

## MODIFIED MOUTHPARTS IN HYDROPHILOUS CAVE MILLIPEDES (DIPLOPODA)

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### ABSTRACT

In several unrelated cave-dwelling millipedes from southern Europe and the Caucasus, the mouthparts are convergently modified: The biting/masticating parts of the mandibles are reduced, whereas the pectinate lamellae are hypertrophied; the medial labral teeth are often reduced, and the gnathochilarium often broader than usual.

Species with modified mouthparts are known in the families Julidae (genera *Leucogeorgia*, *Trogloiulus*, *Typhloiulus*), Blaniulidae (genus *Vascoblaniulus*), and Polydesmidae (genus *Serradium*). Julid and blaniulid species with modified mouthparts tend to have fewer segments than related species.

Available evidence suggests that species with modified mouthparts live in, or at the edge of, subterranean water bodies. It is suggested that the modified mandibles with their enlarged pectinate lamellae function as a kind of filter, screening suspended organic material from the water. The shortened body may be a consequence of a lessened need for pushing power, and perhaps endows the species with a higher speed of locomotion.

### INTRODUCTION

Caves have been invaded independently by numerous unrelated lineages of millipedes. Many of the cave-dwelling species differ from their epigeal relatives in being blind, paler, longer, and having longer legs and antennae, but otherwise they do not show significant morphological deviations. It has been known for a long time that a few of the cave-dwelling Julidae are distinguished by a particular set of modifications of the mouthparts. Prompted by the discovery of such a species belonging to the genus *Trogloiulus*, I reviewed the literature pertaining to this phenomenon, with some interesting results, which are reported on here. Similar cases of mouthpart modification in the families Blaniulidae and Polydesmidae are also discussed.

The material studied derives from the following museums:

MNV: Museo Civico di Storia Naturale, Verona, Italy.

MSNB: Museo Civico di Scienze Naturali, Bergamo, Italy.

NHMS: National Natural History Museum, Sofia, Bulgaria.

NHMW: Naturhistorisches Museum, Vienna, Austria.

ZMUC: Zoological Museum, University of Copenhagen, Denmark.

ZSBS: Zoologische Sammlung des Bayerischen Staates, Munich, Germany (F.R.G.).

### JULIDAE

#### *Leucogeorgia*

Material examined. — The type-series of *L. longipes* Verhoeff, 1930 (ZSBS).

Verhoeff (1930) described the new genus and species *Leucogeorgia longipes* from a cave in the Caucasus. The species deviated from all other julids known at that time in several mouthpart characters: the labrum lacks the usual three median teeth; the biting/masticating parts of the mandibles, viz., the external and internal teeth, and the molar plate, are reduced, whereas the mandibular pectinate lamellae are hypertrophied (terminology from Enghoff, 1979); the gnathochilarium is broader than usual, the lateral palps are enlarged, the lingual lobes very broad, and the setae of the lamellae linguales are mostly apical. A further modification, not noted by Verhoeff, affects the posterior hypopharyngeal node, so characteristic of the Julidae (Enghoff, 1981), which is reduced in *Leucogeorgia* (like in *Typhloiulus ausugi* Manfredi, 1953, *T. edentulus* Attems, 1959, and *Trogloiulus binii*, fig. 4).

Verhoeff was so impressed by the modified mouthparts (as such mouthparts will be

termed in the present paper) that he (1926-32) erected a separate family to accommodate *Leucogeorgia*. The Leucogeorgiidae did not survive for long: Lohmander (1936) demonstrated that *Leucogeorgia* has relatives, viz., species of the genus *Archileucogeorgia* Lohmander, 1936, with perfectly normal julid mouthparts. The two genera are identical in gonopod morphology and are both currently classified in the Julidae. Lohmander (1936) described two species of *Archileucogeorgia* from the Caucasus, one of which was found in a cave. Golovatch (1981, 1983, and in litt.) reports on two further *Leucogeorgia* spp., both troglobites, and several new *Archileucogeorgia* spp., mostly troglobites, from the Caucasus.

### *Trogloiulus* and *Typhloiulus*

Material examined. — The type-series of *Trogloiulus binii* Enghoff, 1985 (MSNB), and numerous specimens of the "normal" *Tr. boldorii* Manfredi, 1940, *Tr. mirus* Manfredi, 1931, and *Tr. minimus* Manfredi, 1935 (MSNB and MNV). — A male topotype of *Typhloiulus ausugi* Manfredi, 1953 (MNV). The holotype of *T. edentulus* (NHMW). A female and a juvenile paratype of *T. longipes* Strasser, 1973 (NHMS). Specimens of the "normal" *T. montellensis* Verhoeff, 1930, *T. psilonotus* (Latzel, 1884), *T. strictus* (Latzel, 1882), and *T. illyricus stygis* Verhoeff, 1933 (ZMUC, MSNB, and ZSBS).

Whereas the modified mouthparts are currently genus-defining in the case of *Leucogeorgia* and *Archileucogeorgia*, this is not so in the Italian-Balkan genera *Trogloiulus* and *Typhloiulus*, which both belong in the somewhat dubious tribe Typhloiulini (Strasser, 1962a).

Strasser (1977) reviewed the North Italian genus *Trogloiulus* Manfredi, 1931, at that time consisting of six species — almost exclusively troglobites, and all with normal mouthparts. But in 1978, Strasser described a seventh species from a cave in Brescia: *Tr. vailatii*, with mouthparts entirely of the *Leucogeorgia* type. A second *Trogloiulus* with modified mouthparts (*Tr. binii*) was described by Enghoff (1985). Figs. 1-7 show scanning electron micrographs of important details in the mouthparts of this species, compared with the "normal" *Tr. boldorii* Manfredi, 1940.

Modified mouthparts in the genus *Typhloiulus* were described by Strasser (1962a, b), as occurring in *T. (Spelaeoblaniulus) serbani* (Ceuca, 1956), *T. (Attemsotyphlus) edentulus* Attems, 1959, and *T. (Stygiulus) ausugi* Manfredi, 1953. Strasser did not mention details of the mandibles in *T. ausugi*, but I found them, like those of *T. serbani* and *T. edentulus*, to be of the *Leucogeorgia* type — with one notable addition, namely that there are five instead of the usual four pectinate lamellae.

*Typhloiulus (Inversotyphlus) longipes* Strasser, 1973, may represent an intermediate stage in the evolution of *Leucogeorgia*-like mouthparts: The clypeus and gnathochilarium are broad (Strasser, 1973), but the mandibles and hypopharynx are unmodified (pers. obs.).

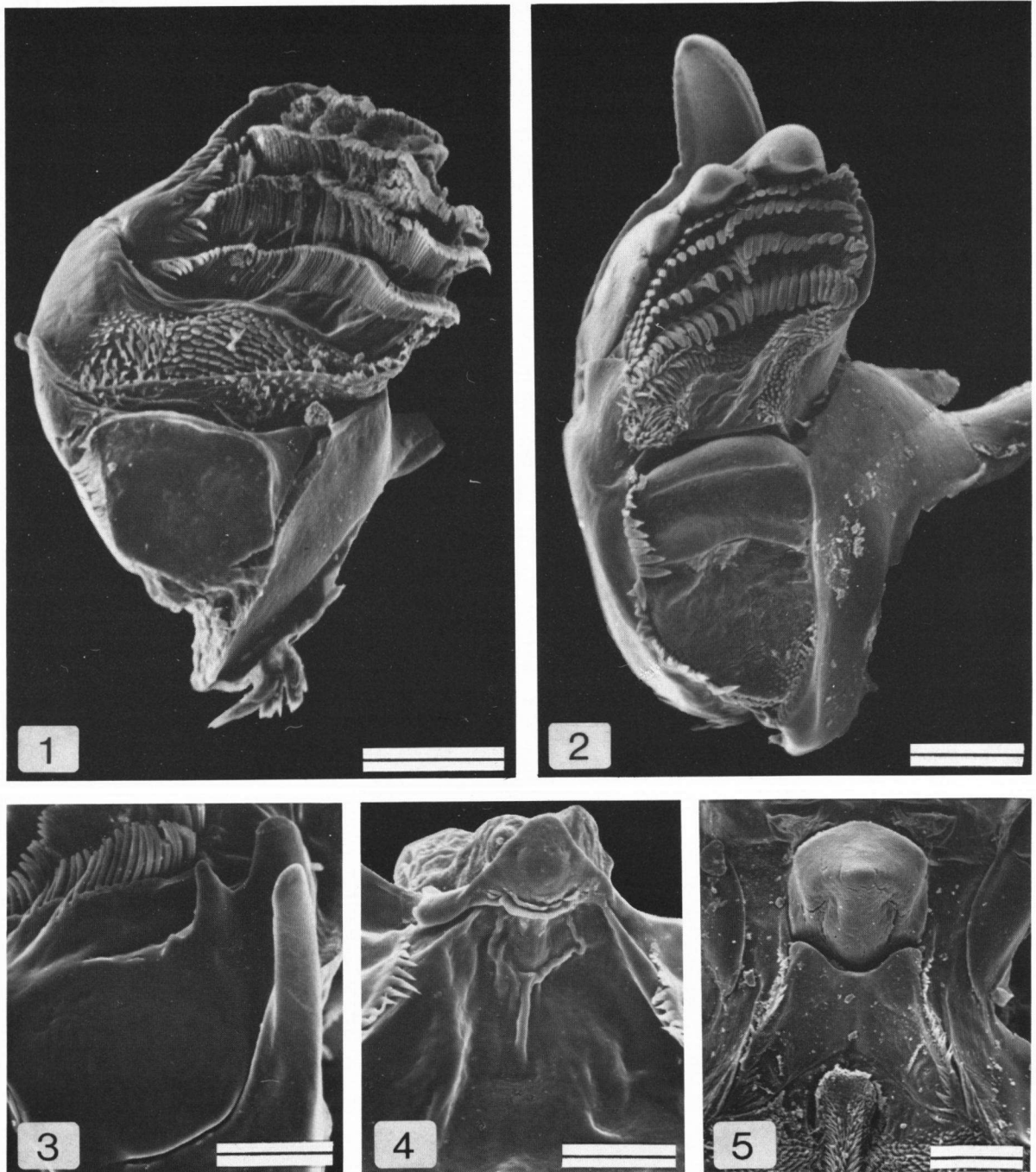
## BLANIULIDAE

### *Vascoblaniulus cabidochei*

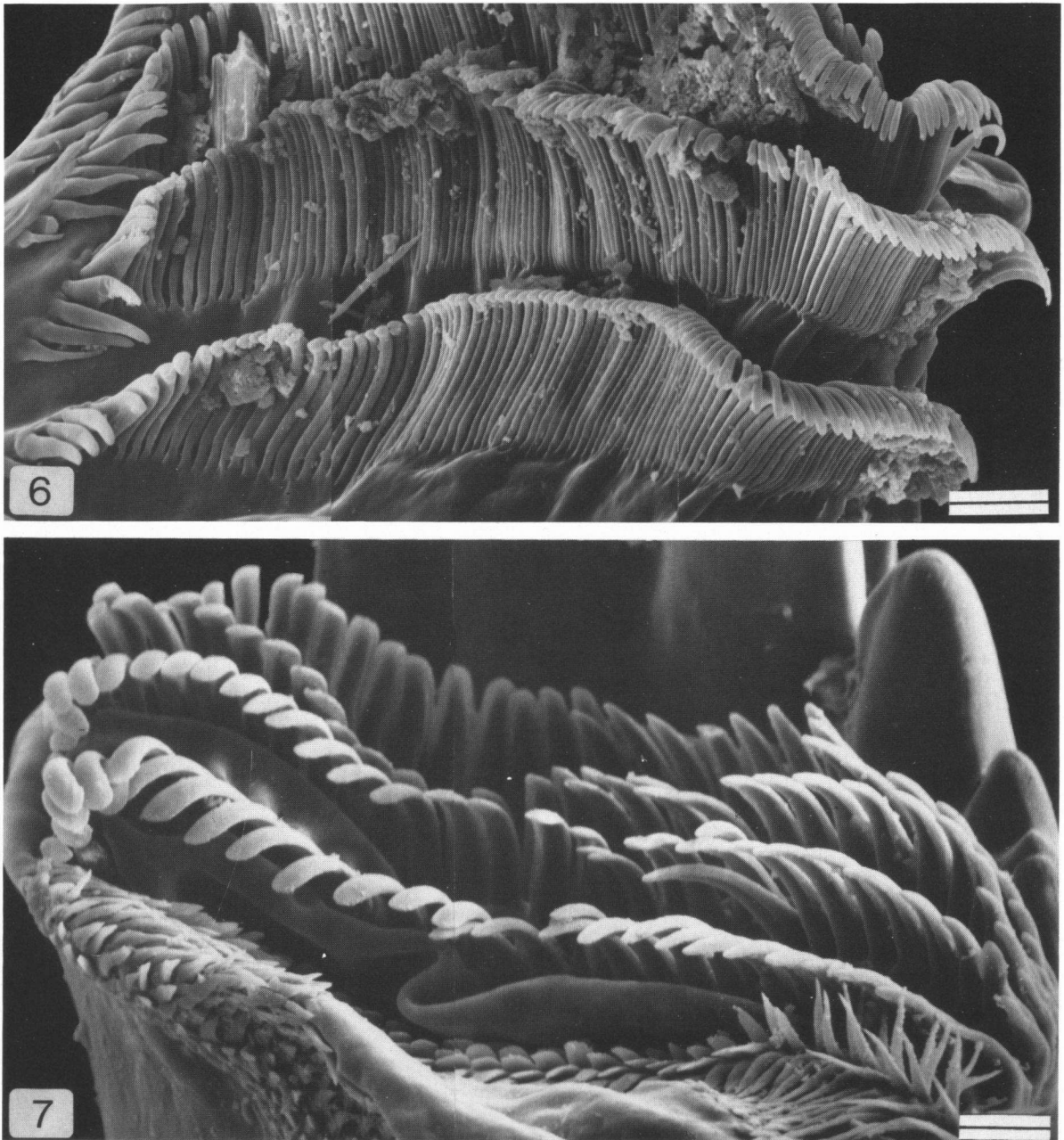
Material examined. — One ♂, one ♀, topotypes (ZMUC, Mauriès ded.). — Numerous "normal" blaniulids.

Mauriès (1967) described the new genus and species *Vascoblaniulus cabidochei* from the famous Pyrenean cave "Gouffre de la Pierre-Saint-Martin". *V. cabidochei* differs from the numerous other cavernicolous blaniulids (genera *Blaniulus*, *Occitaniulus*, *Euzkadiulus*, etc.) in several mouthpart characters: The labrum is broad and bulging and has the median teeth strongly reduced; the mandibles have about a dozen pectinate lamellae instead of the usual four; the gnathochilarium is comparatively short, distally enlarged, and has the external palps very strong (Mauriès, 1967).

I have examined a mandible of a male *V. cabidochei* with scanning electron microscopy and found some further modifications (figs. 8-10). The external tooth seems to be absent altogether; the internal tooth and the molar plate are reduced; the teeth of the pectinate lamellae (11 lamellae in the mandible examined) are extremely long, slender, and densely set.



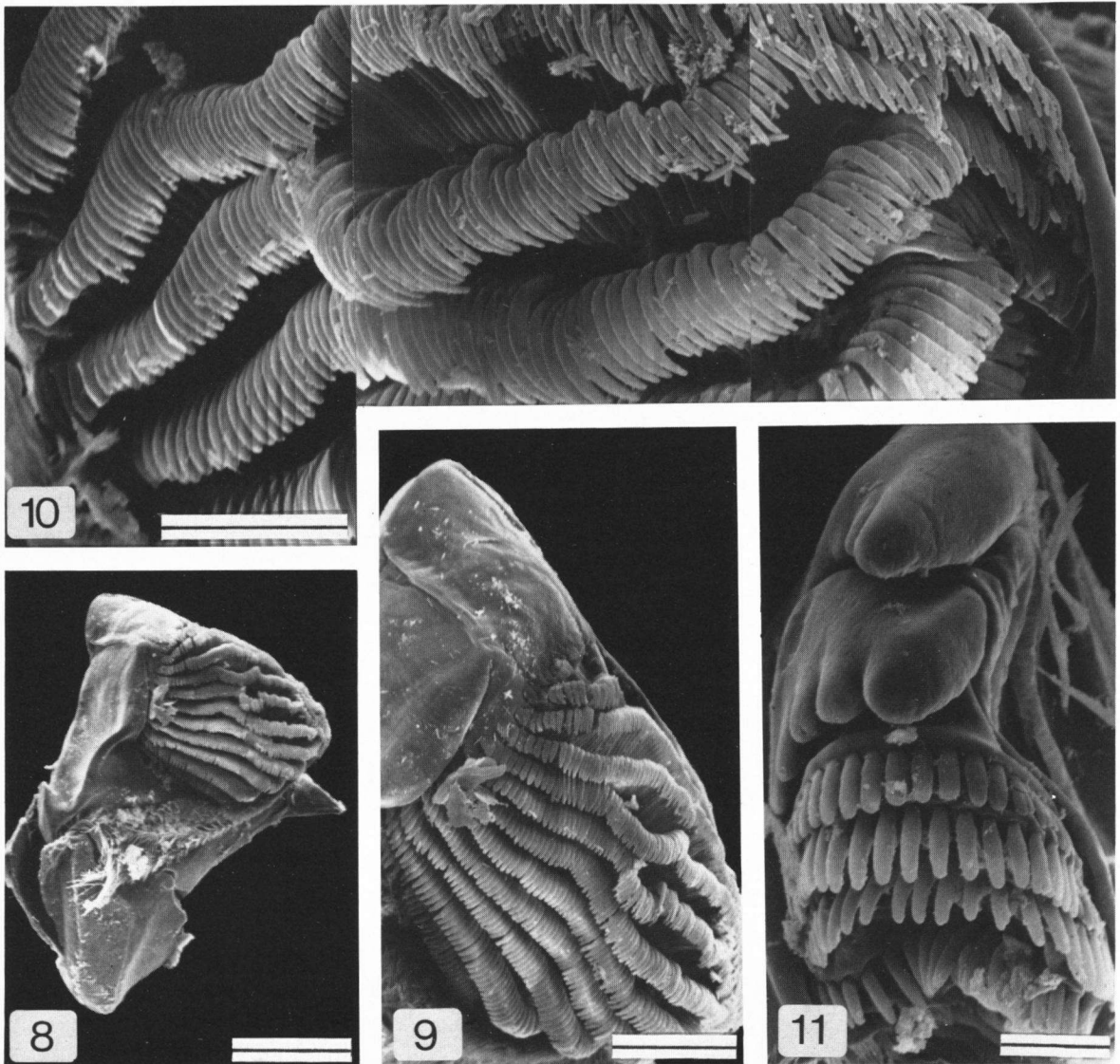
Figs. 1-5. Mouthparts: 1, 3, 4, *Troglolulus binii*; 2, 5, *Tr. boldorii*, a "normal", troglobiont julid. (1-2, left mandible, gnathal lobe; 3, external and internal teeth of right mandible; 4-5, posterior node of hypopharynx). Scales 100  $\mu\text{m}$  (1, 2, 5), 50  $\mu\text{m}$  (3, 4).



Figs. 6-7. Pectinate lamellae: 6, *Troglotulus binii*; 7, *Tr. boldorii*. Scales 20  $\mu\text{m}$ .

Most of these modifications are exact parallels to those found in the julids discussed above. The strongly enlarged number of pectinate lamellae, however, is unique and deserves a comment from a systematic point of view as well: Enghoff (1979, 1981) found that the possession of four (rarely five) pectinate

lamellae instead of a higher number is a synapomorphy for the julid superfamilies Blaniuloidea + Nemasomatoidea + Juloidea. *V. cabidochei* appears to be a potent falsifier of this hypothesis (and it is quite embarrassing that I overlooked Mauriès' report when I wrote the above-cited papers). Several other



Figs. 8-11. Mandibular gnathal lobes with pectinate lamellae: 8-10, *Vascoblaniulus cabidochei*; 11, *Noptoiulus kochii* (Gervais) a "normal" blaniulid. Scales 100  $\mu\text{m}$  (8), 50  $\mu\text{m}$  (9), 20  $\mu\text{m}$  (10, 11).

characters, however, indicate that the large number of lamellae is a secondary modification: *V. cabidochei* exhibits several of the blaniulid apomorphies mentioned by Enghoff (1981): anterior male legs with leaflike setae, penis single, anterior gonopods without flagella, vulval invaginations deep. The characteristic blaniulid mandibular forceps is absent, but so it is in several other taxonomically scattered

blaniulids as well — these probably are cases of secondary reduction. The arrangement of ocelli escapes evaluation in this blind species.

The enlarged number of pectinate lamellae is paralleled, although on a much smaller scale, in *Typhloiulus ausugi* where the number of lamellae (five) is still within the "allowable" limits.



## POLYDESMIDAE

*Serradium* sp.

Material examined. — One juv. ♀ (17 segments) of *Serradium* sp. from "Grotta dell'Acqua" del Ponte de Veja, S. Anna d'Alfaedo, Italy, 16.IV.1983, leg. Caoduro (MNV). — Specimens of the "normal" polydesmids *S. hirsutipes* and *S. longicorne* (ZMUC, Pisoni and Osella ded.).

In material of cavernicolous millipedes from northern Italy I found a single juvenile specimen of the genus *Serradium*, in which the pectinate lamellae are remarkably enlarged, and the external and internal teeth diminished, in comparison with the "normal" species *S. hirsutipes* Verhoeff, 1941, and *S. longicorne* (Silvestri, 1894) (figs. 12-15). Labrum and gnathochilarium of the specimen are identical to those of *S. hirsutipes* and *S. longicorne*. This is, to my knowledge, the first recorded instance of "leucogeorgioid" mouthpart modification in the order Polydesmida.

## BODY SHAPE

The typhloiulines with modified mouthparts are remarkably short-bodied compared with congeneric species. Adults of *Typhloiulus edentulus* have 33-38 segments (Attems, 1959; Strasser, 1962b; the record of 58 segments by Attems (1951) is erroneous), *T. ausugi* also has 33-38 segments (Manfredi, 1953; Strasser, 1971), and *T. serbani* has 29-35 segments (Ceuca, 1956, 1961). *T. longipes*, with only partly modified mouthparts, has 37-41 segments (Strasser, 1973). Other species of *Typhloiulus* have 39-79 segments (Strasser, 1962a). (*T. staregai* Strasser, 1973, has normal mouthparts and 32-40 segments. It is, however, not a typhloiuline (pers. obs.).)

*Trogloiulus vailatii* has 30-34 segments (Strasser, 1978), *Tr. binii* (fig. 17) has 27-30. Other *Trogloiulus* spp. have 41-87 segments (Strasser, 1977) (fig. 19).

The difference is less clear-cut in *Leucogeorgia* and *Archileucogeorgia*: *L. longipes* with 28-34 segments (fig. 16) has the same body shape as the modified typhloiulines, but other species of

*Leucogeorgia* have 49-54 segments (Golovatch, 1983 and in litt.). *Archileucogeorgia* spp. have 36 - ca. 60 segments (Lohmander, 1936, Golovatch, in litt.).

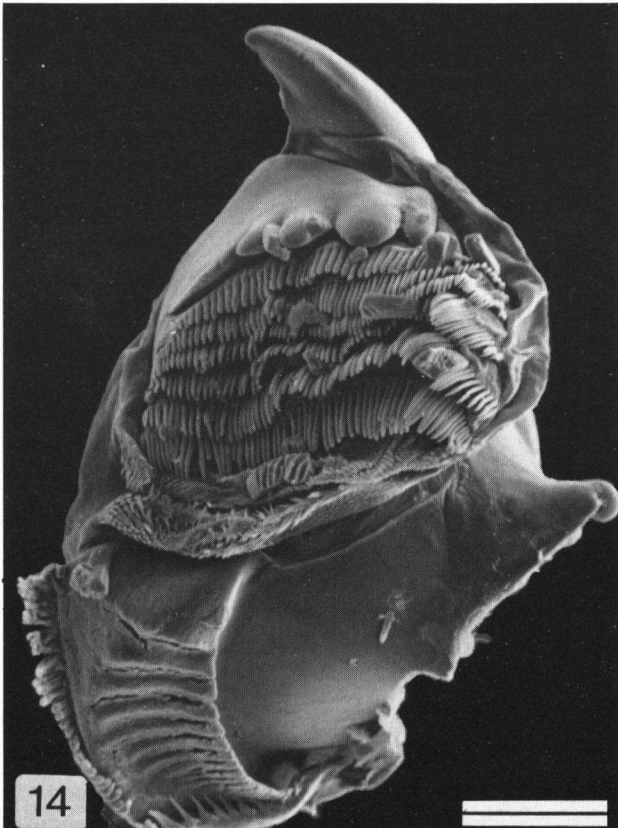
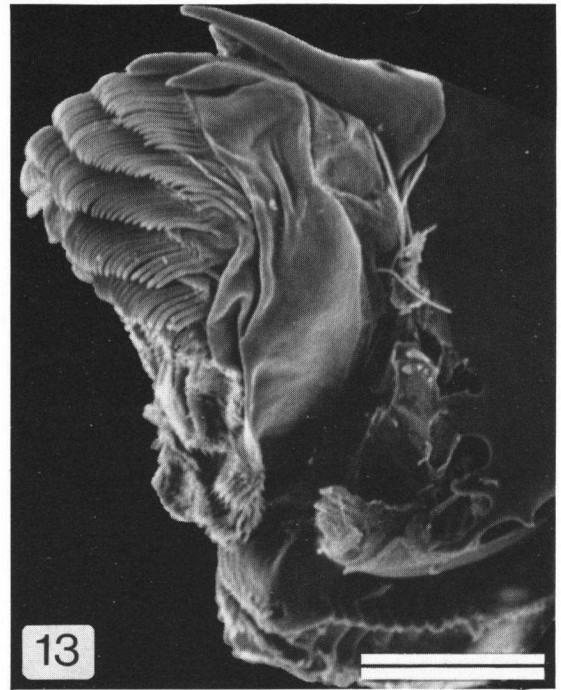
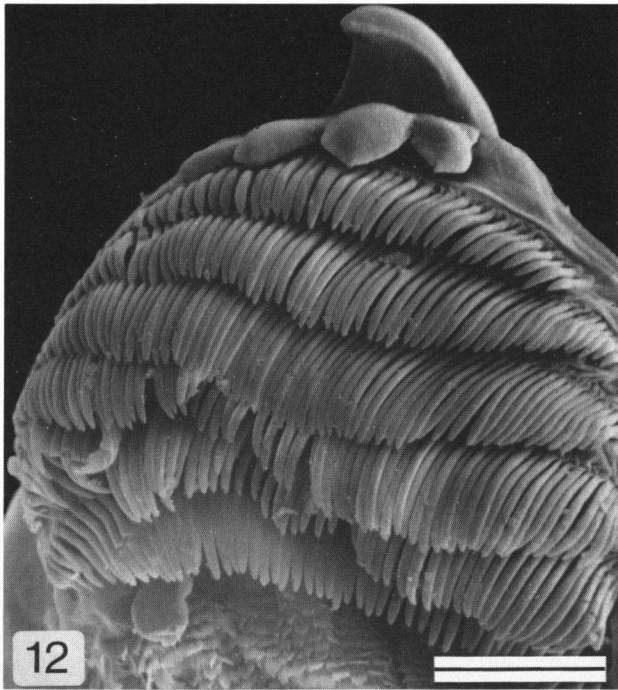
*Vascoblaniulus cabidochei* (fig.18) has 40-44 segments and thus lies in the lower end of the range covered by other cavernicolous blaniulids (Brölemann, 1923; Demange, 1981). *V. cabidochei* is further characterized by particularly stout legs.

The Polydesmidae are generally short-bodied, and *Serradium* sp. from "Grotta dell'Acqua" bears no signs of further shortening (only one juvenile known, however).

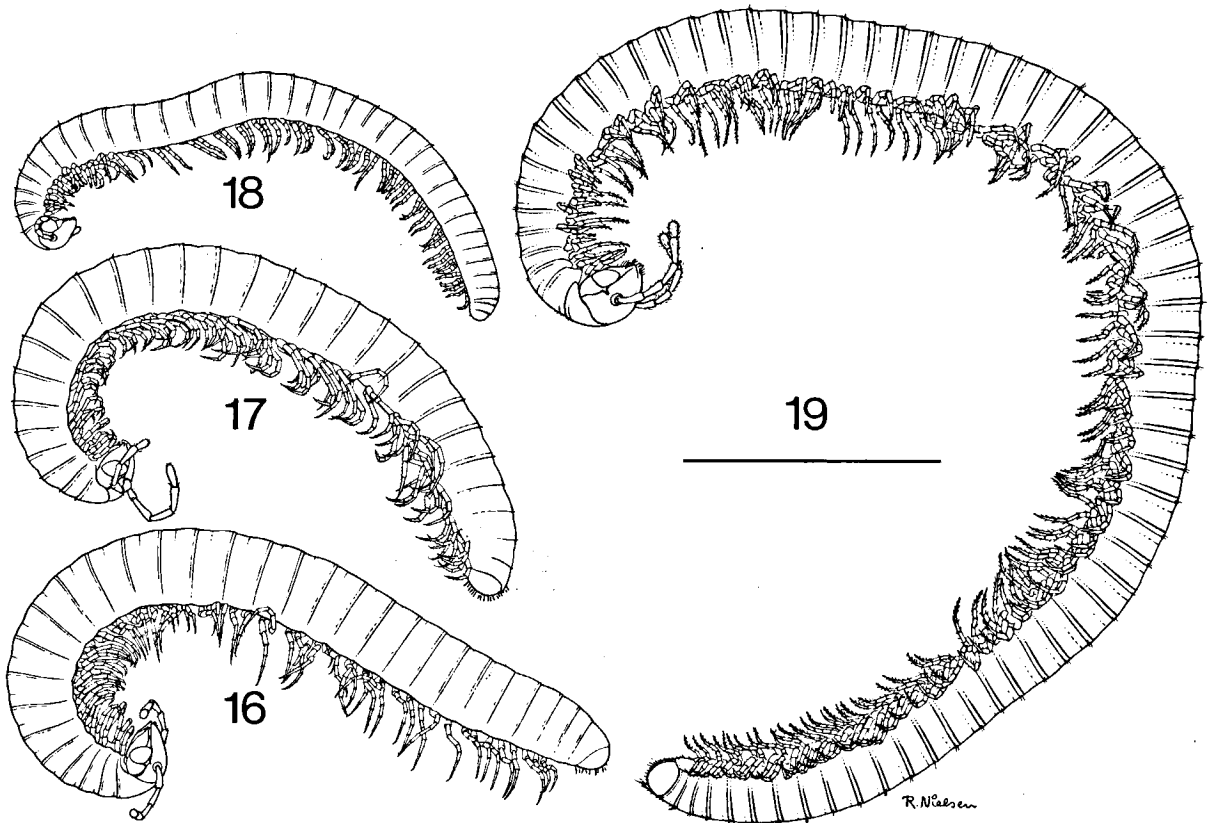
## HABITAT

The bionomically best known of the species with modified mouthparts is *Trogloiulus vailatii*. Strasser (1978) cites D. Vailati, who wrote (translated from Italian): "The millipedes were collected in an active meander in the above-mentioned cave, called 'branch of the waterfalls' because of the presence of many waterfalls. The waterfalls change, in periods of small flow, into a film of water running over the vertical parts of the canal excavated in the rock ... When collected, the adult diplopods were heading upstream, covered by at least a couple of millimeters of water, whereas the juvenile stadia could be found at the sides, where only the spray was reaching. The air temperature was 8.7 °C, the water temperature 7.5 °C".

Limited information is available on the other julids with modified mouthparts, but what there is suggests that they may live like *T. vailatii*: *Leucogeorgia longipes* was collected in puddles (Verhoeff, 1930). *L. rediviva* Golovatch, 1983, and *L. n. sp.* inhabit "very humid parts of the caves" (Golovatch, in litt.). *T. serbani* was found "partly on the cave wall, partly on stones near subterranean water. Both walls and stones were wet" (Ceuca, 1956, translated from Rumanian). No habitat information is available on *T. edentulus* and the nominate forms of *T. ausugi*, but *T. a. gentianae* was found "on wet, clayey walls of the ... cave" (Strasser,



Figs. 12-15. Left mandibular gnathal lobes: 12-13, *Serradium* sp. from "Grotta dell'Acqua"; 14-15, *S. longicorne*. Scales 50  $\mu\text{m}$  (12), 100  $\mu\text{m}$  (13-15).



Figs. 16-19. Body shape of species with modified mouthparts (16-18), compared with a "normal" troglolulid (19): 16, *Leucogeorgia longipes*; 17, *Troglolulus binii*; 18, *Vascoblaniulus cabidochei*; 19, *Troglolulus boldorii*. Robert Nielsen del. Scale 5 mm.

1971, translated from German), and *T. a. fimbriatus* was found in a cave about which Strasser (1971) wrote (translated from German): "The spring cave, which is well known and often visited because of its built-in old church, has been often and thoroughly investigated, without a *Typhloiulus* having been found before. Its rarity might be explained by the fact that the cave is sometimes flooded". The cave in which *Troglolulus binii* was collected is described by Bini (1977) who further informs (R. Pisoni, in litt.) that the sampling sites for the species are always very muddy, because they are often flooded. *Vascoblaniulus cabidochei* fits into this picture too (Mauriès, 1967; Cabidoche, 1968): "Among the species living in this cavity, *Vascoblaniulus cabidochei* should be especially emphasized: it is localized very differently from the

remaining fauna ... and is never found together with *Aphaenops* [a genus of carabid beetles] and other encountered species which come to baits. (This is in contrast to what one can usually see in numerous caves at low altitude in the same region, where diplopods of the genus *Typhloblaniulus* [= *Blaniulus*] litterally swarm on baits.) This new genus described by Mauriès is thus quite distinct: in addition to morphological criteria its ecology is quite different because it is the only species which frequents the banks of subterranean watercourses ..." (Cabidoche, 1968: 670, translated from French).

The *Serradium* from "Grotta dell'Acqua" nicely rounds off the pattern of hydrophily: it was collected under stones in the bed of the little brook of the cave (G. Osella, in litt.).



## HABITAT OF RELATED SPECIES

Only scant habitat information on "normal" cave julids could be extracted from the literature. This in itself may indicate that these species do not occur in very special habitats, unlike at least some of the species with modified mouthparts.

Golovatch (in litt.) reports on "many new *Archileucogeorgia* inhabiting very wet caves ... However, some *Archileucogeorgia* have been found on relatively dry walls in caves, and some even in the forest litter (epigeically)".

*Trogloiulus minimus* has been collected "on rotting wood" and "under water collector (sewer)" (unpublished material in MSNB, Enghoff det.).

*Typhloiulus bureschi* Verhoeff, 1926, has been found on moist clay and in bat guano (Guéorguiev & Beron, 1962). *T. strictus* (Latzel, 1882) occurs in accumulations of decaying plant and animal waste (Negrea & Negrea, 1979). *T. albanicus* Attems, 1929, was found under stones at a cave entrance (Strasser, 1962a). *T. illyricus* Verhoeff, 1929, was found abundantly on an accidentally introduced sheaf in a Slovenian cave (Strasser, 1966), but *T. illyricus stygis* was collected on moist stalagmites and on clay and wood in a very wet cave with clay and many muddy puddles (Verhoeff, 1933).

Brölemann (1923: 411) writes about the habitat of cavernicolous blaniulids that species of *Blaniulus* (= *Typhloblaniulus*) and *Archichoneiulus* have been collected in abundance on bat guano, on stalagmitic flows and on decomposing vegetable and animal debris. They have also been found eating old drops of stearin (from the candles of speleologists) or mould growing upon them. (See also above under *Vascoblaniulus cabidochei*.)

*Serradium hirsutipes* and *S. longicorne* have been collected in numerous North Italian caves, some with, others without water. (G. Osella, R. Pisoni, in litt.). The only available exact habitat notes, however, concern an undescribed *Serradium* species with normal mouthparts, which was found in great numbers on the walls and on various organic materials (wood, etc.) in an artificial cave near Bergamo (R. Pisoni, in litt.).

## DISCUSSION

The foregoing sections indicate an interesting "syndrome". The affected species have their mouthparts modified; in particular, the biting parts of the mandibles are reduced, whereas the pectinate lamellae are hypertrophied. The species tend to be short-bodied, and available habitat information suggests that most, if not all of them, favour very wet habitats and might deserve the designation semiaquatic. Related species with normal mouthparts (and longer bodies) appear to occupy other, less wet, habitats in the caves (*Typhloiulus illyricus stygis* seems to be an exception. I have examined this species and ascertained that its mouthparts are normal.)

It is remarkable that the syndrome recurs in three families and that within the Julidae, it has apparently evolved several times independently: The *Leucogeorgia*, *Typhloiulus*, and *Trogloiulus* species with modified mouthparts all have close relatives with normal mouthparts. The three *Typhloiulus* species involved are even classified in three different subgenera!

## POSSIBLE FUNCTIONAL SIGNIFICANCE

*Modified mouthparts*

The function of julid mouthparts was described by Fechter (1961), and Manton (1964) described the mandibular function of a species belonging to the related order Spirostreptida. According to these authors, the external and internal teeth of the mandibles pick up food particles which are then ground between the molar plates. In the case of Julidae, the molar plates grind the food against the hypopharyngeal node (which is characteristic of the Julidae and one further family, the Trichoblaniulidae, see Enghoff, 1981). According to Fechter (1961), the pectinate lamellae also assist in the picking up and grinding of food particles. (Verhoeff (1926-32: 138) interpreted the pectinate lamellae as grooming organs; however, B. D. Valentine (in litt.), who has studied grooming in 14 families of millipedes, has never seen the pectinate lamellae being used for grooming.)

The median labral teeth are used as an anchor during burrowing (Fechter, 1961).

The modifications described in the preceding sections must obviously affect these functions profoundly. Verhoeff (1930) hypothesized that the enlarged pectinate lamellae of *Leucogeorgia* scrape off particles of some soft substance present in large quantity. He suggested this substance to be either fine, moist ooze or more or less decayed guano. Strasser (1978) found that several specimens of *Trogloiulus vailatii* had their preoral cavity stuffed with some extraneous substance in such quantities that it prevented them from "closing their mouth". He suggested that the specimens might have been captured while "grazing" under water and that the substance might be ooze, but hardly bat guano. I found the gut contents of *Trogloiulus binii* to consist of extremely fine-grained material which could not be identified, not even under the scanning electron microscope.

Based on this scant evidence I can only follow Verhoeff in hypothesizing that these species feed on some soft, fine-grained material. The indications for hydrophily lead to the suggestion that the enlarged pectinate lamellae function as a kind of filter.

The reduction of the labral teeth may be correlated with non-burrowing habits of the species involved. The gnathochilarial modifications escape evaluation at present but certainly have a functional aspect, since they are paralleled in several unrelated lineages.

### *Body length*

A large number of body segments increases the pushing power a millipede is able to exert (Manton, 1954). The possibly hydrophilous julids and blaniulids with modified mouthparts probably have little need for burrowing. The comparatively short body with long legs, quite reminiscent of certain Paradoxosomatidae (order Polydesmida) probably results in higher speed of locomotion, when compared with the related longer species. The very strong legs of *Vascoblaniulus cabidochei* also recall certain

species of the order Polydesmida. A correlation between hydrophily and high speed of locomotion is thus suggested.

### CONCLUSION

The evidence presented here, although fragmentary and insufficient, clearly indicates that the "modified mouthparts syndrome" constitutes a significant feature in the adaptation of cave-dwelling millipedes. That there is a particular functional aspect of the modifications (probably adaptations to the recovery of suspended food in subterranean waterbodies) is indicated by the taxonomic isolation of the species affected.

So far, the phenomenon has been found only in a quite restricted area: from northern Italy over the Balkan countries to the Caucasus. The reason for this may be either that cave millipedes of other regions are less well-known, or that they belong to taxa whose mouthparts are not pre-adapted for this kind of modification.

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