

Gelyelloida, a new order of stygobiont copepods from European karstic systems

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Abstract

A new order, Gelyelloida, is proposed for *Gelyella* Rouch & Lescher-Moutoué, 1977 (ex Harpacticoida), an enigmatic genus of freshwater-inhabiting copepod from European karstic systems. The new order is characterized by a unique combination of generalised gnathostomous mouth parts and unusual derived features, some of them suggesting a possible neotenic origin for the order. It is suggested that gelyellids have had a long evolutionary history and separated as an early offshoot of the main cyclopoid lineage.

Introduction

Lang, in his monograph of the harpacticoids (1948), recognized or established 32 families. Since his monograph, only three new families have been discovered, viz. Latiremidae Bozic, 1969, Namakosiramiidae Ho & Perkins, 1977 and Gelyellidae Rouch & Lescher-Moutoué, 1977.

The most enigmatic of these new families is the Gelyellidae; the first record of *Gelyella* was from Saint-Gély-du-Fesc, Hérault, France (Rouch & Lescher-Moutoué, 1977), where *G. droguei* was obtained by continuous filtration of subterranean water from a karstic system at a depth of 60 m. Rouch & Lescher-Moutoué (1977) placed the species in a new family, particularly on account of the peculiar combination of characters from both 'polyarthran' and 'oligoarthran' lineages within the Harpacticoida. They recognized also a certain superficial similarity with the genus *Cerviniella* Smirnov, 1946 (Cerviniidae). Consequently, the alignment of the gelyellids within the order has been the subject of controversy.

A second species, *G. monardi*, has recently been obtained from a Swiss karstic system (Gorges de l'Areuse, Jura neuchâtelois) by Moeschler & Rouch (in press). Due to the conservative nature of the morphology within the genus, the discovery of a second member of the family apparently yielded no new evidence (Moeschler & Rouch, in press) on relationships.

After re-examination of the type material of *G. droguei* it is clear that the family should be excluded from the Harpacticoida and comprise a separate order, the Gelyelloida ordo nov., more closely allied to the Cyclopoida than the Harpacticoida.

Material and methods

This re-examination is based on type specimens of *Gelyella droguei* obtained from Saint-Gély-du-Fesc and retained in the personal collection of Dr. Rouch, Laboratoire souterrain du CNRS, Moulis.

Before dissection, the habitus was drawn in lactophenol and body length measurements were made. Specimens were dissected in lactic acid and the dissected parts were individually positioned in lactophenol mounting medium. Preparations were sealed with glyceel.

Gelyella droguei was examined by scanning electron microscopy (SEM) with a JEOL JSM-840 microscope. Specimens of both sexes were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter coated with gold.

All figures have been prepared using a camera lucida. The terminology and presentation of the setal formulae are adopted from Lang (1948, 1965). The terms *pars incisiva*, *pars molaris* and *lacinia mobilis* are omitted in the description of the mandibular gnathobasis (Mielke, 1984). Boxhall's (1985, pp. 341-344) terminology for the mandible and the maxilliped and that of Huys (in press) for the caudal ramus structure are followed.

Abbreviations used in the text and figures are: P1-P6 = first through sixth legs.

Systematics

Gelyelloida ordo nov.

Diagnosis. First pedigerous somite free and about equal in size to the following somite. No distinct body articulation between prosome and urosome. Genital double-somite in the female without any trace of subdivision. Except for anal somite abdominal somites relatively short. Anal operculum present, unarmed. Caudal rami longer than wide, each furnished with 7 setae.

Integument of body somites not strongly chitinized, somitic sensillae lacking. Male anal somite provided with several rows of pores laterally.

Rostrum thick, not fused with cephalosome, sensillae absent. Antennula indistinctly 14-segmented in female, 9th segment with aesthetasc; 13-segmented and geniculate (between 11th and 12th segment) in male, 8th segment with aesthetasc and probably sensory seta. Antenna with

basis, 3-segmented endopodite and 7-segmented exopodite. Mandible with well developed gnathobasis; basis with 1 seta; exopodite indistinctly 5-segmented; endopodite 2-segmented. Maxillula with praecoxal non-articulating endite, surface without setae; coxa with well developed endite, epipodite absent; basis with 2 setose lobes; exo- and endopodite unisegmented. Maxillar syncoxa with 3 endites; basis with cylindrical endite; endopodite 3-segmented. Maxilliped stenopodial, cyclopoid-like; syncoxa with 5 setae; basis with 2 setae; endopodite 2-segmented.

Swimming legs fairly reduced. Fourth and fifth pair of legs totally absent. Intercoxal plate ('coupler') of P1-P3 absent; coxae of both sides fused. Leg 1-3 with 1- (female) or 3-segmented (P2-P3 in male) exopodite; endopodite vestigial or absent. Male 6th leg represented as an asetose lobe.

Sexual dimorphism in antennula, P2-P3 (exopodite 3-segmented, endopodite defined at base), P6, anal somite and in genital segmentation. Male with 2 spermatophores.

Small-sized (300-400 μm); free-living; freshwater-inhabiting, stygobiont (karstic systems).

Family Gelyellidae Rouch & Lescher-Moutoué, 1977

Diagnosis. As for ordo.

Type and sole genus: *Gelyella* Rouch & Lescher-Moutoué, 1977

Genus Gelyella Rouch & Lescher-Moutoué, 1977

Diagnosis. Gelyellidae. Endopodite of leg 1 vestigial (represented as 1 seta) or absent. Endopodite of leg 2-3 a small segment (male) or process (female) with 1 apical seta. Basis of P3 without outer seta. Seta- and spine formulae as follows:

	Exopodite		Endopodite
P1	(1-2)13		0(0-1)0
	♀	♂	
P2	(1-2)14	0.0(1-2)12	010
P3	114	0.0.112	010
P4	-	-	-

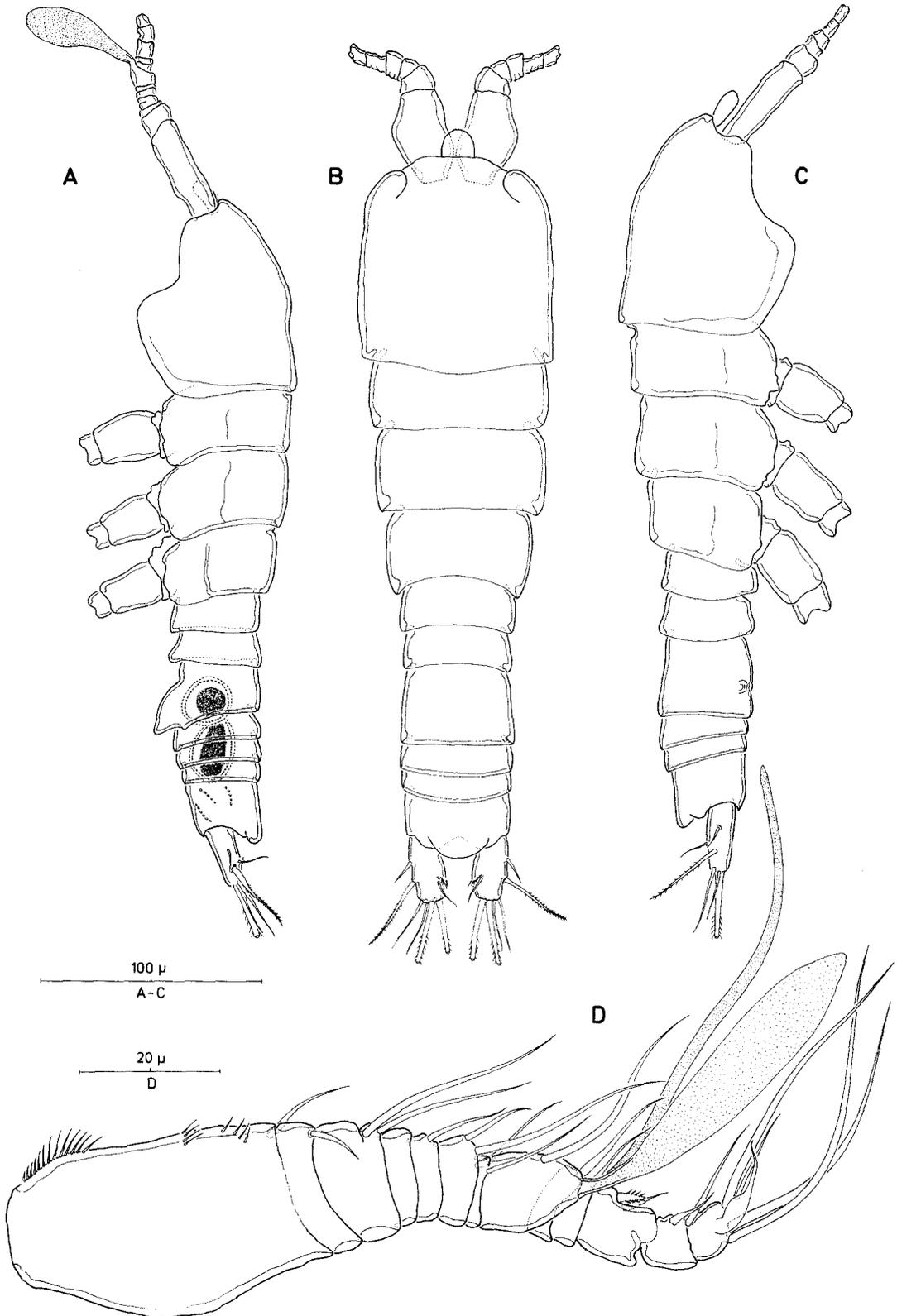


Fig. 1. *Gelyella droguei*. A. Male, lateral side; B. Female, dorsal side; C. Female, lateral side; D. Antennula, male.

Type species: *G. droguei* Rouch & Lescher-Moutoué, 1977 (by monotypy).

Other species: *G. monardi* Moeschler & Rouch, in press

Gelyella droguei Rouch & Lescher-Moutoué, 1977
Redescription: FEMALE (Figs. 1-B,C). Body length: 320–346 μm ($n = 3$) rostrum and caudal rami included; 298–312 μm ($n = 3$) rostrum and caudal rami excluded.

Body subcylindrical, slightly tapering towards 5th thoracic somite, constricted between thoracic somites. Colourless and transparent. No distinct separation between prosome and urosome.

Rostrum (Figs. 1-A,B,C) well developed, rounded, thick, tip pointing downwards, without any sensillae, defined at base. Cephalic shield as long as wide, forming on either side a distinct fold ventrally, without any ornamentation. Nauplius eye absent. First pedigerous somite free. Genital double somite rectangular, wider than long, without any trace of subdivision; genital field simple, without remnants of P6. Antepenultimate and penultimate abdominal somites smallest. Anal somite with smooth anal operculum. Somitic sensillae totally absent.

Caudal rami (Fig. 3-C) slightly converging, about twice as long as maximum width; inner margin with a spinular row, furnished with 7 setae; anterolateral accessory seta (I) smallest, anterolateral (II) and posterolateral (III) setae plumose and accompanied with some spinules at the base, outer terminal seta (IV) plumose and confluent at base with the strongly developed inner terminal seta (V), terminal accessory seta (VI) also strongly developed and having some spinules at the base, dorsal seta (VII) small and smooth.

Antennula (Fig. 2-A) indistinctly 14-segmented, segmentary boundaries not clearly defined in the middle part; first segment strongly developed, nearly as long as the remaining segments combined, furnished with some spinular rows in the proximal half and 2 setae in the distal half; 2nd segment partially subdivided along the inner rim and having 2 setae; 3rd and 4th segments with 1 seta each; 5th one with 4 slender setae; 6th

through 9th segments not totally separated from each other dorsally and provided with 1, 0, 1 and a long, probably sensory seta with a basally fused aesthetasc, respectively; 10th and 11th segments very small and having 1 seta each; 12th one bare; 13th segment with 2 setae; 14th having 6 slender setae and a minute hook shaped process at the tip.

Antenna (Fig. 3-E). Coxa not well developed. Basis strongly developed and armed with several spinular rows. Exopodite 7-segmented; 3rd-6th segments smallest; 7th segment with some minute spinules, 1 small and 3 long setae distally; other segments with 1 inner seta each. Endopodite 3-segmented; proximal segment with 1 inner seta; middle segment with an oblique spinular row and 4 slender setae; distal segment as long as preceding ones combined, furnished with 7 slender setae distally.

Mandible (Fig. 2-B). Gnathobasis with several sharp teeth. Basis with several spinular rows and 1 inner seta. Exopodite indistinctly 5-segmented; first segment bare and fused with 2nd one along posterior side; segments 2 and 3 with 1 seta each; 4th segment along anterior side not clearly separated from 5th and bearing 1 seta; 5th segment with 3 distal setae. Endopodite 2-segmented; first segment shortest and having 3 inner setae; distal segment with 7 setae along anterior edge.

Maxillula (Fig. 2-C). Praecoxxa with well developed non-articulating endite (arthrite) having 9 strong spines. Coxa with 1 strong claw, 3 slender setae and a spinular row at the subcylindrical endite. Basis with 2 setose lobes; proximal lobe with some minute spinules and 3 setae; distal lobe with 3 setae. Endopodite unisegmented, furnished with 4 lateral and 5 terminal setae. Exopodite unisegmented, outer side spinulose, having 3 slender setae distally.

Maxilla (Fig. 3-F). Syncoxa with 3 endites; proximal endite with 3 setae and not clearly defined; middle and distal endites subcylindrical and with 2 setae each. Basis forming a long endite, furnished with 1 seta at base, 1 seta along both proximal and distal lateral margins and 1 strong claw and 1 seta distally. Endopodite 3-segmented; proximal and middle segments bearing a strong claw and a slender seta each; distal segment with 1 claw and 3 slender setae.

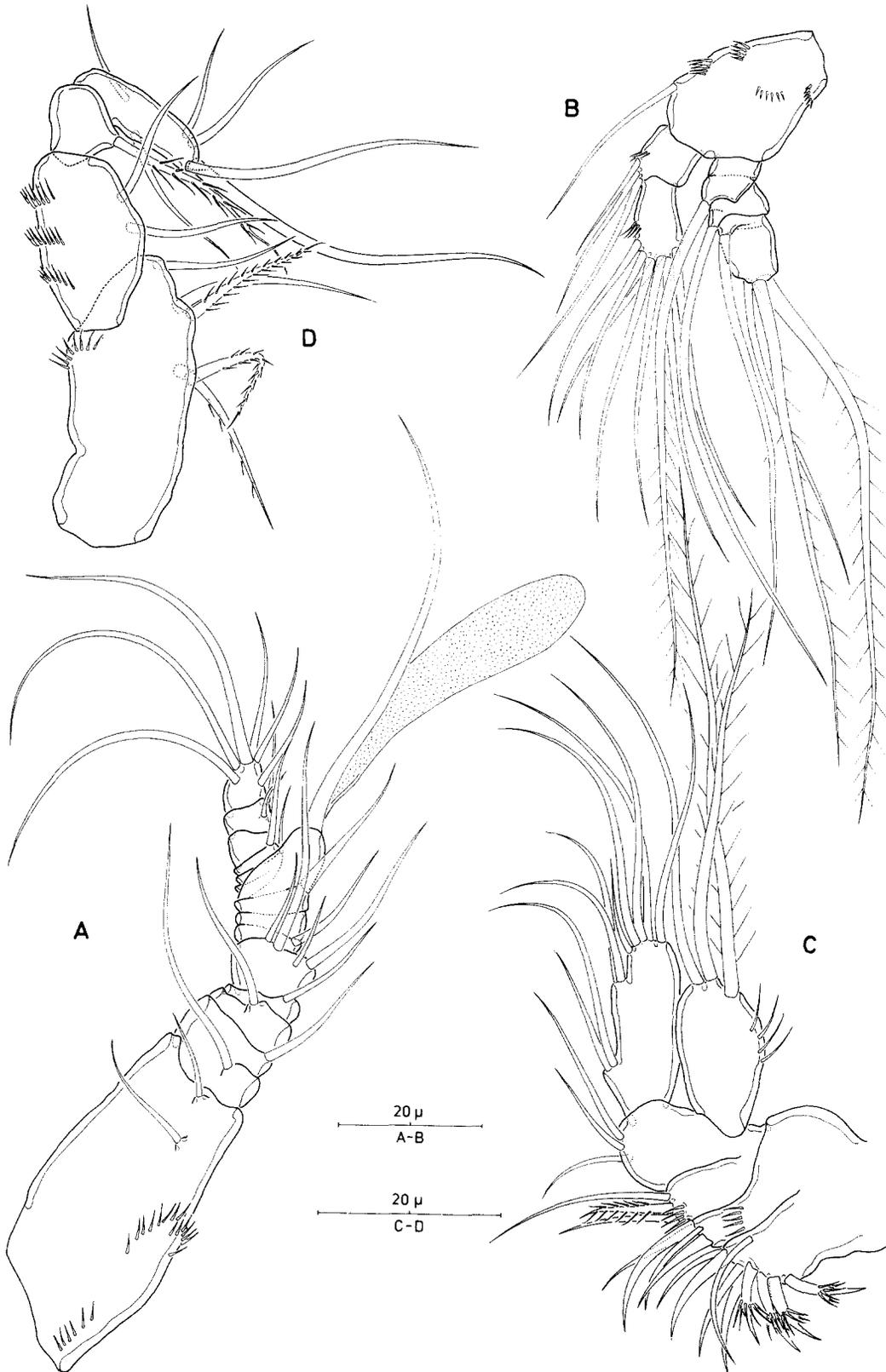


Fig. 2. *Gelyella droguei*. A. Antennula, female; B. Mandibular palp; C. Maxillula; D. Maxilliped.

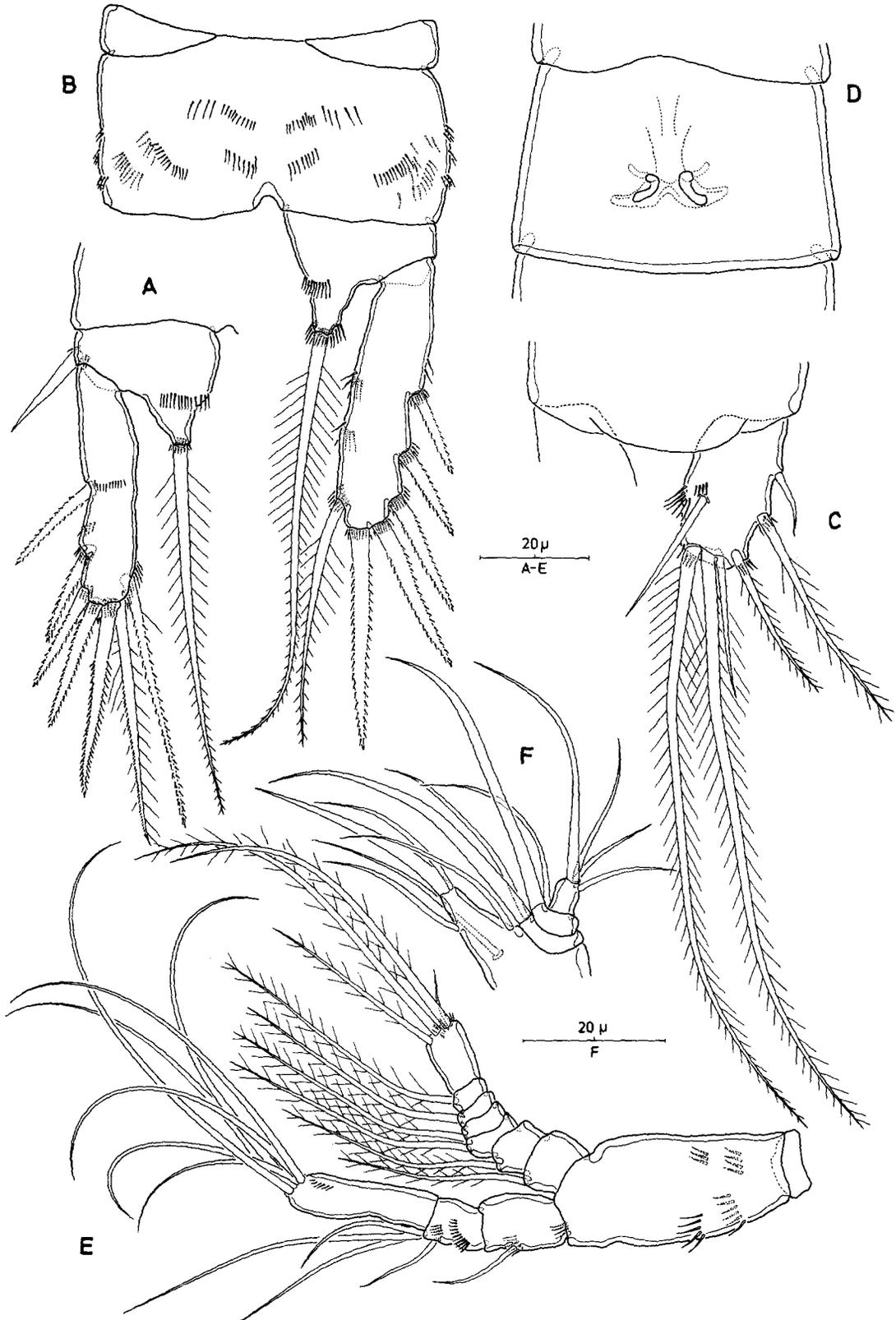


Fig. 3. *Gelyella droguei*. A. P2, female; B. P3, female; C. Caudal ramus, dorsal side; D. Genital double-somite, ventral; E. Antenna; F. Basis and endopodite of maxilla.

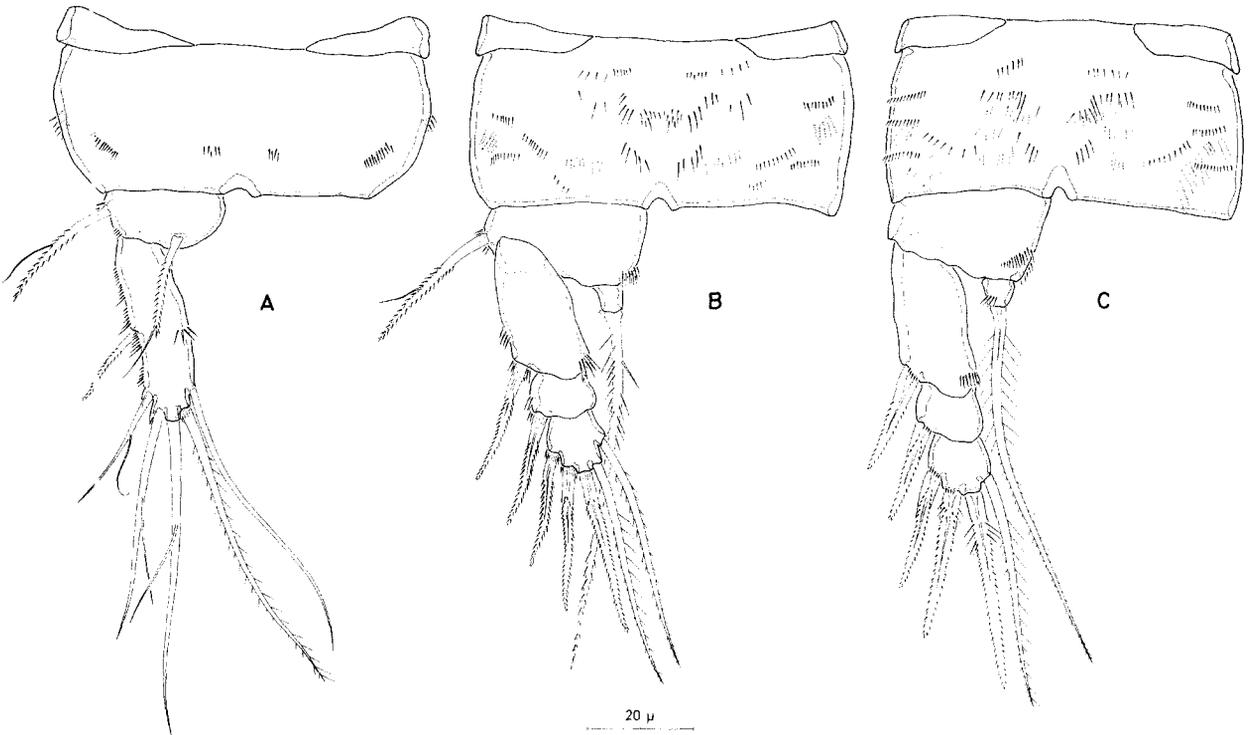


Fig. 4. *Gelyella droguei*. A. P1; B. P2, male; C. P3, male.

Maxilliped (Fig. 2-D). Stenopodial, cyclopoid-like, slender. Praecoxa and coxa completely fused into large syncoxa having 3 plumose and 2 smooth setae along the inner margin. Basis with several spinular rows at the outer side and 2

slender inner setae. Endopodite 2-segmented; proximal segment forming a small process with a plumose seta; distal segment longest and bearing 6 setae.

Labrum unarmed.

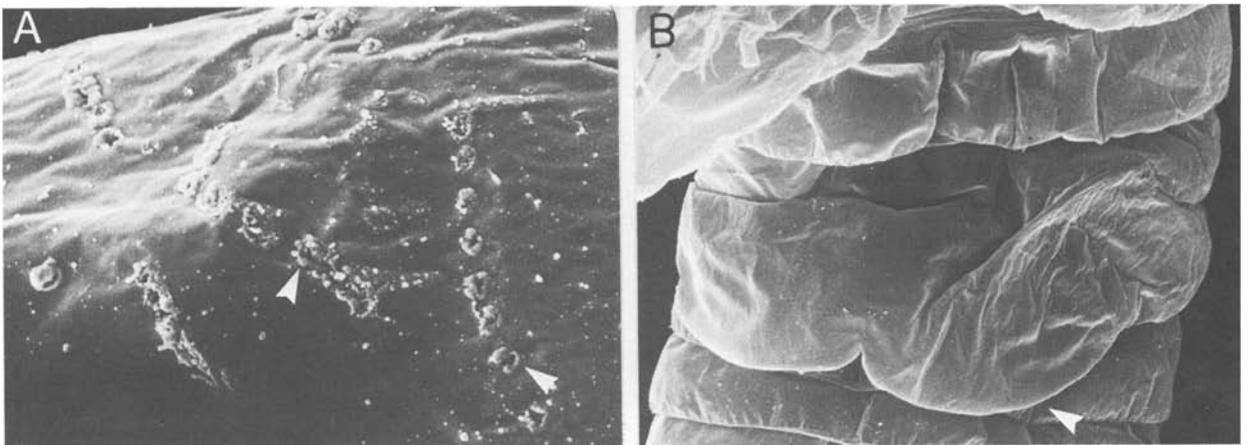


Fig. 5. *Gelyella droguei* (SEM-photography). A. Pore pattern on male anal somite; B. Fifth and sixth free thoracic somites of male, ventral side (arrow indicating P6)

Swimming legs fairly reduced; 4th and 5th pair of legs totally absent. Praecoxa of P1-P3 a small triangular plate at the outer proximal corner; coxae of both sides fused into a broad plate with several rows of diminutive spinules but devoid of setae; intercoxal plate (coupler) absent.

P1 (Fig. 4-A). Outer spine of basis bipinnate and having a long flagellum at about middle edge. Exopodite unisegmented; outer margin spinulose and furnished with a bipinnate spine; distal part forming 2 hook shaped processes and bearing 5 setae, of which the 3 outer ones have a flagellum. Endopodite represented as a flagellum-bearing bipinnate spine.

P2 (Fig. 3-A). Basis confluent with unisegmented endopodite; provided with a strong outer spine. Exopodite unisegmented, having 2 hook shaped processes and 7 setae. Endopodite small, not defined at base and with a long plumose distal seta.

P3 (Fig. 3-B). Basis confluent with unisegmented endopodite; devoid of outer spine. Exopodite unisegmented and bearing 6 spines. Endopodite as in P2.

MALE (Fig. 1-A). Body length 325–340 μm ($n = 3$) rostrum and caudal rami included, 305–332 μm ($n = 3$) rostrum and caudal rami excluded. General body shape and ornamentation as in female. Sexual dimorphism in antennula, P2, P3, P6, anal somite and in genital segmentation.

Abdominal somites 1–3 short. Anal somite provided with several characteristic pores which are arranged in rows both laterally and ventrolaterally (Fig. 5-A). Two spermatophores.

Antennula (Fig. 1-D). 13-segmented, geniculate between 11th and 12th segments; first segment largest, with several spinules and 1 seta; 2nd segment not totally separated from preceding one, furnished with 1 seta; 3rd segment having 2 setae and partially subdivided along the inner rim; 4th–6th segments small and bearing 0, 1 and 3 setae, respectively; 7th segment smallest and furnished with 1 seta; 8th segment with 1 lateral seta and forming into a distinct process with a probably sensory seta and a long aesthetasc at the top; 9th–10th segments with 1 seta each; 11th seg-

ments armed with a short bipinnate spine and a spiniform seta; 12th segment with 1 spiniform seta and 1 slender seta; last segment bearing 4 slender setae at the distal edge and a strong hook shaped process which is swollen at the basis.

Other mouthparts and P1 exactly the same as in female.

P2 (Fig. 4-B). Praecoxa and fused coxae as in female; no coupler. Basis with a flagellum-bearing outer spine and some spinules along the inner margin. Exopodite 3-segmented; proximal segment longest and having a bipinnate spine; middle segment shortest with 1 bipinnate spine; 3rd segment with 2 outer spines, 1 distal spine and 2 inner setae. Endopodite unisegmented and defined at the base; furnished with a long slender seta distally.

P3 (fig. 4-C). Praecoxa and fused coxae as in female; no coupler. Basis without outer spine; furnished with some spinules along inner edge. Exopodite 3-segmented; proximal and middle segments as in P2; distal segment with 2 outer spines, 1 distal spine and 1 inner seta. Endopodite as in preceding leg.

P4-P5 totally absent.

P6 (Fig. 5-B) on either side represented (?) as a small protruding lobe without setae or spinules.

Discussion

The unusual bodyplan of the gelyellids, with a unique combination of plesiomorphies and advanced characters, has led most workers to regard the family as ancient or as a missing link between the 'Polyarthra' and the 'Oligoarthra'. Although I consider that they have been a separated group long enough to obscure a great deal of their relationships with other copepods, there is no positive evidence to support this interpretation. Gelyellids are placed between the 'Polyarthra' and the 'Oligoarthra' merely for want of exact knowledge where to place them.

Gelyellidae possess (1) an antenna with a 7-segmented exopodite and a 3-segmented endopodite, and (2) a primitive mandibular palp with a 2-segmented endopodite. These are characters exclud-

ing *Gelyella* from the 'Oligoarthra'. On the contrary, they have lost the inner coxal spine on the swimming legs and the coxal epipodite of the maxillula. Furthermore, the exopodite of the mandibular palp is 5-segmented whilst it is unisegmented in the Canuellidae and in *Longipedia*. All these features exclude the Gelyellidae from the 'Polyarthra'.

For these reasons it is not surprising that gelyellids are invoked several times as models for the missing link between the 'Polyarthra' and the 'Oligoarthra' (Rouch & Lescher-Moutoué, 1977; Wells, 1979; Moeschler & Rouch, in press) whilst other workers (e.g. Dussart, 1984) simply ignored them in their phylogenetic trees.

Bowman & Abele (1982) – in their recent classification of the Crustacea – considered the Gelyellidae to be an infraorder incerta sedis and gave it equal status to Lang's (1948) higher 'oligoarthran' categories, viz. Maxillipedasphalea, Exanechentera and Podogennonta.

Por (1984) suggested that the Gelyellidae diverged from the general harpacticoid stem after the split off of the Cerviniidae because the abdominal muscles do not penetrate the last abdominal somite. In my opinion the phylogenetic significance of these muscles is exaggerated in Por's (1984) system. Moeschler & Rouch (in press) state that such abdominal muscles are present in the anal somite of *G. monardi*. Furthermore, in Mormonilloida (Boxshall, 1985) and in many 'oligoarthran' families (Huys, unpubl.) and some calanoids (Huys, unpubl.), the ventral abdominal muscles extend into the last abdominal somite. The presence or absence of ventral muscles in the anal somite should therefore be used with caution in constructing phylogenetic schemes.

Both Rouch & Lescher-Moutoué (1977) and Moeschler & Rouch (in press) pointed out the striking similarity in certain characters between *Gelyella* and some Cerviniidae. There is certainly some resemblance between *Cerviniella* and *Gelyella*; both exhibit an analogous reduction of the swimming legs, but the resemblance does not include the mouthparts and must be due to convergence.

Moeschler & Rouch (in press) stated that the real number of antennular segments could not be detected with certainty due to the weak segmentary boundaries. In their description of *G. droguei* Rouch & Lescher-Moutoué (1977) figured 5 segments for the female and 9 for the male and in both sexes the sole aesthetasc is located on the 4th segment. The same condition was found in *G. monardi*, although it appears that the constituent segments are not equivalent in both species. According to Moeschler & Rouch (in press) these differences indicate that the number of antennular segments in male *Gelyella* may have to be increased to 12. Interference microscopy revealed a 13-segmented condition in the male and 14 segments in the female. In Harpacticoida this number never exceeds 9 in the female and 11 in the male. Female harpacticoids typically have the proximalmost aesthetasc on the 4th segment (a few exceptions exist, e.g. some Canuellidae on the 3rd one). In *Gelyella* it is situated on the 9th segment. Gelyellidae have a haplocer antennula in the male with the aesthetasc standing on the 8th segment. In male harpacticoid antennules, when haplocer, the proximalmost aesthetasc is fixed at the same position as in the female, viz. the 4th segment.

Moeschler & Rouch (in press) had difficulties in determining the segmentation of the mandibular exopodite. Personal observations revealed a somewhat cryptic 5-segmented condition. This is also found in Calanoida, Platycopioida and some Misophrioida; harpacticoids have at most a 4-jointed exopodite in the mandible.

Gelyellids are reminiscent of the Cyclopoida in the detailed structure of the postantennular mouthparts (viz. antenna with elongated basis and 1 seta on proximal endopodite segment; maxillula with reduced epipodite and 1-segmented endopodite; stenopodial maxilliped with 2 setae on the basis). All these characters are shared by the Cyclopoida and related parasitic groups (Poecilostomatoida and Siphonostomatoida). This set of features is sufficiently complex that, unless contrary evidence were forthcoming, it constitutes a strong synapomorphic suite.

The Gelyellidae can be regarded as the group

standing closest to the ancestral form of this monophyletic cluster, because of the retention of the 7-segmented antennal exopodite in the adult. The genital double-somite without any trace of subdivision apparently evolved several times within this lineage. Whilst this character state seems to be the rule for the Gelyelloida, Siphonostomatoida and free-living Cyclopoida, fully separated genital segments are retained in some species of *Hemicyclops* (Humes, 1965) and most parasitic cyclopoids.

The Gelyellidae exhibit many unusual characters, for example the absence of an intercoxal coupler (interpodal bar) uniting the two members of the 1st-3rd pairs of swimming legs. In *Gelyella* the simultaneous beating of the left and right members of a leg pair is apparently determined by the fused coxae, which is unique among free-living copepods. The loss of the inner coxal spine is probably linked to this fusion. The loss of this spine in Mormonilloida and Platycopioida is probably due to convergence.

Somatic sensillae are present in members of all the orders examined (Calanoida, Mormonilloida, Misophrioida, Harpacticoida, Cyclopoida and Siphonostomatoida), yet are definitely absent in the Gelyellidae. Male *Gelyella* exhibit a unique pore pattern on the sides of the anal somite.

It needs further research to reveal the real nature of the paired ventral lobes of the 7th thoracic somite. If these structures turn out to represent the 6th pair of legs, the retention of the latter – though the 4th and 5th legs are wanting – can be regarded as a character of great phylogenetic significance. All podoplean groups, except for the Mormonilloida(?), have retained the sixth leg, regardless of the often drastic reductions of the other legs.

On the basis of the unusual, and in some cases unique characters of the Gelyellidae it is impossible to place them in one of the currently recognized copepod orders and it is therefore proposed to raise the family to ordinal level. The unique features combined with the generalised gnathostomous mouthparts indicate that the Gelyelloida *ordo nov.* have had a long evolutionary history, separated as an early offshoot of the main cyclo-

poid lineage, during which the exploitation of the freshwater environment of subterranean karstic systems took place.

The weakly defined major body articulation and segmentary boundaries of the antennula and mandibular exopodite, the small body size, the profound reduction of the swimming legs, the loss of P4 and P5, the less chitinized integument and the complete absence of somitic sensillae suggest a possible neotenic origin for the order.

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References

- Bowman, T. E. & L. Abele, 1982. Classification of recent Crustacea. In L. Abele (ed.), *The biology of Crustacea: Systematics, the fossil record, and biogeography*. Academic Press, NY, London 1: 1–27.
- Boxshall, G. A., 1985. The comparative anatomy of two copepods, a predatory calanoid and a particle-feeding mormonilloid. *Phil. Trans. r. Soc. London B311*: 303–377.
- Dussart, B., 1984. A propos du répertoire mondial des calanoides des eaux continentales. *Crustaceana Suppl. 7*: 25–31.
- Humes, A. G., 1965. New species of *Hemicyclops* (Copepoda, Cyclopoida) from Madagascar. *Bull. Mus. comp. Zool. Harv.* 134: 159–259.
- Huys, R., 1988. A redescription of the presumed associated *Caligopsyllus primus* Kunz, 1975 (Harpacticoida, Para-

- mesochridae, Paramesochrinae) with emphasis on its phylogenetic affinity with Apodopsyllus Kunz, 1962. *Hydrobiologia*, 162: 3-19.
- Lang, K., 1948. *Monographie der Harpacticiden*. Håkan Ohlsson, Lund, 1682 pp.
- Lang, K., 1965. Copepoda Harpacticoidea from the Californian Pacific coast. *K. svenska Vetensk Akad. Handl.* 10: 1-560.
- Mielke, W., 1984. Some remarks on the mandible of the Harpacticoida (Copepoda). *Crustaceana* 46: 257-260.
- Moeschler, P. & R. Rouch, in press. Découverte d'un nouveau représentant de la famille des Gelyellidae (Copepoda, Harpacticoida) dans les eaux souterraines de Suisse. *Crustaceana*, in press.
- Por, F. D., 1984. Canuellidae Lang (Harpacticoida, Polyarthra) and the ancestry of the Copepoda. *Crustaceana Suppl.* 7: 1-24.
- Rouch, R. & F. Lescher-Moutoué, 1977. *Gelyella droguei* n.g. n.sp., curieux harpacticide des eaux souterraines continentales de la nouvelle famille des Gelyellidae. *Annls. Limnol.* 13: 1-14.
- Wells, J. B. J., 1979. Keys to aid in the identification of marine harpacticoid copepods. *Amendment Bulletin No. 2. Zool. Publ. Victoria Univ. Wellington* 73: 1-8.