The enigmatic *Cleopatra broecki* Putzeys, 1899 of the Congo River system in Africa – re-transfer from *Potadomoides* Leloup, 1953 (Caenogastropoda, Cerithioidea, Paludomidae)

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Abstract

While the lacustrine gastropods from the great East African lakes, most notably of Lake Tanganyika, with their local endemisms and spectacular species flocks have found attention among both malacologists and more recently evolutionary biologists, our knowledge of gastropods of the central African rivers is still insufficient. In the course of a systematic revision of fluviatile paludomids of the genus *Potadomoides* Leloup, 1953, and in context with a study on the origin of the lacustrine gastropod radiation in Lake Tanganyika, type and other material of the constituent taxa from several museum collections was studied. Re-investigating the type material housed in the Musée Royal L’Afrique Centrale in Tervuren, Belgium (MRAC), and of additional material found in the collection of the Museum of Comparative Zoology of the Harvard University in Cambridge, Mass. USA (MCZ), provided new geographical, conchological as well as anatomical evidence (with respect to the operculum and radula). Hitherto only known from the original description, these new findings allow here to re-transfer *C. broecki* Putzeys, 1899 from *Potadomoides* to *Cleopatra* Troschel, 1856.

Introduction

"The old river in its broad reach rested unruffled at the decline of day, after ages of good service done to the race that peopled its banks, spread out in the tranquil dignity of a waterway leading to the uttermost ends of the earth." – Joseph Conrad, 1899: Heart of Darkness

The great East African lakes, and most notably those in the Rift such as Lake Tanganyika and Lake Malawi, are generally regarded as hotspots of aquatic biodiversity, with local endemisms and spectacular species flocks of various animal groups. As these lakes provide natural laboratories, i.e. exemplary settings for studies on evolutionary processes of intra-lacustrine speciation and adaptive radiation, their faunas have received considerable scientific attention (see e.g. reviews in Coulter 1991; Rossiter & Kawanabe 2000; Danley & Kocher 2001; Kocher 2004). Providing another instructive model for understanding evolutionary processes, such as speciation and radiation, the gastropod assemblage of Lake Tanganyika has also stirred much interest among malacologist and evolutionary biologists (Glaubrecht 2008; see also review of literature therein).

At the same time, though, the knowledge of freshwater molluscs in adjacent regions of Africa is still scarce. In particular, the gastropod fauna of the central African rivers is insufficiently studied, mainly due to continuous adversary logistical and/or political reasons. However, as has been pointed out by Glaubrecht & Strong (2007: 397), not only lakes such as in particular ancient Tanganyika but also the enormous Congo River drainage provide stable evolutionary systems, both in their own right and with distinct inherent en-

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vironmental dimensions. Consistent with this view is the hypothesis that at least part of the fauna of Lake Tanganyika might be older than the lake itself, its basin thus potentially functioning as an evolutionary reservoir since the Miocene, as we have anticipated recently for its paludomid gastropods (Glaubrecht 2004; Wilson et al. 2004).

With emphasis starting to shift to non-lacustrine settings in studies not only of African cichlid fishes (e.g. Kocher 2005; Joyce et al. 2005) but also of Asian and African cerithioidean gastropods (e.g. Glaubrecht 2004; Glaubrecht & Köhler 2004; Glaubrecht & Strong 2007; Köhler & Glaubrecht 2010; Köhler et al. 2010), lacustrine species flocks are not necessarily to be seen as evolutionary dead ends. Quite to the contrary, it can be expected that the potentially repeated switch of limnic taxa between riverine and lacustrine habitats during the course of their evolution guaranteed their survival, and at the same time provided ample evolutionary opportunities for speciation and radiation under various conditions, as Glaubrecht (2004) and Glaubrecht & Strong (2007) have suggested for African paludomid gastropods.

It is this context that renders the fluviatile gastropods from Central Africa of special interest. Equal to great lakes such as Tanganyika and Malawi, the Congo River and its easternmost tributaries have an outstanding rich species assemblage, not only of unique molluscs, that deserve more attention. Unfortunately, the material basis as well as our knowledge for many of the constituent members for long has remained regrettably poor. Despite them being demonstrably of considerable interest for evolutionary biology, no large-scale exploration of limnic habitats in the Congo Basin has been undertaken for several decades now, and I am not aware of any more recent collections of relevant material from the Congo River, rendering even the oldest and poorest museum collection records of great importance.

**Figure 1.** The Congo River drainage in Central Africa, with the occurrences of *Cleopatra broecki* in its tributary, the Aruwimi River, and of species attributed to *Potadomoides* Leloup, 1953. Basoko, as locus typicus given for *C. broecki* zonata; see text for more; * = locus typicus of the type species *Potadomoides pelseneeri*; ▲ = *Potadomoides bequaerti*; ■ = *Potadomoides hirta*; ○ = *Potadomoides schoutedeni*. Scale bar = 100 km.
Among the enigmatic freshwater gastropods, for which we lack most biological information since their first descriptions, are species of the paludomid genera Cleopatra Troschel, 1856 and Pseudocleopatra Thiele, 1928 that occur also in the drainages of the Congo River system in the Central African Basin. To date, the systematic placement of several of their species is essentially based on shell characters alone, since operculum and radulae or other anatomical characters remained unknown.

For example, in a short note the Belgian malacologist S. Putzeys (1899) described Cleopatra broecki, that later authors, e.g. Mandahl-Barth (1967) and Brown (1994: 131), transferred to the genus Potadomoides Leloup, 1953, a taxon with species occurring in the Lualaba and Luvua tributary of the upper Congo River as well as a single species, viz. the type P. pelseneeri Leloup, 1953, disjunctly distributed in the delta of the Malagarasi River that flows into eastern Lake Tanganyika (Fig. 1). These taxa are of particular interest in relation to the ancestry of the radiation of the so-called „thalassoid“ (i.e. marine-like) gastropod fauna of Lake Tanganyika. It was long assumed, according to Brown (1994: 129), that among the living gastropods Potadomoides had the strongest claim for consideration in relation to the ancestry of this Tanganyikan radiation. While addressing the question of the origin of the Tanganyikan gastropod radiation (Glaubrecht 1996, 2008) and systematically revising the fluviatile Potadomoides (Glaubrecht & Strong 2007) it was established, however, that this taxon is not ancestral to the entire endemic species flock of thalassoid Tanganyikan gastropods. Instead, it was suggested that a fluvio-lacustrine clade Nassopsinae, uniting two lacustrine taxa (Lavigeria and Vinundu) with the fluviatile Potadomoides, apparently represents an early independent lineage of East African paludomids that until recent times survived in and adjacent to Lake Tanganyika. Consequently, while Potadomoides does certainly not serve as a suitable model for the majority of the thalassoid gastropods, it might serve as a model for an African paludomid with the potential to colonize not only fluviatile but also lacustrine habitats (Glaubrecht 2004, 2008).

In the course of an ongoing systematic revision of African paludomids, types and other material of constituent taxa from several museum collections were studied. In comparison with the types of Potadomoides and species of Cleopatra I will here investigate additional type material housed in the collection of the Musée Royal L’Afrique Centrale in Tervuren, Belgium, as well as material found in the collection of the Museum of Comparative Zoology of the Harvard University in Cambridge, Mass., USA (MCZ). Radulae retrieved from dried soft bodies found with the latter sample help to elucidate the radula morphology of C. broecki which was unknown to date (Fig. 5). For radula comparison a sample of the type species Cleopatra bulimoides, from Medinet el Fajum in Egypt from the ZMB collection (ZMB Moll. 31148-1), was studied.

Methods and terminology for shell measurements follow Glaubrecht (1996). Drawings were done using a Leica 9.5 binocular microscope with camera lucida. Radulae were prepared from re-hydrated soft bodies found within the shell, and photographed using a Jeol 6300F Scanning Microscope at ZMB with standard procedures. Formula for radular tooth descriptions are as follows. Rachidian: numbers of denticles on the left side/median denticle(s)/numbers of denticles on the right side. Lateral teeth: inner cusps/branched denticles/outer cusps. Marginal teeth: number of cusps on inner marginal tooth + number of cusps on outer marginal tooth.

The name used throughout this paper for the former Belgian Congo, later known as Zaire, is Democratic Republic of Congo (DRC).

On the taxonomic history of Cleopatra broecki

The systematic placement of Cleopatra broecki remained uncertain for over a century. The Belgian malacologist S. Putzeys (1899) published a very short scientific note of six printed pages only, devoid of any other information and presenting basically the diagnoses for several, mostly terrestrial gastropods, for example species of Cyclophorus and Streptaxis, before adding in a last brief paragraph the description of a new limnic paludomid species, which is depicted in his text-figure 16.

Unfortunately, nothing is known as to who collected and/or brought back Putzeys’ gastropod material from the Congo, which suffered at that time under King Leopold II. Since the European nations’ Berlin Congo conference of 1884–1885 on colonial influences in Africa, the euphemistically so-called “Congo Free State” was de facto Leopold’s private colony before being turned in 1908 into the Belgian Congo until 1960 [with a regime of terror leading to the decimation of approximately three to ten million people from 1885 to 1910 (see Hochschild 1998); as described e.g. in Joseph Conrad’s (1899) famous novella “Heart of darkness”, first published as three-part magazine series, coincidentally in the same year as Putzeys’ taxa; see epitaph].

In his revision of African freshwater snails the German malacologist Kobelt (1909: 383) listed broecki within the genus Cleopatra, but discussed its affinity also to Viviparus and Bellamy, while Pilsbry & Be-
quaert (1927: 296) accepted the original placement within Cleopatra. It was later the Danish malacologist Mandahl-Barth (1967) who suggested transferring this species to Leloup’s (1953) new and, at that time, monotypic genus Potadomoides. Adding to P. pelseneeri Leloup, 1953, which is known to only occur in the former Congo River system to the east of Lake Tanganyika, viz. the Malagarasi River (Fig. 1), Mandahl-Barth (1967) also transferred three other species from the upper Congo River system. These three species, viz. P. bequaerti, P. hirta and P. schoutedeni, were originally described by Dautzenberg & Germain (1914) as mem-

bers of the widespread African genus *Cleopatra*. How-
ever, all three of them actually exhibit radula features very similar to Leloup’s *P. pelseneeri*. Mandahl-Barth (1967) examined (and in one case depicted) the radula of these three new *Potadomoides* species, which were recently re-discovered and studied by Glaubrecht & Strong (2007). However, in case of *broecki*, Mandahl-Barth neither figured nor described the radula.

According to him, Putzeys’ original description, al-
beit being rather brief, “indicates a *Potadomoides rather than a Cleopatra*” (Mandahl-Barth 1967: 130). Himself being brief there (with only five lines on this taxon), he did not further specify as to why this should be the case. However, Mandahl-Barth added, “a final decision must be postponed until the radula is known”. Later, Brown (1994: 130–131, fig. 62d) has redrawn the original shell figure (apparently without studying the types), and also allocated *broecki* within *Potado-
moiides*, albeit “with hesitation only”, since radula and operculum were unknown. This species since then re-
ceived no further attention or study. It was, however,
excluded from their study on *Potadomoides* by Glaubre-
cht & Strong (2007: 393), for the reason of new data being available, which is presented here.

**Systematic Part**

**Paludomidae**

**Cleopatra Troschel, 1856**

This genus of paludomid Cerithioidean (for a discus-

sion of the familial affiliation see Glaubrecht 2008), is characterized by mostly ovate, medium-sized shells with generally more or less sharply pointed, but often eroded (or decollated) spire with up to six whorls, that are mostly rounded in cross-section and usually have a distinct shoulder. The whorls are generally smooth, sometimes slightly angulated, with a sculpture consist-
ing essentially of growth lines only; however, some spe-
cies also exhibit spiral elements, such as keels or ridges; often these are not very pronounced. The aperti-
ture is usually higher than wide, angular above and rounded or slightly produced below. The outer margin is flattened and mostly evenly rounded. Shell colour is mostly beige to brown, sometimes dark brown; in some species with several smaller spiral bands. The opercu-

lum is thin, concentric, with spiral, slightly eccentric nucleus, concave and of mostly dark horny colour. Some 17 species are known from Africa and Madagascar; a modern revision is lacking but desperately needed. For more details see e.g. Mandahl-Barth (1967), Brown (1994) and Glaubrecht (1996).

**Cleopatra broecki** Putzeys, 1899

*Cleopatra broecki* Putzeys, 1899, Annales de la Société Royale Malacologique de Belgique, Bulletins des Séances 34: 60, fig. 16.

*Cleopatra broecki zonata* (as var. *zonata*) Putzeys, 1899, Annales de la Société Royale Malacologique de Belgique, Bulletins des Séances 34: 60.


(?) *Potadomoides broecki* – Brown 1980 [1994], Freshwater snails of Africa: 114, fig. 64d [p. 130, fig. 62d].

Type locality, “Trouvé sur des valves d’Aethéries de la rivière Aruwimi, affluent du Congo”; Aruwimi River, today DR Congo, Oriental Province (Fig. 1). Although not given more precisely by Putzeys (1899) in his original description, and hitherto overlooked, it is nevertheless possible to restrict the type locality to Basoko according to the label associated with the holotype of Putzeys’ var. *zonata*, for which he stated in the text that the habitat is “memé provenance” (as that of the nominal *broecki*). This doubtlessly refers to the large vil-

lage or today’s city of the same name, located at the eastern shore of the Congo River, just north of where the Aruwimi enters.

Type material. C. *broecki*: Lectotype, by present designation (MRAC 47.360; from Aruwimi River, ded. Putzeys 1935); this shell (Fig. 2c) agrees best with Putzeys’ original text-figure and the shell measure-
ments given. One paratype (MRAC 47.361; Aruwimi River, ded. Putzeys 1935) (Fig. 2d). Holotype of *zonata* (MRAC 47.362) from the same series and with the location “Basoko” stated on the label (Fig. 2e).

Additional material examined. Here attributed to *Cleopatra broecki*: A series of n = 13 specimens (MCZ 171520), from “near Luozi, Kas-
bunzi, Zaire [= Congo]; coll. W. Watson; acc. no. 1027” (see Fig. 2f). The location lies at the northern bank of the lower Congo River, north

![Figure 3. Shells of *Cleopatra broecki*, MCZ 294126; from 3 km E of Inga, N of Matadi, lower Congo River mainstream, E bank of river; from fish stomach, coll. T. Roberts, D. Stewart, 1 Aug 1973. Scale: 1 cm.](image)
of Matadi. Also attributed here to *C. broecki* a smaller series of $n = 4$ specimens (MCZ 294126), also from lower Congo River, N of Matadi: “23 km E of Inga, Zaire [= Congo] River mainstream (E bank of river) (5°27.5 S, 13°36 E), from fish stomach; coll. T. Roberts, D. Stewart, 1 Aug 1973” (Fig. 3).

**Taxonomic remarks.** Although not directly indicated in his note, Putzeys (1899) apparently named this species after the then active and known Belgian malacologist Ernest van den Broeck. He described it based on a small series of only three shells, as can be judged from the types that came to the MRAC in 1935, according to the cryptic label information. In his report Putzeys differentiated, next to two larger shells (Figs 2c–d) also one variety *zonata* for a slightly smaller, banded shell. The latter was already considered by Pilsbry & Bequaert (1927) to be conspecific, which is agreed on here from the comparison of the respective types (see Fig. 2e). For the full taxonomic history of the changing generic affiliation of *broecki* see above.

**Description.**

**Shell** (Fig. 2). Shells are smooth and thick; the only sculptural element is a faint *anwachsstreifung*. The shells have a weakly angular periphery, with short transverse ridges on upper whorls. The lectotype (MRAC 47.360), as designated herein (Fig. 2c), was originally stated to measure 10.5 x 6.5 mm, with a 6 mm long aperture (Putzeys 1899). The syntype series comprised $n = 3$ shells with the following parameters: height = 9.23 (sd 1.01) and width = 6.90 (sd 0.70). The height to width ratio is here calculated as $h/w = 74.99$ (sd 6.01). Shell measurements are given in Table 1; compare also Figure 6.

The shell measurements for the additional material from the MCZ series (Figs 2f and 3) are also given in Table 1. For the $n = 13$ shells (MCZ 171520) the parameters are quite similar to the type series: height = 8.5 (sd 1.08), width = 6.8 (sd 0.93), although with a higher $h/r$ ratio = 81.06 (sd 5.60) and 85.8 (sd 6.67), respec-

| Table 1. Shell parameters of the types of *Cleopatra broecki*, and additional material attributed in the present paper to this taxon from the MCZ collection. Note that the apex of all shells is decollated. Measurements given in mm; x = arithmetic mean, sd = standard deviation. |
|---------------------------------|-----------------|---------|---------|---------|
| **Paludomidae** | **repository** | **height** | **width** | **whorls** |
| *Cleopatra broecki* | MRAC 47.360 lectotype | 10.1 | 6.9 | 3 |
| | MRAC 47.361 paralectotype | 9.5 | 7.6 | 2 |
| | MRAC 47.362 type | 8.1 | 6.2 | 3 |
| | x: | 9.2 | 6.9 |
| | sd: | 1.01 | 0.70 |
| | **height** | **width** | **whorls** |
| *Cleopatra broecki* | MCZ 171520, $n = 13$ | 9.0 | 7.3 | 2 |
| | 6.9 | 5.7 | 3 |
| | 9.4 | 7.9 | 2 |
| | 10.6 | 8.1 | 2 |
| | 9.4 | 7.9 | 2 |
| | 9.6 | 7.7 | 2 |
| | 8.2 | 6.6 | 2 |
| | 8.8 | 7.1 | 2 |
| | 7.8 | 6.3 | 2 |
| | 7.2 | 6.9 | 2 |
| | 7.4 | 5.7 | 3 |
| | 7.3 | 5.2 | 3 |
| | 8.3 | 6.6 | 2 |
| | x: | 8.5 | 6.8 |
| | sd: | 1.08 | 0.93 |
| | **height** | **width** | **whorls** |
| *Cleopatra broecki* | MCZ 294126, $n = 4$ | 8.9 | 7.1 | 4 |
| | 9.8 | 9.0 | 3 |
| | 10.4 | 9.5 | 2 |
| | 10.6 | 8.5 | 2 |
| | x: | 9.9 | 8.5 |
| | sd: | 0.76 | 1.03 |
tively, as it is the case of the second, smaller series (MCZ 294126).

Operculum (Fig. 4). Among the shells of the original syntype series one detached operculum was found, which is attributed to the lectotype of *C. broecki* (MRAC 47.360), due to size and fit with the aperture of this particular shell. As typical for *Cleopatra*, it is concentric and with a spiral nucleus. Only the nucleus, positioned slightly eccentric with respect to the columellar side, is paucispiral, lamellar, and of less than half the length of the operculum (Fig. 4a). The same pattern was found in one operculum of *Cleopatra broecki* from the additional series (MCZ 171520) from Kibunzi (Fig. 4b). Here the nucleus is deeply concave with knob-like intrusions on the ventral side. Again, when compared to the operculum of the type species *Cleopatra bulimoides* (MRCA), we find this to be also concentric, with eccentric and spiral, lamellar nucleus, of less than half the entire length (Fig. 4c).

Anatomy. The animal is unknown, as no soft bodies were found with the original type series. The radulae described below originate from dried soft bodies found and extracted from the additional shells in the MCZ (171520), here attributed to *C. broecki* based on shell parameters and operculum. The only features visible in the dried-up animals were the black colour of body, with a pigmented, whitish stripe along the right side running to the propodium. Apparently, they lack a clearly invaginated genital gutter or any other features related to reproductive organs in this place, but have a smooth mantle edge without papillae.

Radula (Fig. 5). The radulae found in shells attributed here to *Cleopatra broecki* (MCZ 171520, from Kibunzi) is clearly distinct, in particular with respect to the rachidian and laterals, from that known in all radulae of *Potadomoides*; for comparison and description see Glaubrecht & Strong (2007). While all known four species of the latter genus exhibit a narrow rachidian tooth, slightly more than 1.5-fold larger than wide, tapering to a V-shaped base, and with only few, mostly three cusps of the 1/1/1 pattern only, the central tooth in *Cleopatra*, here shown for *Cleopatra bulimoides* (ZMB Moll. 31148-1, from Medinet el Fajum) (Figs 5a–c) and that found in *C. broecki* (Figs 5d–f), appears to be different in essential features.

The rachidian of *C. broecki* is of roughly squarish to rounded shape, nearly as wide as high, with up to 15 denticles (7/2/7) at the upper edge (Figs 5a–b). This is also found in *C. bulimoides* (Figs 5d–e) as well as other *Cleopatra* species; for *C. ferruginea* see also Glaubrecht (1996) and radula figures in Pilsbry & Bequaert (1927: 289). Lateral teeth in *C. broecki* (Fig. 5d) again bearing many small denticles, mostly of a 2–3/1/9 + pattern, of roughly triangular shape; with the central denticle pronounced, larger and bluntly rounded, and the outer flankng denticles decreasing in size to continue in the relatively short lateral extensions. Inner and outer marginal teeth moderate long, both with a row of up to 18 or 20 very small denticles.

In the $n = 2$ radulae studied for the *C. broecki* material the ribbon consists of between 60 to 82 rows, as compared to about 60 rows in $n = 2$ radulae in *C. bulimoides* (this study) and 70, 76 and 82 rows, respectively, found in *Potadomoides* species (Glaubrecht & Strong 2007).

Distribution and Ecology. Reported originally only from the Aruwimi River, a tributary of the River Congo, northwest of Kisangani (Fig. 1). However, nothing more is known as to the precise occurrences of this taxon along this river that originates far to the east, in the mountainous region of the eastern shoulders of the Rift Valley, close to Lake Albert, at the border of the DR Congo and Uganda. I searched, albeit in vain, for those locations that Putzeys (1899) gave for the terrestrial snails also described in his short paper (e.g. Manyéma, forêt de Micici, forêt de Waregga, and Nseudwé etc.).
Based on the inclusion of additional material attributed here to *Cleopatra broecki* based on the evidence presented above, the distributional range of the species expands further downstream along the Congo River, to include also its lower reaches N of Matadi, with two locations known now at Inga, on the E bank of the Congo River mainstream, and at Luozi near Kibunzi, at the northern bank of the lower Congo. However, as detailed above, the type locality should be restricted to Basoko, immediately at the confluence of the Aruwimi with the Congo River.

According to a note in Putzeys (1899: 60), *broecki* was found there on the shells of *Etheria*. It is an oyster-like, sessil freshwater bivalve of equatorial Africa, with today recognized a single species, *Etheria elliptica* Lamarck, 1807 (the “Nile or Congo Oyster”), within the Etheriidae Deshayes, 1830. As an edible clam it is harvested by local people along African rivers as traditional food.

**Discussion**

As is evident from the continuous confusion of species of *Cleopatra* and *Potadomoides* in earlier accounts (see historical review above), the shells of those taxa in question here are quite similar to each other. However, re-investigation of the types of *C. broecki* and the comparison of now available data on shell, operculum, ra-
dula and geographical occurrence allows to differentiate between both genera and to re-transfer this species.

Characters used in systematic placement

The overall shell shape of relevant paludomids from the Congo River drainage, given as shell height versus shell width, reveals that not only *Potadomoides* species (including the type *pelseneeri*) but also other *Cleopatra* species (including the type *bulimoides*) can be differentiated from *C. broecki*. In the compilation of the data for Figure 6 I have used the height and width parameters for these taxa to show the occupation of different morphospace in three *Potadomoides* and four *Cleopatra* species, with *C. broecki* being distinguishable from all, but closest to the type *C. bulimoides*. In contrast to the latter two relatively small-shelled species, *C. johnstoni* and in particular *C. ferruginea* clearly stand out as taxa with larger shells.

The data presented here for the operculum of the lectotype of *C. broecki* for the first time clearly reveals a concentric one with paucispiral, slightly eccentric nucleus, as it is also found in *Cleopatra* and *Pseudocleo-patra* (see Glaubrecht 1996). With this the species is to be distinguished from *Potadomoides*, where the operculum was found to be paucispiral with sub-central nucleus on the columellar side (see Glaubrecht & Strong 2007: fig. 5).

Radula features have been proven to be of great systematic value not only in many gastropod taxa in general, but in particular among the different lineages of freshwater Cerithioidea (Glaubrecht 1996, 1999, 2006, 2008). Thus, next to the operculum that allows to now link the relevant sample MCZ 171520 to the MRAC types of *broecki*, the most conclusive evidence for re-transferring this species to *Cleopatra* comes from its radula features. The radula in *Potadomoides* reveals a series of tooth and dentine features that clearly distinguish it from that in *Cleopatra* (see e.g. Brown 1994; Glaubrecht 1996; Glaubrecht & Strong 2007). Among this, most importantly the rachidian, lateral and marginals of the *Cleopatra* species studied so far are all of different shape, and they all bear regularly far more cusps than found in the four *Potadomoides* species. The narrow, tall rachidian in the latter is clearly distinct from the squarish to round and much wider central tooth in *Cleopatra* including *broecki*, as is the often spatula-like broad central denticles of the rachidian and lateral. Most strikingly, however, in all *Potadomoides* species, we found the outer and inner marginal teeth to be dissimilar, with the inner ones with major cups being very broad and spatula-shaped (Glaubrecht & Strong 2007: fig. 6), whereas in all *Cleopatra* species known so far the denticles of the marginals are much more numerous and of similar size and shape in the inner and outer ones.

Therefore, based on the similarity of their radulae with the type species *pelseneeri*, Mandahl-Barth (1967) correctly assigned and transferred Dautzenberg & Germain’s (1914) former *Cleopatra* species *bequaerti*, *hirta* and *schoutedeni* to LeLoup’s (1954) *Potadomoides*.

![Figure 6](museum-zoosyst.evol.wiley-vch.de)

**Figure 6.** Shell shape of paludomids from the Congo River drainage, here given as shell height vs. shell width, showing the occupation of different morphospace by three *Potadomoides* and four *Cleopatra* species, respectively; including the type species *P. pelseneeri* and *C. bulimoides* in comparison with *Cleopatra broecki*. 
Lacking this particular piece of evidence, though, he was only wrong in the case of *Cleopatra broecki*.

**On the occurrence and distribution of *Cleopatra broecki***

Glaubrecht & Strong (2007) have reconstructed and commented on the compelling disjunct distribution of *Potadomoides*, with *P. pelseneeri* being restricted to the delta region of the Malagarasi River east of Lake Tanganyika, whereas the three congeneric species *P. bequaerti*, *P. hirta*, and *P. schoutedeni* inhabit the Congo River with its tributaries Lualaba and Luvua (but apparently not the Lukuga), west of the Tanganyikan Rift (see Fig. 1). Thus, concerning the distribution as reconstructed here and the restricted type locality of *Cleopatra broecki* at the confluence of the Aruwimi with the Congo River, the occurrence in the Oriental Province of the DRC seems to be sufficiently separate from that of the remaining *Potadomoides* species.

However, given our poor state of knowledge on the fluviatile malacoфаuna in the eastern Congo River system, the possibility can, of course, not be excluded that the actual distributional range of both taxa is larger, rendering their occurrence less disjunct, parapatric or maybe even sympatric. Nevertheless, in concert with the morphological data provided herein, the biogeographical facts known to date lend additional support to the removal of *broecki* from *Potadomoides* and its assignment to *Cleopatra*. In contrast to the restricted range of the former, congeneric species of *Cleopatra* seems to occur widely distributed from west to east across central Africa, and reaching all the way from the north through the extensive Nile drainage system to the southern parts of Africa, expanding even to the island of Madagascar (see Brown 1994).

**Conclusion**

The available data presented here reveals, as it was first anticipated in Glaubrecht & Strong (2007: 393), that *Cleopatra broecki* does in fact not represent a member of *Potadomoides*. Based on conchological, operculum and, in particular, radula characters, in concert with the outlying geographical occurrence in the Aruwimi River of the northeastern part of the upper Congo River system, it is suggested that *broecki* is actually a constituent member of the widely distributed African *Cleopatra*. By contrast, as was shown earlier, the known occurrences of *Potadomoides* are all restricted to the upper most, i.e. south-eastern tributaries of the Congo River drainage, viz. the Luvua and Lualaba as well as, east of Lake Tanganyika, the Malagarasi River.

Unfortunately, since nothing more is known on the anatomy of this species, quite some interesting questions in this context remain unresolved, such as e.g. that on potential (ovo-)viviparity in riverine paludomid gastropods from the vast Congo region to the west of ancient Tanganyika, of which this reproductive mode has been suggested earlier as key innovation for lacustrine colonization, speciation and radiation; for critical discussion and literature see Glaubrecht (2008).

Hopefully, in the future new data will come to light for congeneric taxa of *Cleopatra*, as their occurrence to the west and north of the Tanganyikan basin and drainage might eventually help to better understand the origin of the lacustrine malacoфаuna of this ancient lake. In contrast to the long held assumption of an *in situ* radiation of its “thallassoid” species flock, Lake Tanganyika has possibly functioned as a reservoir for ancient African lineages, implying that the now lacustrine taxa originated elsewhere (in the west). As long, however, as the fluviatile gastropod fauna of adjacent river systems in Central and East Africa is not better known, eventually founded on new collections of relevant material especially from the Congo River drainage, even the oldest and poorest museum collection records – such as in case here of Putzeys’ *broecki* – remain important in context of reconstructing the evolutionary history of riverine and lacustrine gastropod radiations in Africa.

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