On the taxonomic position of the genera *Archeocyprideis* and *Kavalacythereis* of the *Cyprideis* species flock (Crustacea, Ostracoda) in Lake Tanganyika (East Africa), with the first description of the appendages

by Karel WOUTERS & Koen MARTENS

Abstract

The Cyprideis species flock of Lake Tanganyika presently consists of 17 formally described species in 6 genera. The appendages of two of these species and genera, nl. of Archeocyprideis tuberculata DUCASSE & CARBONEL 1994 and Kavalacythereis braconensis WOUTERS 1979, remained thus far unknown. The soft parts of these species are here described for the first time, while their valves are redescribed and – illustrated. New, as well as established, features are used to determine the taxonomic position of these species and genera within the Tanganyikan Cyprideis species flock.

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

Résumé

Sur la position taxinomique du genre *Archeocyprideis* et *Kavalacythereis* du species flock *Cyprideis* (Crustacea, Ostracoda) du lac Tanganyika (Afrique), avec une première description de leurs appendices.

Le « species flock » Cyprideis du lac Tanganyika consiste actuellement en 17 espèces formellement décrites et 6 genres. Les appendices de deux de ces espèces et genres, Archeocyprideis tuberculata DUCASSE & CARBONEL 1994 et Kavalacythereis braconensis WOUTERS 1979, demeuraient inconnus jusqu'à présent. Une description de leurs parties molles est donnée ici pour la première fois, ainsi qu'une redescription et de nouvelles illustrations de leurs valves. La position taxinomique de ces espèces et genres au sein du « species flock » Cyprideis du Tanganyika est déterminée sur la base de caractères bien établis et également nouveaux.

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

Introduction

There are at least 5 separate ostracod radiations in Lake Tanganyika (MARTENS, 1994), of which the *Cyprideis* species flock has been most intensively studied (KISS 1960, ROME 1962, WOUTERS 1979, 1988a, b, WOUTERS & MARTENS 1992, 1994, 1999, in press, DUCASSE & CARBONEL 1993, 1994). The knowledge of this species flock increases pro-

gressively as new collections become available. Seventeen species (16 endemic) in 6 genera (4 endemic) have to date been described. Of two of these species, namely of Archeocyprideis tuberculata DUCASSE & CARBONEL and of Kavalacythereis braconensis WOUTERS, the morphology of the soft parts was thus far unknown. The chaetotaxy of the appendages of these taxa is here described and illustrated for the first time, while also their valve structure is redescribed. These data allow us to refine the taxonomic position of these genera and species within the Tanganyikan Cyprideis species flock. A phylogenetic analysis based on a morphological data matrix comprising the whole of the known species flock will be presented elsewhere; this tree will be used to falsify the analyses based on molecular data (SCHÖN et al. in press).

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). 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 Archeocyprideis DUCASSE & CARBONEL, 1994

AMENDED DIAGNOSIS

Elongated valves with bluntly pointed, triangular posterior margin; hinge tripartite, median element bipartite with short antero-median element; valve surface ornamented with pits and nodes or smooth; vestibula absent; medial seta on fourth segment of antennula medium-sized; exopodite of antenna three-segmented; first thoracic leg in males weakly asymmetrical, first right leg being only slightly broader than left one.

Archeocyprideis tuberculata DUCASSE & CARBONEL, 1994 (Pl. 1, figs 1-11, Pl. 3, figs 1-6)

1994 Archeocyprideis tuberculata n. sp. - DUCASSE & CARBONEL, p. 99-100, Pl. 1, fig. 1-9, pl. 2, fig. 1-9, pl. 3, fig. 1-8. 1999 Archeocyprideis tuberculata - ALIN et al., p. 1031.

TYPE LOCALITY

D.R. Congo, Lake Tanganyika, Burton Bay, near Mutambala River mouth (DUCASSE & CARBONEL, 1994)

MATERIAL INVESTIGATED

- D.R. Congo, between Moliro and Vua, dredged at a depth of 8 m. Leg.: L. STAPPERS, 25 november 1912 (station number 1718): two dissected males (O.C. 2363, 2364)
- D.R. Congo, Bracone Bay, Kabala (= Kavala) Island, dredged at a depth of 3 m. Leg.: L. STAPPERS, 18 January 1913 (station 1975): a male and a female carapace (O.C. 2370).
- Burundi, near Cape Mvugo, road Bujumbura-Rumonge, km 117, collected at 1000 m from the shore, at a depth of 4.5 m. Leg.: A. CALJON, 16 February 1990 (station 900): two dissected females (O.C. 2368, 2369).
- Tanzania, Kipili Islands, (S 7°27'122" E 30°34'116"), collected with hand net at a depth of 2-5 m, on sand and gravel. Leg.: K. MARTENS & B. GODDEERIS, 26 May 1992 (station 92/03): one dissected female (O.C. 2367).
- Tanzania, swampy area, N. of cliff, c 18 km NE of village Kanyasa (S 5°40'185" E 29°53'272"), collected with a PONAR grab on sand amongst rocks, at a depth of 7 m. Leg.: K. MARTENS & B. GODDEERIS, 2 June 1992 (Station 92/52): one dissected male (O.C. 2365)
- Tanzania, transect opposite main outlet of Malagarasi River, collected with Ponar, at a depth of 1.5 m, on fine sand. Leg.: K. MARTENS & B. GODDEERIS, 2 June 1992 (station 92/58): one dissected female (O.C. 2366).

AMENDED DIAGNOSIS

Valves heavily calcified; valve surface with indistinct reticulation and five to six knob- to rib-like protuberances; distal shield of hemipenis with anvil-shaped terminal margin; central lobe club-shaped; terminal segment of antennal exopodite short.

DESCRIPTION

Medium-sized, elongated and well-calcified valves (Pl. 3, Fig. 1, 2). Dorsal margin straight, with distinct anterior and posterior cardinal angles. Anterior margin obliquely rounded, ventral margin weakly sinuous, and posterior margin protruded in a triangular posterior extremity, with blunt tip situated near the middle. Valve surface with indistinct reticulation and with five to six knob- to rib-like protuberances. Left valve somewhat higher than the right one, and female valves higher than those of the male. Postero-ventral knob hollow in females, not in males.

Male carapace (Pl. 3, Fig. 4) in dorsal view somewhat fusiform, with lateral margins convex, but irregular, due to the presence of ribs and knobs; anterior extremity pointed, posterior one rather blunt; largest width situated somewhat beyond the middle.

Female carapace (Pl. 3, Fig. 5) wedge-shaped in dorsal view, with almost straight, but irregular lateral margins, due to the presence of ribs and knobs. Anterior extremity blunt and bifid, posterior one broadly blunt. Largest width situated posterior to the middle, at about 9/10 of the length.

Anterior and postero- ventral fused zones wide, posterior one moderately wide, with numerous, sometimes branched marginal pore canals (Pl. 1, Fig. 1, 2); few false pore canals. Anterior and posterior vestibula absent. Hinge strongly developed, tripartite and consisting of anterior, median and posterior elements; median element short and bipartite. Hinge of right valve (Pl. 1, Fig. 1): anterior element with about fourteen dorso-ventrally elongated toothlets; antero-median element with three subcircular sockets; postero-median element a bar-like structure with about seven indistinctly delineated toothlets; transition between postero-median element and posterior element indistinct; posterior element consisting of about six slightly bifid toothlets. Left valve hinge complementary (Pl. 1, Fig. 2).

Antennule (Pl. 1, Fig. 3) five-segmented; first segment short and broad; second segment elongate, about twice as long as wide, third and fourth segments short and fifth segment elongate and narrow; antero-distal seta of second segment relatively short, reaching slightly beyond the tip of the last segment; third segment with one, and fourth segment with two strong claws; medial seta of fourth segment medium-sized, reaching to margin of fourth segment. Fifth segment with a short claw and a long aesthetase, fused at the base with a long seta

Antenna (Pl. 1, Fig. 4) with three-segmented exopodite and four-segmented endopodite; third segment of endopodite with three short postero-distal claws and a long seta; claws of forth segment long.

First leg only slightly dimorphic in the male: left leg (Pl. 1, Fig. 8) slender, as in the female; right leg (Pl. 1, Fig. 9) with somewhat broadened second, third and fourth segments.

Second leg dimorphic in the male; right leg (Pl. 1, Fig. 5) 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. 7) as in the female.

Third leg (Pl. 1, Fig. 6) not dimorphic, but long and slender, set with bundles of setulae, and with long and very slender

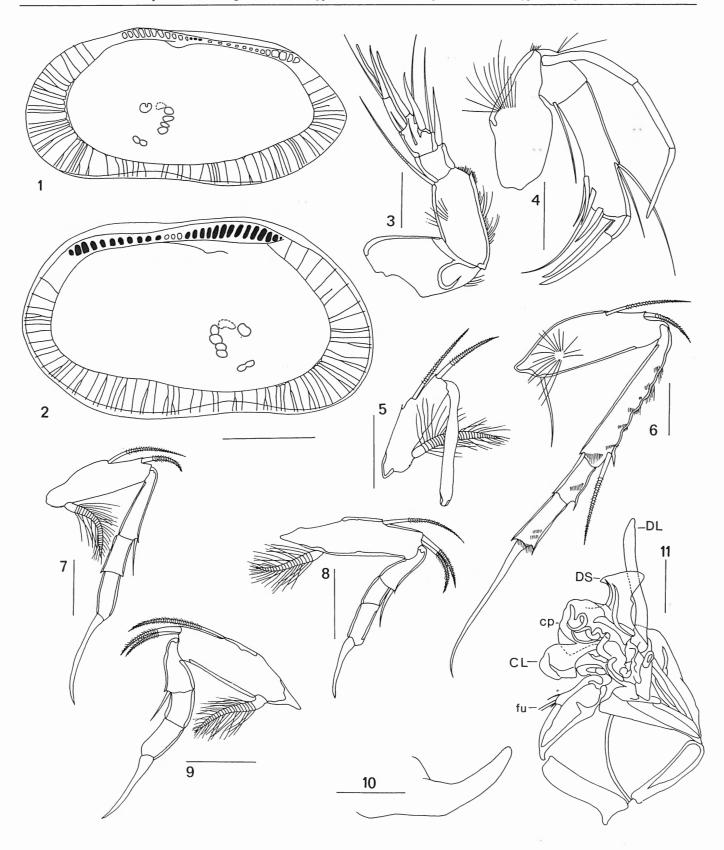


Plate 1. – Archeocyprideis tuberculata DUCASSE & CARBONEL, 1994. Lake Tanganyika (for localities see under "Material investigated"). Fig. 1. Right valve, internal view, male (O.C. 2364). Fig. 2. Left valve, internal view, female (O.C. 2366). Fig. 3. Antennule, male (O.C. 2365). Fig. 4. Antenna, male (O.C. 2369). Fig. 5. Right second leg, male (O.C. 2363). Fig. 6. Third leg, male (O.C. 2363). Fig. 7. Left second leg, male (O.C. 2363). Fig. 8. Left first leg, male (O.C. 2365). Fig. 9. Right first leg, male (O.C. 2365). Fig. 10. Abdominal extremity, female (O.C. 2369). Fig. 11. Hemipenis, male (O.C. 2365). Scales: Fig. 1-2: 200 μm; Fig. 3-10: 50 μm.

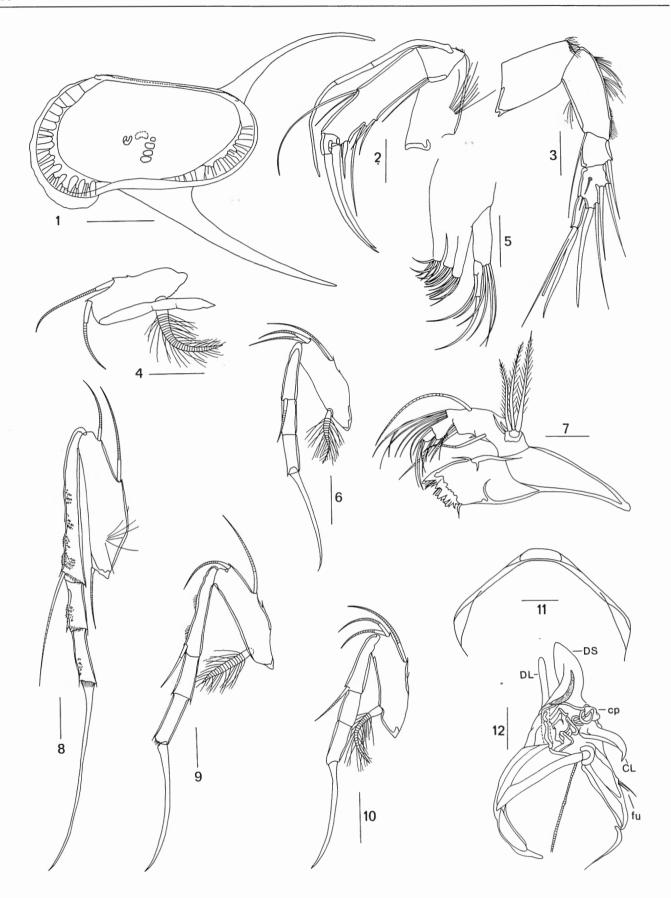


Plate 2. – *Kavalacythereis braconensis* WOUTERS, 1979. Lake Tanganyika, Burundi, Cape Mvugo. Fig. 1. Right valve, internal view, male (O.C. 2372). Fig. 2. Antenna, male (O.C. 2372). Fig. 3. Antennule, male (O.C. 2372). Fig. 4. Right second leg, male (O.C. 2372). Fig. 5. Maxillule, male (O.C. 2373). Fig. 6. Left first leg, male (O.C. 2373). Fig. 7. Mandible, male (O.C. 2373). Fig. 8. Third leg, male (O.C. 2372) Fig. 9. Left second leg, male (O.C. 2373). Fig. 10. Right first leg, male (O.C. 2373). Fig. 11. Hypostome fork, male (O.C. 2373) Fig. 12. Hemipenis, male, (O.C. 2373). Scales: Fig. 1-2: 200 μm; Fig. 3-10: 50 μm.

terminal claw.

Hemipenis (Pl. 1, Fig. 11) with distal shield (DS) relatively small and anvil-shaped; distal lobe (DL) long, narrow and weakly sinuous with blunt distal end; copulatory process (cp) large, semi-circular; central lobe (CL) large, club-shaped. Female abdominal extremity (Pl. 1, Fig. 10) with a crescent-shaped process; furcae small.

MEASUREMENTS

Males: L 0.69 - 0.72 mm, H 0.33 - 0.36 mm Females: L 0.67 - 0.80 mm, H 0.34 - 0.42 mm

REMARKS

The present species is a brooder. In two of the dissected females the postero-dorsal pouch contained: 4 eggs and 3 nauplii in O.C. 2366 and 10 eggs and 2 nauplii in O.C. 2367.

OCCURRENCE

Archeocyprideis tuberculata is known from the type locality, Burton Bay, near Mutambala River mouth, D.R. Congo (DUCASSE & CARBONEL, 1994). The original description of the species was based exclusively on valves and carapaces. Material with appendages was found in 5 of the localities cited above.

DISCUSSION

Up to now, only one species of the genus Archeocyprideis has been described: Archeocyprideis tuberculata DUCASSE & CARBONEL, 1994. Our ostracod collections of Lake Tanganyika, however, contain 2 specimens of a second species in the genus, Archeocyprideis sp. A sp.nov. : one male from Gitaza (Burundi), collected on sand at a depth of 20 m (station NURC III.34), and one female from te bay South of Kibwesa (Tanzania), collected on sand at a depth of 20 m (station LT92/ 24). This new species, thus far not formally decribed, can be distinguished from A. tuberculata by the completely smooth valves (in both sexes), and especially by the very different morphology of the hemipenis, which has a distally rounded triangular dorsal shield and an elongated, wedge-shaped central lobe. The third segment of the antennal exopod is also much longer and narrower in the new species. Interestingly, both A. tuberculata and the new species have a very similar valve shape, with bluntly pointed, triangular posterior margin in lateral view and no vestibula. As the new species also conforms to the structural features diagnostic for Archeocyprideis, it doubtlessly belongs to this genus. More material is needed before this new species can be described, as a detailed assessment of the intraspecific variability is vital for the characterisation of ancient lake ostracods (MAR-TENS, 1994).

Genus Kavalacythereis WOUTERS, 1979

AMENDED DIAGNOSIS

Medium-sized to large smooth valves with postero-dorsal and ventro-lateral hollow spines; large anterior and posterior vestibulum; numerous compound marginal pore canals; hinge tripartite, with anterior anti-slip bar in the left valve; antennal exopodite three-segmented; medial seta on fourth segment of antennula short to medium-sized; dimorphism between left and right male first leg indistinct.

Kavalacythereis braconensis WOUTERS, 1979 (Pl. 2, figs 1-12, Pl. 4, figs 1-9)

1979 Kavalacythereis braconensis gen.n., sp.n. - WOUTERS, p. 180-184, Pl. 1, figs 1-8, Pl. 2, figs 1-7.

1987 Kavalacythereis braconensis Wouters, 1979 - Lethiers & Crasquin, p. 419, pl. 1, figs 14-15.

1990 Kavalacythereis braconensis Wouters, 1979. - Schornikov & Michallova, p. 141, fig. E.

1994 Kavalacythereis braconesis Wouters, 1979 - Martens, figs 1a-b. 1999 Kavalacythereis braconensis Wouters, 1979 - Martens & Schön, p. 903, fig. K.

TYPE LOCALITY

D.R. Congo, Lake Tanganyika, Kavala Island, Bracone Bay, 12 m, sand (Wouters, 1979).

MATERIAL INVESTIGATED

- Burundi, near Cape Mvugo, dredged at a depth of 20 m, on sand and rocks. Leg.: K. MARTENS, 28 September 1991 (station 91/06): one dissected male (O.C. 2373) and one female right valve (O.C. 2377).
- Tanzania, swampy area, N. of cliff, c 18 km NE of village Kanyasa (S 5°40'185" E 29°53'272"), collected with a PONAR, at a depth of 7 m, on sand amongst rocks. Leg.: K. MARTENS & B. GODDEERIS, 2 June 1992 (station 92/52): one dissected male (O.C. 2372).
- Zambia, Mayimba, near Kalambo River (S 08° 36' 32" E31° 11' 45"), collected by SCUBA at a depth of 13 to 6 m, on sand. Leg.: K. MARTENS, 5 April 1995 (station 95/07): two dissected males (O.C. 2376, 2377), one female whole mount (O.C. 2375) and 20 adult males, females and juveniles preserved in ethanol (O.C. 2379).

AMENDED DIAGNOSIS

Medium-sized smooth valves, with long postero-dorsal and ventro-lateral hollow spines; height 50-55 % of length; postero-dorsal brood pouch of female elongate; anterior flange strongly developed; spiky hairs on anterior and posterior margin absent; hemipenis with elongate triangular dorsal shield, small copulatory process and hook-like central lobe.

DESCRIPTION

Valves (pl. 2, Fig. 1, Pl. 4, Fig 1,-4) medium-sized, completely smooth and translucent; dorsal margin straight, ventral margin slightly sinuous; both margins tapering towards the posterior end; anterior margin obliquely rounded, posterior margin evenly rounded; maximum height situated anteriorly to the middle, near the transition from the anterior to the dorsal margin; cardinal angles indistinct; large flange, extending along the entire anterior margin, raising from the valve surface at an angle of about 45°, and slightly lobed at its distal margin; in dorsal view appearing as a large collarlike structure surrounding the entire anterior margin; valves with two long and slender hollow spines, ventro-lateral spine with a broad, somewhat dorso-ventrally flattened base; postero-dorsal spine only weakly curved, pointing obliquely upward, with an angle of about 120° in males and of about 140° in females; female specimens (Pl. 4, Fig. 2) with a large, elongate pouch-like widening of the postero-dorsal area, with the postero-dorsal spine at the distal extremity of the pouch; carapace in dorsal view (without spines) fusiform in males (Pl. 4, Fig. 6), with the maximum width situated in the middle; female carapace in dorsal view (Pl. 4, Fig. 5) wedgeshaped, with maximum width situated at the extreme posterior.

Inner lamella (Pl. 2, Fig. 1) moderately wide, with well developed selvage; wide anterior and narrow posterior vestibulum; marginal pore canals numerous and strongly branched anteriorly, less so posteriorly.

Hinge weakly developed, tripartite, and consisting of anterior, median and posterior element; median element indistinctly bipartite. Hinge of right valve (Pl. 2, Fig. 1, Pl. 4, Fig. 3, 7): anterior element small with about 9 toothlets; anteromedian element very long (reaching to the middle of the valves) with an indistinct number of small sockets; posteromedian element a crenulated bar, with numerous, small toothlets; posterior element with 8 to 10 small toothlets. Hinge of left valve (Pl. 4, Fig. 4, 8, 9) complementary (Pl. 2, Fig. 4, 8, 9), but with a large anti-slip bar, obliquely inserted below the anterior element (only in the left valve).

Strong sexual dimorphism: females with large postero-dorsal brood pouch, and female valves markedly longer than male ones.

Antennule (Pl. 2, Fig. 3) five-segmented; first segment subrectangular; second segment twice as long as broad; antero-distal seta of second segment long, reaching almost to the end of the fifth segment; third and fourth segment short, with long claw-like setae; fifth segment long and slender with a long weakly developed claw and a long aesthetasc, fused at the base with a long seta. Medial seta of fourth segment rather short, not reaching to the distal margin of the segment.

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

First leg in the male only very weakly dimorphic: left leg (Pl. 2, Fig. 6) as in the female, with slender segments; right leg (Pl. 2, Fig. 10) almost identical, but with only slightly broader second, third and fourth segments.

Second leg strongly dimorphic in the male: left leg (Pl. 2,

Fig. 9) as in the female, with long and slender curved terminal claw; right leg (Pl. 2, Fig. 4) strongly reduced and weakly sclerotized; terminal segments small and delicate and indistinctly three-segmented.

Third leg (Pl. 2, Fig. 8) not dimorphic, elongate and very hirsute, with very long, slightly curved slender terminal claw. Hemipenis (Pl. 2, Fig. 12) with a leaf-like, somewhat subtriangular distal shield (DS); distal lobe (DL) long (but shorter than DS) and straight with rounded distal extremity; copulatory process (cp) very small and indistinctly lobed; central lobe (CL) large and hook-shaped.

Abdominal extremity in the female a wedge-shaped process, apparently carrying setae, and probably a more complex structure, needing further research on new material; furcae moderately large.

MEASUREMENTS

Males: L 0.74 - 0.84 mm, H 0.40 - 0.46 mm Females: L 0.87 - 0.95 mm, H 0.43 - 0.52 mm

REMARKS

The present species is a brooder. In one of the dissected females the postero-dorsal pouch contained 4 eggs (O.C. 2375).

OCCURRENCE

Kavalacythereis braconensis is known from the type locality, Bracone Bay, Kavala Island, D.R. Congo (WOUTERS, 1979). The original description of the species was based exclusively on valves and carapaces. Material with appendages was found in the three localities listed above.

DISCUSSION

Up to now, only one species in the genus Kavalacythereis had been described: K. braconensis WOUTERS, 1979. Our ostracod collections of Lake Tanganyika, however, contain a number of empty valves from various localities and one female with appendages from Gitaza (Burundi, depth 20m) of a second species in the genus, Kavalacythereis sp. A. sp.nov. This new, presently undescribed, species differs from K. braconensis in its larger size and higher valves (both in males and females), by the smaller anterior vestibulum and the less branched marginal pore canals. The new species is moreover characterised by the presence of large spiky setae along the anterior and posterior valve margins and by the fact that the medial seta on the fourth segment of the antennula is significantly shorter than in the type species. As no male specimens with soft parts have thus far been found, this new species cannot be described until new material is available.

General Discussion

The valve and soft part characteristics of both Archeocyprideis tuberculata and of A. sp. A. sp. nov. clearly

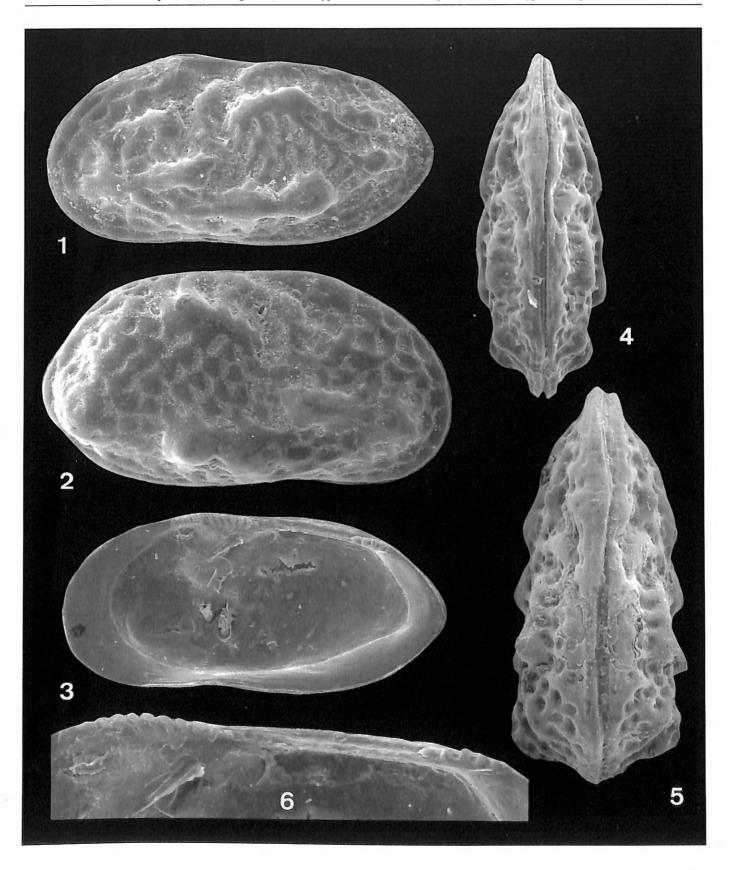


Plate 3. – Archeocyprideis tuberculata DUCASSE & CARBONEL, 1994. Lake Tanganyika (for localities see under "Material investigated"). Fig. 1. Left valve, lateral view, male (O.C. 2364). Fig. 2. Right valve, lateral view, female (O.C. 2366). Fig. 3. Right valve, internal view, male (O.C. 2364). Fig. 4. Male carapace, dorsal view (O.C. 2370). Fig. 5. Female carapace, dorsal view (O.C. 2370). All magnifications: 120 X.

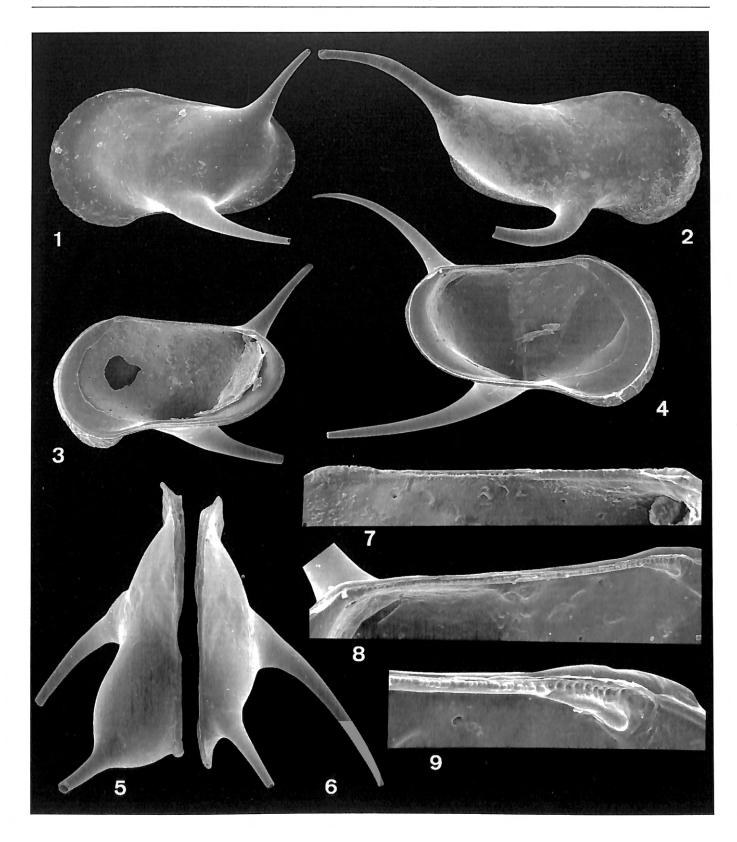


Plate 4. – *Kavalacythereis braconensis* WOUTERS, 1979. Lake Tanganyika (for localities see under "Material"). Fig. 1. Left valve, lateral view, male (O.C. 2372). Fig. 2. Right valve, lateral view, female (O.C. 2377). Fig. 3. Right valve, internal view, male (O.C. 2372). Fig. 4. Left valve, internal view, male (O.C. 2376). Fig. 5. Female left valve, dorsal view (O.C. 2374). Fig. 6. Male right valve, dorsal view (O.C. 2376). Fig. 7. Male right valve, hinge (O.C. 2372). Fig. 8. Male left valve, hinge (O.C. 2376). Fig. 9. Male left valve, anterior part of hinge, showing "anti-slip bar" (O.C. 2376). All magnifications: 120 X.

constitute a separate set of features, which justifies the allocation of these species to a separate genus. These features are: absence of vestibulum; triangular and bluntly pointed posterior margin in lateral view; medium-sized medial seta on 4th segment of antennula; 3-segmented exopodite of antenna; indistinct dimorphism between male right and left first leg. Although the valve shapes in both groups is very different, Archeocyprideis seems most closely related to Romecytheridea. In the latter genus, the vestibulum is also reduced to almost absent, while the dimorphism between left and right first legs in the male is equally indistinct.

Both species of Kavalacythereis (K. braconsensis and K. sp. A sp.non.) clearly belong to a distinct genus, as their carapaces have striking and unique morphologies. The soft part features support the validity of Kavalacythereis as a good and separate genus, but more importantly they also confirm that this genus forms part of the Tanganyikan Cyprideis species flock. The very aberrant valve features in this genus (completely smooth valves, with unusually long and hollow dorsal and ventral spines and large vestibulum) indeed separate this genus from all others in the Tanganyikan flock. The appendage morphology confirm this distinct place of Kavalacythereis within the flock by the absence of dimorphism in male left and right second leg. Other soft part features, however, confirm the relationship between Kavalacythereis and Romecytheridea.

WOUTERS & MARTENS (in press) and MARTENS et al. (in press) discuss the value of ancient lake biota, especially ostracods, for the discussion on the biological reality and the mode of origin of genera. They conclude that arguments for both gradual and saltatory origin of genera can be found in the analysis of ancient lake species flocks. The present paper confirms several statements. Firstly, soft part features confirm presumed pathways of evolution and speciation, for example the very aberrant valve morphology in Kavalacythereis is matched by an exceptional soft part feature, namely the absence of dimorphism in the first male leg. Secondly, in spite of this, soft part morphology is clearly more conservative than valve morphology, which appears to be more plastic and faster evolving. Finally, the confirmation of the presence of at least a second species in both Kavalacythereis and Archeocyprideis, thus far the last presumed monospecific genera in this flock, strengthens the validity of these genera. It also confirms the fact that they are relatively old (SCHÖN et al. in press) and that, most likely, at least intra-generic evolution and speciation was more gradual than saltatory.

Acknowledgements

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References

ALIN, S.R., COHEN, A.S., BILLS, R., GASHAGAZA, M.M., MICHEL, E., TIERCELIN, J.-J., MARTENS, K., COVELIERS, P., MBOKO, S.K., WEST, K., SOREGHAN, M., KIMBADI, S. & NTAKIMAZI, G., 1999. Effects of landscape disturbance on animal communities in Lake Tanganyika, East Africa. *Conservation Biology*, 13(5): 1017-1033.

DUCASSE, O. & CARBONEL, P., 1993. *Tanganyikacythere* nov. gen. (Cytherideinae, Ostracoda) du Lac Tanganyika: systématique des valves, données écologiques. *Geobios*, 26(4): 427-447.

DUCASSE, O. & CARBONEL, P., 1994. Cytherideinae (Crustacea, Ostracoda) récents du Lac Tanganyika. *Archeocyprideis tuberculata* n.gen., n.sp.: systématique, distribution, écologie. *Revue de Micropaléoniologie*, 37(2): 97-112.

KISS, R., 1959. Quelques ostracodes nouveaux et intéressants de la région de l'extrémité nord du Lac Tanganyika. Revue de Zoologie et de Botanie africaines, 59(1/2): 81-105.

LETHIERS, F. & CRASQUIN, S., 1987. Reconnaissance des milieux profonds de la Paléotéthys à l'aide des ostracodes. *Bulletin de la Société géologique de France*, (8), 3(3): 415-423.

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. & SCHÖN, I., 1999. Crustacean biodiversity in ancient lakes: a review. *Crustaceana*, 72(8): 989-910.

MARTENS, K., K. WOUTERS, G. MAZEPOVA & I. SCHÖN (in press). Geniation and the genus concept in ancient lakes. *Verhandlungen der Internationalen Vereinigung für Limnologie* 27.

ROME, DOM R., 1962. Ostracodes. Résultats scientifiques Exploration hydrobiologique du Lac Tanganika, 3(8): 1-305.

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

SCHORNIKOV, E.I. & MICHAILOVA, E.D., 1990. Ostracoda Bythocytheridae at early stage of development: comparative morphology, paleoecology and evolutionary pathways. Nauka Publishers, Moskva, 278 pp (in Russian).

WOUTERS, K., 1979. Kavalacythereis braconensis gen.n., sp.n., a remarkable new cytheracean ostracod genus and species from Lake Tanganyika (Zaire). Annales de la Société royale zoologique de Belgique, 108(3-4): 179-187.

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 know-ledge 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 know-ledge 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.

WOUTERS, K. & MARTENS, K., 1999. Four new species of the Cyprideis species flock (Crustacea: Ostracoda) of Lake Tanganyika. Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Biologie, 69: 67-82.

WOUTERS, K. & MARTENS, K., in press. On the *Cyprideis* species flock (Crustacea, Ostracoda) in Lake Tanganyika, with the description of four new species. *Hydrobiologia*.

K. WOUTERS & K. MARTENS
Koninklijk Belgisch Instituut
voor Natuurwetenschappen
Vautierstraat 29
B-1000 Brussels, Belgium
e-mail: kwouters@kbinirsnb.be
martens@kbinirsnb.be