones become apparent, approximately 25 µm long, ending abruptly, and hollow. According to R.M. Kristensen (in litt.) such hollow formations are an indication for chemoreception, as known from other crustaceans. Uropods with a chemosensory function are clearly an evolutionary novelty in Cirolanidae.

In all these cases complete loss of the ability of the uropods to function as steering appendages is evident. As documented in several publications this is in direct relation with the small bodies of water available, and sometimes also with the highly unstable hydrological regime. In my opinion another mechanism working in parallel could be involved, as response to life in such an environment: a shift from actively searching for living prey in the water mass, to scavenging on the bottom.

Rudimentation and novelty in pleopods

In a vast majority of stygobitic cirolanids, and even in a stygophilous species such as *Saharolana seurati*, the endopodites of pleopods III-V are devoid of marginal setation (something seen only in very few marine species, according to Bowman & Franz 1982). Moreover, in some stygobitic species the endopodites of *all* pleopods are without marginal setation and often of small size, in some of them even the setation of the exopodites, or at least of some of them, being very reduced or absent (cases of more accentuated rudimentation of setation: *Mexilana saluposi* Bowman, 1975, *Skotobaena monodi*, *S. mortoni*, *Speocirolana*

thermydronis Cole & Minckley, 1966, *S. zumbadora* Botosaneanu *et al.*, 1998, *Sphaerolana interstitialis*, *S. karenae*, *Zulialana coalescens*). The exceptions (i.e.: stygobitic species with marginal setation, even if sometimes sparse, of Pl. III-V or at least III-IV endopodites) are very few but highly significant: *Arubolana aruboides* (Bowman & Iliffe, 1983); *Bahalana geracei* Carpenter, 1981; *B. mayana* Bowman, 1987; *B. yagerae* (Carpenter, 1994); *Cirolana* (*C.*) *troglexuma* Botosaneanu & Iliffe, 1997; and *Metacirolana ponsi* Jaume & Garcia, 1992. All of these 6 species are inhabitants of caves with water of full marine – or at least high-salinity (mostly 35‰, in one case 21‰), whereas all remaining ones are freshwater (sometimes brackish water) species. It is, for instance, highly significant that fresh- or brackish water species congeneric with those enumerated above lack setation on the endopodites of Pl. III-V: *Arubolana imula* Botosaneanu & Stock, 1979; *A. parvioculata*; *Bahalana cardiopus*.

One thing is evident: reduction of pleopod setation (and size) is associated with life in subterranean water of low salinity; it may be added that in a rather extensive discussion of this problem (Carpenter 1994) the loss of pleopod setation in most stygobitic cirolanids is considered as being more associated with high O₂ concentration than with lower salinity. Nevertheless: loss of pleopod setation is clearly a character evolved under selection pressure in the hypogean aquatic environment of low(er) salinity, and can be associated, at least in many cases, with reduction or loss of the natatory ability of the pleopods.

In a few stygobitic species there is a degree of general rudimentation of the pleopods, not equalled in any marine species. *Faucheria faucheri* has very small and polymorphic pleopods covering only 1/2 of the sternal face of the pleotelson, the rami of Pl. I-II being reduced to narrow chitinous straps; *Faucheria* is definitely unable to use such pleopods for swimming (Racovitza 1912).

Finally, 5 stygobitic species in 4 different genera share a remarkable character never present in any marine cirolanid: deeply split (bilobed), endopodites of Pl. III-V. It was a regrettable error of mine to state in the original description of *Jamaicalana pleoscissa* Botosaneanu & Iliffe, 1997, that this character is uniquely present in this species. In Fig. 27 only Pl. V is illustrated for *Cirolana* (*Anopsilana*) *pleoscissa*, *Skotobaena monodi*, *Zulialana coalescens*, and *Sphaeromides raymondi* Dollfus, 1897; but the situation is similar for Pl. III-IV (also *Skotobaena mortoni* has similarly split endopodites). We have here at the same time rudimentation *and* novelty clearly associated with subterranean life. Despite slight differences in morphological detail, the significance of such a structure is likely fundamentally the same in all these species: maybe either enhancement (in rela-

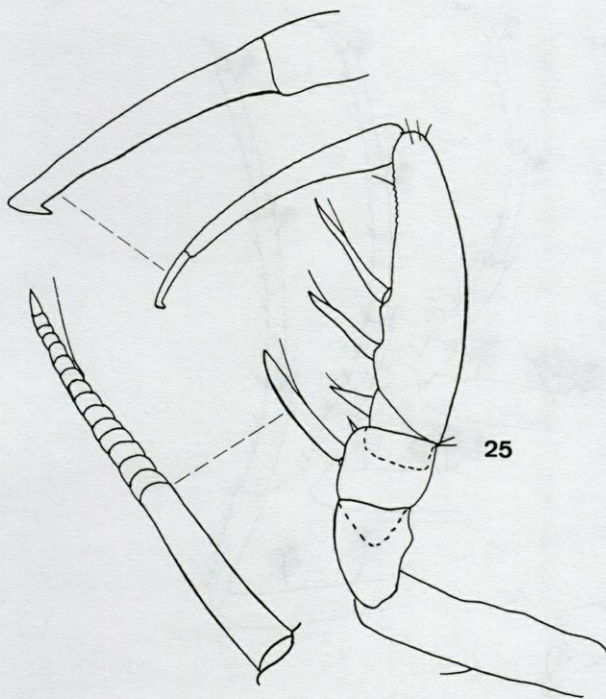


Fig. 25. – *Yucatalana robustispina* Botosaneanu & Iliffe, 1999, left PI, with one of the huge spines and the unguis more strongly magnified (from the original description).

tion with transition from marine water to lower ionic concentrations), or lowering (in relation with metabolic economy) of O₂ consumption. But its significance could be different: according to Wägele (1992: 564) the pleopod endopodites are mainly involved in osmoregulation, in contrast with the respiratory exopodites. Anyway, I am tempted to consider such situations as being diametrically opposed to that found in species of the small marine genera *Bathynomus* and *Parabathynomus*, with their “grapes” of gills on all pleopod endopodites (*B.*) or coxopodites (*P.*).

Some particular structures in hypogean species

In *Sphaeromides polateni* Angelov, 1968, a troglostygobiont from Bulgaria, All are sexually dimorphic, the last peduncular article in the ♂ (Fig. 24) being not only strongly widened, but also twisted, in a manner helping the male to take hold of the 1st pereionial epimera of the female during mating (Angelov 1968: 212). It is possible that the sexual dimorphism described for the propodus of PIII of *Typhlocirolana margalefi* (Pretus, 1986: 100, fig. 5) is a similar case. Is there some relation between hypogean life and such structures? It is possible that a structure efficient in holding mates has its selective value in the special conditions characterizing the hypogean environment.

Shape and armament of the various articles of the gnathopod – and other pereopods – are subject to infinite variation. But it is possible that the odd situation found in the gnathopod of *Yucatalana robustispina* (Fig. 25) remains unequalled either in marine or in stygobitic species: well developed – although not very dilated – propodus, with palmar margin serrate distally; extremely elongate dactylus; unusually long unguis ending in a small hook; armature of merus, carpus, and propodus reduced to a small number of very long spines, all curiously annulated in their distal half (such a structure of the propodial spines previously known only for *Cirolanides texensis* Benedict, 1896); all this in strong contrast with all following pereopods. These peculiarities point to feeding on living prey (of minute size certainly, taking into account the small size and frail habitus of the cirolanid). But to what extent this is related to hypogean life, remains unanswered.

Bowman (1992) describes in *Cirolanides texensis* a “precocious gnathopod development”. His illustration (here reproduced: Fig. 30) shows, to the same scale, the gnathopod in a 5.7 mm juvenile, and a 13 mm adult ♂, from the same sample, the conclusion being that the juvenile propodus has grown allometrically at nearly twice the rate of the body, and that clear differences between the two are seen in the shape of the propodial palm and in the length of the dactylus, all this suggesting “a need for the juvenile to handle objects that a gnathopod developing isometrically could not cope with”. A similar situation has not been described for another cirolanid.

Generally speaking, sexual dimorphism in Cirolanidae is described as slight, if not practically absent (of course, if abstraction is made of the modified PI. II and the presence of penes/genital papillae in the ♂♂, or of oostegites and of modified maxillipeds in ♀♀ with oostegites). In a few marine species (in the genera *Booralana*, *Limicolana*, *Metacirolana*...), or in the species of *Annina*, some of them to some extent stygophile, a rather strong sexual dimorphism is present (see, i.a., discussion in Bowman & Iliffe 1991). Nevertheless, I believe that nowhere in the family is the sexual dimorphism so conspicuous as that displayed by the uropods of 3 related species of the stygobitic genus *Speocirolana*: *S. lapenita* Botosaneanu & Iliffe, 1999 (Fig. 28), *S. pubens* Bowman, 1981 (Fig. 29), and probably also *S. guerrai* Contreras-Balderas & Purata-Velarde, 1981 – all from Mexico.

The propodial organs

Racovitza (1912: 238-241, 246) gave the first description of curious organs discovered on the propodus of pereopods II and III in both sexes of

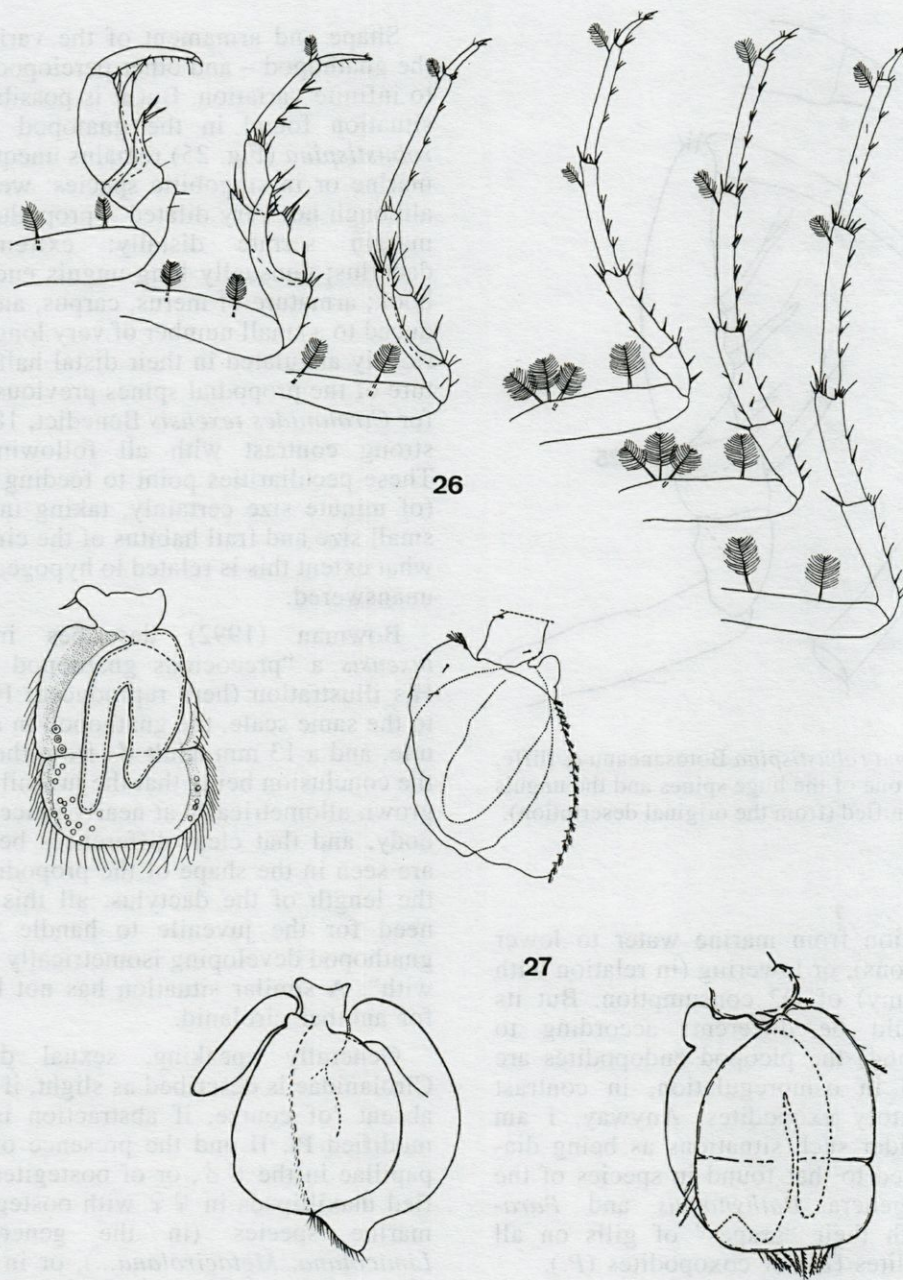


Fig. 26. – *Bahalana yagerae* (Carpenter, 1994), left pereiopods of a mature male (from the original description). – Fig. 27. – Pleopod V of *Cirolana (Anopsilana) pleoscissa* (Botosaneanu & Iliffe, 1997) (above, left), *Skotobaena monodi* Ferrara & Lanza, 1968 (above, right), *Zulialana coalescens* Botosaneanu & Vilorio, 1993 (below, left), and *Sphaeromides raymondi* Dollfus, 1897 (below, right); first three from the original publications, last one from Racovitza 1912.

Typhlocirolana moraguesi Racovitza, 1905; he coined for them the term “propodial organs” and offered a detailed discussion on their structure and possible significance. These organs are rather large round or elliptical “blades” externally placed on the anterior surface of the propodus; separated from its cuticula by a thin membrane, they are relatively easily detached (which could explain their absence in some examined specimens). Their surface looks like a honeycomb, but the cells of this honeycomb are, in fact, complex organites de-

scribed in detail by Racovitza by means of sections (Fig. 21 shows a sectioned propodial organ, and a detail with a few organites); he describes the organ surface as being covered by truncate hexagonal pyramids, on each pyramid an externally concave disk being placed. The propodial organs –of a type never described in other crustaceans or arthropods– are tentatively considered by Racovitza as being adhesive organs, the “disks” maybe acting as suckers. To this day, no other explanation for their function has been proposed; apparently not having

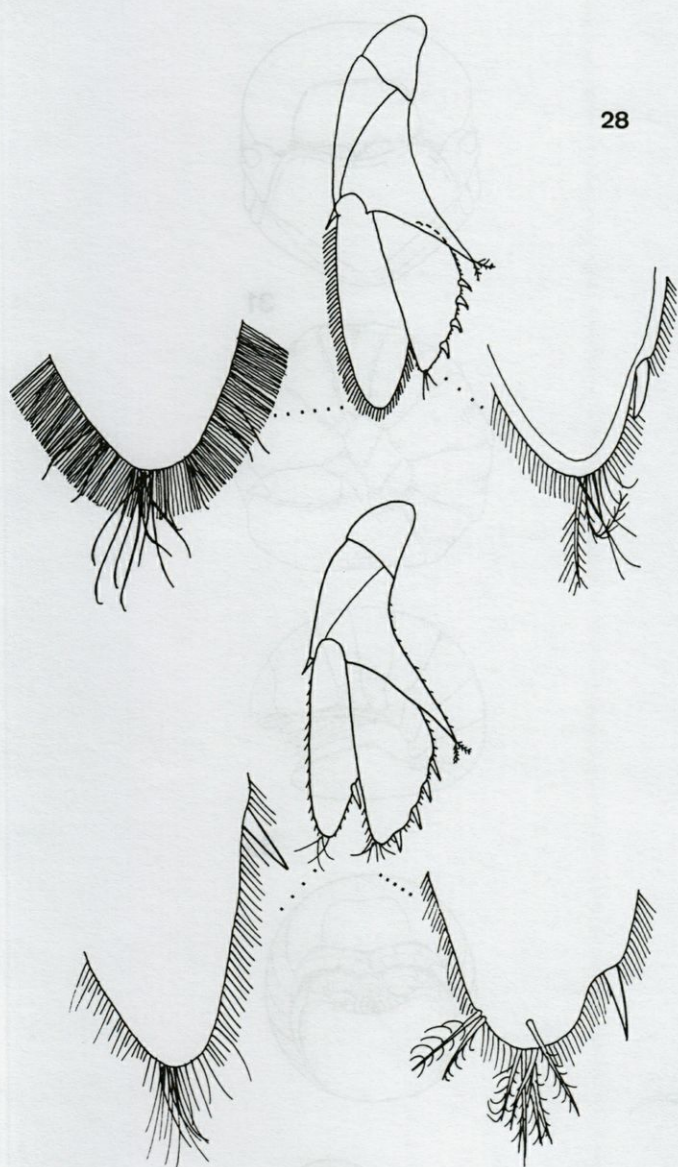


Fig. 28. – *Speocirolana lapenita* Botosaneanu & Iliffe, 1999, ♂ left uropod (above) and ♀ left uropod (below), both with strongly magnified apices of exo- and endopodite (from the original description).

any nervous connection they cannot be sensory, or equilibrium organs.

Subsequently, propodial organs were mentioned and sometimes illustrated for adults of several species in the closely related genera *Typhlocirolana* and *Turcolana*. The situation is complex, because in some species they were not found, whereas in others they are present in both sexes, or only in the males, but always on the propodus of P II and P III (although – Nourisson 1956 – such an organ was found only on P III in a ♂ of *Typhlocirolana gurneyi* Racovitza, 1912). Propodial organs were not found in *Typhlocirolana leptura*, *T. margalefi* Pretus, 1986, *Turcolana pamphyliæ* Botosaneanu

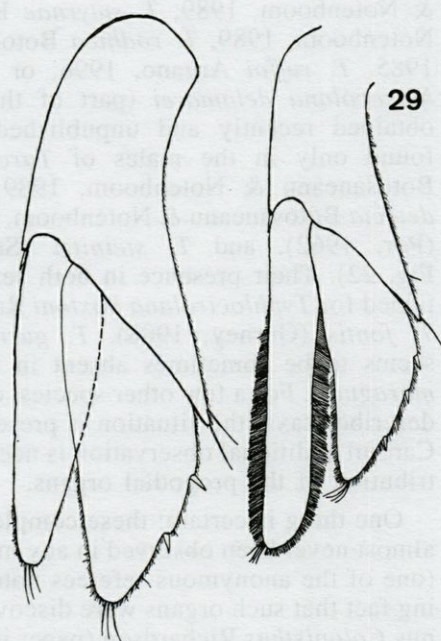
& Notenboom, 1989, *T. smyrnae* Botosaneanu & Notenboom, 1989, *T. rodhica* Botosaneanu *et al.*, 1985, *T. ruffoi* Argano, 1996, or in the related *Marocolana delamarei* (part of this information obtained recently and unpublished). They were found only in the males of *Turcolana adaliae* Botosaneanu & Notenboom, 1989 (Fig. 23), *T. detecta* Botosaneanu & Notenboom, 1992, *T. reichi* (Por, 1962), and *T. steinitzi* (Strouhal, 1960; Fig. 22). Their presence in both sexes was ascertained for *Typhlocirolana buxtoni* Racovitza, 1912, *T. fontis* (Gurney, 1908), *T. gurneyi* (where it seems to be sometimes absent in the ♀, and *T. moraguesi*. For a few other species, or not formally described taxa, the situation is presently unsettled. Careful additional observation is needed on the distribution of the propodial organs.

One thing is certain: these complex organs have almost never been observed in any marine cirolanid (one of the anonymous referees notes the interesting fact that such organs were discovered in the genus *Colopisthus* Richardson (paper in press); and it would be absurd to believe that several generations of carcinologists have failed to observe them. They are thus a remarkable novelty in a phyletic line entirely subterranean-adapted of the family, this contradicting an idea expressed by Racovitza (1912: 247): [the propodial organs] “... ne semblent pas pouvoir être attribués à la vie souterraine; ils devaient caractériser la lignée avant la colonisation souterraine”.

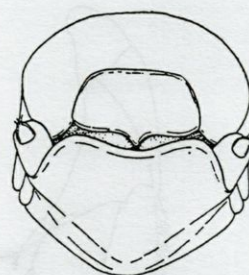
Volvation

The ability of rolling the body more or less completely into a ball is known in several groups of Arthropods; in Isopoda it is observed in several widely distant groups, being in some of them a very frequent phenomenon (for instance in the aquatic suborder Sphaeromatidea, or in various terrestrial taxa, groups for which excellent studies have been published on the volvational mechanism and the morphological implications of volvation). Various explanations of its utility have been offered, the most plausible – and supported by some published information – being that it is the result of a defense reflex enabling animals to avoid being grasped by potential predators and protect the tender ventral parts of the body with their appendages, as well as the brood.

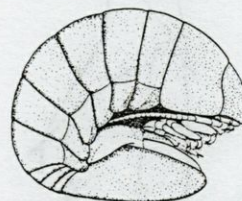
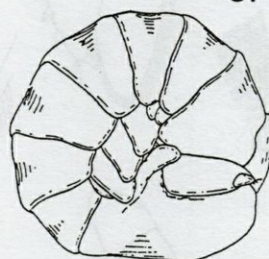
It is significant that, whereas no case of volvation, even incipient, is known in marine Cirolanidae, several such cases are known in phylogenetically widely distant subterranean species, this being evidence that “Il se peut que l’enroulement soit acquis après la colonisation souterraine sous l’influence de la lutte pour l’existence” (Racovitza 1912), that “... la volvation a pu se voir acquise en rapport avec la vie



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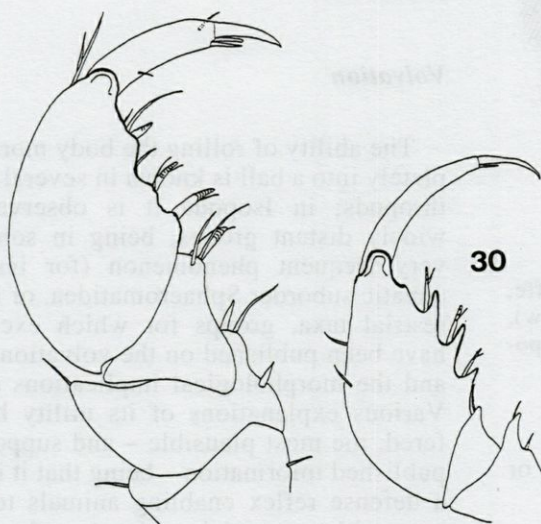
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Fig. 29. – *Speocirolana pubens* Bowman, 1981, uropod of ♀ (left) and of ♂ (right) (from the original description). – Fig. 30. – *Cirolanides texensis* Benedict, 1896, right PI of a mature ♂ (left) and of a juvenile (right) (from Bowman, 1992). – Fig. 31. – *Faucheria faucheri* (Dollfus & Viré, 1900), ♀ rolled into a ball, frontal and lateral view (from Racovitza 1912). – Fig. 32. – *Skotobaena mortoni* Monod, 1972, rolled into a ball, lateral and frontal view (from the original description). – Fig. 33. – *Marocolana delamarei* Boutin, 1993, rolled into a ball (from the original description).

endogée” (Monod 1972), and of “... the existence, in the subterranean aquatic environments, of ecological conditions favourable to the adaptive suc-

cess of this behavioural feature” (Argano & Pesce 1980).

Not all cases of volvational ability in stygobitic cirolanids are described with enough detail, and in some cases uncertainty reigns about the degree to which volvation is achieved. Volvation can be "perfect" or "almost perfect" in *Creaseriella anops* (Creaser, 1936); *Faucheria faucheri* (Fig. 31; detailed description of morphological implications, and considerations about "origine de l'enroulement": Racovitza 1912); and *Zulialana coalescens* (observations on morphological implications, and field and aquarium observations on the volvational behaviour: Botosaneanu & Vilorina 1993). In *Marocolana delamarei* (Fig. 33) the volvation observed on living animals is described as complete (Boulouar *et al.* 1993) – but it is possibly imperfect. Despite the genus name and a short note in the original description, the situation in *Sphaerolana* is not clear: in specimens of *S. interstitialis* and *S. affinis* kept in alcohol, I have observed only a slight tendency to volvation; moreover, in Cole & Minckley (1970) we find that in a mixed population of these two species, the 2nd one "appeared unable to roll tightly when disturbed". "Imperfect" volvation, but with specific differences inside a genus, was reported for *Skotobaena* (Fig. 32; discussion on morphological implications and on behaviour: Monod 1972); and for *Turcolana* (especially discussion, partly based on observations on living animals, in Botosaneanu & Notenboom 1989; for some species ability to roll completely into a ball was reported, but this is contradicted by published illustration and should be taken with caution).

Several observations were made on volvation as a direct reaction to disturbance by coexisting animals, or by man. And it is quite plausible that in a cave pool the impact of mighty, turbulent animals like crustaceans or fishes on blind and sensitive cirolanids may be stronger than in the open sea. Finally, that volvation may act as protection against dessication, was observed in *Zulialana coalescens* (Botosaneanu & Vilorina, 1993); taking into account the fact, several times noticed, that cave cirolanids have the habit of leaving their aquatic environment for roaming in its vicinity, this is possibly a rather frequently acting survival strategy.

Paedomorphy in Bahalana yagerae

A situation unique for Cirolanidae (although known in several other isopod groups: Gnathiidae, Protognathiidae, a few Anthuridae, some deep sea Asellota) was described by Carpenter (1994) for *Dodecalana yagerae*, a species inhabiting fully marine caves on Grand Bahama Island: the existence of only 6 pairs of pereopods in all mature males and females caught. The fact that P III-VI (Fig. 26) in this species are all longer than any pereopods in

specimens of the same size of the closely related *Bahalana geracei*, could be, according to Carpenter, an adaptation to compensate for the instability accompanying loss of P VII. This is a case of paedomorphy: is there a direct relation between it and hypogean life? Not necessarily, but to all appearances there is one. It should be added that in the marine genus *Seychellana*, PVII is strongly reduced.

Facts related to "K-strategy"

K-Selection implies, i.a.: reduced reproductive effort, low number of offspring, and delayed maturity. For various groups of stygobitic animals there is at present abundant evidence of low reproductive rates (few but large, yolky eggs produced; reduced populations) and increased longevity (heterogeneity in age class structure of the populations), all this in contrast with the situation in related epigean taxa. The rather scarce, and not always rigorous evidence for Cirolanidae, does not contradict this pattern.

In the marsupium of a ♀ of *Yucatalana robustispina* only 3 very large eggs were found (Botosaneanu & Iliffe 1999) but that of another specimen was filled with 10 large pulli. A single pullus was found in the marsupium of a ♀ of *Skotobaena mortoni*, and this "laisse à penser que le nombre des œufs par ponte est très réduit et peut-être même limité à un seul" (Monod 1972). In the marsupium of a specimen of *Cirolanides texensis* ssp. *mexicensis* Botosaneanu & Iliffe, 2001, I have found 10 big eggs. There are several observations on species of the *Typhlocirolana-Turcolana* lineage; despite inconsistency of terminology used in various publications, one apparently interesting pattern emerges: eggs (?), if present, are found in the general cavity, oostegites having never been observed in this group. In 3 ♀ of *Turcolana reichi* "ovaires jaunes et pleins d'œufs immatures" were observed (Por 1962). In *T. rodhica* ♀ was found "à ovocytes mûrs visibles dorsalement par transparence" (Botosaneanu *et al.* 1985; "ovocytes" is, possibly, an error). The ♀ allotype of *T. pamphylliae* was described and illustrated (Botosaneanu and Notenboom 1989) as having "two large eggs... inside the 6th pereopodal segment". And Racovitza (1912) describes 1 ♀ of *Typhlocirolana gurneyi* as having one dozen eggs in the general cavity – which would be a record for stygobitic Cirolanidae, should this observations be confirmed. All this is evidence for internal brooding of eggs in *Typhlocirolana-Turcolana* (ovovivipary is recorded for very few epigean – marine or from continental water – cirolanids, as well as for the epigean and slightly stygophilic, fresh/brackish water *Annina lacustris*). This evidence should be compared with the situation found

in some epigeal – mostly marine – Cirolanidae. *Annina mesopotamica* (Ahmed, 1971): “mean 24 eggs” (Salman, Oshana & Ali 1996); *Bathynomus giganteus* Milne Edwards, 1879: 26 eggs (Lloyd 1908); *Cirolana harfordi* (Lockington, 1877): 18-68 eggs per brood (Johnson 1976); *Eurydice pulchra* Leach, 1815 and *E. affinis* Hansen, 1905: 30-45 and, respectively, 18-29 eggs (Jones 1970); *Exciorolana braziliensis* Richardson, 1912: 10-27 “embryoes” or “huevos” (Zuñiga *et al.* 1985); “Number of eggs per brood ranged from 4 to 17 (Dexter 1977); *Exciorolana chiltoni* (Richardson 1905): “average 30.7 eggs (Klapow 1970); *Natatolana borealis* (Lilljeborg, 1851): “The number of eggs, embryos and larvae found in the marsupia varied from 23 to 77, averaging 50.9” (Johansen 1996); *Pseudolana concinna* (Hale, 1925): mean 13.29 and mean 27.80 eggs in two different populations (Dexter 1985); *P. towrae* Bruce, 1983: 18-24 eggs (Dexter 1985).

In numerous subterranean cirolanid species conspicuous intrapopulational differences in size of mature specimens were noticed. In a populational study of *Antrolana lira* Bowman, 1964, adults in two populations measured between 9 and 21 mm (Collins & Holsinger 1981). In a population of *Speocirolana pelaezi* (Bolivar y Pieltain, 1950) mature females measuring between 8.5 and 31 mm were found (Botosaneanu & Iliffe 1999). Dwarf mature specimens as small as 5 mm and as 3 mm were found by Carpenter (1981) in the otherwise large *Bahalana geracei* and, respectively, *B. mayana*; the same author found, in many months of laboratory observation on *B. geracei*, only one moulting specimen. *Jamaicalana pleoscissa* was described from a ♀ specimen measuring 10 mm, the only other specimen being a fully developed dwarf ♀ of only 3.6 mm.

DISCUSSION

How to explain the fascinating diversity of morphological and other adaptive responses of stygobitic Cirolanidae? Ideas formulated by Danielopol & Rouch (1991) could be summarized as follows.

1. *The subterranean aquatic environment is more complex than considered in traditional biospeology.* This seems to be true in the light of recent research. From the three main factors recognized as essential in classical biospeology (complete darkness, scarcity of trophic resources, environmental constancy), the first one is indisputably of paramount importance. Concerning the 2d one, it is presently evident that, if oligotrophy is often – but certainly not always – one element of the trophic factor, others should be equally well taken

into consideration: sources, quality, patchiness, seasonal variation of available trophic resources; moreover, an aspect which could prove to be of some importance: the feeding modes (trophic categories) of the members of an assemblage of hypogean living species. And a specification is indispensable concerning the 3d factor: indeed, quite frequently the habitats of subterranean Cirolanidae, especially in karstic environments and even more so in tropical ones, are characterized by an extremely unstable hydrological regime (water depth and flow, current speed, turbidity...), or chemical regime (salinity stratification and fluctuations in anchialine or other near-shore environments...). All this represents quite serious constraints of the rigorous subterranean habitats.

2. *Animals display a great variety of adaptive responses to this environment/there is a positive relationship between subterranean habitat diversity and these adaptive responses.* This idea is well supported by evidence presented in this paper.

The answer for some of the questions asked in the present paper will be found by more thorough study of the trophic factor (see above) and of the biocenotic factors (exact composition of the biocenoses, population densities, interspecific relations).

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