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A revision of some Asian and African freshwater clams assigned to *Corbicula fluminalis* (Müller, 1774) (Mollusca: Bivalvia: Corbiculidae), with a review of anatomical characters and reproductive features based on museum collections

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Abstract

A study of museum specimens of the genus *Corbicula* from the western Asiatic part of its range (Middle East, the Caucasus and Central Asia) has provided the following diagnostic anatomical characters for *Corbicula fluminalis* (Müller, 1774): siphons narrow with circular apertures; siphonal papillae rather scarce: about 40 around inhalant siphon (one or two rows) and 12–20 around exhalant siphon (one incomplete row); ring of dark pigment usually present internally at base of each siphon; papillae of fused mantle lobes and free mantle edge numerous, the first organised in one or two rows; radial muscles of mantle edge well developed and arranged in bands. Presence of hermaphroditic specimens, biflagellate type of spermatozoa indicating clonality, and incubation of D-shaped 190–217 μm long larvae in gills were also shown for this taxon. Two conchologically different morphotypes referred to in literature as *C. fluminalis* s. str. and *C. purpurea* (Prime, 1864) show also slight differences in size of spermatozoa and may represent different clonal lineages. The lots from North Africa possess the same characters as one of the Asian morphotypes, thus taxonomic distinctness of *C. fluminalis consobrina* (Cailliaud, 1827) is not supported. In contrast, *C. africana* (Krauss, 1848) distributed in Lake Malawi and South Africa and treated in some modern reviews as another subspecies of *C. fluminalis* differs by the patterns of shell sculpture, the lower number of siphonal papillae, the absence of pigmentation on the siphons and their papillae, and the size of spermatozoa; its distinctness is therefore supported, but close affinity to *C. fluminalis* needs confirmation. All studied African morphotypes are identical in their mode of reproduction. The new data on the anatomy and reproduction of *C. fluminalis* show strong similarities between this taxon and the 'eastern' incubating species *C. fluminea* (Müller, 1774), but these taxa can be distinguished by their shell characters. The Chinese estuarine non-incubating *Corbicula* earlier assigned to *C. fluminalis* shows different anatomical and reproductive characters and is re-considered as *C.cf. japonica* (Prime, 1864). These results are discussed in the framework of *Corbicula* phylogeny based on molecular characters.

Introduction

Freshwater bivalve molluscs of the genus *Corbicula* are widely distributed in natural state across tropical and subtropical regions of Africa, Asia, the Malay Archipelago, the Philippines, New Guinea and Eastern Australia (Morton, 1986). During the Pleistocene interglacials, the genus also occurred in Europe (Meijer & Preece, 2000). In the 20th century, these clams were introduced in both

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[†] Deceased

Americas and in Europe (Britton & Morton, 1979; Araujo et al., 1993; Ituarte, 1994; Swinnen et al., 1998). Rapidly expanding their range and constituting a potential danger to the native aquatic communities, these invasive freshwater bivalves became the focus of multidisciplinary investigations (Morton, 1986; Kennedy et al., 1991; Kinzelbach, 1991; McMahon, 1999; Rajagopal et al., 2000; Siripattrawan et al., 2000; Renard et al., 2000; Mouton, 2001; Pfenninger et al., 2002).

The study of *Corbicula* is not only important from the perspective of ecological invasions, but also because of this taxon's unique characteristics amongst bivalves. Its reproductive biology in particular is of general interest to evolutionary research. First of all, this genus is distinguished by a wide spectrum of reproductive strategies, ranging from indirect development with free swimming larvae to incubation of larvae in gills till the stage of benthic juveniles (Morton, 1986; Kennedy et al., 1991; Byrne et al., 2000; Rajagopal et al., 2000). While the first mode is typical for estuarine *Corbicula* species tolerant to brackish water, the second one is restricted to freshwater taxa (Morton, 1986; Rajagopal et al., 2000; Siripattrawan et al., 2000). Furthermore, remarkable chromosome polymorphism including high level of polyploidy (up to 4*n*) was discovered among East Asian incubating taxa (Okamoto & Arimoto, 1986; Komaru & Konishi, 1999; Qiu et al., 2001). Finally, non-reductive biflagellate spermatozoa and the development from an exclusively paternal genome (androgenesis) were reported for incubating *Corbicula* species from Japan and China (Komaru et al., 1997, 2000). Morphologically similar sperm was also observed in Australian *Corbicula* (Byrne et al., 2000). On the base of these data, Siripattrawan et al. (2000) suggested that most freshwater nominal taxa within the genus *Corbicula* are actually clonal lineages. In contrast, uni-flagellate sperm was observed in estuarine *C. japonica* Prime, 1864, and in lacustrine endemic taxa from the Japanese Lake Biwa and the lakes on Indonesian islands Sumatra and Sulawesi (Komaru et al., 1997; Siripattrawan et al., 2000; Glaubrecht et al., 2003). Association of this sperm type with sexual reproduction was suggested in all cases, but no strict correlation with the particular reproductive strategy (releasing free swimming veligers vs incubation of juveniles in gills) was noted, since the taxa with the uni-flagellate spermatozoa demonstrated all strategies known within the genus *Corbicula*. Surprisingly, only diploid specimens were reported until now from Europe; evidence for hybridisation between different lineages on this continent was also provided (Pfenniger et al., 2002).

But despite intensive studies of native Asian and introduced *Corbicula* populations (clones), the taxonomy within this genus is still unresolved. There is no agreement between investigators neither about the general number of valid species which vary, for example in China from six (Prashad, 1929) to only two (Morton, 1986), nor about the species identity of the morphotypes recorded in America and Europe (Ituarte, 1984, 1994; Morton, 1986; Kinzelbach, 1991; Araujo et al., 1993; Swinnen et al., 1998; Siripattrawan et al., 2000; Pfenniger et al., 2002). The confused taxonomy of *Corbicula* and discrepancies between the descriptions of morphological and reproductive characteristics cited for the same species name by different authors hamper both fundamental and applied investigations of this important freshwater molluscs group.

One of the main problems is the taxonomic status and geographic range of the Müller's (1774) species *Corbicula fluminalis* (originally placed in *Tellina*). Given the type locality in Euphrates River, this taxon was once treated as 'Western' *Corbicula*, a geographic vicariant of the 'Eastern' *Corbicula fluminea* (Müller, 1774), described from China (Zhadin, 1952). Kinzelbach (1991, 1992) basically agreed with this view. Mandahl-Barth (1988) and Daget (1998) assigned to *Corbicula fluminalis* most of the African taxa (some of them were treated as subspecies). In contrast, Izzatullaev (1980) distinguished alongside *C. fluminalis* several other valid Central Asian species. In his general revision of Asian *Corbicula*, Morton (1979, 1986) considered *Corbicula fluminalis* to be an estuarine species distributed across Asia (including China) and Africa, an ecological vicariant of the strictly freshwater and equally wide-spread *C. fluminea*. In this revision another Asian estuarine taxon, *Corbicula japonica*, was tentatively synonymised to *C. fluminalis*. However, the later Japanese authors (Harada & Nishino, 1995; Komaru et al., 1998) did not accept this suggestion, and continued to treat *C. japonica* alongside the other insular taxa

(*Corbicula leana* Prime, 1864 and *Corbicula sandai* Reinhardt, 1878) as a distinct valid species.

Besides the uncertainty about the natural range of *C. fluminalis,* there is a discrepancy in literature concerning its introduction in Europe. Kinzelbach (1991) assigned extant European morphotypes to *C. fluminea* and *Corbicula fluviatilis* (Müller, 1774). However, recent authors (Swinnen et al., 1998; Rajagopal et al., 2000; Renard et al., 2000) identify the second form, distinguished by the high triangular shell and restricted to the lower courses of rivers, as *C. fluminalis*. Until now, *C. fluminalis* is not recorded in North America (Britton & Morton, 1979; Siripattrawan et al., 2000).

While some of the authors mentioned (Izzatullaev, 1980; Mandahl-Barth, 1988; Kinzelbach, 1991, 1992; Komaru et al., 1998; Swinnen et al., 1998) used only shell characters to diagnose *Corbicula* species, Britton & Morton (1979) suggested several anatomical diagnostic characters, such as number, arrangement and colouration of siphonal papillae. They showed that on the base of these characters the estuarine Chinese taxon identified by them as *C. fluminalis* was distinct from *C. fluminea* populations in Hong Kong and North America. Anatomical studies of *C. fluminea* populations in Europe (Araujo et al., 1993) and China (Chen et al., 1995) corroborated the diagnosis of Britton & Morton (1979). At the same time, differences in anatomical characters among Japanese taxa were reported (Harada & Nishino, 1995). However, the anatomical review of *C. fluminalis* remained incomplete, since neither the populations from West Asia representing *C. fluminalis* s.str., nor any of the presumably conspecific African taxa were included.

The mode of reproduction and development is also considered to be an important diagnostic taxonomic character in *Corbicula*, thus *C. fluminalis* is described in modern literature as a non-incubating species, in contrast to the incubating *C. fluminea* (Morton, 1986; Rajagopal et al., 2000). Noteworthy, Izzatullaev (1980) considered the mode of reproduction as being a generic character, including all incubating species in the genus *Corbiculina*, but this view was not accepted by later authors. As for anatomy, the study of reproduction of *Corbicula* was mainly restricted to populations from East and Southeast Asia (Morton, 1982, 1986; Komaru et al., 1997, 2000; Glaubrecht et al., 2003), North America (Britton & Morton, 1979; Kennedy et al., 1991) and Europe (Araujo et al., 1993; Rajagopal et al., 2000; Mouton, 2001). Observations from West and Central Asia and from Africa remain sparse and controversial (Mandahl-Barth, 1954; Izzatullaev, 1980).

Some samples presumably of *C. fluminalis* were included in recent molecular analyses. Noteworthy, molecular analysis of European samples, all identified as conspecific on morphological criteria, produced different clusters, suggesting the existence of at least one cryptic taxon (Renard et al., 2000). According to a phylogenetic analysis of all available sequence data carried out by Pfenninger et al. (2002), different morphotypes of *Corbicula* from Asia, Australia, North America and Europe (including those from Europe and Israel originally identified as *C. fluminalis*) form a cluster with poorly resolved relationships, with only *C. japonica* and a species from Madagascar forming outgroups.

From the above it can be concluded, that *C. fluminalis* is still a poorly known taxon. In addition to sequence data from different parts of its presumed range, adequate data on anatomy and reproduction mode are urgently needed in order to define its status and the status of dubious forms. In particular, it is important to know, what anatomical characters and mode of reproduction has to be attributed to *C. fluminalis* from the type area (Euphrates River) and adjacent river drainages. To this purpose, we revised available museum collections, searching for preserved specimens morphologically most similar and geographically nearest to the type lot. In addition, several African and East Asian morphotypes assigned in modern literature to *C. fluminalis* were studied, in order to check stability of anatomical and reproductive features within this species or species complex.

Material and methods

The lectotype of *Tellina fluminalis* Müller, 1774 deposited in the Zoological Museum of the University of Kopenhagen (ZMUK) was examined. Other relevant material (preserved specimens or shells with dry body tissue) was obtained from the Museum für Naturkunde, Humboldt Universität zu Berlin (acronym ZMB based on the former name – Zoologisches Museum Berlin), Senckenbergsmuseum in Frankfurt/Main (SMF), Danish Bilharziasis Laboratory in Charlottenlund, Denmark (DBL), and from the Zoological Institute in St. Petersburg, Russia (ZIN). Collection details of the studied lots, arranged according to geographic regions are provided below (localities are shown in Fig. 1). The system of labelling in ZIN collection is based on the systematic catalogue (separate numbering within each species), therefore original identifications are also given in these cases.

1. West and Central Asia: Orontes River, Homs (Hims), Syria, leg. Nägele, undated, ZMB 50930 (dry); Samarkand, Uzbekistan, leg. Sänger, undated, ZMB 19409 (dry), 102850 (wet); Azerbajdžan, leg. 1915, det. Ya. Starobogatov, ZIN: *C. fluminalis* No. 32 (wet); Samarkand, Uzbekistan, leg. 18.07.1928 B. Prikhodko, det. Ya. Starobogatov, ZIN: *C. purpurea* Prime, 1864, No. 49 (wet); altogether eight preserved specimens examined.
2. North Africa: Freshwater channel, Suez, Egypt, leg. Jickeli, undated, ZMB 23225 (dry), 23632 (wet); Fajum (Al-Fayyum), Egypt, leg. Schweinfurth, undated, ZMB 31140 (dry); Ismailia (Al-Ismailiya), Egypt, leg. Schweinfurth, undated, ZMB 32268 (dry); Nile at Barrage, leg. 25.11.1965, colln. Mandahl-Barth, DBL (wet); Clot Bay, Egypt, leg. Yunker, det. Y. Starobogatov, ZIN, *Corbicula consobrina* (Cailliaud, 1827), No. 9 (wet); altogether 10 preserved specimens examined.
3. African Great Lakes and South Africa: Edward Lake, ZMB 103056 (wet); Lake Malawi, Mangoche, Palm Beach, Malawi, leg. M. Glaubrecht 03.1995, det. A. Korniushin, ZMB

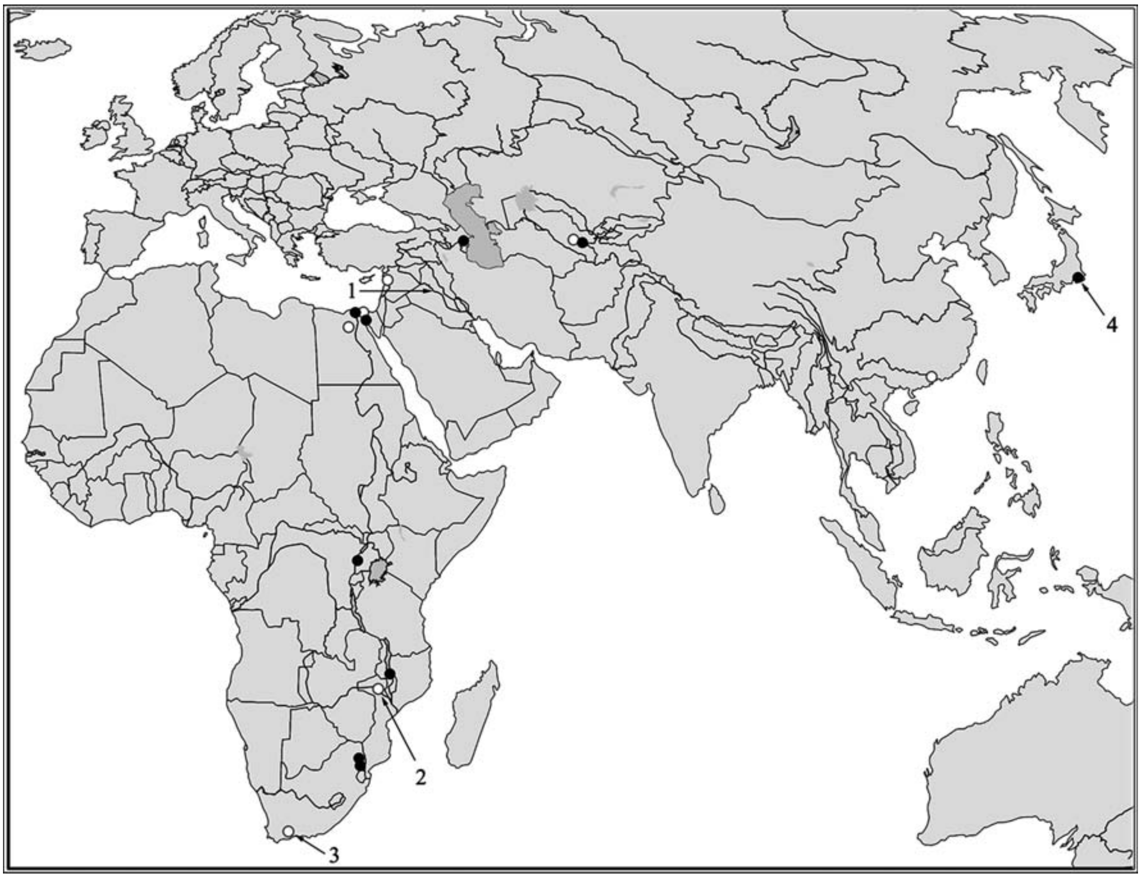

Figure 1. A map showing localities of *Corbicula* available for this study: 1 – type area of *C. fluminalis* – Euphrates River (exact localilty unknown). 2 – type locality of *C. astartina* – Zambezi River at Tette. 3 – type localilty of *C. africana* – Gauritz River. 4 – locality of the comparative material of *C. japonica* – Yeddo (Tokyo). Open circles – localities of shell material; black circles – preserved lots.

Table 1. Shell measurements and morphometric indexes of the studied lots

Species and lot	*n*	Measurements of largest specimen, mm				Indexes, M ± SD		
		L	H	W	H/L	$2W/H$	U/L	HH/H
C. fluminalis, lect. ZMUK	1	29.9	29.7	11.1	0.99	0.75	0.54	0.111
C. fluminalis, ZIN No. 32	1	22.4	22.2	8.3	0.99	0.75	0.58	0.095
C. fluminalis, ZMB 50930	3	20.6	19.2	7.4	0.94 ± 0.05	0.81 ± 0.09	0.52 ± 0.03	0.101 ± 0.017
'*C. purpurea*', ZMB 102850	4	23.3	20.5	7.2	0.90 ± 0.03	0.72 ± 0.02	0.50 ± 0.02	0.087 ± 0.015
C. f. consobrina, ZIN No. 9	1	27.2	26.6	9.2	0.98	0.69	0.47	0.068
C. f. consobrina, ZMB 32268	8	30.5	26.5	8.7	0.89 ± 0.03	0.69 ± 0.05	0.47 ± 0.02	0.084 ± 0.010
C. f. consobrina, ZMB 31140	5	24.2	20.2	7.3	0.87 ± 0.02	0.72 ± 0.01	0.44 ± 0.04	0.083 ± 0.004
C. f. cunningtoni ZMB 103056	7	13.3	12.7	4.9	0.87 ± 0.05	0.72 ± 0.08	0.48 ± 0.04	0.068 ± 0.007
C. f. africana, syntype, ZMB 28486	1	13.0	10.9	3.6	0.84	0.66	0.46	0.064
C. f. africana, ZMB 102632	10	13.5	11.3	4.0	0.87 ± 0.03	0.72 ± 0.03	0.55 ± 0.11	0.102 ± 0.001
C. f. africana, SMF 10381a	3	11.6	9.1	3.0	0.80 ± 0.02	0.68 ± 0.03	0.46 ± 0.01	0.070 ± 0.017
C. japonica, ZMB 32884	4	31.4	30.5	8.9	0.92 ± 0.04	0.59 ± 0.02	0.43 ± 0.02	0.083 ± 0.004
Corbicula cf. japonica ZMB 35461, 26951	7	39.1	35. 3	13.0	0.91 ± 0.08	0.66 ± 0.04	0.43 ± 0.05	0.087 ± 0.007

L – shell length, H – shell height, W – width of one valve, U – distance between anterior edge and umbo, HH – breadth of hinge plate under umbo, N – number of measured specimens, M – mean value, SD – standard deviation.

102632 (wet); South Africa, River Gauritz, syntypes of *Corbicula africana* Krauss, ZMB 28486, SMF 5780 (dry); South Africa, East Transvaal, Letaba River at Letaba Camp, leg. 1931, colln. F. Haas, SMF10381a (wet); South Africa, East Transvaal, Sabie River at Lower Sabie Camp, leg. 1931, colln. F. Haas, SMF 219527 (wet); altogether more than 20 preserved specimens examined.

4. China: Canton, different collectors, ZMB 35461, 26951, 38399 (dry); China, exact locality not given, coll. Dunker, ZMB 103057 (wet specimen).

Syntypes of *C. astartina* (Martens, 1859) (Zambezi at Tette, Mozambique, ZMB 4655, dry) and numerous representative specimens of *C. japonica* (Yeddo, Japan, ZMB 32884, wet) were studied as comparative material.

Shell characters referred to in taxonomic descriptions and reviews (Izzatullaev, 1980; Morton, 1982, 1986; Mandahl-Barth, 1988; Araujo et al., 1993; Harada & Nishino, 1995; Swinnen et al., 1998) were checked in each lot. In addition to the conventional measurements (i.e. length, height and width of shell) the width of hinge under umbo (see Araujo et al., 1993) and distance between anterior edge of valve and umbo were measured. The indexes obtained are cited in Table 1. Statistical comparisons were based on the two-tail t-criterion. The sculpture pattern of shell (average number of ribs per cm) was recorded for each specimen, in large shells ribs were only counted in the median part. Dry specimens containing remains of soft body tissues were examined for presence of larval shells, tissues were dissolved in hot 5% KOH solution.

All anatomically studied lots are preserved in 70% alcohol. Animals were dissected, mantle and gills being in some cases removed for careful examination. Pieces of mantle edge were stained by eosine (water solution) and embedded in Canada Balsam for microscopic study of mantle muscles. Gonads were examined *in situ*, presence of sperm and eggs was checked also in squash preparations and by scanning electron microscopy (SEM). The treatment with hexamethyldisilazane (HMDS) after Nation (1983) and spotting with gold-palladium were used by the SEM study. Larvae were prepared for SEM by rinsing in alcohol, drying up and spotting with gold–palladium. Observations were performed on

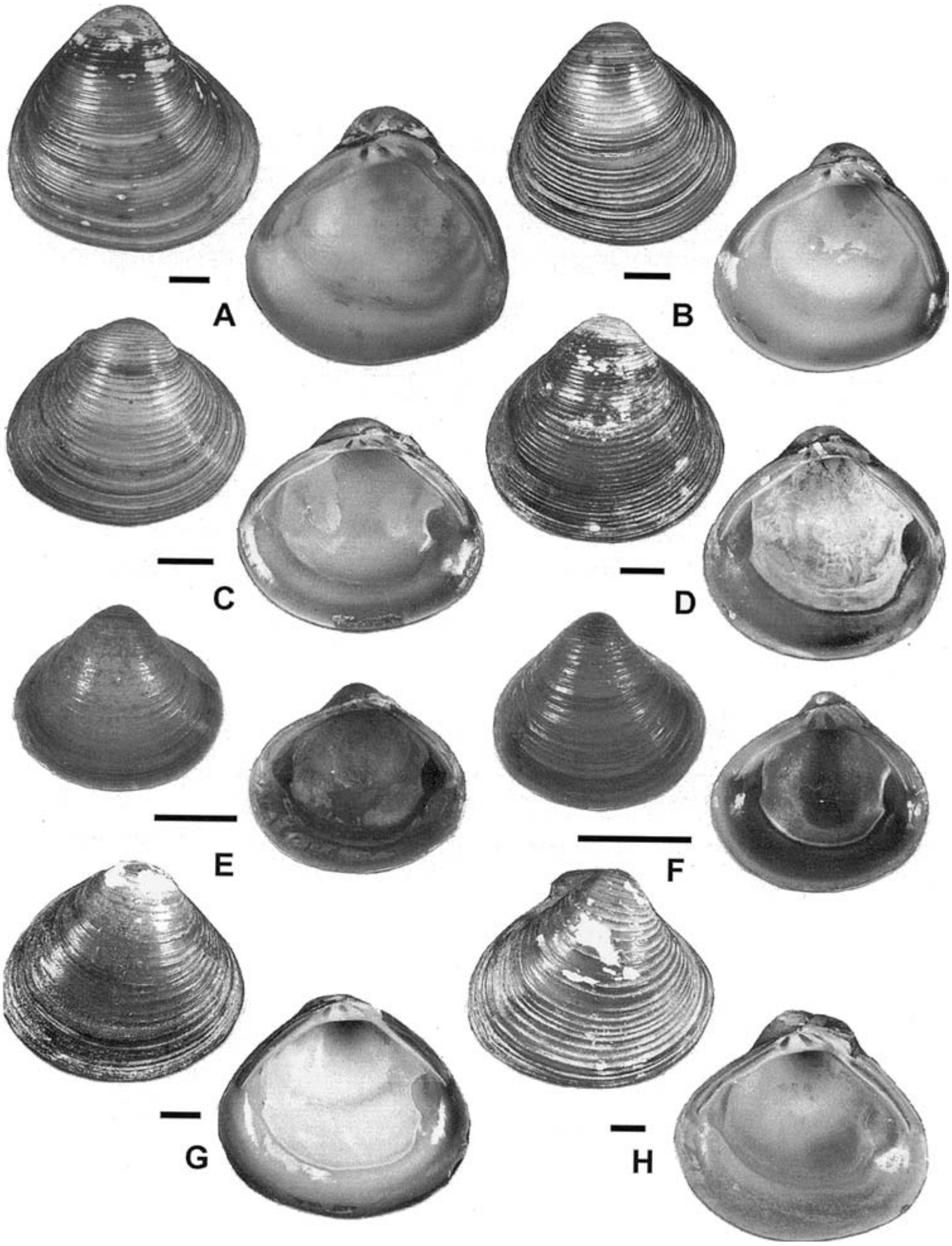

Figure 2. Representative shells of the studied *Corbicula* morphotypes: (A) *C. fluminalis*, lectotype ZMUK; (B) *C. fluminalis* s.str., ZIN, No. 32; (C) '*C. purpurea*', ZIN, No. 49; (D) *C. fluminalis consobrina*, ZIN, No. 9; (E) *C. f. cunningtoni*, ZMB 103056; (F) *C. f. africana*, ZMB 102632; (G) *C. japonica*, ZMB 32884. (H) *Corbicula* sp., China, ZMB 103057. Scale bar 5 mm.

LEO 1450VP microscope; pictures were saved as digital images. Spermatozoa and larval shells were measured on photographs, shell length was taken parallel to the hinge edge.

Standard photographic and video equipment was used while drawings were made with the help of *camera lucida*.

Results

Shell characters

Material from the Middle East, the Caucasus and Central Asia included two shell morphotypes. The shells from Azerbajdžan identified as *Corbicula* *fluminalis* (ZIN, No. 32) were relatively high (height almost equal to length), with rather broad hinge plate and thick lateral teeth (Fig. 2B, Table 1). They were morphologically closest to the lectotype of the species (Fig. 2A), and therefore are further referred to as *Corbicula fluminalis* s. str. The umbo of larger specimens was distinctly shifted posteriorly (Table 1), and this character can also be observed in the lectotype. A similar morphotype was found in Syria (ZMB 50930). The morphotype from Samarkand (ZIN, No. 49; ZMB 19409, 102850) representing *C. purpurea sensu* Izzatullaev (1980) differs by its lower shell with centrally placed umbo and narrower hinge (Fig. 2C). However, no statistically significant differences between this form and the typical *C. fluminalis* were detected (Table 1). Sculpture in both morphotypes was similar, consisting of rather pronounced, sharp, narrow and regularly spaced ribs (13–16 per cm) agreeing well with that of the lectotype of *C. fluminalis* (14–15 ribs per cm); periostracum was dull, outer side of valves yellow or light brown, and inner side light purple.

The specimens from North Africa were similar to the flatter Asian form; the only noticeable difference was their larger size (Fig. 2D, Table 1). Sculpture and shell colouration were almost identical to the Asiatic *C. fluminalis*. The North African specimens labelled as *C. consobrina* (e.g. ZIN, No. 9) were very similar to North African specimens originally identified as *C. fluminalis* (ZMB 23225, 236432, 31140, 32268), and thus all studied North African forms could be treated as belonging to a single morphotype, which according to the latest review on African *Corbicula* (Daget, 1998) has to be referred to as *C. fluminalis consobrina* (Cailliaud, 1827).

In contrast, shells from African Great Lakes (Fig. 2E and F) were distinctly smaller than the forms from the Middle East and North Africa, and distinguished by their sculpture: 22–26 ribs per cm in shells from Lake Malawi identified as *C. fluminalis africana* (Krauss, 1848) and almost smooth shells from Lake Edward, consubspecific to *C. fluminalis cunningtoni* Smith, 1906 (according to Daget, 1998). Colouration of these forms was variable, externally from pale yellow to dark brown (sometimes greenish-brown), internally from white to deep purple. Samples from South Africa were similar in their shell characters to those from Lake Malawi, differing only in values of several indexes (Table 1). It is noteworthy, that the lots in the F. Haas' collection originally identified *C. astartina* (SMF 10381a) were not specifically distinguishable from the types and other representative specimens of *C. f. africana*. Therefore, they were re-identified as the latter taxon. At the same time, the syntypes of *C. astartina*, also revised by this study differed in their elongated compressed shells and widely spaced ribs.

Representative specimens of *Corbicula japonica* (Fig. 2G, Table 1) included in this study were characterised by compressed shells with anteriorly shifted umbo, broad, unevenly spaced ribs, and bright glossy periostracum. External colouration was dark brown, internal white with darker area at posterior end. The shells from China (Fig. 2H) were similar in form to *C. japonica*, but differed by their large size (up to 39 mm long) and more pronounced sculpture (though also broad spaced and irregular). Bright glossy periostracum was clearly observed in fresh shells. Differences in shell width index ($2W/H$) and position of umbo (U/L) between Japanese and Chinese shells on one hand, and those from the Middle East and Central Asia on the other, were statistically significant ($p < 0.05$), but distinction of the former from the North African samples was less pronounced (Table 1). Pattern of sculpture and structure of periostracum were more consistent among the studied East Asian lots than shell measurements.

Mantle characters

Siphons of *Corbicula* from Uzbekistan, Azerbajdžan, and Egypt, as seen in fixed specimens (Figs 3A–C and 4A), were tubular, with narrow circular apertures. Rather broad pigmented ring (black or brown) is present at the base of each siphon (Fig. 3A and C), except for one specimen from Azerbajdžan. Siphonal papillae were unpigmented. Inhalant siphon was surrounded by 35–45 (usually about 40) papillae unevenly arranged in two rows, papillae of internal row were longer than those of external one; exhalant siphon had 12–20 small papillae arranged in one incomplete row. Papillae of the fused mantle lobes in front of

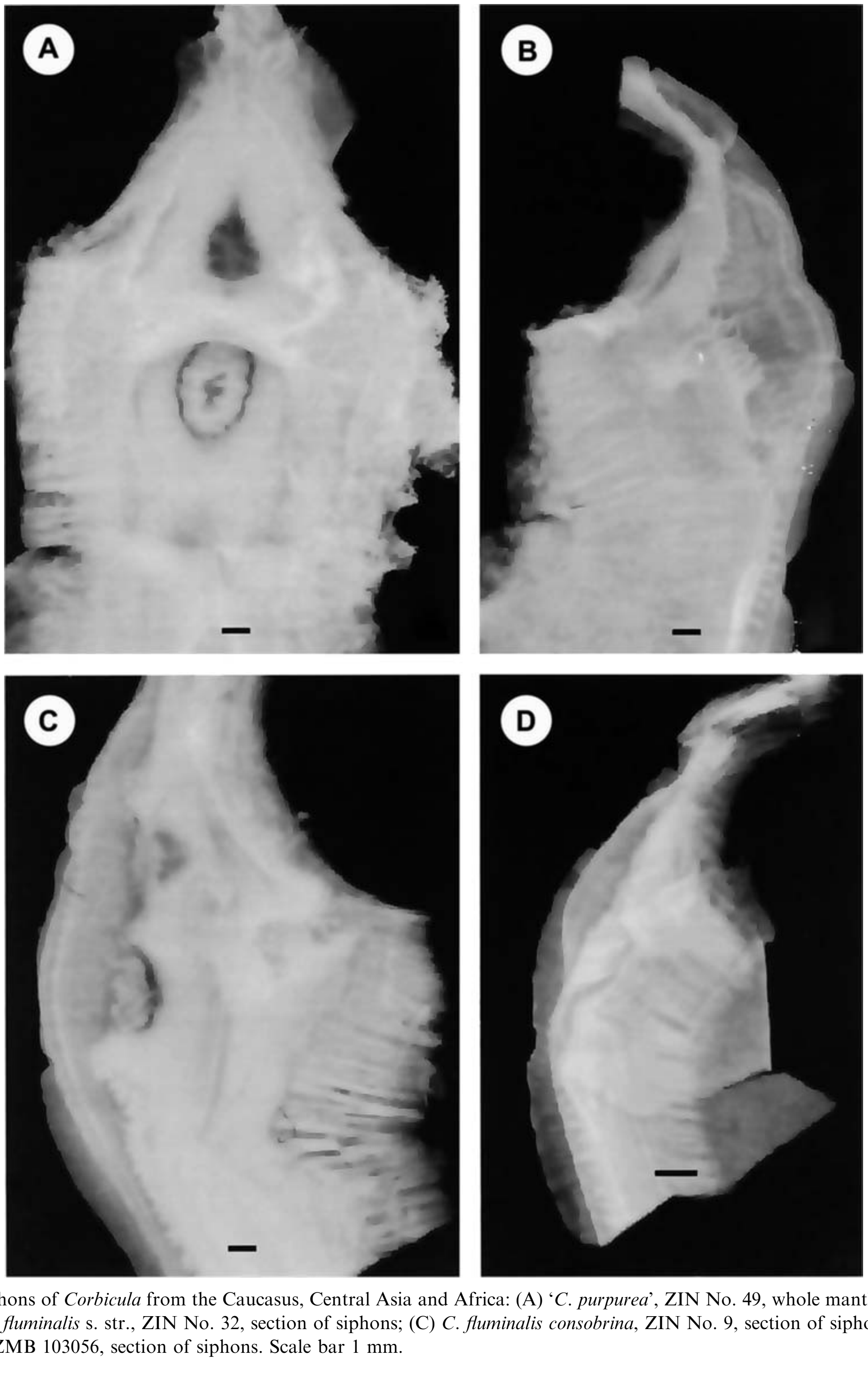

Figure 3. Siphons of *Corbicula* from the Caucasus, Central Asia and Africa: (A) '*C. purpurea*', ZIN No. 49, whole mantle, view from inside; (B) *C. fluminalis* s. str., ZIN No. 32, section of siphons; (C) *C. fluminalis consobrina*, ZIN No. 9, section of siphons; (D) *C. f. cunningtoni*, ZMB 103056, section of siphons. Scale bar 1 mm.

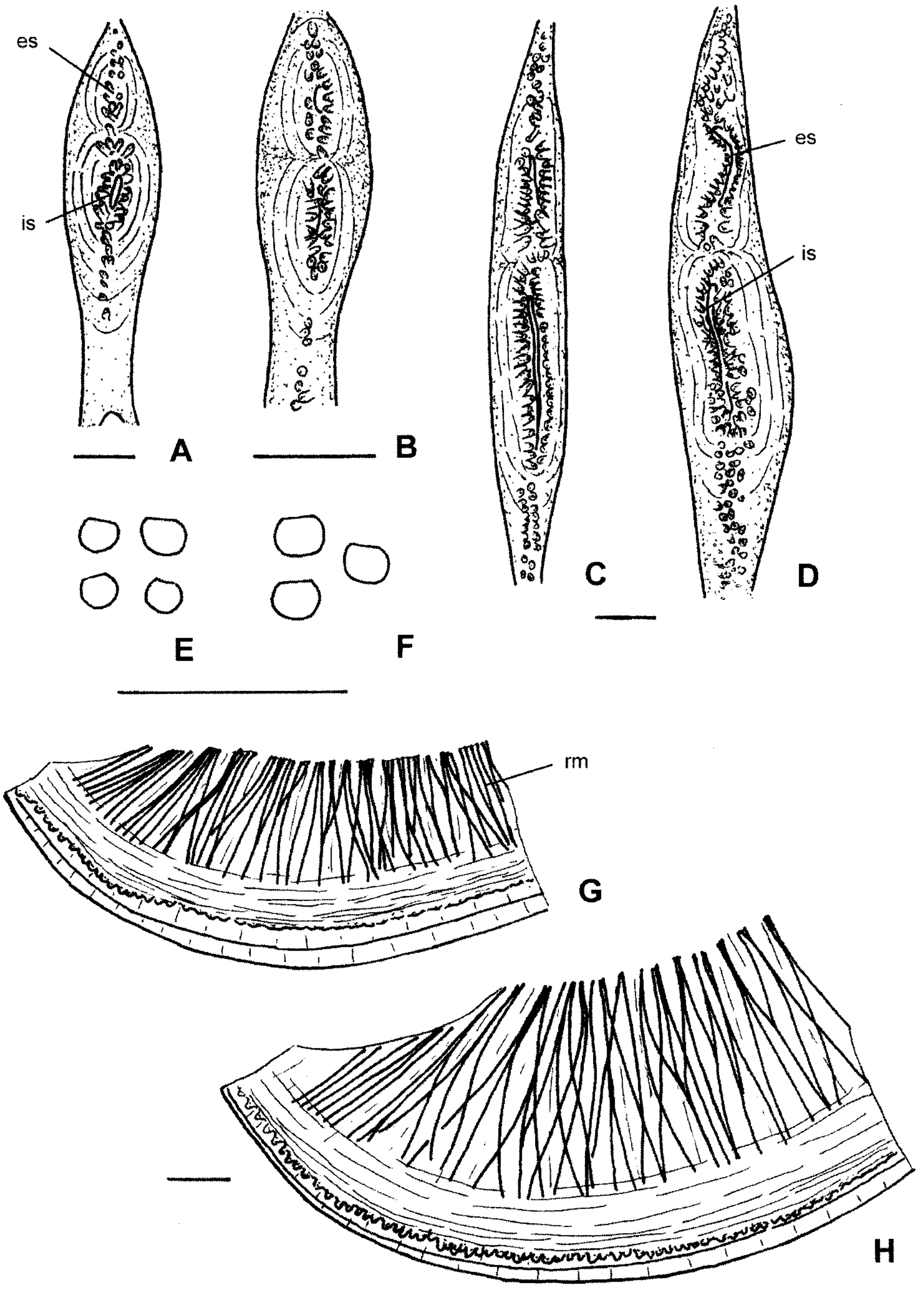

Figure 4. Some anatomical details of the studied *Corbicula*: (A–D) outside view of siphons in *C. fluminalis* s.str., ZIN No. 32 (A); *C. fluminalis africana*, ZMB 102632 (B); *C. japonica*, ZMB 32884 (C) and *Corbicula* sp. from China, ZMB 103057 (D); (E–F) Larvae from gills of '*C. purpurea*', ZIN, No. 49 (E) and *C. f. consobrina*, ZIN, No. 9 (F); (G–H) Musculature of mantle edge in *C. fluminalis*, ZMB 102850 (G) and *C. japonica*, ZMB 32884 (H); es – exhalant siphon, is – inhalant siphon, rm – radial mantle muscles. Scale bar 1 mm.

siphons were organised in one or two uneven rows. Marginal papillae of the free mantle edge were densely arranged. Circular siphonal apertures surrounded by black pigment were distinguishable also in dry specimens from Syria, but papillae could not be observed.

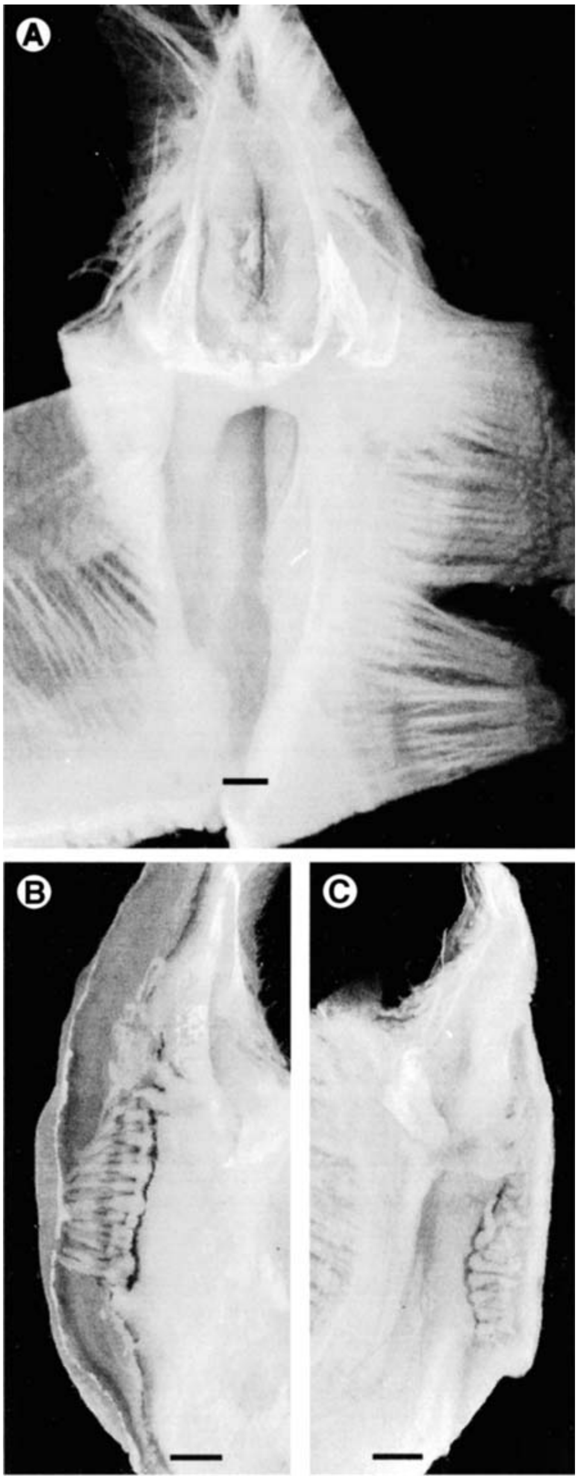

Figure 5. Siphons of *Corbicula* from Japan and China: (A–B) *C. japonica*, ZMB 32884 (A – whole mantle, view from inside, B – section of siphons); (C) *Corbicula* sp. from China, ZMB 103057, section of siphons. Scale bar 1 mm.

Central and South African taxa were characterised by the same form of siphons (Figs 3D and 4B), but the number of inhalant siphon papillae is apparently lower: from 15 in small specimens from Lake Malawi up to 25 in larger ones from Lake Edward. Pigmented rings are absent. Papillae of the fused mantle lobes and free mantle edge are similarly arranged, as in *C. fluminalis* from Central Asia.

Corbicula japonica and the conchologically similar Chinese form differed from the above described taxa in having broader siphons with slit-like apertures (Figs 4C, D and 5). The siphonal papillae were distinctly more numerous: not less than 80 around inhalant siphon (organised in three rows), and about 30 around exhalant siphon (one complete row). Siphons were poorly pigmented internally, having only a narrow dark stripe at the base of each inhalant siphon papilla, another dark spot is seen in the middle of each large papilla (Fig. 5B and C); small papillae of inhalant siphon and papillae of exhalant siphon were pale yellowish, without any spots or stripes. External surface of siphons and internal surface of mantle edge around siphons were dark brown. Papillae of the fused mantle lobes were numerous and arranged in several rows. Marginal mantle papillae were similar to those of the other studied taxa.

Radial mantle muscles of *C. fluminalis* were well developed and densely arranged along the mantle edge, with individual bundles not distinguishable (Fig. 4G). In contrast, radial muscles of *C. japonica* were weaker, and their arrangement is loose, individual bundles being separated (Fig. 4H).

Reproduction

Examination of gonads in all available specimens of *Corbicula fluminalis* s.str. from Azerbajdžan (ZIN, No. 32), '*Corbicula purpurea*' from Uzbekistan (ZMB 102850), and *C. fluminalis consobrina* from Egypt (ZMB 23632), recovered simultaneous presence of oocytes and sperm (see example on the Fig. 6A–C). In the most numerous sample of *C. f. africana* (SMF 10381a), this condition was found in two of 15 specimens studied, while only oocytes were observed in other animals. Spermatozoa were not found in specimens from the lakes Edward and Malawi. The examined material is too sparse to make final conclusions on the expression

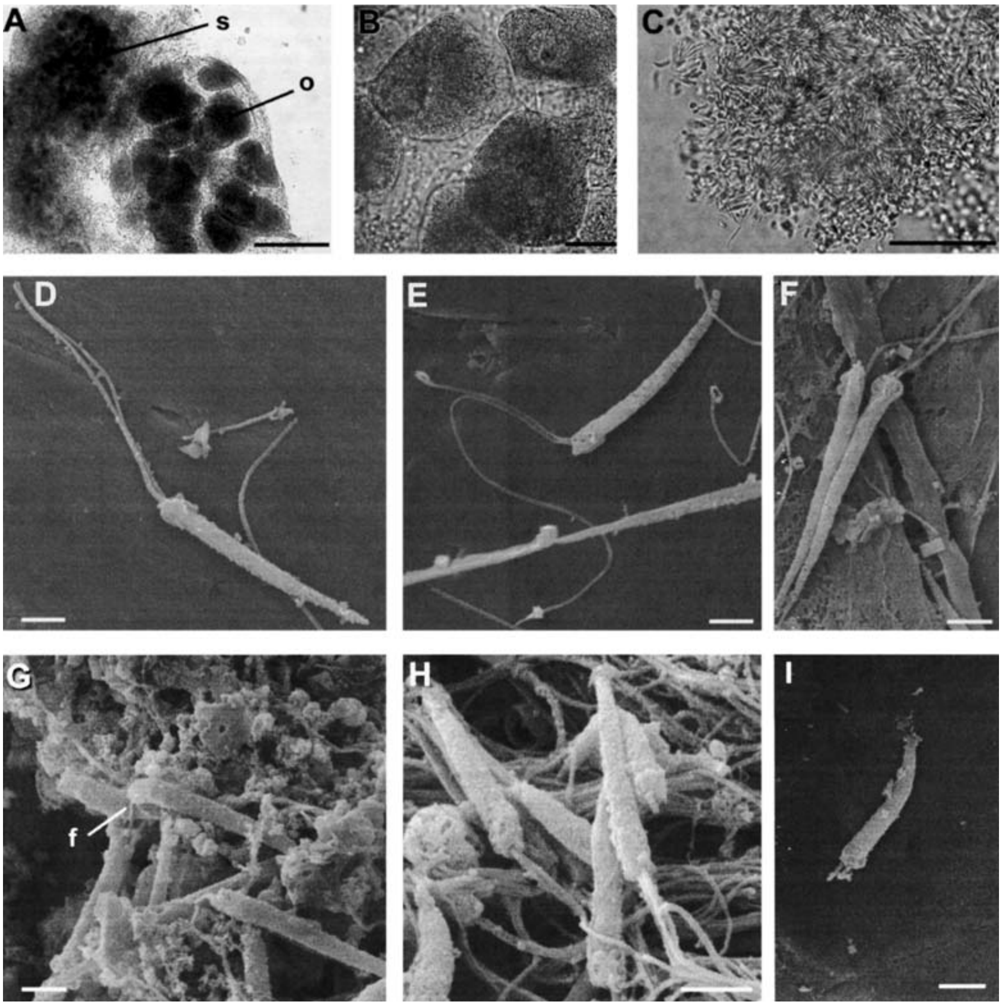

Figure 6. Gonad structure and sperm morphology of *C. fluminalis*; A – adjacent egg and sperm follicles in the gonad of *C. fluminalis* s. str., ZIN No. 32; B – oocytes; C – sperm from the same specimen; D – SEM image of a spermatozoon from the same specimen; E–F – SEM images of spermatozoa from '*C. purpurea*', ZMB 102850; G – sperm of *C. f. consobrina*, ZMB 23632 (SEM); H–I – spermatozoa of *C. f. africana*, SMF 10381a; s – sperm, o – oocytes, f – flagelli. Scale bars: A – 200 μm; B–C – 50 μm; D–I – 2 μm.

Table 2. Measurements of spermatozoa and incubated larvae in the specimens of *Corbicula* studied

Species and lot	*n* (spermatozoa)	Head length, μm, $M \pm$ SD	*n* (larvae)	Shell length, μm, $M \pm$ SD	Prodissoconch length, μm, $M \pm$ SD
C. fluminalis, ZIN No. 32 (sperm and larvae)	5	10.7 ± 0.69	6	206 ± 4	185 ± 11
'*C. purpurea*', ZMB 102850 (sperm), ZIN No. 49 (larvae)	5	12.8 ± 0.47	5	185 ± 11	Not measured
C. f. consobrina, ZMB 23632 (sperm), ZIN No. 9 (larvae)	5	12.3 ± 0.76	6	215 ± 9	Not measured
C. f. africana, SMF 10381a (sperm) ZMB 102632 (larvae)	5	6.8 ± 0.38	5	199 ± 8	183 ± 14

n – number of measurements, *M* – mean value, SD – standard deviation.

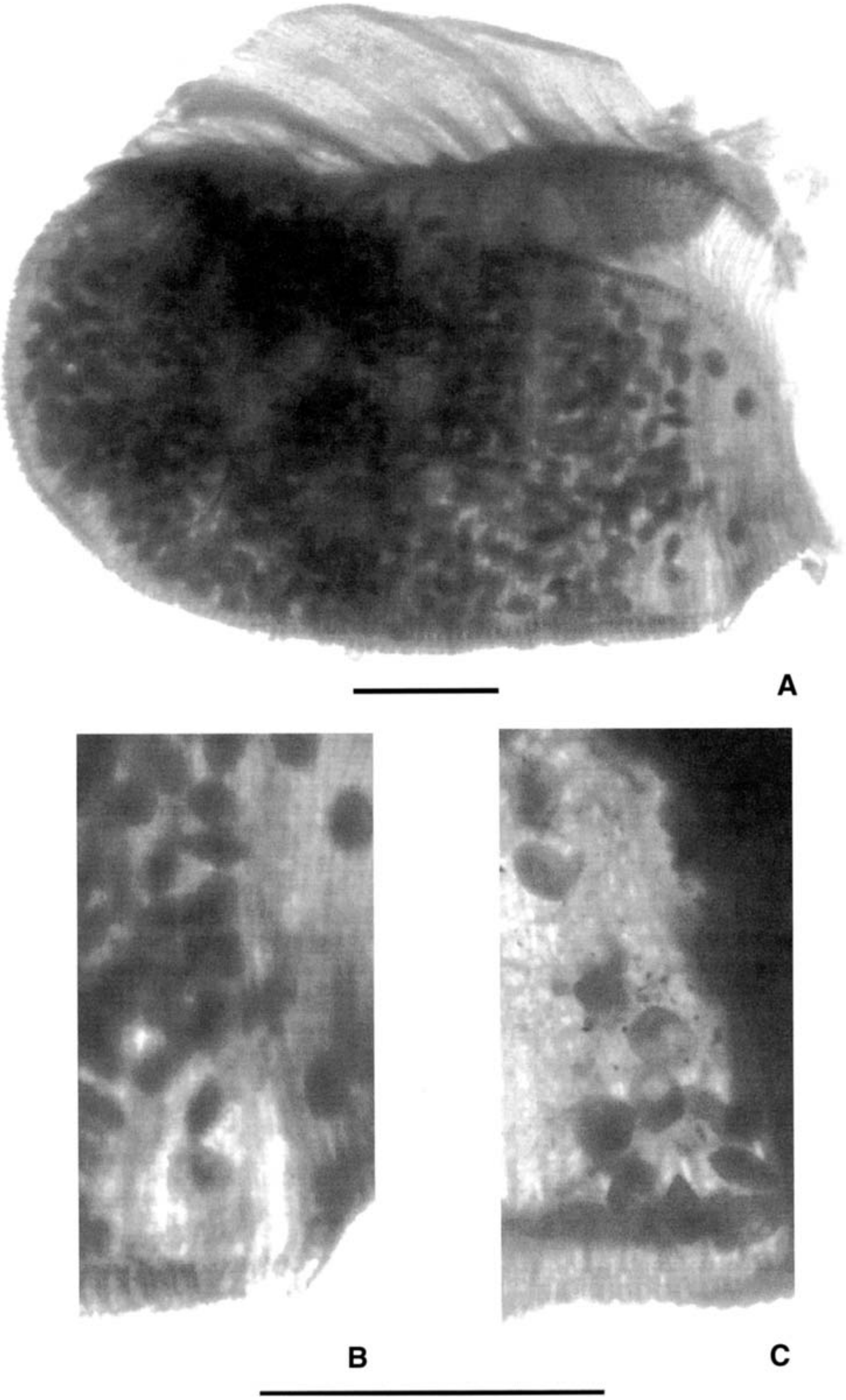

Figure 7. Larvae in gills of *Corbicula fluminalis*: (A, B) *C. fluminalis africana*, ZMB 102632; (C) *C. fluminalis* s. str., ZIN, No. 32, inner demibranch partly removed. Scale bar 1 mm.

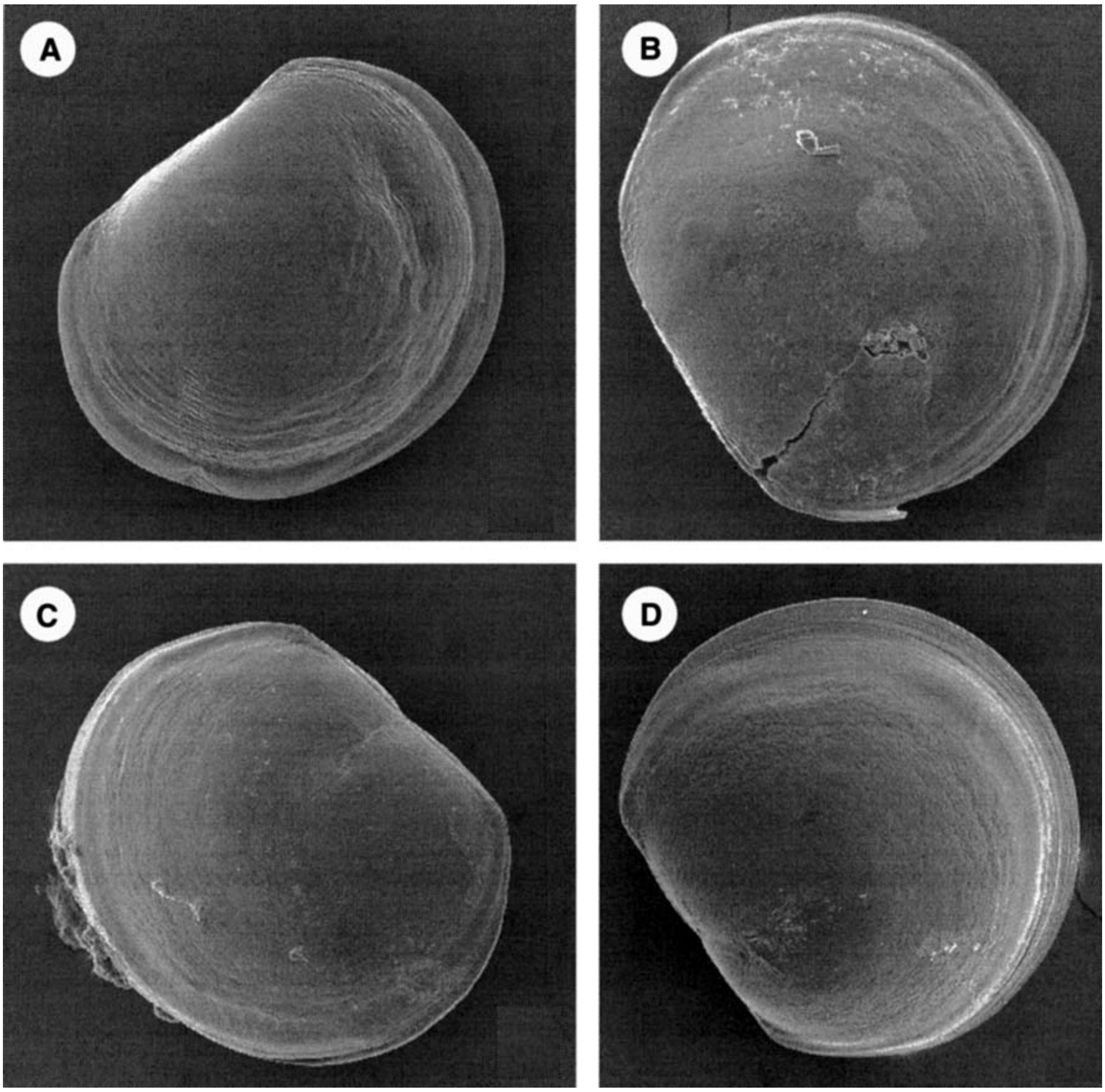

Figure 8. Larvae of *Corbicula fluminalis* extracted from gills (SEM): (A, B) *C. fluminalis* s.str., ZIN, No. 32; (C, D) *C. fluminalis africana*, ZMB 102632. Scale bar 30 μm.

of sexuality in *C. fluminalis*, but presence of hermaphroditic specimens in all studied morphotypes is confirmed; moreover, such specimens constitute a considerable part in most of the sampled populations. It should be also noted, that no functional males (specimens containing only sperm) were detected by the present study.

SEM observations have shown, that spermatozoa of all above mentioned morphotypes are biflagellate (Fig. 6). At the same time, remarkable variability in the head size was observed (Table 2). The smallest spermatozoa were obtained from *C. f. africana*, and those of *Corbicula fluminalis* s.str. were slightly, but significantly ($p < 0.01$) smaller than spermatozoa of '*C. purpurea*' and *C. f. consobrina*; the differences between the two latter taxa was not significant. It is noteworthy, that the differences in sperm morphology between Asian and African morphotypes corroborated the differences in shell characters.

No sperm was found in the available preserved material representing the Chinese morphotype assigned to *C. fluminalis*.

Specimens with incubated larvae in gills were found in all Asian and African morphotypes studied. In addition to the samples mentioned in Table 2, larvae were observed in specimens from the following lots: ZMB 23632, 32268, DBL (all from Nile River, *C. fluminalis consobrina*); ZMB 103056 (Lake Edward, *C. f. cunningtoni*); and SMF 10381a, 219527 (South Africa, *C. f. africana*). Up to several hundreds larvae could be located between gill lamellae in the inner demibranch (Fig. 7). In gravid specimens from Central Africa, developing larvae were densely packed, filling almost all available interlamellar space (Fig. 6A), while in other samples the larvae were distributed unevenly (Fig. 7C).

All larvae obtained from gills were D-shaped (Figs 4E, F, 7 and 8). Larval shells were weakly calcified and fragile, the hinge edge was straight, and no hinge structures were seen. The size of larvae was also similar (Table 2), ranging between 190 and 217 μm. The largest larvae (206–217 μm) were found in *C. consobrina* from Egypt, larvae of *C. fluminalis africana* from Lake Malawi were relatively small (190–208 μm).

The boundary between prodissoconch I and II was distinguishable on SEM pictures of intramarsupial larvae (Fig. 8); prodissoconch I size varied between 170 and 198 μm (Table 2), and prodissoconch II was seen as a narrow marginal band. No pores (punctal canals) could be distinguished.

No larvae were found in gills of *C. japonica* and in the studied Chinese specimens.

Discussion

Shell morphology and nomenclature

Considering the close fit in shell characters with the lectotype, the high form collected in Azerbajdžan and Syria can be identified as *C. fluminalis sensu* Müller. It should be noted that Russian authors (Izzatullaev, 1980) restricted their concept of *C. fluminalis* to this form. It is also similar to the 'saddle-like' European morphotype, referred to as *C. fluminalis* in literature (Rajagopal et al., 2000; Pfenninger et al., 2002).

The other Central Asian morphotype, identified by Izzatullaev (1980) as *C. purpurea* agrees well in its conchological characters with the original description and figures of this species from Tigris River (Prime, 1864). However, the species distinctiveness of *C. purpurea* is questionable, if the variability of shell dimensions in the genus is taken into account (Morton, 1986; Mandahl-Barth, 1988; this study) as well as the similarity in sculpture patterns with *C. fluminalis* s. str.

Discussing the status of North African *Corbicula*, both Van Damme (1984) and Mandahl-Barth (1988) noted that forms occurring in this area are morphologically hardly separable from Asiatic *C. fluminalis*. The former author recognised *C. consobrina* as a valid species, stressing, however, that it forms a 'superspecies' with *C. fluminalis*. In contrast, Mandahl-Barth (1988) failed to distinguish *C. consobrina* even as a geographical race of *C. fluminalis*. The most recent account of African *Corbicula* was provided by Daget (1998) who distinguished on this continent several geographically separated subspecies of *C. fluminalis*, namely *C. f. consobrina* (Cailliaud, 1927) (Nile basin and West Africa), *C. f. cunningtoni* Smith, 1906 (Lakes Victoria, Edward and Albert), *C. f. tanganyicensis* (Crosse, 1881) (Lake Tanganyica) and *C. f. africana* (Krauss, 1848) (East and South Africa from Lake Malawi to the Cape Province). Conchological characters of specimens included in the present study generally agree with this classification. However, the absence of a clear distinction between *C. f. consobrina* and the presumably Asian nominative subspecies of *C. fluminalis* (particularly the more elongated and flattened morphotype of the latter) should be pointed out. It should be also noted, that *C. f. africana* lives in South Africa sympathrically with *C. astartina*, differing from the latter taxon in its shell morphology (Mandahl-Barth, 1988; the present study).

Chinese specimens included in the present study correspond in their shell characters with the description of specimens from the Pearl River near Canton (China) and identified as *Corbicula cf. fluminalis* by Morton (1982: 5, pl. 2). Though similar to the lectotype of *C. fluminalis* because of its relatively high shell (see Fig. 2A and H), the Chinese morphotype differs in having irregular widely spaced ribs and glossy periostracum. In these characters, it is similar to *C. japonica*, as described by Harada & Nishino (1995).

Anatomy

Differences in siphonal characters between *C. fluminalis* s.str. and the Chinese '*C. fluminalis*' (*sensu* Britton & Morton, 1979; Morton, 1982, 1986) were detected in the study. Samples from Central Asia, the Caucasus, Middle East and North Africa representing *C. fluminalis* are almost identical in anatomy. Moreover, their narrow tubular siphons with relatively scarce papillae (especially around the exhalant aperture) and internal dark rings at the base are quite similar to siphons of *C. fluminea* (Britton & Morton, 1979; Araujo et al., 1993; Chen et al., 1995) and *C. leana* (see Harada & Nishino, 1995). On the other hand, siphonal characters of the Chinese form discussed here (slit-like form, with numerous exhalant siphon papillae and peculiar pattern of colouration) agree well with those of *C. japonica* (Harada & Nishino, 1995; this study). Thus, assignment of this morphotype to *C. fluminalis* and synonymisation of *C. japonica* with *C. fluminalis* (Morton, 1986) are not supported by the present anatomical investigation.

The low number of siphonal papillae observed in *C. fluminalis africana* and *C. f. cunningtoni* might be explained by the small size of these morphotypes. A correlation between the number of papillae and size was reported by Harada & Nishino (1995). Weak pigmentation of siphons and papillae may be peculiar to the African taxa but the siphons of the studied African *Corbicula* are basically of the same type as those of *C. fluminalis* and *C. fluminea*.

Reproduction

Presence of hermaphroditic specimens (containing both sperm and oocytes) and the biflagellate type of sperm shown for the Asian and African populations of *C. fluminalis s. lato* included in the present study suggest that they have basically the same mode of reproduction as *Corbicula fluminea*, *C. leana* and *C. australis* (Morton, 1986; Araujo, 1993; Byrne et al., 2000; Komaru et al., 1997, 2000). Sperm morphology is especially informative in this aspect, since spermatozoa with two flagelli were shown to be non-reductional, thus indicating clonality (Komaru et al., 1997; Siripattrawan et al., 2000).

In contrast to *C. fluminalis* in its present understanding, estuarine *Corbicula* from China and Japan are dioecious and apparently reproduce sexually (Morton, 1982, 1986). *Corbicula japonica* has uni-flagellate spermatozoa (Komaru et al., 1997), while sperm morphology of the Chinese estuarine *Corbicula* remains unknown. The reproductive features reported here for *C. fluminalis* differ also from that of the lacustrine Indonesian taxa studied by Glaubrecht et al. (2003), where either oocytes or spermatozoa (of the uni-flagellate type) were found in the dissected animals and no hermaphroditic specimens were detected. Since the same methods were applied in the last cited work and the present study, the observed peculiarities could hardly be artifacts. It is also noteworthy, that sexually reproducing freshwater species of *Corbicula* have, according to the available data, rather limited distribution, being restricted to Lake Biwa and several localities on Sumatra and Sulawesi (Siripattrawan et al., 2000; Glaubrecht et al., 2003). In contrast, clonal lineages are distributed throughout the range of the genus from Australia and Japan to the Caucasus and Africa.

Differences in the size of spermatozoa among *Corbicula* were also reported in literature. With the head size of 16–25 μm (depending on the level of ploidy), the biflagellate spermatozoa of the Chinese *C. fluminea* and Japanese *C. leana* (Komaru & Konishi, 1996; Qiu et al., 2001) are markedly larger than those of *C. fluminalis*. It is also interesting, that the South African *Corbicula f. africana* is close in this parameter to *C. australis* from Australia, with its spermatozoan head length of 9.3 μm on average (Byrne et al., 2000).

While the present observations on the larval incubation of African *Corbicula* agree with the data of literature (Mandahl-Barth, 1954), the reports on Central Asian populations were controversial. Izzatullaev (1980) observed shelled larvae in the samples identified by him as *Corbiculina tibetensis* (Prashad, 1929) and *Corbiculina ferghanensis* (Kursalova & Starobogatov, 1971), which are very similar in their shell morphology to *Corbicula purpurea*, as described in the present study. At the same time, *C. fluminalis* s. str. was described by him as non-incubating (Izzatullaev, 1980). The data on reproduction of European populations identified as *C. fluminalis* are also controvercial: some authors (Rajagopal et al., 2000) describe them as non-incubatory, while other observations (Kinzelbach and collaborators, unpublished) showed the presence of intrabranchial larvae similar to those of *C. fluminea*. Several possible explanations for these contradictions can be forwarded.

First of all, some characters of the studied larvae, such as the small size of the shell (not exceeding 217 μm), and narrow prodissoconch II indicate that the period of their incubation might be very short. According to the literature (Kennedy et al., 1991), released larvae in *Corbicula fluminea* are larger (up to 250 μm). The same size (250 μm) was reported for *C. australis* by Byrne et al. (2000), while intramarsupial larvae up to 350 μm long and even larger juveniles were found in some taxa from Indonesian islands (Glaubrecht et al., 2003). Noteworthy, the prodissoconch size measured in this study (mean value 183.9 μm, $n = 11$) is only slightly smaller than that reported by Kennedy et al. (1991) for *C. fluminea* (mean value 196.9 μm), thus the difference in the final size of the larvae is mainly due to the less developed prodissoconch II. According to King et al. (1986), the larvae of *C. fluminea* are released 100–125 h after fertilization. Taking into account, that the period of intrabranchial development in *C. fluminalis* may be even shorter, the probability of overlooking incubation even by seasonal sampling (Rajagopal et al., 2002) is rather high.

Furthermore, we cannot exclude that incubation in *C. fluminalis* is facultative. Scarcity of gravid *C. fluminalis* in museum collections seems to corroborate this suggestion. The mode of reproduction, as well as other biological features in species of the genus *Corbicula* may also depend on environmental conditions and thus be a populational characteristic, as already suggested by Morton (1986). In any case, assignment the designation of incubating and non-incubating Central Asian morphotypes to different species and even genera based on the fact if they are incubating or not (Izzatullaev, 1980) is unfounded. In particular the presence of larvae in gills of *C. fluminalis* s. str. and '*C. purpurea*' treated as non-incubating in the above mentioned paper is shown here. It seems therefore probable, that all morphotypes of *Corbicula* represented in Central and West Asia have the same mode of reproduction, which is a short-termed (possibly facultative) incubation of larvae. This hypothesis, however, should be confirmed by seasonal collecting in representative populations from different regions, especially from West Asia, accompanied by the careful examination of gills, in addition to the study of gonads. Reproductive biology of European *Corbicula* also needs closer investigation.

In any case, the larval development of *C. fluminalis* from Central Asia and Africa is apparently different from that of *C. japonica* and '*C. fluminalis*' from China, where incubation was never observed, despite numerous studies including seasonal field observations as well as histological examination of gonads and gills (see Morton, 1986, for a review). Though occasional incubation in these taxa cannot be excluded (Morton, 1982, 1986), it should be very rare.

Taxonomic implications

As already stressed by Morton (1979, 1986), the taxonomy and nomenclature of *Corbicula* is extremely complicated, because numerous taxa were described without providing solid diagnostic characters. There are many contradictions in the recent literature on the subject (Izzatullaev, 1980; Van Damme, 1984; Mandahl-Barth, 1988; Daget, 1998), which cannot be discussed in detail because of the rather limited material included in the present study and lack of molecular data. In additon, the clonal origin of many *Corbicula* lineages (Siripattrawan et al., 2000, present study) hampers taxonomic revision, since application of taxonomic names to such lineages is still disputable, and the knowledge of their ancestry is needed. Therefore, no final taxonomic decisions could be provided on this stage.

However, it seems necessary to evaluate the different views developed in literature in the light of the new data on anatomy and reproduction. First of all, the study of materials which were morphologically and geographically closest to the lectotype of *C. fluminalis* suggests that this name in its original sense (Müller, 1774) was given to a freshwater clonal lineage of *Corbicula* characterised by biflagellate sperm and short-termed incubation of larvae in gills. Another Asian morphotype distinguished by differences in its shell dimensions and referred to in literature as *C. purpurea* (Prime, 1864; Izzatullaev, 1980) is characterised by the same reproductive features; its distinctness is supported here by slight differrences in spermatozoan head length. This morphotype may represent another clonal lineage sympathrically occuring with *C. fluminalis* s. str. in the Middle East, the Caucasus and Central Asia. However, the species distinctness of the two mentioned Asian morphotypes seems improbable at this stage of investigation, given their similarity in shell sculpture, anatomy and the reproductive characters. The similar situation was recently described in North America, where two conchologically and genetically different lineages related to *C. fluminea* (forms A and B) were distinguished (Siripattrawan et al., 2000).

Identity of the North African morphotype to one of the Asian ones ('*C. purpurea*') shown by this study suggests their belonging to one and the same lineage. Thus, distinctness of the North African subspecies, *C. f. consobrina*, is not supported, this point of view being consistent with that of Mandahl-Barth (1988).

In contrast, the morphotype distributed in Lake Malawi and South Africa differs not only in its conchological indexes, but also in coloration of siphons and in size of spermatozoa. Therefore taxonomic distinctness of this morphotype seems probable, and *C. africana* can be treated as a valid name for it. However, its affinity to *C. fluminalis* at subspecific level, as suggested by Daget (1998), should be tested by future studies. The outstanding position of *C. africana* shown on the recently published trees based on COI sequence data (Pfenninger et al., 2002) needs a comment. The search in GenBank for the source of the cited sequence AF 196275 has shown that it represents indeed *C. madagascariensis* Smith, 1906 from Madagascar (under that name the sequence was already published by Siripattrawan et al., 2000). The latter name is treated as a valid species name in modern reviews (Daget, 1998), and no grounds for its synonymisation with *C. africana* were ever provided. Thus, the available sequence data should be attributed to *C. madagascariensis*, and the taxa from the African mainland are still awaiting molecular investigation.

The data on the other possible subspecies from the African Great Lakes (*C. f. cunningtoni* and *C. f. tanganyicensis*) are still too restricted and insufficient for any revision of their status.

The new observations show that *C. fluminalis* s. str. (as defined here) and *C. fluminea* are much more similar in respect of their anatomy and reproductive biology than considered previously (Britton & Morton, 1979; Morton, 1986). Both disputable taxa are characterised by their narrow conical siphons with relatively scarce papillae and internal pigmented rings, biflagellate sperm and incubation of larvae in gills. At the same time, they are distinguishable on the base of their shell characters (especially the patterns of sculpture); also the size of spermatozoa may be a distinctive character. These observations are in a good agreement with the latest molecular analysis (Pfenninger et al., 2002; Glaubrecht et al., 2003), showing *Corbicula* from Israel (where only *C. fluminalis* was previously reported) and *C. fluminea* (represented itself by several geographically separated paraphyletic lineages) as being genetically different and, at the same time, placing all of them in one large clade together with other incubating freshwater *Corbicula*. It is noteworthy, that the latter clade includes both sexual and clonal lineages (as indicated by their uni- and biflagellate type of sperm, respectively) with poorly resolved relationships (Glaubrecht et al., 2003). Therefore, assignment of all freshwater *Corbicula* lineages to one species seems to be ungrounded at this state of knowledge, but a more detailed molecular investigation of these clams is apparently needed.

The distinctness of the Chinese and Japanese estuarine morphs on one hand and *C. fluminalis* on the other in their mode of reproduction corroborate the differences in shell and anatomical characters and disagree with their synonymisation suggested by earlier works (Morton, 1982, 1986). On the other hand, close affinity of the mentioned Chinese morph and *C. japonica* still seems probable. All available molecular data (Siripattrawan et al., 2000; Pfenninger et al., 2002) confirm a distinct phylogenetic position of the latter species. Thus, the Chinese estuarine taxon can provisionally be designated as *Corbicula cf. japonica*, till its status is finally defined by the future investigation of sperm morphology and, especially, molecular genetics.

Concluding remarks

The results of this study show that the morphotypes assigned in the recent literature (Morton, 1986; Mandahl-Barth, 1988; Daget, 1998; Swinnen et al., 1998; Rajagopal et al., 2001) to *Corbicula fluminalis* are heterogeneic, differing not only in their shell characters, but also in anatomy and the mode of reproduction.

The morphotypes from Central Asia, the Caucasus, Middle East and North Africa, including the lots conchologically and geographically nearest to the type lot, are collectively characterised by narrow siphons with scarce papillae and pronounced internal pigmentation, as well as by simultaneous presence of oocytes and sperm in their gonads, biflagellate type of spermatozoa and incubation (possibly facultative) of larvae in the gills. Application of the name *C. fluminalis* is restricted herein to these morphotypes. Differences in shell dimensions and sperm morphology suggest presence of several clonal lineages in the above region, this hypothesis being testable by a detailed molecular investigation. *Corbicula fluminalis* in the present understanding (as a freshwater incubating taxon) is similar in its anatomy and reproductive biology to the East Asian *C. fluminea*, but can be well distinguished from the latter by the shell characters. Status of the both presumably distinct taxa can be finally settled, when a molecular investigation of the principal freshwater *Corbicula* lineages is completed.

Presence of another distinct taxon distributed in Lake Malawi and South Africa is also supported by the anatomical characters and sperm morphology; this taxon is referred to as *C. africana*. *Corbicula* populations from other African Great Lakes are similar in their anatomical characters to *C. africana*, but their sperm morphology remains unknown.

Interpretation of *C. fluminalis* as an estuarine dioecious non-incubating taxon suggested in some earlier works (Morton, 1982, 1986) is apparently wrong. As shown here, the Chinese estuarine *Corbicula* differs from *C. fluminalis* and is similar to *C. japonica* both in anatomy (broader siphons with numerous papillae and other pattern of pigmentation) and reproductive biology (absence of incubation); it is therefore provisionally designated as *Corbicula cf. japonica*. In the light of these data, molecular investigation of the non-incubating Chinese *Corbicula* is needed.

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