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Four new species of the *Cyprideis* species flock (Crustacea: Ostracoda) of Lake Tanganyika

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Abstract

Four new species, belonging to three genera, of ostracods from Lake Tanganyika are described: *Romecytheridea longior* sp. nov., *Cyprideis spatula* sp. nov., *Cyprideis profunda* sp. nov. and *Mesocyprideis pila* sp. nov. The *Cyprideis*-flock now consists of 13 formally described species (all endemic) in six genera (five endemic), although extant collections hold at least 10-15 more species belonging to this flock. However, as the material of these taxa is mostly insufficient to allow description, new collections are urgently required, especially along the Congolese coastline and on rocky shores. None of the genera in this flock are monospecific, and together with the discovery of new soft part characters diagnostic at the generic level, this strengthen the validity of these genera in Lake Tanganyika. The geographical and ecological distribution of the four species is briefly discussed. The hypothesis that (presumed) ancestral species of *Cyprideis* occur in deeper water only, while species from the derived genera in the flock occur in the littoral is confirmed for three of the four new species presently described; *Cyprideis spatula* sp.nov., however, is found in the upper littoral.

Key words: taxonomy, morphology, ancient lakes, Tanganyika, speciation, *Cyprideis*, species flock, Ostracoda.

Résumé

QUATRE NOUVELLES ESPÈCES DU GROUPE *CYPRIDEIS* (CRUSTACEA, OSTRACODA) DU LAC TANGANYIKA

Quatre nouvelles especes du Lac Tanganyika, apppartenant à trois genres, sont décrites: *Romecytheridea longior* sp. nov., *Cyprideis spatula* sp. nov., *Cyprideis profunda* sp. nov. et *Mesocyprideis pila* sp. nov. Le groupe *Cyprideis* se compose à présent de 13 espèces formellement décrites (toutes endémiques) réparties en six genres (dont cinq endémiques), bien que les collections existantes comprennent encore au moins 10-15 autres espèces appartenant à ce groupe. Cependant, le matériel relatif à ces taxons étant le plus souvent insuffisant pour permettre leur description, de nouvelles collections sont nécessaires d'urgence, particulièrement en provenant des côtes congolaises et des côtes rocheuses. Aucun des genres de ce groupe n'est monospécifique, et, si l'on tient compte du diagnostic au niveau générique des nouveaux caractères des parties molles, ceci corrobore la validité de ces genres dans le Lac Tanganyika. La distribution géographique et écologique des quatres espèces est traitée rapidement. L' hypothèse selon laquelle des espèces ancestrales (présumées) de *Cyprideis* n'apparaîtraient que dans les eaux plus profondes alors que des espèces des genres dérivés au sein du groupe apparaîtraient au littoral, est confirmée pour trois des quatres nouvelles espèces décrites ici; l'on rencontre, cependant, *Cyprideis spatula* sp. nov. dans le littoral supérieur.

Mots-clefs: taxonomie, morphologie, lacs anciens, Tanganyika, spéciation, *Cyprideis*, species flock, Ostracoda.

Introduction

Lake Tanganyika in East Africa is the second largest and second oldest body of unfrozen surface freshwater in the world after the Siberian Lake Baikal. Both lakes have a high extant biodiversity, which is invariably largely endemic (MARTIN, 1994, COULTER, 1994). It has been argued repeatedly (recent review in MARTENS, 1997) that ancient lakes in general, and the two oldest ones Baikal and Tanganyika in particular, are excellent sites for evolutionary studies. Endemic species flocks presently exist in the cradle in which they originated, which allows one to reconstruct local environmental conditions under which these lineages evolved.

Non-marine ostracods invariably have extensive radiations in ancient lakes (MARTENS, 1994). As mostly similar groups (primarily Candonidae, Cytherideinae and Limnocytheridae) occur in the different lakes, comparative analyses of these flocks are particularly illuminating with regard to tempo and mode of speciation in different basins and factors affecting evolution and speciation.

Ancient lake ostracods are also of prime importance in evolutionary studies because they have an excellent fossil record. Ostracod valves constitute abundant microfossils, and timing of appearances of certain forms and species allows absolute calibration of molecular clocks. In groups without extensive fossils records, such as nematodes and rotifers, such clocks can at best be relative.

Finally, present concern about conservation of biodiversity, especially that of ancient lakes, requires permanent monitoring programs to assess human impact on endemic faunas. Again, ostracods will be ideal model organisms for such programs as their local fossil record will show past natural cyclicity in biodiversity, against which present dynamics can be assessed. This way, natural changes in biodiversity can better be distinguished from alterations caused by human impact.

Two closely related lineages (belonging to the same subfamily) of ancient lake ostracods are the *Cytherissa*-flock in Baikal and the *Cyprideis*-flock in Tanganyika. Morphological and molecular phylogenetic reconstructions of both flocks are presently under way (SCHÖN *et al.* 1998), but are hampered by insufficient alpha-taxonomical knowledge of especially the latter flock. Whereas more than 50 (sub-) species of Baikalian *Cytherissa* have presently been described (MAZEPOVA, 1990), only 9 species in the Tanganyikan *Cyprideis*-lineage where thus far formally named. Nevertheless, extant collections indicate that the specific diversity of the Tanganyikan *Cyprideis*-flock is at least of the same order of magnitude as the Baikalian *Cytherissa*-flock. Most of these collections, however, consist of rare specimens or empty carapaces only, making formal description impossible. Continued sampling is therefore of prime importance, because long series of specimens of presently undescribed taxa are needed to evaluate intra-specific variability, especially in valve ornamentation. Such variability is particularly high in Tanganyikan biota and can obscure species boundaries.

The present paper describes 4 new species in 3 genera. Such alpha-taxonomic descriptions are only partial, but nonetheless vital contributions to the studies of the taxonomy and the complex phylogenies of ancient lake biota. Without such basic studies, the above mentioned advanced evolutionary and biodiversity research will remain difficult, if not impossible.

Terminology and abbreviations

The morphology of the copulatory process of *Cyprideis* and related genera is complex and sometimes difficult to interpret with light microscopy. Therefore, some descriptive terms for parts of the hemipenis anatomy, important for taxonomic discrimination, were introduced by WOUTERS & MARTENS (1994). These are again used here. The distal part of the hemipenis consists of two lobes, a larger one, the distal shield (DS) and a smaller one, the distal lobe (DL). The central part of the hemipenis is very complex, and has, among other structures, a ventrally oriented lobe, here called the central lobe (CL), which can be hook-like, club-like or hammer-like in appearance. The fourth structure is the actual copulatory process (cp). As maxillule and mandible appear to have no specific features in the present species flock (see descriptions in WOUTERS & MARTENS 1994), they are not described, nor illustrated for the four new species described herein. Line drawings of the hinge of the valves, finally, illustrate the negative parts (the sockets) in black, the positive parts (the teeth) in white.

Taxonomic descriptions

Superfamily Cytheroidea BAIRD, 1850
Family Cytherideidae SARS, 1925
Subfamily Cytherideinae SARS, 1925
Tribe Cyprideidini KOLLMANN, 1960

Genus **Romecytheridea** WOUTERS, 1988

AMENDED DIAGNOSIS

Elongated valves, hinge tripartite, median element bipartite; valve surface ornamented with pits or nodes; anterior marginal rim present in some species.

Medial seta on fourth segment of antennula medium-sized (c. half the length of terminal segment). Exopodite of antenna three-segmented. First thoracic leg in males asymmetrically developed, but less so than in *Cyprideis s.s.*

Romecytheridea longior sp. nov.
(Pl. 1, figs 1-10, Pl. 5, figs 1-5)

DERIVATION OF NAME

From Latin: *longior* = longer, because of the elongated shape of the valves.

TYPE LOCALITY

Burundi, Lake Tanganyika, bay off village of Karonda, collected with hand net, depth 1 m, in a macrophyte stand. Leg.: K. MARTENS, 26 September 1991 (station n°91/12).

HOLOTYPE

A male with valves stôred dry (O.C.2240a) and dissected limbs preserved in a sealed glycerine preparation (O.C.2240b).

PARATYPES

Three dissected females and 2 dissected males (O.C. 2241-2245), 1 male carapace (O.C. 2246), 1 female carapace (O.C. 2247) and 10 females preserved in ethanol (O.C. 2248).

DIAGNOSIS

Elongate valves, with nearly parallel dorsal and ventral margins, without anterior marginal rim, and without nodes; valves set with small pits (more in males than in females);

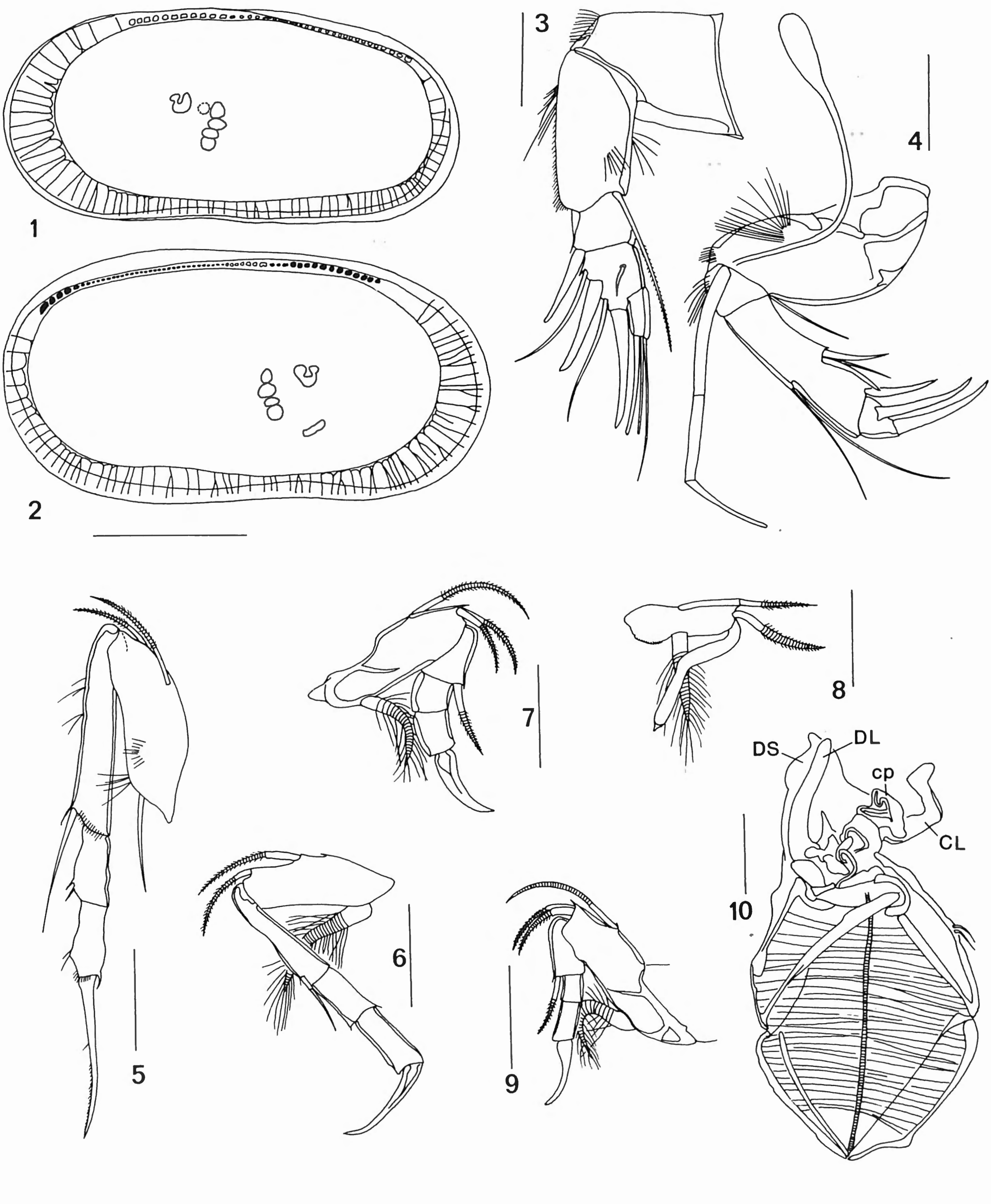

Plate 1. – *Romecytheridea longior* sp. nov., Burundi, Lake Tanganyika, Bay off Karonda Village. Fig. 1. Right valve, internal view, male, holotype (O.C. 2240). Fig. 2. Left valve, internal view, female, paratype (O.C. 2241). Fig. 3. Antennule, female, paratype (O.C. 2241). Fig. 4. Antenna, female, paratype (O.C. 2241). Fig. 5. Third leg, holotype. Fig. 6. Second leg, holotype. Fig. 7. Right first leg, holotype. Fig. 8. Right second leg, holotype. Fig. 9. Left first leg, holotype. Fig. 10. Hemipenis, paratype (O.C. 2244). Scales: Fig. 1-2: 200 μm; Fig. 3-10: 50 μm.

copulatory appendage with zigzag-shaped central lobe, broadly triangular dorsal shield and elongated, weakly curved dorsal lobe.

DESCRIPTION

Medium-sized, elongate, sub-oval, well-calcified valves; valve surface regularly pitted. Left valve somewhat higher than the right one.

Male valves (Pl. 1, Fig. 1; Pl.5, Fig. 1, 3, 4) with weakly convex dorsal margin; anterior and posterior margins broadly rounded; ventral margin straight with a weak antero-ventral concavity; valves with nearly parallel dorsal and ventral margins. Valve surface pitted, with regularly spaced shallow pits. Carapace in dorsal view somewhat fusiform, with nearly parallel lateral margins, and blunt anterior and posterior extremities; largest width situated in the middle.

Female valves (Pl.1, Fig. 2; Pl. 5, Fig. 2, 5) higher than those of the male; dorsal and ventral margins nearly straight; anterior and posterior margins broadly rounded. Carapace in dorsal view wedge-shaped, with evenly convex lateral margins and with the largest width situated posterior of the middle, at c. 4/5th of the length; broadly rounded posterior extremity.

Inner lamella in both sexes moderately wide, with numerous, sometimes branched marginal pore canals (Pl. 1, Fig. 1, 2); few false pore canals. Very narrow, hardly visible anterior and posterior vestibula. Hinge tripartite and consisting of anterior, median and posterior elements; median element bipartite. Hinge of right valve (Pl. 1, fig. 1): anterior element with about fifteen toothlets; antero-median element with three to five small indistinctly delineated sockets; postero-median element a bar-like structure with a large number of small toothlets; transition between postero-median element and posterior element indistinct; posterior element consisting of about seven slightly bifid toothlets. Left valve hinge complementary (Pl. 1, fig. 2).

Antennule (Pl. 1, Fig. 3) five-segmented; first segment short and broad; third and fourth segments short; antero-distal seta of second segment relatively short, reaching to the tip of the last segment; third segment with one, and fourth segment with two strong claws.

Antenna (Pl. 1, Fig. 4) four-segmented, with three-segmented exopodite; claws of third and fourth segments short.

First leg dimorphic in the male: left leg (Pl. 1, Fig. 9) slender, as in the female; right leg (Pl. 1, Fig. 7) with somewhat broadened second, third and fourth segments.

Second leg dimorphic in the male; right leg (Pl. 1, Fig. 8) strongly reduced and weakly sclerotized; first segment of same size as in the female, the following two segments (indistinctly sutured) small and delicate; left leg (Pl. 1, Fig. 6) as in the female.

Third leg (Pl. 1, Fig. 5) not dimorphic, but long and slender, set with bundles of setulae, and with long, slender terminal claw.

Hemipenis (Pl. 1, Fig. 10): distal shield (DS) large and irregularly triangular with a broad base; distal lobe (DL) weakly sinuous with blunt distal end; copulatory process (cp) small and lobed; central lobe (CL) long and narrow, with two right angled curves (zigzag-shaped).

Female abdominal extremity with a crescent-shaped process; furcae small.

MEASUREMENTS

Holotype: Left valve: L 0.60 mm, H 0.29 mm
Right valve: L 0.60 mm, H 0.28 mm

Paratypes:
Males: L 0.56-0.60 mm, H 0.27-0.29 mm
Females: L 0.61 - 0.64 mm, H 0.30 - 0.33 mm

REMARKS

The present species is a brooder. In two of the dissected females the postero-dorsal pouch contained: 2 eggs and 1 nauplius in O.C.2242 (paratype) and 7 eggs and 3 nauplii in O.C.2245 (paratype).

OCCURRENCE

Romecytheridea longior sp. nov. is known from the type locality, Karonda (Burundi), where the species was collected in a macrophyte stand on sand, at a depth of 1 m (leg.: K. MARTENS, 26 Sept. 1991, and from a bay south of Karema (approx. coord. S 6°52', E 30°32' - Tanzania), where the species was collected with a petit PONAR grab, on sand and shell debris, at a depth of 18 m (leg.: K. MARTENS & B. GODDEERIS, 29 May 1992, LT/92-22).

DISCUSSION

Up to now, two other species of the genus *Romecytheridea* have been described: *Romecytheridea tenuisculpta* (ROME, 1962) (redescribed by WOUTERS, 1988a) and *Romecytheridea ampla* WOUTERS, 1988b. The valves of *R. longior* sp. nov. have a comparable elongate shape as the two higher mentioned *Romecytheridea*-species, but lack the antero-marginal rim, and the nodes on the valves. *R. longior* sp. nov. has a zigzag-shaped central lobe, a broadly triangular dorsal shield and a weakly curved dorsal lobe. In *R. ampla* the central lobe is narrow, and only weakly curved; the dorsal shield is distally rounded and triangular, with a much narrower base, the distal lobe is sinuous. The "soft parts" of the male of *R. tenuisculpta* remain to be described. It is interesting to note that the asymmetry in the male first legs is comparable in *R. longior* sp. nov. and *R. ampla* WOUTERS, 1988.

Genus **Cyprideis** JONES, 1857

AMENDED DIAGNOSIS

Rounded valves, hinge tripartite, median element bipartite; valves smooth to ornamented with pits and/or nodes. Medial seta on fourth segment of antennula very small (1/10-1/5 of length of terminal segment). Exopodite on antenna three-segmented. Asymmetry of first male thoracic leg very strong, with large subquadrate terminal segments on right first leg.

Cyprideis spatula sp. nov.
(Pl. 2, figs 1-10, Pl. 5, figs 6-10))

DERIVATION OF NAME

From Latin: *spatula* = small spoon, because of the spoon-shaped process on the dorsal side of the copulatory appendage (*spatula* used as a noun in apposition).

TYPE LOCALITY

Tanzania, Lake Tanganyika, opposite village Kaparamsenge, 5°48'320" S, 29°56'431 E", collected with petit PONAR grab at 5 m deep on silt (leg. K. MARTENS & B. GODDEERIS, June 2nd, 1992).

HOLOTYPE

A male with valves stored dry (O.C.2249a) and dissected limbs preserved in a sealed glycerine preparation (O.C.2249b).

PARATYPES

Two dissected males and 3 dissected females (O.C. 2250-2254), 1 male carapace (O.C. 2255), 1 female carapace (O.C. 2256) and 13 females preserved in ethanol (O.C. 2257).

DIAGNOSIS

Weakly pitted valves, with parallel dorsal and ventral margins; anterior and posterior margins broadly rounded, posterior margin nearly straight; hemipenis with a dorsally implanted spoon-like process (arrowed in Plate 2, Fig. 10).

DESCRIPTION

Valves large and suboval; valve surface with small shallow pits, mostly in the central and posterior regions. Dorsal and ventral margins nearly straight.

Male valves (Pl. 2, Fig. 1, Pl. 5, fig. 7) dorsal and ventral margins straight; anterior and posterior margins broadly rounded; transition between dorsal and posterior margin without an angle.

Female valves (Pl. 2, Fig. 2; Pl. 5, Fig. 8) somewhat higher than male valves, and with distinct posterior cardinal angle.

Female carapace wedge-shaped in dorsal view, with pointed anterior and narrowly rounded, inflated, posterior extremity; maximal width situated posterior to the middle, at nine tenth of the length; male carapace with rounded to somewhat truncate posterior extremities and nearly parallel lateral margins; maximal width near the middle.

Inner lamella moderately wide, with numerous, sometimes branched marginal pore canals; narrow anterior, posterior, and postero-ventral vestibula (Pl. 2, Fig. 1 and 2). Hinge tripartite, and consisting of anterior, median and posterior element; median element bipartite.

Hinge of right valve (Pl. 2, Fig. 1, Pl. 5, Fig. 6): anterior element with about 10 toothlets; antero-median element with an indistinct number (about 14) of partially fused small sockets; postero-median element with numerous, small toothlets; posterior element with 5 to 6 weakly bifid toothlets. Hinge of left valve complementary (Pl.2, Fig. 2).

Antennule (Pl. 2, Fig. 4) five-segmented; first segment broad and short; antero-distal seta of second segment long, reaching to the middle of the terminal claws; third and fourth segment short, with long claws and claw-like setae; fifth segment long and slender with a long weak claw and a long bifurcate aesthetasc.

Antenna (Pl. 2, Fig. 3) four-segmented with three-segmented exopodite; terminal segment small with two strong claws.

First leg dimorphic in the male: left leg (Pl. 2, Fig. 8) as in the female, with slender segments; right leg (Pl. 2, Fig. 7) with broad second, third and fourth segment; fourth segment rectangular and broader than base of terminal claw.

Second leg strongly dimorphic in the male: left leg (Pl. 2, Fig. 6) as in the female, with long curved terminal claw; right leg (Pl. 2, Fig. 5) strongly reduced and weakly sclerotized; terminal segments small and delicate and indistinctly three-segmented.

Third leg (Pl. 2, Fig. 9) not dimorphic, elongate and very hirsute, with long, slightly curved slender terminal claw.

Hemipenis (Pl. 2, Fig. 10) with subtriangular distal shield (DS), distally rounded and with dorsal semicircular expansion; distal process (DP) almost straight to slightly sinuous: copulatory process (cp) small and indistinctly lobed; central lobe (CL) large and club-shaped, with posterior semi-oval shield-like widening with antero-ventral lobed margin. A large spoon-shaped process on the dorsal side, close to the insertion point of the central lobe.

Abdominal extremity in the female a wedge-shaped process; furcae moderately large.

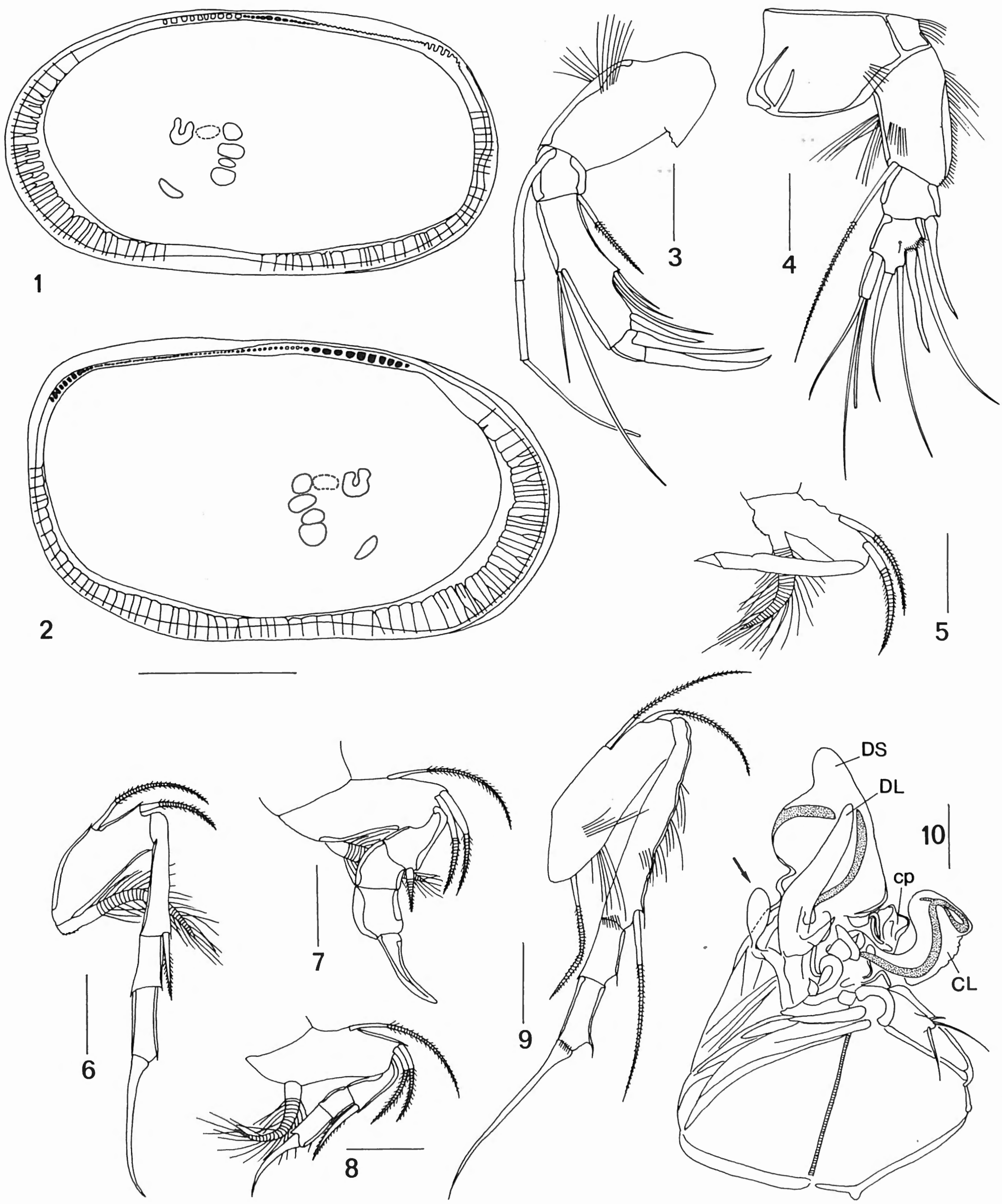

Plate 2. – *Cyprideis spatula* sp. nov., Tanzania, Lake Tanganyika, opposite village Kaparamsenge. Fig. 1. Right valve, internal view, male, holotype (O.C.2249). Fig. 2. Left valve, internal view, female, paratype (O.C. 2250). Fig. 3. Antenna, holotype. Fig. 4. Antennule, holotype. Fig. 5. Right second leg, male, paratype (O.C. 2252). Fig. 6. Left second leg, holotype. Fig. 7. Right first leg, holotype. Fig. 8. Left first leg, holotype. Fig. 9. Third leg, holotype. Fig. 10 Hemipenis, holotype; spoon-shaped process arrowed. Scales: Fig. 1-2: 200 μm; Fig. 3-10: 50 μm.

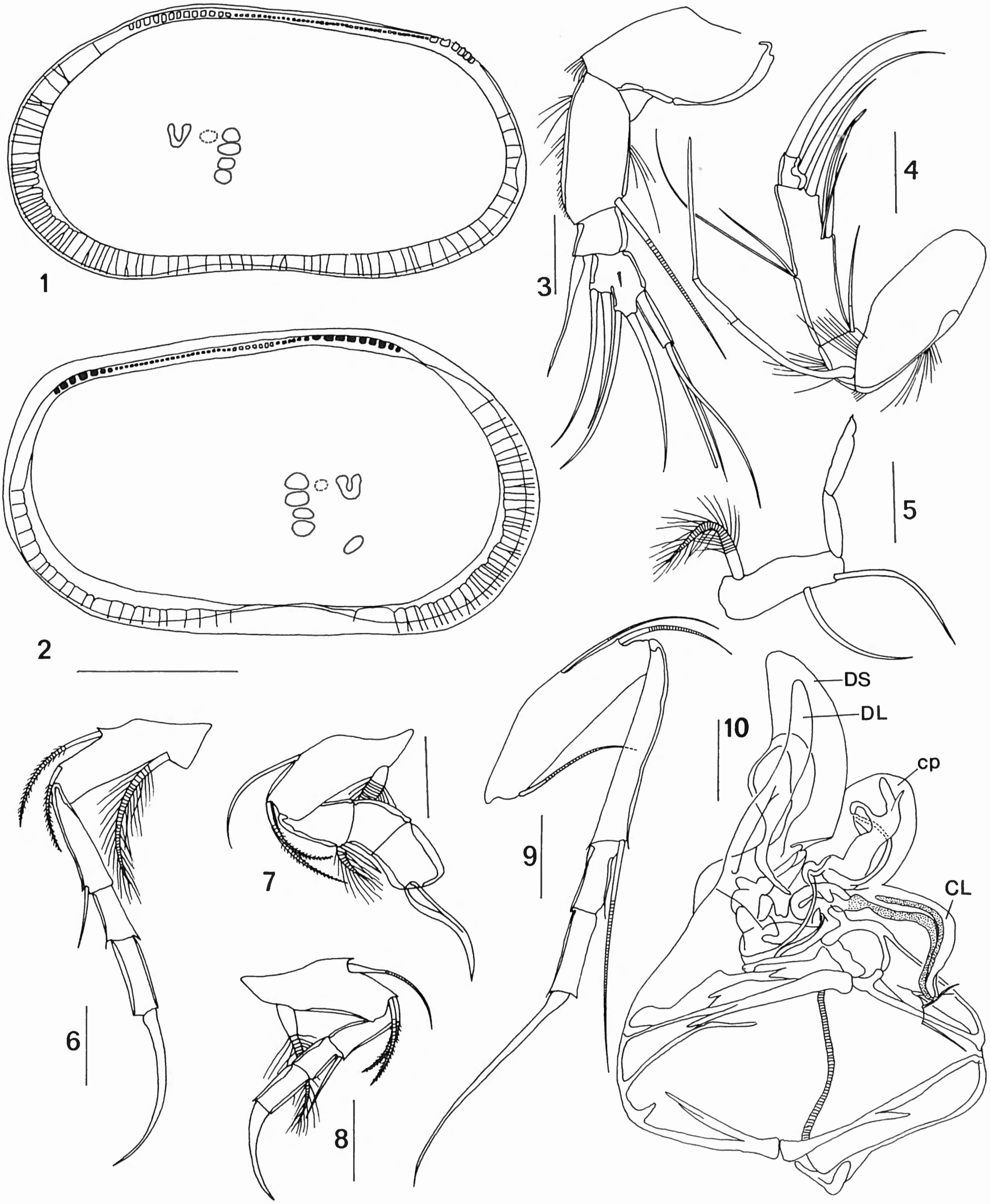

Plate 3. – *Cyprideis profunda* sp. nov., Tanzania, Lake Tanganyika, Bays South of Kibwesa. Fig. 1. Right valve, internal view, male, holotype (O.C. 2263). Fig. 2. Left valve, internal view, female, paratype (O.C. 2264). Fig. 3. Antennule, holotype. Fig. 4. Antenna, female, paratype (O.C. 2265). Fig. 5. Right second leg, holotype. Fig. 6. Left second leg, holotype. Fig. 7. Right first leg, holotype. Fig. 8. Left first leg, holotype. Fig. 9. Third leg, holotype. Fig. 10. Hemipenis, holotype. Scales: Fig. 1-2: 200 µm; Fig. 3-10: 50 µm.

MEASUREMENTS

Holotype: Left valve: L 0.65 mm, H 0.35 mm
Right valve: L 0.64 mm, H 0.34 mm
Paratypes:
Males: L 0.65 - 0.68 mm, H 0.34 - 0.37 mm
Females: L 0.68 - 0.70 mm, H 0.38 - 0.40 mm

REMARKS

The present species is a brooder. In three of the dissected females the postero-dorsal pouch contained: 15 eggs and 5 nauplii in O.C.2251 (paratype), 7 eggs and 1 nauplius in O.C.2254 (paratype) and 6 eggs and 2 nauplii in O.C. 2259 (paratype).

OCCURRENCE

Cyprideis spatula sp. nov. is known from the type locality, Kaparamsenge (Tanzania), where it was collected at 5 m deep on silt (leg. K. MARTENS & B. GODDEERIS, June 2nd, 1992). The species is also known from three other localities: Gitaza (approx. coord. S 3°34' E 29°18' - Burundi), collected with a petit PONAR grab, at a depth of 8 m on sand and mud (leg. K. MARTENS, 27 Sept. 1991), Resha (Burundi), collected with a petit PONAR grab, on fine sand, at a depth of 9.5 m (leg. K. MARTENS, 27 Sept. 1991), and Kaparamsenge (same coordinates as type locality - Tanzania), collected with a petit PONAR grab at 7 m deep, on fine sand (leg. K. MARTENS & B. GODDEERIS, 2 June 1992).

DISCUSSION

Two other species of the genus *Cyprideis* have thus far been decribed from Lake Tanganyika: *Cyprideis mastai* WOUTERS & MARTENS, 1994 and *Cyprideis rumongensis* WOUTERS & MARTENS, 1994. *Cyprideis spatula* sp. nov. differs both from *C. mastai* and from *C. rumongensis* by its parallel dorsal and ventral margins (tapering in the two other species), and by its less developed hinge. Furthermore *C. mastai* has completely smooth valves, whereas *C. spatula* has pitted valves. Finally, *C. spatula* can easily be distinguished by the presence of a dorsally implanted spoon-like process on the hemipenis.

Cyprideis profunda sp.nov.
(Pl. 3, figs 1-10, Pl. 6, figs 1-5)

DERIVATION OF NAME

From Latin *profundus* = deep, because of the occurrence of this species in the deeper part of Lake Tanganyika

TYPE LOCALITY

Tanzania, Lake Tanganyika, Bay south of Cape Kibwesa, collected with a petit PONAR grab at 90 m deep on mud. Leg.: K. MARTENS & B. GODDEERIS, 30 May, 1992 (station LT92/23).

HOLOTYPE

A male with valves stored dry (O.C.2263a) and dissected limbs preserved in a sealed glycerine preparation (O.C.2263b).

PARATYPES

Five dissected females (O.C. 2264-2268), 1 male carapace (O.C. 2269), 1 female carapace (O.C. 2270), and 9 valves and 2 carapaces (O.C. 2271).

DIAGNOSIS

Strongly pitted elongate valves, with narrow anterior inner lamella; central lobe of hemipenis a long and strongly curved process.

DESCRIPTION

Medium-sized, elongate, suboval valves; valve surface covered with large round pits; left valve somewhat higher and longer than right one. Female valves (Pl. 3, Fig. 2; Pl.6, Fig. 2, 5) with weakly tapering dorsal and ventral margins; dorsal and ventral margins straight, anterior margin broadly rounded, posterior margin slightly truncate. Female carapace in dorsal view somewhat wedge-shaped with almost straight lateral margins, pointed anterior extremity and bluntly rounded posterior margin; largest width situated posterior to the middle, at about 8/10 of the length.
Male valves (Pl.3, Fig. 1; Pl. 6, Fig. 1, 4) less high than those of the female; dorsal and ventral margins weakly tapering towards the posterior; dorsal and ventral margins nearly straight; anterior and posterior margins broadly rounded. Carapace in dorsal view with straight and parallel lateral margins and with the largest width situated in the middle; anterior and posterior extremities pointed.
Inner lamella narrow, with numerous, sometimes branched marginal pore canals (Pl. 3, Fig. 1-2. Narrow anterior vestibulum; shallow posterior and postero-ventral vestibulum. Hinge tripartite, and consisting of anterior, median and posterior element; median element bipartite. Hinge of right valve: anterior element with about thirteen toothlets; antero-median element with five to seven small indistinctly delineated sockets; postero-median element with a large number of small toothlets; transition between postero-median element and posterior element indistinct; posterior element consisting of six to seven slightly bifid

toothlets. Left valve hinge complementary (Pl. 3, Fig. 2).
Antennule (Pl. 3, Fig. 3) five-segmented; first segment short and broad; third and fourth segments short; antero-distal seta of second segment long, reaching just beyond distal extremity of fifth segment; posterior setae of third and fourth segments long; difference between setae and claws indistinct.
Antenna (Pl. 3, Fig. 4) four-segmented, with three-segmented exopodite; claws of fourth segment long, curved, and slender; terminal claw long.
First leg dimorphic in the male: left leg (Pl.3, Fig. 8) slender, as in the female; right leg (Pl. 3, Fig. 7) with very broad second, third and fourth segments; third and fourth segments sub-quadrate, and much broader than base of terminal claw; distal claw not centrally, but ventrally inserted.
Second leg dimorphic in the male; right leg (Pl.3, Fig. 5) strongly reduced and weakly sclerotized; first segment of same size as in the female, the following two segment small and delicate but distinctly sutured; left leg (Pl. 3, Fig. 6) normal, with long and strongly curved distal claw.
Third leg (Pl. 3, Fig. 9) not dimorphic, long and slender and with long, slightly curved and very slender terminal claw.
Hemipenis (Pl. 3, Fig. 10) with distal shield (DS) large and elongated triangular, slightly curved; distal lobe (DL) long and weakly sinuous; copulatory process (cp) large and oval, with smooth margin; central lobe (CL) long and elongate, with chitinous bands, bent in the middle in a straight angle; distal end pointing in anterior direction.
Female abdominal extremity crescent-shaped, with medium-sized furcae.

MEASUREMENTS

Holotype: Left valve: L 0.67 mm, H 0.36 mm
Right valve: L 0.66 mm, H 0.34 mm
Paratypes: Females: L 0.65 - 0.68 mm, H 0.36 - 0.39 mm

REMARKS

The present species is a brooder. In four of the dissected females, the postero-dorsal pouch contained: 3 eggs in O.C. 2264 (paratype), 2 eggs and 2 nauplii in O.C. 2266 (paratype), 2 eggs and 2 nauplii in O.C. 2267 (paratype) and 5 eggs and 1 nauplius in O.C. 2268 (paratype).

OCCURRENCE

Cyprideis profunda sp. nov. is only known from the type locality, namely the Bay south of Cape Kibwesa (Tanzania), where is was collected on mud, at a depth of 90 m (leg.: K. MARTENS & B. GODDEERIS, 30 May, 1992).

DISCUSSION

Cyprideis profunda sp. nov. has strongly pitted valves, and therefore can be distinguished from *Cyprideis mastai*, *Cyprideis rumongensis* and *Cyprideis spatula*, having smooth or finely pitted valves. The new species also has a much narrower anterior inner lamella than the former three species, and a much weaker hinge than *C. mastai* and *C. rumongensis*. *Cyprideis profunda* sp. nov. differs from *C. spatula* sp. nov. by the absence of a spoon-like dorsally implanted process on the hemipenis. In *C. profunda* sp. nov., the central lobe is a long and curved process, whereas in *C. mastai*, *C. rumongensis* and *C. spatula* sp. nov., the central lobe is club-shaped.

Genus **Mesocyprideis** WOUTERS & MARTENS, 1992

AMENDED DIAGNOSIS

Valves subtrapezoidal, ornamented with pits, nodes and/or knobs, caudal process and ventro-lateral ala more or less developed; hinge tripartite; median element bipartite.
Medial seta on fourth segment of antennula very long (3x length of final segment). Exopodite of antenna two-segmented. Male first thoracic legs almost symmetrical.

Mesocyprideis pila sp. nov.
(Pl. 4, figs 1-10, Pl. 6, figs 6-10)

DERIVATION OF NAME

From Latin *pila* = pillar, because of the pillar-like pustules on the valves (*pila* is used as noun in apposition).

TYPE LOCALITY

Tanzania, Lake Tanganyika, Bay south of Karema, 6°52' S, 30°32' E, collected on sand with a petit PONAR grab at 3m deep. Leg.: K. MARTENS & B. GODDEERIS, 29 May, 1992 (station LT92/20).

HOLOTYPE

A male with valves stored dry (O.C.2272a) and dissected limbs preserved in a sealed glycerine preparation (O.C.2272b).

PARATYPES

Three dissected males and 7 dissected females (O.C. 2273-2282), 1 male carapace (O.C. 2283), 1 female carapace (O.C. 2284), 17 carapaces and 1 right valve (O.C. 2285) and 2 males and 5 females preserved in ethanol (O.C. 2286).

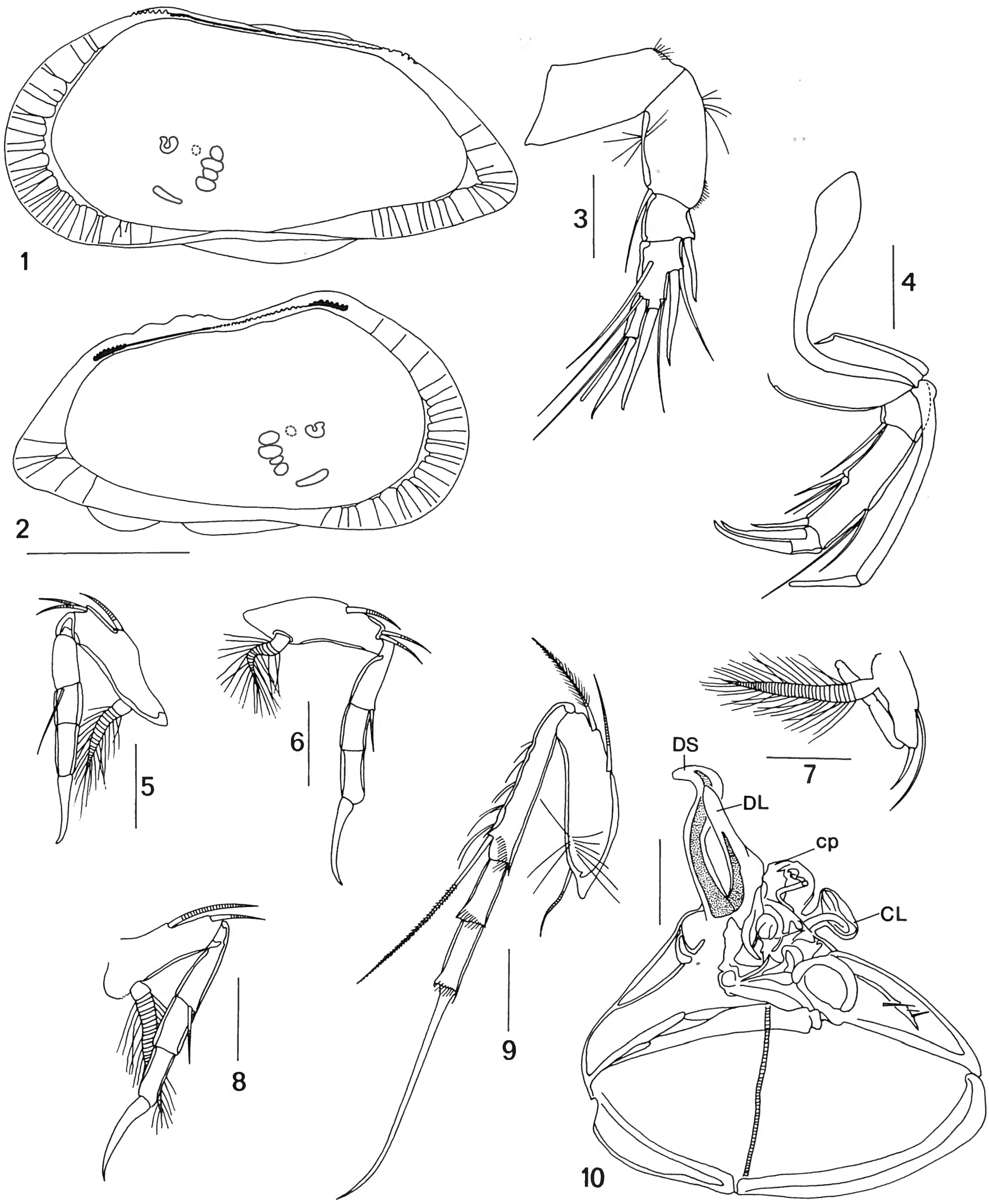

Plate 4. – *Mesocyprideis pila* sp. nov., Tanzania, Lake Tanganyika, Bay south of Karema. Fig. 1. Right valve, internal view, male, holotype (O.C. 2272). Fig. 2. Left valve, internal view, female, paratype (O.C. 2274). Fig. 3. Antennule, holotype. Fig. 4. Antenna, holotype. Fig. 5. Right first leg, holotype. Fig. 6. Left first leg, holotype. Fig. 7. Right second leg, holotype. Fig. 8. Left second leg, holotype. Fig. 9. Third leg, male, paratype (O.C. 2273). Fig. 10. Hemipenis, paratype (O.C. 2273). Scales: Fig. 1-2: 200 µm; Fig. 3-10: 50 µm.

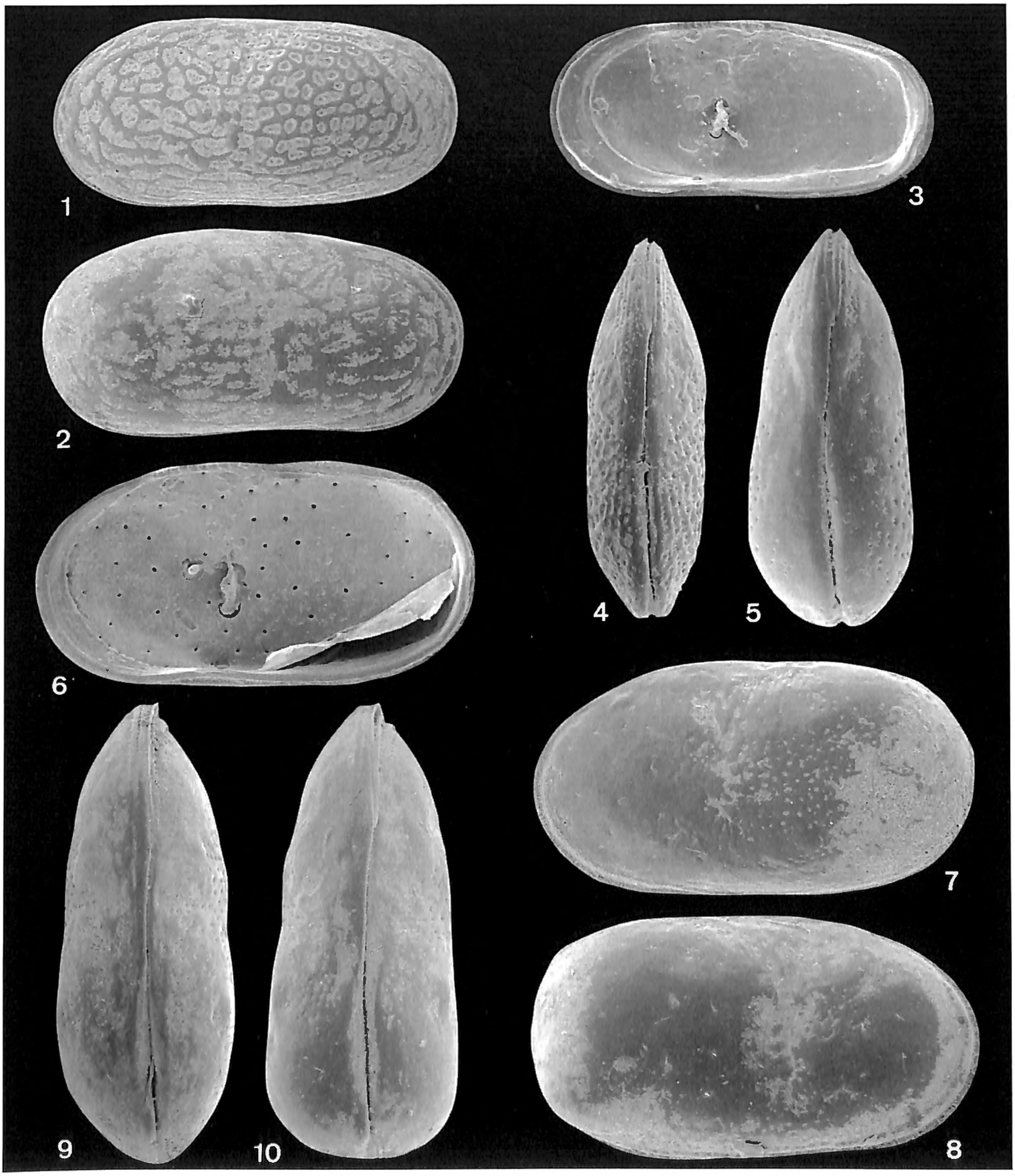

Plate 5.

Figs 1-5: *Romecytheridea longior* sp. nov. Burundi, Lake Tanganyika, Bay off Karonda Village.

Figs 6-10: *Cyprideis spatula* sp. nov., Tanzania, Lake Tanganyika, opposite village Kaparamsenge.

Fig. 1. Left valve, lateral view, male, holotype (O.C. 2240). Fig. 2. Right valve, lateral view, female, paratype (O.C. 2241). Fig. 3. Right valve, internal view, male, paratype (O.C. 2244). Fig. 4. Male carapace, dorsal view, paratype, O.C. 0.C. 2246). Fig. 5. Female carapace, dorsal view, paratype (O.C. 2247). Fig. 6. Right valve, internal view, male, paratype (O.C. 2252). Fig. 7. Left valve, lateral view, male, holotype (O.C. 2249). Fig. 8. Right valve, lateral view, female, paratype (O.C. 2250). Fig. 9. Male carapace, dorsal view, paratype (O.C. 2255). Fig. 10. Female carapace, dorsal view, paratype (O.C. 2256). All magnifications: 120 X.

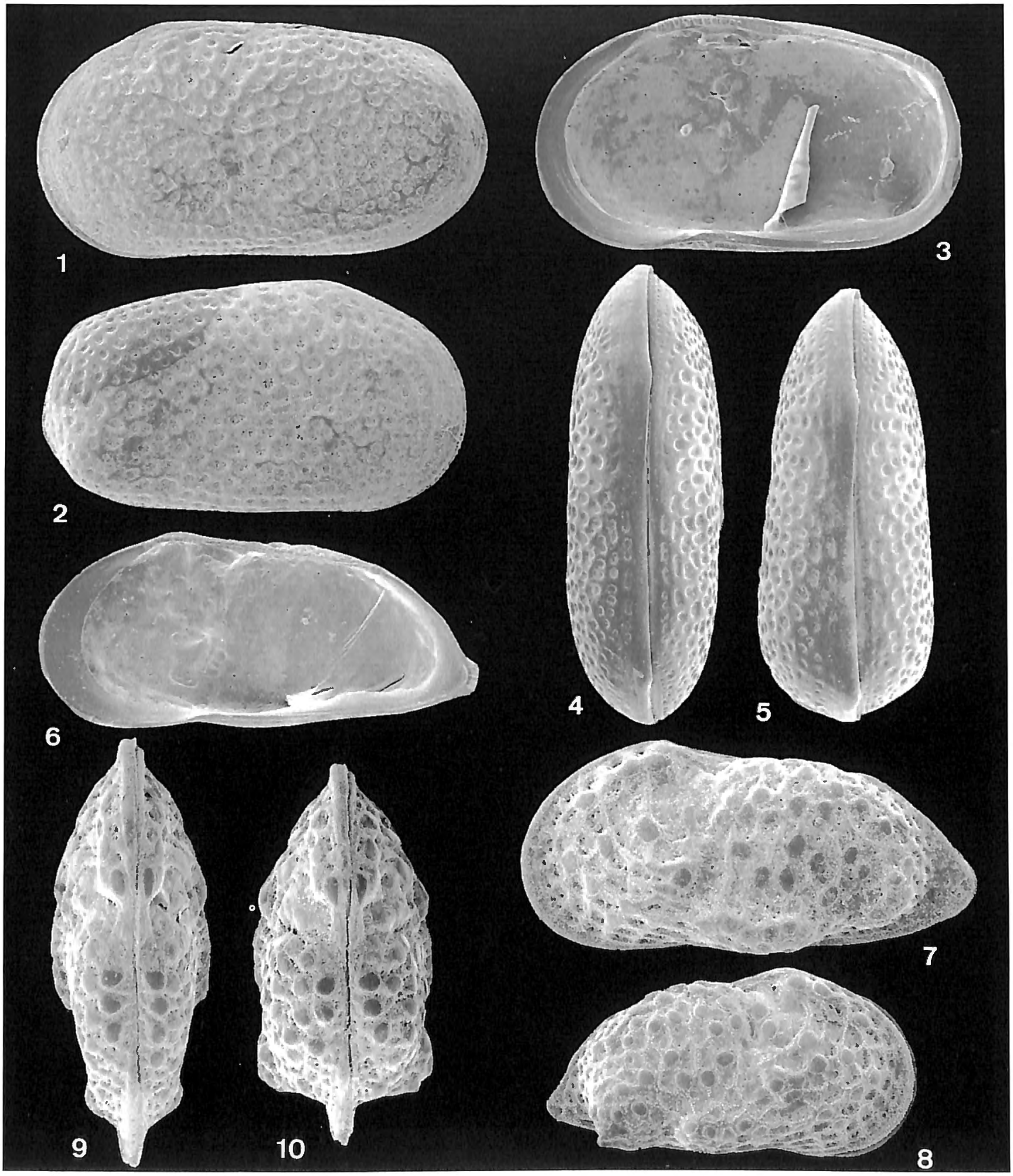

Plate 6.

Figs 1-5: *Cyprideis profunda* sp. nov., Tanzania, Lake Tanganyika, Bays South of Kibwesa. Figs 6-10: *Mesocyprideis pila* sp. nov., Tanzania, Lake Tanganyika, Bay south of Karema.

Fig. 1. Left valve, lateral view, male, holotype (O.C. 2262). Fig. 2. Right valve, lateral view, female, paratype (O.C. 2263). Fig. 3. Right valve, internal view, female, paratype (O.C. 2264). Fig. 4. Male carapace, dorsal view, paratype (O.C. 2269). Fig. 5. Female carapace, dorsal view, paratype (O.C. 2270). Fig. 6. Right valve, internal view, male, paratype (O.C. 2273). Fig. 7. Left valve, lateral view, male, holotype (O.C. 2272). Fig. 8. Right valve, lateral view, female, paratype (O.C. 2274). Fig. 9. Male carapace, dorsal view, paratype (O.C. 2283). Fig. 10. Female carapace, dorsal view, paratype (O.C. 2284). All magnifications: 120 X.

DIAGNOSIS

Subtrapezoidal valves, with ventro-lateral alae; valve surface strongly ornamented, with pillar-like knobs, surrounded by small pustules; posterior vestibulum triangular; dorsal shield of hemipenis narrow and sinuous; central lobe club-shaped with broad distal extremity.

DESCRIPTION

Valves (Pl. 4, Fig. 1, 2, Pl. 6, fig. 7-10) small, subtrapezoidal to wedge-shaped, with anterior margin evenly rounded, and posterior margin produced in a blunt postero-ventral corner. Dorsal margin strongly sloping, but straight, with distinct anterior and posterior cardinal angles; ventral margin slightly sinuous. Male valves markedly longer than those of the female. Surface set with a reticulation pattern, and with large, round pillar-like thickenings, surrounded by a large number of very small pustules; ventro-lateral expansion (ala), consisting of two large nodes (more pronounced in the females) and one large node in the males (the posterior node being less developed).
Carapace in dorsal view showing strong sexual dimorphism. Very narrow in males, with convex lateral margins (with exception of the protruding ventro-lateral ala); maximum width situated somewhat in front of the middle; posterior extremity narrow, and sharply delineated; eye spots clearly visible. Female carapace much wider, with a strongly inflated appearance; lateral margins nearly parallel; posterior extremity, as in the male, narrowly pointed.
Inner lamella moderately wide, with a shallow anterior, and a small triangular posterior vestibulum; numerous, sometimes branching, marginal pore canals.
Hinge weakly developed, and individual elements difficult to see; hinge tripartite, and consisting of anterior, median and posterior element; median element bipartite. Hinge of right valve (Pl. 4, Fig. 1): anterior element with six to eight toothlets; antero-median element a crenulated groove, with the number of indistinctly delineated sockets difficult to count; postero-median element a crenulated bar, consisting of a large number of small and indistinct toothlets; transition between postero-median element and posterior element indistinct; posterior element consisting of about five to six small and slightly bifid toothlets. Left valve hinge complementary (Pl. 4, Fig. 2).
Antennule (Pl. 4, Fig. 3) with five segments, generally stout and broad. First and second segment set with brushes of setulae. Third and fourth segment with three claw-like setae; fifth segment rectangular, with one small claw, and a bifurcate aesthetasc.
Antenna (Pl. 4, Fig. 4) with four segments and a large two-segmented exopodite; terminal claws stout, but short.
First leg indistinctly dimorphic in the male: left leg (Pl. 4, Fig. 6) slender, as in the female; right leg (Pl. 4, Fig. 5) as the left one, but second and third segments somewhat shorter, and distal seta of second segment markedly shorter.
Second leg dimorphic in the male; right leg (Pl. 4, Fig. 7) strongly reduced and weakly sclerotized; first segment of same size as in the female, the following two segment short and delicate but distinctly sutured; left leg (Pl. 4, Fig. 9) normal, with short distal claw.
Third leg (Pl. 43, Fig. 9) not dimorphic, long and slender, set wish brushes of setulae, and with long, slightly curved and very slender terminal claw.
Hemipenis (Pl. 4, Fig. 10): distal shield (DS) a narrow and sinuous process; distal lobe (DL) short and almost straight, with tapering lateral margins; copulatory process (cp) small and subcircular; central lobe (CL) large and club-shaped.
Female abdominal extremity wedge-shaped, with small furcae.

MEASUREMENTS

Holotype: Left valve: L 0.67 mm, H 0.32 mm
Right valve: L 0.66 mm, H 0.31 mm
Paratypes: Males: L 0.63 - 0.67 mm, H 0.30 - 0.32
Females: L 0.56 - 0.60 mm, H 0.20 - 0.32 mm

REMARKS

The present species is a brooder. In three of the dissected females the postero-dorsal pouch contained: 5 eggs and 2 nauplii in O.C. 2275 (paratype), 6 eggs and 1 nauplius in O.C. 2276 (paratype) and 5 eggs and 1 nauplius in O.C. 2282 (paratype).

OCCURRENCE

Mesocyprideis pila sp. nov. is known from the type locality, the Bay of Karema (Tanzania), where is was collected on sand at a depth of 3m (leg.: K. MARTENS & B. GODDEERIS, 29 May, 1992). The species was also found in two other localities, namely the Kipili Islands (coord. S 7°27'122" E 30°34'116" - Tanzania), collected with a hand net at 2 - 5 m (Leg.: K. MARTENS & B. GODDEERIS, 27 May 1992; no. LT/92-03), and Mkangasi (coord. S 6°35'901" E 30°16'279" - Tanzania), collected with a hand net, on sand, at 3 m deep (leg.: K. MARTENS & B. GODDEERIS, 30 May 1992, no. LT/92-22).

DISCUSSION

Only one other *Mesocyprideis*-species, *M. irsacae* (KISS, 1959), is known from Lake Tanganyika. As far as the overall shape of the valves is concerned, *M. irsacae* and *M. pila* sp.nov. show some resemblance. *Mesocyprideis pila* sp. nov., however, has a much stronger ornamented valve surface, with pillar-like knobs, surrounded by small pustules. Furthermore, the caudal process on the valves of *M. pila* sp.nov. (especially in the males), is much more developed. Male carapaces of *M. pila* sp.nov., in dorsal view, are markedly less wide than those of *M. irsacae*. The posterior vestibulum in *M. pila* sp.nov. is triangular, whereas there is hardly a vestibulum present in *M. irsacae*, and if present, it is not triangular and very shallow. The posterior extremity of the carapace (in both male and female) of *M. pila* sp.nov. is a narrow, pointed projection. In *M. irsacae*, the posterior extremity of the carapace is blunt. The dorsal shield of the hemipenis is a narrow, sinuous process in *M. pila* sp. nov., and broad and triangular in *M. irsacae*. The central lobe is club-shaped, with a very broad distal extremity in *M. pila* sp.nov. and only slightly inflated in *M. irsacae*.

General Discussion

SPECIFIC DIVERSITY

The 4 new species described in the present paper, bring the total of formally described species in the Tanganyikan *Cyprideis*-flock to 13 (all endemic), distributed over 6 genera (5 endemic). The actual number of extant species in this flock is difficult to estimate, but existing collections, mostly consisting of single specimens or empty carapaces, show that several other species, and maybe even genera, await description. At least another 10-15 species have been identified. However, given the fact that most of the Congolese coast (more than 1/3 of the total Tanganyikan shoreline) as well as most rocky shores around the lake (see below) remains largely unexplored, the total number of extant taxa may be much higher.

GENERA IN ANCIENT LAKES

Compared to species, genera are poorly understood evolutionary units. Whereas a recent review listed not less than 22 different species concepts (MAYDEN, 1997), only 3 genus concepts have thus far been recognised (ALLMON, 1992): the *Phenetic* genus concept (genera are clusters of morphologically closely related species, with morphological gaps separating the clusters - MAYR, 1969), the *Phylogenetic* (or cladistic) concept (monophyletic clusters of species with the same ancestor - WILEY, 1981) and the *Hybridisability* concept (species belonging to the same genus can produce viable, albeit mostly sterile, hybrids - DUBOIS, 1988). Geniation, the process through which genera originate, is often seen as speciation taken one step further (MAYR, 1970). Other authors regard supra-specific cladogenesis as a special process, primarily differing from speciation by a much faster rate of evolutionary change (STANLEY, 1998, DUBOIS, 1988).
Ancient lakes are ideal sites to study this question and to test the above hypotheses on supra-specific cladogenesis. The question is presently being investigated using both morphological and molecular methods and comparing the Baikalian and the Tanganyikan flocks (MARTENS *et al.* in press). However, some preliminary observations are possible at this stage, especially after the description of the present species. Firstly, if geniation is a gradual process, then the incidence of intermediate forms between otherwise valid genera must be higher than in other water bodies. This is so because extant forms live in the cradle where they originated. WOUTERS & MARTENS (1994) reported that *Tanganyikacythere caljoni* sp.nov. is indeed to some extent intermediate between *T. burtonensis* and *Cyprideis s.s.* But no further intermediate species between the other genera have thus far been found. Secondly, it appears that far less monotypical genera exist in the ostracods of Lake Tanganyika than was previously thought. After WOUTERS (1988) described a second species in the genus *Romecytheridea*, the present paper adds a third species to this genus and a second one to *Mesocyprideis*. Both *Tanganyikacythere* and *Cyprideis* were already known to be represented by more than one species in the lake. At least one new species of the last two genera, *Kavalacythereis* and *Archaeocyprideis,* has already been found, albeit thus far in insufficient material to allow formal description. Finally, most of these genera were originally defined on valve characters only. As ostracod valves are known to have a higher adaptive plasticity than soft parts (MARTENS, 1998), this threw additional doubt on the validity of the different genera in the Tanganyikan *Cyprideis*-flock. The present descriptions of species belonging to different genera, however, has revealed additional soft part features diagnostic of the genera: two- or three-segmented exopodite on the antenna, size of the medial seta on the fourth segment of the antennula and degree of asymmetry between left and right first leg in males.
These additional soft part features, as well as the apparent absence of monospecific genera, strengthen the taxonomic validity of the Tanganyikan genera in the *Cyprideis*-flock. The presence of an intermediate form between two genera in at least one case, as well as the said absence of monospecific genera, offers support to the gradualistic view of geniation, without however completely excluding the possibility of quantum geniation in some cases.

BATHYMETRIC DISTRIBUTION AND SEDIMENT TYPE

WOUTERS & MARTENS (1994) postulated that the ancestral species of the Tanganyikan flock, i.e. belonging to the genus *Cyprideis*, occur in the deeper waters of the lake. This statement can now be refined (Table 1). Firstly, of the two new *Cyprideis* species described here, one confirms to this hypothesis, occurring at or near the oxygen limit at 90 m depth, the other falsifies it, occurring in the upper littoral (above 10 m). The two other new species described here, both belonging to supposedly derived genera, conform to the pattern and occur in shallow water only. Secondly, shallow and deep in Tanganyika have completely different meaning than in Baikal, where the littoral extends to about 200 m (20 m in Tanganyika), while the Baikalian abyss is oxygenated down to it deepest point, c 1700 m (below 100-200 m, Tanganyika is anoxic).

Table 1. – Aspects of ecological distribution of thirteen species of Cyprideidini (Cytherideinae) in Lake Tanganyika, based on living material only.

Species	Number of localities	Depth	Sediment type
Littoral fauna			
Archaeocyprideis tuberculata	5	1.5-8 m	fine sand-gravel
Kavalacythereis braconensis	1	20 m	sand & rocks
Mesocyprideis irsacae	2	1 m	macrophytes/sand
Mesocyprideis pila sp.nov.	3	2-5 m	sand and gravel
Romecytheridea tenuisculpta	1	7 m	sand and rocks
Romecytheridea ampla	1	8 m	sand
Romecytheridea longior sp.nov.	2	1-18 m	sand & shell debris
Tanganyikacythere burtonensis	6	1-20 m	sand
Tanganyikacythere caljoni	1	1 m	sand
Cyprideis spatula sp.nov.	4	5-9.5 m	fine sand, silt
Deep water fauna			
Cyprideis mastai	3	40-90 m	mud
Cyprideis rumongensis	1	50 m	coarse sand
Cyprideis profunda sp.nov.	1	90 m	mud

Nevertheless, bathymetric segregation appears present in both lakes, albeit in a compressed version in Tanganyika. Finally, only phylogenetic analyses will show if the species of *Cyprideis* presently living in Tanganyika are indeed ancestral, or at least belong, to the same monophyletic flock of Tanganyikan endemics. If at least some of the four *Cyprideis* species would turn out to be palaeoendemics, and unrelated to the rest of the flock, the presently recognised flock would be polyphyletic. This can only be investigated by including several non-Tanganyikan *Cyprideis* species in the phylogenetic analysis.

Most species in this flock were thus far found on sand, while two deep-water species of *Cyprideis* occur on mud. However, this factor is closely linked to bathymetry. Most sandy flats in Tanganyika indeed occur in shallow waters, while deep water sediments mostly consist of mud or fine silt. A sediment type presently underrepresented in the collections is rocky slopes. Down to about 30-40 m such habitats can be sampled using SCUBA, but there are presently no good techniques to collect meiobenthos from rocks below 40 m, as most dredges and grabs cannot be used in such conditions and it is too deep to use SCUBA.

Conclusions

The *Cyprideis* species flock in Lake Tanganyika is a potentially very useful model group for both evolutionary studies (especially in comparison to the Baikalian *Cytherissa* flock) and for biodiversity assessments. However, more taxonomic work is urgently required, i.e. (1) collecting additional material, especially from the western (Congolese) shore and from rocky slopes lake wide, (2) alpha-taxonomic descriptions of species and genera, (3) providing illustrated identification keys and (4) integrating molecular and morphological phylogenies. The present paper contributes to the second aim.

References

ALLMON, W.D., 1992. Genera in Paleontology: definition and significance. *Historical Biology*, 6: 149-158.

DUBOIS, A., 1988. The genus in zoology: a contribution to the theory of evolutionary systematics. *Mémoires du Muséum national d'Histoire naturelle*, 140: 1-122.

MARTENS, K., 1994. Ostracod speciation in ancient lakes: a review. In: MARTENS, K., B. GODDEERIS & G. COULTER (eds.), Speciation in Ancient Lakes. *Advances in Limnology*, 44: 203-222.

MARTENS, K., 1997. Review: Speciation in Ancient Lakes. *Trends in Ecology and Evolution*, 12: 177-182.

MARTENS, K., 1998. Sex and ostracods: a new synthesis. In: MARTENS, K. (ed.). Sex and Parthenogenesis – evolutionary ecology of reproductive modes in non-marine ostracods. Backhuys Publ., Leiden: 295-321.

MAYDEN, R.L., 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. In: CLARIDGE, M.F., H.A. DAWAH & M.R. WILSON (eds.), Species. The Units of biodiversity. Chapmann & Hall, N.Y.: 381-424.

MAYR, E., 1969. Principles of systematic zoology. Mc Graw-Hill, N.Y., 429 pp.

MAYR, E., 1970. Populations, species and evolution. Harvard University Press, Cambridge, 453 pp.

MAZEPOVA, G., 1990. Rakushkovye ratchi (Ostracoda) Baikala - Sibirskoe Otdelenie Akademia Nauk SSSR, Novosibirsk, 470 pp.

SCHÖN, I., VERHEYEN, E. & MARTENS,K., in press. Speciation in ancient lake ostracods: comparative analysis of Baikalian *Cytherissa* and Tanganyikan *Cyprideis*. *Verhandlungen der Internationalen Vereins für Limnologie*, 27.

STANLEY, S.M., 1998. Introduction 1998. Macroevolution then and now. In: Stanley S.M., Macroevolution, Pattern and process (2nd ed.). John Hopkins University Press, Baltimore, xiii-xxxviii.

WILEY, E. O., 1981. Phylogenetics. Wiley Interscience, N.Y.

WOUTERS, K., 1988a. On *Romecytheridea tenuisculpta* (ROME). *Stereo-Atlas of Ostracod Shells*, 15(2): 97-100.

WOUTERS, K., 1988b. On *Romecytheridea ampla* WOUTERS sp.nov. *Stereo-Atlas of Ostracod Shells*, 15(2): 101-106.

WOUTERS, K. & MARTENS, K., 1992. Contribution to the knowledge of Tanganyikan cytheraceans, with the description of *Mesocyprideis* nom.nov. (Crustacea, Ostracoda). *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Biologie*, 62: 159-166.

WOUTERS, K. & MARTENS, K., 1994. Contribution to the knowledge of the *Cyprideis* species flock (Crustacea: Ostracoda) of Lake Tanganyika, with the description of three new species. *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Biologie*, 64: 111-128.

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