

On *Korannacythere* gen.nov. (Crustacea, Ostracoda), a new genus of temporary pool limnocytherids from southern Africa, with the description of three new species and a generic reassessment of the Limnocytherinae

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Abstract

A new genus *Korannacythere* and three new species, *K. devriesi* spec. nov., *K. ugiensis* spec. nov. and *K. hamerae* spec. nov. are described from rockpools on the Korannaberg and the Drakensberg (South Africa). The new genus is characterized by the following main features: absence of pronounced sexual dimorphism in both valve and non-copulatory soft part morphology, a nearly adont hinge, aberrant chaetotaxy of A2 and simplicity of hemipenis structure (no clasping organ, simple copulatory process). *Korannacythere* gen.nov. is here lodged in the Limnocytherini, but, because of the adont hinge and the absence of at least a part of the clasping organ in the hemipenis, it occupies an isolated position within this tribe. The generic taxonomy of the Limnocytherinae is reassessed, and an evolutionary scenario (exemplified by both a reduction in hinge structure and the increasing size of the furca in the hemipenis) is proposed.

Korannacythere gen.nov. is the second limnocytherid genus occurring exclusively in temporary habitats, the other one being the monospecific genus *Ovambocythere* MARTENS, 1989. As both species belong in different tribes, and as several other limnocytherids have meanwhile also been reported from non-permanent habitats, it is accepted that Limnocytherinae in general have the ability to produce drought-resistant stages. The evolutionary significance of this ability for the success of non-marine ostracod lineages is briefly discussed.

Key words: taxonomy, morphology, sexual selection, diapause, evolutionary ecology.

Résumé

Un nouveau genre *Korannacythere* et trois nouvelles espèces, *K. devriesi* spec. nov., *K. ugiensis* spec. nov. et *K. hamerae* spec. nov. sont décrits des mares rocheuses du Korannaberg et du Drakensberg (Afrique du Sud). Le nouveau genre se distingue par les principaux caractères suivants: absence de dimorphisme sexuel prononcé aussi bien dans la valve que dans la morphologie des parties molles non copulatoires, charnière pratiquement dépourvue de dents, chétotaxie aberrante de A2 et structure simple de l'hémipénis (absence d'organe préhenseur, processus copulatoire simple).

Afin de déterminer la position du nouveau genre, la taxonomie générique est réévaluée et un scénario évolutif est proposé

pour les groupes faisant partie de cette sous-famille (illustré par la réduction de la structure de la charnière et l'augmentation des dimensions de la furca dans l'hémipénis). *Korannacythere* gen.nov. est classé ici parmi les Limnocytherini, mais en raison de la charnière dépourvue de dents et de l'absence d'organe préhenseur dans l'hémipénis, il occupe une position isolée au sein de cette tribu.

Korannacythere gen.nov. est le second genre de limnocytherides apparaissant exclusivement dans des habitats temporaires, le premier étant le genre monospécifique *Ovambocythere* MARTENS, 1989. Etant donné que les deux genres appartiennent aux tribus différentes et que, entretemps, plusieurs autres limnocytherides ont également été signalés dans des habitats non-permanents, l'on considère que les Limnocytherinae, en général, ont la capacité de développer des phases durant lesquelles ils résistent à la sécheresse. L'importance évolutive de cette capacité pour la prospérité des lignées d'ostracodes non-marins est brièvement discutée. Un scénario évolutif est élaboré à partir des informations disponibles concernant la morphologie, la distribution et l'écologie du nouveau genre et des nouvelles espèces.

Mots clefs: taxonomie, morphologie, sélection sexuelle, diapause, écologie évolutive.

Introduction

Temporary habitats in the semi-arid to arid areas of southern Africa have a remarkably high diversity and endemism, even at a supra-specific level. With regard to non-marine Ostracoda, the biodiversity of these habitats appears to be comparable only to that of ancient lakes such as Lake Tanganyika (MARTENS, in press). Some of the extensive radiations in these habitats can logically be expected, such as that of the giant ostracods of the subfamily Megalocypridinae (MARTENS, 1986, 1987), which show special adaptations to life in temporary environments. Other groups, however, are not even expected to occur in such habitats, let alone be speciation prone there. *Ovambocythere milani* MARTENS, 1989 (species and genus endemic to northern Namibia) was the first limnocytherid ever to be raised from completely desiccated mud, and the discovery of this taxon actually constituted counter

evidence to the long-held belief that species of the superfamily Cytheroidea were unable to produce drought-resistant stages.

The present paper describes a second new genus and three new species of temporary pool limnocytherids (from rockpools on both the Korannaberg and the Drakensberg in South Africa). After a brief generic reassessment of the post-Cretaceous Limnocytherinae as a whole, it is established that *Korannacythere* belongs to a different lineage within the Limnocytherinae than does *Ovam-bocythere*: the former belongs in the Limnocytherini, the latter in the Leucocytherini. This corroborates the opinion that the ability to produce drought-resistant stages in limnocytherids is not a freakish event, but is more widely spread amongst the members of at least this subfamily in the Cytheroidea than was previously accepted. The evolutionary implications of this deduction are briefly discussed. The new species furthermore shows a number of morphological peculiarities, and their potential taxonomic significance is also discussed.

Abbreviations used in text and figures

Hemipenis

cp	copulatory process
cs	caudal seta
dej	ductus ejaculatorius
dl	distal lobe
f (1-3)	furcal setae 1 - 3
fu	furcal ramus
pl	proximal lobe
po	entrance pore
trab	moveable trabecule
vej	vesicula ejaculatoria

Other soft parts

A1	Antennula
A2	Antenna
exo	exopodite of A2
Md	Mandibula
M×1	Maxillula
P (1)	First walking leg (= first thoracopod T1)
P (2)	Second walking leg (= T2)
P (3)	Third walking leg (= T3)
fu	Furca (in female)
go	Genital operculum (female)

Valves

H	Height of valves
L	Length of valves
RV	Right valve
LV	Left valve
act	anterior cardinal tooth
acs	anterior cardinal socket

Illustrated (type-)specimens

The following registered specimens have been used for illustrations:

Korannacythere devriesi gen. et spec. nov.

AM.OST1A (holotype): 1(A-K), 2A,B.
 AM.OST1B (allotype): 2(C-H).
 OC.1866 (3 paratypes) (KM.1889): 7G,,H,N,O;
 (KM.1891): 7J; (KM.1892): 7I.
 OC.1867 (paratype): 7C,D,M.
 OC.1868 (paratype): 7E,F.
 OC.1869 (paratype): 7A,B.
 Remarks: illustrated specimens of Figs. 7K (KM.1893) and 7L (KM.1894) are lost.

Korannacythere ugiensis gen. et spec. nov.

AM.ECR160A (holotype): 3C-F, 9C,D.
 AM.ECR160B (allotype): 4A-H.
 OC.1871 (paratype): 3B, 9A,B,J.
 OC.1872 (paratype): 9G.
 OC.1873 (2 paratypes) (KM.2076): 9I; (KM.2077): 9H.
 OC.1874 (2 paratypes) (KM.2078): 9F; (KM.2079): 9E.
 OC.1875 (paratype): 3A.

Korannacythere hamerae gen. et spec. nov.

AM.OST2A (holotype): 5A-G.
 AM.OST2B (allotype): 6A-G, 10G,H.
 OC.1878 (paratype): 10F.
 OC.1881 (3 paratypes) (KM.2090): 10D; (KM.2091):
 10E; (KM.2092): 10C.
 OC.1882 (paratype): 10A,B.
 OC.1885 (3 paratypes): (KM.2108): 10N; (KM.2109)
 10K; (KM.2110): 10M.
 OC.1886 (2 paratypes): (KM.2111): 10O; (KM.2112):
 10L,P.
 OC.1887 (paratype): 10I,J.

Taxonomic descriptions

Subclass Ostracoda LATREILLE, 1806
 Order Podocopida G.W. MÜLLER, 1894
 Suborder Podocopina G.W. MÜLLER, 1894
 Infraorder Cytherocopina GRÜNDEL, 1967
 Superfamily Cytheroidea BAIRD, 1850
 Family Limnocytheridae KLIE, 1938
 Subfamily Limnocytherinae KLIE, 1938
 Tribe Limnocytherini KLIE, 1938

Korannacythere gen. nov.

Type species: *Korannacythere devriesi* gen. nov. spec. nov. (here designated).

Derivation of name: after the type locality of the type species: Korannaberg, north of Bloemfontein, South Africa.

Other species: *K. hamerae* spec. nov.; *K. ugiensis* spec. nov. (see below).

Diagnosis: small genus (≤ 0.5 mm), with nearly adont hinge (act in RV absent, pct in RV minute or absent, hinge bar in LV smooth) and almost no sexual dimorphism in valve shape and structure. Marginal pore canals few, c 10 along anterior margin, short and straight, not branched; fused zone narrow.

A2 with three curved apical claws, two proximal ones spinous, in both sexes; exopodite shorter in males than in females (length of this exopodite in both sexes species specific). Hemipenis simple, with both upper ramus (UR) and lower ramus (LR) of clasping organ (CO) absent; furca with a short base and three setae, not hyper developed, copulatory process (cp) simple, sickle-shaped.

Remarks

Of the three endclaws on the A2, the two proximal ones are situated closely together and are sub-equal in shape. Therefore, even at high magnification with light microscopy, only two endclaws (one proximal and one distal) are visible in most specimens. Nevertheless, the presence of three claws has been confirmed in all three species with SEM.

Additional generic features: External valve sculptures well developed in most populations, with ventral ala and dorso-lateral sulci. Width of valves sub-equal in both sexes, females being slightly wider, greatest width in the middle or in the anterior half. Three walking limbs (P1-3) with two dorsal and 1 ventral setae well developed on first segment. Lateral aesthetasc on penultimate segment of A2 small, one accompanying seta very large, the other minute.

Remark: differential diagnoses and ecology of the following species are treated in the general discussion.

Korannacythere devriesi spec. nov.

(Figs 1, 2, 7, 8 (A-F))

Type locality: sandstone rockpools at the top of Korannaberg, Excelcior district, Eastern Freestate. Approx. coordinates: S 28°51'13" E 27°13'51". Altitude: 1710 masl. Size of pools ranging from 1-50 m², depth 5-40 cm and period of inundation from 1 week to over 4 months. The new species was not found in the most short-lived pools.

Accompanying ostracod fauna: *Sarscypridopsis gregaria*, *Isocypris priomena*, *Heterocypris incongruens*.

Type material: All material was collected by Mr Ch. DE VRIES, either directly from the inundated rockpools, or raised from dried mud in the lab. Both lots of specimens were used for descriptions and illustrations. The holotype and allotype are both cultured specimens.

HOLOTYPE: a male, with soft parts dissected in glycerine in a sealed slide and valves stored dry in a cavity-slide (no. AM-OST1A).

ALLOTYPE: a female, with soft parts dissected in glycerine in a sealed slide and valves stored dry in a cavity-slide (no. AM-OST1B).

PARATYPES: a tube with c 10 specimens (AM-OST1C); several dissected and dried specimens in slides (OC.1866-1870).

Deposition of material: the holotype, allotype and ten paratypes are deposited in the Albany Museum, Freshwater Biology Section, Grahamstown (South Africa). The other paratypes are deposited in the Ostracod Collection of the Royal Belgian Institute of Natural Sciences, Brussels (Belgium).

Derivation of name: After Mr Chris DE VRIES (Bloemfontein), who collected the material.

Abbreviated diagnosis

Valves with straight, sloping dorsal margin. A1 with apical seta on second segment present. Exopodite on A2 in males not reaching beyond edge of second segment, in females reaching tip of penultimate segment, endclaws short, about 1.5 times the length of terminal segment. Glans on cp delated, base internally swollen. Apical seta on second segment of P(3) reaching tip of penultimate segment.

Extended diagnosis: small species, with straight dorsal margin sloping in caudal direction; anterior margin widely rounded, recurving abruptly towards the ventral margin; external valve sculptures prominent. A1 with apical seta on second segment. A2 with three short and stout endclaws, c 1.5 times the length of the terminal segment, proximal ones serrate; exopodite twice as long in female as in male: reaching the tip of the penultimate segment in the former, not reaching beyond the edge of the second segment in the latter. P1 the smallest walking limb. Hemipenis with copulatory process sickle-shaped, with delated glans and with base additionally widened at internal curvature; lobe dl sub-triangular, anterior margin with an additional curve in the middle.

Description of male

Valves with dorsal margin straight over 3/4-4/5 of the total length, sloping towards the caudal side, frontal margin more broadly rounded than caudal margin, frontal margin recurving abruptly towards ventral margin. No calcified inner lamella; posterior fused zone narrower than anterior fused zone, both with few (c 10 each) short, narrow and straight marginal pore canals, line of concrecence not entirely parallel to valve margin. Four central muscle scars, two ventral scars oblique. Hinge nearly adont, act absent, pct in RV very weakly built; intercardinal bar in LV smooth. External valve sculptures prominent, in dorsal half with two prominent and one smaller bulbous,

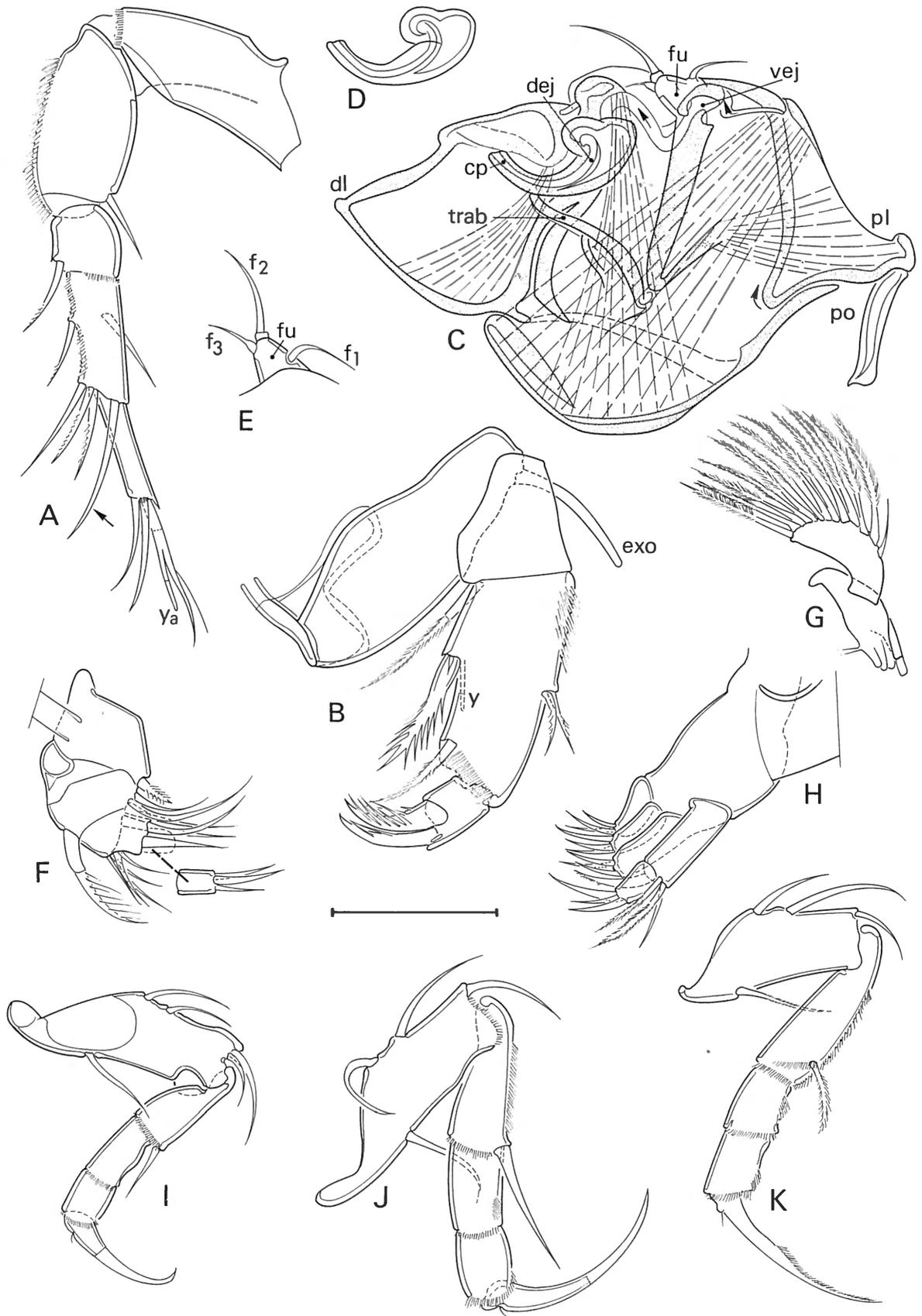


Fig. 1. – *Korannacythere devriesi* gen. et spec. nov., male.

A. A1. B. A2. C. Hemipenis. D. Idem, detail of copulatory process. E. Idem, detail of furca. F. Mandibular palp. G. Mx1. H. Idem, chaetotaxy of palp and endites. I. P1. J. P2. K. P3.

Scale = 33 μm for A-F, H-K; 81 μm for G.

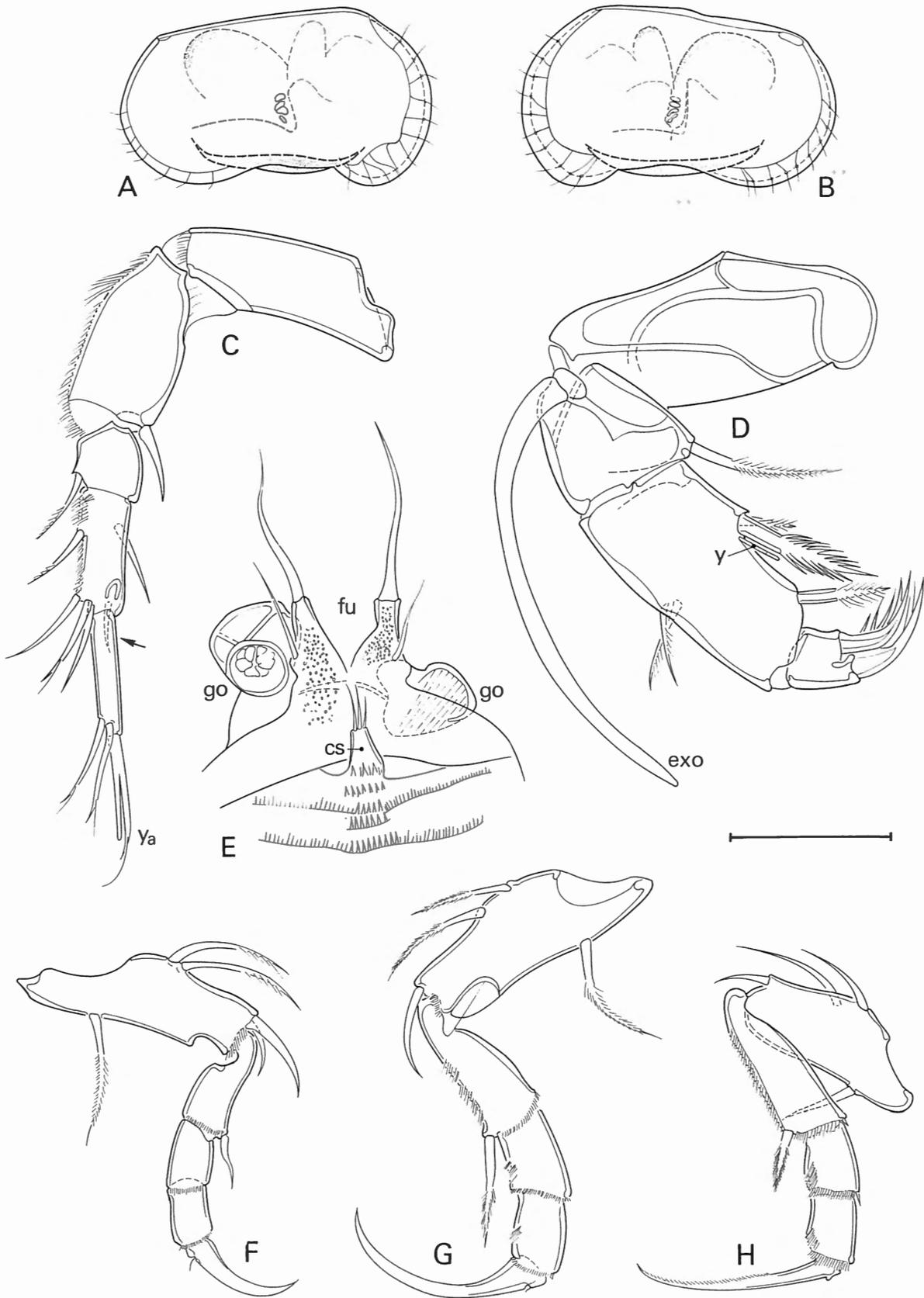


Fig. 2. – *Korannacythere devriesi* gen. et spec. nov., female.

A. LV, internal view. B. RV, internal view. C. A1. D. A2. E. Caudal part of body, showing furcae, genital operculae and caudal seta. F. P1. G. P2. H. P3.

Scale = 33 μ m for C-H; 315 μ m for A,B.

interspaced with two sulci, in ventral half with an inversed T-shaped ala. Carapace pointed at both anterior and posterior side in dorsal view, greatest width situated in the anterior half; closed valve edges forming a sharp ridge along both frontal and caudal margins, including part of dorsal and ventral margins, only absent in medio-dorsal and medio-ventral region.

Eye large and pigmented.

A1 (Fig. 1A) with second and third segments each with one apical seta; penultimate segment with 2 lateral and 4 apical setae, ventro-apical seta being the largest, terminal and penultimate segments of similar length, terminal segment with 2 apical setae and one fused seta/aesthetasc, the seta being the longest, fused part of this structure almost half of the total length of aesthetasc; most setae (incl. the one fused with the aesthetasc) claw-like and flagellated.

A2 (Fig. 1F) with exopodite only slightly longer than second segment, this segment with one apical seta, almost as long as 3rd (penultimate) segment. This penultimate segment with two short dorso-lateral setae, a huge and serrate ventro-lateral seta, accompanied by a short and weak aesthetasc and a degenerate second seta, apically with one stout seta. Terminal segment small, with three unusually short and stout claws, proximal ones set with long spines.

Mandible with coxa without special features. Palp (Fig. 1E) with segments seemingly partly fused. First segment with one apical seta and respiratory plate. Second segment with one huge dorsal seta and two (one long, one short) ventral setae. Third segment with a group of five subequal dorsal setae and two longer ventral setae. Fourth segment with three apical setae. Fifth segment with three setae.

Maxillula with respiratory plate (Fig. 1G) normal, without hyperdeveloped rays. Three endites and one palp (Fig. 1H); first palp segment elongate, with a group of three normal apical setae, and one large seta inserted near the base of the distal palp segment, second palp segment subrectangular, set with three apical setae.

Three walking limbs with chaetotaxy following the general limnocytherid pattern and not showing any significant modification.

P(1) (Fig. 1I) relatively small, with first segment bearing two dorsal, one long ventral and two unequal knee-setae, second segment with one short apical seta; terminal claw short and solid.

P(2) (Fig. 1J) larger; first segment with 2 dorsal, 1 long ventral and 1 knee-seta, second segment with one long apical seta, as long as the terminal two segments combined; terminal claw long, solid and curved.

P(3) (Fig. 1K) the largest walking limb, first segment as in P(2), apical seta on second segment shorter than 3rd segment; apical claw long, weakly sclerified and hirsute. Hemipenis (Fig. 1B) of remarkably simple structure. Furca (Fig. 1D) with short, subtriangular base and three setae, f2 being the longest. Copulatory process (Fig. 1C) simple, sickle-shaped, with squarish base and dilated glans. Lobe dl blunt and sub-triangular, with an addi-

tional curvature in the middle of the anterior margin. Medial trabecule nearly straight.

Caudal seta in-between both hemipenes (not illustrated) large and stout, consisting of one sub-rectangular base and three apical setulae.

Description of female

Valves (Figs. 2A, B, 7A, B, I, J) as in the male, but slightly wider in dorsal view and with anterior margin somewhat more broadly rounded (Note: differences in valve shape illustrated here are extremes, most specimens show less sexual dimorphism).

A1 (Fig. 2C) as in the male.

A2 (Fig. 2D) with exopodite reaching tip of penultimate segment, i.e. about twice as long as in the male; smallest accompanying seta to lateral aesthetasc on penultimate segment as long as the aesthetasc. Other aspects of chaetotaxy as in the male.

Mandible and Maxillula as in the male.

P(1)-(3) (Figs. 2F-H) with chaetotaxy as in the male, including relative lengths of setae, P(1) relatively larger than in the male.

Genital operculae simple. Furcae (Fig. 2E) large, with triangular base, one long apical seta and one shorter lateral seta, the latter inserted close to the base. Caudal seta large and stout, consisting of one sub-rectangular base and three apical setulae. Abdomen with series of spinuous setae.

Measurements (in μm)

♀ : L = 412-442 (n = 4), H = 273 (n = 2), W = 194-206 (n = 2).

♂ : L = 406-436 (n = 7), H = 230-261 (n = 5), W = 176-182 (n = 2).

Korannacythere ugiensis spec.nov.

(Figs 3, 4, 9)

Type locality

Rockpool on the top of Prentjiesberg, near Ugie (Southern Drakensberg, Eastern Cape, South Africa) (RSA/93/033). Collected on 30.3.1993 by K. MARTENS, F.C. DE MOOR, H. BARBER-JAMES and F. WEIR. Approx. coordinates: S 31°08'48" E 28°08'18", Altitude c. 2000 masl. pH = 7.0, $K_{25} = 10 \mu\text{S/cm}$, Temperature = 25 °C.

Accompanying ostracod fauna: *Cyprilla paludum*, *Plesiocypridopsis* spec.

Type material

c 50 males and females from the above locality.

HOLOTYPE: a male, with soft parts dissected in glycerine in a sealed slide and valves stored dry in a cavity-slide (no. AM-ECR.160A).

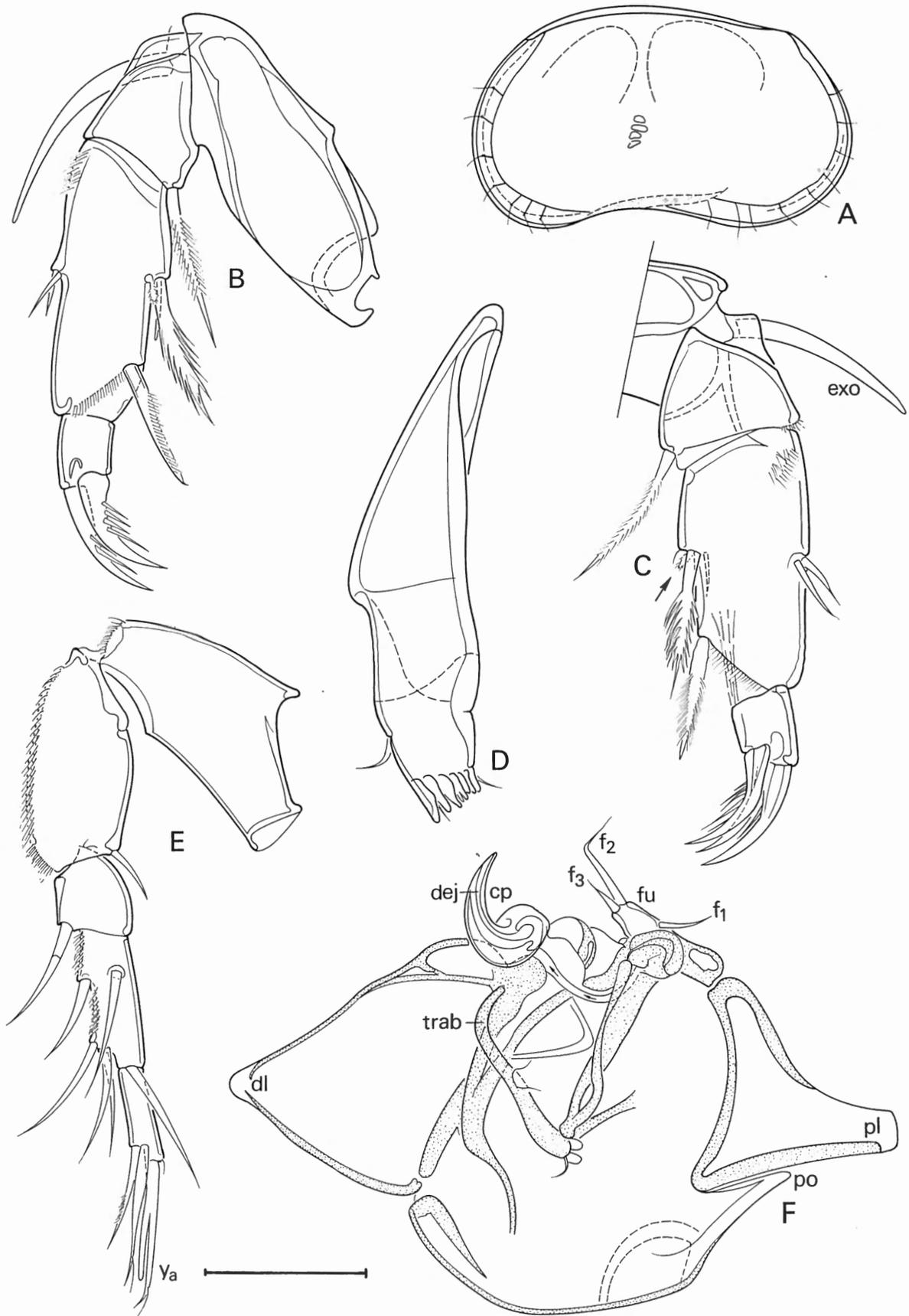


Fig. 3. — *Korannacythere ugiensis* gen. et spec. nov., male.

A. RV, internal view. B. A2 with long exopodite (small form). C. A2 with short exopodite (large form). D. Md coxa. E. A1. F. Hemipenis.

Scale = 33 μ m for B-F; 315 μ m for A.

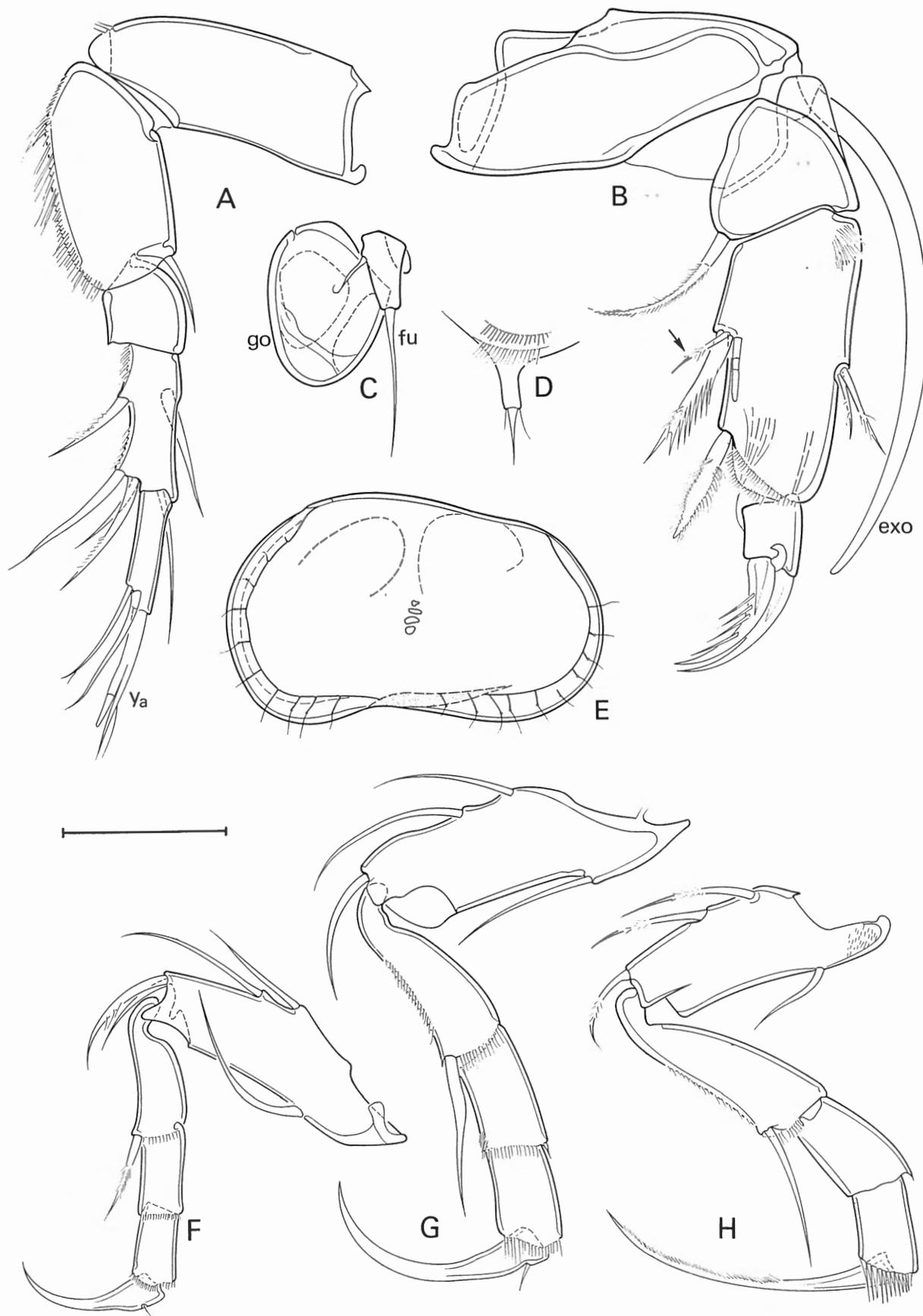


Fig. 4. – *Korannacythere ugiensis* gen. et spec. nov., female.
 A. A1. B. A2. C. Furca and genital operculum. D. RV, internal view. F. P1. G. P2. H. P3.
 Scale = 33 μ m for A-D, F-H; 315 μ m for E.

ALLOTYPE: a female, with soft parts dissected in glycerine in a sealed slide and valves stored dry in a cavity-slide (no. AM-ECR.160B).

PARATYPES: a tube with c 10 specimens (AM-ECR.160C); several dissected and dried specimens in slides (OC.1871-1876).

Deposition of material: the holotype, allotype and ten paratypes are deposited in the Albany Museum, Freshwater Biology Section, Grahamstown (South Africa). The other paratypes are deposited in the Ostracod Collection of the Royal Belgian Institute of Natural Sciences, Brussels (Belgium).

Derivation of name: after the town closest to the type locality, Ugie.

Abbreviated diagnosis

Valves with rounded dorsal margin. A1 with apical seta on second segment present. Exopodite on A2 in males reaching beyond edge of second segment, in females reaching tip of terminal segment, endclaws about twice as long as terminal segment. Glans on cp pointed, base narrow. Apical seta on second segment of P(3) reaching tip of terminal segment.

Extended diagnosis

Valves more rectangular, with anterior and posterior margins in both sexes equally broadly rounded, and with dorsal margin curved, not straight; external valve ornamentation in type population less prominent than in the preceding species. A1 with apical seta on second segment. A2 with exopodite in males reaching beyond edge of second segment, almost halfway the penultimate segment in most specimens, exopodite in females reaching tip of terminal segment, lateral seta on penultimate segment slightly less robust, apical claws in both sexes slightly longer than in the preceding species (c twice as long as terminal segment).

Hemipenis with dl subtriangular, more pointed than in the preceding species, anterior margin almost straight, without additional curve, cp sickle-shaped, with pointed glans and with base narrow and symmetrically curved (Fig. 3F). P(3) with apical seta on second segment reaching tip of terminal segment.

Remarks

Two morphological forms of this species were present in the type locality: a more abundant and smaller one, where males had exopodites on the A2 reaching almost halfway the penultimate segment (Fig. 3B) and a more rare, larger form, with slightly shorter male A2 exopodites, which still reach beyond the edge of the second segment (Fig. 3C). There were no differences in other aspects of the morphology. As this species is at present known from its type locality only, it is difficult to interpret intra-specific variability and both forms are here included in the same

species. The holotype belongs to the smaller form with longer exopodite.

Measurements (in μm)

♀ : L = 467 (n = 1), H = 273 (n = 1)

♂ : L = 467-515 (n = 8), H = 273-321 (n = 6), W = 236 (n = 2).

Korannacythere hamerae spec.nov.

(Figs. 5, 6, 8 (G-K), 10)

Type locality

eChibini minor Tarn, Loteni, KwaZulu Natal, coll. 18.3.1996 (K. MARTENS & M. HAMER) RSA/96/030, S 29°23'01" E 29°32'29", altitude 2400 masl. $K_{25} = 13.1 \mu\text{S/cm}$, temperature = 24 °C, pH = 7.2.

Accompanying ostracod fauna: *Isocypris priomena*, *Megalocypris durhani*. Remark: the record of the latter taxon is noteworthy, as this is the first time this genus and species is found outside of the coastal area of the Cape Province. Although the type of locality is typical of the species, both the geographical position and the altitude are highly remarkable.

Type material

c 50 specimens from the above locality.

HOLOTYPE: a male, with soft parts dissected in glycerine in a sealed slide and valves stored dry in a cavity-slide (no. AM-OST2A).

ALLOTYPE: a female, with soft parts dissected in glycerine in a sealed slide and valves stored dry in a cavity-slide (no. AM-OST2B).

PARATYPES: a tube with c 10 specimens (AM-OST2C); several dissected and dried specimens in slides (OC.1878-1887).

Deposition of material: the holotype, allotype and ten paratypes are deposited in the Albany Museum, Freshwater Biology Section, Grahamstown (South Africa). The other paratypes are deposited in the Ostracod Collection of the Royal Belgian Institute of Natural Sciences, Brussels (Belgium).

Derivation of name: the species is named after Dr Michelle HAMER (Pietermaritzburg), for her continuous help with field work in KwaZulu Natal and for providing ostracod material from various other parts of southern Africa. This is also in acknowledgement of her significant contribution to the knowledge of the biology and taxonomy of southern African Anostraca and of temporary pool ecology in general.

Other material investigated

RSA/95/012 Crane Tarn 5, Mzimkhulwana Nature Reserve. c 10 × 15 m, almost entirely on rocks, shallow

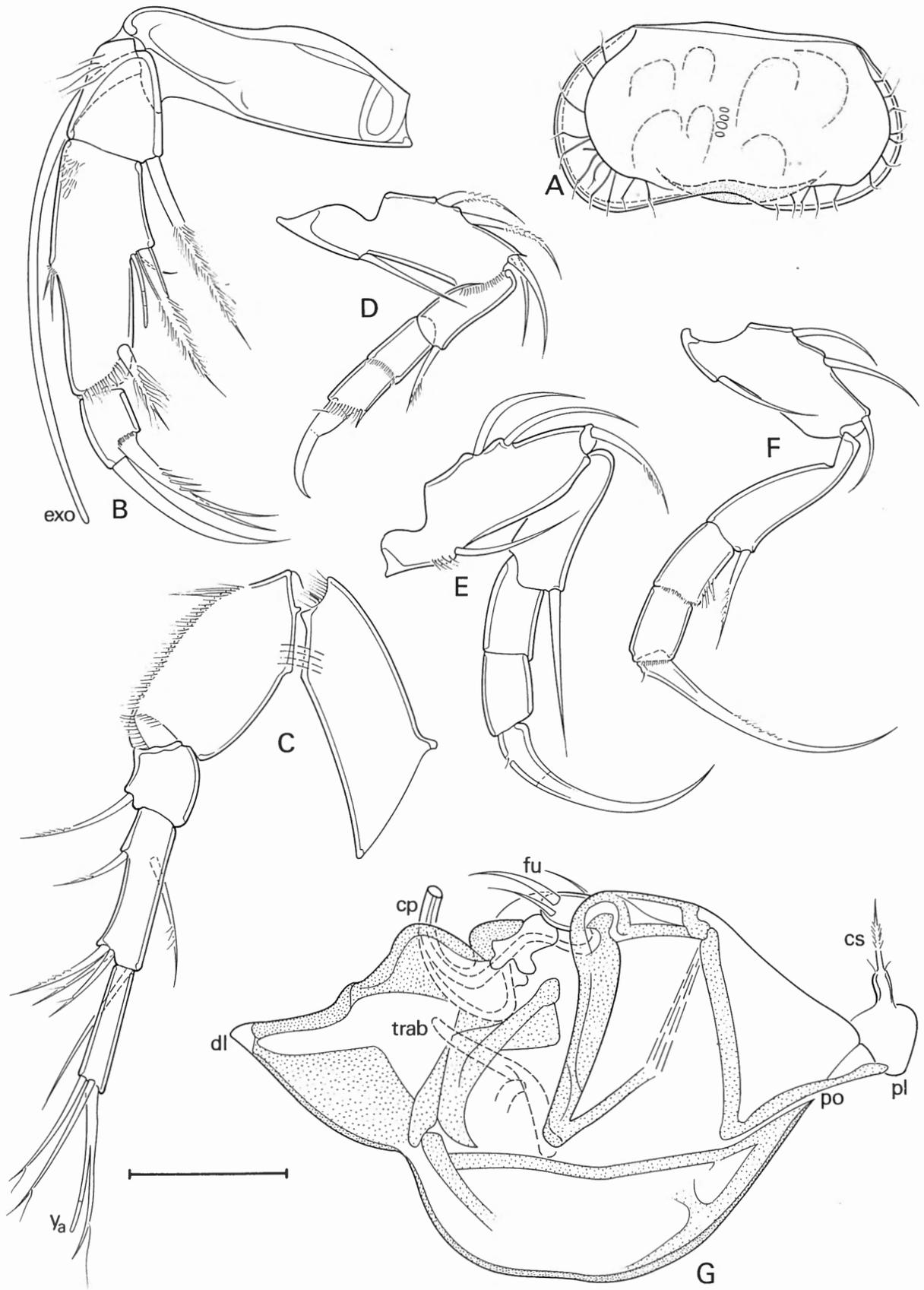


Fig. 5. – *Korannacythere hamerae* gen. et spec. nov., holotype male.
 A. RV, internal view. B. A2. C. A1. D. P1. E. P2. F. P3. G. Hemipenis.
 Scale = 33 μ m for B-G; 315 μ m for A.

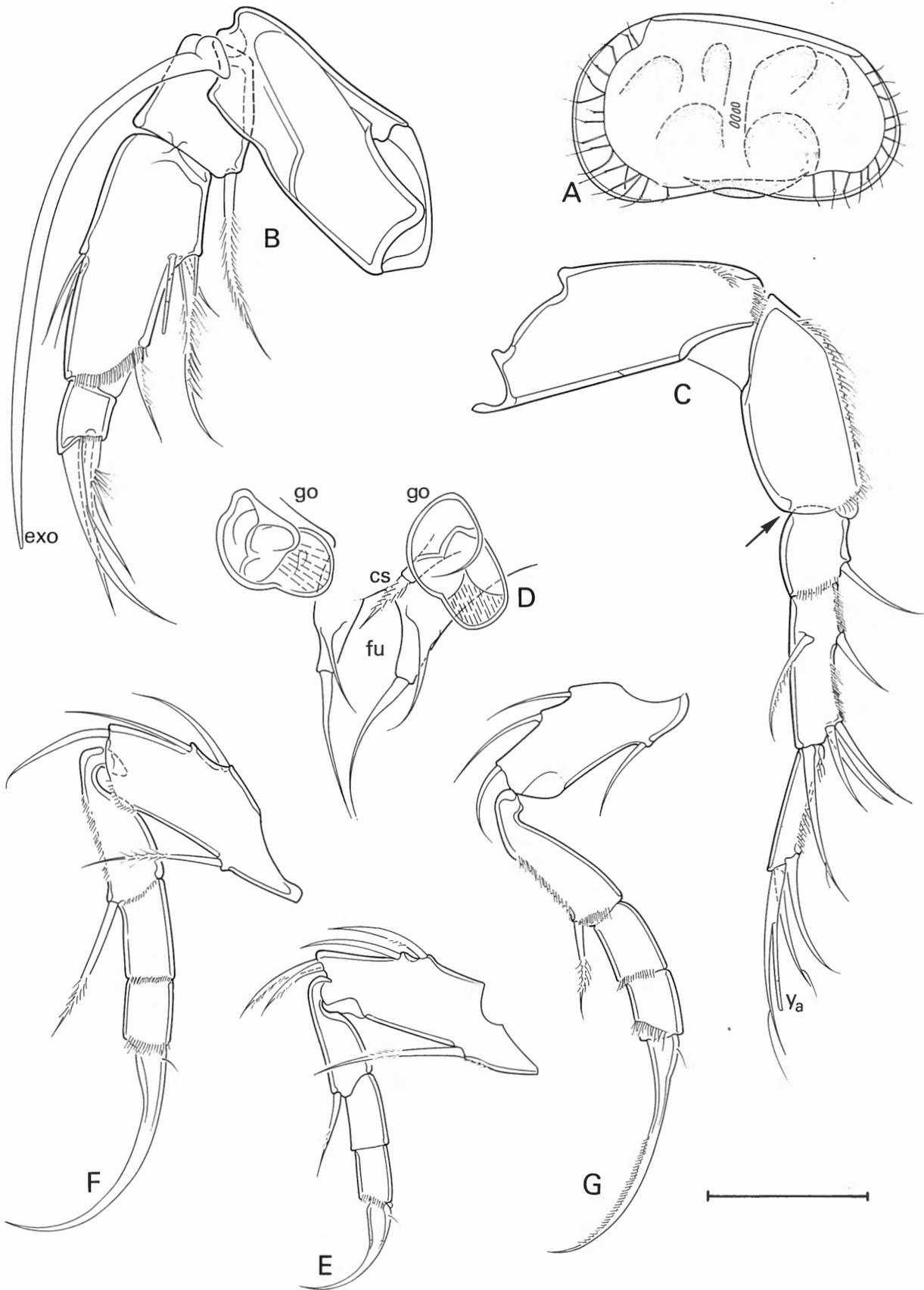


Fig. 6. – *Korannacythere hamerae* gen. et spec. nov., allotype female.
 A. RV, internal view. B. A2. C. A1. D. Caudal part of body, showing furcae, genital operculae and caudal seta.
 E. P1. F. P2. G. P3.
 Scale = 33 μ m for B-G; 315 μ m for A.

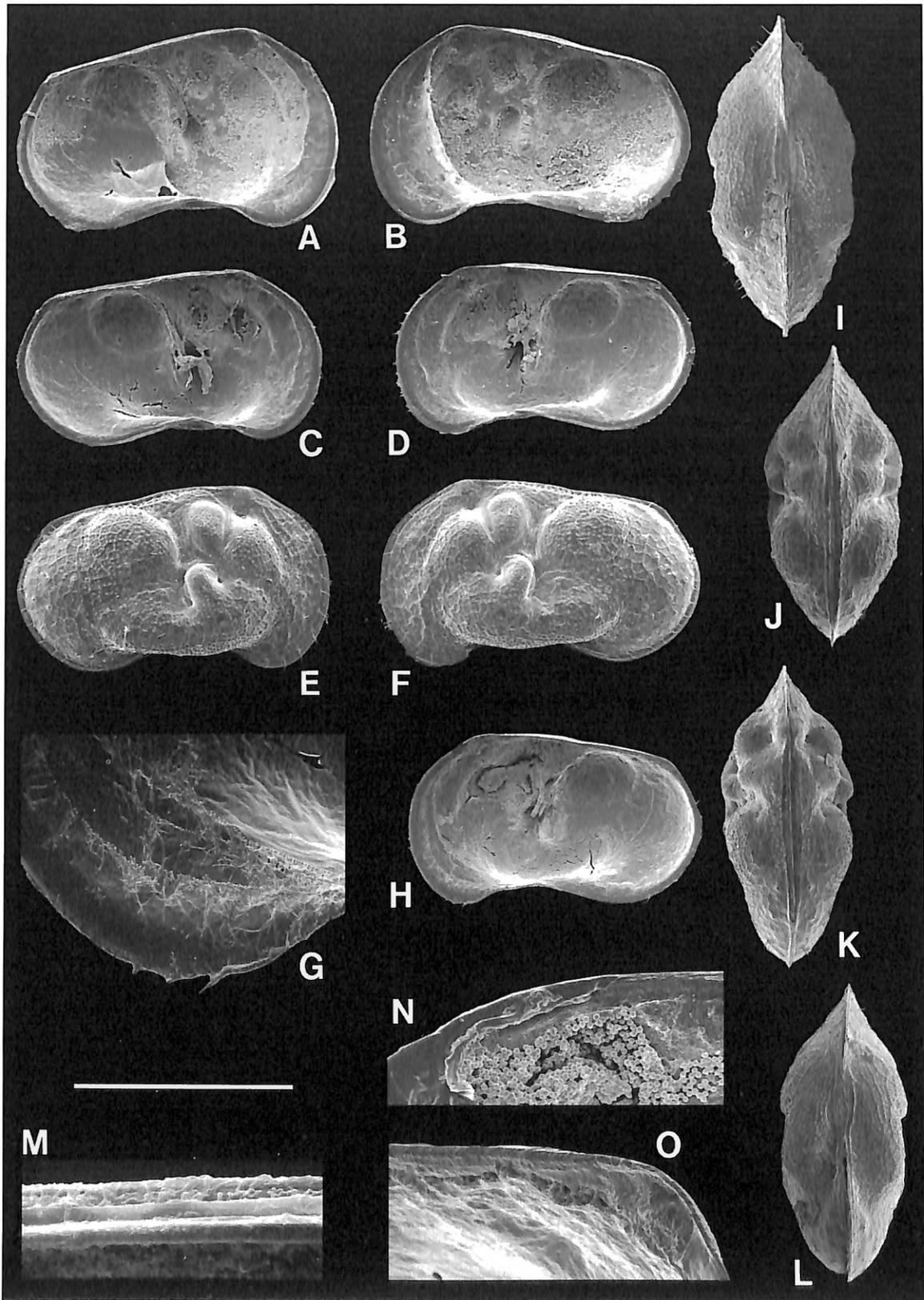


Fig. 7. – *Korannacythere devriesi* gen. et spec. nov.

A. ♀, LV, internal view. B. ♀, RV, internal view (same specimen). C. ♂, LV, internal view. D. ♂, RV, internal view (same specimen). E. ♂, RV, external view. F. ♂, LV, external view (same specimen). G. ♂, RV, internal view, detail anterior. H. ♂, RV, internal view. I. ♀, Cp, ventral view. J. ♀, Cp, dorsal view. K. ♂, Cp, dorsal view. L. ♂, Cp, ventral view. M. ♂, LV, internal view, detail cardinal bar. N. ♂, RV, internal view, detail antero-dorsal part, showing absence of act. O. ♂, RV, internal view, detail postero-dorsal part, showing absence of pct. Scale = 36 μm for N-O; 74 μm for G; 269 μm for M; 303 μm for A-F, H-L.

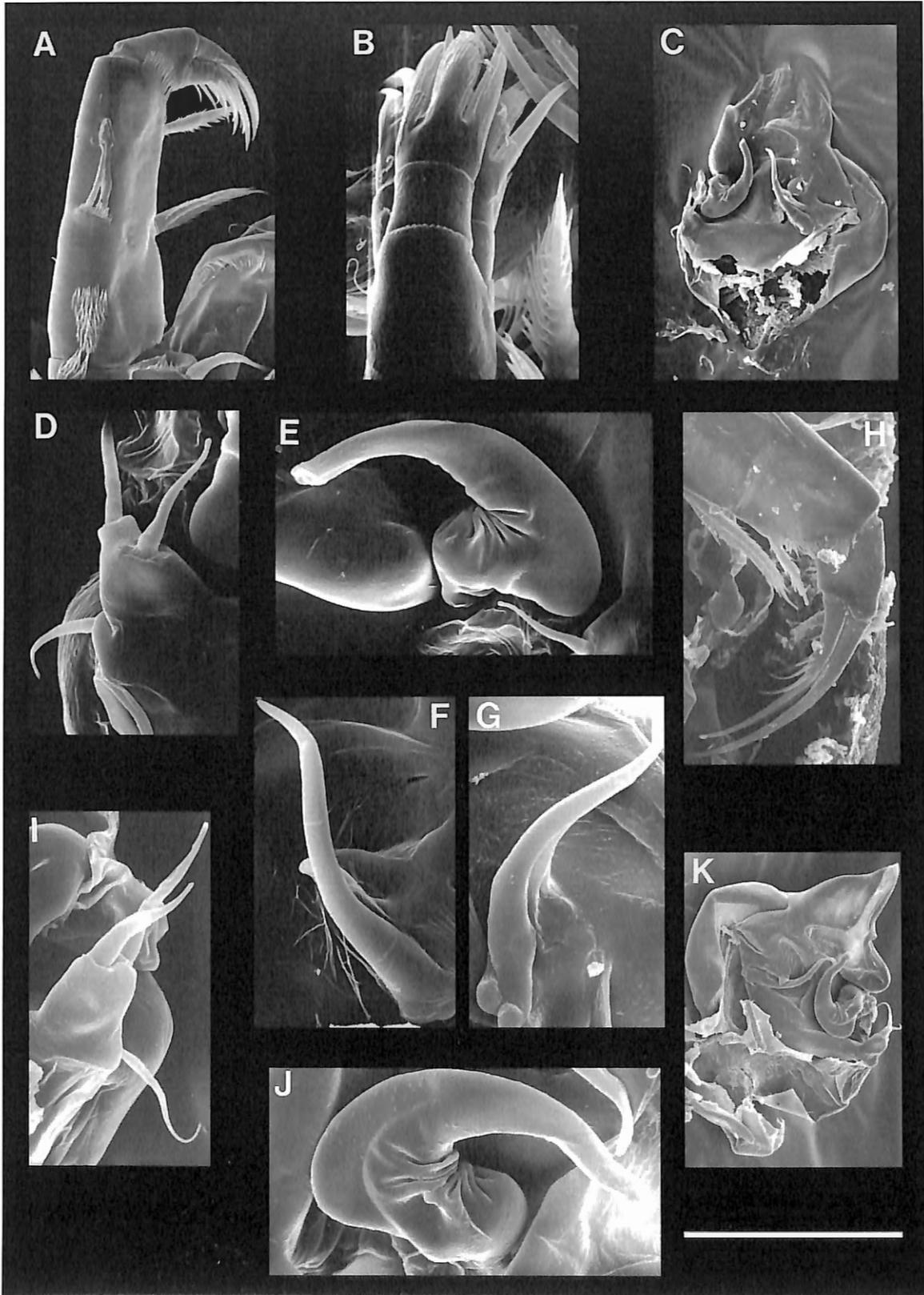


Fig. 8. – *Korannacythere devriesi* gen. et spec. nov. (A-F) and *K. hamaerae* gen. et spec. nov. (G-K).

K. devriesi: A. ♂, A2, lateral view. B. ♂, A2, detail of endclaws in ventral view. C. ♂, Hemipenis. D. ♂, hemipenis, detail of furca. E. ♂, hemipenis, detail of copulatory process. F. ♂, hemipenis, detail of moveable trabecule.

K. hamaerae: G. ♂, hemipenis, detail of moveable trabecule. H. ♂, A2, lateral view. I. ♂, hemipenis, detail of furca. J. ♂, hemipenis, detail of copulatory process. K. ♂, Hemipenis.

Scale = 16 μm for B; 19 μm for D; 26 μm for E-G, I, J; 38 μm for H; 42 μm for A; 104 μm for C, K.

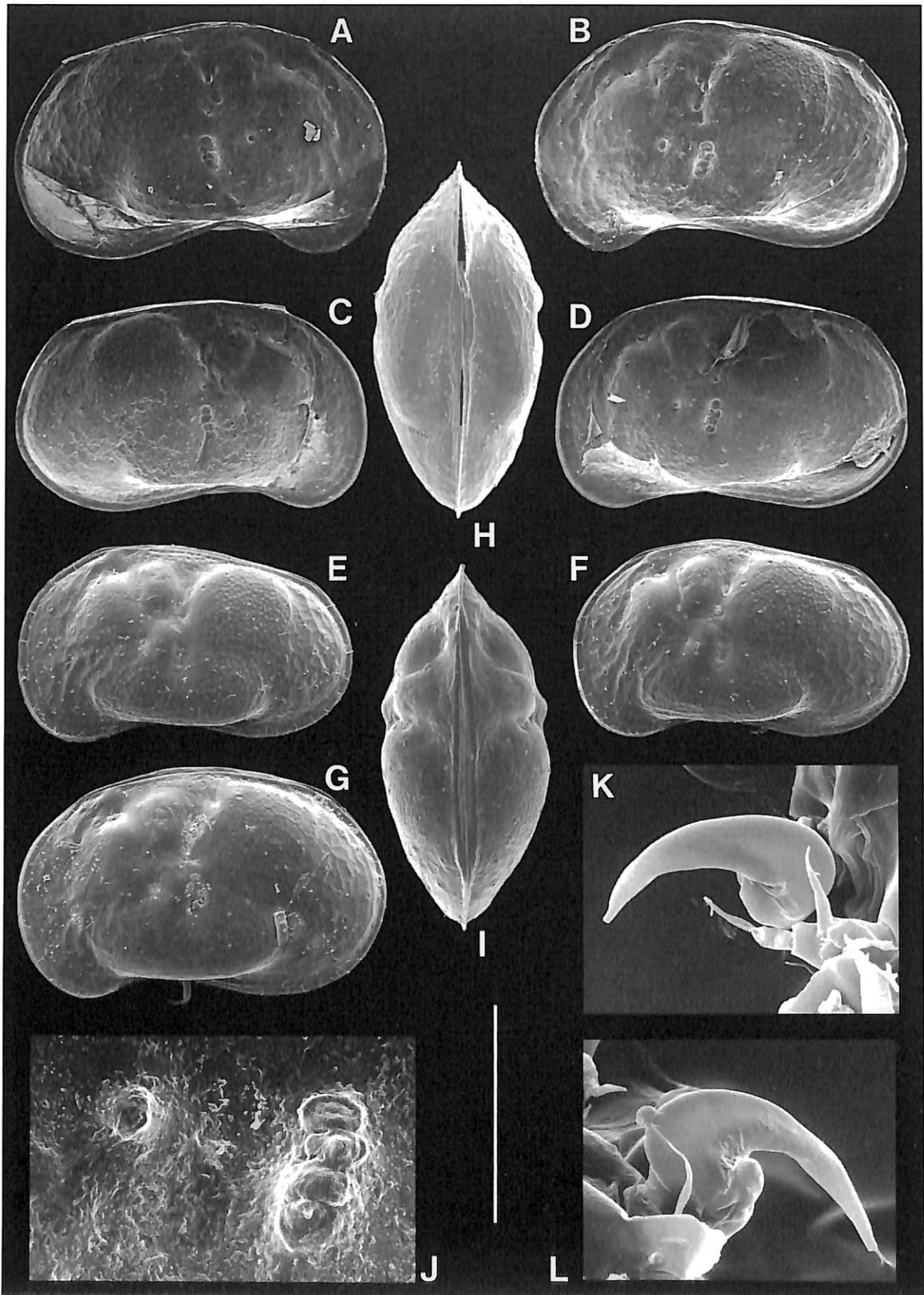


Fig. 9. – *Korannacythere ugiensis* gen. et spec. nov.

A. ♂, LV, internal view. B. ♂, RV, internal view (same specimen). C. ♂, LV, internal view. D. ♂, RV, internal view (same specimen). E. ♀, Cp, left lateral view. F. ♂, Cp, left lateral view. G. ♂, Cp, left lateral view. H. ♂, Cp, ventral view. I. ♂, Cp, dorsal view. J. ♂, RV, internal view, detail of central muscle scars. K. ♂, hemipenis, detail of furca and copulatory process. L. ♂, hemipenis, detail of copulatory process (different angle).
Scale = 70 μm for J; 250 μm for K-L; 303 μm for A-I.

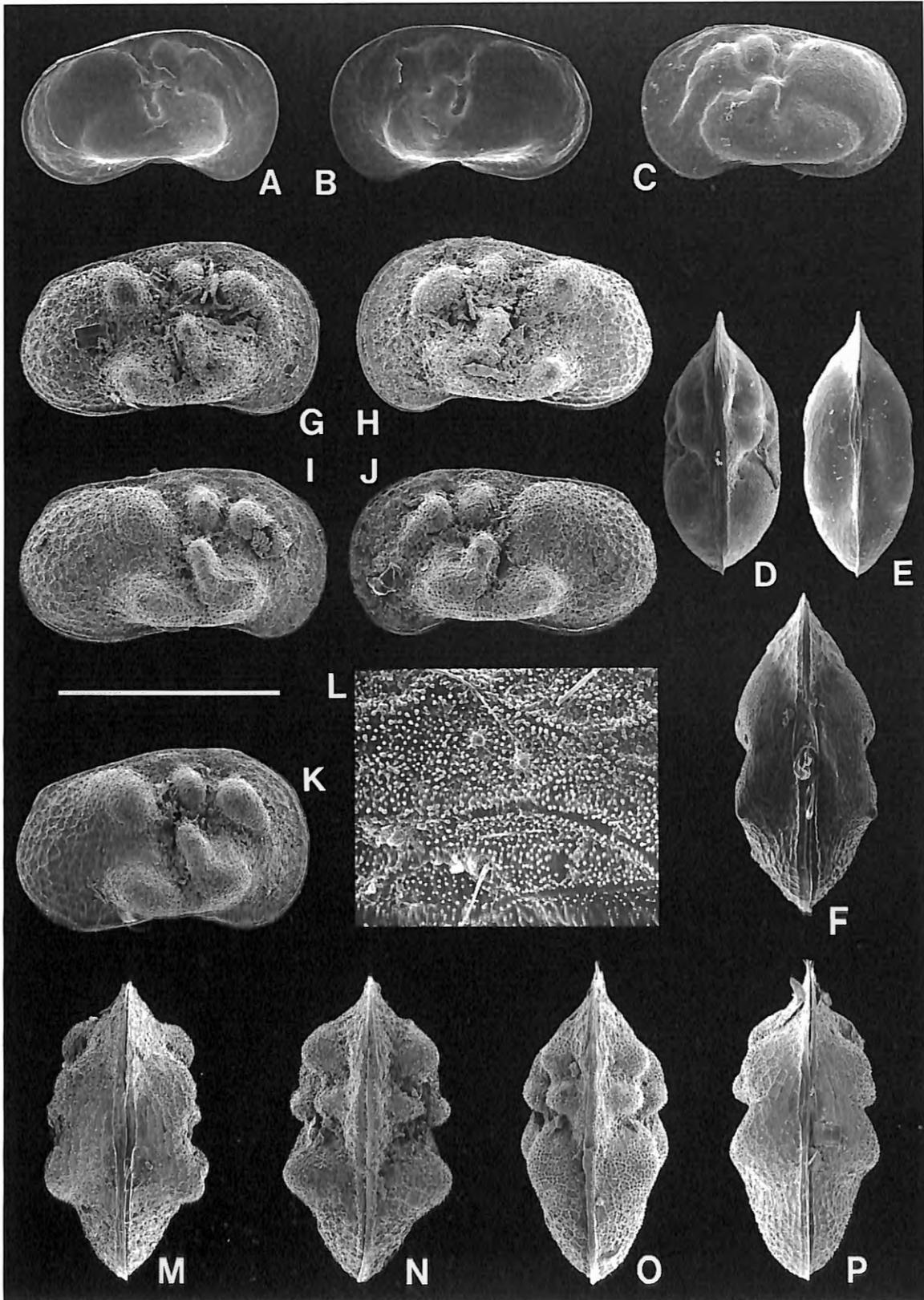


Fig. 10. – *Korannacythere hamerae* gen. et spec. nov. (A-F from Tarn 3 at The Lakes - largest population; G-P from type population at eChibini minor Tarn).

A. ♀, LV, internal view. B. ♀, RV, internal view (same specimen). C. ♀, Cp, left lateral view. D. ♀, Cp, dorsal view. E. ♀, Cp, ventral view. F. ♀, Cp, ventral view. G. ♀, RV, external view. H. ♀, LV, external view (same specimen). I. ♂, RV, external view. J. ♂, LV, external view (same specimen). K. ♀, CP, right lateral view. L. ♂, Cp, ventral view, detail of surface structure. M. ♀, Cp, ventral view. N. ♀, Cp, dorsal view. O. ♂, Cp, dorsal view. P. ♂, Cp, ventral view.

Scale = 34 μm for L; 303 μm for G-K, M-P; 417 μm for A-F.

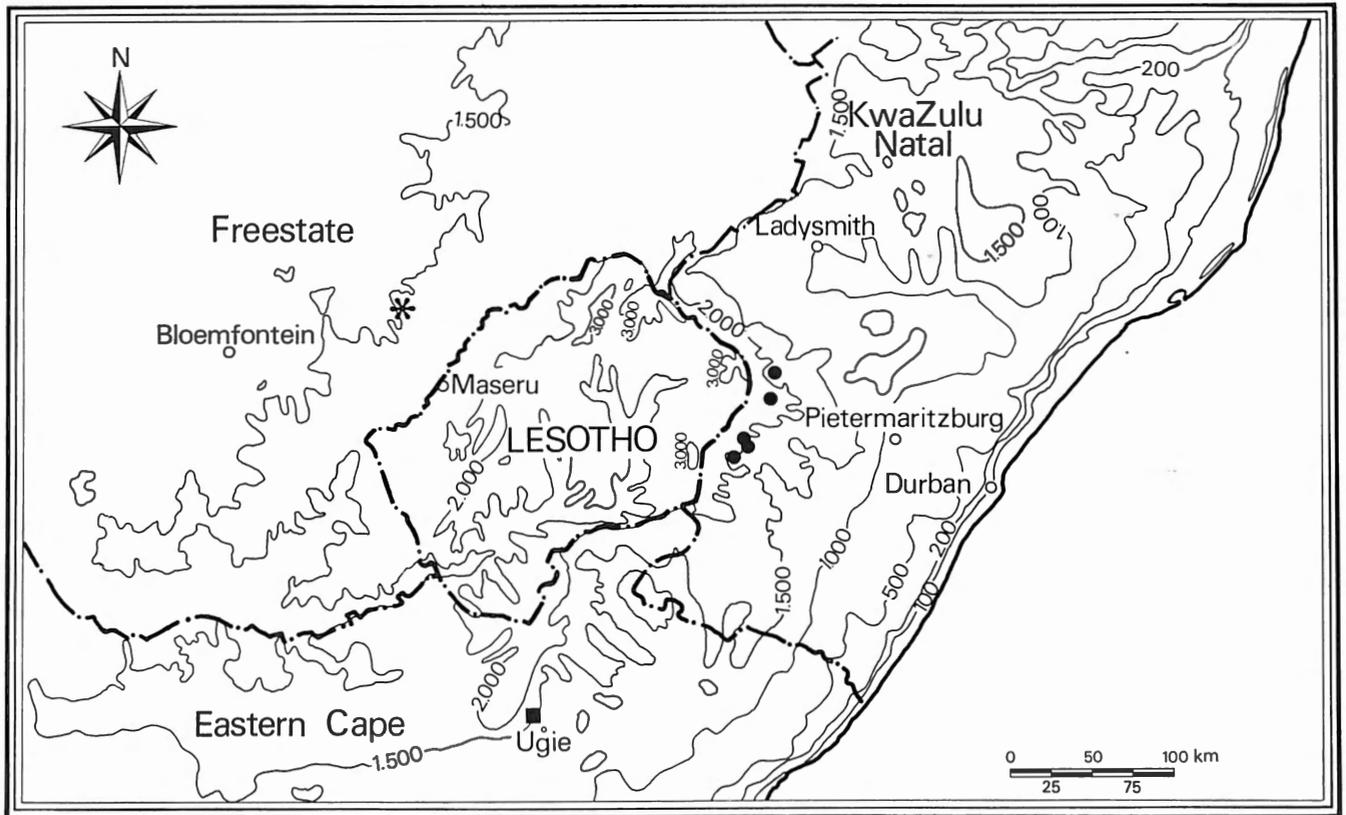


Fig. 11. – Distribution of *Korannacythere* gen. nov. around the Drakensberg. Closed dots = *K. hamerae* spec. nov.; closed square = *K. ugiensis* spec. nov., asterisk = *K. devriesi* spec. nov.

(max 20 cm), clear water, few sedges, small submerged macrophytes. pH = 7.5, temperature = 22.0°C, S 29°42'52" E 29°19'27", altitude = 2000 masl.

RSA/95/014 Sentinels plateau Pool 1, near Giant's Cup Trail, Cobham State Forest. Diameter c 10m, shallow, Sphagnum-like mosses and grasses, clear water with little open surface. pH = 7.6, temperature = 17.0°C, S 29°38'26" E 29°24'18", altitude = 1975 masl.

RSA/95/017 Sentinels plateau Pool 4, W-side of plateau, near Giant's Cup Trail, Cobham State Forest. 20 × 50 m, very marshy, many sedges. pH = 5.5, temperature = 17.0°C, S 29°38'00" E 29°23'38", altitude = 2000 masl.

RSA/95/040 Lake 3, 'The Lakes', Giant's Castle Game Reserve, c 5 km N of main Camp. Largest pool, relatively shallow, on rocky bottom, many small submerged grasses. pH = 6.5, temperature = 22.8°C, S 29°14'31" E 29°33'02", altitude = 1950 masl. The species was found in the same locality during a second sampling trip RSA/96/024, 1996.03.16.

Abbreviated diagnosis

Valves with dorsal margin both rounded and sloping. Apical seta on second segment of A1 absent. Exopodite on A2 in males reaching beyond tip of terminal segment,

females reaching halfway endclaws, the latter about three times as long as terminal segment. Glans on cp delated, with external base expanded. Apical seta on second segment of P(3) reaching slightly beyond tip of penultimate segment.

Extended diagnosis

Valves large (generally largest species) with dorsal margin both rounded and sloping, posterior margin significantly less curved than anterior one, external valve ornamentation in type population more prominent than in both preceding species; other populations with less developed ornamentation. Apical seta on second segment of A1 absent in both sexes. A2 with exopodite in males reaching beyond edge of terminal segment, in females reaching halfway the endclaws, lateral seta on penultimate segment slightly less robust, but reaching beyond edge of penultimate segment, apical claws in both sexes significantly longer and more slender than in the preceding species (c three times as long as terminal segment). Hemipenis with dl subtriangular, more pointed than in the two preceding species, anterior margin concave, with additional central curve, cp sickle-shaped, with delated glans and with base expanded on the external corner (Fig. 5G). P(3) with apical seta on second segment reaching slightly beyond edge of penultimate segment.

Measurements (in μm)

♀ : L = 400-500 (n = 11) [406-442 (n = 6) and 492-500 (n = 5)], H = 236-292 (n = 8), W = 194-230 (n = 5).

♂ : L = 424 (n = 4), H = 230 (n = 2), W = 200-206 (n = 2).

Discussion

TAXONOMY OF THE LIMNOCYTHERINAE

The taxonomy of the Limnocytheridae KLIE, 1938 has remained confused for a very long time. COLIN & DANIELOPOL (1978, 1980) first introduced order into it by establishing the presence of two subfamilies within this group: the Limnocytherinae KLIE, 1938 and the Timiriaseviinae MANDELSTAM, 1960. Subsequent revisions and descriptions of new genera have largely

increased our knowledge of the taxonomy and distribution of this group (SCHORNIKOV, 1986; KRSTIC, 1987; KRSTIC & SCHORNIKOV, 1993; MARTENS, 1989, 1990a,b, 1991, 1992, 1994, 1995; DANIELOPOL et al., 1990). A phylogenetic analysis of the genera of the Timiriaseviinae will be presented elsewhere; a preliminary reassessment of the genera in the Limnocytherinae is here presented in Table 1. It is necessary to do this here in order to assess the correct position of *Korannacythere* gen. nov.

DANIELOPOL et al. (1990) divided the Limnocytherinae into four tribes: Limnocytherini, Leucocytherini, Cytheridellini and Dinarocytherini (change of rank). Since the Cytheridellini have been transferred to the Timiriaseviinae (MARTENS, 1995), the nominate subfamily is left with three tribes, which are mainly distinguished on the basis of the hinge: Limnocytherini have a smooth cardinal bar in LV and simple cardinal teeth in the RV, of which

Table 1: Preliminary grouping of Recent and Fossil genera in the post-Cretaceous Limnocytherinae

1. Tribe: Limnocytherini KLIE 1938

Abbreviated Diagnosis: hinge antimerodont, hinge bar smooth, act present or absent, pct nearly always present. Hemipenis with copulatory process never spiralled.

1.1. *Limnocythere*-lineage

Characteristics: furca in hemipenis small, marginal pore canals straight, clasping organ generally well developed and consisting of several processes (exception: *Korannacythere* n. gen.).

Genera: *Limnocythere* BRADY, 1868 (= *Limnocythere* BRADY, 1868; = *Limnocytheridea* G.W. MÜLLER, 1912; = *Acanthopus* VERNET, 1928); *Galolimnocythere* SCHORNIKOV, 1973; *Limnocytherina* NEGADAEV-NIKONOV, 1967, *Korannacythere* gen.nov.

1.2. *Neolimnocythere*-lineage

Characteristics: hemipenis with furca large to very large, marginal pore canals straight.

Genera: *Neolimnocythere* DELCHAUX, 1928, *Paracythereis* DELACHAUX, 1928 (= *Pampacythere* WHATLEY & CHOLICH, 1974 (fossil)).

1.3. *Paralimnocythere*-lineage

Characteristics: marginal pore canals branched; ventral setae on basal segment of at least P2-3 strongly reduced or absent; furcal setae in hemipenis relatively large.

Genera: *Paralimnocythere* CARBONNEL, 1969 (= *Relictocytherina* NEGADAEV-NIKONOV, 1968 (fossil); non *Paralimnocythere* WANG, 1989); *Kiwicythere* MARTENS, 1992.

2. Tribe: Leucocytherini DANIELOPOL & MARTENS, 1990

Abbreviated Diagnosis: hinge bar crenulate, act present or absent, pct with 1-3 lobes. A1 and P3 often (not always) with sexual dimorphism; hemipenis with furcal setae large, UR and LR simple.

Genera: *Leucocythere* KAUFMANN, 1892; *Ovambocythere* MARTENS, 1989; *Potamocythere* SCHORNIKOV, 1986; *Athalocythere* SCHORNIKOV, 1986, *Prolimnocythere* KARMISCHINA, 1970 (fossil); *Elkocythereis* DICKINSON & SWAIN, 1967 (fossil).

3. Tribe: Dinarocytherini KRSTIC, 1987 (exclusively fossil).

Abbreviated Diagnosis: hinge amphidont, hinge bar crenulated, act and pct present; LV with anterior (+ sometimes posterior) cardinal tooth.

Genera: *Dinarocythere* KRSTIC, 1987; (? = *Scordiscia* KRSTIC & SCHORNIKOV, 1993); *Cladarocythere* KEEN, 1972.

often the act, and sometimes also the pct, is reduced. The Leucocytherini have a crenulated cardinal bar in the LV and cardinal teeth in the RV that are generally well developed and where especially the pct often consist of 2 or 3 lobes. Dinarocytherini also have a well-developed hinge, with crenulated bar in LV, but with the cardinal bar in LV showing an additional anterior, and sometimes also an additional posterior tooth (amphidont). As the development of an additional tooth on the edge of a crenulated bar is basically a very minor addition, it is possible that the Dinarocytherini and the Leucocytherini will in time turn out to be the same group. At present, however, it is useful to maintain the three tribes separate, in order to show the evolution within the Limnocytherinae from well-developed amphidont hinge, over modified antimerodont to lophodont and nearly adont in the new genus described herein. Note that the direction of this evolutionary scenario is entirely hypothetical and can only be established with some degree of certainty after the type of the ancestral limnocytherid, i.e. the ancestor of both the Timiriaseviinae and the Limnocytherinae, has been established.

Whereas the Dinarocytherini at present have a rather limited known diversity, it appears that Leucocytherini have been far more successful than was originally thought: not less than four extant and two fossil genera can be allocated to this lineage (*Athalocythere* and *Prolimnocythere* were correctly assigned to this group by KRSTIC & SCHORNIKOV (1993); *Elkocythereis* is here assigned to this tribe). No evolutionary pathways are as yet apparent within this lineage.

Within the Limnocytherini, however, a pattern is emerging as new data are becoming available. There are at present three main lineages within this tribe, and most characteristics are in the morphology of the hemipenis. The first is the actual *Limnocythere* lineage, in which the subgenera *Limnocytherina* and *Galolimnocythere* are here reassigned a generic status and to which *Korannacythere* gen.nov. is here added. Most North American *Limnocythere* s.l. species actually belong in *Limnocytherina* (e.g. DELORME, 1971), while at least *L. goersbachensis* DIEBEL, 1961 and *L. baikalensis* MARTENS & MAZEPOVA, 1992 also belong in *Galolimnocythere*. Note further that within *Limnocythere* itself, there are at least 3 sub-lineages: *Limnocythere* s.s. with large UR on the hemipenis (largely Holarctic); the *L. thomasi* group without an UR on the hemipenis (African) and the *L. stationis* lineage, with aberrant valve shape (caudally sloping dorsal margin) and small P3; its hemipenis structure is not known (Palaeartic, Africa and maybe Australia). This entire group has straight marginal pore canals, mostly a well-developed clasping organ and a small furca incorporated in the hemipenis.

The second group in the Limnocytherini is characterized by branched pore canals and a gradual increase in size of the furca in the hemipenis. The Palaeartic *Paralimnocythere*, especially speciose in the Balkan Lakes, still has a relatively small furca in the hemipenis, but the Pacific *Kiwicythere* already shows hyperdevelopment of

this structure. MARTENS (1992) doubted the monophyletic origin of the branched radial pore canals, but as no solid arguments against monophyly are available, this is still the most parsimonious hypothesis.

The tendency towards hyperdevelopment of the furcal basis and setae in the hemipenis is furthered in the third lineage, which consists of the South American *Neolimnocythere* and *Paracythereis*. The radiation of Neotropical limnocytherids is ill-understood and needs urgent elaboration; especially the wide radiations on the Altiplano, in Lake Titicaca and other lagunas, will prove highly informative for the evolution of the Limnocytherinae as a whole. If the neolimnocytherids are indeed derived from a paralimnocytherid ancestor, then at least some remnants of branched pore canals must be visible in the most plesiomorphic taxa of the South American group. The alternative scenario, that neolimnocytherids and paralimnocytherids have evolved from a common ancestor, is equally plausible. Note, finally, that not all Neotropical limnocytherids belong to the *Neolimnocythere* lineage: also *Limnocythere* s.s. and *Leucocythere* s.s. occur on the Altiplano (MOURGUIART, 1992; MARTENS & MOURGUIART, unpubl.).

The above evolutionary scenario thus relies on series of progressively changing character states in both valves (reduction of hinge structure) and soft parts (hemipenis: general and increasing size and complexity of furca in hemipenis). It is self-evident, however, that this hypothetical phyletic scheme at present relies on incomplete data sets; a cladistic analysis with complete data matrix will be presented elsewhere.

DIFFERENTIAL DIAGNOSIS OF *KORANNACYTHERE* GEN. NOV.

Relying on the above discussion, the taxonomic position of *Korannacythere* can now be argued in full. The genus belongs in the Limnocytherini because of the smooth hinge bar, the normal (not hyperdeveloped) furca in the hemipenis, and the absence of any modification of the P3 in males. Within the Limnocytherini, it differs from the *Paralimnocythere*-group by the straight marginal pore canals and the presence of a ventral seta on the basal segment of the three walking limbs, and from the *Neolimnocythere*-group by the normal (not hyperdeveloped) furca in the hemipenis. It differs from *Limnocythere* s.s. and *Limnocytherina* by the absence of a clasping organ in the hemipenis and the reduction of the posterior cardinal tooth (pct) of the hinge. In *Limnocythere* s.s., there is furthermore nearly always a large sexual dimorphism in valve shape, while female valves are either rectangular or with dorsal margin sloping anteriorly. The *L. stationis* lineage in *Limnocythere* also has a posteriorly sloping dorsal margin, like in *Korannacythere devriesi* gen. et spec. nov. and *K. hamerae* gen. et spec. nov., but has a well-developed pct on the RV; this lineage might in time also merit a separate (sub-) generic status (see below). *Korannacythere* gen.nov. shows

morphological similarities with *Galolimnocythere*, but differs from it at least in hinge structure (well-developed cardinal teeth in *Galolimnocythere*), morphology of hemipenis (furca, clasping organ, complexity of copulatory process) and respiratory plate of Mx1 (absence of hyperdeveloped rays). In short, the new genus is lodged in the *Limnocythere* s.l. group of the Limnocytherini, but occupies an isolated position within it. Its closest relative might be the *L. stationis*-lineage.

MORPHOLOGY OF KORANNACYTHERE GEN. NOV.

The most peculiar morphological aspects of the new genus are the almost absent sexual dimorphism in the structure of valves and in the soft parts and the simplicity of the hemipenis. The following are the only differences between the sexes:

- valves with slightly more broadly rounded caudal margin and slightly wider in dorsal view in females; small and variable differences between the sexes in lateral outline;
- exopodite of the A2 longer in females than in males - this is so especially in *K. devriesi* and *K. ugiensis*;
- stronger reduction of the second accompanying seta to the aesthetasc Y in males.

According to the theory of sexual selection by the female choice, males have several specific morphological structures by which females can establish conspecificity and by which the male stimulates the female into accepting him for copulation and hence reproduction (EBERHARD, 1985; ANDERSSON, 1994). The Limnocytheridae as a whole are generally good examples of this, with males in several species and genera showing specific hyperdevelopment of several aspects of their copulatory module (the set of structures and morphologies in the male, used to stimulate the female: furcal structures in hemipenis, clasping organ, antennae and walking limbs - DANIELOPOL et al., 1990). The present species and genus has a relatively small and very simple hemipenis structure, and this explains at least partly the similarity in valve structure between both sexes: the aberrant (more elongated, and with posterior expansions) male valve shape in other taxa has indeed been correlated with the hyperdevelopment of the external hemipenis structures (DANIELOPOL et al. loc. cit.). Thus, a relatively small hemipenis without such large expansions does not necessitate enlargement of the valves and smaller valves will reduce the size and structure of the hemipenis. It will be shown below that it is most parsimonious to accept that the hemipenis structure simplified under restraint of a smaller carapace and not the other way around.

Note, moreover, that inter-specific differences in hemipenis structure are minimal between these species (only the actual copulatory processes differ slightly) and that, due to the mineral-poor habitats of these species, the carapace shape is generally very variable.

The absence of prominent species-specific characters in valves and hemipenis, however, is amply compensated by

the interspecific differences in the morphology of the A2; especially in length of the exopodite, length and shape of apical claws and shape and setulation of the three major ventral setae of the endopodal segments. The length of the exopodite of the A2 decreases progressively from *K. hamerae* over *K. ugiensis* to *K. devriesi*. In all species, the female exopodite is longer than the male one, largely so in *K. devriesi* and slightly in *K. hamerae*. As these exopodites are long in all other limnocytherid genera, and short exopodites can thus be considered apomorphic, a tendency to a decreasing exopodite size from East to West can thus be accepted. This tendency is paralleled by a change in the length of the endclaws, which become shorter and stouter, and a progressive reduction (in the male) of the smallest accompanying seta of the lateral aesthetasc on second endopodal segment.

From experience with other limnocytherid (DANIELOPOL et al., 1990) and non-limnocytherid ostracod lineages (MARTENS, 1987), we know that the male A2 is indeed known to be actively involved in clasping during copulation. The fact that the above characters are furthermore sexually dimorphic within the species, offers additional support to the hypothesis that in this genus recognition of the male by the female is to a large degree effected by the morphology of the A2 and not by the hemipenis structures as is the case in most limnocytherids.

Why this shift in importance from hemipenis to A2 has occurred in this lineage of the Limnocytherinae, where sexual selection is mostly based on plastic hemipenis structures, is at present a matter of speculation, and this can best be done in an inverse way. The sexual and specific morphological differences in the A2 replace the normal differences in hemipenis morphologies and this is so because the hemipenis structure is highly simplified, with a reduction of the entire clasping organ. This simplification of the hemipenis is related to a reduction in carapace size. The overall size reduction of the animal can be either a pre-adaptation to the temporary environment (but then it needs to be specified why these animals became so small in the first place) or an adaptation through natural selection to and within these high altitude rockpools. It may be that the exceptional habitat is related to an overall reduction in size and a uniformity in valve shape, because of four possible reasons: low mineral content of the water, type of drought-resistant stages, predation and nutrient-depletion. (1) The low ionic content in the water of temporary rockpools on the Drakensberg sandstone (EC = c 10 μ S/cm, which is close to distilled water) indeed affects the species of *Korannacythere*, as they often live with weakly to nearly uncalcified valves, and it probably also caused the nearly adont hinge structure in this lineage. Smaller carapace size would then be advantageous as smaller, weakly calcified valves are more easily strengthened by shape and sculptures than larger ones. (2) It is not known to date how the temporary pool cytheroids survive the dry periods in their habitat. Cypridinae all have drought-resistant eggs, but it is possible that Limnocytherinae survive differently, i.e. as desiccated cryptobiotic juveniles (like in some copepods) or

in adult torpidity; especially in the latter case, again size reduction is advantageous. (3) Even in predator-poor environments such as temporary pools, longer-lived pools are not completely devoid of predation, both by vertebrates (fish, frogs) and by invertebrates (Notostraca, Coleoptera, etc). As this genus prefers long-lived temporary habitats, its size reduction can offer convenient protection against such predators. (4) A final, more esoteric, argument holds that, like in subterranean environments, temporary rockpools are nutrient-poor. Small size is an advantage when food sources are limited. These arguments support the natural selection hypothesis, with the consequential shift in species-specific characteristics for female-male recognition from hemipenis to A2.

There are a number of other morphological peculiarities, which can only be conveniently evaluated comparatively within the whole of the Limnocytherini. For example, both males and females, especially in *Korannacythere devriesi* gen. et spec. nov., have a relatively large caudal seta, consisting of a solid base, with three apical setulae. Female abdomens (Fig. 2E) furthermore bear typical rows of spinuous setulae; these are most likely remnants of ancient segmentation. These features will not be discussed here.

ECOLOGY OF *KORANNACYTHERE* GEN. NOV. AND EVOLUTIONARY RELEVANCE OF DIAPAUSE IN NON-MARINE OSTRACODS

The genus and species have thus far only been found in temporary rockpools in the Drakensberg area of South Africa. Together with *Ovambocythere* MARTENS, *Korannacythere* gen. nov. is thus far the only limnocytherid genus known to occur exclusively in temporary habitats and to have been raised directly from completely desiccated mud. It is most interesting to note that these genera belong to two separate lineages, the Leucocytherini and the Limnocytherini. Although no other cytheroid genera are especially adapted to temporary habitats, there are several other limnocytherid species reported from non-permanent habitats. Both *Leucocythere algeriensis* MARTENS, 1990 from the Sahara and *L. helenae* MARTENS, 1991 from the Eastern Cape are described from temporary habitats. Species of the *Limnocythere stationis* - group have on several occasions been found in temporary pools in Europe (VAVRA, 1891) as well as in East Africa (MCKENZIE, 1971 as *L. notodonta* VAVRA, 1906) and in Australia (DE DECKKER, 1981 as *Limnocythere dorsosicula*). Therefore, it seems plausible that diapause did not develop convergently in both lineages, but rather that the ancestors of at least the Limnocytherinae were also able to produce drought-resistant stages. WHATLEY (1988, 1990a,b, 1992) explained the relative success of the Cypridoidea, compared to the other two non-marine lineages Cytheroidea and Darwinuloidea, primarily by the exclusive development of such drought-resistant stages (combined with par-

thenogenesis and ability to swim) in the former lineage. If diapause also existed in the ancestral limnocytherids, then these arguments must be reassessed. Either the presence of diapause in Cypridoidea is less important for their success (both in density and in diversity, MARTENS in press) in non-marine habitats than deemed before, with then maybe the swimming power becoming the prime factor, or the mechanism of producing drought-resistant stages is different in the two superfamilies and more efficient in the Cypridoidea. This subject is of the utmost importance from an evolutionary biology point of view and merits further elaboration.

All three new species were found in very comparable habitats, namely in temporary rockpools (so-called 'kop-pies') on sandstone in the Drakensberg (including isolated outcrops of the Maluti mountains, such as Korannaberg) at an altitude of c 2000 masl (1700-2400m). Thus far, the new genus was not found in tarns at lower altitudes, nor in pools on the Lesotho plateau (c 3000 masl), although such habitats were also sampled. Invariably, waters of these rockpools had very low conductivity (c 10-20 $\mu\text{S.cm}^{-1}$) and a generally neutral pH. Most localities show an assemblage of pools with different sizes, depth and structures and hence different length of inundation. The new species invariably occurred in the longer-lived pools, with an inundation period of several months.

HISTORICAL BIOGEOGRAPHY

The new genus is at present endemic to the Drakensberg area and the following scenario is thus based on the presently known distribution and polarity of morphological characters as inferred above.

Korannacythere hamerae spec. nov. occurs along the entire eastern Escarpment of the Drakensberg in KwaZulu Natal, *K. ugiensis* spec. nov. is found in the southern part of the actual Drakensberg and *K. devriesi* spec. nov. to the west, i.e. in the Korannaberg area of the Maluti Mountains. The latter two species are known from their type locality only, but further research in the area is expected to yield new localities, as was the case in *K. hamerae*, which is now known from nearly every suitable habitat along the eastern Escarpment. The northern side of the Drakensberg area remains to be explored.

It was inferred above that the morphological changes in A2 indicate a reduction in exopodite length and a reduction in length of endclaws, as indeed all other species in the Limnocytherini have a long exopodite and rather long claws. Combining these patterns with the present distribution, it can be accepted that *K. hamerae* spec. nov. is the species with the most plesiomorphic character states, while *K. devriesi* spec. nov. has the most apomorphic features. As these species appear to be absent from the high altitude pools on the Lesotho plateau (c 3000 masl), the so-called 'High berg' could have acted as an effective barrier around which speciation occurred. Note that the isolation is at present incomplete (although species have as yet not been found sympatrically), as such rockpools at this altitude

occur semi-continuously around the entire Drakensberg. If this distribution pattern is a genuine relict of *in situ* evolution, then speciation occurred parapatrically along a geographical cline. The tempo of speciation might have been enhanced by the effect of sexual selection (see above). As was said above, this scenario is based on present distribution and new records outside of the Drakensberg area will either invalidate or corroborate this hypothesis. The faunal relationships between the Drakensberg and the Cape Fold Mountains are documented, and relicts of a much wider distribution of the genus could be found there. Also connections with the East African mountainous areas are possible.

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