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Contribution to the knowledge of the *Cyprideis* species flock (Crustacea : Ostracoda) of Lake Tanganyika, with the description of three new species

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Abstract

Three new species of ostracods from Lake Tanganyika are described : *Tanganyikacythere caljoni* sp. nov., *Cyprideis mastai* sp. nov. and *Cyprideis rumongensis* sp. nov. The type species of the genus *Tanganyikacythere* DUCASSE & CARBONEL, 1993, *T. burtonensis*, is extensively redescribed, including the morphology of male and female soft parts which was thus far unknown. Two other species in this genus, *T. banzaensis* DUCASSE & CARBONEL, 1993 and *T. mondegueri* DUCASSE & CARBONEL, 1993, are here formally sunk into synonymy with *T. burtonensis*, which is here for the first time also reported outside Lake Tanganyika. The geographical and ecological distribution of the four species is briefly discussed and some preliminary remarks on the radiation of the *Cyprideis* species flock in Lake Tanganyika are offered.
Key words : taxonomy, morphology, ancient lakes, speciation.

Résumé

Trois nouvelles espèces d'ostracodes du lac Tanganyika sont décrites : *Tanganyikacythere caljoni* sp. nov., *Cyprideis mastai* sp. nov. and *Cyprideis rumongensis* sp. nov. L'espèce-type du genre *Tanganyikacythere* DUCASSE & CARBONEL, 1993, *T. burtonensis*, est redécrite amplement, y compris la morphologie des parties molles mâles et femelles, inconnue jusqu'à présent. Deux autres espèces de ce genre, *T. banzaensis* DUCASSE & CARBONEL, 1993 and *T. mondegueri* DUCASSE & CARBONEL, 1993, sont ici formellement réduites en synonymie avec *T. burtonensis*, signalé ici, pour la première fois, également hors du lac Tanganyika. La distribution géographique et écologique des quatre espèces considérées est discutée brièvement et quelques remarques préliminaires sont proposées concernant la radiation du *Cyprideis* 'species flock' dans le lac Tanganyika.
Mots-clefs : taxonomie, morphologie, lacs anciens, spéciation.

Introduction

Lake Tanganyika is the largest, deepest and oldest lake in the African Rift Valley (COULTER, 1994) and the second largest body of unfrozen freshwater in the world after Lake Baikal. While the average depth of the lake is close to 570 m, with its deepest point being 1470 m, only the top 150-200 m of water are oxygenated. This relatively thin section of the lake therefore harbours all Metazoic life, of which at present close to 1300 species in more than 580 genera are described. It is generally accepted that this constitutes only part of the extant biodiversity. Most taxa are furthermore endemic to the lake, or at least to its drainage basin.With regard to the ostracods, 64 lacustrine species (of which 94 % are endemic) in 16 genera (38 % endemic) have at present been described and reported. MARTENS (1994), however, estimated that not less than 200 species in approximately 25 genera are presently extant. This implies that still a considerable amount of alpha-taxonomical work remains to be done. One of the most important and interesting radiations of Tanganyikan ostracods is formed by the *Cyprideis*-species flock, presently consisting of nine species (all endemic) in six genera (five endemic). The most recent additions to the taxonomy of this species flock were presented by WOUTERS (1979, 1988a, b), WOUTERS & MARTENS (1992) and DUCASSE & CARBONEL (1993, 1994).

The present contribution presents a reassessment of the genus *Tanganyikacythere* DUCASSE & CARBONEL, 1993, a redescription, including description of soft part morphology, of its type species as well as the description of a new species in this genus and of two new species in the related genus *Cyprideis*.

Terminology and abbreviations

As the morphology of the copulatory process of *Cyprideis* and related genera is complex and sometimes difficult to interpret with light microscopy, some descriptive terms for parts of the hemipenis anatomy, possibly of importance for taxonomical discrimination, are here introduced. 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).

On the female abdomen, the size of the furcae (fu) and of the abdominal extremity (AE) are of importance.

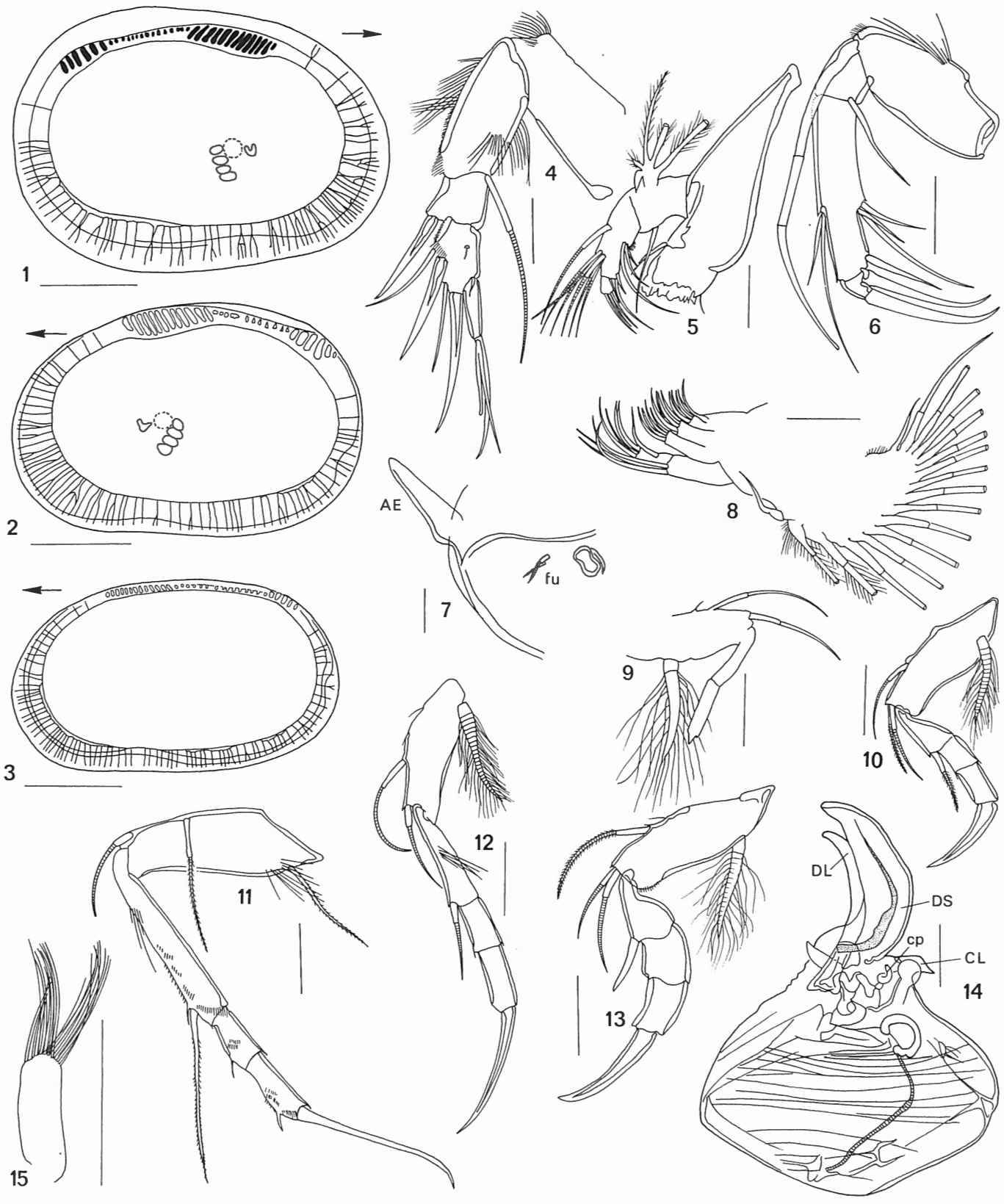


PLATE 1. – Tanganyikacythere burtonensis *Ducasse & Carbonel, 1993. Fig. 1. Female left valve, internal view (O.C. 1730); Fig. 2. Female right valve, internal view (O.C. 1730); Fig. 3. Male right valve, internal view (O.C. 1724); Fig. 4. Female antenna (O.C. 1730); Fig. 5. Female mandible (O.C. 1730); Fig. 6. Male antenna (O.C. 1724); Fig. 7. Abdominal extremity, female (O.C. 1730); Fig. 8. Maxilulla, male (O.C. 1724); Fig. 9. Right second leg, male (O.C. 1724); Fig. 10. Left first leg, male (O.C. 1724); Fig. 11. Third leg, male (O.C. 1724). Fig. 12. Left second leg, male (O.C. 1724); Fig.13. Right first leg, male (O.C. 1724); Fig. 14. Hemipenis (O.C. 1724); Fig. 15. Brush-like organ (O.C. 1724). Scales : Fig. 1-3 : 200 µm; Fig. 4-14 : 50 µm.*

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 **Tanganyikacythere**
DUCASSE & CARBONEL, 1993

AMENDED DIAGNOSIS

Remark : the present diagnosis amends the original one mainly in soft part anatomy. In order to serve the needs of the present paper, the characters are here presented in contrast to those of the genus *Cyprideis*.
Valves with spherical appearance (more elongated in *Cyprideis*). Hinge in right valve completely positive or with maximum 2-3 small sockets in the anterior part of the median element (this negative part in right valve much larger in *Cyprideis*). Fused zone wider than in *Cyprideis*, with many long, sometimes branched, pore canals.
Females with small furcae (larger in *Cyprideis*); abdominal extremity (AE) wedge-shaped (crescent-shaped in *Cyprideis*). Males with first and especially second walking limbs highly dimorphic; first legs less dimorphic than in *Cyprideis*. Hemipenis with central lobe (CL) small, hook-like (large and club-shaped in *Cyprideis*).

Tanganyikacythere burtonensis
DUCASSE & CARBONEL, 1993
(Pl. 1, Fig. 1-14, Pl. 5, Fig. 1-19)

SYNONYMY

Tanganyikacythere burtonensis nov.sp. - DUCASSE & CARBONEL, 1993, p. 434-436, pl. 1, fig. 1, pl. 2, figs 1-4.
Tanganyikacythere banzaensis nov.sp. - DUCASSE & CARBONEL, 1993, p. 438-439, pl. 2, figs 5-8, pl. 3, figs. 1-7.
Tanganyikacythere mondegueri nov.sp. - DUCASSE & CARBONEL, 1993, p. 440-443, pl. 4, figs 1-7.

MATERIAL

Lake Tanganyika : 7 dissected males and 8 dissected females (O.C. 1724 - O.C. 1739); 70 females and 7 males preserved in alcohol (O.C. 1745 - O.C. 1747).
Lake Mobutu Sese Seko (= ex Lake Albert) : 3 dissected males and two dissected females (O.C. 1740 - O.C. 1744); 11 females and 15 males preserved in alcohol (O.C. 1768 - O.C. 1769).

Figured specimens :
Lake Tanganyika, Burundi :
O.C. 1724, 1726, 1728, 1729 : Road Bujumbura-Rumonge, Km 117, near Cape Mvugo, depth : 4.5 m, leg. A. CALJON, 17 Febr. 1990 (station 900).
O.C. 1730, 1731 : Karonda Village, depth 1 m, in bamboo stand, leg. K. MARTENS, 26 Sept. 1991 (sample LT 91/12).
Lake Tanganyika, Tanzania :
O.C. 1736 : bay S. of Cape Kibwesa, depth : 20 m, leg. K. MARTENS & B. GODDEERIS, 30 May 1992 (sample LT 92/24).
Lake Mobutu Sese Seko (= ex Lake Albert), Zaire :
O.C. 1740, 1744 : Kasenyi, depth 0.1 m, between algae, leg. J. VERBEKE, 12 Dec. 1953 (station C4051a).

DIAGNOSIS

Female valves spherical; right valve with completely positive hinge. Postero-ventral inner lamella not notably wider. Hemipenis with both distal shield and distal lobe crescent-shaped.

DESCRIPTION

Medium-sized, very thick and heavily calcified carapaces; general appearance spherical; right valves markedly lower than left ones, especially in females. Valves completely smooth and shiny, except for a few small and shallow pits, the latter not always visible.
Female valves (Pl. 1, Fig. 1, 2; Pl. 5, Fig. 1-4, 7-10, 13, 15) : dorsal margin more or less convex; parts of the dorsal margin sometimes nearly straight; anterior and posterior margins broadly rounded, with almost no marked transitions between the dorsal and ventral margins; ventral margin slightly convex to almost straight, with an antero-ventral concavity in the right valve; dorsal and ventral margins tapering towards the anterior; maximum height in posterior third of the valves; carapace in dorsal view with pointed anterior and rounded posterior extremity; largest width situated posteriorly, giving the carapace an inflated appearance (brood pouch).
Male valves (Pl. 1, Fig. 3; Pl. 5, Fig. 5, 6, 11, 12, 14) : more elongate, i.e. less high than female ones; dorsal and ventral margins only slightly convex, and nearly parallel; carapace in dorsal view with pointed anterior and posterior extremities and slightly convex, nearly parallel lateral margins.Inner lamella moderately wide in the female, much less so in the male. Numerous straight, sometimes bifurcated marginal pore canals (see Pl. 1, Fig. 1, 2, 3); very indistinct small (sometimes absent) vestibula in the antero-ventral and postero-ventral areas. Muscle scar pattern consisting of a row of

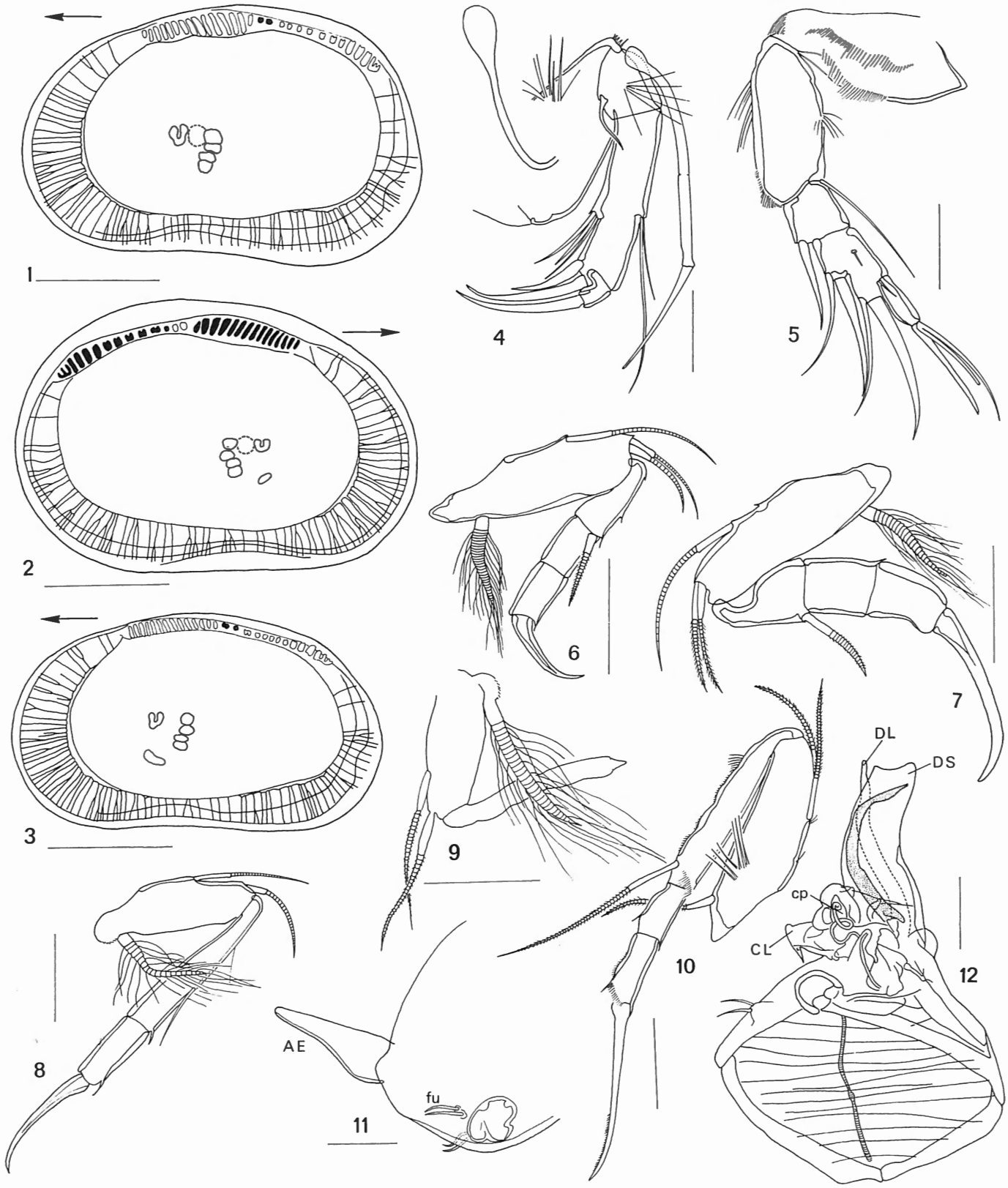


PLATE 2. – Tanganyikacythere caljoni *sp. nov., Lake Tanganyika, Burundi, Karonda Village. Fig. 1. Right valve, internal view, female, allotype (O.C. 1749); Fig. 2. Left valve, internal view, female, paratype (O.C. 1750); Fig. 3. Right valve, internal view, male, holotype (O.C. 1748). Fig.4. Antenna, holotype; Fig. 5. Antennule, holotype : Fig. 6. Left first leg, holotype; Fig. 7. Right first leg, holotype; Fig. 8. Left second leg, holotype; Fig. 9. Right second leg, holotype; Fig. 10. Third leg, holotype; Fig. 11. Abdominal extremity, allotype; Fig. 12. Hemipenis, holotype. Scales : Fig. 1-3 : 200 µm; Fig. 3-12 : 50 µm.*

four oval adductor scars, a V-shaped frontal scar, and a nearly circular fulcral point. Hinge strongly developed in the female, much less so in the male. Hinge completely positive in the right valve and negative in the left one. Right valve : anterior element of hinge consisting of about twelve large, elongated, obliquely oriented toothlets; median element consisting of about 12 to 15 small toothlets; posterior element consisting of about six, obliquely oriented elongate toothlets, the latter smaller than those of the anterior element. Hinge of left valve complementary, with a comparable number of sockets. Anterior and posterior elements of male hinge much less developed, i.e. with smaller toothlets (Pl. 1, Fig. 1-3; Pl. 5, Fig. 16-19).

Antennule (Pl. 1, Fig. 4) : composed of five segments, generally stout and broad. First segment about the same width and length as the second segment. Both of these segments set with brushes consisting of long fine hairs, second segment furthermore with a long ringed distal seta reaching beyond the tip of the terminal segment. Third segment subquadrangular, with a stout antero-distal claw. Fourth segment oblong, of an irregular shape, set with six setae : four anterior setae consisting of two fine setae and two claws and two additional very short setae, one on the outer lateral surface, near mid-length, the other near the postero-distal corner. Fifth segment narrow, rectangular, distally with one weakly developed claw and a bifurcate aesthetasc, the latter slightly longer than half the accompanying seta.

Antenna (Pl. 1, Fig. 6) with four segments and a large three-segmented exopodite; second segment small, with one ventro-distal seta; third segment long and narrow, with two antero-median setae, and two short postero-median setae and a very long aestethasc. Terminal segment minute, set with two strong claws.

Mandible (Pl. 1, Fig. 5) with a stout and broad coxa, without special features; palp indistinctly four-segmented; first segment with respiratory plate bearing two long, one medium-sized and two very short rays. For setation of other segments, see Pl. 1, Fig. 5.

Maxillule (Pl. 1, Fig. 8) with a large respiratory plate bearing 17 rays, a two-segmented palp and three endites. First palp segment with four ringed setae; second palp segment with one lateral and four distal setae. Endites with an unknown number of distal setae; first endite with a large and stout lateral seta.

First leg a four-segmented walking limb; first segment almost as large as three terminal segments combined, bearing two knee-setae, one dorsal seta and a large root-like plumose and ringed ventral seta. Second segment with a long distal seta and terminal segment with a stout claw. This leg dimorphic in males : right leg (Pl. 1, Fig. 13) with broader and heavier second, third and fourth segments, and with slightly shorter distal seta on second segment; left leg (Pl. 1, Fig. 10) as in the female.

Second leg strongly dimorphic in the male. Left second leg (Pl. 1, Fig. 12) as in the female, with elongate and slender segments; first segment with one dorsal seta, one knee-seta and large root-like plumose and ringed ventral seta. Second segment with one distal seta and fourth segment with long and slender claw. Male right second leg (Pl. 1, Fig. 9) with normal, although less chitinized first segment but with segments two and three strongly reduced and weakly chitinized.

Third leg (Pl. 1, Fig. 11) not dimorphic; first segment with one dorsal seta, one knee-seta and one normal ventral seta (not root-like as in other legs) : second segment very elongate, with long distal seta, reaching slightly beyond the tip of the terminal segment; fourth segment with long and terminally curved claw.

Hemipenis (Pl. 1, Fig. 14) with a large muscular basal part and a distal copulatory complex consisting of a crescent-shaped distal shield (DS), a crescent-shaped distal lobe (DL), a rounded and rather indistinct copulatory process (CP) and a small hook-like central lobe (CL). At the proximal side of this central lobe, a club-like thickening is implanted on the distal part of the basal muscular body.

Brush-like organs (Pl. 1, Fig. 15) elongate, each set with numerous long fine apical hairs.

Abdominal extremity in the female (Pl. 1, Fig. 7) a wedge-shaped process; furcae small.

MEASUREMENTS

Males :	L	0.68-0.71 mm
	H	0.38-0.44 mm
Females :	L	0.68-0.80 mm
	H	0.44-0.56 mm

REMARKS

The present species is a brooder. In four of the dissected females the postero-dorsal pouch contained eggs and nauplii : 6 eggs in no. O.C. 1727, 8 eggs and 4 nauplius larvae in O.C. 1729, 10 eggs in O.C. 1784 and 3 eggs in O.C. 1736.

OCCURRENCE

Tanganyikacythere burtonensis is a common species in Lake Tanganyika. It has been described by DUCASSE & CARBONEL (1993) from Burton Bay (Zaire). In our collections we have large amounts of empty valves and carapaces from different localities in the lake. Living specimens, however, are far less common. Specimens with preserved limbs, and which were hence living in situ at the time of collecting, were found at the following localities.

Burundi : near Cape Mvugo (depth 4.5 m and 20 m, leg. : A. CALJON, 16 Febr. 1990) and near Karonda (depth 1 m, on sand) (leg. : K. MARTENS, 26 Sept. 1991).

Tanzania : swampy area directly north of cliff between

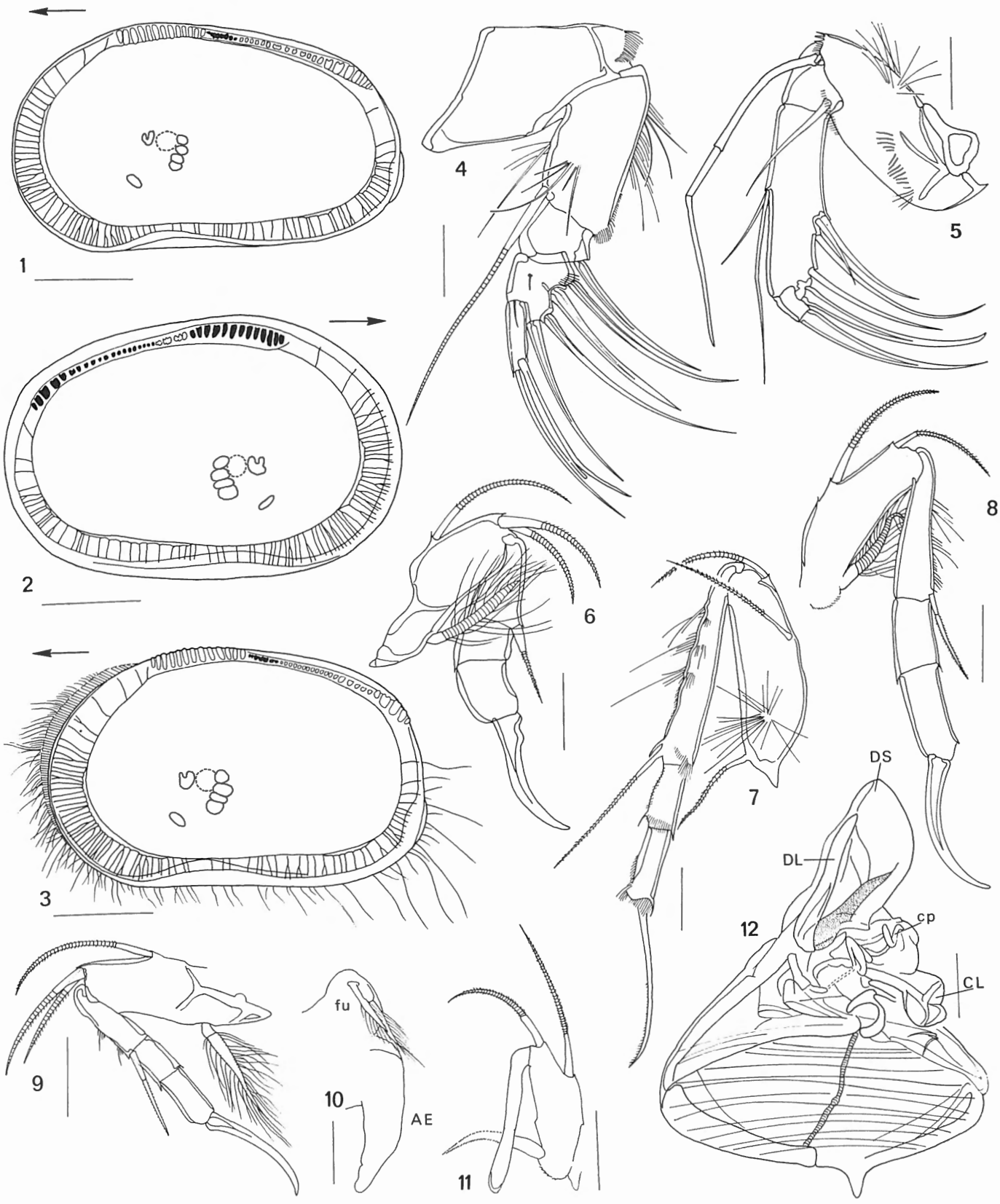


PLATE 3. – Cyprideis mastai *sp. nov., Lake Tanganyika, Burundi, off delta of river Nyengwe. Fig. 1. Right valve, internal view, male, holotype (O.C. 1753); Fig. 2. Left valve, internal view, female, allotype (O.C. 1754); Fig. 3. Right valve, internal view, female, allotype; Fig. 4. Antennule, holotype; Fig. 5. Antenna, holotype; Fig. 6. Right first leg, holotype; Fig. 7. Third leg, holotype; Fig. 8. Left second leg, holotype; Fig. 9. Left first leg, holotype; Fig. 10. Abdominal extremity, female, paratype (O.C. 1756). Fig. 11. Right second leg, holotype; Fig. 12. Hemipenis, holotype. Scales : Fig. 1-3 : 200 µm; Fig. 4-12 : 50 µm.*

Kungwe and Kabogo (S 5°40'185", E 29°53'272") (depth 7 m, on fine sand) and in a bay south of Cape Kibwesa (depth 20 m, on sand) (leg. K. MARTENS & B. GODDEERIS, 1992).
Zambia : Bay of the river Luvu, dredged at a depth of 8 to 15 m (leg. L. STAPPERS, 1913).
Finally, the species also occurs in Lake Mobutu Sese Seko (= ex Lake Albert). It was collected near Kasenyi, by J. VERBEKE in 1953 at a depth of 0.1 m. These specimens are somewhat less spherical in outline, and less strongly calcified (Pl. 5, Fig. 9-12). In soft parts anatomy, and more in particular in the structure of the copulatory organ, however, there are no differences with the specimens from Lake Tanganyika.
The depth distribution of the species, as can be judged from the available living material, seems to be between 0.1 m and 20 m.

DISCUSSION

Tanganyikacythere burtonensis is the type species of the genus *Tanganyikacythere*. In comparison with *T. caljoni* sp. nov. it has a completely positive hinge in the right valve, and can therefore easily be distinguished from it (see also discussion under *T. caljoni* and general discussion). DUCASSE & CARBONEL (1993) described three distinct species from Burton Bay, namely *T. burtonensis, T. banzaensis* and *T. mondegueri*. These species are synonymized here because we were unable to clearly and unequivocally separate them. The most important characteristics used by DUCASSE & CARBONEL (1993) to distinguish these taxa are the shape and the size. It is obvious that there is a high degree of variability, but we observed all possible intermediates between the shapes of the species of DUCASSE & CARBONEL. As far as the size is concerned, our material as a whole is furthermore smaller than the measurements reported by them. The largest specimen in our collection is 0.80 mm long, the smallest 0.68 mm long. The highest and lowest value mentioned by DUCASSE & CARBONEL is 0.89 mm (for *T. burtonensis*) and 0.68 (for *T. mondegueri*). The distinction between the three species on the basis of shape and size was not statistically analyzed, and hence is difficult to interpret. On the basis of the soft parts, finally, we were unable to see differences between the specimens presumably belonging to the three species. We therefore accept *T. burtonensis* as representing a single variable species. Whether this variation is environmentally or genetically induced is not yet clear, and certainly needs further research. It is furthermore not at all surprising to encounter a highly variable species in a genus which is closely related to the genus *Cyprideis*.

Tanganyikacythere caljoni sp. nov.
(Pl. 2, Fig. 1-12, Pl. 6, Fig. 1-8, Pl. 8, Fig. 9)

Derivation of name : the species is named after the late Dr. A. CALJON, who collected part of the material studied in this paper, in appreciation of his valuable contributions to the limnology and algology of Lake Tanganyika.
Type locality : Lake Tanganyika, Burundi, Bay in front of Karonda Village, depth 1 m, in bamboo stand, collected with handnet (leg. K. MARTENS, 26 Sept. 1991, station no. LT91/12).
Holotype : a male with valves (O.C. 1748a) and dissected limbs (O.C. 1748b). Allotype : a female with valves (O.C. 1749a) and dissected limbs (O.C. 1749b).
Paratypes : two dissected females (O.C. 1750 and 1751) and 11 females and 6 males preserved in alcohol (O.C. 1752).

DIAGNOSIS

Female valves less spherical than in the preceding species; right valve with a short antero-median negative element in the hinge (2-3 sockets). Postero-ventral inner lamella wider. Hemipenis with distal shield narrow and apically truncate, distal lobe slender and weakly sinuous.

DESCRIPTION

Medium-sized, very thick and heavily calcified carapaces, general appearance sub-spherical. Right valve lower than left one, especially in the female. Valves covered with small shallow pits in the central area.
Female valves (Pl. 2, Fig. 1-2; Pl. 6, Fig. 2, 3, 5) : dorsal margin convex in left valve, with broadly rounded anterior and posterior margin; ventral margin weakly convex; dorsal margin in right valve less convex, and with subtruncate posterior margin; ventral margin slightly concave; carapace in dorsal view oval, with pointed anterior and rounded posterior extremity; maximum width just behind the middle.
Male valves (Pl. 2, Fig. 3; Pl. 6, Fig. 1, 4) more elongate than female ones; carapace in dorsal view oval, with evenly curved lateral margins; largest width in the middle.
Inner lamella broad, with a characteristic widening of this lamella in the postero-ventral area. Hinge of right valve not completely positive. Long anterior element with oblong, obliquely oriented toothlets. Median element consisting of two parts, an antero-median part with two or three small sockets (negative) and a postero-median element consisting of a few small toothlets (positive). Transition from postero-median element to posterior element indistinct. Posterior element consisting of relatively small, weakly bifid toothlets. Left valve hinge complementary (Pl. 2, Fig. 1; Pl. 6, Fig. 6-8).

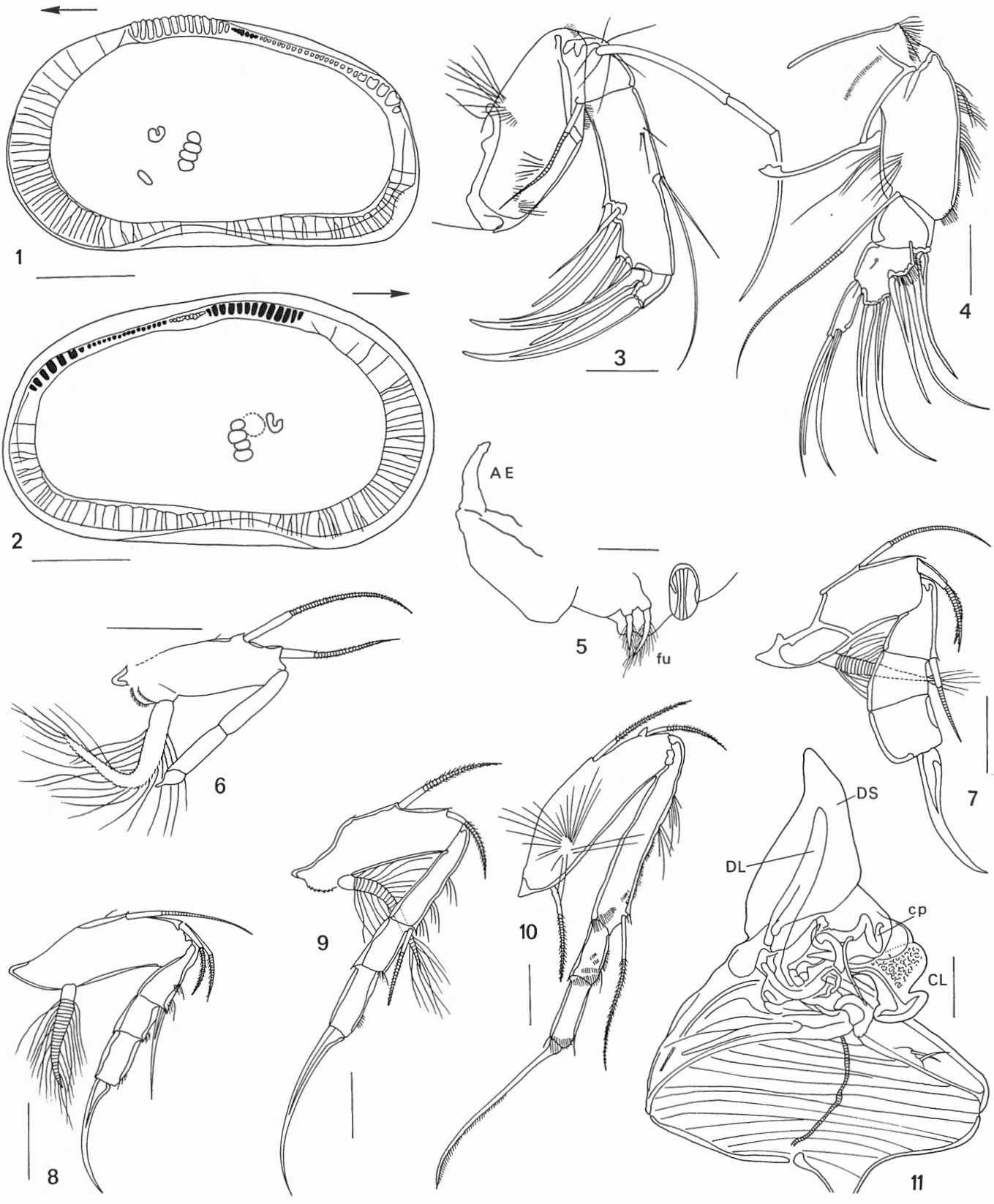


PLATE 4. – Cyprideis rumongensis *sp. nov., Lake Tanganyika, Burundi, off delta of river Dama, near Rumonge. Fig. 1. Right valve, internal view, female, allotype (O.C. 1766); Fig. 2. Left valve, internal view, allotype; Fig. 3. Antenna, holotype (O.C. 1765). Fig. 4. Antennule, holotype; Fig. 5. Abdominal extremity, allotype. Fig. 6. Right second leg, holotype; Fig. 7. Right first leg, holotype; Fig. 8. Left first leg, holotype; Fig. 9. Left second leg, holotype. Fig. 10. Third leg, holotype; Fig. 11. Hemipenis, holotype. Scales : Fig. 1-2 : 200* μm*; Fig. 3-11 : 50* μm.

Antennule (Pl. 2, Fig. 5) : five-segmented with first and second segment of sub-equal size; distal seta of second segment reaching to the middle of the fifth segment; medio-lateral and antero-dorsal setae of fourth segment very small; aesthetasc of fifth segment almost as long as the weakly developed claw.
Antenna (Pl. 2, Fig. 4) : four-segmented; distal seta on second segment short; exopodite three-segmented : terminal claws relatively short.
First leg dimorphic in the male; left leg (Pl. 2, Fig. 6) slender as in the female, second, third and fourth segments of right leg (Pl. 2, Fig. 7) slightly broader than in left leg; terminal claw in right leg twice as long as in left leg.
Second leg dimorphic in the male; right leg (Pl. 2, Fig. 9) strongly reduced and weakly scleritized; first segment as in the female, the following two segments (indistinctly sutured) small and delicate. Left leg (Pl. 2, Fig. 8) normal.
Third leg (Pl. 2, Fig.10) : not dimorphic, long and slender, and with a long and weakly curved terminal claw.
Hemipenis (Pl. 2, Fig. 12) : distal shield narrow and apically truncate; distal lobe slender and weakly sinuous; copulatory process lobed; central lobe small and hook-like, with a sharp postero-ventrally oriented beak-like projection.
Female abdominal extremity (Pl. 2, Fig. 11) with a wedge-shaped process; furcae small.

MEASUREMENTS

Holotype :
Left valve : L 0.63 mm, H 0.38 mm
Right valve : L 0.63 mm, H 0.36 mm
Allotype :
Left valve : L 0.68 mm, H 0.47 mm
Right valve : L 0.67 mm, H 0.44 mm
Paratypes :
Females : L 0.65-0.69 mm, H 0.44-0.47 mm
Males : L 0.62-0.65 mm, H 0.36-0.40 mm

REMARKS

The present species is a brooder. In one of the dissected females the postero-dorsal pouch contained 9 eggs and 4 nauplii (O.C. 1750, paratype).

OCCURRENCE

Tanganyikacythere caljoni sp. nov. is known from the type locality only, Karonda (Burundi), where the species was collected with a handnet in a bamboo stand on sand, at a depth of 1 m (leg. K. MARTENS, 26 Sept. 1991), and where it occurs together with *Tanganyikacythere burtonensis.*

DISCUSSION

Tanganyikacythere caljoni sp. nov. differs from the type species, *T. burtonensis,* in the shape of the valves, which is less spherical, by the subtruncate posterior extremity, particularly in the right valve, and probably also by the shallow pits on the lateral surface. The inner lamella has a characteristic widening in the postero-ventral area, which can easily be observed in transmitted light, even when the valves are closed. Furthermore, the hinge is not completely positive or negative as in *T. burtonensis.* The short median element is divided in an antero- and a postero-median element. The antero-median element consists of a few toothlets in the left valve and sockets in the right one. Finally, *T. caljoni* has an apically truncate distal shield, whereas this shield is crescent-shaped in *T. burtonensis.*

Genus **Cyprideis** JONES, 1857

Cyprideis mastai sp. nov.
(Pl. 3, Fig. 1-12, Pl. 7, Fig. 1-9)

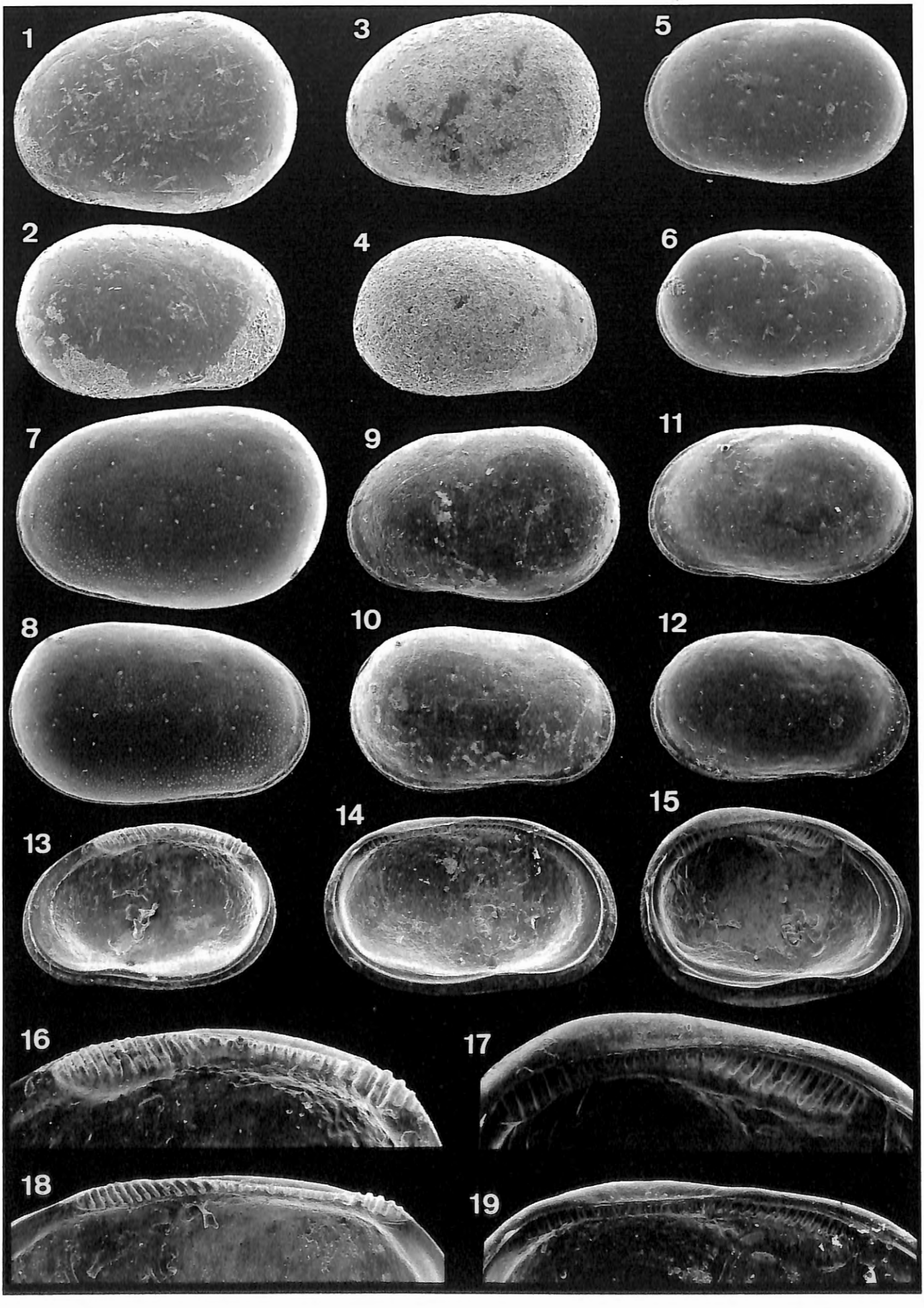
Derivation of name : in honour of Dr. Mukwaya Gashagaza MASTA (Centre for Research in Natural Sciences, Uvira, Zaire), who managed to maintain a high standard of scientific research in his institute, even during the most difficult of times.
Type locality : Lake Tanganyika, Burundi, in front of delta of river Nyengwe, depth 40 m (leg. K. MARTENS, 25 Sept. 1991, station LT91/10).
Holotype : a male specimen with valves (O.C. 1753a) and dissected limbs (O.C. 1753b).
Allotype : a female specimen with valves (O.C. 1754a) and dissected limbs (O.C. 1754b).
Paratypes : three dissected males and two dissected females (O.C. 1755-1759), 28 empty valves and carapaces (O.C. 1760-1762) and 6 females preserved in alcohol (O.C. 1763-1764).

DIAGNOSIS

Valves subtrapezoidal, with posterior end truncate. Hemipenis with distal shield irregularly triangular, apically rounded; central lobe large and club-shaped, with chitinized bands. Valves smooth and shiny, sometimes very finely pitted.

DESCRIPTION

Large, elongate, sub-trapezoidal thick valves; valve surface smooth and shiny; in some specimens rare and very shallow pits. Left valve somewhat higher than right one. Female valves (Pl. 3, Fig. 2, 3; Pl. 7, Fig. 2, 3) : left valve with weakly tapering dorsal and ventral margins; dorsal margin convex to almost straight, ventral margin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straight, anterior and posterior margins broadly rounded; right valve with parallel dorsal and ventral margins, almost straight dorsal margin and straight ventral margin with concavity in oral region; anterior margin broadly rounded, posterior margin somewhat truncate. Carapace in dorsal view somewhat wedge-shaped with weakly convex lateral margins and with largest width situated posteriorly, at about 4/5 of the length.

Male valves (Pl. 3, Fig. 1; Pl. 7, Fig. 1, 4-6) : less high than female ones, and with dorsal and ventral margins tapering towards the posterior in both the left and the right valve; dorsal and ventral margins nearly straight; anterior and posterior margins broadly rounded in left valve; right valve with broadly rounded anterior margin and with oblique, somewhat truncate posterior margin. Carapace in dorsal view with evenly convex lateral margins and with the largest width situated in the middle.

Inner lamella moderately wide, with numerous, sometimes branched marginal pore canals (see Pl. 3, Fig. 1-3). Hinge tripartite and consisting of anterior, median and posterior elements; median element bipartite. Hinge of right valve : anterior element : about thirteen toothlets; antero-median element : five to seven small indistinctly delineated sockets; postero-median element : a large number of small toothlets; transition between postero-median element and posterior element indistinct; posterior element consisting of five to six slightly bifid toothlets. Left valve hinge complementary (Pl. 3, Fig. 1-3; Pl. 7, Fig. 7-9).

Antennule (Pl. 3, Fig. 4) five-segmented; first segment short and broad; third and fourth segments short; antero-distal seta of second segment long, reaching to the middle of the terminal claw; posterior setae of third and fourth segments long, with claw-like appearance.

Antenna (Pl. 3, Fig. 5) : four-segmented, with three-segmented exopodite; claws and setae of third and fourth segments long and slender; terminal claw long.

First leg : dimorphic in the male : left leg (Pl. 3, Fig. 9) slender, as in the female; right leg (Pl. 3, Fig. 6) with broad second, third and fourth segments; fourth segment subquadrate, and much broader than base of terminal claw.

Second leg : dimorphic in the male; right leg (Pl. 3, Fig. 11) strongly reduced and weakly scleritized; first segment of same size as in the female, the following two segments (indistinctly sutured) small and delicate; left leg (Pl. 3, Fig. 8) normal.

Third leg (Pl. 3, Fig. 7) : not dimorphic, long and slender, set with bundles of hairs, and with long, slightly curved slender terminal claw.

Hemipenis (Pl. 3, Fig. 12) : distal shield large and irregularly triangular; distal lobe almost straight to weakly sinuous; copulatory process rounded and somewhat lobed; central lobe large and club-shaped, with chitinized bands.

Female abdominal extremity (Pl. 3, Fig. 10) crescent-shaped, with large furcae.

MEASUREMENTS

Holotype :
Left valve : L 0.82 mm, H 0.49 mm
Right valve : L 0.81 mm, H 0.46 mm
Allotype :
Left valve : L 0.79 mm, H 0.54 mm
Right valve : L 0.82 mm, H 0.49 mm
Paratypes :
Males : L 0.77-0.84 mm, H 0.45-0.51 mm
Females : L 0.75 - 0.83 mm, H 0.47 - 0.55 mm

REMARKS

The present species is a brooder. In two of the dissected females the postero-dorsal pouch contained eggs : 10 eggs in O.C. 1754 (allotype) and 11 eggs in O.C. 1757 (paratype).

OCCURRENCE

Cyprideis mastai sp. nov is known from three localities.
Burundi : off the delta of the river Nyengwe, dredged at a depth of 40 m on sandy mud, and off Karonda village, dredged at a depth of 50 m on mud (leg. K. MARTENS, 25 and 26 Sept. 1991).
Tanzania : bay S. of Cape Kibwesa, collected with a PONAR sampler at a depth of 90 m on mud (leg. K. MARTENS & B. GODDEERIS, 29 May 1992).

DISCUSSION

Cyprideis mastai sp. nov. differs from *C. rumongensis* sp. nov. by its subtrapezoidal valves, with truncate posterior margin in the female right valve. It also differs by the structure of the hemipenis. Only a limited

◁ PLATE 5. – Tanganyikacythere burtonensis *Ducasse & Carbonel, 1993. Fig. 1 - 7 and 13 - 19 : Lake Tanganyika; Fig. 9 - 12 : Lake Mobutu Sese Seko (= ex Lake Albert). Fig. 1. Left valve, female (O.C. 1730); Fig. 2. Right valve, female (O.C. 1730); Fig. 3. Left valve, female (O.C. 1726); Fig. 4. Right valve female (O.C. 1726); Fig. 5. Left valve, male (O.C. 1731); Fig. 6. Right valve, male (O.C. 1731); Fig. 7. Left valve, female (O.C. 1736); Fig. 8. Right valve, female (O.C. 1736); Fig. 9. Left valve, female (O.C. 1744); Fig. 10. Right valve, female (O.C. 1744); Fig. 11. Left valve, male (O.C. 1740); Fig. 12. Right valve, male (O.C. 1740); Fig. 13. Right valve, internal view, female (O.C. 1729); Fig. 14. Left valve, internal view, male (O.C. 1728); Fig. 15. Left valve, internal view, female (O.C. 1729); Fig. 16. Hinge, right valve, female (O.C. 1729); Fig. 17. Hinge, left valve, female (O.C. 1729); Fig. 18. Hinge, right valve, male (O.C. 1728); Fig. 19. Hinge, left valve, male (O.C. 1728). Magnifications : Fig. 1-15 : 68 X; Fig. 16-19 : 150 X.*

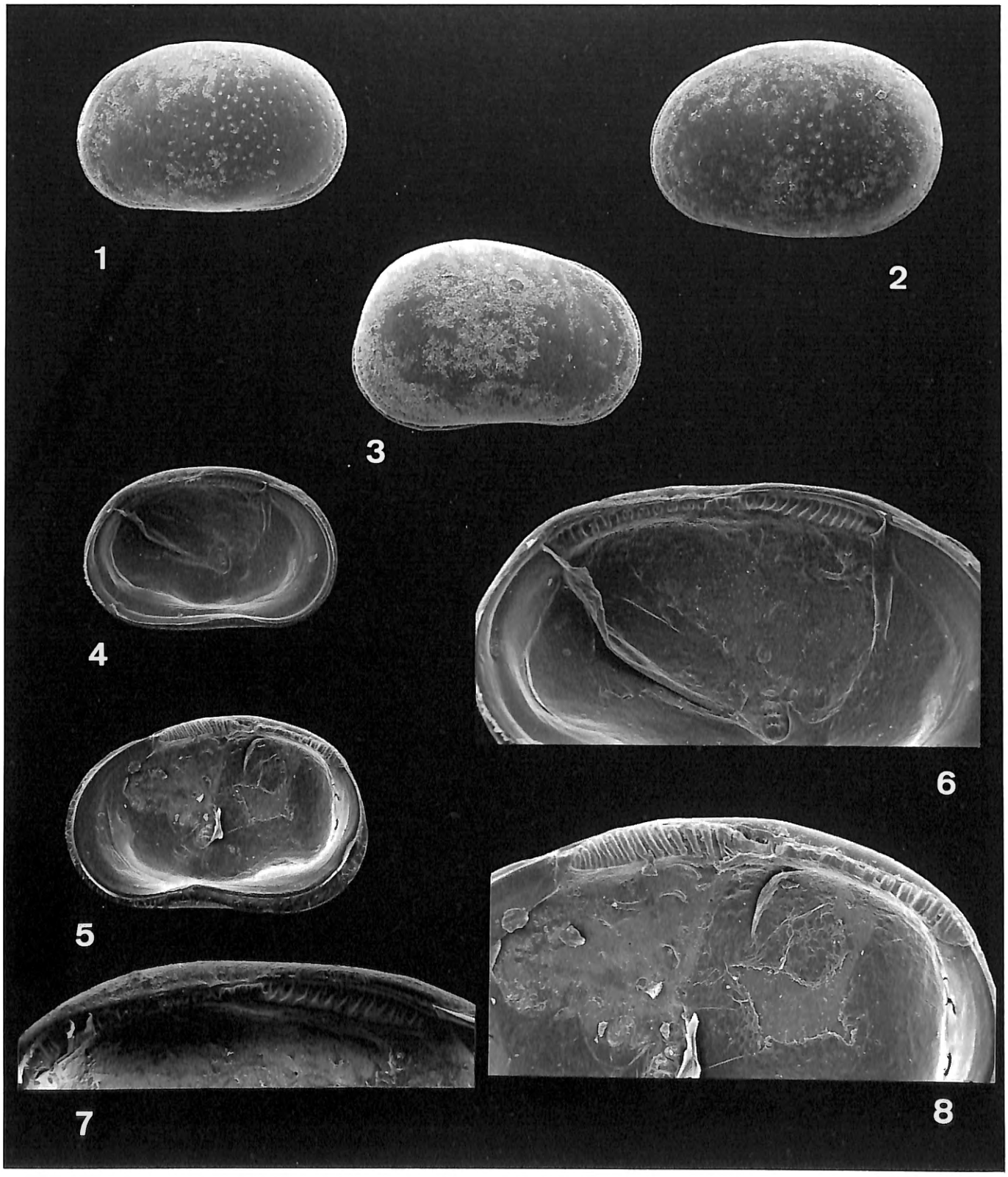

PLATE 6. – Tanganyikacythere caljoni *sp. nov. Lake Tanganyika, Burundi, Karonda Village. Fig. 1. Left valve, male, holotype (O.C. 1748); Fig. 2. Left valve, female, paratype (O.C. 1750); Fig. 3. Right valve, female, allotype (O.C. 1749); Fig. 4. Left valve, internal view, holotype; Fig. 5. Right valve, internal view, female, paratype (O.C. 1750); Fig. 6. Hinge, left valve, holotype. Fig. 7. Hinge, left valve, female, paratype (O.C. 1751); Fig. 8. Hinge, right valve, female, paratype (O.C. 1750). Magnifications : Fig. 1-5 : 70 X; Fig. 6-8 : 160 X.*

number of specimens of this new species was found, and maybe there is more variability in the valves than is shown by this material.

Cyprideis rumongensis sp. nov.
(Pl. 4, Fig. 1-11, Pl. 8, Fig. 1-8)

Derivation of name : after the village of Rumonge (Burundi).
Type locality : Lake Tanganyika, Burundi, delta of river Dama, near Rumonge, depth 50 m, coarse sand with algae (leg. K. MARTENS, 26 Sept. 1991, station LT 91/21).
Holotype : a male specimen with valves (O.C. 1765a) and dissected limbs (O.C. 1765b).
Allotype : a female specimen with valves (O.C. 1766a) and dissected limbs (O.C. 1766b).
Paratype : a male empty carapace (O.C. 1767).

DIAGNOSIS

Valves subtrapezoidal, but relatively more elongated. Hemipenis with distal shield subtriangular, distally bluntly pointed; central lobe large and club-shaped, with posterior semi-oval shield-like widening with rough surface. Type population with external valve surface pitted.

DESCRIPTION

Large, elongate, subtrapezoidal, thick valves; valve surface with shallow pits, mostly in the central region, and with knob-like swellings in the antero-dorsal and the dorso-median area. Left valve somewhat larger than right one. Dorsal and ventral margins tapering towards the posterior.
Male valves (Pl. 8, Fig. 1, 3, 4) : dorsal margin weakly convex; ventral margin nearly straight; anterior margin broadly rounded; posterior margin narrow and obliquely rounded.
Female valves (Pl. 4, Fig. 1-2; Pl. 8, Fig. 2, 5) somewhat higher than male valves, and dorsal and ventral margin less tapering.
Female carapace ovoid in dorsal view, with pointed anterior and rounded posterior extremity; maximal width near the posterior two third of the length; male carapace with pointed extremities and nearly parallel lateral margins; maximal width near the middle.
Inner lamella moderately wide, with numerous, sometimes branched marginal pore canals (see Pl. 4, Fig. 1 and 2). Hinge tripartite, and consisting of anterior, median and posterior element; median element bipartite. Hinge of right valve : anterior element : about 13 toothlets; antero-median element : an indistinct number (about 10) of partially fused small sockets; postero-median element about 17 small toothlets : posterior element 5 to 6 weakly bifid toothlets; the transition between the toothlets of the postero-median element and the toothlets of the posterior element is not clearly separated. Hinge of left valve complementary (Pl. 8, Fig. 6-9).
Antennule (Pl. 4, 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. 4, Fig. 3) four-segmented with three-segmented exopodite; terminal segment small with two strong claws.
First leg dimorphic in the male; left leg (Pl. 4, Fig. 8) as in the female, with slender segments; right leg (Pl. 4, Fig. 7) with broad second, third and fourth segment; fourth segment squarish and much broader than base of terminal claw.
Second leg strongly dimorphic in the male; left leg (Pl. 4, Fig. 9) as in the female, but right leg (Pl. 4, Fig. 6) strongly reduced and weakly sclerotized; terminal segments small and delicate and indistinctly three-segmented.
Third leg (Pl. 4, Fig. 10) not dimorphic, elongate and hirsute, with long, slightly curved slender terminal claw.
Hemipenis (Pl. 4, Fig. 11) with triangular distal shield, dorsal margin sinuous with distal concavity and convex ventral margin; distal process almost straight to slightly sinuous : copulatory process rounded and indistinctly lobed; central lobe large and club-shaped, with posterior semi-oval shield-like widening with rough surface.
Abdominal extremity in the female (Pl. 4, Fig. 5) crescent-shaped, with large furcae.

MEASUREMENTS

Holotype :
Left valve : L 0.85 mm, H 0.43 mm
Right valve : L 0.83 mm, H 0.43 mm
Allotype :
Left valve : L 0.89 mm, 0.51 mm
Right valve : L 0.87 mm, H 0.48 mm
Paratype :
Left valve : L 0.86 mm, H 0.47 mm

OCCURRENCE

Cyprideis rumongensis sp. nov. is known from the type locality only, namely the delta of the river Dama, near Rumonge, where it was dredged at a depth of 50 m on coarse sand and algae (leg. K. MARTENS, 26 Sept. 1991).

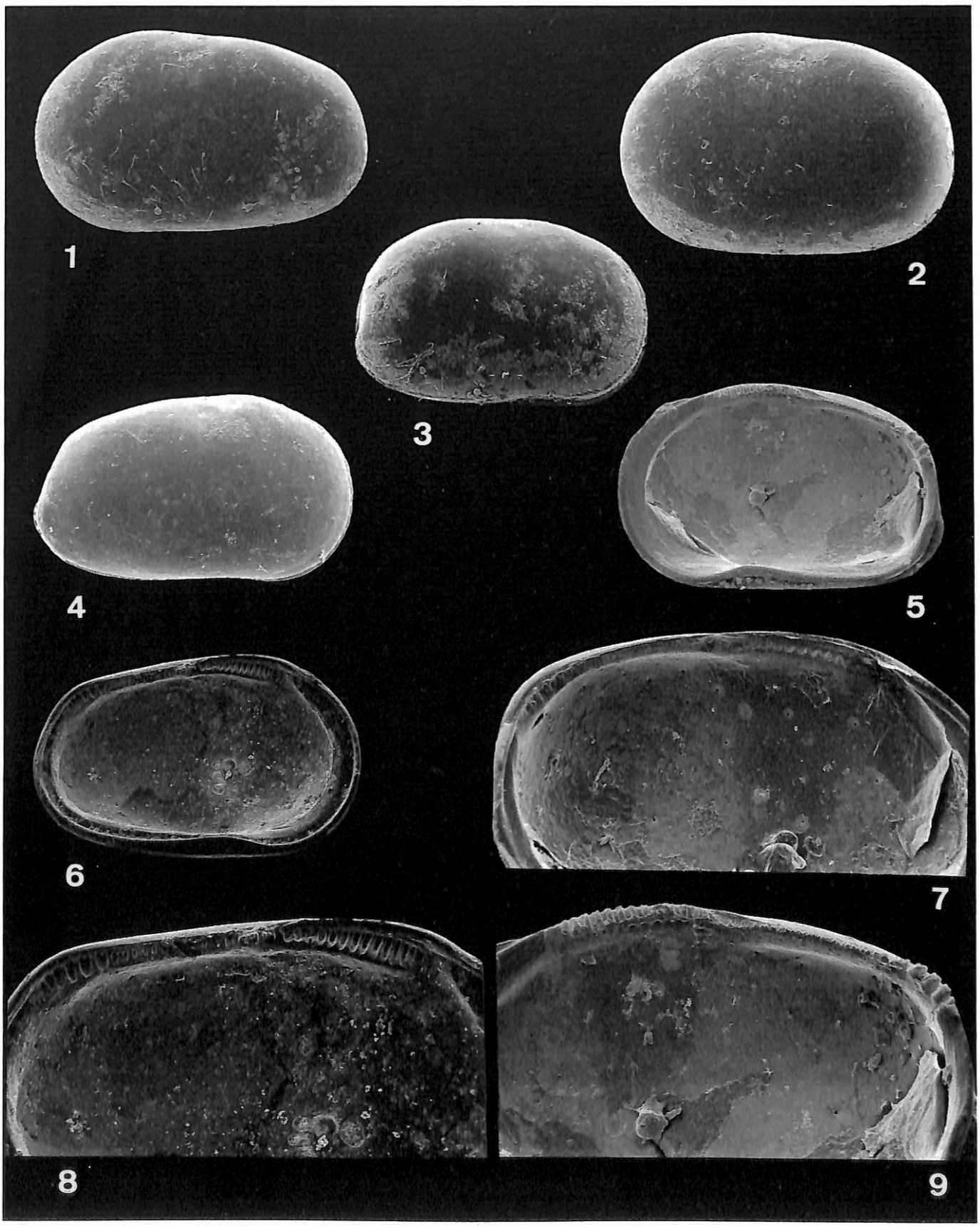

PLATE 7. – Cyprideis mastai *sp. nov., Lake Tanganyika, Burundi, off delta of river Nyengwe. Fig. 1. Left valve, male, holotype (O.C. 1753); Fig. 2. Left valve, female, allotype (O.C. 1754); Fig. 3. Right valve, female, paratype (O.C. 1756); Fig. 4. Right valve, male, paratype (O.C. 1755); Fig. 5. Right valve, internal view, male, paratype (O.C. 1757); Fig. 6. Left valve, internal view, male, paratype (O.C. 1755); Fig. 7. Hinge, left valve, female, paratype (O.C. 1756); Fig. 8. Hinge, left valve, male, paratype (O.C. 1755); Fig. 9. Hinge, right valve, female, paratype (O.C. 1757). Magnifications : Fig. 1-6 : 70 X; Fig. 7-9 : 130 X.*

DISCUSSION

Cyprideis rumongensis sp. nov. differs from *C. mastai* sp. nov. by the more elongate shape of the valves, the tapering dorsal and ventral margin in the female right valve, and probably also by the presence of shallow pits and indistinct tubercles on the valve surface. The hemipenis is also different, with a large triangular distal shield, and typically with a club-shaped central lobe bearing a posterior semi-oval shield-like widening with rough surface. Only three specimens of this new species were found, and therefore no information is available on the possible variation of the valve characters.

General Discussion

TAXONOMIC POSITION OF *TANGANYIKACYTHERE*

The genus *Tanganyikacythere* was erected primarily on the basis of the completely positive hinge of the right valve. While the amended generic diagnosis presented here allows for a minor antero-median negative element in this valve, this character still distinguishes the genus from *Cyprideis*, as well as from the other Cyprideidini in Lake Tanganyika (such as *Romecytheridea, Mesocyprideis, Archaeocyprideis, Kavalacythereis*). Meanwhile, it is here also demonstrated that a number of important soft part features (the hook-like distal process on the hemipenis and the small furcae and wedge-shaped abdominal extremity in females) further characterize the genus, which unites *T. burtonensis* and *T. caljoni*.

These species resemble, especially by their round shape, the genus *Neocyprideis,* which is a common component of late Cretaceous to Early Miocene brackish water faunas (KEEN, 1990). The hinge in *Neocyprideis* is, however, tripartite (positive, negative, positive in the right valve). This is in contrast to the quadripartite hinge in *Cyprideis* and the tripartite, but completely positive (or nearly so) hinge in *Tanganyikacythere*. The evolution from 'primitive' *Neocyprideis* over *Neocyprideis* to *Miocyprideis* constitutes a separate line within the Cytherideinae (COLIN & CARBONEL, 1990). In the second line, starting from the genus *Fabanella* over *Sarlatina* to *Cyprideis*, the median element of the hinge (negative in the right valve, positive in the left valve) becomes gradually shorter. Within this group, *Cyprideis* has a relatively short median element, which then becomes very short in *Tanganyikacythere caljoni* and disappears completely in *T. burtonensis*. Relying on the evolution of this feature, *Tanganyikacythere* appears to constitute the most recent element of this entire lineage. Although the anatomy of the hinge thus clearly separates *Neocyprideis* from *Tanganyikacythere,* the similarity in external morphology between the two genera is striking and constitutes a case of homeomorphy by convergent evolution. A similar case of convergence in Tanganyikan ostracods exists between *Tanganyikacypris* and *Tanganyikacythere* (WOUTERS *et al.*, 1989, MARTENS 1994).

THE *CYPRIDEIS* SPECIES FLOCK IN LAKE TANGANYIKA

The *Cyprideis* species flock in Lake Tanganyika, foreshadowed by WOUTERS (1990) and DANIELOPOL *et al.* (1990), now consists of nine described species in six genera : *Archaeocyprideis tuberculata* DUCASSE & CARBONEL, 1994; *Cyprideis mastai* sp. nov.; *Cyprideis rumongensis* sp. nov.; *Kavalacythereis braconensis* WOUTERS, 1979; *Mesocyprideis irsacae* (KISS, 1959); *Romecytheridea tenuisculpta* (ROME, 1962); *Romecytheridea ampla* WOUTERS, 1988; *Tanganyikacythere burtonensis* DUCASSE & CARBONEL, 1993 and *Tanganyikacythere caljoni* sp. nov.

As several new taxa presently await description (WOUTERS 1990), we will refrain from presenting a phylogenetic analysis. It is, however, clear that this group is important in the lake, both with regard to densities (if compared to other benthic ostracods) as with regard to diversity. All genera are closely related and can at times be hard to separate and one could indeed question the use and validity of these taxa. The problem of the genus concept in ancient lakes, such as Lake Tanganyika, was briefly discussed by MARTENS (1994) and MARTENS *et al.* (1994). Genera are supra-specific, to a large extent artificial, units, which serve to unite groups of related species and are mostly thought to be fully disjunct. However, it is not completely unexpected that in ancient lakes, where most endemics live in the cradle where they originated, intermediate forms and morphologies between species-clusters can and will exist. If in such conditions one accepts that genera should be fully disjunct, then large and broadly defined genera will have to be used, such as for example the genera *Cytherissa* (57 species and subspecies) and *Candona* (53 species and subspecies) in Lake Baikal (MAZEPOVA, 1990, 1994). In the case of the Cytherideinae of Lake Tanganyika, such an approach would probably include all species in *Cyprideis*. The alternative solution, splitting these large genera into phylogenetic units, will encounter problems with intermediate taxa, so that the resulting genera might not always be fully disjunct. As we apply the latter approach, the species *Tanganyikacythere caljoni* sp. nov., to some extent intermediate between *T. burtonensis* and *Cyprideis*, is still included in the former genus. We feel that this approach better reflects the degree of radiation and the internal relationships of the flocks within the lake basins. This approach, however, is prone to cause substantial discussion; the generic taxonomy of cichlid fishes of African ancient lakes for example (GREENWOOD, 1981) is presently already a hotly debated subject.

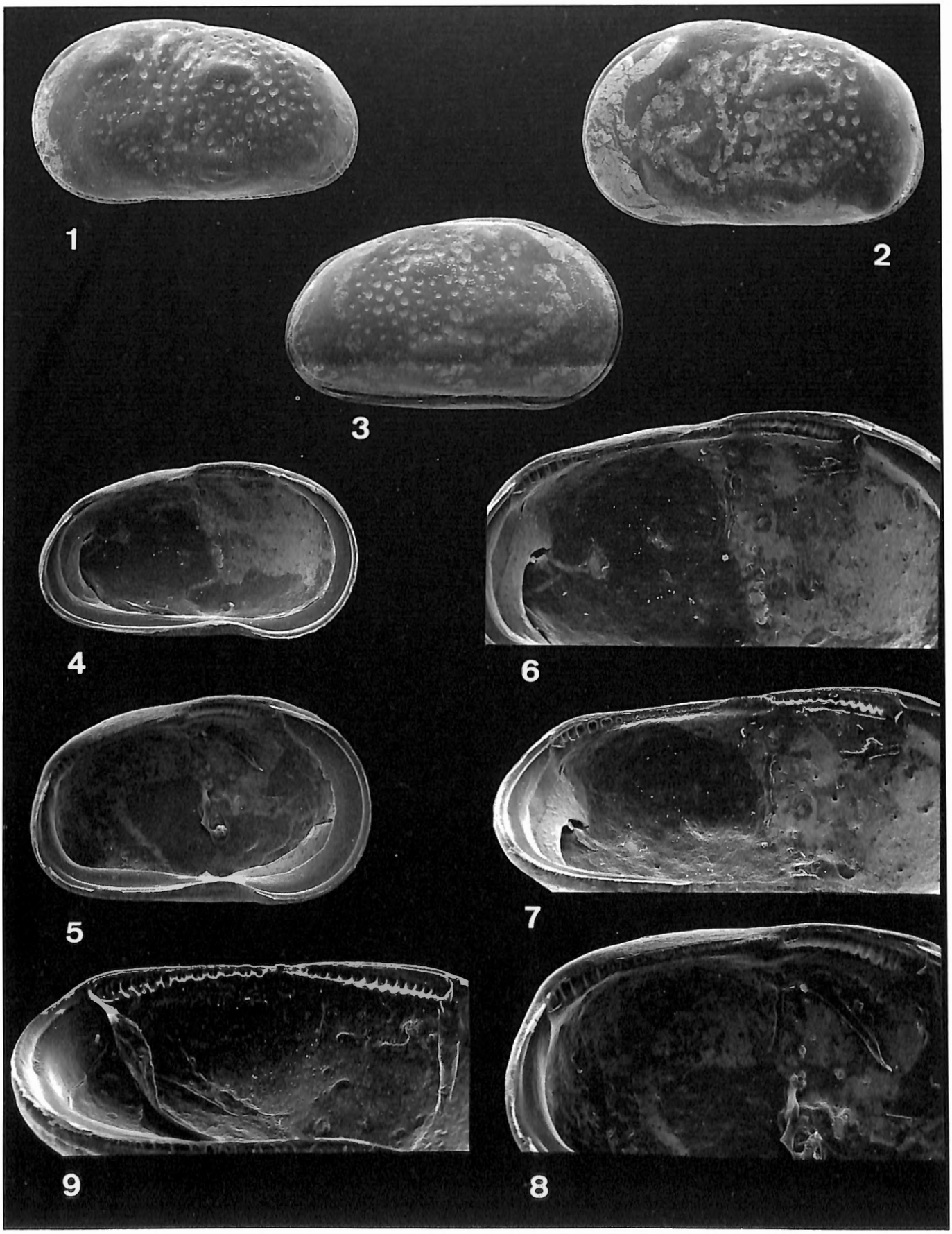

PLATE 8. – Fig. 1-8 : Cyprideis rumongensis *sp. nov., Lake Tanganyika, off delta of river Dama, near Rumonge. Fig. 1. Left valve, male, holotype (O.C. 1765); Fig. 2. Left valve, female, allotype (O.C. 1766); Fig. 3. Carapace, right valve view, male, paratype (O.C. 1767). Fig. 4. Left valve, internal view, holotype; Fig. 5. Left valve, internal view, allotype; Fig. 6. Hinge, left valve, allotype; Fig. 7. Hinge, left valve, holotype, inclined; Fig. 8. Hinge, left valve, female, allotype. Fig. 9.* Tanganyikacythere caljoni *sp. nov., Lake Tanganyika, Burundi, Karonda Village, hinge, left valve, holotype, inclined.Magnifications : Fig. 1-5 : 70 X; Fig. 6-9 : 130 X.*

Table 1.
Aspects of ecological distribution 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
Romecytheridea tenuisculpta	1	7 m	sand and rocks
Romecytheridea ampla	1	8 m	sand
Tanganyikacythere burtonensis	6	1-20 m	sand
Tanganyikacythere caljoni	1	1 m	sand
Deep water fauna			
Cyprideis mastai	3	40-90 m	mud
Cyprideis rumongensis	1	50 m	coarse sand

ECOLOGY AND DISTRIBUTION

Research on the taxonomy, biology and ecology of benthic invertebrates in ancient lakes is still hampered by the logistic difficulties to collect sufficient living material. It is at present impossible to give an assessment of the biology and distribution of the *Cyprideis* flock in Lake Tanganyika. Table 1 summarizes the isolated data on living material that are presently available. We refrain from including instances where ecological variables are derived from localities with (sub)fossils only. It is indeed impossible to deduce in which conditions these animals once lived, i.e. to establish their ecological requirements, relying only on the circumstances where the dead valves were found.

From Table 1, it would appear that the highest diversity of Cytherideinae occurs primarily in shallow waters of the upper littoral. Four species can occur in the shallow surf zone; these species are well adapted to these high energy zones as they all have strong, heavily calcified valves. Two species appear to be restricted to deeper waters; these belong to the cosmopolitan genus *Cyprideis*. Further research is of course needed to investigate if genuine *Cyprideis* species are indeed excluded from the shallow littoral. Another example were endemic ostracods are confined to the shallow littoral, can be found in the three species of the endemic genus *Tanganyikacypridopsis,* which have thus far been found living between 0 and 9 m deep (MARTENS, 1985).

Most taxa occur on coarse sediments (fine sand to sand); only one species was found living on mud in three different localities (*C. mastai*). It should be noted that muddy sediments are relatively rare in the oxygenated zone of Lake Tanganyika and generally occur in the deeper parts only.

Most Tanganyikan Cytherideinae appear to be brooders, and eggs and/or nauplii have actually been observed in the brooding pouch. This mode of reproduction has been cited as one of the intrinsic factors promoting speciation in ancient lakes (COHEN & JOHNSTON, 1987; MARTENS, 1994), and could be at least partly responsible for the success of this particular lineage in Lake Tanganyika.

The presence of *Tanganyikacythere burtonensis* in Lake Mobutu Sese Seko (ex Lake Albert) is intriguing. This species is therefore not, or no longer, a genuine Tanganyika-endemic and there are two possible explanations for this. *Tanganyikacythere* might originally have had a much wider distribution, including waterbodies outside of Lake Tanganyika, much like the concept of 'superflock' used by GREENWOOD (1994) for the haplochromine fish of Lake Victoria, Kivu and Edward amongst others. More likely, because we are dealing with two disjunct populations of one and the same species, the population in Lake Albert might constitute a (sub)recent introduction; this hypothesis can readily be falsified by investigating fossil ostracods in cores from Lake Albert.

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