

# THE SYSTEMATIC POSITION OF *UNIO CAFFER* (PELECYPODA: UNIONOIDA: UNIONIDAE)

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## ABSTRACT

Some anatomical, adult shell and larval features of *Unio caffer* Krauss are described and compared to those reported in previous accounts of this and other species. The findings necessitate the removal of *U. caffer* from the nominal genus *Cafferia* Simpson, for which it is the type species, and its return to the genus *Unio* Philipsson, in the Unionidae: Unioninae. *Cafferia* consequently becomes a junior subjective synonym of *Unio*.

*Unio caffer* is characterized in part by zigzag beak sculpture, dimorphic septal spacing between the marsupial, outer (comparatively dense) and the non-marsupial, inner (more distant) demibranchs and also within the marsupial demibranchs, the presence of perforated marsupial septa and imperforate non-marsupial septa, the occurrence of hermaphrodites in some but apparently not all populations, production of subtriangular glochidia with a hook at the ventral margin of each valve, short-term incubation of larvae in the marsupial demibranchs, and by its disjunct occurrence in the southern Ethiopian region (other *Unio* occurring only in the Palearctic).

These adult shell and anatomical features relate this species to those of several nominal genera in the Oriental region, although the latter are distinguished from it by the production of subovate, hookless glochidia.

## INTRODUCTION

Nearly all African freshwater mussels belong to the Unionoida: Amblemidae (e.g., *Caelatura* Conrad) and to the Muteloida: Mutelidae (mostly *Aspatharia* Bourguignat and *Mutela* Scopoli). Animals of the former group incubate glochidial larvae in all four demibranchs (cf. Heard & Guckert 1971), whereas those of the latter incubate lasidium-like, haustorial larvae only in the two inner demibranchs (Fryer 1961; Parodiz & Bonetto 1963). Species of those two families range over much of the Ethiopian region south of the Sahara Desert, and also extend down the Nile drainage. Among the Unionoida: Unionidae, in which glochidia are incubated just in the two outer demibranchs (Heard & Guckert 1971; Morrison 1973), allegedly true *Unio* Philipsson (whose adult animal and larval features are unknown) occurs in the northernmost part of Africa, north of the Sahara Desert, i.e., in the southernmost western Palearctic region. The only unionid in the Ethiopian region is *Unio caffer* Krauss (Figure 1). This species, for which Connolly (1939) listed three nominal subspecies (viz., *Unio caffer* s.s., *U. c. verreauxi* 'Charpentier' Küster and *U. c. connollyi* Pilsbry), has been recorded from the Republic of South Africa, south-eastern Rhodesia and allegedly but doubtfully Malawi (Haas 1936: 49, 1969a: 159-166; Connolly 1939: 604-610).

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*Unio caffer* Krauss, 1848, was originally designated as the type species of *Cafferia* Simpson, 1900, a taxon conchologically established as a section of *Nodularia* Conrad [= *Unio* Philipsson, 1788, *vide* Ortmann (1918a)]. Connolly (1912) elevated *Cafferia* to generic rank, and emended the specific name *caffer* to *caffra* to agree with the gender of the generic-group name *Cafferia*. Simpson (1914) subsequently recorded *Cafferia* as a section of *Unio*, and Pilsbry & Bequeart (1927), Thiele (1935) and Connolly treated it as a subgenus of that group. More recently, Haas (1936, 1969a, 1969b) and Modell (1942, 1949, 1964) have considered *Cafferia* to be a valid, monotypic genus, and Haas (1969a) treated the subspecies listed by Connolly (1939) as synonyms of *C. caffra*. Modell (1964) reported *Cafferia* from the Upper Cretaceous of the Transvaal, Republic of South Africa, and from Eocene deposits in France, whereas Haas (1969b) recorded only Pleistocene fossils ('. . . in der Kalahari zwischen Oranje und Kunene' *vide* Haas 1969a: 156).

Simpson (1900) originally placed *U. caffer* in the Unionidae: 'Hyrianae' [= Hyriidae Swainson *vide* Parodiz & Bonetto (1963) and Heard & Guckert (1971), in which glochidia are incubated in only the two inner demibranchs], and later (1914) listed it in the Unionidae: Unioninae. Ortmann (1918b), Thiele (1935) and Haas (1969a, 1969b) also classified *Unio caffer* in that subfamily, whereas Pilsbry & Bequeart (1927), Haas (1936) and Connolly (1939) placed it simply in the Unionidae. Modell (1942) originally employed *Cafferia* as the type genus of his new unionid subfamily Cafferiinae, but later (1964) recorded it in the Unionidae: Rectidentinae. All of the above classifications, except those of Ortmann (1918a, 1918b) were based on shell characters.

Several classifications of freshwater mussels, or naiades, based on shell-structure have been proposed (Simpson 1900, 1914; Modell 1942, 1949, 1964; Haas 1969a, 1969b), although some workers have employed anatomical and reproductive features to define superfamilial, familial and subfamilial taxa (Ortmann 1910, 1911a, 1911b, 1912; Parodiz & Bonetto 1963; Heard & Guckert 1971; Heard 1974). Animal characters have also been used to define generic limits (e.g. in the Unionidae: Lampsilinae of the Nearctic region), but less widely because of the lack of such information about the type and other species of most nominal generic-group taxa. However, as noted by Heard & Guckert (1971), classifications based on soft-part anatomy and reproduction often differ significantly from those based on shell characters.

The purposes of this paper are to describe what are considered to be the systematically significant animal features of *Unio caffer* Krauss, and, with an evaluation of shell characters, to provide an interpretation of the phylogenetic position and affinities of this species.

#### MATERIALS AND METHODS

The nine shells and animals upon which this report is based were collected on 17 July 1972 at the Lundi River [Sabi-Save drainage] at Chilonga Crossing, about 24 km south of Chiredzi, Chiredzi District, south-eastern Rhodesia. The shell lengths ranged from 35.8 to 57.3 mm ( $\bar{x}$ : 46.8  $\pm$  7.1). Voucher specimens have been deposited in the Museum of Zoology, University of Michigan (catalogue number MZUM-234710).

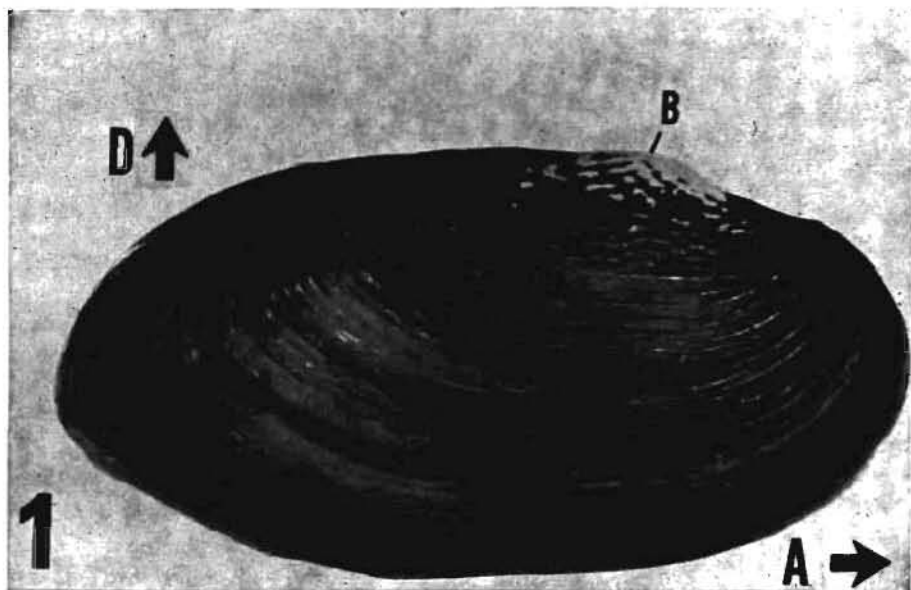


FIGURE 1

Shell (right valve) of *Cafferia caffra*.

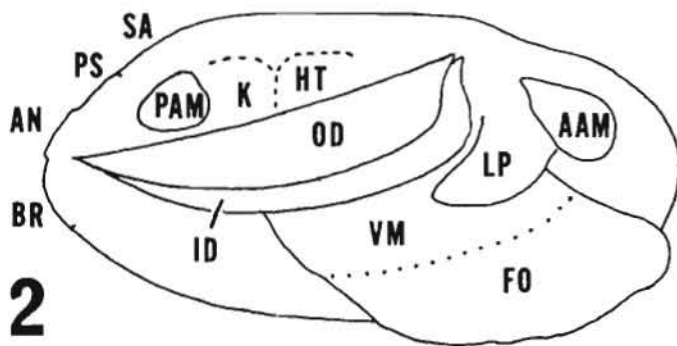


FIGURE 2

Lateral aspect of general anatomical organization (right valve and mantle below the suprabranchial chamber removed). For abbreviations see page 56.

The adult naiades were narcotized with 10 per cent sodium nembutal, fixed in 10 per cent formalin, and preserved initially in 1 per cent propylene phenoxetol and subsequently in 70 per cent ethyl alcohol. After the animals were removed intact from the shells, gross dissection revealed most features; measurements were taken with vernier calipers. The sex of each individual was determined by removing parts of the visceral mass containing the gonads and preparing them for histological examination: paraffin embedding, sectioning at a thickness of 10  $\mu\text{m}$ , and staining with Harris' hematoxylin and alcoholic eosin. Portions of the outer and inner demibranchs of each individual were also removed and prepared for histological examination; shells of any glochidial larvae present in the marsupial demibranchs were decalcified with a 1 per cent solution of hydrochloric acid in 70 per cent ethyl alcohol prior to embedding.

Seven of the nine animals were gravid, and some incubating larvae were removed from each marsupial demibranch and studied with a compound microscope; measurements were taken with a calibrated ocular micrometer.

#### ANATOMICAL DESCRIPTION OF ADULTS

Posterior margins of mantle sheets not united internally, but drawn together by the diaphragm; the latter, consisting only of the ctenidia, posteriorly separating the suprabranchial chamber from the branchial chamber. Supra-anal opening present (Figure 2, 3), separated from the anal (excurrent) opening by a superficial pallial suture nearly as long as the anal opening; anal opening about two-thirds as long as the supra-anal opening; branchial (incurrent) opening about twice as long as the anal opening, not separated from the latter by a pallial union. Inner surface of inner lobe of mantle sheets simple, i.e. without papillae, except at the branchial opening. Branchial papillae arranged in three rows, long and tereted, only rarely bifid apically; most anterior row with the largest and fewest papillae, the size decreasing and the number increasing to the most posterior row. Pigmentation pattern on inner surface of inner lobe of posterior end of mantle sheets (Figure 3) consisting of a dense concentration of melanin, forming a distinct band, along the apex of the supra-anal opening and the adjacent pallial suture; small 'flaps' of anal opening covered with heavy dusting of rust-orange pigment, and containing irregularly interspersed blotches of melanin; branchial vestibule with heavy dusting of rust-orange pigment on all papillae, but becoming fainter anteriorly, and with superficial light dusting of melanin around the bases of and between the papillae. Edge of mantle sheets anterior to the branchial opening not united by a pallial suture, and simple (i.e. lacking flaps, papillae, caruncles and crenulae).

Dorsal margin of outer lamella of outer demibranchs united with the inner surface of the mantle for all but the most posterior 1–2 mm, leaving the diaphragm incomplete; dorsal margin of inner lamella joined for its entire length to the dorsal margin of the apposing outer lamella of the inner demibranchs. Dorsal margin of inner lamella of inner demibranchs attached to the visceral mass (abdominal sac) for about its most anterior tenth, free from the visceral mass for the next posterior half, and united with the dorsal margin of the apposing inner lamella of the other inner demibranch for its most posterior two-fifths.

Outer lamella of both outer and inner demibranchs of greater height than the inner lamella; each lamella of the inner demibranchs higher than the corresponding lamella of the outer demi-

branches, but the interlamellar connections (septa) in the outer demibranchs higher than those in the inner demibranchs (Figure 4).

Interlamellar connections in all four demibranchs developed as septa that run parallel to the filaments. Septa comparatively distantly spaced (averaging about 16 filaments flanking the intervening water-tubes) throughout the inner demibranchs (Figure 5, 6), and in the posterior fifth to third of the outer demibranchs (Figure 7); septa densely spaced (averaging about seven filaments flanking the intervening water-tubes) in the anterior two-thirds to four-fifths of the outer demibranchs (Figure 7, 8). Distantly spaced septa continuous, complete, imperforate;

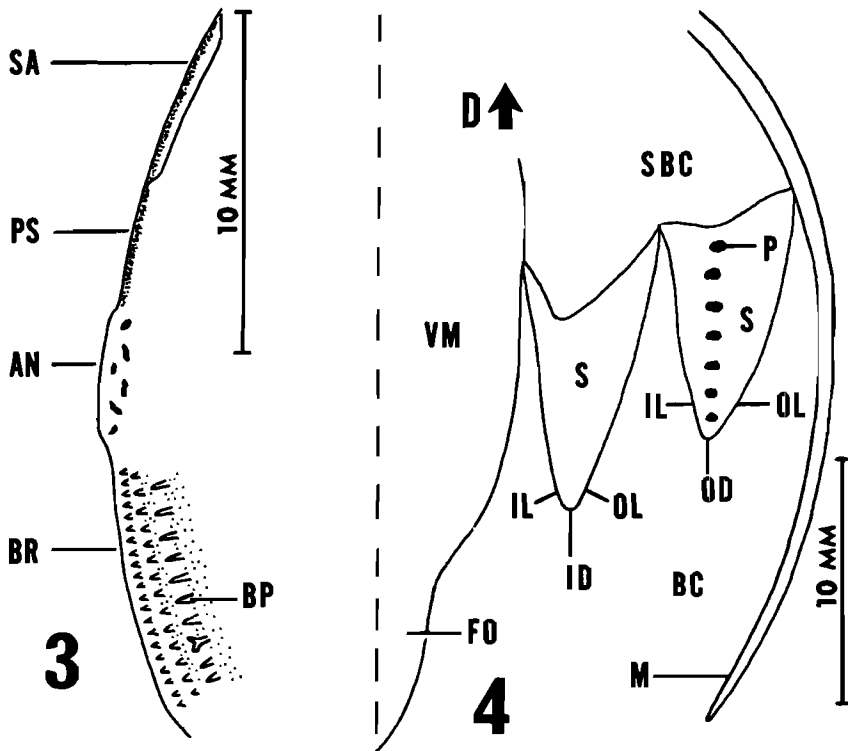


FIGURE 3 (left)

Medial surface of mantle openings and pallial suture. Melanin distribution is the only pigmentation pattern shown.

FIGURE 4 (right)

Transverse section of one side of the animal.

For abbreviations see page 56.

densely spaced septa vertically perforated, with 5–10 small holes per septum (Figure 4: *P*). All water-tubes and septa in all four demibranchs simple, not vertically divided as in the outer, marsupial demibranchs of the Unionidae: Anodontinae (Heard 1975). Only the outer two demibranchs marsupial, and just in the region of the densely spaced, perforated septa (Figure 7).

Labial palpi about one-third as long as the inner demibranchs, and not contiguous with them; palp height nearly half their length. Outer palpi laterally attached to the inner surface of the mantle for nearly two-thirds of their length; inner and outer palpi basally joined to each other for about two-thirds to three-quarters of their length.

All nine individuals were hermaphroditic (Figure 9). The amount of ovarian tissue predominated over that of testicular tissue; monoecious acini were not observed. Both eggs and sperm were present in each animal. According to Heard's (1975) classification of the kinds of monoecious naiades, based on the predominance of one of the types of gonadal tissue and the nature of the septal spacing in the marsupial demibranchs in each individual, this species is a female-hermaphrodite.

No digenetic or aspidogastreaan trematode infestations were found among the nine naiades, although nymphal and adult stages of an unidentified water-mite (Hydracarina) were observed between the outer and inner demibranchs in five of the animals.

#### LARVAE

The larval type observed was a glochidium of subtriangular shape, 0,21 mm long and 0,21 mm high at maximum size, and with an externally punctated, bivalved shell bearing a multi-spined hook at the ventral maring of each valve (Figures 10–13). Of the seven gravid animals, six contained larvae still encapsulated in their individual fertilization membranes, and one possessed seemingly infective glochidia which had escaped from the membrane. The larval shells in each gravid adult were of similar size and constituted a single brood.

#### DISCUSSION

Ortmann (1918*b*) provided a prior anatomical account of *Unio caffer* Krauss, basing his description on specimens from Natal and the Transvaal, Republic of South Africa. The present findings on this species disagree in several important aspects with those of Ortmann, who reported subtriangular but hookless glochidia, indicated the species to be dioecious, described a complete diaphragm, and stated that all septa were imperforate.

Ortmann (1918*b*) considered that, since other features of *U. caffer* were similar to those in several European *Unio* which possess hooked larval shells, the hookless glochidia that he found in this species may have been immature. Although he cited slightly larger glochidia (0,23–0,25 mm long by 0,20–0,21 mm high) than those described here, we conclude that the present hooked larvae were further developed than those which he observed. A similar case has been reported for an Australian hyriid naiad, *Velesunio ambiguus* (Philippi), in which the glochidial valves bear hooks only late in development (cf Hiscock 1951; McMichael & Hiscock 1958).

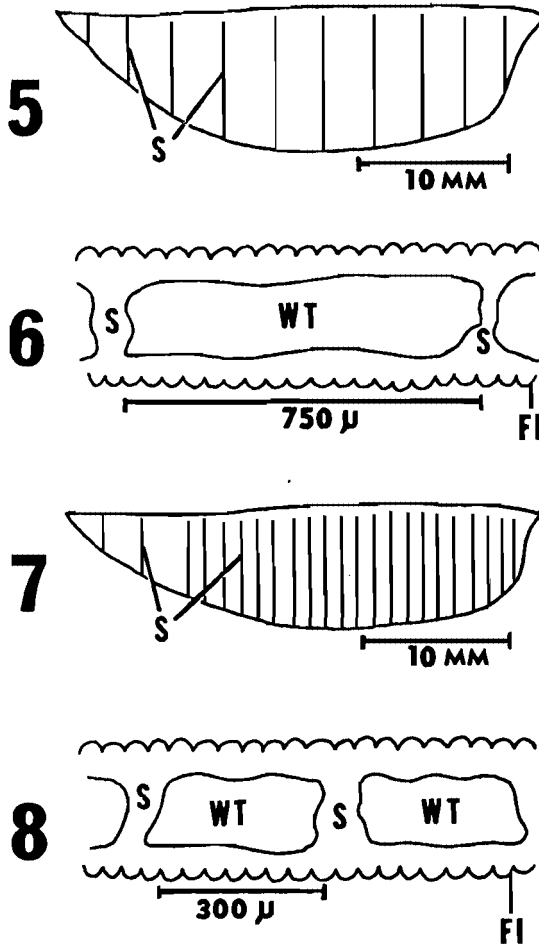


FIGURE 5

Lateral aspect of non-marsupial, inner demibranch with the outer lamella removed to show the organization of septal spacing. Compare Figure 7.

FIGURE 6

Frontal aspect of a portion of the non-marsupial, inner demibranch with comparatively long water-tubes. Compare Figure 8.

FIGURE 7

Lateral aspect of marsupial, outer demibranch with the outer lamella removed to show the organization of septal spacing. Compare Figure 5.

FIGURE 8

Frontal aspect of part of the marsupial portion of the outer demibranch, with comparatively short water-tubes. Compare Figure 6.

For abbreviations see page 56.

The discrepancy between the sexual natures of the specimens of *U. caffer* studied by Ortmann (1918b) and by us suggests that monoecious animals might not occur in all populations. Such differences are known in some Unionidae: *Anodonta* Lamarck (Heard 1975), as well as in some muteloid Mutelidae: *Aspatharia* Bourguignat (Heard unpublished). Ortmann's typically careful attention to anatomical differences between males and females gives us confidence in his description of his material.

The difference between the present and Ortmann's (1918b) findings on the diaphragm is enigmatic, although the nature of the diaphragm in the Unionidae is not as significant a character-state as is the nature of the septa.

Ortmann (1911b, 1912, 1914) previously described some anatomical features of *Unio pictorum* (Linnaeus, 1758) [type species of *Unio* Philipsson], *U. crassus* Philipsson and *U. tumidus* Philipsson from Germany. He reported only imperforate septa, although he mentioned (1912: 275) 'non-marsupial' anterior and posterior ends of the marsupial, outer demibranchs in *U. pictorum* and *U. crassus* (dimorphic septal spacing?). In partial contrast, Haas (1924) described and illustrated perforated septa in the marsupial demibranchs of *U. pictorum* and *U. elongatus* C. Pfeiffer from Spain, and he noted that the marsupial septa were more densely spaced than were non-marsupial septa.

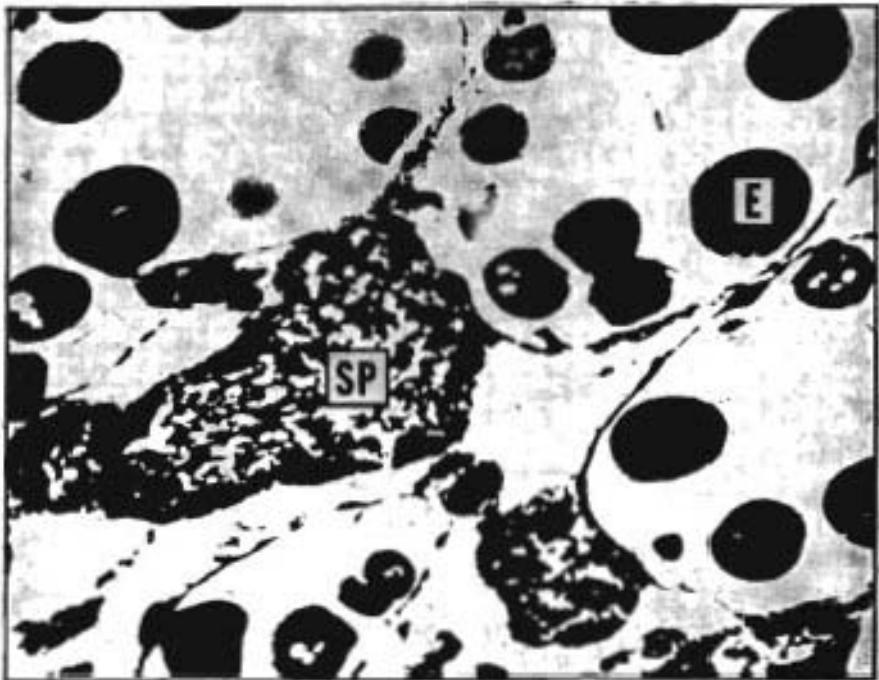


FIGURE 9

Hermaphroditic gonad of *C. caffer*.



Haas (1924) also described perforated marsupial septa in gravid *Potomida littoralis* (Lamarck) (Amblemidae), and suggested that these perforations might vanish during the non-gravid interval between consecutive breeding cycles. However, he did not detail the nature of marsupial septa in non-gravid *Unio*. Ortmann's (1911*b*, 1912) earlier reports of imperforate marsupial septa in *Unio* were based largely on non-gravid females, but his later (1914) material contained gravid animals. Why septal perforations were not present (or, if present, not described) is unknown. Because of purported similarities in anatomy, larval shell-shape, and in adult shell-shape and beak sculpture between European *Unio* and *U. caffer* Krauss, Ortmann (1918*b*) advised retaining the latter in the genus *Unio*.

A conchological feature commonly used to determine generic membership of unionoid naiades is beak (i.e. umbonal) sculpture (Ortmann 1912: 228–230). Three general patterns occur, each with several variations: zigsag (V- or W-shaped ridges), radial and concentric. In some cases, the beak sculpture has been secondarily lost. Many species originally placed in *Unio* have since been relocated in other nominal genera, and those remaining in that genus are customarily regarded as occurring only in the Palearctic region (Haas 1969*a*: 18–60). Although it is considered that congeneric species exhibit the same general kind of beak sculpture, Haas (1969*a*, 1969*b*) recently listed two kinds for *Unio*: several forms of concentric sculpture in western Palearctic species, and several forms of the zigzag kind in species of the eastern Palearctic. However, Ortmann (1918*a*) previously noted that all Palearctic *Unio* have zigzag beak sculpture, with the pattern being pronounced in the eastern *U. douglasiae* Griffith & Pidgeon (type of *Nodularia* Conrad) and much obliterated in the western *U. pictorum*. Ortmann (1918*a*) considered *Nodularia* to be a synonym of *Unio* because of their common pattern of beak sculpture, and because he also found only imperforate marsupial septa in *U. douglasiae*. Haas (1922) did not give details of the marsupial septa in his anatomical description of *U. douglasiae*, and that species should be re-examined for perforated septa. Perforated marsupial septa are present in other species of the eastern Palearctic (e.g. *U. biwae* Kobelt from Japan: Heard unpublished).

*Unio caffer* Krauss, of the southern Ethiopian region, also has zigzag beak sculpture, which pattern extends over part of the rest of the shell (Figure 1). Therefore, because of the kind of beak sculpture and the marsupial anatomy (*viz.* perforated and imperforate septa and dimorphic septal spacing) common to *U. caffer* and *U. pictorum*, we concur with Ortmann's (1918*b*) recommendation and replace the former in the genus *Unio*. *Cafferia* Simpson, 1900, is thus treated as a junior subjective synonym of *Unio* Philipsson, 1788. This action extends the known range of the *Unio* group, and suggests that *U. caffer* is a biogeographic relict.

Other unionids with very similar anatomy and pattern of beak sculpture to *U. caffer* are *Conradens cambojensis* (Sowerby) [= *Uniandra conradens rustica* (Lea) *vide* Brandt (1974); not cited by Haas (1969*a*)] from Thailand (Ortmann 1917; also personally verified) and *Lamellidens consobrinus* (Lea), *L. marginalis* (Lamarck) and *L. thwaitesii* (Lea) [all = *L. testitudinarius* (Spengler) *vide* Haas (1969*a*)] from India (Ortmann 1911*a*; Bloomer 1931). In addition, *Hyriopsis bialatus* Simpson and *H. myersiana* (Lea) from Thailand possess similar anatomical features, but have concentric beak sculpture (Ortmann 1916; Woodward 1965; personally verified). Unlike those of *Unio caffer*, however, the glochidia of those species of *Hyriopsis* Conrad, *Lamellidens* Simpson and *Uniandra* Haas, all of the Oriental region, are of subovate shape (height always greater than length) and lack hooks.

Inaba (1941) and Higashi & Hayashi (1964) described and illustrated subtriangular, hooked glochidia for several unionids from the south-eastern Palearctic region (Korea and Japan): some species of *Cristaria* Schumacher and *Lanceolcra* Conrad, *Unio biwae* and *U. douglasiae*. The beak sculpture is concentric in *Cristaria* and modified-zigzag in the others, and none possess the secondary structural organization of the marsupial demibranchs of the Unionidae: Anodontinae, the species of which also produce subtriangular, hooked glochidia (Ortmann 1910, 1911a, 1912; Heard 1975). Although Haas's (1922) anatomical descriptions are superficial, some similarities between *Unio caffer* and *Lanceolaria grayana gladiolus* (Heude) may be seen. His statement regarding that subspecies (page 293) that 'Die Septen der äusseren Kieme sind vollständig [in context: of full, maximum height]; sie stehen dicht und, besonders in der Mitte,

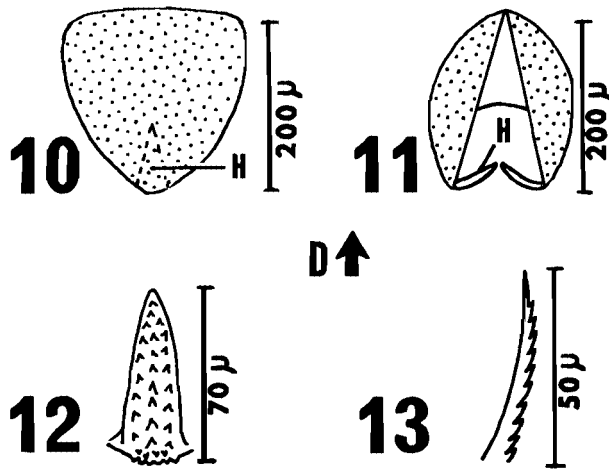


FIGURE 10

Lateral aspect of glochidial larva (one valve).

FIGURE 11

End view of both valves of larval shell.

FIGURE 12

Ventral aspect of spined hook.

FIGURE 13

Lateral aspect of spined hook.

For abbreviations see page 56.

etwas unregelmässig' suggests that these marsupial demibranchs have dimorphic septal spacing and that the central septa are perforated. Nevertheless, *Lanceolaria* and other nominal generic-group unionid taxa in the Oriental and eastern Palearctic regions have a rather characteristic adult shell shape that is distinct from that of *Unio*, and the relationships of these groups to the latter are still unclear.

Modell (1942) erected the subfamilial taxon *Cafferiinae* for *Cafferia caffer* entirely for conchological reasons, stating (page 189) that 'Diese etwas isoliert stehende Gruppe hat ihre nächsten Verwandten in den Contradentinae Südostasiens'. The type genus of the latter, *Contradens* Haas [( = *Uniandra* Haas, *vide* Brandt (1974)], contains species that are anatomically similar to *Unio caffer* (Heard unpublished). However, as already noted here, the larval forms of the two groups differ, and intrasubfamilial variation in naiad larval form is known only in the Nearctic Unionidae: *Lampsilinae*, in which four-spined, celtiform glochidia occur in *Proptera Rafinesque* and subovate, hookless larvae occur in the other nominal genera (Ortmann 1910, 1912). Modell's (1964) later placement of *Cafferia* in the Unionidae: *Rectidentinae* was in error because the type species of that subfamily, *Rectidens prolongatus* (Drouet), is an amblemid (Haas 1922).

Several earlier authors placed *Unio caffer* in the Unionidae: *Unioninae sensu* Ortmann (1910 *et seq.*), an assemblage from which Heard & Guckert (1971) separated the *Amblemidae* (*non* *Amblemidae sensu* Morrison 1955, 1973). This species, as well as others of *Unio*, belong to the Unionidae *sensu* Morrison (1973), but not to Morrison's (1955) earlier concept of that family.

In treating the recent North American naiades, Heard & Guckert (1971) defined subfamilial limits partly on anatomical grounds, partly according to the larval shape and presence or absence of hooks on the glochidial shell, and partly on the duration and season(s) of larval incubation in the marsupial demibranchs. The states of all of these characters distinguish the *Unioninae s.s.* from other subfamilial groups.

As concerns the brood habit, Palearctic *Unio* are gravid only in the summer (Ortmann 1911b, 1914; Higashi & Hayashi 1964). Ortmann's (1918b) observations on gravid *U. caffer* led him to consider that larval incubation in that species could begin in July, i.e. in winter in southern Africa. The present findings, based on material collected in mid-July, suggest that the presumably nearly infective larvae might be brooded for at least another month. Therefore, despite regional variation in the 'season', which may coincide with the yearly low water level in streams, species of *Unio* have comparatively rapid larval development.

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#### ABBREVIATIONS

A	anterior	K	kidney (metanephridium)
AAM	anterior adductor muscle	LP	labial palp
AN	anal (excurrent) opening	M	mantle
B	beak (umbone)	OD	outer demibranch
BC	branchial chamber	OL	outer lamella
BP	branchial papilla	P	perforation through septum
BR	branchial (incurrent) opening	PAM	posterior adductor muscle
D	dorsal	PS	pallial suture
E	egg	S	interlamellar septum
FI	filament	SA	supra-anal opening
FO	foot	SBC	suprabranchial chamber
H	hook	SP	spermatozoa
HT	heart	VM	visceral mass
ID	inner demibranch	WT	water-tube
IL	inner lamella		

#### REFERENCES

- BLOOMER, H. H. 1931. A note on the anatomy of *Lamellidens marginalis*, Lamarck, and *L. thwaitesii*, Lea. *Proc. malac. Soc. Lond.* 19: 270-272.
- BRANDT, R. A. M. 1974. The non-marine aquatic Mollusca of Thailand. *Arch. Molluskenk.* 105: 1-423.
- CONNOLLY, M. 1912. A revised reference list of South African non-marine Mollusca; with descriptions of new species in the South African Museum. *Ann. S. Afr. Mus.* 11: 59-306.
- CONNOLLY, M. 1939. A monographic survey of South African non-marine Mollusca. *Ann. S. Afr. Mus.* 33: 1-660.
- FRYER, G. 1961. The developmental history of *Mutela bourguignati* (Ancey) Bourguignat (Mollusca: Bivalvia). *Phil. Trans. R. Soc.* 244B: 259-298.
- HAAS, F. 1922. Bemerkungen über asiatischen Najaden, im Anschlusse an die von Dr. M. Kreyenberg in der chinesischer Provinz Tschili gesammelten Binnenmollusken. *Abh. Ber. Mus. Nat. - u. Heimatk. (Naturk. Vorgesch.)* Magdeburg, 3: 287-316.
- HAAS, F. 1924. Anatomische Untersuchungen an europäischen Najaden. I. *Arch. Molluskenk.* 56: 66-82.
- HAAS, F. 1936. Binnen-Mollusken aus Inner-Afrika, hauptsächlich gesammelt von Dr. F. Haas während der Schomburgk-Expedition in den Jahren 1931/32. *Abh. senckenb. naturforsch. Ges.* 431: 1-156.

- HAAS, F. 1969a. Superfamilia Unionacea. *Tierreich*, 88: x + 663.
- HAAS, F. 1969b. Superfamily Unionacea. In: *Treatise on Invertebrate Paleontology*, ed. R. C. Moore. Part N: Mollusca. Vol. 1 Bivalvia. Lawrence: Univ. Kansas Press.
- HEARD, W. H. 1974. Anatomical systematics of freshwater mussels. *Malacol. Rev.* 7: 41–42.
- HEARD, W. H. 1975. Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). *Malacologia*, 15: 81–103.
- HEARD, W. H. & GUCKERT, R. H. 1971. A re-evaluation of the recent Unionacea (Pelecypoda) of North America. *Malacologia*, 10: 333–355.
- HIGASHI, S. & HAYASHI, K. 1964. On the larvae of fresh-water bivalves in the Lake Biwa-Ko. *Bull. Jap. Soc. scient. Fish.* 30: 227–233.
- HISCOCK, I. D. 1951. A note on the life history of the Australian freshwater mussel, *Hyridella australis* Lam. *Trans. R. Soc. S. Aust.* 74: 146–148.
- INABA, S. 1941. A preliminary note on the glochidia of Japanese freshwater mussels. *Annotnes zool. jap.* 20: 14–23.
- KRAUSS, F. 1848. *Die Südafrikanischen Mollusken. Ein Beitrag zur Kenntniss der Mollusken des Kap- und Natallades und zur geographischen Verbreitung derselben, mit Beschreibung und Abbildung der neuen Arten.* Stuttgart: Ebner & Seubert.
- LINNAEUS, C. 1758. *Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis locis.* Ed. 10. Holmiae: Laurentii Salvii.
- MCMICHAEL, D. F. & HISCOCK, I. D. 1958. A monograph of the freshwater mussels (Mollusca: Pelecypoda) of the Australian region. *Aust. J. mar. Freshwat. Res.* 9: 372–503.
- MODELL, H. 1942. Das natürliche System der Najaden. *Arch. Molluskenk.* 74: 161–191.
- MODELL, H. 1949. Das natürliche System der Najaden. 2. *Arch. Molluskenk.* 78: 29–48.
- MODELL, H. 1964. Das natürliche System der Najaden. 3. *Arch. Molluskenk.* 93: 71–126.
- MORRISON, J. P. E. 1955. Family relationships in the North American freshwater mussels. *Rep. Am. malac. Un.* 1955: 16–17.
- MORRISON, J. P. E. 1973. The families of the pearly freshwater mussels. *Bull. Am. malacol. Un.* 1973: 45–46.
- ORTMANN, A. E. 1910. A new system of the Unionidae. *Nautilus*, 23: 114–120.
- ORTMANN, A. E. 1911a. The anatomical structure of certain exotic naiades compared with that of the North American forms. *Nautilus*, 24: 103–108, 114–120, 127–131.
- ORTMANN, A. E. 1911b. The classification of the European naiades. *Nautilus*, 25: 5–7, 20–23.
- ORTMANN, A. E. 1912. Notes upon the families and genera of the najades. *Ann. Carneg. Mus.* 8: 222–365.
- ORTMANN, A. E. 1914. Studies in najades. *Nautilus*, 28: 28–34.
- ORTMANN, A. E. 1916. The anatomy of the nayad *Hyriopsis myersiana* (Lea). *Nautilus*, 30: 85–87.
- ORTMANN, A. E. 1917. The anatomy of *Contradens cambojensis* (Sow.) (Nayades). *Nautilus*, 30: 106–108.
- ORTMANN, A. E. 1918a. The identity of the nayad-genus *Nodularia* Conrad with *Unio* Retzius. *Nautilus*, 31: 128–131.
- ORTMANN, A. E. 1918b. The anatomy of two African nayades, *Unio caffer* and *Spatha wahlbergi*. *Nautilus*, 31: 75–78.

- PARODIZ, J. J. & BONETTO, A. A. 1963. Taxonomy and zoogeographic relationships of the South American naiades (Pelecypoda: Unionacea and Mutelacea). *Malacologia*, 1: 179–213.
- PHILIPSSON, L. M. 1788. *Dissertatio historiconaturalis sistens nova testaceorum genera*. Sweden: Univ. Lund.
- PILSBRY, H. A. & BEQUEART, J. 1927. The aquatic mollusks of the Belgian Congo. With a geographical and ecological account of Congo malacology. *Bull. Am. Mus. nat. Hist.* 53: 69–602.
- SIMPSON, C. T. 1900. Synopsis of the naiades, or pearly fresh-water mussels. *Proc. U.S. natn. Mus.* 22: 501–1044.
- SIMPSON, C. T. 1914. *A descriptive catalogue of the naiades or pearly fresh-water mussels*. Detroit: B. Walker.
- THIELE, J. 1935. *Handbuch der systematischen Weichtierkunde*. Stuttgart: G. Fischer.
- WOODWARD, F. R. 1965. The morphology of *Hyriopsis myersianus* (Lea, 1856) and *Pseudopar-reysia johnseni* gen. nov. sp. nov. (Unionidae: Bivalvia). *Vidensk. Meddr dansk naturh. Foren.* 128: 205–219.