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A Review of the Genus Cavernocypris Hartmann (Ostracoda, Cypridopsinae): Systematics, Ecology and Biogeography

by

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Abstract: The genus *Cavernocypris* Hartmann, 1964 is revised. *Cavernocypris lindbergi* Hartmann, 1964 is shown to be synonymous with *Cavernocypris subterranea* (Wolf), which is the type-species of the genus. *Cypridopsis shadini* Akatova, 1950 and *Cypridopsis coreana* McKenzie, 1972 are transferred into the genus *Cavernocypris* (these are two new combinations). *Cavernocypris shadini* nov. comb. is shown to be synonymous with *Cavernocypris subterranea.* A new species, *Cavernocypris wardi* n. sp. from Colorado, USA, is described. The descriptions of *C. subterranea* and *C. coreana* are completed. The genus *Cavernocypris* at present includes three species: *Cavernocypris subterranea* (Wolf, 1920), *Cavernocypris coreana* (McKenzie, 1972) nov. comb. and *C. wardi* n.sp. The phylogenetic relationships between the three species are discussed. *C. coreana* seems to be the most primitive.

Data on the ecology of the three species are presented. The *Cavernocypris* species show a preference for oligotrophic, slow-flowing, cold waters; they actively colonize subsurface habitats: the interstitial milieu of riverbed sediments, springs and caves. The species are shown to have several preadaptive morphological characters (e.g. the carapace shape, the reduced carapace size and reduced antennal natatory setae) for colonization of the subterranean habitats. The biogeographic data lead the authors to hypothesize that the *Cavernocypris* species migrated into subsurface waters many times, independently forming subterranean populations.

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1. INTRODUCTION

The Cypridopsinae Kaufmann, 1900 is one of the most common group of freshwater ostracods living on all the continents. Unfortunately the systematics of this group is only poorly understood and therefore the taxonomic

identifications are very difficult. Thorough morphological and phylogenetic studies are lacking for most of the Cypridopsinae genera. During the last 50 years the ostracodologists accepted the idea that within the Cypridopsinae many morphological characters belonging both to the carapace and the limbs are conservative and offer few opportunities for a fine taxonomic analysis. This is why such a genus like *Cypridopsis* Brady, 1867 sensu lato is an enormous group comprising species from all the continents and from various types of environments which obviously belong to different evolutive lineages. A careful morphological analysis of the genus *Potamocypris* Brady, 1870 and part part of the genus *Cypridopsis* s.str. has clearly demonstrated that is possible to differentiate species using both fine details of the carapace and of the appendages (Meisch, 1984, 1985 and 1989).

In the present paper we carefully analyse the morphology, the ecology and biogeography of the species of the genus *Cavernocypris* Hartmann, 1964. This will allow us to reconstruct a phylogenetic lineage called *Cavernocypris* that we shall follow in time and space. This study will be of interest not only for the specialized ostracod taxonomists but also for those working on the general problem of the origin of the subterranean aquatic fauna. Each of the three *Cavernocypris* species occurs in subsurface habitats. From our study on functional morphology as well as from present day and past ecological and geographical distributions one can reconstruct why and how representatives of this phyletic lineage colonized various subterranean habitats.

At present there is an active debate about the origin of the hypogean dwellers within the scientific community dealing with the subterranean fauna. Are most of the troglobites relics of an old and specialized epigean fauna which took refuge underground at various periods of time or do they represent expansive epigean species which actively colonized the underground milieu (for a review see Rouch & Danielopol, 1987)?

Because species of *Cavernocypris* are widely and abundantly distributed -e.g. *C. subterranea* (Wolf) commonly occurs in Central and Western Europe, other species are known from Asia and North America - one can use these species for experimental work in evolutionary studies. For such investigations it is always necessary, as a prerequisite, to have good morphological descriptions, a precise taxonomy, a good knowledge of the ecology and the biogeography of the various representatives of a phyletic group. The present paper should, at least partly, contribute to these aims. In the longer term our review should stimulate other students to continue the investigation on Cypridopsinae and particularly on the *Cavernocypris* group.

2. MATERIAL

From 1981 to 1983, during several stays at the Limnological Institute of Mondsee (Austria), one of us (P.M.) examined very numerous specimens of *Cavernocypris subterranea* collected by G. Bretschko near Lunz am See (Austria) during an ecological survey study of an alpine brook. The same author (P.M.) provided specimens collected by D. Barthélémy, J. Gibert and

Ph. Vervier in several springs in the French Jura mountains. One of us (C.M.) provided several samples from the W. Klie collection (deposited in ZMH): (a) two samples from springs in Germany (near Bad Pyrmont, leg. W. Klie, see Klie 1925, 1927 and 1938), (b) one sample from France (near Nancy, leg. R. Dolbec, see Dolbec 1947), (c) one sample from Belgium (near Néblon, leg. Leruth, see Leruth 1939) and (d) one sample from Poland (Silesia, at 'Reyersdorf', leg. Stammer). The same author provided the type-material of *C. lindbergi* from Afghanistan (Hartmann collection, deposited in ZMH). The British Museum (Nat. Hist.) provided one of us (D.L.D.) with material of *C. coreana* collected in two caves in South Korea. J. D. Ward (USA) sent us (D.L.D. and P.M.) to samples from Colorado (USA) of a hitherto not described *Cavernocypris* species. This species will be described herein as *Cavernocypris wardi* n. sp. Finally, Dr E. Pietrzeniuk sent one of us (D.L.D.) Holocene specimens of *C. subterranea* from Weimar (GDR). A detailed list of the material examined is given at the end of this work. After careful study of this material, we are able to revise the taxonomy of the genus and to give a contribution to the ecology, biogeography and evolutionary tendencies of the *Cavernocypris* lineage.

It should be noticed that the original material upon which Wolf (1920) described *C. subterranea* no longer exists (Dr Stocker, pers. comm. to D.L.D.). So the redescription presented here is based on specimens from Lunz/See in Austria. The sites where *C. subterranea* occurs permanently belong to the experimental field RITRODAT. It is therefore easy to have access to living specimens of *C. subterranea* at any time. The RITRODAT area at Lunz offers the unique opportunity of a better approach to the ecology of *C. subterranea* and in the future to continuing studies on this species.

3. SYSTEMATICS

Abbreviations used in the text: LV, RV = left valve and right valve; L = length; H = height; B = width; ZMH = Zoological Institute and Zoological Museum of the Univerity of Hamburg (D); ICZN = International Code of Zoological Nomenclature (1985); SEM = scanning electron microscope. The limb descriptions follow the model proposed by Broodbakker & Danielopol (1982). The description of the antenna of the male of *C. coreana* follows the model proposed by Martens (1987).

3-1. The present state of the Cypridopsinae taxonomy

Systematic position of the genus *Cavernocypris* Hartmann, 1964: Class Ostracoda Latreille, 1806 - Subclass Podocopa Müller, 1894 - Order Podocopida Sars, 1866 - Superfamily Cypridoidea Baird, 1845 - Family Cyprididae Baird, 1845 - Subfamily Cypridopsinae Kaufmann, 1900 - Tribe Cypridopsini Kaufm., 1900 with the genus *Cavernocypris* Hartmann, 1964.

The following is a brief description of the taxonomic history and diagnostic features of the Cypridopsinae.

The subfamily Cypridopsinae within the Cyprididae was created by Kaufmann (1900) for the former cypridid genera bearing reduced, flagellum-like furcal rami. The genus *Cypridopsis* Brady, 1867 was designated as the typical genus.

It was not until recently that Malz (1977) was able to add a carapace feature to Kaufmann's diagnosis of the Cypridopsinae: the anteroventral part of both valves of the cypridopsines shows an enlarged, crescent shaped fused marginal zone (see Malz 1977 for further explanations and figures). This feature now also allows to asssign fossil specimens without ambiguity to the Cypridopsinae. The known *Cavernocypris* species all share this cypridopsine feature (see figs 3A-C,E, 6A,B, 7A,B, 11A,B in this work).

Later on, the Cypridopsinae were raised to family rank (see for instance Hartmann & Puri 1974, Swain 1976, McKenzie 1982). According to McKenzie (1982) and De Deckker (1979b), the Cypridopsidae comprise the following three subfamilies:

(1) Cypridopsinae Kaufm., 1900 (with the genus *Cavernocypris*),
(2) Callistocypridinae Schornikov, 1980,
(3) Pseudocyprettinae Klie, 1932.

Nevertheless it should be noticed that De Deckker (1979a,b), who adopts the family Cypridopsidae, seriously doubts that the cypridopsids form a monophyletic lineage; and he states that if the Cypridopsidae are not monophyletic, then the Cypridopsinae should be reintegrated into the Cyprididae at subfamilial level. The same opinion is expressed by Martens (1985), who consequently rejects the family Cypridopsidae and reintegrates the Cypridopsinae within the Cyprididae at subfamilial level. The discussion on the classification problem of the Cypridopsidae-Cypridopsinae goes beyond the scope of this work. Nevertheless, as we favour the opinion expressed by De Deckker (1979a,b) and Martens (1985), we herein consider the Cypridopsinae as forming a subfamily within the Cyprididae.

At present, the following 13 living and 2 fossil genera are assigned to the Cypridopsinae (after McKenzie 1982 and Martens 1985, completed):

Cypridopsis s.str. Brady, 1867
Plesiocypridopsis Rome, 1965
Sarscypridopsis McKenzie, 1977
Kapcypridopsis McKenzie, 1977
Cavernocypris Hartmann, 1964
Potamocypris Brady, 1870
Zonocypris Müller, 1898
Neozonocypris Klie, 1944
Neocypridopsis Klie, 1940
Notiocypridopsis De Deckker, 1981
Austrocypridopsis McKenzie, 1982
Tanganyikacypridopsis Martens, 1985
Tungucypridopsis Victor, 1983
Curvopsis Malz, 1977
Cavernopsis Malz, 1977

The last two genera are only known from fossil records. Only the first four of these genera are of importance here and will be compared with *Cavernocypris*.

3-2. Diagnosis of the genus *Cavernocypris* Hartmann, 1964

The genus *Cavernocypris* was created by Hartmann (1964) for the cypridopsine species *Cavernocypris lindbergi* (this species will be shown to be a junior synonym of *Cavernocypris subterranea* in this work), collected in three caves in Afghanistan.

Cavernocypris subterranea was originally described by Wolf (1920) as belonging in the genus *Cypridopsis.* This can be understood if one bears in mind that the genus *Cypridopsis* until recently served to group most of the cypridopsine species bearing a cylindrical terminal joint on the maxillular palp (the species having this joint distally enlarged, i.e. spatula-like, are assigned to the genus *Potamocypris).* Later on, when it became clear that the *Cypridopsis* s.l. species in fact belong to different evolutionary lineages, McKenzie (1971 and 1977) proposed to split the genus into three separate genera - i.e. *Cypridopsis* s.str., *Plesiocypridopsis* (formerly introduced by Rome 1965 as a subgenus of *Cypridopsis)* and *Sarscypridopsis* - and introduced the new and related genus *Kapcypridopsis* (see McKenzie, 1977). On that date, *C. subterranea* still remained within the genus *Cypridopsis.* But more recently, Wouters (1983) became aware of the fact that *'Cypridopsis' subterranea* perfectly fits in the diagnosis of the genus *Cavernocypris* as given by Hartmann (1964) and he transferred the species into the genus *Cavernocypris.*

Diagnosis of the genus *Cavernocypris* Hartmann, 1964:
A genus with the characters of the Cyprididae - Cypridopsinae. LV bigger than RV. Ventral closure of the carapace: the LV overlaps the RV. Marginal zones of the valves: selvage peripheral (not displaced inwards) on the whole circumference of both valves; the anterior, posterior and ventral margin with a well developed fused zone, showing numerous and regularly disposed marginal pore canals. The inner lamella broad to very broad anteriorly and posteriorly; an inner list present on the ventral and ventroposterior end. The ventral marginal zone of both valves with a distinct outer list (see Fig. 1 E,F). Surface of valves smooth or with small pits. Carapace small (inferior to 0.80 mm), elongate in lateral view, the dorsal margin being distinctly arched.

Swimming setae of the antennae very short, scarcely extending beyond the proximal margin of the penultimate A2 joint. Distal joint of the maxillular palp cylindrical (not distally enlarged), 3rd masticatory lobe of the maxillule with 2 'Zahnborsten'. Respiratory plate of the maxilla reduced (with 2 to 4 filaments in the known species). Endopodite of the 1st thoracopod distinctly elongate. Seminiferous tubes of the male enrolled in a simple loop (not spirally enrolled) in the anterior part of the carapace (see Fig. 7 B). Furcal rami flagellum-like in the female, absent in the male.

Remark: the absence of the furcal rami in the male most probably is a common feature of all Cypridopsinae (for further information see Martens & Meisch, 1985).

The genus *Cavernocypris* now includes three species, one of which (*C. wardi* n. sp.) is described as new herein (see below). These species are: *C.*

subterranea (Wolf, 1920) Wouters, 1983, *C. coreana* (McKenzie, 1972) nov. comb. and *C. wardi* n. sp. (described below). A fourth species, *C. shadini* (Akatova, 1950), is most probably synonymous with *C. subterranea* (see below).

3-3. Redescription of *Cavernocypris subterranea* (Wolf, 1920)

The following redescription is based on the examination of female specimens collected in the interstitial underground waters of the Seebach, a brook near Lunz am See in Austria (leg. G. Bretschko). These specimens were then compared with material from (a) West Germany (springs near Bad Pyrmont, leg. W. Klie, see Klie 1925); (b) France (near Nancy, leg. R. Dolbec, Klie collection); (c) eastern France (several karstic springs in the Jura mountains, leg. J. Gibert, D. Barthélémy and Ph. Vervier). (See also the detailed list of the material examined at the end of this work).

Carapace in lateral view (Fig. 1 D) distinctly elongate, its height slightly less than half its length (H/L = 0.48 for LV; = 0.46 for RV).
Both valves subequal, the LV being slightly longer and higher than the RV. In dorsal view (Fig. 1 A-B, C), both ends nearly equally rounded, the LV extending beyond the RV anteriorly and posteriorly.
Ventral closure of the carapace: the LV overlaps ('embraces') the RV.
Ventral margin of both valves with an outer list (Fig. 1 E,F).
Marginal zones of the valves: selvage totally peripheral on both valves (a generic character); fused zone broad on the anterior and posterior marginal zone, very broad on the ventral margin, distinctly enlarged in the anteroventral part (this latter feature characterizes the whole cypridopsine group), with numerous regularly disposed marginal pore canals (Fig. 3 A,B). The ventral and posterior ventral marginal zone on both valves with a very weak inner list (Fig. 2 A-F); anteriorly and posteriorly the membraneous part of the inner lamella very broad on both valves (Fig. 2 A-H).
Surface of valves smooth, except for a central transverse band covered with small shallow pits. This pitted area may be reduced or even absent (Fig. 1 A-D).
The eye is small and with black pigment; it is present in both epigean and hypogean populations. Colour of carapace: whitish to yellowish.
Size: L = 695 μm ($\pm$ 17 μm; n = 24); H = 335 μm ($\pm$ 14 μm); B = 320 μm ($\pm$ 21 μm). Size limits of the specimens of the whole material examined: 0.58-0.72 mm.

Appendages: Antennula (A1) 7-jointed (Fig. 3 G): I: A - 1l (pl), P - 2l (pl) / II: A - 1m / III: A - 1m, P - 1s / IV: A - 2l, P - 2s / V: A - 2l, P - 1l - 1s / VI: A - 2l -1s (α), P - 2l / VII: D - 3l - y_a.
The 1st joint shows a transversal row of delicate setae. The Rome organ (2nd joint) is weakly developed. The posterior setae of the 2nd and 4th joints are shorter than the length of the 3rd joint. The aesthetasc y_a is 3.6 x longer than the 7th joint.

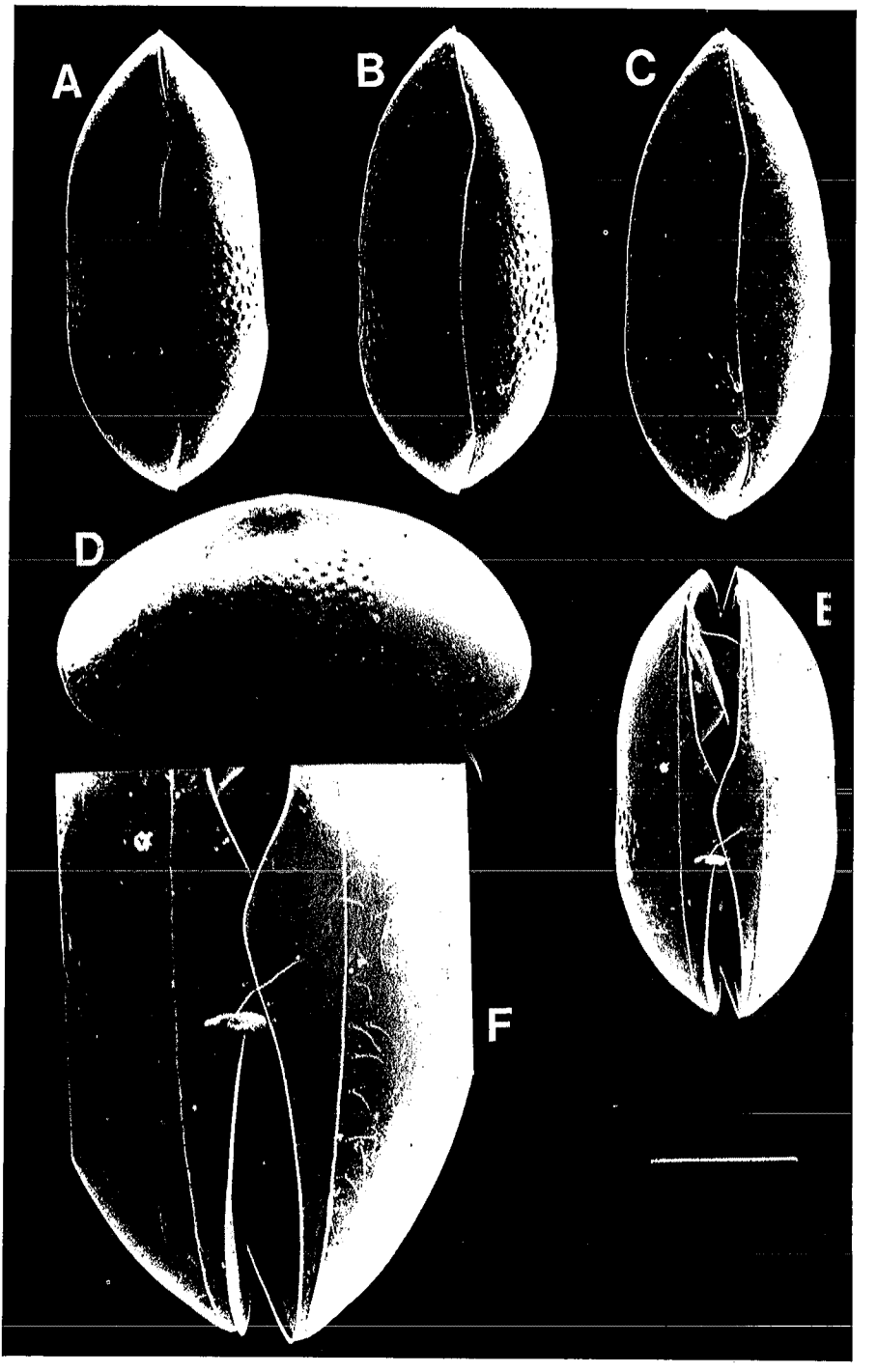


Fig. 1. - *Cavernocypris subterranea* (female). - A, B and C: carapace in dorsal view. D: carapace in lateral view. E: carapace in ventral view. F: posterior end of carapace in ventral view (detail of E). A and D-F from D-Bad Pyrmont (Klie collection, ZMH), B-C from A-Lunz. Scale: 0.20 mm for A-E, 0.09 mm for F.

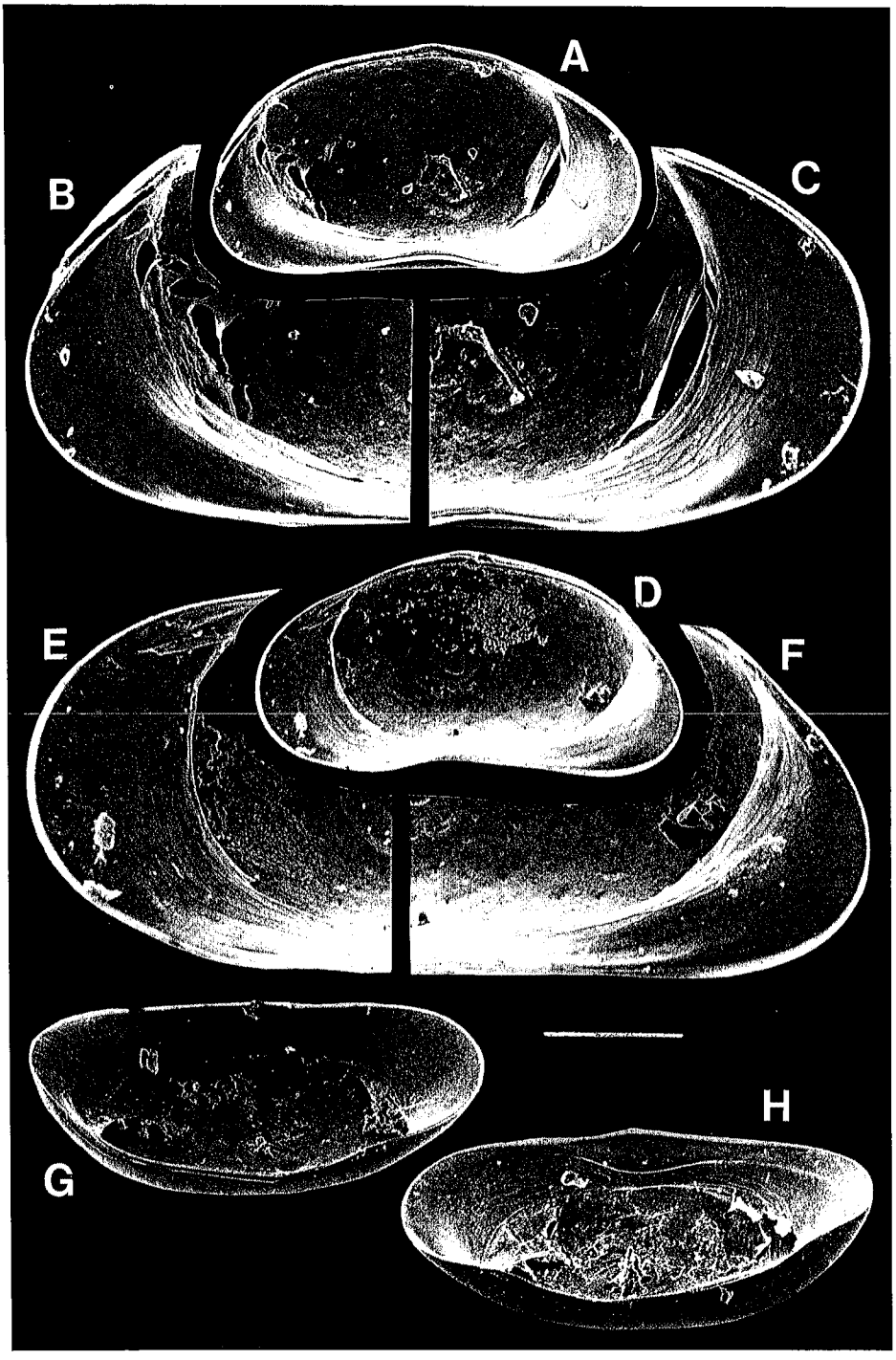


Fig. 2. - *Cavernocypris subterranea* (female). - A: left valve, inner view. B: posterior detail of A. C: anterior detail of A. D: right valve, inner view. E: anterior detail of A. F: posterior detail of A. G: right valve, inner inclined view. H: left valve, inner inclined view. A-F from D-Bad Pyrmont (Klie collection). G-H from A-Lunz. Scale: 0.20 mm for A,D,G,H; 0.12 mm for B,C,E,F.

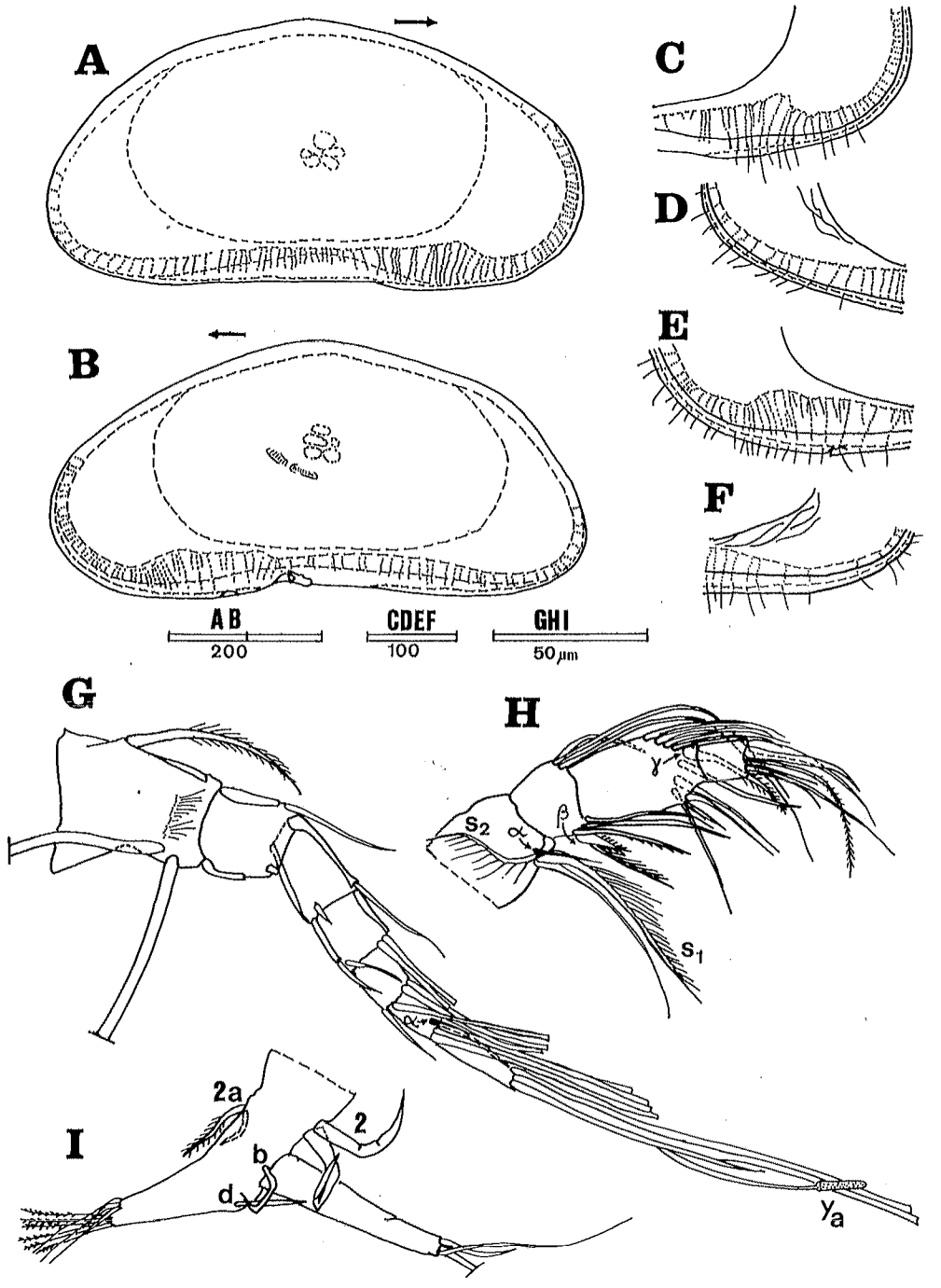


Fig. 3. - *Cavernocypris subterranea* (female, A-Lunz). - A: right valve, external view. B: left valve, external view. C,D: left valve, inner view, anteroventral (C) and posteroventral (D) margin. E,F: right valve, inner view, anteroventral (E) and posteroventral (F) margin. G: antennula. H: mandibular palp. I: maxilla.

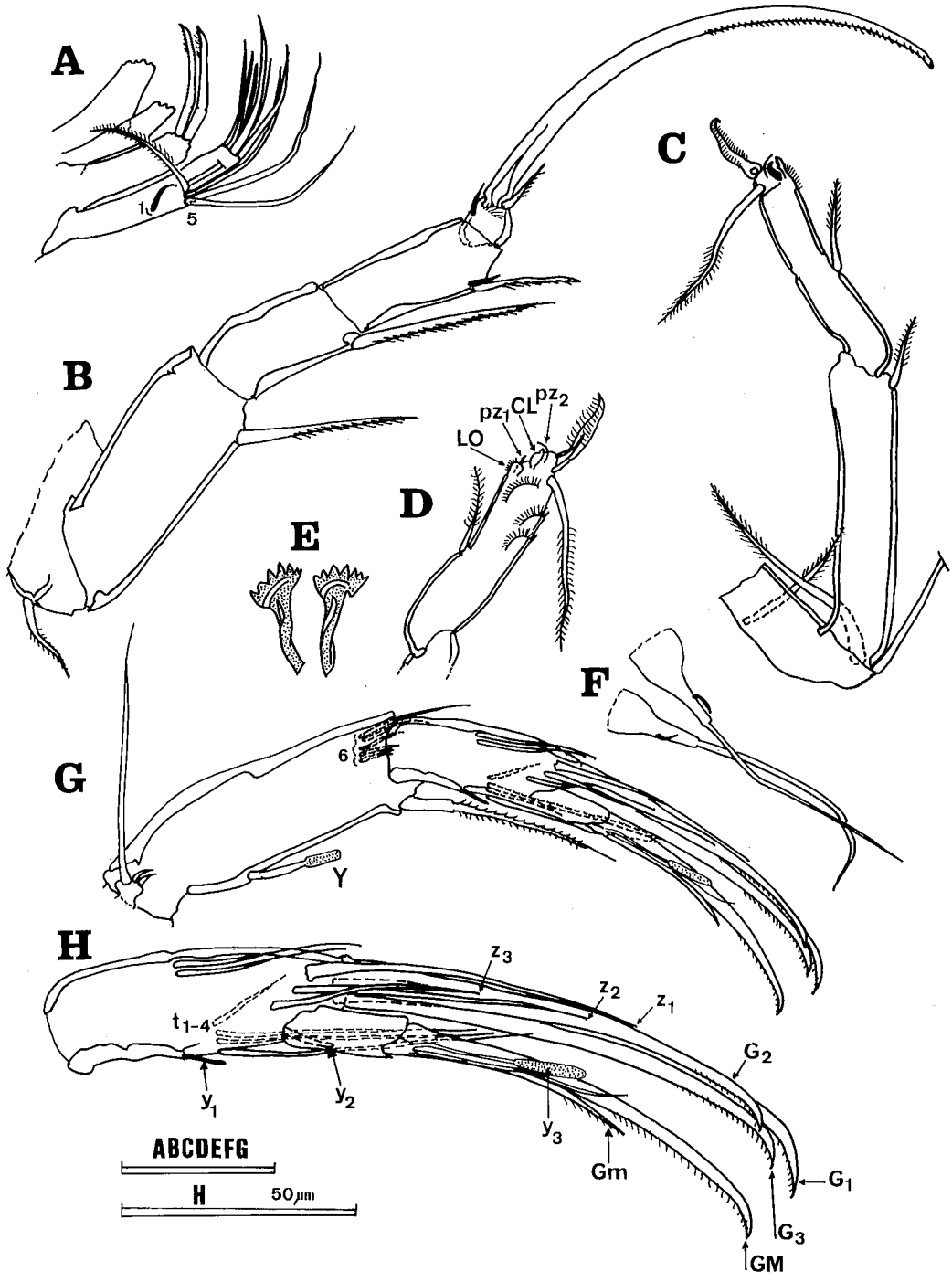


Fig. 4. - *Cavernocypris subterranea* (female, A-Lunz). - A: maxillula and maxillular palp. B: 1st thoracopod. C: 2nd thoracopod. D: detail of the distal part of the 2nd thoracopod. E: rake-like organs. F: furca. G: antenna. H: detail of the distal part of the antenna.

Antenna (A2) (Fig. 4 G,H). Pr: P - 1l / Exo: 1m - 2s / EI: A - 6s, P - Y - 1 m (pl) / EII + III: A - 2s, P - y_1 - 1s(t_4) - 3m($t_{1,2,3}$), D - y_2 - 1s(z_1) - 2m($z_{2,3}$) - 2m (G2,3: ser) - 1l (G1: ser) / EIV: D - 2m (GM et Gm: ser) - 1m - y_a.
The aesthetasc Y is relatively long for a cypridopsine; its length equals 33% of the length of EI. The natatory setae are very short; they scarcely extend beyond the proximal end of the next joint (EII-EIII); only the sixth seta reaches the middle of the next joint. The t and z setae are not modified. The claws G1, G2 and G3 are subequal, their length equalling respectively 106%, 93% and 96% of the length of the EI joint; all three of them are delicately serrate. The GM claw is quite long, it extends to the tip of the G1 claw and equals 84% of the length of the EI joint. The Gm claw is shorter (53% of the length of EI). GM and Gm are serrate. The aesthetasc y_3 is well developed (43% of the length of EI) and associated with a simple seta; its sensitive hyaline part is well developed (34% of its length).

Mandibular palp (Mdp) (Fig. 3 H). I: In - 1s (α) - Im - 1m (S1: pl) - 1m (S2: pl) / II: In - 3m - 1m (pl) - 1s (β), Ex - 3l / III: In - 2s, Ex - 4m, D - 3m - 1s (γ: pu) / IV: D - 2s - 2m - 2m(cs: pu).
The α seta is smooth, the β and γ setae are feathery. The three setae on the inner margin of the 2nd joint are smooth, the 4th is feathery.

Maxillular palp (Mxup) (Fig. 4 A): I: Ex - 1s - 1m (pu) - 4l (pu) / II: D -6m. The palp bears 6 setae (5+1) on the outer margin of the 1st joint.

Maxilla (Max) (Fig. 3 I): Pr: A - 2s (a and a'), In - 2s(d,b?) / Mastic: D - 9m / Exo: 2m(pl) / E: D - 2s - 1m. The exopodite of the maxilla bears 2 feathery branchial filaments.

First thoracopod (T1) (Fig. 4 B): Pr: A - 1s / EI: A - 1m (pl) / EII: A - 1m (pl) / EIII: A - 1s - 1s(pl) / EIV: P - 1s, D - 1s(pl) - 1l(G: ser). The distal claw is about 3x as long as the 2nd joint.

Second thoracopod (T2) (Fig. 4 C,D): Pr: P - 1s(pl), A - 2m(pl) / EI: P -1s(pl) / EII + EIII: P - 1s(pl) / EIV: P - 4s(LO, pz_1, pz_2), D - 1s(pl) - 1m(pl). The pincer organ is normal for a cypridopsid; it bears 2 well developed, serrate setae, a hairy lobe (LO) associated with a seta (pz_1) and a beaklike claw (CL) dorsally showing a small seta (pz_2); on the EII+EIII there are three series of very fine setae (called M1, M3 and M4).

Furca (Fu) (Fig. 4 F) strongly reduced, the proximal part bearing a short curved seta; the distal part is flagellum-like (a cypridopsine character).

The genital fold of the female bears several chitinised pieces. There is no copulatory hook.

Males unknown: parthenogenetic reproduction for all the different populations known at present.

Infraspecific variability

We would like to point out that the comparison, side by side, of the specimens from Lunz described above with those from Germany (springs near Bad-Pyrmont, leg. Klie), from France (springs of the southern Jura

mountains and a spring of Meurthe-et-Moselle) and from Afghanistan (type-specimens of *C. lindbergi)* did not reveal any difference justifying a taxonomic separation at sub-specific level.

Petkovski (1962) carefully described the subspecies *C. subterranea germanica* after specimens collected in East Germany. According to this author, the subspecies *germanica* differs from the nominal form:
(a) by the carapace form in dorsal view: both ends equally rounded in *C. subt. germanica*; anterior end somewhat sharply pointed and posterior end more rounded in the nominal form according to Wolf's original figure (but Wolf's drawing shows a carapace which is not totally closed!);
(b) the ornamentation of the valves: valves with central pits in the *germanica* form; valves smooth in the nominal form, relying on the fact that the pits are not mentioned in Wolf's original description.

After careful examination of our samples, we are able to point out that, ad (a): the dorsal view of perfectly closed carapaces of *C. subterranea* shows nearly equally rounded ends in all our specimens (see Fig. 1 A-C) and not, as shown on Wolf's original figure and as believed by Petkovski, a more rounded posterior end;
ad (b): the central pits on the valves are present in most of the specimens, but are missing in some of them (Fig. 1 C). As Wolf (1920) did not mention the presence of these pits in his original description, we must assume that he simply overlooked this character or that he examined specimens with smooth valves.

In conclusion: in our opinion, the establishment of the subspecies *germanica* is not justified. It should be noted that Löffler (1963) expressed the same opinion).

3-4. *Cavernocypris lindbergi* Hartmann, a junior synonym of *C. subterranea*

Hartmann's (1964) original description of *Cavernocypris lindbergi* was based on specimens collected in caves in Afghanistan. The type-material of the species is deposited in the Zoological Museum in Hamburg (reg. n. 27646, Hartmann collection). It comprises one glycerine tube including about 50 female specimens (most of them are juveniles, only some are adult females). The valves of these specimens are severely decalcified, but nevertheless the characteristic transverse pitted band is still recognizable. The examination of the type-specimens allowed one of us (C.M.) to confirm the detailed original description of the species, except for one character: contrary to Hartmann's statement, the type-specimens bear a flagellum-like furca (the furcal rami could be observed in 1 of 2 dissected specimens). It should be noted that the very reduced furca is easily lost during the dissection and that such a loss most probably explains the erroneous statement in the original description.

Furthermore, the careful examination of the type-specimens and their comparison side by side with our material belonging to *C. subterranea,*

showed that the *C. lindbergi* specimens share all the features (on the carapace and on the appendages) of *C. subterranea.* In conclusion, *C. lindbergi* has to be considered as being synonymous with *C. subterranea,* the latter being the senior synonym.

3-5. Synonymy of *Cavernocypris shadini* (Akatova, 1950) with *Cavernocypris subterranea* (Wolf)

The original description of *Cypridopsis shadini* Akatova, 1950 was based on specimens collected in the springs of a brook in the USSR, in the area of the Chozhambio kolkhoz in Tadjikistan, Central Asia. The original description suggests that the species belongs without any possible doubt in the genus *Cavernocypris (Cavernocypris shadini* nov. comb.). Furthermore, all the taxonomic characters, except two, are in perfect agreement with the description of *C. subterranea.* The two features which form exception are (1) the surface ornamentation of the valves: the valves are said to be smooth in *C. shadini.* But the pits may easily be overlooked and are not always present in *C. subterranea* (see above); (2) the penultimate joint of T1 (walking leg) is not divided in fig. 9:6 (Akatova, 1950, p. 104). But in the text (p. 104), which according to the ICZN has priority over the figure, this joint is explicitly said to be divided. Furthermore, it should be noticed that *C. shadini* and *C. subterranea* (as *C. lindbergi)* were both collected in Central Asia. This consideration too makes the synonymy between the two names very plausible.

We would like to conclude that the synonymy of *C. shadini* with *C. subterranea* is very likely. Nevertheless, it cannot be considered as being absolutely certain until confirmed later by the examination of the type-specimens (if they still exist) or of specimens coming from the type-locality.

3-6. *Cavernocypris coreana:* additional description

Cavernocypris coreana nov. comb. was described as *'Cypridopsis' coreana* by McKenzie (1972) after examination of specimens collected in several caves in South Korea. The author was aware that the species obviously does not belong in the genus *Cypridopsis* s.str., which fact he marked by the quotation-marks. He writes: "...I cannot assign them (i.e. the specimens) as yet with confidence to any other described cypridopsine genus". This genus is the genus *Cavernocypris.* The original description of the species by McKenzie (1972), as well as our own examination of part of the type-material shows that the species bears the generic features of the genus *Cavernocypris.*

The structure of the marginal zones of the valves of *C. coreana* comes very close to that of *C. subterranea.* Only one single difference can be seen (compare Figs 2 A-F and 5 A-F): on the posterior marginal zone, both valves show a distinct inner list (Fig. 5 A-F). This list is very weak or absent on the

posterior marginal zones of the valves of *C. subterranea* (Fig. 2 A-F). Concerning the chaetotaxy of the appendages and also the structure of the hemipenis, the following details can be added to the original description given by McKenzie (1972). This addition is based on the examination of 4 dissected specimens (2 males and 2 females) of *C. coreana elongata* deposited in the British Museum (Nat. Hist., reg. n. 1970-2-10-6). These specimens come from the Mosan-gul Cave, Kwansan-ri, South Korea, 25.4.1966.

The antennula (Fig. 7 C and 8 C) is 6-jointed, the 3rd joint is fused with the 4th; the chaetotaxy of these two joints is as in *C. subterranea.* Aesthetasc y_a long (5.5 X the length of the 7th joint). No apparent sexual dimorphism was noted.

The antenna (Fig. 6 G and 7 F) bears 5 + 1 short natatory setae, the longest being the 6th (sensitive) seta. Aesthetasc Y long (40% of the length of EI). For the female, the chaetotaxy of the 2nd and 3rd joint, with 'normal' t and z setae, is identical with that found in *C. subterranea.* The lengths of the G1, G2 and G3 claws equal respectively 120%, 107% and 113% of the length of EI; the GM and Gm claws equal respectively 92% and 40% of the length of EI. The aesthetasc y_3 is long, with 42% of the length of EI, its sensitive hyaline part being poorly developed (20% of its total length). The male has a reduced number of setae: only 2 't' setae and 2 'z' setae (the z_1 is claw-like and as long as G1). The G3 claw is reduced to a thin short seta.

Maxillular palp (Fig. 6 E and 7 D) with 6 (5+1) setae on the 1st joint.

Maxillar epipod (Fig. 8 E and 9 C,D) with 4 feathery branchial filaments (see Fig. 9 A-D for the maxillar endopods). The hemipenis (Fig. 9 H,I) is sub-triangular; lateral shield duck-head shaped, its length equalling 165% of the medial shield; the labyrinth is of the cypridopsine type; the distal part of the spermiductus with a semicircular loop; part 'e' bears a sclerotized ring and a distal plumose part. The 2 dissected males have Zenker organs with 12 whorls.

Besides the nominal form, *C. coreana coreana,* McKenzie (1972) described the subspecies *C. coreana elongata,* which differs by the following characters: the *elongata* subspecies is more elongate in lateral view (but the author reports that the population from one cave comprises intermediate specimens!); the *elongata* specimens are smaller (0.66 mm, 0.72 mm for the nominal form) and the Zenker organ of the males has only 6-8 whorls (8-9 in *C. coreana coreana).* Further studies will show if the distinction of two separate subspecies is justified or not.

3-7. *Cavernocypris wardi* n. sp.

Type-material: 18 specimens collected by pumping the interstitial groundwater of the South Platte River, Colorado (USA), at a depth of 0.50 m. See the description of the locality in Pennack & Ward (1986). Holotype: 1 dissected female specimen on a microscopic slide. Paratypes: 3 dissected female specimens and 13 adult and juvenile females preserved in alcohol.

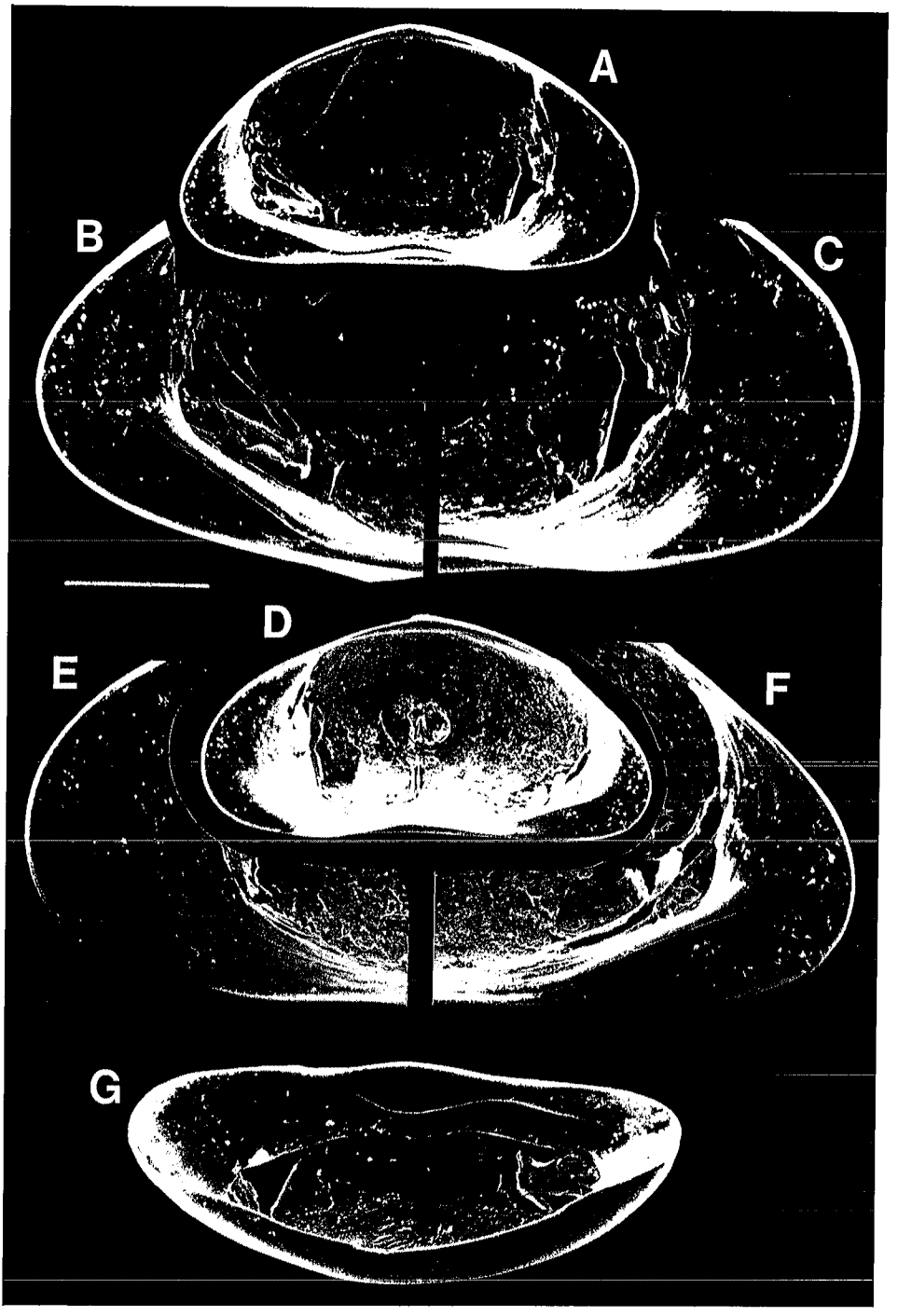


Fig. 5. - *Cavernocypris coreana elongata* (female, Kwansan-ri, South Korea). - A: left valve, inner view. B: left valve, posterior detail of A. C: left valve, anterior detail of A. D: right valve, inner view. E: right valve, anterior detail of D. F: right valve, posterior detail of E. G: left valve, inner inclined view. Scale: 0.20 mm for A,D; 0.10 mm for B,C,E,F; 0.16 mm for G.

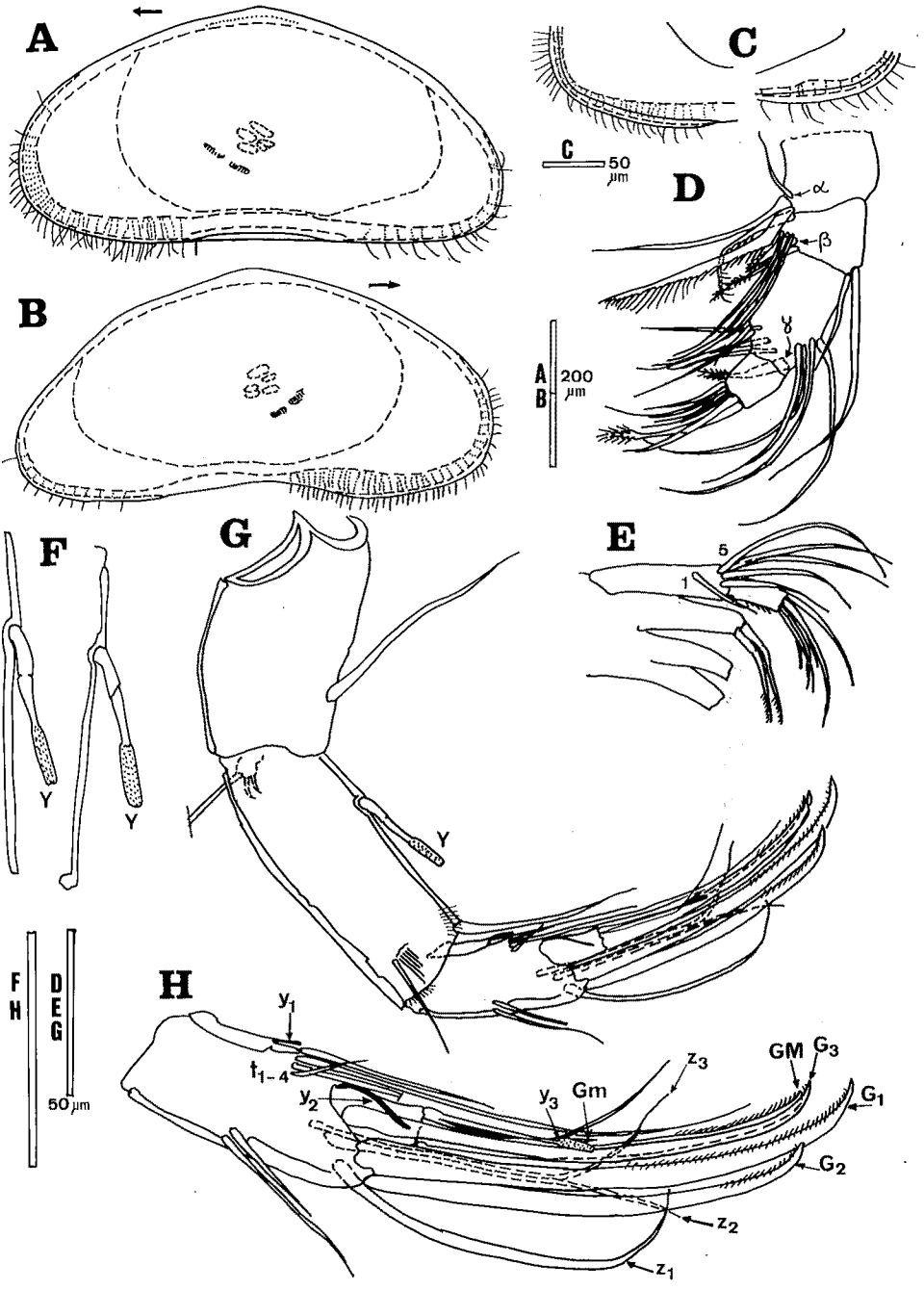


Fig. 6. - *Cavernocypris coreana elongata* (female, Kwansan-ri, South Korea). - A: left valve, external view. B: right valve, external view. C: right valve, anteroventral (left) and posteroventral (right) margin. D: mandibular palp. E: maxilla. F: aesthetasc Y (on A2). G: antenna. H: detail of the distal part of the antenna.

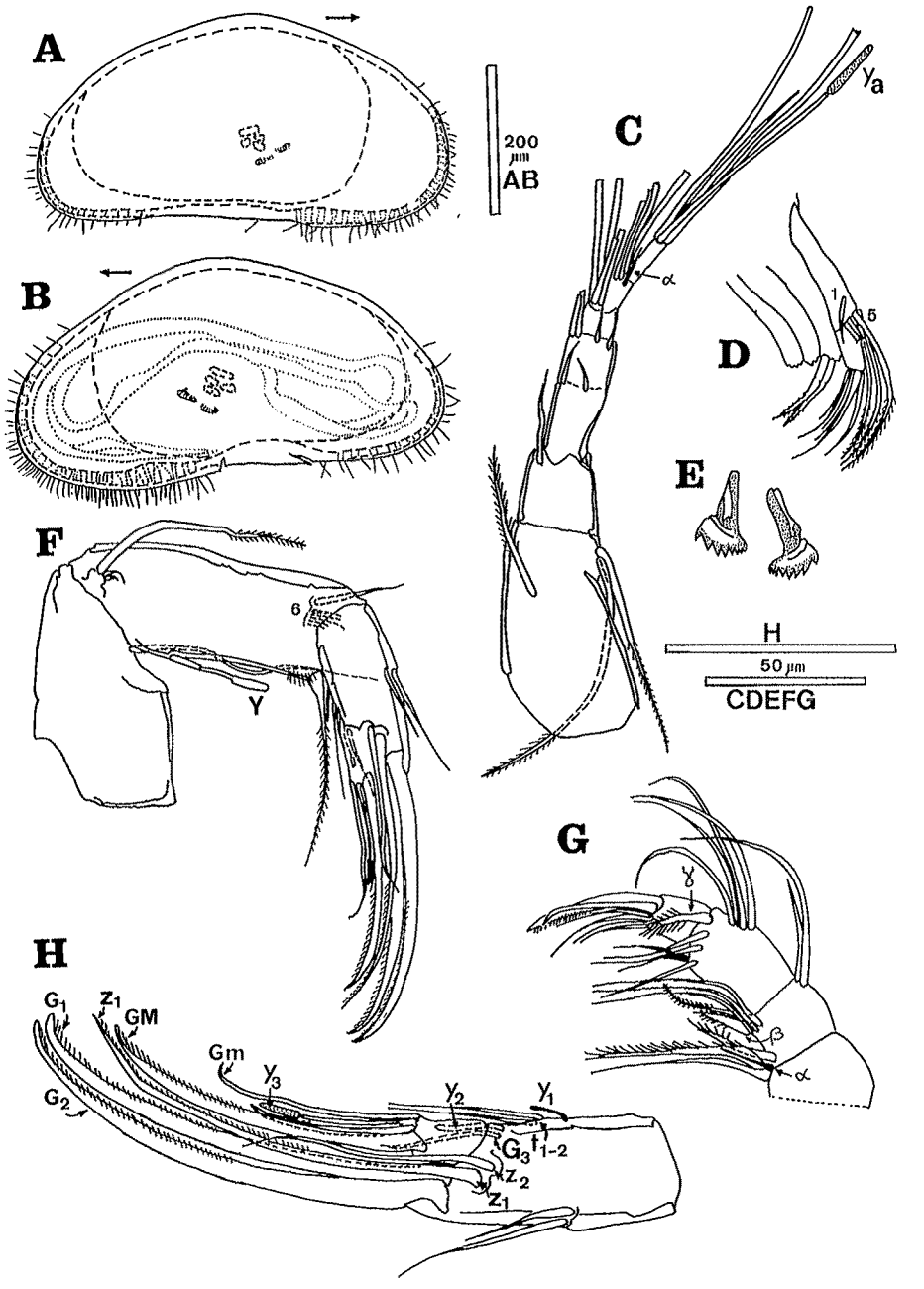


Fig. 7. - *Cavernocypris coreana elongata* (male, Kwansan-ri, South Korea). - A: right valve, external view. B: left valve, external view. C: antennula. D: maxillula. E: rake-like organs. F: antenna. G: mandibular palp. H: detail of the distal part of the antenna.

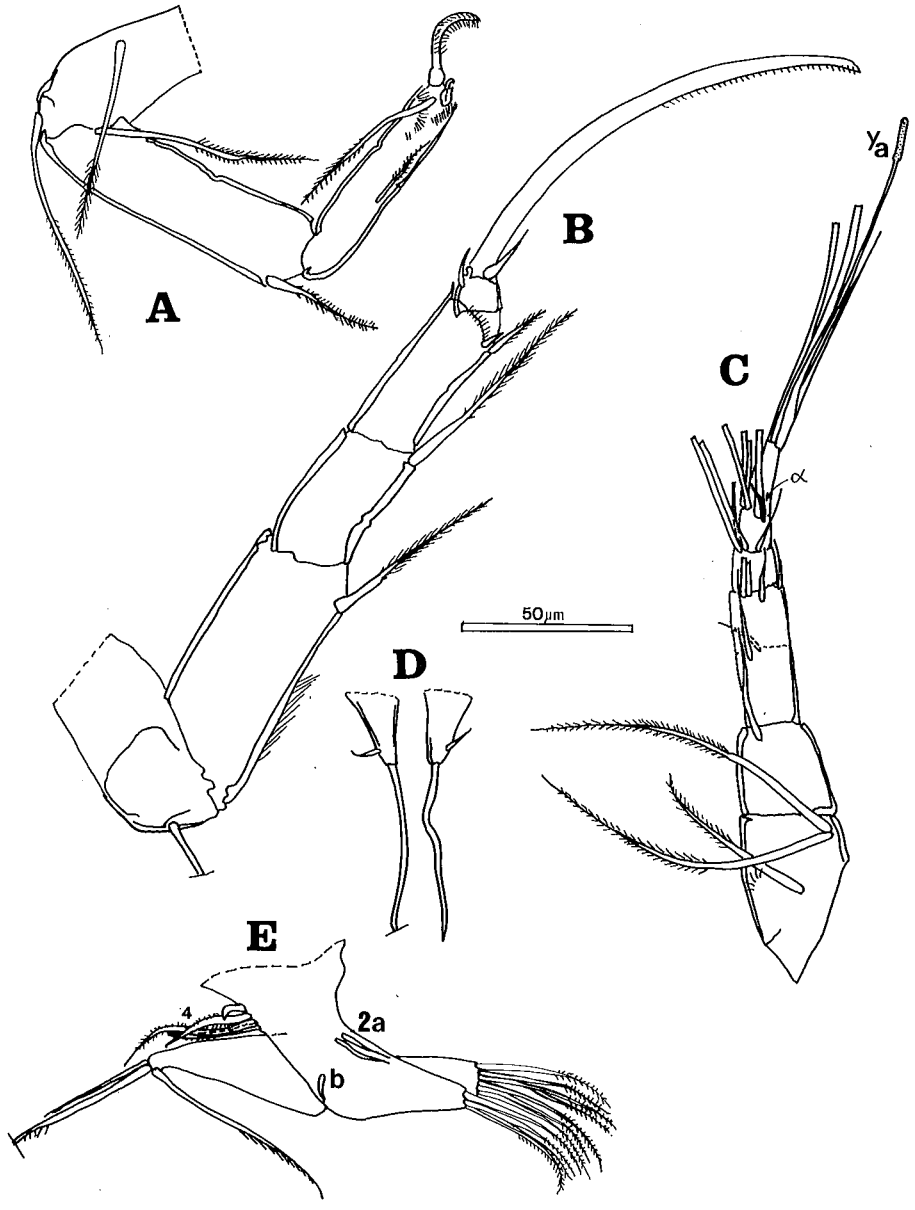


Fig. 8. - *Cavernocypris coreana elongata* (female, Kwansan-ri, South Korea). - A: 2nd thoracopod. B: 1st thoracopod. C: antennula. D: furca. E: maxilla.

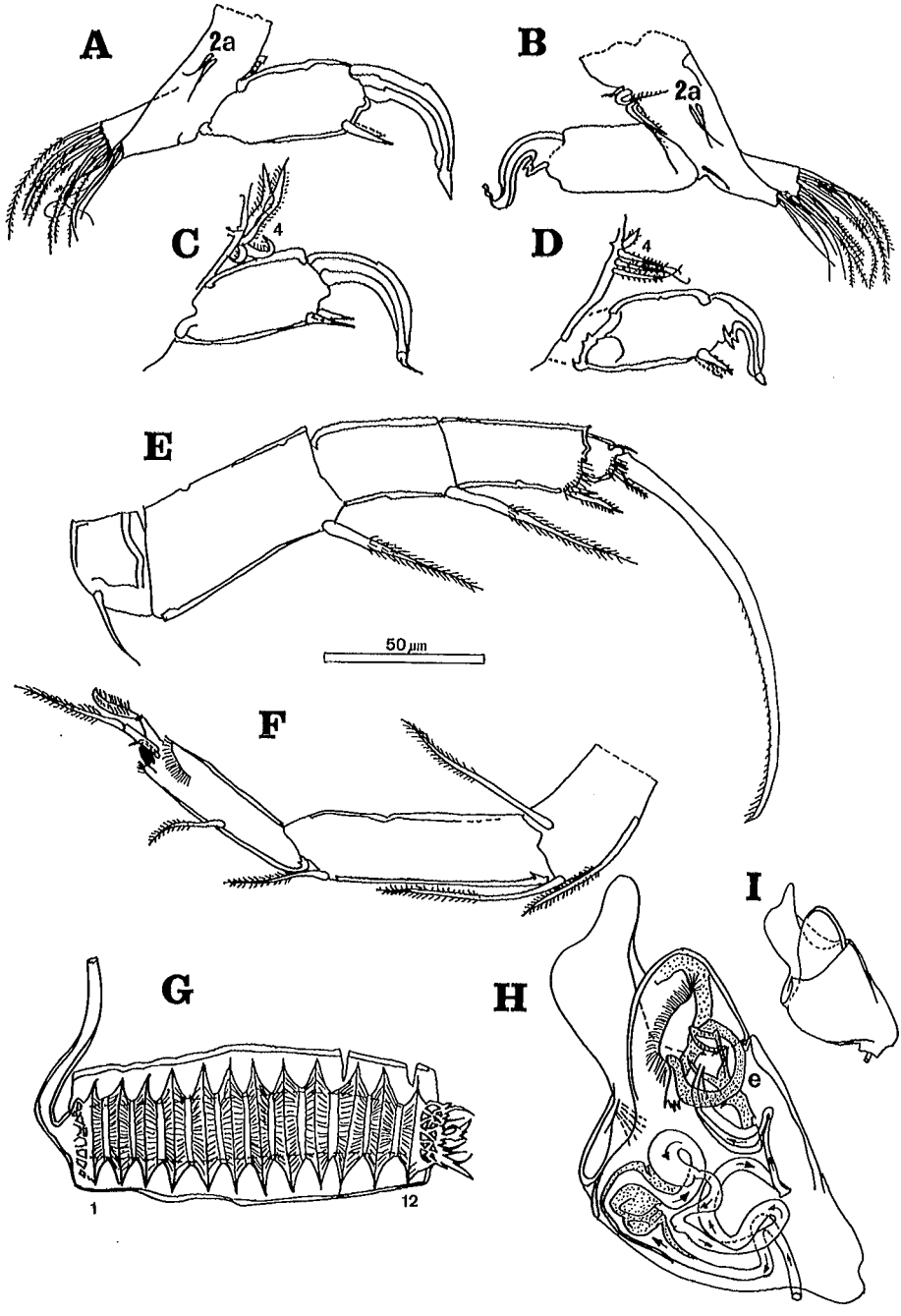


Fig. 9. - *Cavernocypris coreana elongata* (male, Kwansan-ri, South Korea). - A,B,C,D: maxillae of two different males (A,C: right prehensile organs, B,D: left prehensile organs). E: 1st thoracopod. F: 2nd thoracopod. G: Zenker organ. H: right hemipenis, inner view. I: right hemipenis, general shape.

The holotype and the paratypes will be deposited in the US National Museum for Natural History (Washington D.C.).

Type-locality: South Fork of the South Platte River (39° 5' 26"N and 105° 10"W), 46 km SSW of Denver, Colorado, USA. *C. wardi* n. sp. is hitherto only known from the type-locality.

Derivation of name: the species is dedicated to Dr James V. Ward, who collected the type-specimens.

Description

C a r a p a c e very similar to that of *C. subterranea,* but smaller (see below). The following differences are found (compare Figs 2 and 10): the posterior dorsal angle is less developed and the posterior margin is more evenly rounded in the present species. The anterior and posterior zone of both valves show a distinct inner list which joins the ventral and the dorsal margin.

Surface of valves smooth, of whitish to yellowish colour.
Size: LV: L= 530 μm; H = 260 μm; H/L = 0.49.
RV: L = 515 μm; H = 250 μm; H/L = 0.48.
B = 200 μm; B/L = 0.27 mm.

A p p e n d a g e s: A n t e n n u l a (A1; Fig. 11 E) 7 jointed. I: A - 1l (pl), P-2l (pl) / II: A - 1s / III: A - 1m, P - 1s / IV: A -2l, P -2s / V: A - 2l, P - 2m / VI: A - 2l -1s (α), P - 2l / VII: D -3l - y_a.
The chaetotaxy of the antennule is identical with that of *C. subterranea,* except for the second joint, on which the anterior seta is shorter in the new species (it does not reach the length of the 3rd joint) and the 5th joint, the 2 posterior setae of which are nearly of equal length (they slightly extend beyond the distal end of the 7th joint). The aesthetasc y_a is long (8x the length of the 7th joint).

A n t e n n a (A2; Fig. 11 C,D): Pr: P - 1l / Exo: 1m - 2s / EI: A - 6s, P - Y -1m(pl) / EII and EIII: A - 2s, P - y_1 -1s(t_4) -3m($t_{1,2,3}$), D - y_2 - 1 m(z_3) - 2l ($z_{1,2}$) -3l(G1,2,3: ser) / EIV: D - 1s - y_3 - 1m (Gm: ser) - 1l (GM: ser).
The chaetotaxy of the antenna is identical with that of *C. subterranea* (i.e. natatory setae very short, t and z setae normal in number and position). Slight differences in the length of the claws and aesthetascs exist. Aesthetasc Y is 38% of the length of EI. The G1, G2 and G3 claws are of subequal length (their sizes equal respectively 130%, 120% and 120% of the length of the EI joint). The GM claw is long (105% of the length of the EI joint). The Gm claw is shorter (63% of the length of EI). Aesthetasc y_3 is short (30% of the length of EI); its sensitive hyaline part is poorly developed (26% of its total length).

M a n d i b u l a r p a l p (Mdp; Fig. 11 F):
I: In - 1s (α) - 1l - 1m(s1:pl) - 1l(s2:pl) / II: In -3m -1m(pl) - 1s(β), Ex - 2m - 1l / III: In - 2s, Ex - 4m, D -4m (γ: pl) / IV: D - 2s - 2m - 2m(cs:pu).
The α seta is smooth, the β and γ setae are feathery. The 3 setae in the middle of the interior margin of the 2nd joint are smooth, the 4th is feathery.

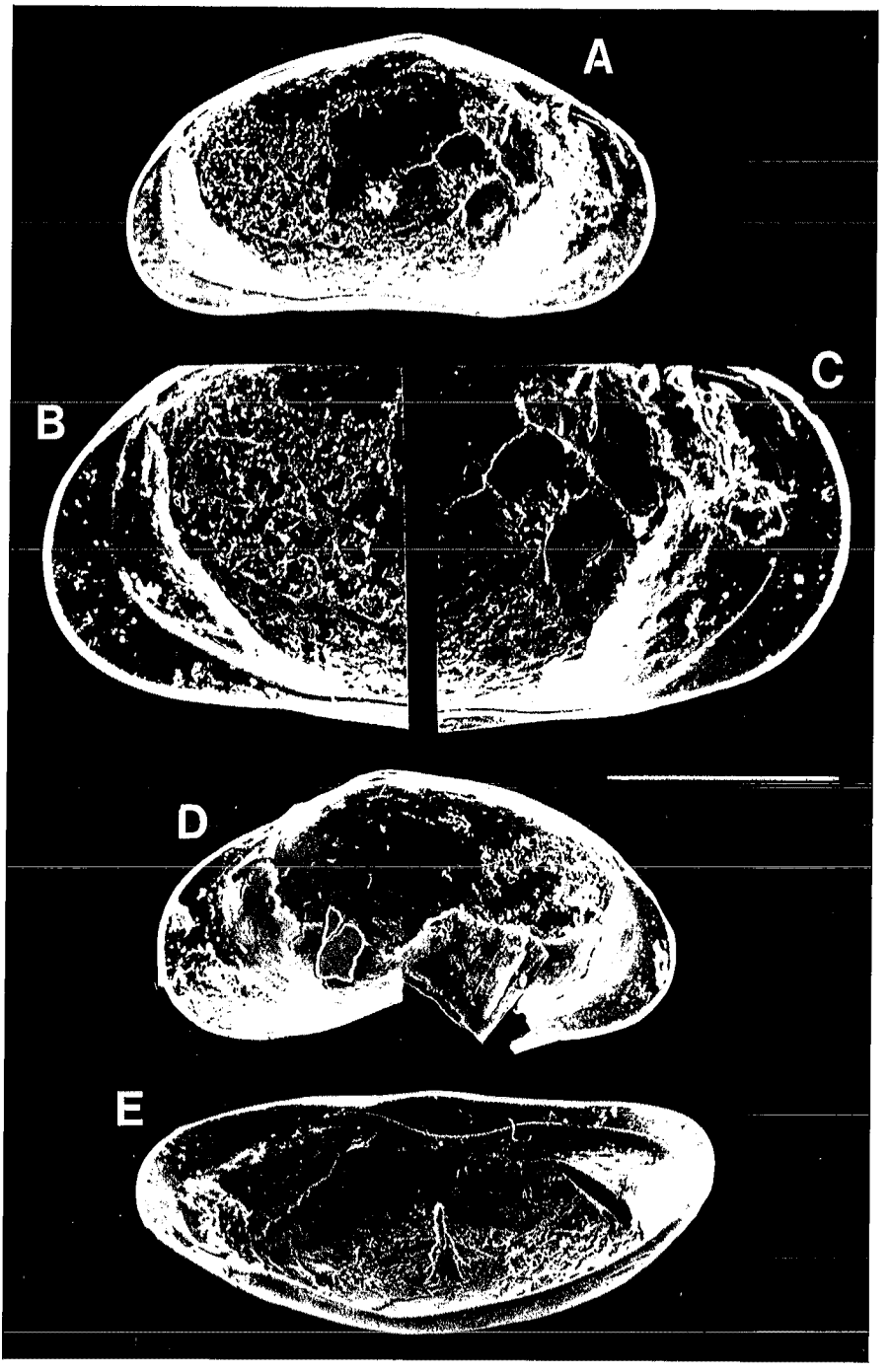


Fig. 10. - *Cavernocypris wardi* (female, Colorado, USA). - A: left valve, inner view. B: left valve, posterior detail of A. C: left valve, anterior detail of A. D: right valve, inner view. E: left valve, inner inclined view. Scale: 0.20 mm for A,D; 0.13 mm for B,C; 0.18 mm for E.

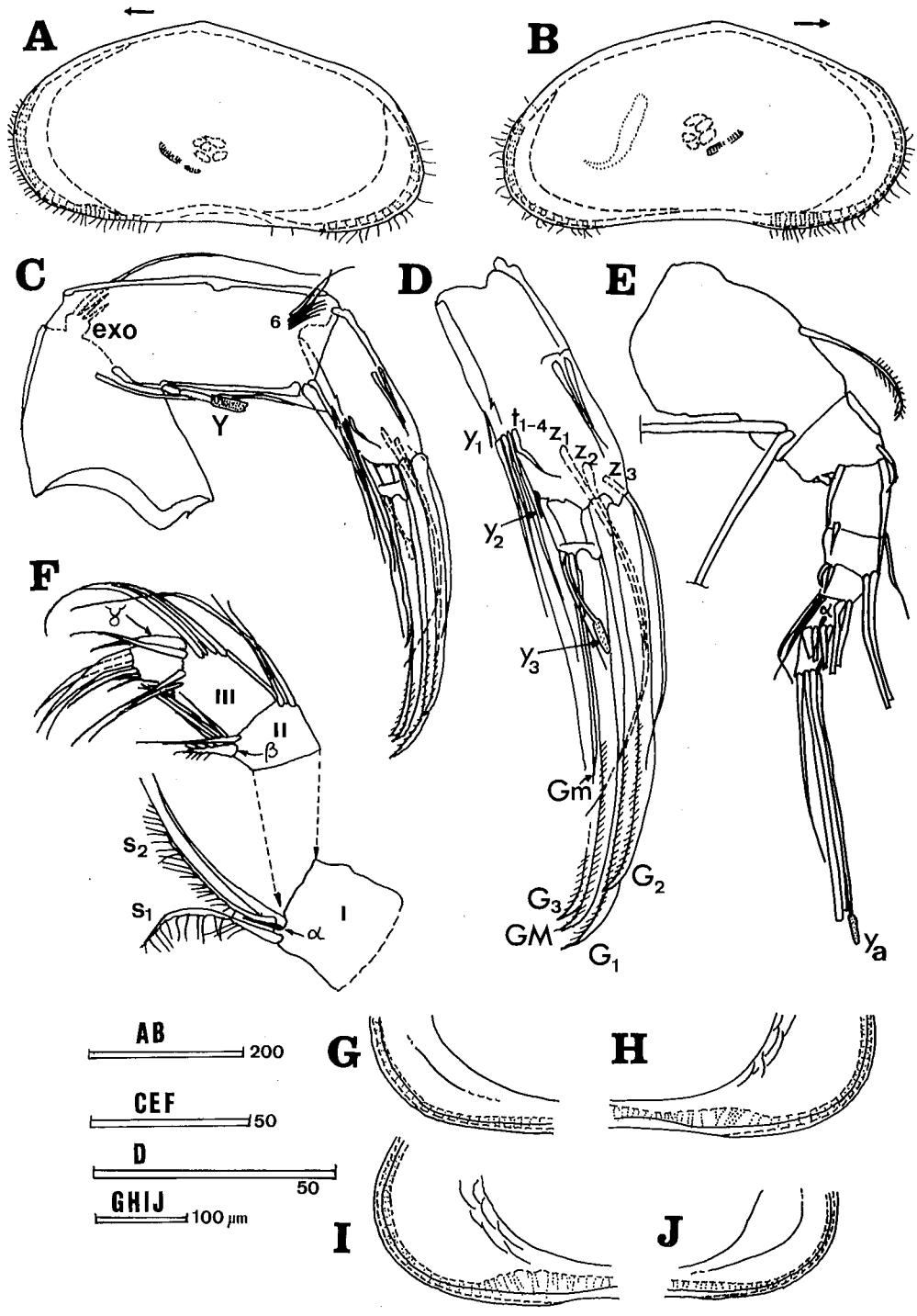


Fig. 11. - *Cavernocypris wardi* (female, Colorado, USA). - A: left valve, external view. B: right valve, external view. C: antenna. D: detail of the distal part of the antenna. E: antennula. F: mandibular palp. G,H: left valve, inner view, detail of the anteroventral (H) and posteroventral (G) margin. I,J: right valve, inner view, detail of the anteroventral (I) and posteroventral (J) margin.

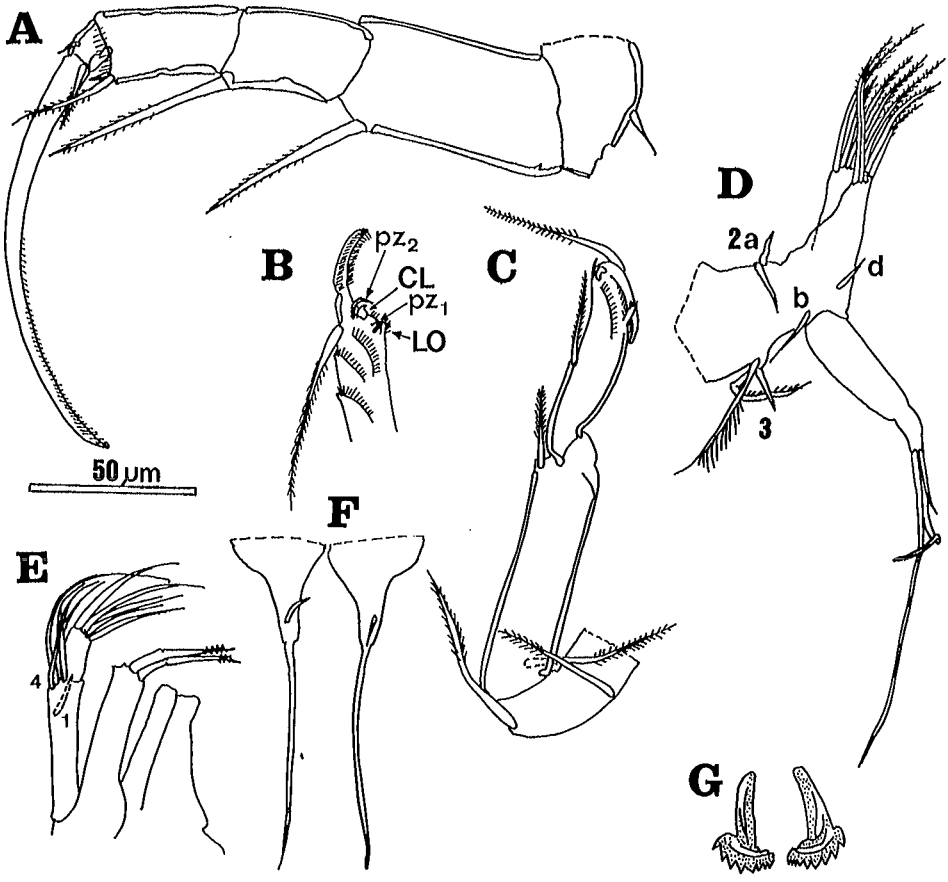


Fig. 12. - *Cavernocypris wardi* (female, Colorado, USA). - A: 1st thoracopod. B: detail of the distal part of the 2nd thoracopod. C: 2nd thoracopod. D: maxilla. E: maxillula. F: furca. G: rake-like organs.

Maxillular palp (Mxup; Fig. 12 E): I: Ex - 1s - 3m - 1l / II: D - 5 m - 1s. The palp bears 5 setae (4 + 1) on the external margin of the 1st joint (there are 6 setae in *C. subterranea).*

Maxilla (Max; Fig. 12 D): Pr: A - 2s (a and a'), In - 2s (d,b) / Mastic.: D -10m / Exo: P - 2s(pl) - 1m(pl) / E: D - 2s - 1m.
The exopodite of the Max bears 3 feathery branchial filaments (2 in *C. subterranea).*

First thoracopod (T1, walking leg; Fig. 12 A): Pr: A - 1s / EI: A - 1m(pl) / EII: A - 1m(pl) / EIII: A - 1s - 1s(pl) / EIV: P -1s, D - 1s(pl) - 1l(G:ser).

Second thoracopod (T2, cleaning leg; Fig. 12 B,C): Pr: P - 1s(pl), A -2m(pl) / EI: P - 1s(pl) / EII + EIII: P - 1s(pl) / EIV: P - 4s(LO, pz_1, pz_2), D -1s(pl) -1m(pl).
The chaetotaxy of T1 and T2 is identical with that described for *C. subterranea.*

Furca (Fu; Fig. 12 F) strongly reduced, slightly conical and bearing a short, curved seta; the distal part is flagellum-like, as in all cypridopsines.

Genital fold of the female without a copulatory hook.

A small pigmented eye, similar to that of *C. subterranea,* present. The male is unknown: parthenogenetic reproduction in the only population which is hitherto known.

3-8. Phylogenetical affinities between the *Cavernocypris* species

It is important to reconstruct phylogenetical relationships of this ostracod group because our long-term aim is a better understanding of the evolutionary history of *Cavernocypris.*

Within the Cyprididae family, the exopodite of the maxilla displays, in many cases, a constant number (i.e. 6) of setae. Within the genus *Cavernocypris,* the number of setae varies between 2 and 4. *C. coreana* with 4 setae, comes closest to the more primitive Cyprididae; *C. wardi,* with 3 exopodite setae, shows a more derived state and *C. subterranea,* with 2 setae, is the most apomorphic *Cavernocypris.*

On the A1, the 3rd and 4th joints are fused in *C. coreana,* separated in *C. subterranea* and *C. wardi.* The 1st joint of the Mxu palp bears 5+1 setae in *C. coreana* and *C. subterranea,* only 4+1 setae in *C. wardi.*

Considering the mode of reproduction, the bisexual reproduction is a primitive state and the parthenogenesis is a derived one. Once again, *C. coreana* appears more primitive than the other two species. We would like to point out that the morphological data presented above do not reveal any close phylogenetic affinities between the three species; however, *C. coreana* is shown to have retained more primitive characters.

3-9. Taxonomic relationships between *Cavernocypris* and the closely related cypridopsine genera

The genus *Cavernocypris* has to be compared with the following cypridopsine genera: *Cypridopsis* s.str. (type-species: *C. vidua), Sarscypridopsis* (type-species: *S. aculeata*), *Plesiocypridopsis* (type-species: *P. newtoni*), *Kapcypridopsis* (type-species: *K. barnardi*) and *Potamocypris* (type-species: *P. fulva).*

Cavernocypris and *Cypridopsis* can be readily separated from the genera listed above by the mode of ventral carapace closure: in *Cypridopsis* s.str. and in *Cavernocypris* the LV ventrally embraces the RV, i.e. the ventral marginal zone of the LV overlaps the marginal zone of the RV. The opposite carapace closure is found in *Plesiocypridopsis, Sarscypridopsis* and *Potamocypris.*

Cavernocypris differs from *Cypridopsis* s.str. by:
(a) the carapace shape in lateral view: the carapace is elongate (H/L = about 0.50) in *Cavernocypris* and subovate (H/L distinctly superior to 0.50) in *Cypridopsis* s.str.;
(b) the structure of the anterior and posterior marginal zones of the valves: in *Cypridopsis* s.str. there is a well-developed inner list showing as a double fold, and the inner lamella is narrow on the posterior marginal zone; in *Cavernocypris* this inner list is either absent or only weakly developed on the posterior and posteroventral margin (see figs 2, 5 and 10) and, when present, the posterior list does not show as a double fold; the inner lamella on the posterior margin is broad to very broad (same figs);
c) the pigmentation of the carapace: the carapace of *Cavernocypris* is whitish to yellowish, while the *Cypridopsis* s.str. species are greenish and often show several dark transverse bands;
d) the swimming ability: the *Cavernocypris* species bear strongly reduced A2 swimming setae, which render them unable to swim. Most of the *Cypridopsis* s.str. species, on the contrary, bear long swimming setae and hence are good and active swimmers;
(d) the ecology: *Cavernocypris* inhabits stenotherm cold waters, springs, the littoral zone of mountain lakes and underground waters, while the *Cypridopsis* species inhabit the littoral zone of lowland lakes, ponds etc. and develop during the summer, in relatively high temperatures.

Kapcypridopsis is another genus which seems to come close to *Cavernocypris* (see also McKenzie, 1977). It shares with *Cavernocypris:*
(a) the presence of a very broad inner lamella on both the anterior and posterior margins of both valves;
(b) *K. barnardi* McKenzie, which is the type-species of the genus, bears very short swimming setae, a feature which characterizes the *Cavernocypris* species;
(c) there seems to be no distinct inner list on either valve (see Figs 6,1 and 7,1 in McKenzie, 1977; but the absence of this list should be checked on SEM figures). Unfortunately, the original description of *K. barnardi* does not mention the ventral carapace closure; this makes a further analysis of the

relationship between both genera impossible. Nevertheless, in *K. asymmetra* De Deckker, 1981, which is the second species hitherto assigned to the genus, the RV ventrally overlaps the LV. If this feature shows to be a generic character, then *Kapcypridopsis* and *Cavernocypris* can be readily separated. At present, the most valuable character separating *Cavernocypris* and *Kapcypridopsis* is the carapace shape: subovate (H/L = 0.60) in *Kapcypridopsis* and distinctly more elongate (H/L about 0.50) in *Cavernocypris).*

4. ECOLOGY

4-1. *Cavernocypris subterranea*

4-1-1. Habitat types

C. subterranea lives in the following types of habitats: (a) springs, (b) streams fed by springs, (c) river and alluvial bed sediments, (d) deep layers of marshy soils, (e) caves, (f) littoral zone of mountain lakes, sometimes in relation with submerged springs.

a) The occurrence of *C. subterranea* in limnocrene springs was quite often reported (Wolf, 1920; Klie, 1925, 1937; Akatova, 1950; Absolon, 1974, 1975; Dittmar, 1955; Wegelin, 1966; Petkovski, 1962; Danielopol, 1965; Ronneberger, 1975; Fox, 1967; Nüchterlein, 1969; Janz, 1983, 1988; Wouters & Bless, 1986; unpublished data of K. Wouters from springs in northern France, at Strouanne and P. Marmonier from the southern French Jura mountains). Absolon (1974) investigated the distribution of *C. subterranea* in limnocrene springs which discharge into small pools formed behind tufa dams. *C. subterranea* is dominant in the upper limnocrene springs close to the subsurface environment. It colonizes the lower pools but its abundance there decreases sharply.

b) Dittmar (1955) collected *C. subterranea* in Germany (FRG, Sauerland) among aquatic mosses and filamentous algae in several small brooks flowing from springs and also in the small stream which unites the brooks. Wouters (1983) recorded the species "in the sandy bottom of a shallow fast running brook in a woodland" in Belgium at Ethe-Buzenol.

c) Generally the riverbed sediments were investigated using the method of digging holes in the gravel bars and filtering the interstitial water which fills the holes (the Karaman-Chappuis method). Using this method, *C. subterranea* was collected by Prof. J. Schwoerbel in the Black Forest (FRG, sediments of the Wutach river; see Löffler, 1961), Löffler (1963) reports the finding of the species in Lower Austria (the Seebach at Lunz, the Ybbs at Langau) and in Tyrol (around Innsbruck). In southern Poland, Sywula (1981) sampled the species in bed sediments of various brooks belonging to the drainage sytems of the rivers Odra, Wistula and Dniestr. Dr G. Bretschko and his associates collected the species in the bed sediments of the See-

bach, a mountain torrent at Lunz (Austria) during the RITRODAT research program, using fixed stand pipes (see section 4-1-3-1 below).

d) In Thuringia (GDR), *C. subterranea* frequently occurs in damp soils on the slopes of hills and in superficial aquifers formed by poorly permeable rocks. The waters of these soils are drained artificially by pipes and then collected in numerous wells. The groundwater flows out through rheocrene springs or more seldom through limnocrene springs (Ronneberger, 1975). This is also the case in Upper Austria, in the village of Wangau (close to Mondsee), where one of us (D.L.D.) collected the species.

e) Numerous populations were found in subterranean habitats to which access is given by wells dug for drinking water supply. This is the case of the specimens collected by Wolf (1920) near Basel in Switzerland. Sywula (1981) collected *C. subterranea* in southern Poland in wells situated in the environs of Krakow, Zakopane and Klodzko; most of the wells were located close (25 - 300 m) to streams (Sywula, partially unpublished data, pers. comm. to D.L.D.).

f) Hartmann (1964, under *C. lindbergi*) mentions the occurrence of the species in three caves in Afghanistan. We ourselves identified the species in a sample from a drip pool in the Grotta di Castello Tesino (Italy), at 70 m from the entrance (leg. F. Gasparo, Triest).

g) Wolf (1920) recorded the species from the Lower Fluela lake (2300 m a.s.l.) in Switzerland and Dr G. Bretschko collected it in the Grüner See in the Austrian Alps (Hochschwab) close to a karstic spring and also in the littoral zone of the lake (in less than 1 m depth) (Löffler, 1963; Bretschko, 1966).

The palaeohabitats in which *C. subterranea* has been found in Central Europe (i.e. Bavaria, Thuringia and Bohemia) by Absolon (1973), Diebel & Pietrzeniuk (1975, 1977, 1978, 1980, 1984), Diebel & Wolfschläger (1975) and Pietrzeniuk (1985) are tufa deposits dating from the Eemian Interglacial and postglacial (Middle Holocene) times. The sediments are sandy humose or silty sands. They were deposited in marshy conditions by slow-flowing lime-rich springs. Thienemann (1950) showed that in Thuringia such habitats developed in large areas during a moderately mild climatic period. In such a palaeohabitat, *C. subterranea* lived both at the surface and in the interstitial space of the coarser matrix of the sediment. M. Handl (unpubl.) found the species in a littoral palaeohabitat, dating from the Late Glacial, in the Haleswiessee, a shallow karstic lake near Mondsee, Upper Austria. Absolon (1975a) studied recent and fossil ostracods from springs and tufa pools at Krivoklat in Bohemia (CSSR). The ostracod associations which became fossilized in the tufa pools around the carbonate rich springs during the Atlanticum (about 6000 years B.P.) are very similar to those living at present in habitats situated nearby. Absolon (op. cit.) suggested that *C. subterranea* already lived in these springs during the rather warm and wet climatic period of the Middle Holocene, and that it has persisted there up to the present day.

4-1-2. Physical and chemical characteristics of the habitats

The following parameters will briefly be analysed: (a) water temperature, (b) water flow, (c) oxygen concentration, (d) substrate, (e) carbonate concentration, (f) pH.

a) *C. subterranea* prefers low water temperatures. Most of the values indicated in the literature vary from 6° to 12°C (Wolf, 1920; Wegelin, 1966; Dittmar, 1955; Ronneberger, 1975; Janz, 1983). These are typical values for mountain lotic habitats, springs and subsurface waters in Central Europe.

b) *C. subterranea* lives in slow-flowing waters. Records of the species from totally stagnant waters are rare. In the littoral zone of the Grüner See in Austria, the species has been found near a sublacustrine karstic spring. Likewise, the interglacial and mid-Holocene deposits in Central Europe in which the species was found, were deposited in slow-flowing waters (see data in Absolon and Diebel & Pietrzeniuk, op. cit.). Data on the precise conditions that exist in the Fluela lake, Switzerland (Wolf, 1920), and on the water regime (i.e. stagnant or flowing) in the cave pools in Afghanistan in which the species was found, are lacking. In the Italian Alps, the species was collected in a pool filled by "dripping water" (Gasparo, unpubl.).

The interstitial environments inhabitated by *C. subterranea are* commonly characterized by flowing (not stagnant) water. This is the case with all the superficial soils located on steep slopes (e.g. the Thuringian localities around the Orla drainage system investigated by Ronneberger, 1975, 1987, pers. comm. to D.L.D.) and also with the habitats sampled at Wangau (Austria, D.L.D., unpubl.) and with the Seebach sediments at Lunz (Bretschko, 1983).

c) *C. subterranea* lives in well-oxygenated waters, reaching 80% - 100% of O_2 saturation, or more than 4 mg/l. This is the case for the localities examined by Dittmar (1955, FRG, Sauerland), Wegelin (1966, GDR, Thuringia) and Bretschko (pers. comm. to D.L.D., RITRODAT area at Lunz, Austria).

C. subterranea was never collected in the stagnant waters of the dead arms of the Danube or in the slowly percolating ground water in areas like the lowest terrace of the Danube, in Lower Austria (Danielopol, 1976, 1983). But one specimen has been found by Dr G. Bretschko and his students in the sediments of the main channel of the Danube at Altemwörth, near Krems. In this area, the Danube has all the characteristics of a mountain river, with high speed water flow (about 2 m/s); the interstitial water of the channel is certainly well oxygenated. At Lunz, the species does not occur in the dead arms of the Seebach (see below) which contain a high amount of fine sediments and where the water is stagnant during part of the year. The species has never been found in polluted waters with high oxygen demand. For instance, Löffler (1963) collected the species in the bed sediments of the Ybbs river, at Langau, upstream from a papermill, but not in the lower part of the river, where the sediments are organically polluted and poorly oxygenated.

d) Substrate: Wolf (1920) mentioned that *C. subterranea* avoids the localities where muddy sediments accumulate. The species does not occur in

flocculent lacustrine sediments like those found in eutrophic lakes. In running waters, it prefers hard substrates like those formed by the sandy gravelly river deposits (e.g. the RITRODAT area at Lunz).

e) Carbonate richness: Löffler (1961) noted that *C. subterranea* occurs mainly in waters with high calcium content. This is true for many areas such as the RITRODATarea, the caves in Europe and Central Asia, but not for areas like the Sauerland in FRG (Dittmar, 1955).

f) pH: Generally, the water pH indicated for *C. subterranea* in the literature is above 7. However, Dittmar (1955) and Ronneberger (1975) mentioned the occurrence of the species in waters with pH values from 5.4 to 7.3.

4-1-3. The distribution in space and time of *C. subterranea* within the sandy gravel sediment of the Seebach, an Austrian mountain brook

C. subterranea is a small ostracod moving fast among the grains of the substrate. When these animals are observed under the stereo-microscope (D.L.D. worked with this species at the Biological Station at Lunz) it can be seen that they dig with their pointed anterior carapace among the grains and disappear into the sediment where they stay for long periods of time. The animals feed on organic particles. Their behaviour suggests that the species is thigmotactic and possibly negatively phototactic.

More details about the ecological preferences of *C. subterranea* are given by the study of its spatial distribution in the interstitial habitats in an Austrian alpine brook: the Seebach.

4-1-3-1. Study area and methods

The Seebach, an alpine brook in the Austrian Alps, is situated in the drainage system of the Danube river. The sites studied belong to the RITRODAT area, which was described by Bretschko (1983); the area is approximately 100 m long by 30 m wide, with three different geomorphological parts (Fig. 13):

- a curved main channel on the right side, with coarse sediments and high flow velocity;
- a central gravel bar, frequently out of water, with more finely grained sediments;
- a secondary arm, on the left side, with finely grained sediments (sandy) and more or less stagnant superficial water during summer.

The main chemical parameters are very stable in time; discharge rates are highly variable according to the mountainous and karstic character of the catchment area. The surface water temperature is low (annual mean: 6.5°C; Bretschko, 1981) with moderate annual variations (from 2°C to 11.2°C); the interstitial water temperatures at -60 cm depth are very close to the surface ones (annual mean: 6.3°C to 6.8°C according to the station considered; annual variations: from 2°C to 12°C; Bretschko, pers. comm.).

Table 1. - RITRODAT project: Sampling periods for vertical and horizontal studies.

A - Spatial distribution of fauna in the groundwater in the banks of the Seebach

1979:	1980:
August 17 and 20	January 18 and 21
September 17 and 20	February 18 and 21
October 22 and 25	March 17
November 19 and 22	April 21 and 24
December 17 and 20	

B - Spatial distribution of fauna in the under-flow of the Seebach (+ sampling periods)

Years	Dates	Horizontal	Vertical
1980	April 21 and 24		+
	May 19 and 22		+
	June 16 and 19		+
	July 18 and 21		+
	September 5 and 8	+	+
	October 20 and 23	+	+
	December 8 and 12	+	+
1981	February 6 and 12	+	+
	April/May 30 and 6	+	+
	July 3 and 9	+	+
	November 9 and 16	+	+
1982	February 19 and 25	+	+
	May 21 and 28	+	+

Table II. - Sampling depths of the vertical distribution study (station 12 B).

Dates	Number of pipes and sampling depths
April, May, June 1980	3 pipes at 0, -20, -40, -60 cm
July, September, October, December 1980; February and April/May 1981	3 pipes at 0 cm 2 pipes at -20, -40, -60, -80 cm
July, November 1981, February, May 1982	3 pipes at -40, -50, -80, -100 cm

The sampling method used to pick up the interstitial fauna ("standpipe method" in Bretschko, 1981 and 1983) collects animals that are either moving actively or drifting inside the sediments. A plastic pipe 7 cm in diameter with a row of holes at its extremity, was pushed down into the sediments; the holes can be opened and closed from the surface. Two samples were taken at each station and the pipes were left open during two periods of three days. The animals collecetd were than pumped out with a hand pump. Thus, the capture abundance was proportional to the real abundance of animals surrounding the pipes and with their activity during the sampling period.

The spatial distribution has been studied following two different approaches:

- a horizontal distribution study, at 20 cm depth, at 13 stations (Fig. 13): 10 stations with one pipe each in the main channel, 2 stations with respectively 3 and 2 pipes on the gravel bar, and 1 station with one pipe in the secondary arm of the river. This study was carried out from September 1980 to May 1982, with 18 sample series (Table 1). It was completed by another one which deals with the spatial distribution of ostracods in the banks: 8 stations (marked with an 'R' in Fig. 13) were sampled from August 1979 to August 1980, with 17 sample series (Table 1).

- a vertical distribution study was carried out in the two stations on the gravel bar (stations 4B and 12B, Fig. 13), from April 1980 to August 1982, with 28 samples (Table 1). At the beginning, the different depths sampled were 0, -20, -40 and -60 cm. At station 12B, the depths varied during the study because the gravel bar sediments moved downstream and covered the pipes: the sampling depth relative to the surface increased although the pipes themselves did not move (Table 2).

4-1-3-2. Results

■ Horizontal distribution of *C. subterranea* in the RITRODAT area.

C. subterranea is abundantly captured in most of the stations of the main channel (2Z1, 22Z3, 10A1, 16C1 and 18A1; Fig. 13) and in the sediments of the gravel bar (4B and 12B; Fig. 13). But the species is less common in the part of the channel where the flow velocity is highest and the sediment most coarse (6Z2, 8Z2 and 10Z2, Fig. 13), and in the secondary arm (8C4, Fig. 13) where the surface water is stagnant during part of the year and where fine particles (gypsum sand, G. Bretschko, pers. comm.) are laid down by the river.

In the samples collected in the banks (the sampling sites located between 5 to 25 m away from the stream, Fig. 13) *C. subterranea* is the dominant species (it appears in 40% of the samples) together with *Pseudocandona bilobata* (a hypogean dweller that appears in 37% of the samples). The abundance of the captures is generally low (never more than 12 specimens for one sample) and *C. subterranea* is more abundant in the samples from the right bank of the brook (stations R15 and R5; Fig. 13).

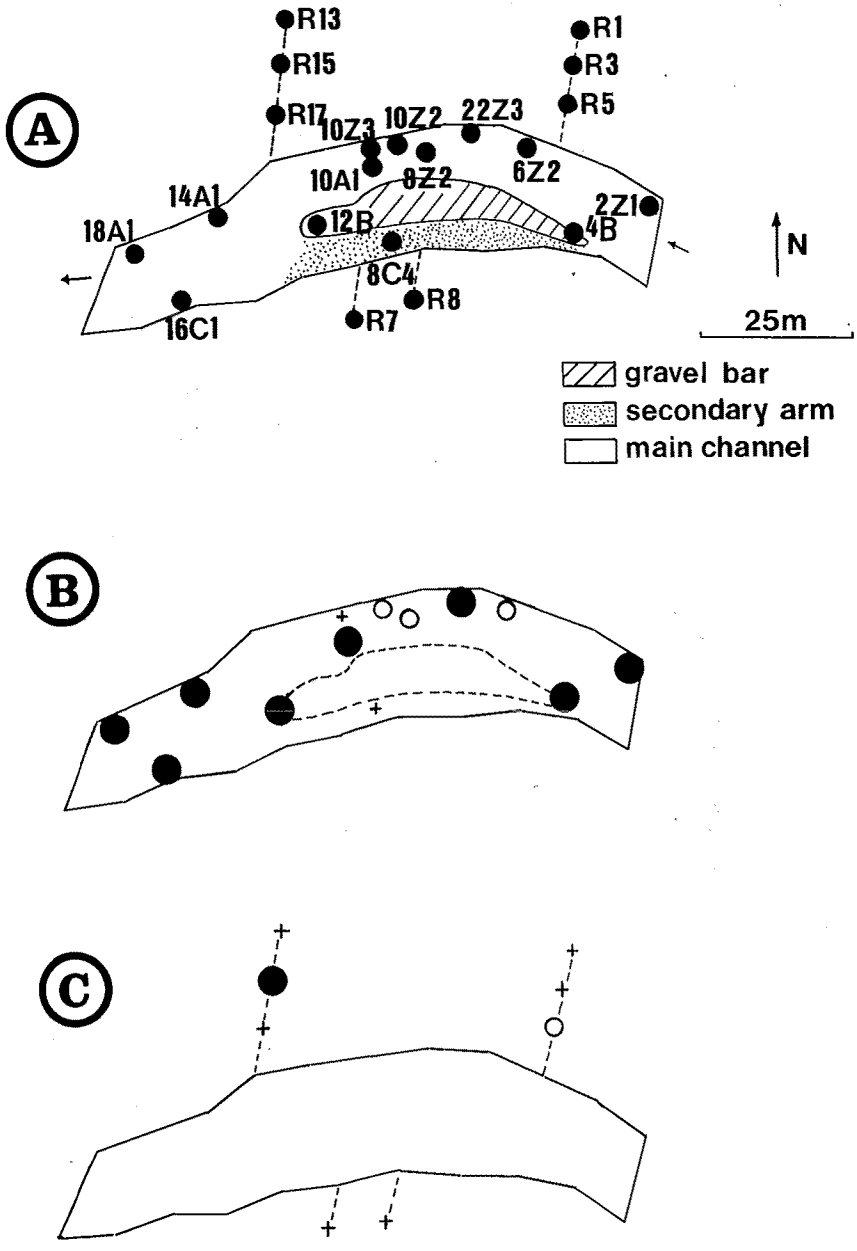


Fig. 13. - Spatial distribution of *C. subterranea* in the bedsediments of the Seebach (RITRODAT AREA).
A: position of the stations. B: spatial distribution in the channel of the stream, at 20 cm depth (data collected from Sept. 1980 to May 1982). C: spatial distribution in the banks of the stream (data collected from August 1979 to April 1980). Black dots: specimens present in more than 75% of the samples. White dots: specimens present in 50-74% of the samples. Cross: specimens present in less than 50% of the samples.

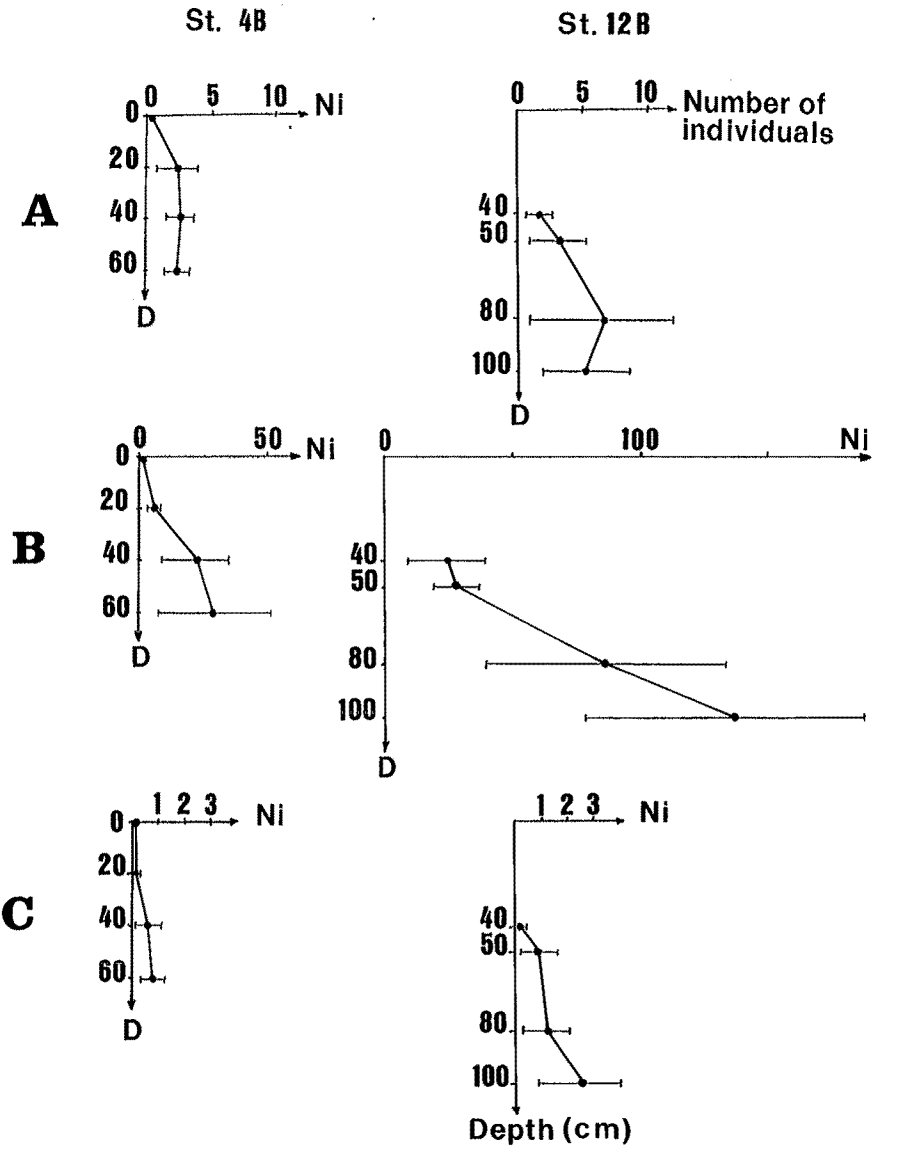


Fig. 14. - Vertical distribution of *Candona candida* (A), *C. subterranea* (B) and *Pseudocandona bilobata* (C) in the bedsediments of the Seebach, at the stations 4B and 12B. Points: mean values for samples collected from July 1981 to May 1982 (n = 24 samples); horizontal lines: 95% confidence limit.

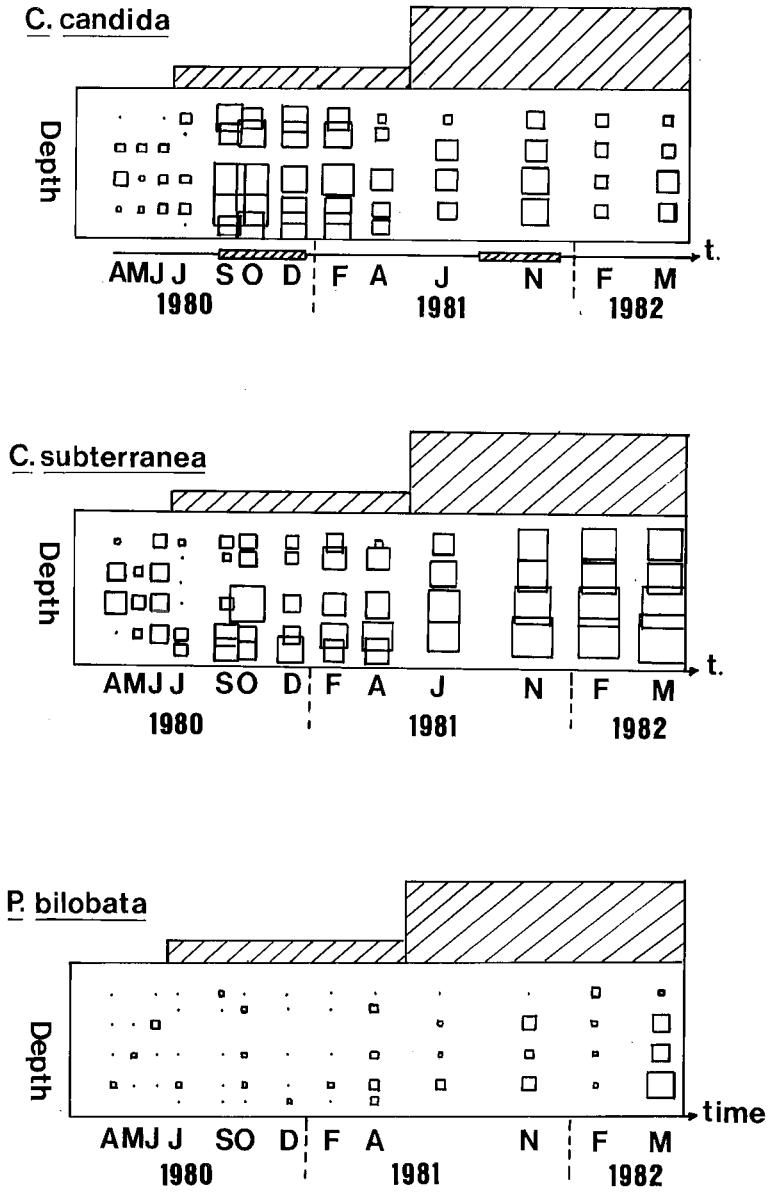


Fig. 15. - Spatial distribution of *Candona candida, C. subterranea* and *Pseudocandona bilobata* at station 12B, from April 1980 to May 1982. Hachured zones: thickness of the newly deposited sediments. Sampling depths: from April 1980 to July 1980: 0, -20, -40 and -60; from Sept. 1980 to Nov. 1981: -10, -20, -40, -60 and -80; from July 1981 to May 1982: -40, -50, -80 and -100 cm.

The comparison of the spatial distribution of this species with that of other ostracod species (Marmonier, 1984, 1985), emphasizes that *C. subterranea* is the most ubiquitous ostracod of the Seebach: the species is able to colonize most parts of the study area, from very lotic habitats to slow-flowing ones and to the ground water environment (in this latter habitat, the species seems to establish permanent populations in only a few stations).

■ Vertical distribution

In both of the stations, *C. subterranea* is found from the surface (i.e. 0 cm depth at station 4B) to the deepest sampling layers (i.e. - 60 cm at station 4B and -100 cm depth at 12B at the end of the study, Fig. 14). *C. subterranea* is more abundant in the deepest layers (in 4B as well as in 12B, Fig. 14). If one compares this vertical distribution with that of *Candona candida* (an epigean dweller) and *Pseudocandona bilobata* (a hypogean dweller), we can see that *C. subterranea* has a very large vertical distribution and holds an intermediate position between the epigean and hypogean species.

■ Reaction to superficial gravel movements

The space/time distribution of *C. subterranea* in station 12B does not show any seasonal cycle (such a seasonal cycle was found for *Candona candida* in autumn 1980 and 1981; Fig. 15). As both adults and juveniles of *C. subterranea* were found in most samples, the species most probably reproduces all year round. The variation of the abundance of the species may be explained by the movements of the superficial sediments: the number of specimens captured increases with the deposition of gravel on the surface of the bed sediments (after September 1980 and July 1981, Fig. 15); the increase began in the deeper layers (i.e. below -60 cm, Fig. 15) and reached the surface layers at the end of the study.

This space/time variation is very similar to that of *Pseudocandona bilobata* (a hypogean species, Fig. 15): the increase of sampling depth, linked to the movement of surface sediments, seems to stimulate the hypogean ostracod populations. (For more details, see Marmonier, 1984, 1985). Considering this modification of the abiotic characteristics of the habitat, *C. subterranea* reacts and behaves more like a hypogean dweller.

4-1-4. Functional morphology

The peculiar structure of the following morphological features of *C. subterranea* can be interpreted as having evolved under the pressure of the environmental conditions under which the species lives:

(a) the shape, size and strength of the carapace;
(b) the amount of pigment in the eye;
(c) the length of the natatory setae on the antenna;
(d) the length of the chemosensorial setae, e.g. the aesthetasc Y;
(e) the length and strength of the endopodial segments and of the distal claws of the antennae and the walking limbs;
(f) the rake-like organs.

(a) Hartmann (1973) showed for marine interstitial ostracods that the elongated carapace and the reduced size of the specimens are adaptive characters connected with life in interstitial systems. But we found no such morphological differences between surface-dwelling *C. subterranea* specimens living in springs and those living in caves and interstitial habitats. It is true that Klie (1925) mentioned that the calcareous lamella of surface specimens living in the Jura mountains is thicker than that of surface specimens living near Bad Pyrmont in an area with Triassic sediments which are poor in carbonates. We were not able to check this statement. Furthermore, we were not able to find out that the carapace of specimens from the Seebach, a habitat which is rich in carbonate, have thick carapaces. For an exact quantification of the thickness of the carapace, special techniques are needed, which were not available to us.

(b) The amount of pigment in the eye: Wolf (1920) mentioned that some of the specimens collected in subterranean waters had no ocular pigment. All the *C. subterranea* specimens we examined had poorly pigmented eyes; we never noticed specimens with unpigmented eyes.

(c) Each of the three *Cavernocypris* species hitherto known has reduced natatory setae on the antennae (Figs 4G, 6G, 7F, 11C). Such short swimming setae prevent the species from swimming. Wolf (1920) considered this character as an adaptation to the subterranean mode of life. Species with reduced natatory setae live in and move upon or dig in the bottom sediments. Moreover, within the Cyprididae-Cypridopsinae, the reduced natatory setae most probably have to be considered as being an apomorphic character. (For instance, in *Cypridopsis vidua,* the type-species of the genus *Cypridopsis,* the natatory setae develop down to the tips of the distal claws). We consider that the reduction of the swimming bristles is due to the blockage of their normal development, a process which occurs convergently in many ostracod groups. This arrested development of the swimming setae is not dependent on the mode of life in subsurface habitats.

(d) Length of the chemosensorial aesthetasc Y: Some of the subterranean ostracod Candonidae, such as the representatives of the genus *Mixtacandona,* which are exclusively hypogean dwellers, have a very long aesthetasc Y (Danielopol, 1973). Because most of the hypogean species with long aesthetascs have no close epigean relatives, it is difficult to decide if the peculiar shape of this organ is the result of an adaptation process to the oligotrophic subterranean environment and a compensating reaction to the lack of the use of the eye. In the case of *C. subterranea* we were fortunate to have the possibility to compare specimens from epigean habitats (a spring near Bad Pyrmont, Germany, springs from the Jura mountains, France) and two hypogean habitats (caves in Afghanistan and riverbed sediments from Austria, at Lunz). We did not find any significant difference between the aesthetasc Y of the epigean and the hypogean *C. subterranea* specimens.

When comparing the total length of the aesthetasc Y of *C. subterranea* with that of *C. vidua* (Fig. 16 C and D) it can be seen that the aesthetasc of *C. subterranea* is longer than that of *C. vidua.* However, we know that only the hyaline distal part is of importance for the chemosensorial process (Anders-

Table III. - Width / length ratios of the three endopodial joints of the 1st thoracopod for *Cypridopsis vidua* and *Cavernocypris subterranea.*

	Cypridopsis vidua	*Cavernocypris subterranea*
E I	87 %	47 %
E II	85 %	57 %
E III	83 %	43 %

son, 1975). If this is true, then the epigean phytophilous species *C. vidua* has a longer distal segment on the aesthetasc than *C. subterranea,* which commonly lives in subterranean waters. So we did not see any indication of a hyperdevelopment of this organ as a compensating process to the life in dark and/or oligotrophic waters.

(e) The length and the strength of the endopodial segments of the walking limb T1 (Table III), of the distal claws of the antenna and of the walking limb (Fig. 16): The benthic ostracod dwellers typically have slightly curved and more or less elongated claws on the antenna as well as on the walking leg (Fig. 16 B and D). The opposite is seen in phytophilous dwellers like *Cypridopsis vidua.* This ostracod swims for short periods and then fixes on the submerged macrophytes. The claws as well as the whole structure of the first thoracopod endopodit are shorter and stronger (Fig. 16 A and C). Moreover, they have more strongly pectinated claws in order to fix more efficiently to the substrate (Fig. 16 C).

(f) The rake-like organs: *C. subterranea* feeds on very fine organic detritus. Its rake-like organs are poorly developed. But *Cypridopsis vidua,* which feeds on coarser detritus and diatoms, has very similar rake-like organs. So the peculiar structure of this organs is not necessarily related to the benthic life of the *Cavernocypris* species either in surface or in subterranean waters.

(g) The carapace pigmentation. Many cypridids living in shallow surface water habitats are distinctly pigmented. For instance, *Cypridopsis vidua* shows dark green or brown to black transversal strips. M. Baninzireki (1988), at the Limnological Institute of Mondsee, documented for this latter species that the colour pattern helps the species to be cryptic on dark background. Fishes, like *Vimba vimba,* find it significantly more difficult to discover it on a dark background than on light-coloured backgrounds. Many animals which are pigmented in surface habitats lose their pigment when living underground (Vandel, 1965). The carapace of all three *Cavernocypris* species is white-yellow. The spring populations of *C. subterranea* are unpigmented like those living in underground waters. A lack of pigment seems to be a characteristic feature of the whole *Cavernocypris* group. A similar case exists in the Candonidae group (Danielopol, 1978).

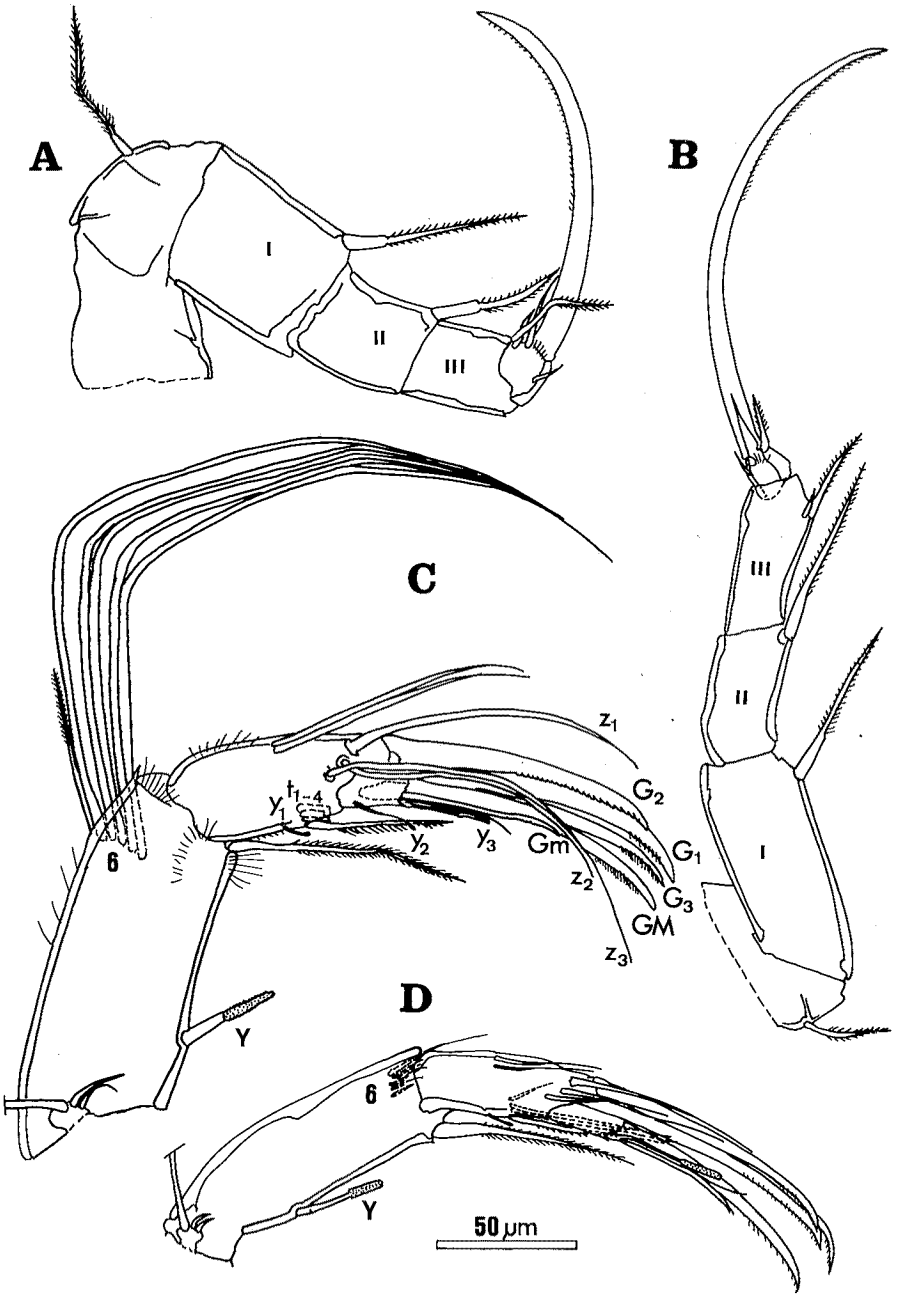


Fig. 16. - *Cypridopsis vidua* (female, A-Mondsee). A: 1st thoracopod. C: antenna. *Cavernocypris subterranea* (female, A-Lunz). B: 1st thoracopod. D: antenna.

In conclusion, we were not able to find any morphological characters which can be interpreted as being involved with or dependent on the environmental conditions in which the species lives; more particularly, there seems to be no character directly related to the life in subsurface habitats. Considering the colonization of this latter environment by *C. subterranea,* it should be noted that this ostracod shows many preadaptive characters enabling it to penetrate and survive in subsurface waters (e.g. the reduced natatory setae and the reduced carapace size). One should remember that Schwoerbel (1967) demonstrated that some water mite species, especially those belonging in the genus *Lania,* which live in riverine interstitial habitats (the so-called hyporheic habitat) can display morphological specialisations like the depigmentation of the body, the reduction of eye structures and of body size. These specialisations are classically found in cave dwelling animals (see a review in Ginet & Decou, 1977).

4-2. Ecological data on the remaining species of the genus *Cavernocypris*

4-2-1. *Cavernocypris wardi* n.sp. from Colorado (U.S.A.)

4-2-1-1. Sampling site and methods

The study site is situated on the South Platte River, Colorado, USA, 46 km SSW of the city of Denver, 1863 m a.s.l. The stream is about 20 m wide, about 1 m deep and unpolluted (high oxygen level), summer water temperatures below 20 °C, the major part of the alluvial deposits being formed by non-friable granitic material (Pennak & Ward, 1986).

Three stations were sampled monthly by Pennak & Ward (op. cit.) from October 1982 to September 1983: station 1 is situated in the stream bed, station 2 is on the shore, 1-2 m from the water edge and station 3 is situated about 19 m from the edge of the stream. Stations 2 and 3 are located on a large gravel bar, the surface of which is about 1 m above the 'normal' water table. The sampling method is that of Bou & Rouch (Bou, 1967; for a description of the apparatus see Bou, 1974): 5 litres of water samples were taken at a depth of 50 cm below the water table. Four vertical distribution studies were realized in the three stations during the study (at -15, -30 and -50 cm, see details in Pennak & Ward, 1986).

4-2-1-2. Results

Ostracods were numerically unimportant in the samples collected. *C. wardi* n. sp. was captured only in station 1 (in the stream bed) in October 1982 and in March 1983. In this station, the species seems to be limited to the under-flow of the river; the species was not captured in stations 2 and 3.

In March 1983, a vertical distribution study was done in the first station. *C. wardi* n. sp. is absent at the -15 cm sampling depth; it occurs only in the -30 cm (9 specimens) and -50 cm (1 specimen) sampling depths.

More recently, Dr J. Ward sent one of us (P.M.) a more complete collection of interstitial ostracods from the South Platte River. *C. wardi* n. sp. was found in a great number of stations located in the superficial layers of gravel as well as in the samples from the under-flow of the river and in the samples from the groundwater of the riverbanks (J. Ward, unpublished data). It seems to be as ubiquitous as *C. subterranea*: it is found from the surface of the bedsediment to the groundwater environment of the riverbanks.

4-2-2. *Cavernocypris coreana* from karstic caves

C. coreana seems to appreciate habitats linked with groundwater: all the specimens were captured in limestone caves in South Korea. The caves are situated at relatively low altitude (from 190 to 650 m a.s.l.) (Ueno et al., 1966; McKenzie, 1972). The water temperatures vary from 8.8 to 14.4 °C (collections and measurements made between 5th and 25th of April 1966). According to Ueno et al. (1966), the caves are connected with or are situated not far from surface rivers; most of the caves show eutrophic conditions (with guano or dead leaves). In the caves, *C. coreana* was captured in pools (Sinryeong-gul Cave, Chilsibri-gul Cave) or only in cave streams (Kwangcheon-seon-gul Cave, Daeya-gul Cave). The same authors also sampled 49 wells in different South Korean cities: *C. coreana* was not captured in any of these wells.

4-3. The colonization of subterranean habitats by *Cavernocypris* species

The migration into subsurface habitats can be well understood when analysing various populations of *C. subterranea*.

There are various possibilities: the species actively colonizes the subsurface habitat or it is pushed passively underground during periods of high water. The active migration can be due to a normal individual cognitive process. In this case the ostracod steadily explores its surroundings and tries to locate its optimal environment (see for instance Danielopol, 1989). There is another possibility: the ostracod retreats into the subsurface habitat, which serves as a refuge, in order to escape environmentally stressful conditions (abiotic or biotic ones) in surface habitats. Angelier (1953, 1962) showed that some oxyphilous water-mites actively colonized subsurface environments during the Pleistocene, when cold water, rich in oxygen, infiltrated the underground in large quantities. This hypothesis was first proposed by Viets (1940). The opposite view was expressed by Husmann (1975) who believes that lotic psychrophilous invertebrates took refuge in subsurface waters during the Pleistocene and the Holocene in order to find cooler waters than those existing in epigean habitats.

The three known *Cavernocypris* species are all psychrophilous, oxyphilous and rheophilous. We believe that they actively colonized the groundwater habitats in those localities where enough oxygen and low temperatures exist in subsurface.

C. coreana lives in an area with a mild climate but colonizes the caves with low water temperature. In the Seebach at Lunz, *C. subterranea* preferentially colonizes the deeper layers of the sediments. There is no temperature difference between the surface and the water flowing at a depth of one metre in the sediment (Bretschko, pers. comm.). As already mentioned, the interstitial water, at a depth of one metre, has a high oxygen content. We have no argument in favour of the hypothesis that any of the *Cavernocypris* species retired into the subterranean habitats because of increasing temperatures in the surface waters. The species still lives in surface habitats with cold water in the alpine area.

C. subterranea is considered by Wolf (1920) as being a glacial relic. Thienemann (1950) believes that the species only recently, i.e. during the Quaternary, penetrated into the groundwater. The occurrence of *C. subterranea* in Central Asia at more than 1000 m a.s.l. in both groundwater and surface water habitats (Akatova, 1950; Hartmann, 1964) and the presence of *C. coreana* in an area of mild climate, indicate that the occurrence of *Cavernocypris* in subterranean habitats is not exclusively dependent on the cold climate events of the Quaternary. However, the water temperature in the above mentioned korean caves remains low (8 - 14 °C, a range of temperature which is similar to that found in Central Europe). The *C. subterranea* populations at Lunz are distributed from 0 to 1 m depth in the riverbed sediments. The animals progressively migrate within the sediment and settle in the deeper layers. We interpret this behaviour as being an active choice. The arrival of new sediments during the high water periods at site 12B (Fig. 13) would theoretically give the animals the possibility to recolonize the upper layers. However (Fig. 15), we see that the population grows in the deepest layer, where the ostracods find more suitable environmental conditions.

Rouch & Danielopol (1987) showed that many invertebrates colonize subterranean habitats because of the fact that they are preadapted and have a wide ecological valence.

C. subterranea shows several preadaptive morphological structures, such as the small carapace size and elongate carapace shape and the structure of the limbs; but the species is already specialized in its thermic and oxygen requirements. Thus *C. subterranea* fits the paradigmatic model of Angelier (1962) well. If Husmann's (1975) refuge model were true, then populations of *C. subterranea* inhabiting groundwater should only be found in lowland regions of Central and Western Europe; moreover, only epigean dwelling populations should be found in the cold mountain water habitats of Central Europe (Switzerland, Austria...) and Central Asia. But this is not the case (see above and also the biogeographic part below) and we have to conclude that Husmann's refuge model is not in agreement with the ecology of *C. subterranea.*

5. BIOGEOGRAPHY

5-1. Geographic distribution of *Cavernocypris*

The representatives of the genus *Cavernocypris* exclusively occur in the Holarctic.

5-1-1. *Cavernocypris subterranea*

Cavernocypris subterranea is known from recent and fossil populations distributed in the Palaearctic, i.e. Europe and Central Asia. In Europe, the species is found in mountainous hilly areas (mainly 200 m a.s.l.) especially (a) in the Alps and in the Carpathians and (b) at lower altitudes in the hilly areas in Central and Western Europe.

(a) In the Jura mountains Wolf (1920) recorded the species from various localities on the northern and eastern side of these mountains, up to 1100 m a.s.l., located mainly in the Basel surroundings (e.g. Passwang, Kellenkopli, Pelzmühlen valley, etc). Wolf (op. cit.) also found the species at 2300 m a.s.l. in the Lower Fluela lake. In the French Jura mountains, the species was collected in numerous karstic springs: at Villards d'Héria, Molinges (Barthélémy, 1984) and Montperreux (Vervier et al., 1986).

In Austria, the species occurs in Tyrol around Innsbruck, between 600 and 1200 m a.s.l. (Löffler, 1963). In the Eastern Alps, *C. subterranea* occurs in Lower Austria, at Lunz, 600 m a.s.l. (Marmonier, 1984) and in the Hochschwab Mountains, at 750 m a.s.l. (Löffler, 1963; Bretschko, 1966). On the southern side of the Alps, *C. subterranea* was found in a cave near Castello Tesino (Trento province) at 925 m a.s.l. (leg. R. Gasparo, Triest).

In the Carpathians, *C. subterranea* was found in Slovakia (Petkovski, 1966) on the slopes of the Homolka Mountain. Other localities are in the Dievcia Valley, in the Dobsina glaciated cave. In Moravia, Absolon (1974) mentioned the species at Sulovskych Skal.

In Poland, Sywula (1974, 1981 and pers. comm. to D.L.D.) found the species in the Sudety, Beskid and Turbacz Mountains, e.g. around the town of Klodzko and Zakopane.

In Rumania, Danielopol (1965) recorded the species from the Moldova spring in the Carpathians at more than 1000 m a.s.l.

(b) In Europe, north of the Alps and Carpathian mountains, *C. subterranea* occurs at lower altitudes (around 200 m a.s.l. and less). In France, K. Wouters (pers. comm. to C.M.) found the species at Strouanne (Pas-de-Calais) in springs situated at the base of a limestone cliff of the North Sea coast. These springs are located about 10 m a.s.l. Other localities were mentioned by Klie (1937), Leruth (1939) and Wouters (1983). They stem from the Ardennes Mountains, e.g. at Hombourg near Liège, at Tohogne and Ethe near Buzenol. Wouters & Bless (1986) reported the species from South Limbourg in the Netherlands.

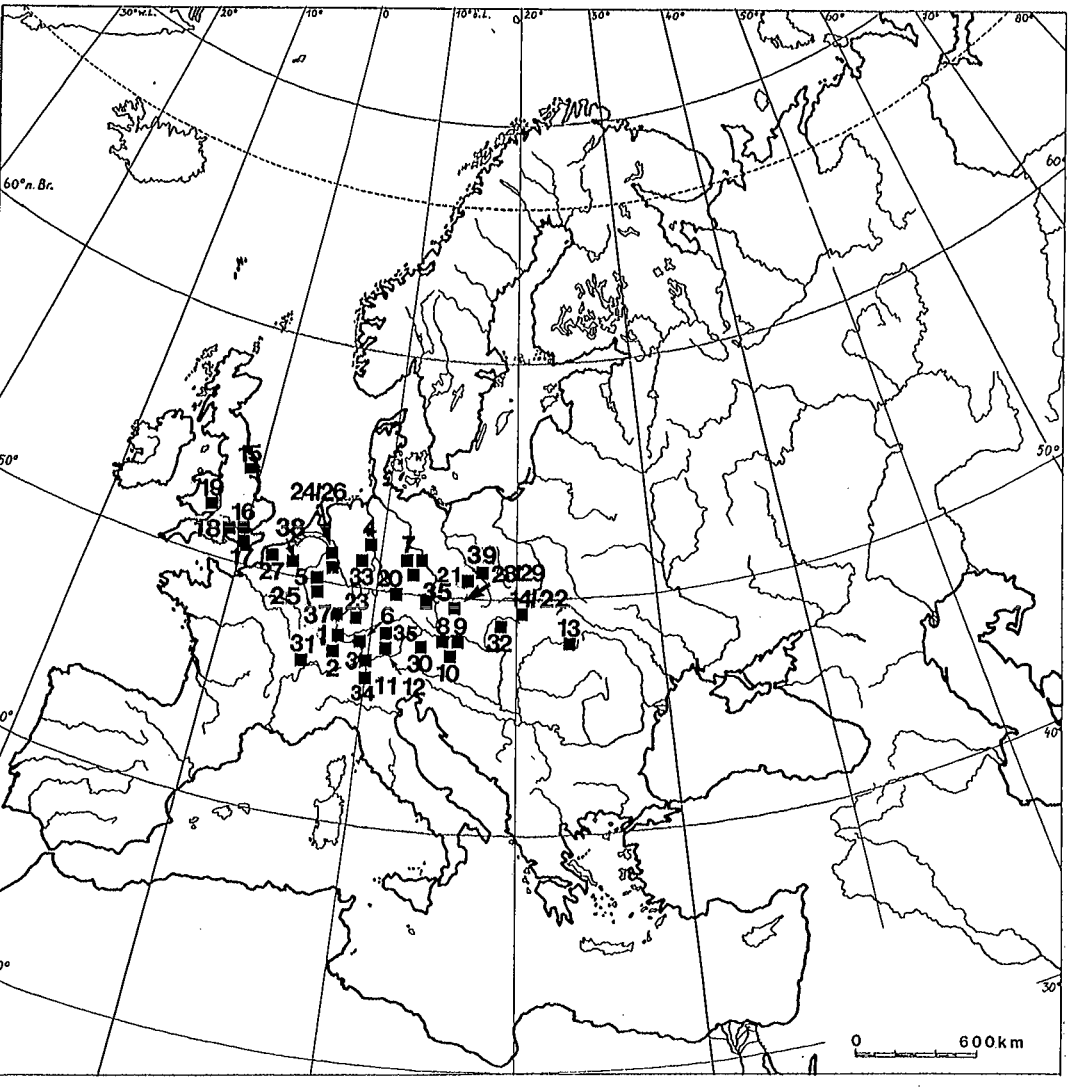


Fig. 17. - *Cavernocypris subterranea*: geographic distribution in Europe.

In the prealpine zone, Löffler (1961) identified the species in the Wutach valley in the Black Forest at about 500 m a.s.l., Janz (1983, 1988) found the species at Schönbuch near Tübingen. In Switzerland, the species was recorded in the Rhine valley close to Basel (Wolf, 1920). In Upper Austria it occurs around Mondsee at less than 500 m a.s.l. (this paper), in Lower Austria, Bretschko and his students found one specimen in the gravel of the Danube river at Altemwörth near Krems, at 200 m a.s.l. In Franconia (FRG) Nüchterlein (1969) collected the species near Erlangen and Nürnberg. In the German Democratic Republic, the species occurs south of Greiz in Thuringia (Petkovski, 1962; Wegelin, 1966). Ronneberger (1975) recorded the species in numerous localities situated in the drainage basins of the rivers Saale, Orla, Schwarza and Roda in Thuringia, south of Erfurt and Jena.

Dittmar (1955) collected the species in a small stream (the Aasbach river) in the Sauerland in the Rothaar mountains (FRG), at 500 to 300 m a.s.l. Absolon (1975) found the species at Krivoklat in Bohemia, west of Prag. Klie (1925) mentioned the species at Bad Pyrmont in the spring of the Löwenser Bach. The same author mentions an unidentified cypridopsine closely related to *C. subterranea* from Körmöcbanya in the Hungarian Carpathians at 1100 m a.s.l. (Klie, 1939; at present, it is not clear which was the exact species examined by the author).

In Great Britain, Fox (1967) found the species (a) in Surrey, in a spring at Paines Hill, (b) in Sussex, in a spring at Newtimber Place, (c) in Buckinghamshire, in a spring near Dagnall, (d) in Yorkshire, in a spring at Malham Tarn and (e) in Breconshire, in the Ffynon Dhu cave at Pen-y-cae. The locality in Yorkshire (about 54° OO'N 1° OO' E) is the northernmost recent locality hitherto known of the species.

As a fossil, *C. subterranea* is known from Holocene travertine (= tufa) sediments from Czechoslovakia (Absolon, 1973) i.e. in Slovakia at Sulov, in Moravia at Pusty Zleb, in Bohemia at Dobromerice, Bilichov, Murichruv Dolec, Krivoklat.

In the German Democratic Republic, Diebel & Pietrzeniuk (1978) mentioned the species from Pleistocene sediments (Eemian Interglacial) at Burgtonna, NW of Erfurt. The same authors (1975, 1980) recorded the species from the Holocene sediments of Bad Langensalza (near Burgtonna) and from Weimar and Bilzingsleben. M. Handl (unpubl.) found the species in the Late Glacial sediments of a shallow lake, the Haleswiessee, near Mondsee (Austria). Krstic (1988) recorded the species (as *C. subterranea germanica*) from Middle Pleistocene sediments in the Middle Banat in Yugoslavia: the species is characterized by the author as being a stagnophile fluviatile species. The last record is the southernmost fossil locality hitherto known for the species in Europe. In northern Europe, Preece et al. (1984) recorded the species in a deposit of early Flandrian tufa (about 9700-6000 B.P.) from Scotland (near Inchrory in Glen Avon, Banffshire). The tufa 'was deposited by springs trickling across wet ground'. This is the northernmost fossil locality of the species in Europe (about 57°09'20''N 3°22'W).

In Central Asia, Hartmann (1964) mentions *C. subterranea* in caves around Kabul and in the Ghourband valley (at Tchachmeh Khadar, Kotuk

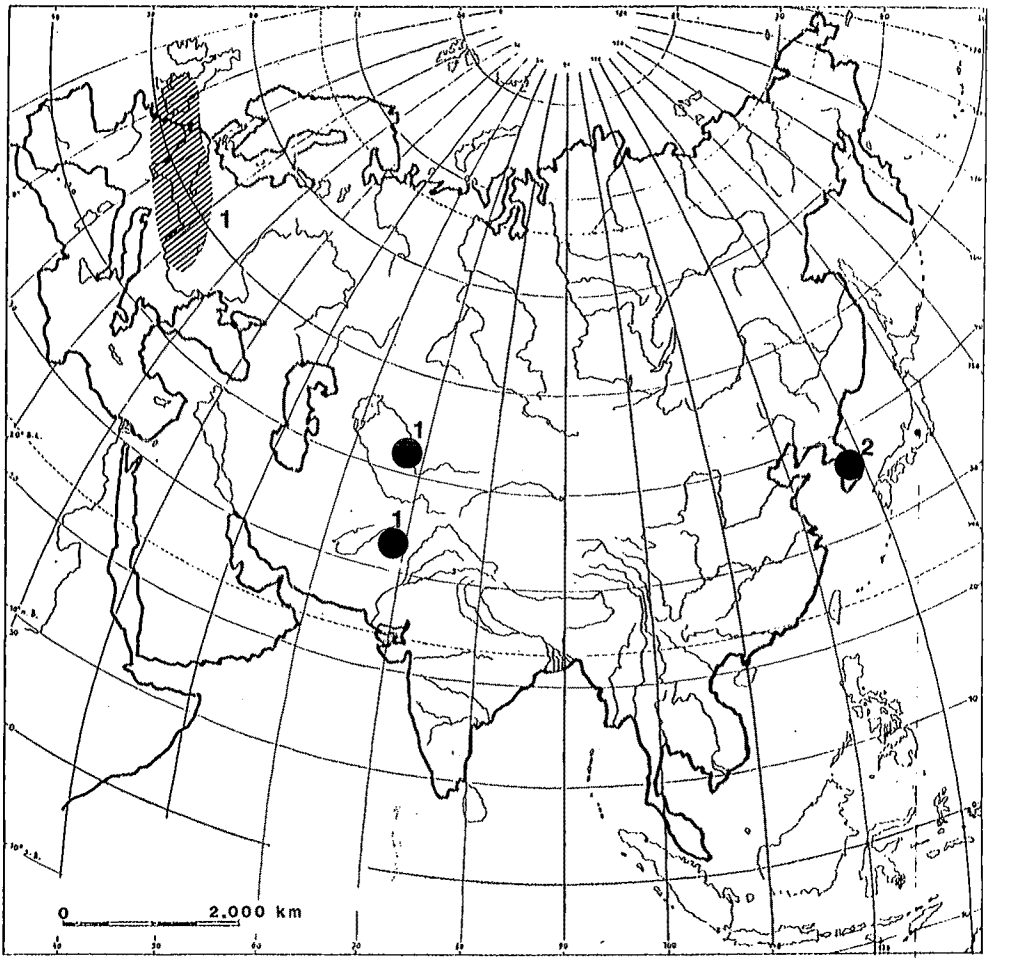


Fig. 18. - World-wide geographic distribution of *C. subterranea* (1) and *C. coreana* (2).

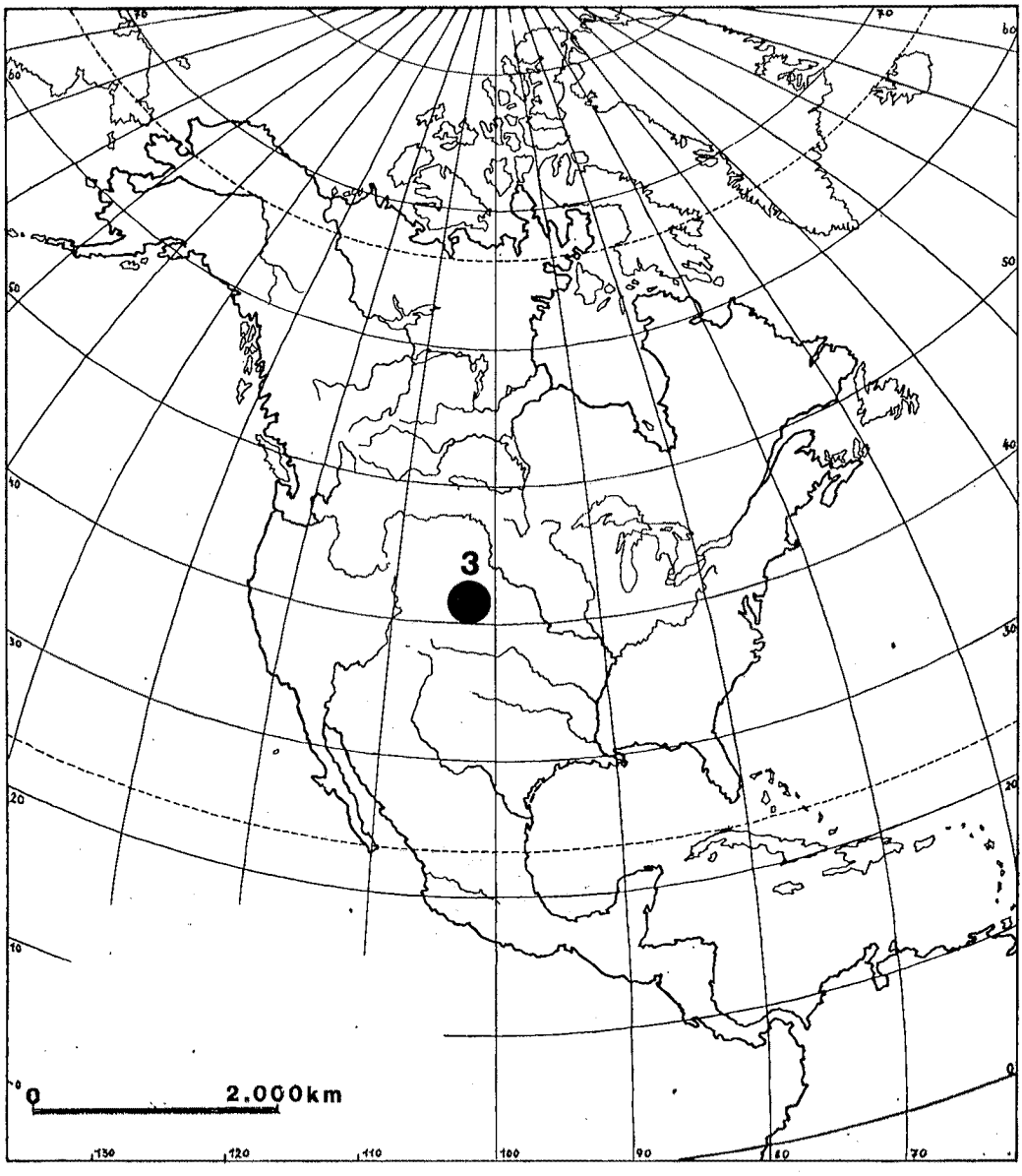


Fig. 19. - Geographic distribution of *Cavernocypris wardi* (3).

and Nayak) at above 2000 m a.s.l. In Tadzhikistan (Soviet Union), Akatova (1950) identified the species in samples collected in high mountain areas from 1000 to 2600 m at Hodjambino, Mazor and Saradjoi.

5-1-2. *Cavernocypris coreana*

C. coreana occurs in several caves in South Korea (McKenzie, 1972) at 36-37° latitude and 128-129° longitude (i.e. Chilsibri-gul, Sinryeong-gul, Daeya-gul, Simbog-gul, Mosan-gul and Kwangcheon-seon-gul). The caves are located in low-lying areas between 190 and 650 m a.s.l. in a wooded zone which has never been glaciated (Frenzel, 1959). It is worth noting that during the last glaciation, glaciers did not develop in Korea and that the snow limit for the southern part of the peninsula was at 2500 m a.s.l. whereas at present it is at 370 m a.s.l. (Frenzel, 1959).

5-1-3. Cavernocypris wardi n.sp.

C. wardi was found in the under-flow of the South Fork of the South Platte River, Colorado, 46 km SSW of the city of Denver (USA), at 1863 m a.s.l. (Pennak & Ward, 1986). Glaciers in that part of Colorado extended down to about 2400 m a.s.l. during the last major glacial recession. So the locality was not glaciated during the Pleistocene (J. Ward, pers. com. to P.M.).

5-2. Origin and dispersal pathways of the *Cavernocypris* species

The present data on the phylogenetical affinities and the biogeography of *Cavernocypris* species offer various possibilities to speculate about their origin and their dispersal pathways. If one accepts that *C. coreana* is the most primitive species, one can postulate that from a center of origin in southern Asia various species migrated westwards towards central Asia and Europe and eastwards towards North America. Klie (1925) speculated that *C subterranea* in Central Europe at Bad Pyrmont (at 52° latitude) is a glacial relic. The species spread there during the Pleistocene cold climate period.

If one accepts Illies' (1983) point of view that the center of origin of a taxon is that with the widest and most continuous distribution, then the European area where *C. subterranea* occurs should be considered as the center of origin of the genus *Cavernocypris.* We reject such hypothetical solutions. Most probably, *Cavernocypris* is an old antequaternary group with a wide geographical distribution. This hypothesis is plausible if we consider the presence of *Cavernocypris* in such distant areas as South Korea, Afghanistan, Western Europe and North America. We propose as a working hypothesis that, at the origin, *Cavernocypris* had a generalized Holarctic distribution. The species occupied cold water habitats mainly in mountain regions

during the Tertiary. From there, during the Quaternary, some species spread in the lowlands. This is the case especially of *C. subterranea* in Western and Central Europe. It first colonized the cold waters of the travertine springs and littoral habitats of lakes in the prealpine and precarpathian zones; it further colonized the 'Mittelgebirge' zones in the Ardennes, Sauerland, Thuringia, Bohemia. Once arrived there, it actively colonized subsurface habitats too and as a result the species is found at present in subsurface and surface habitats which have cold and well oxygenated waters. As Thienemann (1950) noted that during the Late Glacial and at the early Holocene groundwater habitats in northern Europe were poorly developed and most probably badly oxygenated, this may explain why *C. subterranea* did not colonize groundwater habitats in the northern part of the Palaearctic region. Why this species did not colonize surface habitats (e.g. cold springs) in Northern Europe like *Nannocandona faba* (for this latter species, see Marmonier & Danielopol, 1988) remains a puzzle for us.

We know from the research of Löffler (1970) on the *Candonopsis* species from east African mountains (Kenya, Ruwenzori and Marwenzi), that psychrophilous ostracods, restricted to high mountain areas, still exist in tropical-subtropical areas. Danielopol & McKenzie (1977) showed that in Central and Northern Europe *Psychrodromus olivaceus* only occurs in parthenogenetic populations, while the amphigonic populations of this species live in high altitude zones (Caucasus, at 12600 m a.s.l. and Macedonia, at 1200-1300 m a.s.l.). Most probably, the species spread northwards during Quaternary cold climate periods from such mountain areas. Likewise, we consider it possible that *C. subterranea* spread widely during the Quaternary from high mountain prequaternary populations which pre-existed in Central Asia and Europe. The present day distribution of *C. subterranea* in areas covered by ice during the Quaternary (i.e. the Austrian and Swiss Alps) is due to a colonization during the Late Glacial and the Holocene times.

The distribution of *C. coreana* was not dependent on the Quaternary glaciations and apparently was not at the origin of populations which migrated eastwards or westwards.

C. wardi is a species the history of which has to be looked for in North America. There is no evidence that this species originated either from Europe or from South East Asia and spread from there (e.g. via Beringia), as one might postulate for other ostracods like *Cytherissa lacustris* (Danielopol, in prep.).

We now see that the *Cavernocypris* species have always been prone to colonizing cold waters. They migrated into the subsurface waters many times independently forming subterranean populations of *C. subterranea, C. coreana* and *C. wardi.* These independent colonizations of groundwater habitats disagree with the refuge hypothesis, but are in support of the active migration model of Rouch & Danielopol (1987).

6. LIST OF THE EUROPEAN LOCALITIES OF C. SUBTERRANEA (see Fig. 17)

REMARK: the Polish localities were given to D.L.D as a pers. comm. by T. Sywula. Only the formerly published data were included in the list below.

1 Switzerland, environs of Basel, springs and chambers of spring-catchments (most abundant in the valleys of Pelzmühle and Kaltbrunnen)

2 Switzerland, eastern and northern slopes of the Jura mountains, springs

3 Switzerland, the Lower Fluela lake (2300 m a.s.l.) (for 1-3, see Wolf 1920 and 1921)

4 Germany (FRG), near Bad Pyrmont, 2 springs of the 'Löwenser Bach' (Klie 1925, 1938)

5 Belgium, Néblon (Tohogne), spring (Klie 1937, Leruth 1939)

6 Germany (FRG), Black Forest, Wutach basin (the Wutach is a tributary of the Rhine) (Löffler 1961)

7 Germany (GDR), Thuringia: (a) 4 localities (springs) (Petkovski 1962); (b) 49 localities (wells and springs) in the basins of the rivers Saale, Orla, Schwarza and Roda (Ronneberger 1975); (c) 1 spring, about 80 km SSW of Leipzig (Wegelin 1966)

8 Austria, Hochschwab, Grüner See (Löffler 1963, Bretschko 1966)

9 Austria, Ybbs near Langau (Löffler 1963)

10 Austria, Lunz, interstitial riverbed sediments of the Seebach (Löffler 1963, Marmonier 1984 and this work)

11 Austria, near Innsbruck, 5 localities, interstitial milieu (Löffler 1963)

12 Austria, Tyrol, Moosbachtal (Löffler 1963)

13 Rumania, Maramures region, spring of the Moldova (Danielopol 1965)

14 Czechoslovakia, Slovakia, 6 localities (springs) (Petkovski 1966)

15 Great Britain, Yorkshire, near Malham Tarn, spring

16 Great Britain, Surrey, at Paines Hill, spring

17 Great Britain, Sussex, near Newtimer Place, spring

18 Great Britain, Buckinghamshire, near Dagnall, spring

19 Great Britain, Breconshire, at Pen-y-eae, the Ffynon Dhu cave (Fox 1967) (for 15 - 19, see Fox 1967)

20 Germany (FRG), Franconia, springs (Nüchterlein 1969)

21 Poland (South), near Klodzko (Sywula 1981)

22 Poland (South), the Beskid mountains, the stream Potok Olszowy and springs, 10 km NE of Nowy Targ

23 Germany (FRG), Schönbuch near Tübingen (Janz 1981, 1988)

24 Belgium, province of Liège, Hombourg, 2 wells (Wouters 1983)

25 Belgium, Gaume district, at Ethe near Buzenol, a small stream (Wouters 1983)

26 The Netherlands, southern Limburg, a spring at Heerlen-Welten, Putberg (Wouters & Bless 1986)

27 France, coast of the North Sea, near Strouanne, spring (K. Wouters, pers. com.)

28/29 CSSR, Bohemia, springs (Absolon 1975)

30 Austria, village of Wangau, near Mondsee (leg. D.L.D.)

31 France, southern Jura mountains
a) dep. Doubs, commune de Montperreux, Source Bleue (Vervier et al. 1986)
b) dep. Jura, commune de Molinges, sources de l'Enragé and commune de Villards d'Héria, source de l'Héria (Barthélémy, 1984)

32 CSSR, Slovakia, springs at Sulovske Skaly (Absolon 1974)

33 Germany (FRG), Sauerland, near Albaum, the Aabach stream and its springs (Dittmar 1955)

34 Italy, province of Trento, Grotta di Castello Tesino, cave (leg. R. Gasparo, unpubl., pers. comm. to D.L.D.)

35 CSSR, northern Moravia (Mähren), basin of the river Odra (Oder), 2 loc., about 3 and 20 km SW of Ostrava (Kantorek 1976, 1983)

36 CSSR, Bohemia, springs at Krivoklat (Absolon 1975)

37 France, dep. Meurthe-et-Moselle, Villers-les-Nancy, spring-catchment (Dolbec 1947)

38 Belgium, a spring near Wauthier-Braine, about 22 km S of Brussels (leg. A. Van Frausum, pers. comm. to C.M.)

39 Poland, Silesia, a well at Reyersdorf (leg. Stammer) (W. Klie collection)

7. DETAILED LIST OF THE MATERIAL EXAMINED

Cavernocypris subterranea (Wolf, 1920)

1. Austria, near Lunz am See, RITRODAT area on the Seebach, interstitial milieu, leg. G. Bretschko. Many alcohol tubes with very numerous specimens from the ecological study of the underflow od the stream.

2. Germany (FRG), from a spring near Bad Pyrmont, 1 alcohol tube labelled 'Seitenquelle vom Löwenser Bach am Fuße des Schellenberges, 4. August 1923; coll. Klie'. Glycerine tube with more than one hundred specimens. Klie collection (ZMH, reg. n. 1123).

3. Germany (FRG), near Bad Pyrmont, same locality as sub 2, but from 3rd of August 1927. Glycerine tube with several hundred specimens. Klie collection (ZMH, reg. n. 1120).

4. France, near Nancy, dep. Meurthe-et-Moselle, 'source de l'Asnée', Grand Séminaire, at Villers-les-Nancy, leg. R. Dolbec (see Dolbec 1947) Klie collection (ZMH, reg. n. 1121). Glycerine tube with 6 specimens.

5. Poland, Silesia: from a well at Reyersdorf, leg. Stammer 10.8.1939. Klie collection (ZMH, reg. n. 1122. Glycerine tube with 1 valve.

6. Belgium, from a spring near Néblon, leg. R. Leruth 9.8.1936. Klie collection (ZMH, reg. n. 1122). Glycerine tube with 1 specimen and 2 valves.

7. France, springs of the southern Jura mountains, leg. D. Barthélémy, J. Gibert and Ph. Vervier. Alcohol tube with 3 specimens.

8. Afghanistan, from 3 caves, leg. Lindberg. Hartmann collection (ZMH, reg. n. 27646). Glycerine tube with about 50 specimens. Type-material of *Cavernocypris* Hartmann, 1964.

9. Germany (GDR), Holocene specimens from Weimar (Parkhöhle) (voir Pietrzeniuk 1985).

Cavernocypris coreana (McKenzie, 1972)

9. *Cavernocypris coreana coreana elongata*: South Korea, Kwansan-ri, Mosan-gul cave, leg. Y. Morimoto in April 1966 (see McKenzie, 1972). 4 fem., 3 males and 2 juvenils examined: type-specimens of *C. coreana elongata,* deposited in the British Museum (Nat. Hist.), reg. n. 1970-2-10-6.

Cavernocypris wardi n. sp.

10. U.S.A., Colorado, South Fork of the South Platte River, 46 km SSW of the city of Denver (interstitial milieu, 0.50 m depth). Alcohol tube with 18 fem. specimens. Type-material deposited in the Institut Royal des Sc. Nat. de Begique in Brussels.

NOTE: the Klie and the Hartmann collections are deposited in the Zoological Museum of the University of Hamburg. The Klie collection is a permanent loan of the Univ. of Kiel to the Zoological Museum of the Univ. of Hamburg.

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REMARK: The references marked with an asterisk include useful indications for the recent and/or fossil occurrence of *Cavernocypris.*

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