

Revision of the genus *Leucocythere* KAUFMANN, 1892 (Crustacea, Ostracoda, Limnocytheridae), with the description of a new species and two new tribes.

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Summary

The main aim of the present contribution is to provide an unequivocal diagnosis of the genus *Leucocythere*. It appeared, however, that this could only be effected when embodied in a broader taxonomic framework. The subfamily Limnocytherinae is thus divided into four tribes: Limnocytherini, Dinarocytherini, Cytheridellini and Leucocytherini and diagnoses are provided for these taxa. The latter two are new to science, while the rank of Dinarocytherini was changed from subfamily to tribe. Three genera are lodged in the Leucocytherini: *Leucocythere* KAUFMANN, 1892, *Potamocythere* SCHORNIKOV, 1986 and *Ovambocythere* MARTENS, 1989. The former, nominate, genus is characterized and its type species, *L. mirabilis*, is extensively redescribed. A comparative description of a limnocytherinid with a somewhat similar appearance, *Limnocythere (Limnocytherina) sanctipatricii*, is offered. A second species of *Leucocythere*, *L. algeriensis* nov. sp., is described from a temporary pool in Algeria. *L. baltica* (DIEBEL) is retained as a third species in the genus. A large number of fossil records is reassessed. Most of the Asian fossils, previously assigned to *Leucocythere*, do not belong in this genus and a revision of their status appears urgent. Some remarks on the validity and position of *Leucocytherella* are also offered.

L. mirabilis is a cold-stenothermic species, with a preference for oligotrophic waters and fine grained sediments. Its status in Europe can at present best be described as endangered, due to rapid degradation of suitable habitats.

L. algeriensis nov. sp. and *Ovambocythere milani* MARTENS are probably both capable of producing dry resistant stages. This is thus far unique in Cytherids, but the exact taxonomic distribution of this feature remains as yet unknown.

Some comments on the phylogeny and historical biogeography are presented. *Leucocythere* appears to be the more advanced group in the Leucocytherini, the other two genera show more plesiomorphic character states. It is here postulated that the three genera evolved by vicariance from a more widely spread ancestor: *Leucocythere* in Europe, *Potamocythere* in Asia and *Ovambocythere* in Africa. *L. algeriensis* from northern Africa is doubtlessly from Palaearctic stock and its speciation from *L. mirabilis* must have occurred fairly recently. A number of morphological peculiarities of *L. mirabilis* are discussed with special attention for the carapace and for those soft parts that are used for the mating process. In spite of the fact that many of the peculiarities appear maladaptive at first glance, it must be stressed that *L. mirabilis* thus far maintained itself very well in its environment, until recent anthropogenic pollution caused its extinction in many localities.

Keywords: *Leucocythere*, Ostracoda, Leucocytherini, Cytheridellini, morphology, biogeography, functional morphology.

Résumé

Le but principal de cet article est de fournir une diagnose claire du genre *Leucocythere*. Pourtant, il apparaît que ceci ne peut être effectué que

dans un cadre taxonomique plus large. La sous-famille des Limnocytherinae est donc divisée en quatre tribus: Limnocytherini, Dinarocytherini, Cytheridellini et Leucocytherini et des diagnoses sont fournies pour ces taxa. Les deux dernières sont nouvelles pour la science. Trois genres se situent dans les Leucocytherini: *Leucocythere* KAUFMANN, 1892, *Potamocythere* SCHORNIKOV, 1986 and *Ovambocythere* MARTENS, 1989. Le genre nominal est caractérisé et l'espèce-type, *L. mirabilis*, est rédescrite extensivement. Une description comparative est effectuée avec un limnocytherinide semblable: *Limnocythere (Limnocytherina) sanctipatricii*. Une deuxième espèce du genre *Leucocythere*, *L. algeriensis* nov. spec., provenant d'un habitat temporaire en Algérie, est décrite. *L. baltica* (DIEBEL) est retenue comme une troisième espèce de ce genre.

Un important matériau fossile est réexaminé. La majorité des fossiles asiatiques, qui dans le passé étaient considérés comme les *Leucocythere*, ne peuvent plus rester dans ce genre et leur révision reste nécessaire. Quelques remarques sur la validité et la position de *Leucocytherella* sont développées en même temps.

L. mirabilis est sténotherme des eaux froides et marque une préférence pour les eaux oligotrophes et les sédiments fins. Son statut en Europe peut être actuellement considéré comme précaire, étant donné la dégradation rapide de son milieu.

L. algeriensis nov. sp. et *Ovambocythere milani* MARTENS sont probablement tous deux capables de produire des formes résistantes à la sécheresse. Ceci est unique dans les Cythérides, mais la repartition taxonomique exacte de ce caractère n'est pas bien connue.

Quelques commentaires sur la phylogénie et la biogéographie historique sont présentés. *Leucocythere* semble le groupe le plus évolué dans les Leucocytherini; les deux autres genres montrent des caractères plus plésiomorphes. Il est postulé que les trois genres ont évolué par vicariance, d'un ancêtre plus répandu: *Leucocythere* en Europe, *Potamocythere* en Asie et *Ovambocythere* en Afrique. *L. algeriensis* de l'Afrique du Nord provient du stock paléarctique et spéciation de *L. mirabilis* a dû se faire tout récemment. Un nombre de particularités morphologiques de *L. mirabilis* sont discutées, avec une attention spéciale pour la carapace et les pièces molles qui sont utilisées dans la copulation. Malgré qu'à première vue beaucoup de ces particularités ne semblent pas bien adaptées, il est incontestable que *L. mirabilis* se maintient très bien dans son milieu, pourvu qu'une pollution anthropogée récente ne cause pas son extinction dans beaucoup d'endroits.

Mots-clefs: *Leucocythere*, Ostracoda, Leucocytherini, Cytheridellini, Dinarocytherini, morphologie, biogéographie, morphologie fonctionnelle.

1. Introduction

The family Limnocytheridae SARS, 1925 is one of the most common non-marine ostracods groups. The oldest species were found in the early Mesozoic and since that time, this group expanded on all continents

(COLIN & DANIELOPOL 1980, KOZUR 1973, WHATLEY & STEPHENS 1976). Within de Limnocytheridae, COLIN & DANIELOPOL (1978) recognised two distinct phyletic lineages: the Limnocytherinae SARS, 1925 and the Timiriaseviinae MANDELSTAM, 1960. These two subfamilies are defined by both soft part and valve characters. With regard to the latter, it is here stressed that the Limnocytherinae have carapaces with sieve pores, whereas the Timiriaseviinae appear to lack such structures.

The work of COLIN & DANIELOPOL (1978, 1980) has contributed towards a better understanding of the taxonomy of the Timiriaseviinae, but the phylogeny and systematics of the Limnocytherinae still remain highly obscure. It is indeed very difficult to identify phylogenetical relationships between the various limnocytherine ostracod groups. This is due mainly to the fact that many taxa in the past have been described in a superficial and inadequate way, and the only approach to improve on this situation is to (re-)describe the different taxa as careful and complete as possible. Only then can they be integrated in a phylogenetic system. An example of such an approach is the work of MARTENS (1986, 1988) on a subfamily of the Cyprididae. The present paper hopes to contribute towards a similar work on the Limnocytherinae.

The genus *Leucocythere* was erected by KAUFMANN (1892) to comprise a single species, *L. mirabilis*. This remarkable species doubtlessly belongs to the Limnocytherinae (COLIN & DANIELOPOL, 1978). It was first discovered in a number of prealpine lakes in Switzerland (KAUFMANN, loc. cit.) and was subsequently found in other parts of Europe on rare occasions (see below). More recently, however, *L. mirabilis* and several new *Leucocythere* species were described from Eastern Asia, i.e. in the Peoples Republic of China (HUANG 1982A, B, 1985, HUANG *et al.* 1982, 1985, ZHAO 1987A, B, YANG *et al.* 1982). From a biogeographical point of view, these records are highly interesting and require an explanation in terms of evolutionary and historical causes.

The morphology of the single living *Leucocythere* species known to date (*L. mirabilis*) is very peculiar, if compared to other Limnocytherinae. One could therefore ask if KAUFMANN's taxon is not a monstrous *Limnocythere*, a sort of macromutation of a *Limnocythere* like species (for a more detailed account of this subject, see below). An alternative view has been expressed by COLIN & DANIELOPOL (1978), who considered this species as the representative of a distinct phyletic line within the Limnocytherinae, next to the three other lineages: the Limnocytherini and the *Gomphocythere* and *Cytheridella* groups. Both views, however, are highly speculative and demand a re-examination of the systematic and phylogenetic position of the genus *Leucocythere* within the entire subfamily Limnocytherinae. Such a revision would necessarily start with an exhaustive redescription of the type

species. *L. mirabilis*, in order to firmly establish a diagnosis of the genus to which the fossil so-called congeners from Eastern Asia could then be tested. Unfortunately, *L. mirabilis* seems to have all but disappeared from the pre-alpine lakes in Europe during the past 50 years (LOFFLER 1983 A, B, DANIELOPOL *et al.* 1985), mainly due to various forms of anthropogenic pollution. As a good number of specimens is necessary for such a redescription, this appeared a near to impossible task. However, the localisation of a number of healthy populations of this species (SCHARF, pers. comm. - see below), the unexpected discovery of a new species of *Leucocythere* from Algeria by one of us (KM) and the recent description of 2 new limnocytherine genera (*Potamocythere* SCHORNIKOV, 1986 and *Ovambocythere* MARTENS, 1989), clearly related to *Leucocythere*, made the present revision of this group within an evolutionary framework possible. It is our hope that the present contribution will stimulate similar work on related groups, so that our evolutionary and biogeographical models can be corroborated or falsified.

2. Material investigated

2.1. List of Museums and institutions

KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen (Brussel, Belgium)
HNHM	Hungarian Natural History Museum (Budapest, Hungary)
MNHU	Museum für Naturkunde der Humboldt Universität zu Berlin (Berlin, DDR)
LYON	Dept. of Geology, University of Lyon (Lyon, France)
SAM	South African Museum (Cape Town, RSA)
ZIZM	Zoologisches Institut und Zoologisches Museum (Hamburg, DBR)

2.2. Material investigated

Leucocythere mirabilis

* *Mondsee* (Upper Austria): (living and fossil) specimens were collected in the course of an intensive sampling program between 1984 and 1987. For more details, see DANIELOPOL *et al.* (1985, 1988). Fossil material: numerous valves from both the lower sublittoral (6-12 m deep) and from the deeper parts of the lake (20-60 m). Only 8 living specimens were found: 1 ♂ + 1 ♀ at a depth of 20 m in front of Loichbichl; 3 ♀ + 2 juveniles at 12 m depth at side MO-7 (Mooswinkel); 1 juvenile (last instar) at 22 m depth in the southern part of the lake.

* *Attersee* (Upper Austria): 1 living ♀, collected at a depth of 20 m, in front of Weyregg (leg. Dr P. NEWKLA, University of Vienna, Austria).

* *Halleswiessee* (Upper Austria): several fossil (Holocene) specimens (leg. M. HANDL, University of Salzburg).

* *Thunner & Brienzler See* (Switzerland): several subfossil valves and prepared limbs of ♂ and ♀ (leg. Dr B. SCHARF, Mainz).

* *Baltic Sea*, Bothnian Bay at Karvo, opposite Haliluo-toIsland: 1 recent ♂ collected at a depth of 14 m (leg. S. POWELL & T. VALTONEN, University of Jyväskylä, Finland).

* ZIZM nos. 297 a, b: 1 ♂ + 1 ♀ (both Recent) from an astatic ditch on the island of Korfu (coll. T. STEPHANIDES): 2 slides with soft parts.

* MNHU nos. Pr. 2252: 4 fossil valves from Wolfshagen (Northern DDR) (for exact locality: see DIEBEL 1965A, see Figs. 7 H-P)

L. baltica

MNHU nos. 2549 R/c & 2550 R/a-d: 8 syntype valves from Sassnitz (for exact locality: see DIEBEL 1965A).

L. algeriensis

KBIN, nos. OC 1470-1472: 5 adult + 1 juvenile ♂, 11 adult + 2 juvenile ♀ from Oued Tesselata, Tassili-n-Ajjer, Algeria (leg. H.J. DUMONT).

Limnocythere (Limnocytherina) sanctipatricii

Lunz-Mitter See (Lower Austria) and *Mondsee* (Upper Austria): several subfossil and recent specimens of both sexes.

'*Limnocythere*' bressensis

LYON, no. FSL 135206: 3 valves (♀ + juveniles) paratypes from Miocene ("Tortonien lacustre"), Bresse (Eastern France) (leg. Dr G. CARBONNEL).

Gomphocythere obtusata

SAM, no. A11304, c. 30 good ♂ and ♀ in spirit.

Cytheridella ilosvayi

HNHM, no. D 1916-31: 21 specimens (♂, ♀, juveniles) in spirit, but with carapaces mostly decalcified and crushed.

Limnocythere inopinata

KBIN, no. OC1450: dissection of a ♂ + several ♂ and ♀ in spirit, collected from Dojransee, SE Macedonia (leg. T.K. PETKOVSKI).

3. Morphology

3.1. Morphology and terminology of the hemipenis

MARTENS (in press) developed a terminology for the

internal and external anatomy of the hemipenis of *Limnocythere* s.s., meanwhile adopting as many aspects as possible of HIRSCHMANN's (1912) model of the Cytheracean hemipenis. As a similar terminology is used here, we will commence by briefly recapitulating various aspects of the hemipenis morphology in the Limnocytherini and the Leucocytherini nov. trib. (see below). The other two tribes in the Limnocytherinae have a somewhat different type of hemipenis and these are not discussed here.

Hemipenes in these groups are large, occupying c. 1/4-1/3 of the male body cavity and consist mainly of the following parts: (1) the *peniferum*, in which different *rami* are incorporated, (2) a solid mass of different muscles, (3) an internal *labyrinth* and (4) external *copulatory complex*. In Cypridacea, the latter complex is situated internally and furthermore of a very different structure.

In Limnocytherinae, the *peniferum* is a semi-transparent sheet and envelops the muscles and the labyrinth. It has a frontal expansion, the *distal lobe*. Dorsally, a *movable trabecule* is present in some genera (not *Leucocythere*). The *copulatory complex* consists of a clasping organ (with upper and lower rami), a copulatory processus and the furcal setae which in the male are incorporated in the hemipenis. All these structures can have different shapes and functions in phylogenetically different lineages. For example, in *Limnocythere* s.s. and *Limnocythere (Limnocytherina)* it is the lower ramus of the clasping organ (or part of it), which forms the large, often hook-like expansion. In *Leucocythere*, both rami of the clasping organ are reduced to blunt, sclerotised plates and the hook-like structure is more or less formed by a larger furcal seta fl.

3.2. Morphology and terminology of the hinge

There is no consensus in the literature with regard to the nomenclature of the different types of cytheracean hinges. Adding new arguments to this discussion is beyond the scope of the present contribution and we therefore rely largely on the summary presented by HARTMANN (1966). However, as we will have to deal with aspects of this terminology previously applied in the literature on the Limnocytheridae, we will here briefly summarize the morphology of the different hinge types presently under discussion (see Fig. 1).

The different types of hinge that are found in most Limnocytherinae are in reality all variations of the *merodont* type. The most simple variant in the *lophodont* hinge: RV bearing an anterior and a posterior carinal tooth (both smooth) and a smooth intercardinal groove; LV with 2 corresponding cardinal sockets and a smooth intercardinal bar. The hinges present in the Limnocytherini and Leucocytherini are nearly all of a very similar type: frontal cardinal tooth smooth and weakly developed (sometimes nearly absent), posterior tooth mostly consisting of at least 3 lobes; intercardinal bar crenulated to a varying degree. This would approach

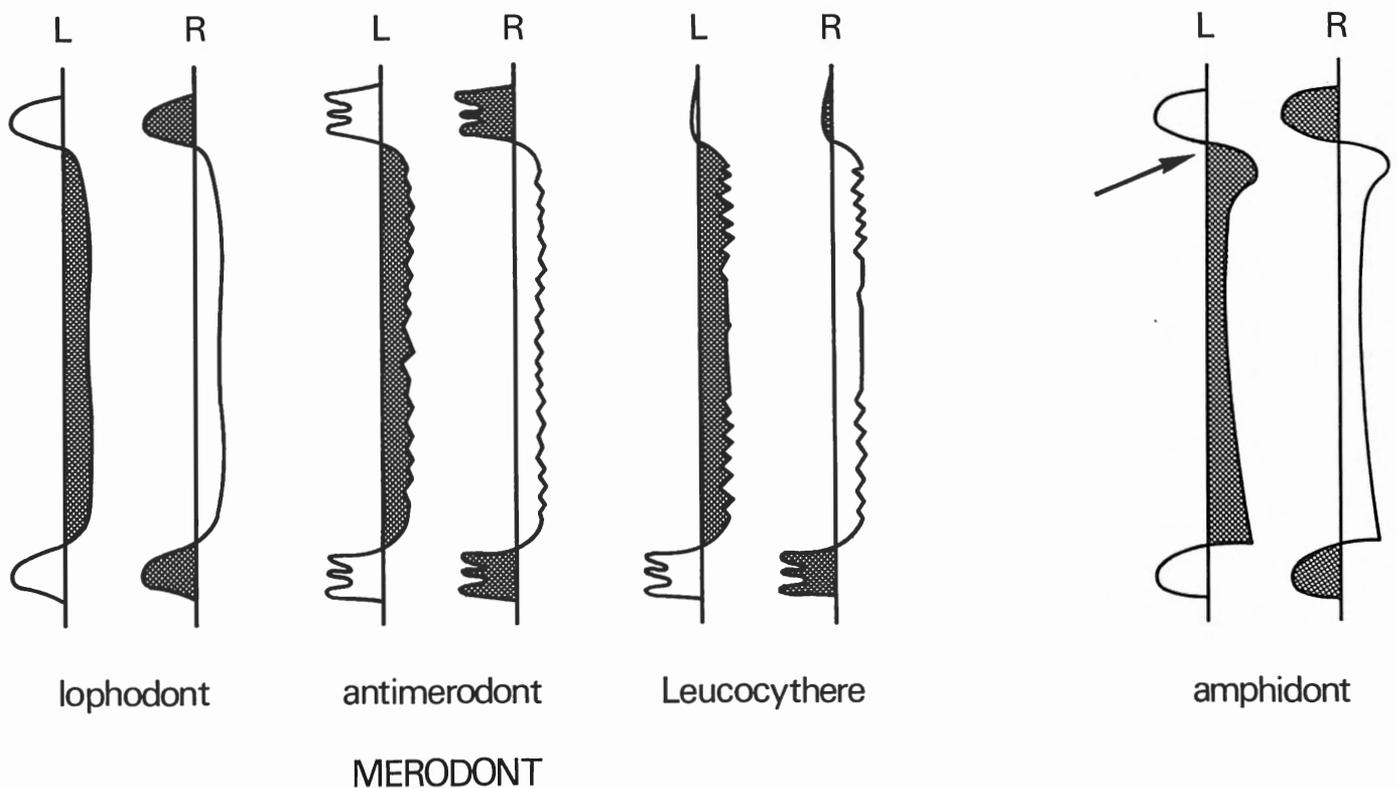


Figure 1. Schematic illustration of various types of hinges in the Limnocytheridae (partly based on Figure 51 in HARTMANN, 1966).

the *antimerodont* variation of the merodont type (HARTMANN, loc. cit.), yet in some species differs from it in the shape and the size of the frontal cardinal tooth on the RV. We are therefore careful in using the latter term and prefer to offer anatomical descriptions, rather than use an approximate term.

KRSTIC (1987) indicated that the Dinarocytherinae have *amphidont* hinges: this is like the lophodont structure, but with an additional (smooth or crenulated) tooth on the LV, posterior to the frontal cardinal socket, corresponding to an additional socket in the RV, just behind the frontal cardinal tooth. Especially figs. 6 and 8 of plate I in KRSTIC (loc. cit.) show this additional tooth on the LV quite clearly. It should furthermore be noted that in the former group, the cardinal bar can have its posterior part somewhat elevated, thus giving the impression that a second tooth is present on the LV. We will return to the latter hinge type when discussing the position of Dinarocytherinae.

3.3. Homology of the walking limbs

We do not wish to express an opinion on the homology of the three walking limbs. Whether the first limb is a second maxilla (Mx2) or the first thoracopod is of little importance for the primary aims of the present contribution. We will therefore use the sympols P(1) - P(3) to indicate these limbs, thus referring to their function and morphology, rather than to their presumed origin and homology.

3.4. Abbreviations used in text and figures

With regard to the nomenclature of the chaetotaxy of the various limbs, we follow the model proposed by BROODBAKKER & DANIELOPOL (1982). Part of the terminology of the hemipenis is similar to the one developed in MARTENS (in press).

Hemipenis

dip	distal part of cp
dl	distal lobe
hp	hook-like processus
mel	medial lobe
mp	medial processus (with lobes a, b, c)
co	clasping organ
cp	copulatory processus
dej	ductus ejaculatorius
f(1-3)	furcal setae 1 - 3
gl	glans of copulatory processus
lp	lateral processus
lr	lower ramus of clasping organ
p(1-4)	parts of the copulatory processus
prp	proximal part of cp
ur	upper ramus of clasping organ

Other soft parts

fu	furca (in female)
GeO	genital operculum (female)

A1	antennula
A2	antenna
Md	mandibula
Mx1	maxillula
P(1-3)	walking limbs
pc	pseudochaetae
s	seta

Valves

H	height of valves
L	length of valves
RV	right valve
LV	left valve

4. Taxonomic descriptions

Subclass	Ostracoda LATREILLE, 1806
Order	Podocopa G.W. MULLER, 1894
Suborder	Podocopa SARS, 1866
Superfamily	Cytheracea BAIRD, 1850
Family	Limnocytheridae KLIE, 1938
Subfamily	Limnocytherinae KLIE, 1938

REMARKS

Diagnosis of both the above family and subfamily were amply provided by COLIN & DANIELOPOL (1978, 1980) and we can at present add little to their work. However, it has to be stressed again that sieve pores have meanwhile been found in nearly all genera of the Limnocytherinae, so the absence of these structure is a feature of the Timiraseviinae, not of the Limnocytheridae as a whole.

KRSTIC (1987) erected the new subfamily Dinarocytherinae (exclusively fossil) within the Limnocytheridae and distinguished it from the nominate subfamily mainly on the basis of the presence of sieve pores. This argument is here clearly falsified. However, Dinarocytherinae can possibly be retained as a valid taxon on the basis of the presence of an amphidont hinge. If so, than this taxon still deserves at most the rank of a tribe, which is the approach adopted here (see below). Taking into account the importance of the differences between both subfamilies presently recognised within the Limnocytheridae (COLIN & DANIELOPOL, 1978, 1980), it is indeed impossible to accept Dinarocytherinae as a separate, third subfamily to date. COLIN & DANIELOPOL (1978) foreshadowed that the Limnocytherinae have to be divided into 4 tribes, at that stage describing 4 so-called 'groups' of genera. We here present somewhat extended diagnoses for three tribes (+ the Dinarocytherini) and assign the known genera to their appropriate groups. *Gomphocythere* and *Cytheridella*, placed in separate 'groups' by COLIN & DANIELOPOL (1978), are here lodged in the same tribe, together with the Australian genus *Gomphodella*. Future research will

show if the Cytheridellini need further subdivision or really constitute one natural group.

It proved impossible to decide upon the correct position of a number of fossil genera: *Denticulocythere* CARBONNEL, 1969; *Cladarocythere* KEEN, 1972; *Stenostroemia* CHRISTENSEN, 1968 and *Prolimnocythere* KARMICHINA, 1970. The position of *Leucocytherella* HUANG, 1982 is discussed in some detail in below.

Tribe *Limnocytherini* KLIE, 1938

ABBREVIATED DIAGNOSIS

Carapace strongly calcified, with a sexual dimorphism in the shape in lateral view, especially of the ventro-caudal margin: male with a strongly convex margin in the posterior part, not so in the female (the latter feature probably related to the strong development of the clasping organs of the hemipenis, see below). In dorsal view, no striking sexual dimorphism, i.e. females not developing brooding pouches. Hinge of the antimerodont variety (see above). No prominent sexual dimorphism in non-copulatory appendages. Hemipenis of the 'horizontal' type, with Ir of co building a large hook-like structure.

Genera: Limnocythere BRADY, 1968 (with at least the subgenera *Limnocythere* s.s. and *Limnocytherina* NEGADAEV-NIKONOV, 1968), *Paralimnocythere* CARBONNEL, 1965 (syn.: *Relictocythere* NEGADAEV-NIKONOV, 1968), (?) *Paracythereis* DELACHAUX, 1928 (nec JENNINGS 1936, nec ELOFSON, 1941, (?) *Neolimnocythere* DELACHAUX, 1928, *Galolimnocythere* SCHORNIKOV, 1973, *Athalocythere* SCHORNIKOV, 1986.

REMARKS

1. We here introduce the term *vertical type* of hemipenis present in the Cytheridellini nov. trib. (see below), and apply *horizontal type* for the hemipenis in the Limnocytherini and the Leucocytherini nov. trib.. The latter type is the one illustrated in the present contribution, with the main body of the hemipenis expanded between the proximal and distal lobes, thus creating a relatively wide margin on which the various parts of the copulatory complex are inserted. Horizontally expanded hemipenes have a more compressed body, with a very simple copulatory complex of which one of the elements forms a huge, sheet-like expansion.

2. The morphology of the hemipenis of the type species of *Limnocythere* s.s. (*L. inopinata*) was redescribed by MARTENS (in press) and the above diagnosis of course largely refers to this taxon. However, at least one other taxon belonging to this tribe is of interest for the present work. *Limnocytherina*, here considered as a subgenus of *Limnocythere*, has a well known European representative: *L. (L.) sanctipatricii* BRADY & ROBERTSON, 1868. LÖFFLER (1983A) wrote that the fact that

Leucocythere mirabilis was found so rarely in a number of pre alpine lakes (e.g. the Attersee) could at least partly be due to the close similarities in carapace morphology between *L. mirabilis* and *L. (L.) sanctipatricii*. In order to avoid confusion in the future, we here present, as an "ex-cursus", a comparative description of the latter species.

Genus *Limnocythere* BRADY, 1867
Subgenus *Limnocytherina*
NEGADAEV-NIKONOV, 1968

DIAGNOSIS

Hemipenis with lr a broad and divided expansion; ur large; furcal setae in ♂ altered to large, broad and sclerified processi

Limnocythere (Limnocytherina) sanctipatricii BR. & ROB., 1868
(Figs. 2, 3, 4, 6(O-R), 10(D-F))

DESCRIPTION OF ♂

Carapace (Figs. 2(A-C), 6(O-R)) convexely expanded in the posteroventral part; anterior margin narrower than the posterior margin, the latter also more broadly rounded. Anterior part of valves with 3rd anterior sulcus (as in *Leucocythere*, see below). Fused zone with longer and straight marginal pore canals (some variability possible in subrecent valves, due to decalcification processes). Dorsal margin straight or slightly concave. Hinge with cardinal sockets on LV, ventrally delineated by a bar, the latter however not closing the elongated socket; intercardinal bar smooth. Carapace ornamentation variable, in well calcified specimens the entire surface covered with shallow fossae, delineated by simple muri, secondary pits sometimes occurring in these fossae. In poorly calcified specimens, however, around anterior dorsal sulci, remaining fossae simple or with very attenuated pits and very slender muri (see plate II in TÖLDERER-FARMER, 1985). A rounded tubercle posterior to the central sulcus possible in some populations.

Non-reproductive soft parts all of the normal *Limnocythere*-type. A1 (Fig. 3B) with distal segment fairly elongated. A2 (Fig. 3D) with inner seta on first endopodial segment large and with distal segment bearing 2 short and smooth claws and one larger and distally pectinated claw. Terminal claw of P(1) (Fig. 3E) weakly serrated at its tip, this claw in P(2) (Fig. 3F) completely smooth and strongly elongated and slender in P(3) (Fig. 3G); the latter limb furthermore with a

stout and plumous ventral seta on the basal segment. Hemipenis (Figs. 4, 10(D-F)) with lr of co large and consisting of different lobes and processi; ur large and consisting of 3 unequal, elongated lobes. Copulatory process with 3 rigid, elongated parts: a stout proximal part, a narrower distal part and the glans. Furca with 2 large sclerified rami (f1 & f3) and 1 short seta (f2). Distal lobe conspicuous.

DESCRIPTION OF ♀

Carapace (Figs. 2(D, E)) shorter than in the ♂, with dorsal margin straight and parallel to the ventral margin.

A1 (Fig. 3A) with distal segment somewhat less elongated than in the ♂. A2 (Fig. 3C) with inner seta on first endopodial segment shorter, distal segment with 3 smooth, equally long claws. No sexual difference in the size and shape of aesthetasc Y. Walking limbs with only slight sexual dimorphism, i.e. in P(3), where a stout and hirsute ventral bristle on basal segments is lacking in the ♀.

REMARKS

1. The last instar already presents a sexual dimorphism in the shape of the carapace. Males of the 8th instar resemble adult females, but are slightly more elongated. Females of this instar (Fig. 2G), on the other hand, have the dorsal margin more oblique and are smaller than their ♂ equivalent. The 7th and 6th instar females (Figs. 2(H, I)) have dorsal margins which are even more oblique.

2. According to TÖLDERER-FARMER (loc. cit.), the variability of the valve ornamentation in *L. (L.) sanctipatricii* is determined by environmental factors. An alternative explanation would be that this variability is genetically cued. Most likely, it is a combination of both in most cases, but solid experimental and in situ data are necessary to substantiate either hypothesis.

Tribe *Dinarocytherini* KRSTIC, 1987
(change of rank)

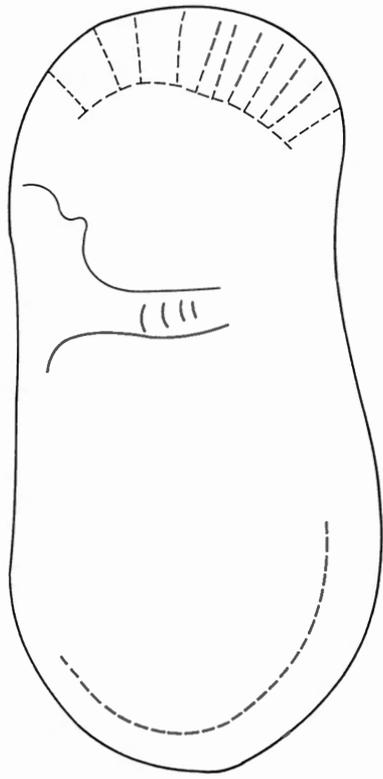
ABBREVIATED DIAGNOSIS

Well calcified valves, with amphidont hinge, i.e. with clearly developed, supplementary anterior cardinal tooth of the LV. Exclusively fossil.

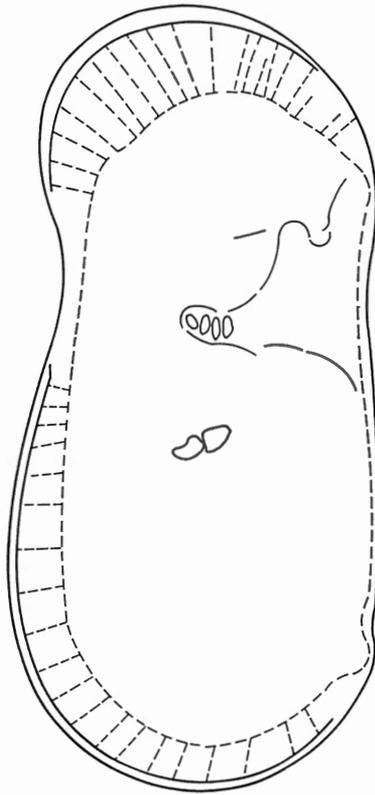
Genera: Dinarocythere KRSTIC, 1987

Figure 2. *Limnocythere (Limnocytherina) sanctipatricii* (BRADY & ROBERTSON). All subfossil valves in external view, collected on various occasions from site MO-7 at Mondsee. A-E= adults, F-I= larval instars.

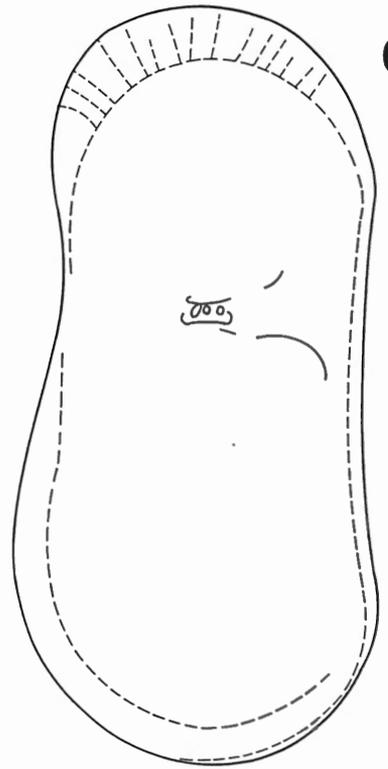
A. ♂, RV. B. ♂, LV. C. Idem. D. ♀, LV. E. ♀, RV. F. ♂, RV, last (8th) larval instar. G. ♀, LV, last (8th) larval instar, H. ♀ (?), LV, 7th larval instar. I. ♀ (?), RV, 6th larval instar. Scale = 333 µm for all figures.



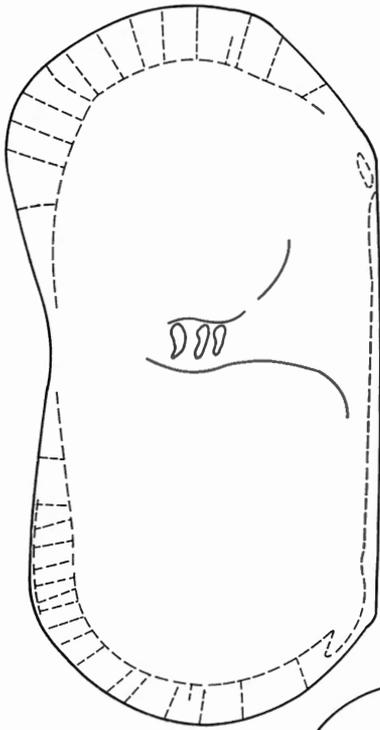
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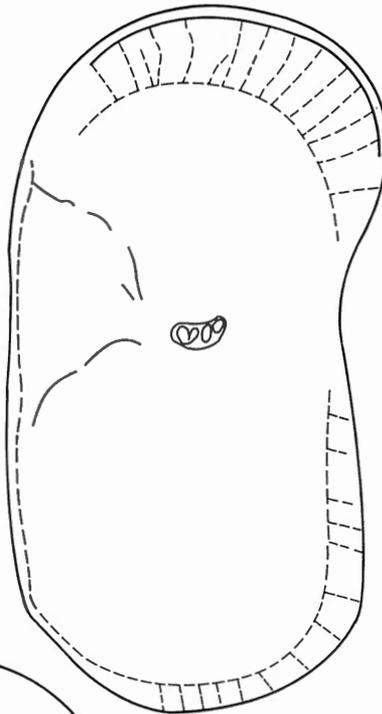
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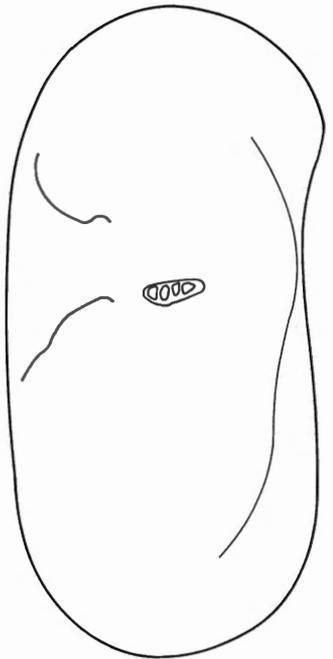
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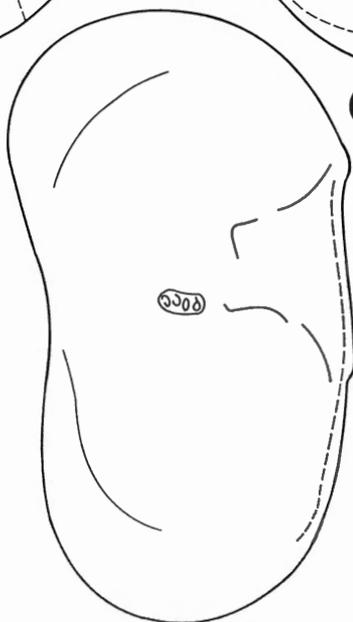
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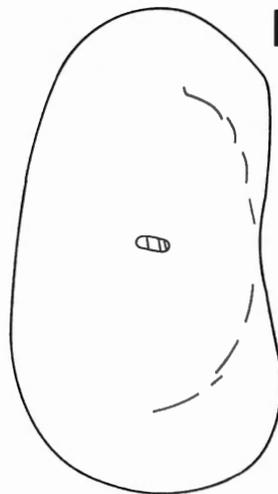
E



F



G



H



I



Tribe *Cytheridellini* D.L.D. & K.M. nov. trib.

ABBREVIATED DIAGNOSIS

Carapace with striking sexual dimorphism in dorsal view, i.e. ♀ caudally with widely dilated valves, forming brooding pouches for eggs and first (2?) instars. Valves with or without additional longitudinal ridges on the external surface. Hinge adont to weakly lophodont. P(3) with or without sexual dimorphism. Hemipenis of the vertical type

Genera: *Cytheridella* DADAY, 1905; *Gomphocythere* SARS, 1924; *Gomphodella* DE DECKKER, 1981.

Tribe *Leucocytherini* D.L.D. & K.M. nov. trib.

DIAGNOSIS

Carapace with 2 vertical sulci near the attachment of the adductor muscles and 1 sulcus in the anterior third; various plications formed through deformation; surface ornamentation consisting of large simple fossae; sieve pores small and sparsely distributed over the valves. Shape subject to considerable sexual dimorphism. In males, carapace in lateral view subrectangular, with anterior margin more broadly rounded than posterior one; ventro-caudal margin straight or slightly convex. Females often with a paedomorphic shape, i.e. anterior margin far more broadly rounded than posterior one and dorsal margin (compared to ventral one) with an oblique position.

Marginal fused zone with (few ?) straight, simple pore canals. Hinge weakly developed: LV with 2 shallow cardinal sockets, rather vaguely delineated and a weakly crenulated intercardinal bar; teeth on the posterior and anterior parts of this bar stronger than on the central part; RV with lamellar shaped (?) cardinal teeth, the anterior one often weak or even hardly developed, posterior tooth consisting of 3 lobes.

Second palp segment of Mx1 with at least 1 seta fused to the inner distal margin of this segment (= without articulation). Third walking limb and furcae with a sexual dimorphism. In females, these structures of the normal *Limnocythere* type; in males the appendage with a gradual reduction of the endopodial segments and furcae (as is common for all (?) *Limnocytherids*) incorporated in the hemipenis; here with strongly sclerified and curved setae. Hemipenis furthermore with short clasping organs and with the lower ramus not hook-like, more lamellar shaped; distal part of the copulatory process spiral shaped.

Genera: *Leucocythere* KAUFMANN, 1892, *Potamocythere* SCHORNIKOV, 1986, *Ovambocythere* MARTENS, 1989.

REMARKS

As the present contribution primarily deals with species of *Leucocythere*, we here present an extended diagnosis of the *Leucocytherini* nov. trib. and only an abbreviated one for the other 3 tribes in the *Limnocytherinae*. However, we feel confident that even those short diagnoses are sufficient to characterize the 3 taxa. In time, however, they should be revised in detail; especially the taxonomy of the nominate *Limnocytherini* requests urgent clarification.

Genus *Leucocythere* KAUFMANN, 1892

Type species: *L. mirabilis* KAUFMANN, 1892

DIAGNOSIS

Carapace weakly calcified, with sexual dimorphism in size and shape: females with a paedomorphic shape and of smaller size than the male. Hinge resembling the antimerodont type (see above), but with anterior cardinal tooth on RV considerably smaller than posterior one; intercardinal bar crenulated, with ridges more pronounced at both extremities than in the center.

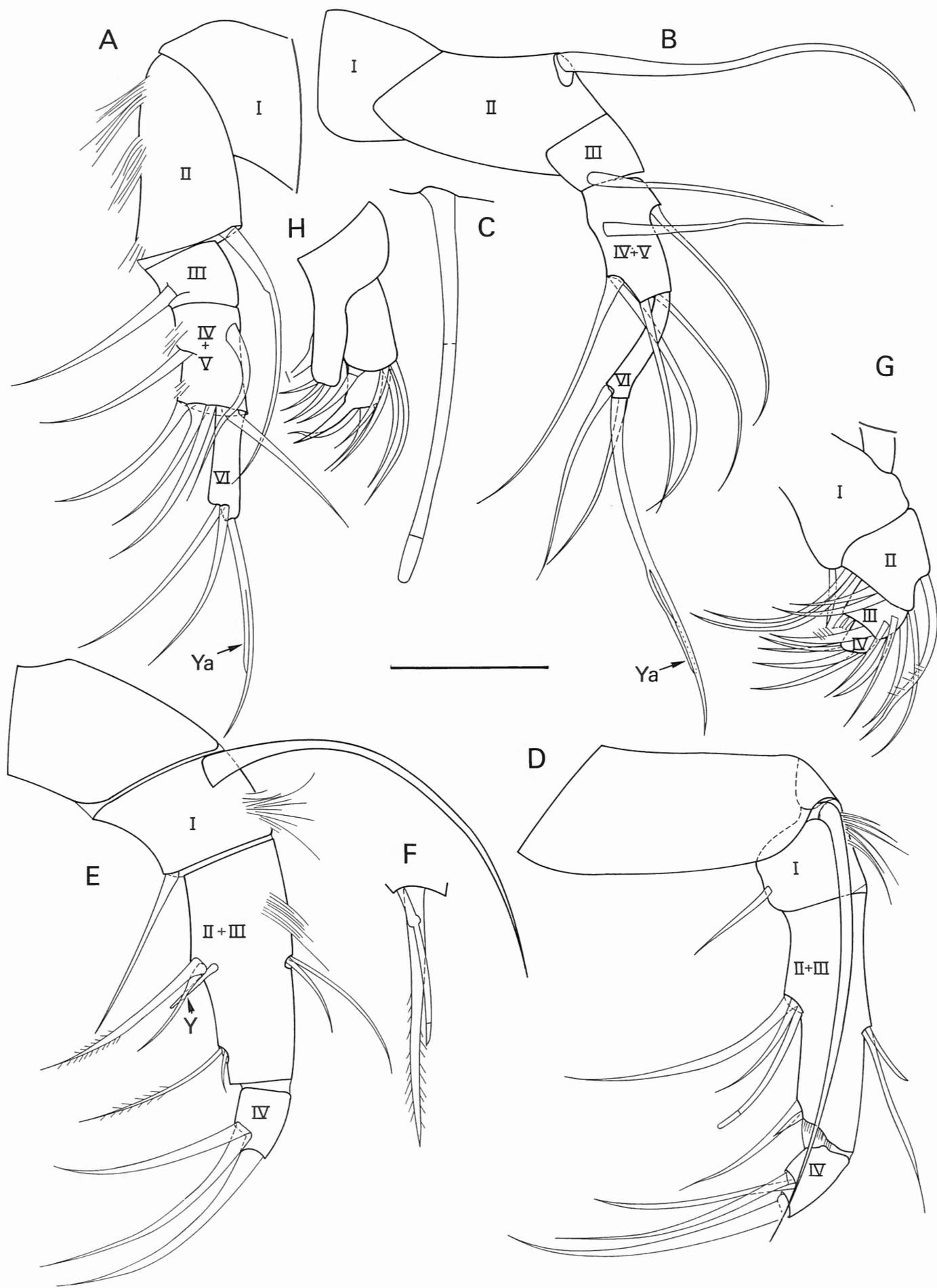
Aesthetasc Y in males longer than the adjacent short seta; seta on first endopodial segment of A2 shorter in males than in females. Third walking limb in males of aberrant shape: first endopodial segment with a hyperelongated and swollen seta and with distal claw long, slender and strongly curved. Male copulatory appendage with reduced clasping organs, consisting of 2 short, poorly sclerified rami; upper ramus furthermore with a lamellar shape; copulatory process shaped as a spiral, distal part of glans tubular.

REMARKS

The original diagnosis proposed by KAUFMANN (1892) consisted of a single morphological character on which the genus could be distinguished from related *Limnocythere* species: the third walking limb in the male has unusually long 'hyaline' bristles. An emended diagnosis, allowing inclusion of both Recent species and of *L. baltica* (see below), is here presented.

RELATIONSHIPS

Leucocythere differs from *Potamocythere* and *Ovambocythere* in a number of valve and soft part characters. Males of the latter 2 groups lack the aberrant P(3) and *O. milani* furthermore differs from both recent *Leucocythere* species in the anatomy of the hemipenis,



especially in the presence of a movable trabecule in the former and in the shape of the copulatory processus and of furcal seta f1, which is of quite a peculiar shape in *O. milani*. The hemipenis of *Potamocythere* needs further descriptions to allow a detailed comparison. Both *Ovambocythere* and *Potamocythere* have the frontal cardinal tooth on the RV far better developed than in *Leucocythere* s.s. and the former genera are furthermore better calcified and have a smaller sexual dimorphism in the carapace length than the species in *Leucocythere*.

***Leucocythere mirabilis* KAUFMANN, 1892**
(Figs. 5, 6(A-N), 8, 9, 10(A-C), 13)

1892 *Leucocythere mirabilis* n. sp. KAUFMANN

DIAGNOSIS

Anterior margins more broadly rounded than posterior ones in both sexes; carapaces never conspicuously sculptured. Hemipenis with furcal seta f2 shorter than half of seta f1, the latter furthermore straight, not hook-like; both ur and lr rounded; copulatory processus spirals, but somewhat less so (more elongated) than in the following species. Sexual dimorphism in structure of both A1 and P(3) conspicuous; the latter with long pseudochaetae on the penultimate segment.

DESCRIPTION OF ♂

Valves (Figs. 5(A, B, E), 6(D, H)) without postero-ventral enlargement; calcification poor; adductor muscle scars visible on the external side of the valves. Dorsal margin possibly concavely curved in the area of the lateral sulci (this margin very weakly calcified and in post mortem condition decaying very fast), but running more or less parallel to the posterior third of the ventral margin. Anterior margins more broadly rounded than posterior ones. In lateral view, two central, transversal sulci visible; in the anterior part of the valves a third sulcus running parallel to the anterior margin; the latter sulcus however not always visible with a normal stereo microscope.

Surface ornamentation consisting of large and simple fossae, no secondary ornamentation as in some specimens of *Limnocythere (Limnocytherina) sanctipatricii*. Sieve pores (Fig. 6M) very small, simple and without circular chitinous reinforcement rims. Hinge approximately anti-merodont (see above), with anterior cardinal tooth on RV weakly developed (Figs. 6(J, K)). Marginal fused zone (Fig. 5(A, B)) narrow, transversed

by 15-20 short and straight radial pore canals. Width of fused zone at the anterior and postero-ventral margins variable (see remark). Length of carapace: 0.83-0.93 mm.

Terminal two segments of A1 (Fig. 8B) long, the distal segment furthermore slightly S-shaped and with an excentric position on the penultimate segment; fused zone between aesthetasc Ya and the adjacent seta about 2,5 times longer than in the female; all setae of the plumose type; anterior surface of the second segment set with long pseudochaetae.

A2 (Fig. 8D) with long pseudochaetae arranged in 1 or 2 rows; all normal setae of the plumose type; distal 3 claws on terminal segment smooth; endopodite slender and relatively long; first endopodial segment with a short subapical seta; aesthetasc Y (Fig. 8C) long (c. 2,5 x longer than in the female), mainly due to extreme elongation of the distal parts of the basal shaft; adjacent seta relatively short.

Gnathobasis of Md with 7 teeth; the external one with 1 sharp point. Md-palp consisting of 4 segments. Inner distal corner of first segment with 1 medium-sized seta. 2nd segment with 1 long and plumose seta on the outer margin and on the inner margin 2 medium-sized and 2 long ones. 3rd segment with 5 medium sized subapical setae, a long and strong seta on the distal margin and 1 long and 1 shorter ones on the inner corner. 4th segment with 4 medium sized distal, claw-like setae. Exopodite a respiratory plate with 6 rays.

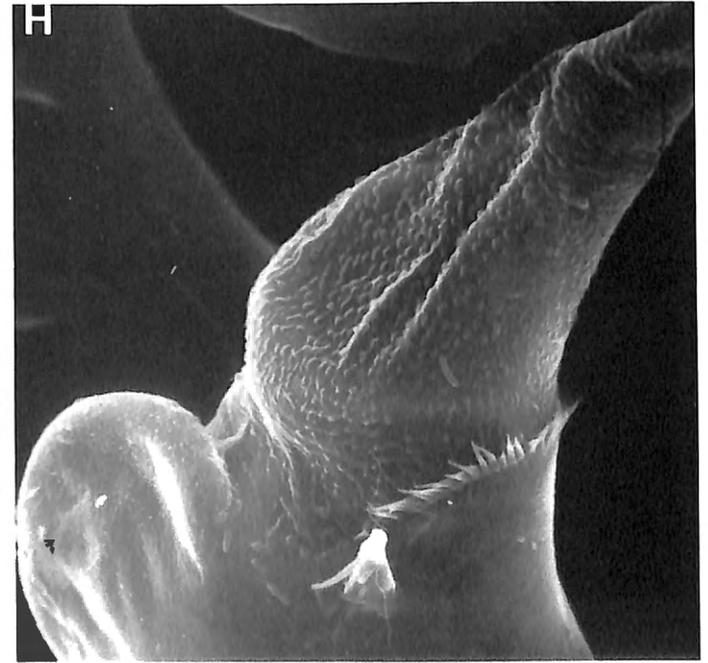
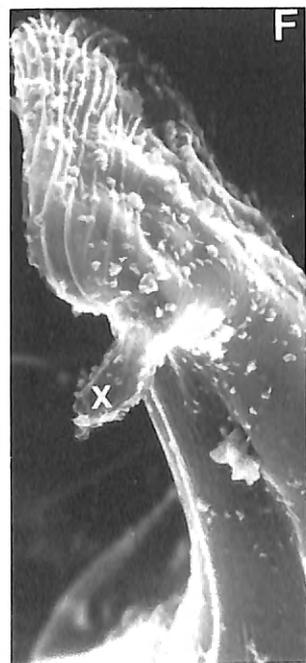
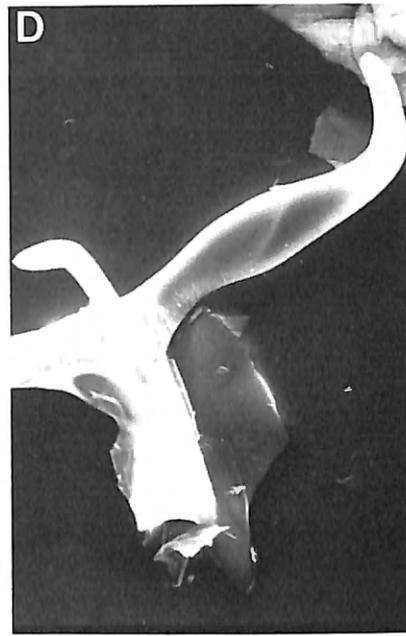
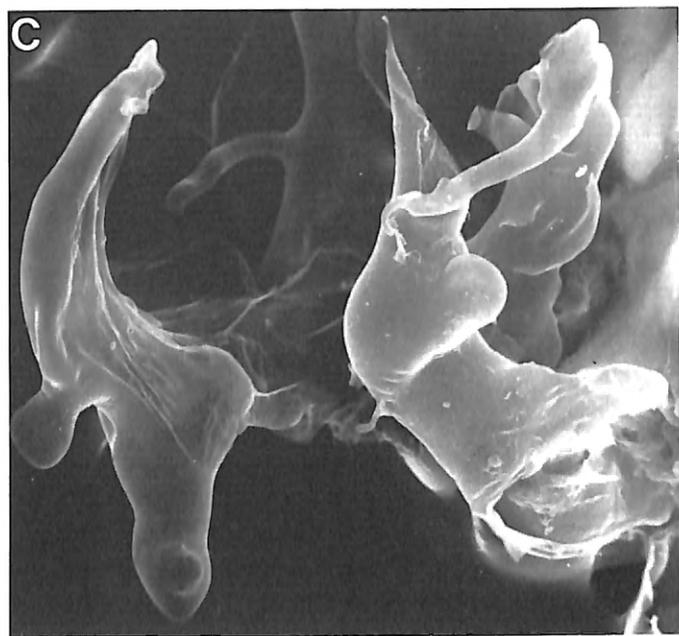
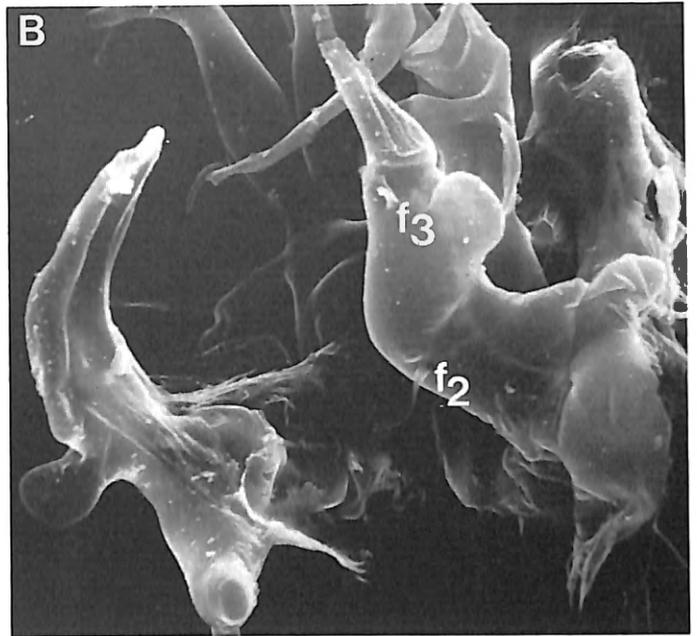
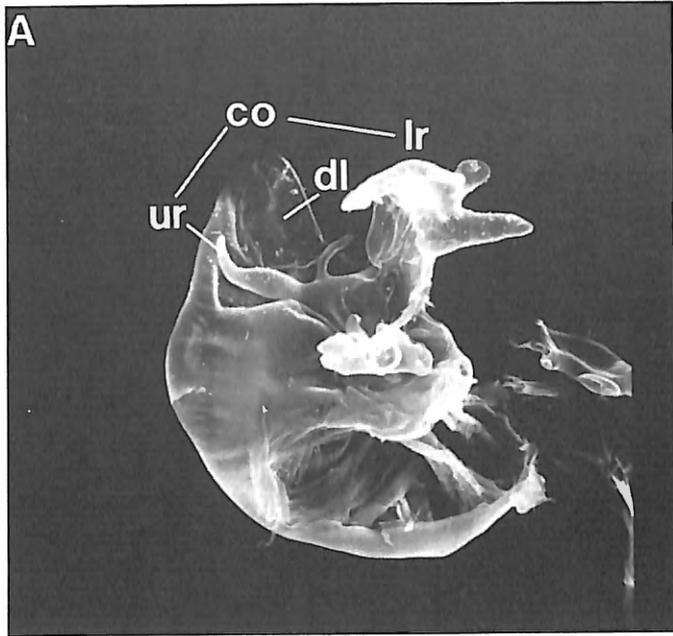
Mx1 with proximal segment of palp bearing 4 setae on the outer distal corner, these setae reaching the tips of the distal claws; inner corner of this palp segment bearing a short, thick seta with a swollen basis. Terminal segment with 1 claw fused to the distal margin (i.e. without articulation) and 2 articulating distal setae.

First 2 walking limbs (Figs. 9E, F) of the normal *Limnocythere* type, without special features: P(1) on basal segment bearing 1 ventral, 2 dorsal and 2 unequal knee-setae. P(2) with only 1 knee-seta. Distal claws on terminal segments with a tiny subbasal seta, several pseudochaetae and a double pectination on the anterior margin (Fig. 9D). Third walking limb (Fig. 9G), however, highly aberrant (see also generic diagnosis): endopodite short; first segment with a giant, smooth seta, this segment also unusually curved; 2nd segment with very long pseudochaetae; distal claw on 3rd segment smooth and S-shaped.

Brush-like organs (Fig. 9H) paired, with only 1 group of setae on the distal margin of the ramus (instead of 2 as figured in KAUFMANN, 1892).

Hemipenis (Figs. 10(A-C)) with a small clasping organ;

Figure 4. *Limnocythere (Limnocytherina) sanctipatricii* (BRADY & ROBERTSON). Anatomy of hemipenis. All from Lunz Mittersee, Austria. Only relative magnifications given, no absolute scales available. A. In toto hemipenis, medial view, (x210). B. Detail of copulatory complex (lr of co and furcal setae) (x530). C. Idem. D. Dissected ur of co (x550). E. Detail of distal part of ur (x2200). F. Detail of lr of co (note the plicated distal part - x2100). G. Detail of distal part of copulatory processus and part of furca (x2100). H. Detail of distal lobe of furca, showing papillate surface (x2100). Note micro-anatomy of co and furca, apparently equipped for a sensorial function during copulation.



upper and lower rami with their distal parts rounded and larger than the proximal parts; ur furthermore lamellar shaped. Peniferum with a large and triangular distal lobe; between the latter lobe and the copulatory process a small medial lobe present; copulatory process spiral shaped and with 4 recognisable parts (p1-p4); distal glans tubular and conical. Furca (Figs. 9(J, K)) incorporated in the hemipenis: ramus a relatively large plate, bearing 2 proximal pappose setae, one stiff and strong (f1), a second slender and flexible (f2); a third distal seta (f3) also articulating on the furcal ramus and completely sclerotised and S-shaped, but without secondary ornamentation.

DESCRIPTION OF ♀

Valves (Figs. 5(C, D), 6(A-C, I-N)) with a different general shape and size (c. 20% smaller than the ♂) and with the dorsal margin somewhat oblique in relation to the ventral margin. Length of carapace: 0.68-0.76 mm. A1 (Fig. 8A) with basic chaetotaxy as in the male, but with 2 terminal segments shorter and with distal segments straight, not S-shaped. Fused zone between aesthetasc Ya and adjacent seta much shorter than in the male.

A2 (Fig. 8E) with chaetotaxy as in the male, except for the following aspects: endopodite (first 2 segments) more stoutly build; subapical seta on first endopodial segment about twice as long as in the male homologue; aesthetasc Y (Fig. 8F) 2.5 x shorter than in the male. Md and Mx1 as in the male (Figs. 8(G, H)).

P(1) (Fig. 9A) stout and with distal claw longer than in the male. Endopodite of P(2) (Fig. 9B) with first segment more elongated, but with the 2 terminal segments shorter than in the male. P(3) (Figs. 9 C, D) of the normal type, not aberrant.

Furca (Fig. 9I) with a stout ramus and 2 plumose (1 lateral, 1 apical) setae f1 and f2.

REMARKS

1. The general shape of adult females of *L. mirabilis* strongly resembles that of juvenile females of both *Leucocythere* and *Limnocythere* s.s. and *Limnocythere* (*Limnocytherina*). We therefore consider the carapace of adult females of this species to have a pedomorphic shape. Last instar males of *L. mirabilis* differ in shape from adult females by their more slender and elongated shape in lateral view.

2. There is a remarkable variability in the width of the marginal fused zone, mainly on the anterior and posteroventral sides. Specimens with more weakly calcified shells have a significantly narrower fused zone and radial pore canals are not always visible in such specimens. In fossils, this could be due to post mortem decalcification processes; in living specimens, this feature could be correlated with age (i.e. time since last moulting).

3. EKMANN (1914) described a sexual dimorphism in the A1 for specimens from Vättern Lake (Sweden): the posterior seta on the 2nd segment would be longer in males than in females. We failed to observe such differences and in this respect our material and observations agree with the descriptions of KAUFMANN (1892) and STEPHANIDES (1948).

Leucocythere algeriensis MARTENS nov. spec. (Figs. 11, 12, 13)

TYPE LOCALITY

Oued Tesselata, Tassili-n-Ajjer, Algeria (26°03'N-08°20'E). Drying pool in temporary river system (locality 415 in DUMONT, 1979). For further description of this locality, see below.

Accompanying fauna: a bisexual population of *Ilyocypris getica* and *Heterocypris* spec.

TYPE MATERIAL AND DEPOSITION

Five adult and 1 juvenile males, 11 adult and 2 juvenile females with valves completely decalcified, but with soft parts in good condition. All material originating from sample 28H, collected on 5.6.1978.

Holotype: 1 male, with soft parts dissected in glycerine on a permanent slide, decalcified valves kept in a separate permanent slide (no. OC 1471).

Allotype: a female dissected and stored as the holotype (no. OC 1472).

Paratypes: c. 10 specimens kept in spirit in toto (no. OC 1470). Deposition: all types are kept in the KBIN (Brussels).

REMARKS

Due to the extreme decalcification of the valves, these cannot be properly described or measured. Nevertheless, the zoogeographical and phylogenetic importance of the present taxon is such (as it is only the second Recent species in the genus), that it was thought necessary to describe *L. algeriensis* sp. n. Furthermore, the new species can immediately be identified on the morphology of the soft parts, especially on the anatomy of the hemipenis and on the morphology of the male P(3) (see below). It is hoped that additional material with good valves will enable proper illustration in the near future.

DIAGNOSIS

Valves in both sexes anteriorly more broadly rounded than posteriorly; female carapace conspicuously sculptured.

Hemipenis with seta f2 large, ur bluntly pointed, Ir rounded, but projecting, copulatory process spirallised; sexual dimorphism on A1 less conspicuous than in

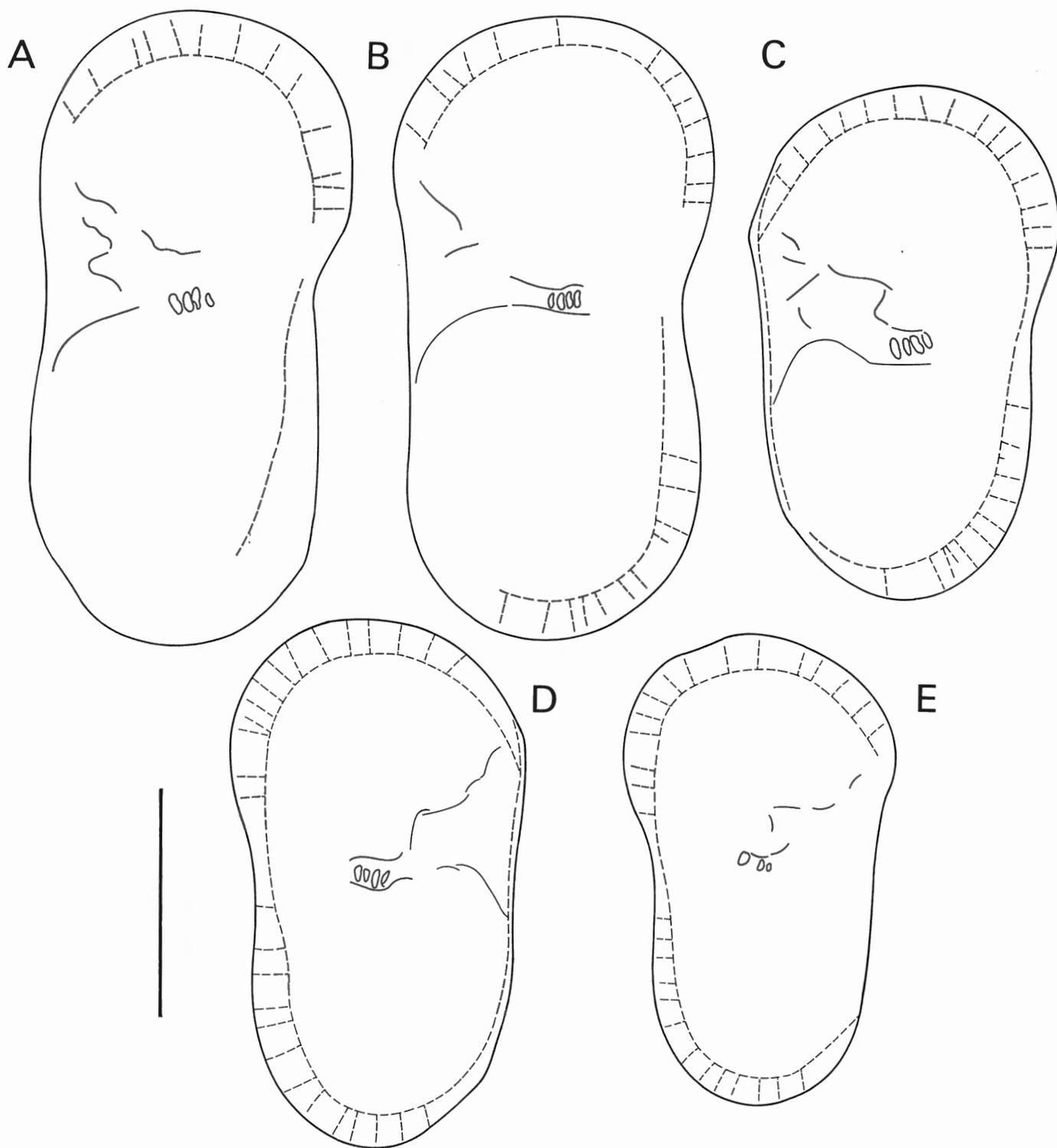


Figure 5. *Leucocythere mirabilis* KAUFMANN. External views of subfossil valves. A, B, E from site MO-7 at Mondsee, C, D, from site Weyregg at Attersee.

A. ♂, RV. B. Idem. C. ♀, RV. D. ♀, LV. E. Last larval instar, LV, ♂. Scale = 333 μm for all figures.

L. mirabilis; P(3) in male typical for the genus, but without large pseudochaetae on penultimate segment.

MEASUREMENTS (in mm - n=3).

Male: L=0.72-0.74; greatest H=0.33-0.35; smallest H=0.28-0.30. Female: L=0.56-0.58; greatest H=0.30-0.32; smallest H=0.28.

DESCRIPTION OF ♂

Valves with lateral sulci prominent, dorsal margin slightly concavely sinuous, caudal margin far more narrower than in the preceding species. L= c. 2,7 x W; greatest width situated in front of the sulci, in dorsal view furthermore caudal margin blunt.

Terminal segment of A1 (Fig. 11A) slightly curved and

with an extreme excentric position, this segment with 2 unequal setae and with a bifurcated aesthetasc Ya. Setulae on second segment short.

A2 (Fig. 11E) with aesthetasc Y reaching beyond insertion of subapical setae on penultimate segment; the latter segment with 1 brush of relatively short setulae. Terminal segment with 3 claws: 1 long and extremely wide claw and 2 unequal, shorter claws of about half the width of the larger.

First segment of Md-palp (Fig. 12H) with respiratory plate carrying at least 4+1 rays and 1 short, but stout apical seta. Second segment with 1 large lateral and 2+2 long apical hairs. Third segment with lateral group of 5 and an apical group of 3 setae. Fourth segment with 4 unequal setae.

Mx1 (Fig. 11C) with palp two segmented; first segment with 5 apical setae, second segment with 3 apical setae, 1 of which not articulating. First endite with 1 large, subapical seta of peculiar shape and c. 6 normal, apical setae.

P(1) (Fig. 12A) with first segment carrying 2 dorsal setae (the distal one being unusually large), 1 ventral seta and 2 unequal knee setae. Apical seta on second segment almost reaching top of terminal segment. Apical claw about as long as 2 terminal segments.

P(2) (Fig. 12 B, C) with 2 dorsal, 2 ventral and 1 knee seta on first segment. Second segment elongated, with 1, short subapical seta. Apical claw weak and shorter than 2 terminal segments combined.

P(3) (Fig. 12D) typical for the genus, with first segment large, the 2 dorsal + 1 knee setae subequal, ventral seta huge. Last 3 segments short and articulating in an angle; apical seta on second segment almost 3x as long as maximum length of first segment. Apical claw whip-like, c. 7/11 of apical seta on second segment. No additional long apical pseudochaetae on penultimate segment.

Hemipenis (Fig. 11F) large, with frontal margin of d1 sinusoid. Furca consisting of 3 processi: seta f1 with a stout base, seta f2 long, f3 a hook-like structure with distal part only weakly sclerotised. ur large and blunty pointed. lr rounded. Copulatory processus as in Fig. 11G, coiled with distal part gradually narrowing and not sclerotised. Three distinctive groups of muscles inserting on 3 different parts of the labyrinth, one additional group of muscles inserting near the ventral corner.

DESCRIPTION OF ♀

Valves shorter and higher than in the male, but also with posterior end narrower; anterior and posterior bulbs prominent on the dorso-lateral sides; a ventro-lateral, longitudinal ridge running along the valve; dorsal margin convexly rounded, greatest width situated in the middle, $L = c. 2,1 \times W$.

All limbs somewhat smaller than in the male. Md and Mx1 without obvious sexual dimorphism.

A1 (Fig. 11B) with second segment carrying 2 tufts of long setulae; terminal segment straight, apical claws on this segment subequal.

A2 (Fig. 11D) with penultimate segment carrying 1 tuft of strikingly long setulae (2-2,5 x as long as in the male); aesthetasc shorter than in the male, not reaching insertion of subapical setae on this segment. Larger claw on terminal segment not as wide as in the male.

P(1) (Fig. 12E) with 2 dorsal setae and 2 knee setae subequal. Apical setae of second segment not reaching halfway terminal segment.

P(2) (Fig. 12F) large, with second segment elongated, but less so than in the male and with apical seta on this segment about as long as the penultimate segment. Apical claw stout and longer than 2 terminal segments combined.

P(3) (Fig. 12G) of normal shape, with all setae long; e.g. apical seta on second segment reaching beyond tip of terminal segment. Furca (Fig. 12I) with two large, subequal setae. Genital operculum elongated as in Fig. 12J.

RELATIONSHIPS

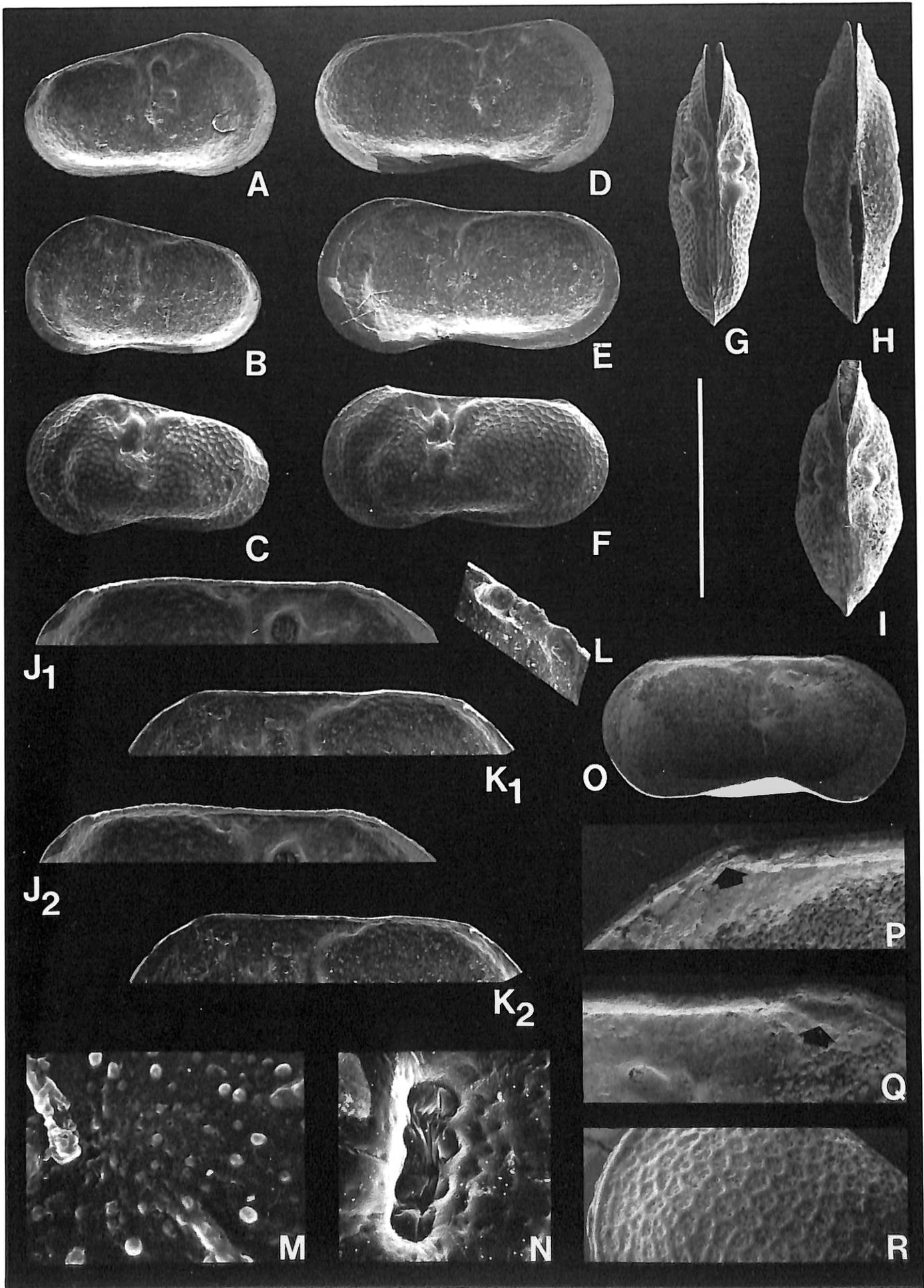
The new species is closely related to *L. mirabilis*, however differs from it in a number of important features, among which the less pronounced sexual dimorphism in the A1, the absence of the long pseudochaetae on the P(3) in males and the morphology of ur, lr, copulatory processus and the size of the seta f1 on the hemipenis. Typical for the female are the long lateral seta on the furca (shorter in *L. mirabilis*) and the pronounced sculpturing of the carapace, which is completely missing in the type species.

Figure 6. *Leucocythere mirabilis* KAUFMANN (A-N) and *Limnocythere* (*Limnocytherina*) *sanctipatricii* (BRADY & ROBERTSON) (O-R). A-J: collected by B. SCHARF (Mainz) from Lake Holzmaar, Eifel region (no. 80-56-1); K-R: collected by D.L.D. from Mondsee (no. MO-LO-22m, 29.08.1985).

L. mirabilis: A. ♀, LV, internal view. B. ♀, RV, internal view; C. ♀, LV, external view. D. ♂, LV, internal view. E. ♂, RV, internal view. F. ♂, LV, external view. G. ♂, Cp, dorsal view. H. ♂, Cp, ventral view. I. ♀, Cp, dorsal view. J1-2. ♀, LV, internal view, hinge (stereo-pair). K1-2. ♀, RV, internal view, hinge (stereo-pair). L. ♀, RV, internal view, detail of posterior cardinal tooth. M. ♀, RV, external view, detail of sieve pore. N. ♀, detail of adductor muscle scars.

L. (L.) sanctipatricii: O. ♀, LV, internal view. P. Idem, detail of anterior cardinal socket. Q. Idem, detail of posterior cardinal socket. R. ♀, RV, external view, detail of surface structure.

Scale = 658 µm for A-I; 526 µm for O; 362 µm for J,K; 238 µm for R; 125 µm for P, Q; 71 µm for N; 66 µm for L; 10 µm for M.



Leucocythere baltica (DIEBEL, 1965)
(Figs. 7(A-G), 13)

1965 *Limnocythere baltica* n. sp., DIEBEL, 1965A

ABBREVIATED DIAGNOSIS

Male with anterior and posterior margins nearly evenly rounded (anterior margin more broadly rounded in *L. mirabilis*), and with hinge on LV better developed: anterior and especially posterior part of intercardinal bar heavily crenulated and elevated, thus creating the impression of at least one additional cardinal tooth in front of the posterior cardinal socket on the LV (see Fig.). Female without special features.

L: ♀ : 0,675-0,775 mm; ♂ : 0,750-0,875 mm (from DIEBEL, 1965A:733).

DISCUSSION

DIEBEL (loc. cit.) described this species from the Pleistocene (Interglacial II) from the environments of the Baltic. Thanks to the efforts of Dr E. PIETRZENIUK, we could investigate part of the type material and some of these specimens are here illustrated. It appears that this species is most closely related to *L. mirabilis*, however differs from it at least in the shape of the male valve and in the anatomy of the hinge. Females of both species cannot readily be distinguished.

It is possible that *L. baltica* will in time turn out to be a junior synonym of *L. mirabilis*, showing nothing but one extreme of a range of variability within the latter species. However, the fact that *L. baltica* is known as a fossil only, prevents comparison of the copulatory appendages, which would immediately yield decisive information as in the case of *L. algeriensis* nov. sp. For the present, we therefore maintain *L. baltica* as a separate species. Future research on intraspecific variability in *L. mirabilis* will illustrate if this conclusion can be corroborated.

5. Discussion

5.1. Questionable *Leucocythere* species

We here defined the genus *Leucocythere* using character states of both carapace and limbs. Especially the morphology of the latter allows for a very straightforward situation with regard to the 2 living species, described above. For both *L. mirabilis* and *L. algeriensis*

nov. sp. there is no indication of limb convergence with other Limnocytherid genera. There are, however, a number of fossil "*Leucocythere*" species of which the carapace agrees closely to the living *Leucocythere* and, on the other hand, there are also a number of fossil taxa, assigned to the latter genus, but with strikingly aberrant valve anatomy. Here, however, we do not have the soft part morphology to assess their proper assignment and not all these cases can readily be solved.

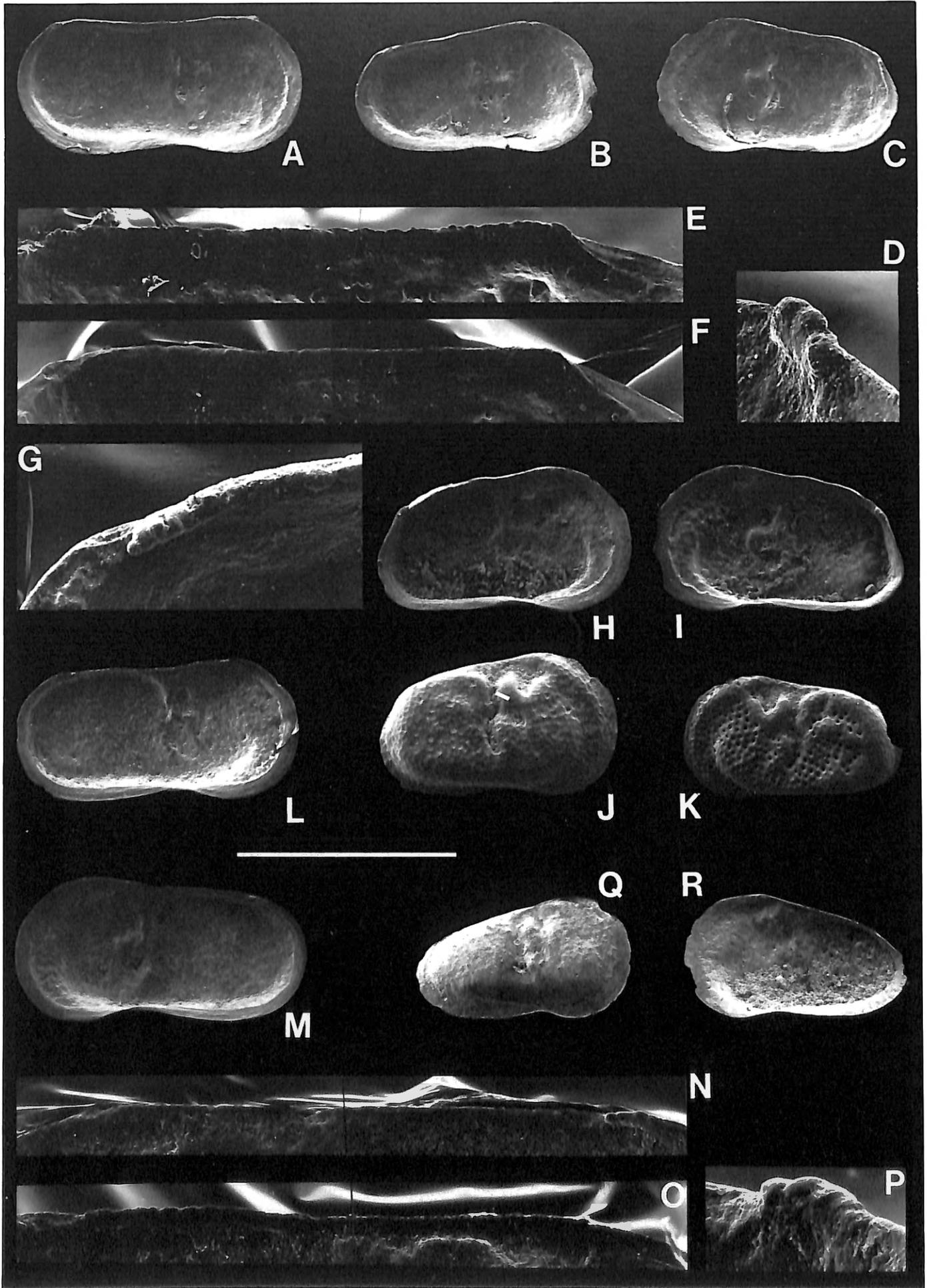
A large number of fossils from the Peoples Republic of China, for example, has been attributed to either *L. mirabilis* itself or to a number of new *Leucocythere* species by various authors in the past decade (for a comprehensive list, see KEMPF's bibliographic index A, suppl. 1986). These taxa are important, mainly because of the biogeographical implications. HUANG (1982A) suggested that *Leucocythere* originated in China in Mesozoic and Cenozoic lakes, which would indicate a very old distribution of this group. *Leucocythere* s.s. was for a long time known from Pleistocene and Recent European aquatic habitats only (see below). Because of this large discrepancy, we will here discuss these Asian taxa in some detail.

L. mirabilis was reported by HUANG *et al.* (1982, 1985) from Middle Pleistocene and Recent sediments from the Xizang Plateau (Tibet) lakes and from late Pleistocene deposits in the Sanggan Valley near Baijing (HUANG, 1985). However, the species figured by HUANG (1982) as *L. mirabilis* does not display differences in length of valves between males and females as in the European material, while also the anterior cardinal tooth on the RV is much stronger than in European *L. mirabilis* we studied. The material figured by HUANG (1985) from Recent sediments of Xizang furthermore looks more like a *Limnocythere* than like a *Leucocythere*. The specimens from Sanggan identified as *L. mirabilis* by HUANG (1985B) does display a sexual dimorphism in size, but there the male has an oblique dorsal margin, while this margin in European populations is largely rounded. The *L. mirabilis* material from Sanggan actually very much resembles *Limnocythere (Limnocytherina) ceriotuberosa* DELORME, 1971. We therefore consider the presence of *L. mirabilis* s.s. in China not yet ascertained.

Some other species described as belonging to *Leucocythere* in HUANG (1982 A, B, 1985) are: *L. dorsotuberosa* HUANG, *L. burangensis* HUANG, *L. debilireticulata* HUANG & YOU, *L. subsculpta* HUANG, *L. subqua-*

Figure 7. *Leucocythere baltica* (DIEBEL), (A-G), Fossil *L. cf. mirabilis* (H-P) and *Leucocythere bressensis* CARBONNEL (Q-R). For registration nos., see section 'material'.

L. baltica: A. ♂, LV, internal view. B. ♀, LV, internal view. C. ♀, RV, internal view. D. *idem*, detail of posterior cardinal tooth. E. ♂, LV, internal view, detail of hinge. F. ♀, LV, *idem*. G. ♂, LV, internal view, detail of posterior. *L. cf. mirabilis*: H. ♀, LV, internal view. I. ♀, RV, internal view. J. ♀, RV, external view. K. ♀, LV, external view. L. ♂, LV, internal view. M. ♂, RV, internal view. N. ♂, LV, internal view, detail hinge. O. ♂, RV, *idem*. P. ♀, RV, internal view, detail of posterior cardinal tooth. *L. bressensis*: Q. ♀ (larval instar), LV, internal view. R. ♀ (*idem*), RV, internal view. Scale = 658 µm for A-C, H-M, Q, R; 204 µm for E, F, N, O; 82 µm for G, P; 69 µm for D.



drata HUANG & YOU, *L. noda* HUANG & YOU, *L. exilitropis* HUANG, *L. latizona* HUANG & YOU, *L. reticulata* HUANG, *L. parasculpta* HUANG, *L. pseudo-sculpta* YANG. These species have, like already discussed for *L. mirabilis*, a very small sexual dimorphism in size of the valves and furthermore have the anterior cardinal tooth of the RV strongly developed, even to such an extent that this tooth is visible with a stereo microscope (not so for European *L. mirabilis*). Some of these species might belong in *Potamocythere* SCHORNIKOV or even in the genus *Limnocythere* s.s.

Leucocythere weimingensis ZHAO, 1987 and *L. plena* ZHAO, 1987 (see ZHAO 1987 A, B) from Pleistocene sediments of Caohai Lake in the South West of China (Guizhan Province) do not look like *Leucocythere*, as these species have their carapaces in dorsal view more inflated, their hinge better developed and are much smaller ($L=0,4-0,5$ mm). These species do not belong to the Leucocytherini as defined above and it can even be questioned if they are genuine Limnocytherinae.

The shape of the valves of both male and female of *Limnocythere bressensis* CARBONNEL, 1969 (Figs. 7(Q, R)) are similar to those of *L. mirabilis* as described above, as there is indeed a sexual dimorphism of the valves comparable to that of present day *L. mirabilis*. However, *L. bressensis* is smaller (the ♂ is 0.8 mm, the ♀ is 0.63 mm) and its hinge is adont and therefore this species does not fit in the Leucocytherini.

The taxonomic position of all these species remains as yet unclear. They cannot be included in *Leucocythere* s.s., nor in any other existing genus (see below). A comprehensive revision of the fossil *Leucocythere* like taxa appears urgent, but this falls outside the scope of the present contribution. It is, however, most interesting to note that this phyletic lineage of the Limnocytheridae has known such an intensive radiation in Asia.

5.2. *Leucocytherella*, a related genus?

HUANG *et al.* (1982, 1985) described the genus *Leucocytherella* with several species from Pliocene to Holocene deposits of the Xizang Plateau. These species have the cardinal teeth on the LV, which is a reverted hinge when compared to *Leucocythere* s.s. At present, *Leucocytherella* cannot be considered as belonging to the tribe Leucocytherini, nor can it readily be lodged in another taxon. Again, a revision of this group appears necessary.

5.3. Ecology and geographical distribution

We have little information on these aspects of the biology of living and fossil Leucocytherini. The existing knowledge will here be summarized.

Living specimens of *Leucocythere mirabilis* have been found mainly in sublittoral and deep lake habitats in central and northern Europe. KAUFMANN (1892) mentioned this species from Brienzer, Thunnen and Geneva lakes in Switzerland, at depths varying between 10 and 40 meters. Dr B. SCHARF (pers. comm.) found this species in the past years still living in the former two lakes. In the Austrian pre-alpine lakes Mondsee and Attersee, this species was found between 12 and 22 m deep, living in the upper centimeters of fine grained sediments. Subfossil and fossil valves occur in Mondsee in sublittoral (6 m) to profundal (30-68 m) sites.

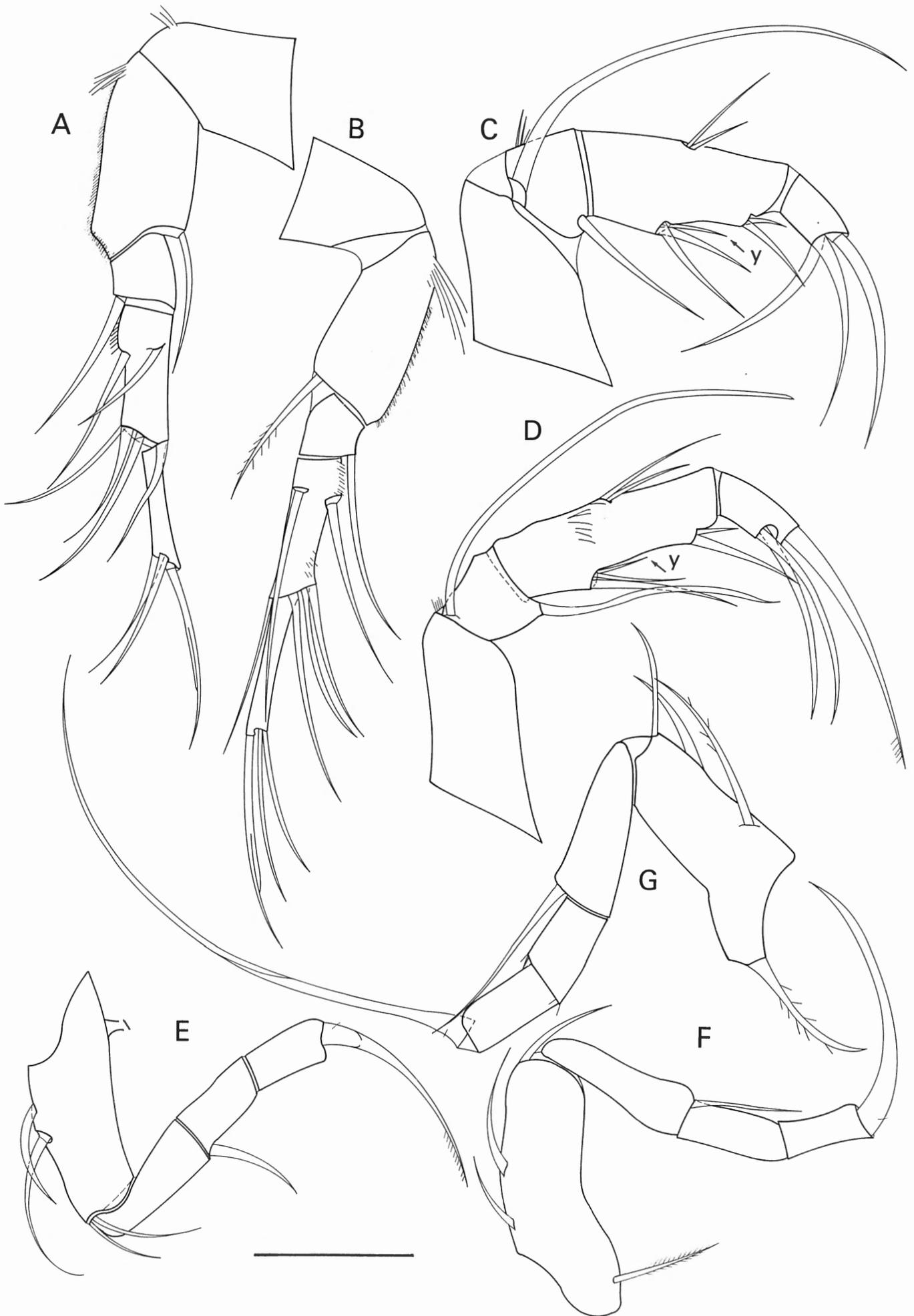
L. mirabilis has been found as fossils in late glacial and postglacial sediments in several pre-alpine lakes in Austria. LÖFFLER (1983) recorded the species in the Traunsee, in several sediment cores taken at depths varying between 140 and 190 m. In all these cores, *L. mirabilis* has a long continuity (see LÖFFLER, loc. cit. fig. 2 and p. 138). In two other prealpine lakes, Mondsee and Halleswiessee, M. HANDL (pers. comm. to DLD) found this species in late glacial Aleröd-Junger Drias) sediments. In Mondsee, this species furthermore stands as one of the first ostracod immigrants after the deglaciation of the surrounding area. It has been found in association with *Candona neglecta*, *Limnocythere (Limnocytherina) sanctipatricii* and *Fabaeformiscandona protzi* in a core taken at 68 m depth in the deepest sediment layers (i. e. at 12 to 14 m sediment depth). In the southern part of this lake, *L. mirabilis* also occurred in the Holocene during the Preboreal and Atlanticum phases (M. HANDL, unpubl. data).

In northern Europe, EKMANN (1914) mentioned this species as living in Lake Vättern at depths ranging from 23 to 34 m. An interesting discovery is the one of SAVOLAINEN & VALTONEN (1983). These authors found *L. mirabilis* living in the north-eastern Bothnian Bay in the Baltic Sea at depths ranging between 12 and 26 m and in areas where salinity usually varies around 3‰. Besides this species, also brackish water ostracods like *Cytheromorpha fuscata*, *Cytherura gibba* and *Cyprideis torosa* occurred.

Between the Alps and northern Europe, only fossil records of *L. baltica* are known. DIEBEL (1965 A, B) found this species in the southern part of the Baltic Sea in late and post glacial sediments from the Mecklenburg Bay (see fig. 1 in DIEBEL, 1965 A, p. 727). As in the case of the Mondsee ostracods, *L. baltica* is one of the first colonizers of the freshwater lake around the Island of Rügen in the Baltic during the deglaciation phase in the interglacial I₁. KRSTIC (1988) mentioned *L. cf. baltica* from the Middle Pleistocene in the SE of the Pannonian

Figure 8. *Leucocythere mirabilis* KAUFMANN. All adults, collected at Mondsee.

A. ♀, A1. B. ♂, A1. C. ♂, A2, detail of aesthetasc Y. D. ♂, A2. E. ♀, A2. F. *Idem*, detail of aesthetasc Y. G. ♀, Md-palp. H. ♀, Mx1, palp and 3rd endite. Scale = 83 µm for A, B, D, G, H; 33 µm for D, F.



Basin, N of Beograd and below the Danube at the border with Roumania. This constitutes the southernmost fossil quotation of a *Leucocythere*.

The oldest occurrences of *L. mirabilis* are those mentioned by DIEBEL & PIETRZENIUK (1969) in the limnic sediments of Süssenborn near Weimar (DDR), during the Elster interglacial in the Middle Pleistocene. Other Pleistocene records are those of DIEBEL & PIETRZENIUK (1977) at Taubach (Travertin sediments) close to Weimar. We here illustrate a number of these specimens (Figs. 7 (H-P)) as *L. cf. mirabilis*, because the shape of the ♀ valve appears somewhat different from present day *L. mirabilis* (compare to Figs. 6 (A-C)).

The southernmost record of *L. mirabilis* is the one of STEPHANIDES (1948: 92), who found this species on the Island of Corfu in a drainage ditch, situated some 150-200 m from the sea and separated from the latter by a shallow marsh. The water of the ditch was slightly saline (2-3‰). This record is most puzzling; a possible explanation for it will be offered in below.

L. mirabilis seems to prefer oligotrophic lakes with fine grained sediments and cold waters. It disappeared at least in Mondsee in the last 50 years from the larger parts of the lake, possibly due to the organic enrichment of the sediments and to the subsequent decrease of the oxygen content at the water-sediment interface (DANIELOPOL *et al.*, 1985, 1988). Interesting enough, *L. mirabilis*, like *Cytherissa lacustris*, started to decrease in abundance before the occurrence of the chronic eutrophication of Mondsee (DANIELOPOL *et al.*, 1985). Compared to *Limnocythere (Limnocytherina) sanctipatricii*, *L. mirabilis* seems more sensitive to the degradation of the limnic environment. In general, it is less abundant than *L. (L.) sanctipatricii*. The key variables responsible for these differences in the quantitative distribution of the two species remain as yet unknown. We suspect them to be oxygen concentration (*L. mirabilis* being more sensitive to low concentrations) as well as the quality of the sediment (grain size? organic content?).

L. mirabilis is doubtlessly a cold stenothermic species. DIEBEL and PIETRZENIUK (1969, 1977) invariably found it in ostracod associations typical of cold waters, i.e. together with *Eucypris pigra*, *Candona rawsoni* and *Potamocypris wolffi*. In the Swiss lakes (KAUFMANN, 1892) as well as in the Bothnian Bay (SAVOLAINEN & VALTONEN, 1983), the species was found with a maximum abundance during spring and summer. The temperature in the latter lake varied between 3.9° and 14.6° C, with a mean temperature of 8.7° C, but during winter, temperatures were practically zero (VALTONEN, pers. comm. to DLD). In lake Vättern, EKMANN (1914) caught the species in June and July. STEPHANIDES

(1948) recorded this species with a peak of abundance in late winter and early spring (February-March), but not from April onwards. This disappearance might be due to the fact that water temperatures in this locality increased above 10° C.

As *L. algeriensis* nov. sp. and *Ovambocythere milani* MARTENS, 1989 are known from their type locality only, even less can be said about their ecology. Nevertheless, they appear to share at least one remarkable ecological trait: the existence of dry resistant stages and an adaptation to temporary habitats.

Tassili-n-Ajjer is a mountaineous plateau in Central Sahara. Whereas the fairly warm canyons which cut through the area are relict pockets for Afro-tropical fauna's, the real plateau has a much harsher climate where relicts of Atlas or even true Palaearctic faunas can survive. Some examples of such relicts are *Bufo viridis*, *Rana ridibunda* and species of the *Barbus calensis* - group (DUMONT, 1979) and a species of the ostracod genus *Pseudocandona* (DANIELOPOL & MARTENS, unpublished).

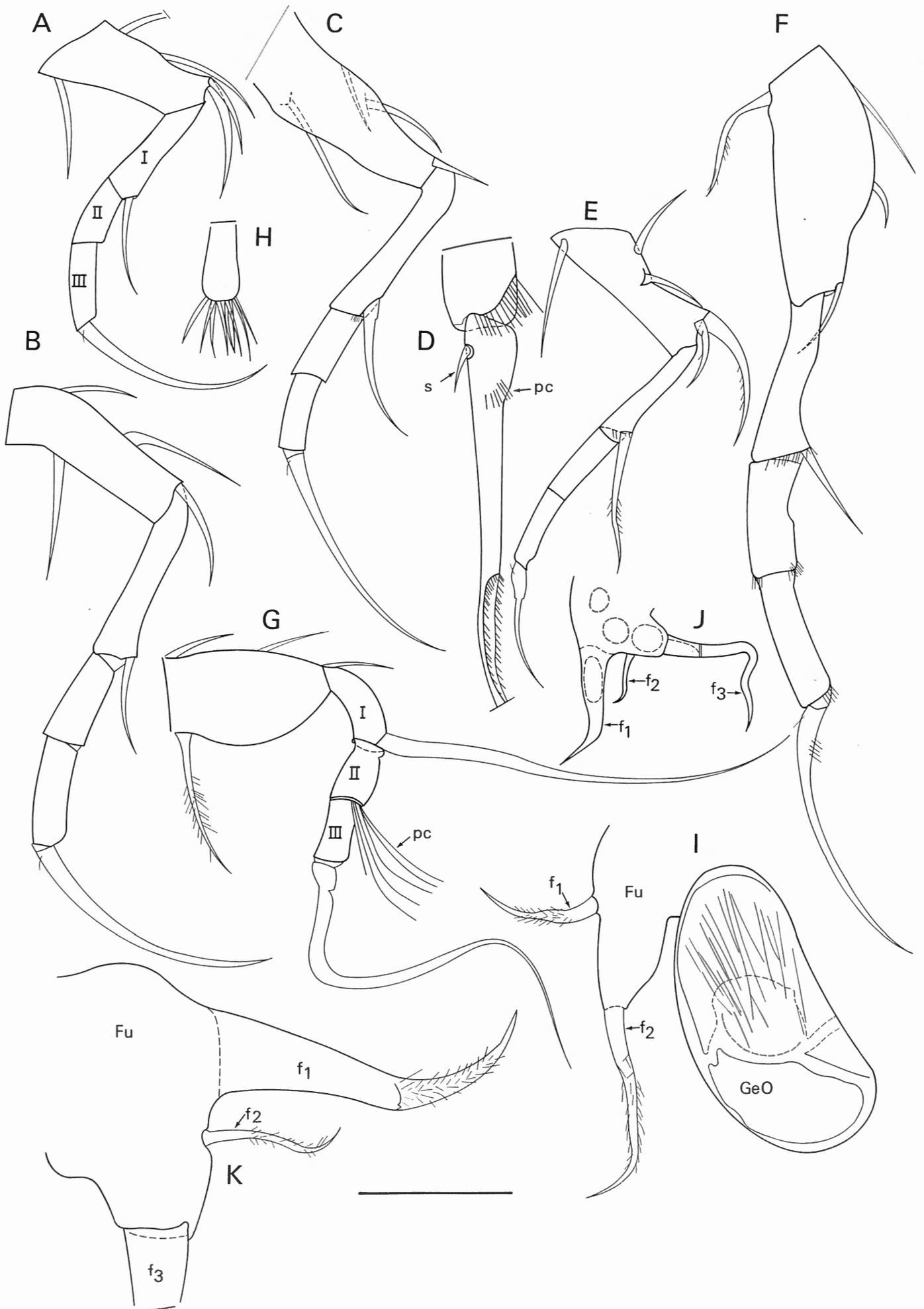
Oued Tesselata is situated on the Fadnoun-plateau, where temperatures frequently drop below zero, especially in winter. The Tassili-n-Ajjer is mostly considered to belong to the northern part of the Sahara, where winter rains are most frequent (these mountains also receive much more rain than the surrounding lowland deserts) and summer rains are fairly rare. The temporary pools in Oued Tesselata thus fill up most frequently in colder periods and it is therefore understandable that a species of *Leucocythere*, generally considered to comprise cold stenothermic forms, can survive in these conditions. The material of *L. algeriensis* sp. n. was collected after a major rainfall in late spring and at that time, temperatures were still quite low.

The type specimens of *O. milani* were raised from completely desiccated mud, collected from a dried vlei in Ovamboland, northern Namibia (MARTENS, 1989). The region is a semi-desert, hot and dry and pools fill up only periodically. Different from *Leucocythere* s.s. and *Potamocythere*, *Ovambocythere* has thus clearly adapted as a temporary pool species in a subtropical region. No other ecological preferences or requirements are known to date, but it is interesting to note that the species was raised from only one of the several pools from which dried mud was collected. This pool did not appear different from all the others in any notable aspect and furthermore yielded specimens of *Sclerocypris exserta* and a species of *Hemicypris*, both very common in temporary pools in this part of Africa.

Ovambocythere milani is thus far still the only Cytherid that was ever raised from completely desiccated mud. Although SARS (in various publications) often described

Figure 9. *L. mirabilis* KAUFMANN. All adults, collected at Mondsee.

A. ♀, P(1). B. ♀ P(2). C. ♀, P(3). D. *Idem*, detail of distal endopodial segment. E. ♂, P(1). F. ♂, P(2). G. ♂ P(3). H. ♂, brush-like organ. I. ♀, furca and genital operculum. J. ♂, furca (as part of hemipenis). K. *Idem*, detail. Scale: 83 µm for A-C, E-I; 33 µm for D, K.



Entomostracan faunas raised from dried mud, he apparently never succeeded in obtaining any cytherids in his aquaria. We do not have such undeniable proof for *L. algeriensis* nov. sp., but the presence of this species in temporary habitats on a desert plateau suggests that it is also capable of surviving as dry resistant stages.

Bearing this in mind, the anomalous occurrence of *L. mirabilis* on the island of Corfu could also be explained. If *L. mirabilis* were to have the same ability to survive in a dry resistant stage, than it could very easily have been brought to this southern locality by passive transport, for example by birds, from more northerly situated localities. The passive transport of eggs or juveniles could also have been effected in other ways. Long range transport of solid particles with a diameter of more than 75 μm was recently recorded to be feasible through air currents in the atmosphere (BETZER *et al.*, 1988). Viability of eggs, transported through the atmosphere, was experimentally checked by SOHN & KORNICKER (1979). THIENEMANN (1950), furthermore, mentioned a case, similar to the one here discussed. The psychrophylic cladoceran *Limnoscida frontosa* SARS, normally living in northern Europe, was observed for a short period of time in central Europe, in a pond in Southern Bohemia. It is furthermore noteworthy that *L. mirabilis* disappeared from its Greek locality when temperatures became too high.

We thus appear to note a tendency towards the presence of dry resistant stages in various species of the Leucocytherini. Whether this ability to produce such stages is present in all Leucocytherini and whether it is furthermore restricted to this group cannot be said to date. However, the answer to this question could have important phylogenetical implications.

Potamocythere murgabensis SCHORNIKOV, 1986, finally, was recently recovered from Pleistocene sediments in the south-eastern part of Pamir in the Karasu Province, Soviet Republic of Tadjikistan (SCHORNIKOV, 1986). Living specimens of this species were found on the bottom of the Murgab stream in the same area (Fig. 13).

As we are not certain if the Chinese fossils belong to the Leucocytherini, their ecology and distribution will not further be discussed here. The same applies for the other Miocene *Limnocythere* species, mentioned by CARBONNEL (1969) and BODINA (1961).

5.4. Phylogeny and historical biogeography

For various reasons, we will not present a complete cladistic analysis of the Leucocytherini here. It indeed would prove nearly impossible to successfully determine the adelphotaxon, which would have to be found in the Limnocytherini. As was mentioned above, however, this tribe is in such a state of taxonomic confusion that to introduce some order, necessary for the said analysis, is beyond the scope of the present paper and in any case

would be impossible without conducting a comprehensive revision. Furthermore, we suspect important members of the Leucocytherini to still be unknown to science, especially in Asia and possibly also in South America. Nevertheless, some remarks on phylogenetic affinities can here be presented.

Within the Leucocytherini, it appears clear that *Leucocythere* is the most evolved member, while both *Potamocythere* and *Ovambocythere* have more plesiomorphic character states. For example, the latter two genera have a general morphology of the A1 and the A2 and of the 3 pairs of walking limbs which still show close similarities to the Limnocytherini. Furthermore, in none of these 2 genera is there a significant difference in carapace size between the 2 sexes as in the case in *Leucocythere* s.s. To decide which of the former two genera is most plesiomorphic, would at this stage be impossible. For this, we would have to rely heavily on the anatomy of the hemipenis. The copulatory appendage of *Potamocythere*, however, remains at present insufficiently known.

Within *Leucocythere*, it is clearly *L. mirabilis* which represents the most apomorphic condition. The A1 of the male of *L. algeriensis* nov. sp. indeed does not display the S-shaped distal segment, while the 3rd walking limb lacks the hyperelongated pseudochaetae on the second endopodial segment and has a less strongly curved distal claw. On the other hand, *L. algeriensis* also has several peculiarities which can be considered as apomorphic specialisations. When compared to an ideal Limnocytherid, one of the distal claws of the male A2, for example, is unusually stout and thick, a sexual dimorphic character absent in all other Limnocytherinae, but which somewhat resembles the distal claw in a number of Timiraseviinae, e.g. the male of *Elpidium* species with the comb-like claw on the A2 (COLIN & DANIELOPOL, 1980). Such features indicate that, not completely unexpected, *L. algeriensis* also has some apomorphic character states of its own. Still, existing evidence seems to indicate that *L. mirabilis* in general is the more advanced species of the two.

The historical biogeography of the group can be reconstructed applying two main methodologies, both fairly rigid and hypothetically constructed: the *center of origin* hypothesis and the *vicariance* model.

(a) If the progression of the morphological differentiation of the Leucocytherini is followed, than one can hypothesize that the origin of this group is situated in Central Asia, somewhat around the present day areal of *Potamocythere murgabensis* SCHORNIKOV, 1986. From there, this lineage could have spread westwards and possibly also eastwards. This would indicate one branch colonizing Africa (*Ovambocythere*) and another one colonizing Europe in the late Neogene and, at a later stage, northern Africa (see below).

(b) If the Upper Miocene species mentioned above (see for example KRSTIC, 1987 and BODINA, 1961) are true Leucocytherini, then one could postulate that during

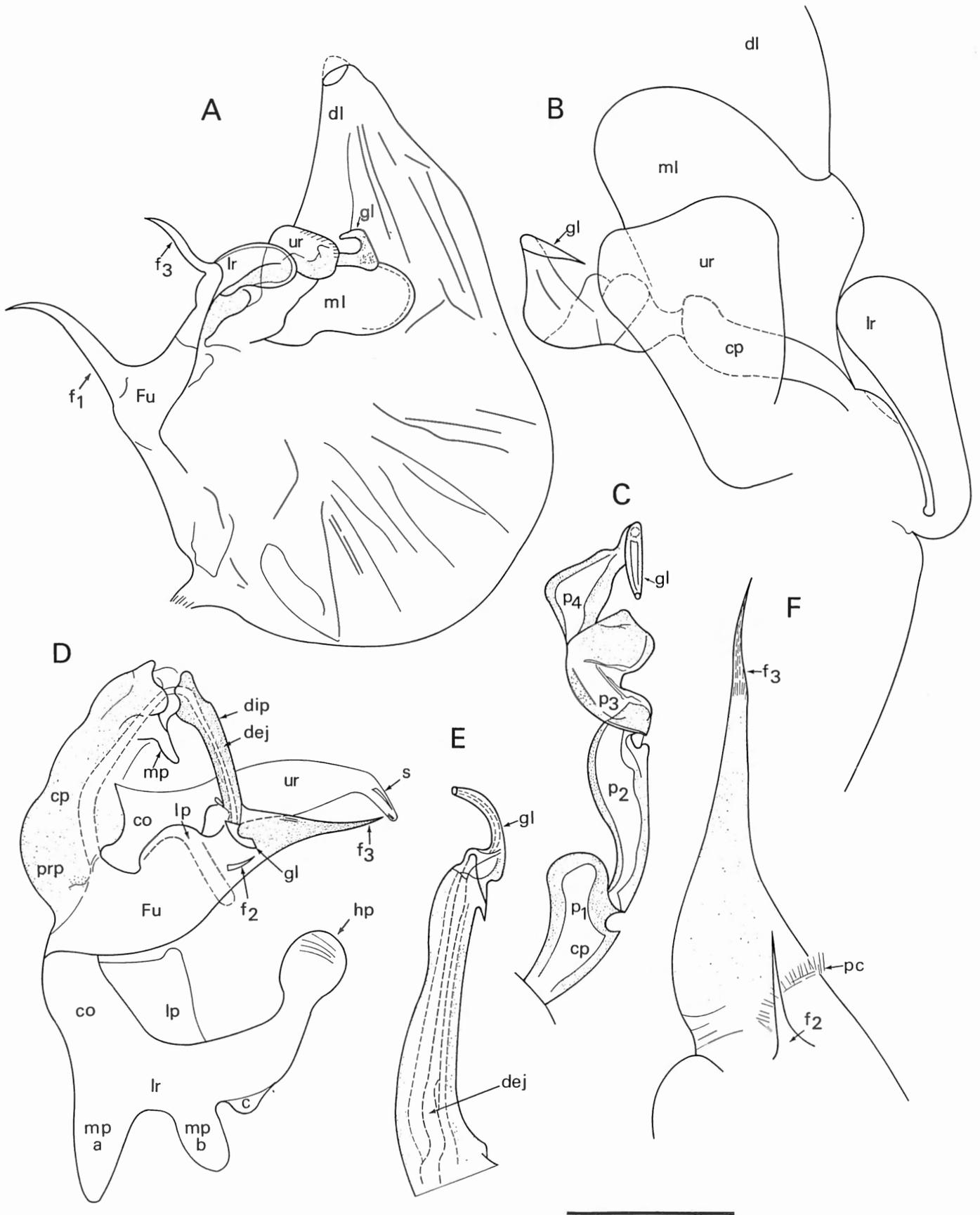


Figure 10. *Leucocythere mirabilis* KAUFMANN (A-C) and *Limnocythere* (*Limnocytherina*) *sanctipatricii* (BRADY & ROBERTSON) (D-F). Detail of hemipenis and male furcal anatomy. All specimens from Mondsee. *L. mirabilis*: A. Medial view of hemipenis. B. Details of co and copulatory processus. C. Detail of copulatory processus. *L. (L.) sanctipatricii*: D. Detail of copulatory complex, with co, copulatory processus and furca. E. Detail of distal part of copulatory processus. F. Detail of furca. Scale = 83 μ m for A; 33 μ m for B-E.

the Tertiary, when a mild climate was governing, a generalised distribution of one or more leucocytherinid ancestors existed over Europe, Asia and Africa. From these ancestors, found during the Pleistocene, some lineages disappeared, others specialised to cold water habitats and spread over large parts of Europe.

To substantiate any of these two scenarios would require far more data than presently available. However, the most parsimonious alternative to date appears to be a combination of the two: the three different genera known to date most likely originated in geographically isolated regions from a more widely distributed ancestor: *Potamocythere* in Asia, *Leucocythere* in Europe and *Ovambocythere* in Africa. The restricted present day distribution of the latter genus of course does not allow for much deduction, but comparison to other South and South-West African ostracods indicates that the actual origin should not necessarily be situated in southern Africa itself. Many groups with their present day distribution mainly restricted to the southern part of Africa (for example a number of genera of the Megalocypridinae) appear to have their center of most intensive speciation situated in East Africa (MARTENS & COOMANS, in press).

With regard to the speciation within *Leucocythere* s.s., we can be somewhat more precise, as this event must have occurred in more recent, hence better documented periods. We can easily accept vicariance effects to have caused the main part of the generic evolution within the tribe. However, with regard to the speciation of the two Recent *Leucocythere* species, we must allow more importance for faunal movements between Europe and North Africa. Simple allopatric speciation caused by the barrier of the Mediterranean is out of the question, if one takes into account the impact of the different glaciations.

If we allow for the fact that the origin of *Leucocythere* s.s. in Palaeartic, and this conforms to both scenarios suggested above, than we must also accept that *L. algeriensis* originated from Palaeartic stock, and does not have a common ancestor with *Ovambocythere* which it does not share with *L. mirabilis*. The direct ancestor of *L. algeriensis* must thus have reached North Africa from Europe and after the genus was already sufficiently evolved as such. The last cold period allowing Palaeartic faunas to penetrate into North Africa was the last stage of the WURM (c. 20000 BP); this was also the most severe of the four glaciations. Exact dating of the speciation between the two *Leucocythere*'s is of course not possible, still it appears likely that *L. mirabilis* and *L. algeriensis* did not split at an earlier stage. Previous glaciations followed too fast after each other for the taxa to have evolved above the subspecific stage. The 2 populations would have been

merged back to one genetic pool. We are not suggesting that this scenario might not have taken place at all; it is on the contrary even quite likely. For a better documented example of such a sequence of (sub)speciation and merging (or extinction) effects, see the discussion on the *Limnocythere* s.s. fauna of the East African Galla lakes in MARTENS (in press and in prep.).

This colonization of North Africa by European ancestral forms, then, could have occurred either through the Atlas Mountains or via the Red Sea Hills or, less probable but not impossible, directly by passive transport over the Mediterranean Sea. The mountainous ridge along the Red Sea has definitely served as a North-South migratory pathway for Palaeartic faunas. This was shown by the discovery of relict populations of the European *Limnocythere stationis* by MARTENS (1984).

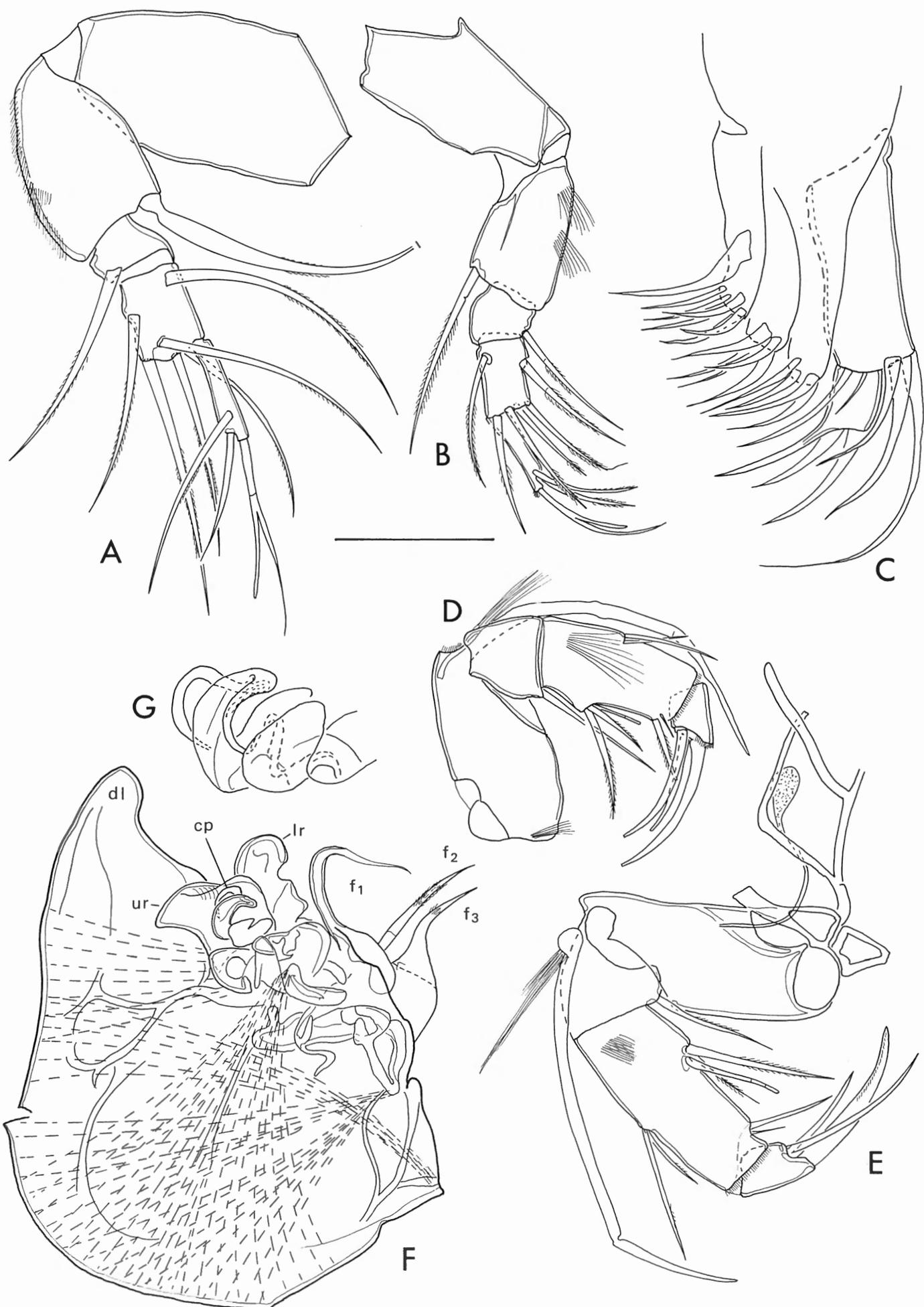
The combination of the present deduction and of the phylogeny proposed here, indicates that *L. mirabilis* should be derived from the recolonizing populations and hence that *L. algeriensis* must be more closely related to Pleistocene European *Leucocythere* than *L. mirabilis* itself, i.e. ♀ of these ancestors should have wide and sculptured valves, unlike those of *L. mirabilis*. This inevitable conclusion seems to urge a re-examination of older European *Leucocythere* fossils. For this to be properly conducted, however, we should first know the exact valve morphology of *L. algeriensis*.

If the Tassili-population of *L. algeriensis* is indeed of the age proposed here, than it must have survived several fairly severe climatic fluctuations. This, however, is not impossible in these mountains. One documented case is the hyperarid period dated at c. 5000 BP by DUMONT (1978) in most of Central Sahara, which wiped out the aquatic faunas in the Air Mountains, but not in the Tassili-n-Ajjer, where for example Nile Crocodiles survived until the 1950.

L. baltica was not included in the present discussion, because still too many uncertainties exist with regard to the position and status of this species. It is, however, not impossible that this species could be found still living to date; at that stage an analysis of the hemipenis morphology should allow an exact assessment of this taxon.

5.5. Functional morphology and evolution (D.L.D.)

The present section will deal with the following questions: what is the evolutionary significance of the peculiar morphology of the various *Leucocythere* species? Did some of these morphological characters represent adaptations or functional solutions to a number of environmental problems? Are they specific solutions, uniquely produced by *Leucocythere* or *Leucocytherini*, or are similar adaptations found in



other taxa as well?

The morphology of an organism can be viewed through a functional analysis of the various character states. We can classify the morphological characters of an ostracod in several functional groups or *modules*. For example, most of the morphological characters of the carapace cooperate to one main function: the protection of the soft body structures. The main part of the A2 and of the walking limbs cooperate as one module to the locomotory function. The sensorial setae of the A1 and A2 and parts of the thoracic legs (especially the third walking limb) as well as the furca and the copulatory appendages participate in the mating process. For the feeding function, we have a module represented by the antennae (parts of their structure), the mandible, the maxillula and, partly, the first walking limb (maxilla?). Parts of some of the limbs, for example the distal endopodial segments of the antennae, are involved in several functional modules at once: in this case the locomotion, the feeding and the mating. We will now discuss some adaptations in a few of these modules.

a. The carapace as the protection module

The calcification of the valves in *L. mirabilis* is very poor and one can well imagine that the anterior sulcus and sometimes also the curved shape of the dorsal margin are both due to deformations of the calcareous walls, which are not strong enough to maintain the convex shape of the valve and the straight shape of the dorsal margin. Still, there are enough compensatory forces which prevent the carapace form being crushed. For instance, a crenulated intercardinal bar increases the strength of the dorsal margin. If this margin shows a deformation in the area of the 2 central sulci, than as a compensation the intercardinal bar, and eventually also the cardinal teeth, should be stronger at the two extremities. This is indeed the case in this group (see descriptions above). Such compensatory reinforcements are known in many examples in both the Plant and Animal Kingdoms, and also even in constructions made by man in different civilisations (d'ARCY THOMPSON, 1961).

Leucocythere shows a strong sexual dimorphism in the shape and size of the carapace. As was already mentioned, the female is smaller and has a paedomorphic shape. One could, now, question the possible adaptive advantages of these peculiarities. For this, we refer to GOULD (1977), who discussed a number of possible adaptive advantages of various forms of paedomorphism. None of these arguments seem to apply to the situation of female *L. mirabilis*. If there is no obvious advantage, than it could very well be that the poor calcification, the paedomorphic shape and the reduced size of the female carapace all are the results of malfunctioning of various morphogenetic processes,

i.e. a slower intensity of calcification and an interruption of the growth and development of the carapace before the individual reaches the adult stage. It appears that such features are by no means peculiar to *Leucocythere* only. Poor calcification and paedomorphic shapes in females can be found in the two other leucocytherinid genera (*Potamocythere* and *Ovambocythere*) and examples are known in some representatives of the Limnocytherini. DELORME (1971) figured such cases for *Limnocythere pseudocrenulata* STAPLIN, *L. ceriotuberosa* DELORME and *L. verucosa* HOFF. *Paracythereis* species from Lake Titicaca (and surroundings) were investigated by us (material from Dr P. CARBONEL) and shows strikingly convergent characters with *Leucocythere*. For example: absence of the posteroventral convexity in males, the intercardinal bar which is more heavily crenulated at both extremities, etc... It should meanwhile also be stressed that these convergences in structure and shape of carapaces between species of *Leucocythere* and *Limnocythere* s.l. prevent us from readily including taxa of which the soft part anatomy is unknown in *Leucocythere*. Other characters of valve anatomy will be necessary to allow a better classification of homeomorphic or convergent fossil limnocytherids. An analysis of the ultra structure of the sieve pores could be one such approach.

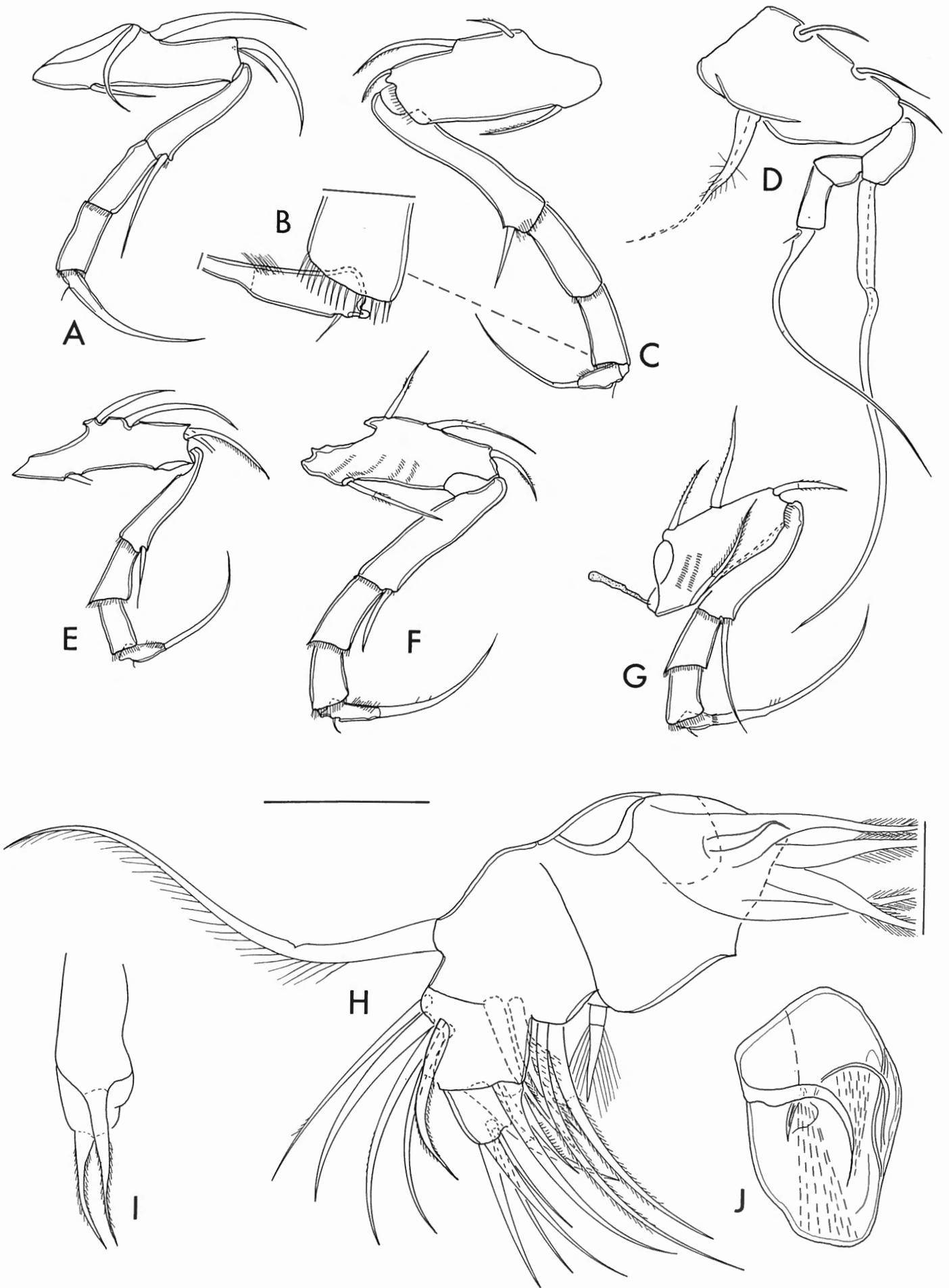
One should note that, in spite of the weak calcification processes, *L. mirabilis* appears to perform very well in its environment and can even be considered as one of the first colonizers of newly available habitats. Finally, it could be that the weakly calcified valves are an adaptation to calcium-poor environments. However, this argument is contradicted by the fact that most of the present day localities of *L. mirabilis* appear to be ion rich waters.

b. Characters contributing to the mating process

The module of the mating process displays the most original characteristics of *Leucocythere*. Firstly, we see an evolutionary trend in the males to produce both hypermorphic and paedomorphic characters. Secondly, we need to discuss the peculiar structure of the clasping organs and of the copulatory processes on the hemipenis. We will attempt to discover if these structure promote a fine 'sexual recognition' in the mating process within the various populations of the species of *Leucocythere*.

The male of *L. mirabilis* displays the hyperdevelopment in size and shape of several morphological characters, e.g. the distal antennular segment (Fig. 8B), the aesthetasc Y (Fig. 8C), the distal seta of the first endopodial segment, the hyperelongated pseudochaetae on the second endopodial segment and the terminal claw of the third walking limb and setae f2 and f3 of the furca (Figs. 9 (G, J, K)). Additionally to the hyperdeveloped structures, one finds a paedomorphic seta on the

Figure 12. *L. algeriensis* nov. sp. (♂ = no. OC 1471, ♀ = no. OC 1472). A. ♂, P(1). B. ♂, P(2). C. ♂, *idem*, detail. D. ♂, P(3). E. ♀, P(1). F. ♀, P(2). G. ♀, P(3). H. ♂, *Md-palp*. I. ♀, *furca*. J. ♀, *genital operculum*. Scale = 81 µm for A, B, D-G; 33 µm for C, H-J.



first endopodial segment of the male A2 and the reduction in size of the endopodite of the third walking limb when compared to the female homologue and to those of the first walking limb in related groups. *L. algeriensis* does not display the hyperdevelopments on the A1 and the A2 or the respective paedomorphic structures listed above. This species furthermore has the distal claw on the P(3) less strongly developed and has the pseudochaetae on the second endopodial segment of this limb of normal (minute) size. Contrary to this, *L. algeriensis* present a hyperdeveloped distal claw on the A2 of the male (Fig. 11E).

The origin of these peculiar developments must now be questioned. At least a number of these morphological traits does not seem to be the result of an adaptive process for the communication of mating (recognition) signals. The distal claw of the P(3) in the male, for example, does not look like an efficient clasping organ to fix the female. It should however be noted that the other leucocytherinid genera, as well as many representatives of *Limnocythere* s.l. also have a somewhat overdeveloped and poorly sclerified distal claw on this limb, although never as prominent as in *L. mirabilis*. We suggest that hyper or hypodevelopment of the above mentioned morphological structures originated through a change in the activity of either the various morphogen substances or of the regulatory genes. For an account on the morphogenetic mechanisms during the ontogenetic development and on the importance of the regulatory morphogen substances, see WOLPERT (1978). The existence of heterochronic genes which regulate the timing of expression of a given morphological trait, has recently been described by RUVKUM & GIUSTO (1989) for the nematode *Caenorhabditis elegans*. The suppression of the activity of such heterochronic genes or their mutation determine arrested developmental evolution of the morphological characters. On the other hand, the existence of redundant information at the subcellular level within an organism, was recently discussed by BRAY & VASILIEV (1989). In the case of *Dictyostelium* mutants, the removal of a single protein will not produce a major functional degradation, because other proteins can maintain this function.

We believe that in some cases an excess of morphogen could have determined the peculiar (retarded) sclerification and the S-shape of the distal claw of the P(3). A prolongation of the developmental time, on the other hand, could produce, in conjunction with an excess activity of the morphogen, a hypergrowth of such

structures, like for example the seta of the first endopodial segment and/or the pseudochaetae on the second segment of this limb of males *L. mirabilis*.

The hyper development of the aesthetasc Y in the male A2 is not an adaptive solution to a better recognition of the female, because the distal, sensorial segment of this structure is not better developed than in other *Limnocytherinae*; the entire elongation is due to the basal segment.

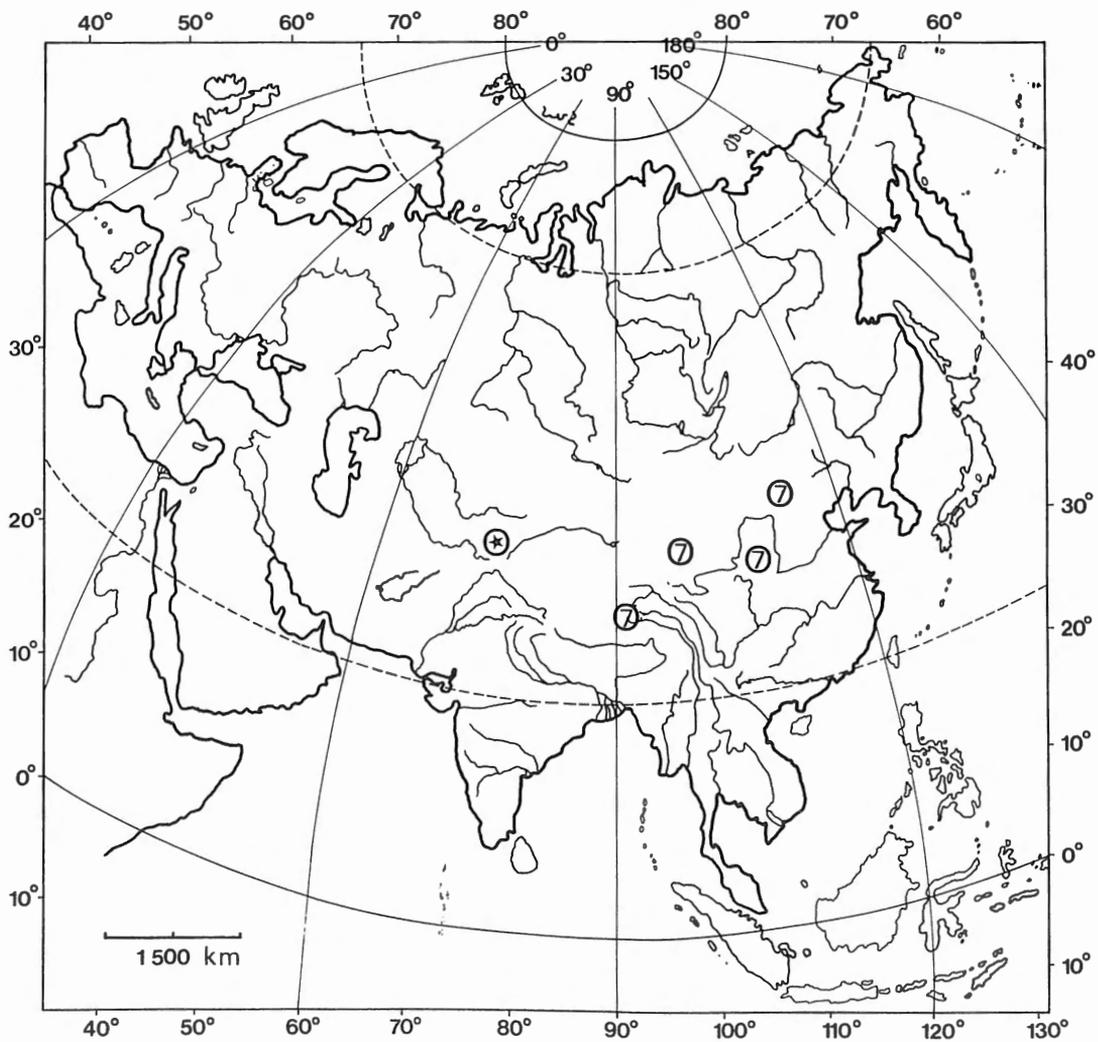
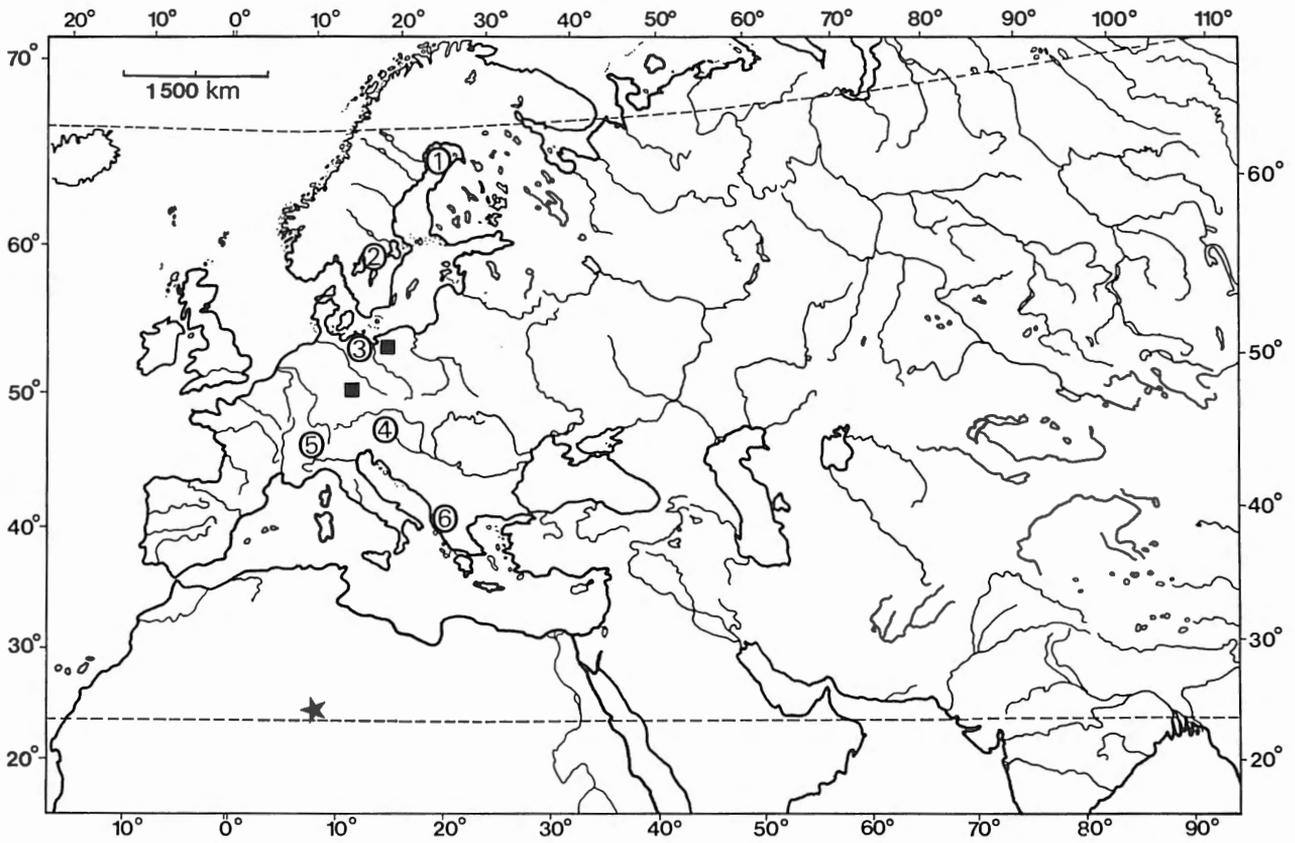
As was discussed above, the S-shaped structure of the distal claw on the P(3) does not represent an efficient clasping organ. But it is possible and even probable that this peculiar structure originated independently of an adaptive function. Whether these structures have been developed for a sexual function, i.e. for discriminating signals sent by the male which can then be specifically recognised by the female (EBERHARD 1985, KANESHIRO 1988) remains to be demonstrated. We believe that this is the case at least for some of the furcal setae in the male.

We now still have to discuss the peculiar structure of the clasping organs and of the copulatory process in Leucocytherini. These structures are clearly poorly developed when compared to those of other Leucocytherid genera (MARTENS, in press). The lower ramus of the clasping organ in *Limnocythere* s.s. consists of a hook-like process and of a lateral process, both with a high diversity of fine structures, which play a role in the male-female recognition during the mating process. In the case of *Limnocythere mirabilis* and *L. algeriensis* as well as for the living representatives of the genera *Potamocythere* and *Ovambocythere*, the clasping organs remain poorly developed: the lower ramus, for example, is lamellar shaped, not hook-like and strongly sclerified. Such a structure does not allow for much variation in tactile recognition. It appears that, to a limited extent, these functions might be taken over by some of the furcal setae, which are better developed than in the Limnocytherini, but these can never reach the same degree of diversification as in *Limnocythere* s.s.

The copulatory process is spiral shaped and has a simple conical glans. In the highly diversified group of *Limnocythere* s.s., the copulatory process seems to be better equipped from a functional point of view. It is better formed by two articulating structures, the distal one, the glans, having mostly a far more complex morphology (MARTENS, in press).

Very likely, it is this absence of sufficient potential for morphological variation in those copulatory structures which prevented the sexual isolation, necessary for

Figure 13. Geographical distribution of Fossil and Recent Leucocytherini (not *Ovambocythere*, restricted to southwestern Africa) and some Fossil species, referred to *L. mirabilis* in the literature. For an appraisal of the latter identifications, see text. Circled figures = *L. mirabilis* (Recent) and *L. cf. mirabilis*. 1: Finland, near Hailuoto Island (Recent). 2: Sweden, L. Vättern (Recent). 3: Northern DDR (Fossil, = *L. cf. mirabilis*). 4: Austria, Mondsee, Traunsee and Attersee (Recent). 5: Switzerland, Brienz and Thuner See (Recent). 6: Greece, Corfu Island (Recent). 7: China (Fossil, = *L. cf. mirabilis*). Black square = *L. baltica* (DIEBEL) (Fossil, Central and Northern DDR). Asterisk = *L. algeriensis* nov. sp. (Recent, Algeria). Circled asterisk = *P. murgabensis* SCHORNIKOV (Recent, USSR).



more extensive radiation and speciation within the genus *Leucocythere*, and the same seems to apply to *Potamocythere* and *Ovambocythere*. The disjunct populations of *L. mirabilis* in northern, central and southern Europe, from where we could examine material (see above), do not show any morphological differentiation in the limbs, copulatory appendages and the carapace, in spite of a nearly complete geographical isolation and ecological differences in habitat. Also, for the moment, both *Potamocythere* and *Ovambocythere* are known in one living species only (SCHORNIKOV 1986, MARTENS 1989).

6. Conclusions

Leucocythere mirabilis could be considered as a 'monstrous *Limnocythere*', if one looks at the various morphological peculiarities of this species. Most of these characters (see above) are maladaptive from a functional point of view and when compared to the ideal mechanical solutions. However, we could see that *L. mirabilis* was perfectly able to colonize lacustrine habitats during the Pleistocene and a number of these lakes have been inhabited by this species up to now. Compared to other European ostracods like *Cytherissa lacustris* and *Limnocythere (Limnocytherina) sanctipatricii*, *L. mirabilis* did very well in maintaining itself as a species, despite these apparently maladaptive characters. Indeed, only the strong eutrophication of these biota could cause its extinction from many lacustrine habitats. Also, once we identified the phylogenetic lineage of the Leucocytherini and its evolutionary trends, we could no longer uphold this view of a 'monstrous' species. *L. mirabilis* is a logical realisation of specific developmental mechanisms, possibly peculiar to this lineage.

The accumulation of the apparently maladaptive traits

in an ostracod species like *L. mirabilis*, however, is only possible when various compensatory morphologies and a certain redundancy in the various types of morphological characters exists. For instance, most Limnocytherinae have three undifferentiated walking limbs. If the P(3) becomes useless for the locomotion function, then still the organism can move by the use of the first 2 walking limbs. The problem of redundant morphological characters in the survival of ostracod species has been discussed by BENSON (1984).

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