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NON-UNIONID FRESHWATER BIVALVES (SPHAERIIDAE, CORBICULIDAE, DREISSENIDAE) OF NORTH AMERICAN FAUNA

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Non-Unionid Freshwater Bivalves (Sphaeriidae, Corbiculidae, Dreissenidae) of North American Fauna. Korniushein A. V. – The article concerns recent representatives of the North American freshwater bivalve mollusks from the three families: Sphaeriidae, Corbiculidae and Dreissenidae. Since only the first family contains aborigine North American species, the paper is focused on this group. The Corbiculidae are represented by a single species (*Corbicula fluminea*) and Dreissenidae by two species (*Dreissena polymorpha* and *D. bugensis*) introduced from Europe and Asia.

Key words: Mollusca, Bivalvia, Sphaeriidae, Corbiculidae, Dreissenidae, North America.

Пресноводные двустворчатые моллюски (Sphaeriidae, Corbiculidae, Dreissenidae) фауны Северной Америки. Корнюшин А. В. – Статья представляет собой обзор современных пресноводных двустворчатых моллюсков Северной Америки из семейств Sphaeriidae, Corbiculidae и Dreissenidae. Особое внимание уделяется сферидам, так как к этому семейству относятся автохтонные североамериканские виды. Два других семейства представлены вселенцами из Европы и Азии – одним видом корбикулид (*Corbicula fluminea*) и двумя видами дрейссенид (*Dreissena polymorpha* и *D. bugensis*), и для них приведены только краткие характеристики.

Ключевые слова: двустворчатые моллюски, Sphaeriidae, Corbiculidae, Dreissenidae, Северная Америка.

Introduction

The manuscript, which was found in the Dr. Alexei V. Korniushein's archive, provides the basis for this article. The manuscript appears to be the chapter of monograph on the North-American fauna. Unfortunately it is unknown for us do this materials were published. For this reason, we believed that the publication of the manuscript in the form of review article is worthwhile. Also the list of North American sphaeriids found at the separate pages from Korniushein's archive was in use and species that were absent in the manuscript are depicted in the article.

The systematic positions and name combinations of mollusks are retained as well as in the author's text. In the cases that Alexei Korniushein used any other name combinations in his publications or manuscripts we cited them in footnote comments, wherever possible. The manuscript of the article was prepared for publication by Dr. I. V. Dovgal. We also thank Mikhail Son (Odessa Branch of the Institute of Biology of the South Seas) for useful information on the mollusk nomenclature.

Means of collection and preparation

Only the largest species of clams can be collected by hand. Smaller specimens should be washed out of the sediment with a sieve. Sediments can be taken by a shovel (in shallow water), a dipnet or a drag dredge (in deeper water). A kitchen sieve can be used for washing, but better results are achieved when the sieve has flat bottom. As follows from the above description of habitats, the places where some mud and debris are accumulated should be searched most carefully. Dead leaves, submerged moss or weeds (inch roots) should be also collected and washed in a sieve.

Small forceps with tapered soft tips are necessary to pick up specimens (which may be very small and fragile) from the sieve. Animals can be taken to the lab for the further preparation in tubes or jars containing water, wet cottonwool, grass or moss (the latter is recommended for the very fragile shells of *Musculium* Link, 1807 and some *Sphaerium* Scopoli, 1777, which may be damaged by shaking in water). When convenient, the whole amount of silt leaves or vegetation can be put in a plastic bag and brought to the lab for washing or sorting.

Dry shells for conchological collections can be kept in boxes; small specimens should be additionally packed in small glass tubes or gelatin capsules. Do not put them directly on cotton wool, as it may be hard to remove them from the cotton fibers. Specimens for anatomical study should be preserved in 70 to 80% ethanol. Neutralized formalin can be also used, but it is not recommended, since it can make the tissues too rigid. The fixative does not penetrate between tightly joined valves; therefore, the animals should be relaxed before fixation. Common narcotizing agents (menthol or barbiturates) can be used, but are not very effective for sphaeriids (exact concentration and time of relaxation should be determined experimentally for each species). Good result gives submerging of animals for several minutes in hot (but not boiling!) water (such material may be good for anatomical preparation, but not available for DNA analysis). If, however, the valves remain closed, one of them should be broken in order to let the fixative in. Special techniques of fixation should be used for histology, electron microscopy etc. When material for DNA sequencing is needed, a stronger alcohol (at least 80%) should be used, and the shells should be necessarily broken in order to ensure fast fixation.

Since internal shell characters (hinge, sometimes muscle scars) are necessary for species identification, it is necessary to open valves. If dried remnants of the soft body hinder opening, the specimen should be carefully heated in a 5% solution of alkali (KOH or NaOH), which dissolves the tissues and facilitate opening. If alkali solution is unavailable, heating in water may also be tried.

In order to expose the soft body for anatomical study, adductor muscles and mantle edge should be carefully detached from the shell with a needle or thin scalpel. Most of the organs are well seen laterally, but the form of nephridium may be clearer when looking from the dorsal side¹.

Details of gill structure are seen much better if the mantle sheets are removed. On the other hand, length of the presiphonal suture and arrangement of mantle muscles are better seen from the inner side of the mantle, therefore it is necessary to separate the mantle from the body. Separation of gills is recommended to expose brood pouches formed on their inner surface. Since the smallest pouches may be covered by the inner (ascending) gill lamella, the latter should be removed, if the exact number of brood pouches, their stage of development and number of embryos are to be determined (for example, for life history studies).

Some standard histological procedures of staining and mounting specimens were suggested for microscopic investigation of mantle and gills (Korniushev, 1995). While the literature on sphaeriid chromosomes is scarce and contains no detailed description of methods, some approaches developed for chromosomes of *Corbicula* Megerle von Muhlfeldt, 1811 can be recommended. Recently, the group was involved in molecular studies (Park, Foighil, 2000), and the methods of such study can be obtained from the special literature.

Living specimens of sphaeriids can be safely kept in a refrigerator for several weeks or even months. It is best to place them in wet cotton wool or moss rather than in water. Most of the species can live in aquarium without any special demands (personal observations). However, this may be problematic for species preferring lotic environments (e. g. *Sphaerium rivicola* (Lamarck, 1818)² or *S. striatinum* (Lamarck, 1818)³).

¹ See figures in A. V. Korniushev's monograph (1996).

² *Rivicoliana rivicola* in Korniushev, 1996.

³ *Amesoda striatina* in A. Korniushev's list of North American species.

Discussion

The recent North American fauna of Non-Unionid freshwater Bivalves includes three families: Sphaeriidae Jeffreys, 1862, Corbiculidae Gray, 1847 and Dreissenidae Gray, 1840. Since only the first family is native, this paper is focused on this group. The other two families are represented by a few species introduced from Europe and Asia and are only described briefly.

Family Sphaeriidae – Fingernail, Pea or Pill Clams

Species diversity and distribution. The Sphaeriidae are distributed all over the world. This family includes at least 150–200 valid species. However, the fauna of some regions are still poorly known and the systematics is not well established. Therefore, it is hard to evaluate the number of species more precisely. According to the latest reviews (Herrington, 1962; Burch, 1975), the North American fauna comprises 38 Sphaeriidae species. The European fauna is almost as rich and includes 25 to 30 species, though the status of some forms is in dispute. Some Russian reviewers recognized many more species (Korniushin, 1996), but this splitting approach is not accepted by West European specialists. Thirteen species are common for both continents, four species, *Sphaerium corneum* (L., 1758), *Pisidium amnicum* (Müller, 1774), *P. henslowianum* (Sheppard, 1823)⁴, *P. supinum* A. Schmidt, 1850⁵, and *P. moitessierianum* (Paladilhe, 1866)⁶ are considered to be introduced from Europe to North America (Burch, 1975; Grigorovich et al., 2000), and one species, *Musculium transversum* (Say, 1829)⁷ was apparently introduced from North America to Europe (Ellis, 1978). Some European species in North America might be overlooked, being described as local species or forms. Holarctic fauna of sphaeriids should be considered as rich. The fauna of the Ethiopian region, which is relatively well studied (Mandahl-Barth, 1988), comprises 29 species, other regions has poorer faunas.

Most of the North American sphaeriid species have transcontinental distribution, but some are more restricted (Burch, 1975). Three species, *Sphaerium nitidum* Clessin, 1876, *Pisidium idahoense* Roper, 1890⁸ and *P. conventus* Clessin, 1877⁹ are distributed only in the northern part of the continent, possibly with isolated populations in the mountains in more southern locations. *Sphaerium fabale* Prime, 1851¹⁰ and *S. patella* Gould, 1850¹¹ form a pair of morphologically similar but geographically separated species, the first being restricted to the eastern part of the continent, and the second to the western part. In the Eastern Hemisphere, similar separation characterizes the European *S. solidum* (Normand, 1854)¹² and the Siberian *S. asiaticum* Martens, 1884¹³. The Central American species *Eupera cubensis* (Prime, 1865) and *Pisidium punctiferum* (Guppy, 1867) are present in the southern states of the USA. One species, *P. ultramon-*

⁴ *Henslowiana henslowianum* in Korniushin, 1996.

⁵ *Henslowiana supina* in Korniushin, 1996.

⁶ *Neopisidium moitessierianum* in Korniushin, 1996.

⁷ *Paramusculium transversum* in Korniushin, 1996.

⁸ *Lacustrina idahoensis* in Korniushin's list.

⁹ *Conventus conventus* in Korniushin, 1996.

¹⁰ *Amesoda fabalis* in Korniushin's list.

¹¹ *Amesoda patella* in Korniushin's list.

¹² *Amesoda (Cyrenastrum) solida* in Korniushin, 1996.

¹³ *Amesoda (Asiocyclas) asiatica* in Korniushin, 1996.

tanum Prime, 1865¹⁴ is restricted to several localities in Oregon and northern California. Other species with limited distribution are known from the ancient lakes: Ochrid in the Balkans, Baikal in Siberia, Biwa in Japan, Tanganyika in Africa and Titicaca in South America. The highest species diversity of sphaeriids in North America is observed in the Great Lakes region (Burch, 1975).

Classification. According to Burch (1975), the family is divided in three sub-families: Euperinae Heard, 1965 with the genera *Eupera* Bourguignat, 1854 and *Byssanodonta* d'Orbigny, 1846, Sphaeriinae Jeffreys, 1862 with the genera *Sphaerium* and *Musculium* and Pisidiinae Baker, 1927 with a single genus *Pisidium*. The *Eupera* are restricted to the tropical regions of Africa and America, with the greatest diversity in South America. *Byssanodonta* is a monotypical South American genus; while the remaining genera are cosmopolitan and their range coincide with the range of the family. The generic classification is hardly final, since heterogeneity of anatomical characters was found in all the named genera, and a phylogenetic analysis, which is necessary to construct the natural system of the group, has still not been carried out. It is also possible that at least Euperinae, with their very peculiar morphology and mode of reproduction, deserve the status of a separate family. Subgeneric classification is even more uncertain, since none of the suggested classifications take into account all the global fauna. Burch (1975) divides the North American *Sphaerium* species between two subgenera – *Sphaerium* s. str. and *Herringtonium* Clarke, 1973, and *Pisidium* between three subgenera – *Pisidium* s. str., *Cyclocalyx* Dall, 1903 and *Neopisidium* Odhner, 1921.

Morphological and biological peculiarities. The species of this family are the smallest among freshwater bivalves and, probably, among bivalves in general. Some sizes of the adult animals (*Pisidium moitessierianum* (Paladilhe, 1866) for example) do not exceed 2.5 mm, though most of the species are somewhat larger, from 3 to about 15 mm long. The largest North American species, *Sphaerium simile* (Say, 1816)¹⁵, may reach 20 mm. The European species, *Sphaerium rivicola* (Lamarck, 1818)¹⁶ is even bigger, it can range up to 25 mm long.

The sphaeriid shell is usually round or oval, but in some species may be trigonal or tetragonal (trapezoid). The position of the umbo may be anterior (*Eupera*), central (*Sphaerium* and *Musculium*) or posterior (*Pisidium*). The outer surfaces often bear concentric sculpture: ribs (larger elements with interval about 0.5 mm) or striae (fine sculpture with interval 0.025–0.1 mm). Tiny pores (3–5 μm in diameter) are usually noticeable on the internal surface. The scars of the two adductors are well marked, while the smaller scars of siphonal retractors are sometimes noticeable, lying near those of posterior adductors or being attached to them. The mantle line is usually weakly marked, and never forms a sinus; the scars of mantle muscle bundles may be visible above this line.

The sphaeriid hinge is typically heretorodont and consists of cardinal, anterior and posterior lateral teeth (Cox et al., 1969). The left valve bears two cardinal teeth and two lateral teeth, one anterior and one posterior; the right valve has one cardinal and two lateral teeth. The lateral teeth are markedly reduced in the Australian taxon *M. lacustre*, and all hinge teeth are reduced in the *Byssanodonta*.

The ligament is visible and external in some species (e. g. *Sphaerium simile*, *M. transversum* (Say, 1829)). In a majority of the taxa, it is covered dorsally by a thin layer of calcified material and thus not visible. In species of the subgenus *Pisidium* (*Odhneripisidium* Kuiper, 1962), the ligament is introverted, e. g. deeply submerged between valves.

¹⁴ *Euglesa ultramontane* in Korniushev's list.

¹⁵ *Cyclas similis* in Korniushev, 1996 and *Amesoda similes* in Korniushev's list.

¹⁶ *Rivicoliana rivicola* in Korniushev, 1996.

The soft body structure is characterized by some peculiar features that may be associated with the small size of these mollusks. The mantle usually forms two ventral fusions dividing the exhalant (anal), inhalant (branchial) and pedal openings. Species of *Eupera*, *Byssanodonta*, *Sphaerium* and *Musculium* have tubular exhalant and inhalant siphons, separate (in the first two genera), or partially joined to each other. The genus *Pisidium* is characterized by the broad (funnel-like) exhalant siphon and the absence of the inhalant siphon. Branchial opening may be retained (e. g. *P. amnicum*, *P. casertanum* (Poli, 1791)¹⁷ or absent (e. g. *P. moitessierianum*, *P. conventus*). The pedal opening is usually a long slit, but in some species (*Eupera* spp., *P. subtruncatum* Malm, 1853¹⁸, *P. milium* Favre, 1927¹⁹) it is shortened because of progressive development of the presiphonal suture (mantle fusion dividing inhalant opening from the pedal slit). In contrast to corbiculid or venerid bivalves in which the siphons are contracted by two broad muscle bands, the siphonal muscles of sphaeriids form several pairs of retractors, hence the absence of the pallial sinus.

The foot is usually well developed and extendable (capable for a great extension). It is a borrowing organ in the majority of species. In contrast, the especially long, motile, worm-like foot of *Sphaerium corneum* gives this animal ability to creep on the water plants. A functional byssus gland is found in the larvae of some species (Mackie et al., 1974), however, adult animals retain a byssus only in the *Eupera* and *Byssanodonta*. The latter peculiarity is apparently associated with their mode of life (see below).

The gills are characterized by a certain reduction of the outer demibranch (outer demibranch is always lower than inner one). The most profound reduction is a characteristic of *Pisidium*: in all species, except *P. idahoense*, the outer demibranch has only one lamella and does not overlap the inner one, and in many species (those lacking inhalant mantle opening) it disappears completely. As in the majority of filter-feeding bivalves, gills of sphaeriids have two basic functions: respiration and collecting food. The reduction of the size of gills definitely leads to the diminution of their respiratory and food-collecting surface, and is, therefore, correlated with the size of the animal.

The configuration of the nephridium is a taxonomic character. The excretory organs of sphaeriids (nephridia) are progressively developed, in contrast to the typical voluminous bivalve nephridium. The excretory organ in this group is a long specifically packed tube. Progressive development of the nephridium can be seen as an adaptation to the freshwater environment which is hypoosmotic and needs intensification of the osmoregulatory function usually carried out by excretory organs.

All sphaeriids are hermaphrodites. The gonads are relatively big, extended to the dorsal side of the animal in *Eupera* and *Byssanodonta*, and small, placed behind the foot in the other genera. Some sphaeriid species are distinguished by remarkably high chromosome numbers (Burch, Huber, 1966; Burch et al., 1998) which in all probability resulted from polyploidy. The only diploid species known is *Sphaerium corneum* with $2n = 36$. However, the family is still poorly studied in this respect.

The most remarkable feature of sphaeriids is the incubation of their young in the gills of the parent animal. *Eupera* and *Byssanodonta* produce large eggs rich in yolk, which develop between the lamellae of the inner demibranch. In the other genera, specialized organs for breeding, brood pouches or marsupia, are produced by inner demibranch filaments. In *Sphaerium* and *Musculium*, several pouches develop in each gill simultaneously and release their young successively, while in *Pisidium* formation of a new pouch is possible only after release of the previous brood.

Sphaeriids usually have one or two breeding seasons per year. Those from habitats with stable temperature, such as deep-water lake populations or tropical species, may

¹⁷ *Euglesa (Euglesa) casertana* in Korniuschin, 1996.

¹⁸ *Pseudeupera subtruncata* in Korniuschin, 1996 and *Euglesa subtruncata* in Korniuschin's list.

¹⁹ *Tetragonocyclus milium* in Korniuschin, 1996.

reproduce year round. Details for particular species are provided by W. H. Heard (1965, 1977), C. Meier-Brook (1970) and I. J. Holopainen and I. Hanski (1986). Incubation of larvae in brood pouches may last from one month (in smallest pisidia) up to several months. After release from pouches, the young continue their growth lying freely in the gill (extra-marsupial larvae), and then leave the parent through its siphons. Compared to bivalves with veliger larvae, sphaeriids are characterized by low fecundity. The number of offspring released by one parent in one breeding season does not exceed several dozens. *Eupera* and *Musculium* species, as well as *Pisidium amnicum*, are characterized by the highest fecundity (sometimes more than 50 young per gravid adult), most *Sphaerium* and *Pisidium* species release up to 20 young, and *P. conventus* may incubate simultaneously only 2 to 3 larvae.

It is notable, that newly released *Sphaerium* already have mature gonads (the young begin to produce their own eggs and sperm even at the end of the incubation period) and soon form the first brood pouches (Heard, 1977). This peculiarity was not found in *Musculium* and *Pisidium*. On the other hand, *Musculium* species are characterized by relatively rapid growth and reach their final size in 60–70 days, while *Sphaerium* need 4 to 8 months to mature, and *Pisidium* about a year. The life span of *Musculium* species is about a year; in *Sphaerium* and *Pisidium* it is up to 5 years. Populations and species from northern countries are characterized (on the average) by slower growth and a longer life span (Holopainen, Hanski, 1986).

Most of the sphaeriids are borrowing. The larger species (*Sphaerium*, *Musculium*, *Pisidium amnicum*) only partly submerge in sediments, with their siphons stretching into the water. They are typical filter-feeders and consume mainly phytoplankton (Lopez, Holopainen, 1987). Most of these species are apparently not very mobile, except *Sphaerium corneum*, which often occurs openly, on submerged vegetation (personal observations) and can move almost as fast as snails move. Small *Pisidium* species are typically completely submerged in bottom sediments, dwelling in long blind burrows, and their feeding mode is defined as interstitial suspension-feeding (Lopez, Holopainen, 1987). Interstitial bacteria probably form the main part of their diet. Some species of sphaeriids may occur among submerged leaves (*Musculium lacustre* Müller, 1774, *Pisidium casertanum*) or mosses (*P. obtusale* (Lamarck, 1818), *P. milium*). North American *Eupera* combine burrowed (infaunal) and attached (epifaunal) modes of life, while some South American *Eupera* and the only species of *Byssanodonta* are strictly epifaunal and attach by a byssus to rocks, stones or other hard substrata (Ch. Ituarte, personal communication).

Habitats. Sphaeriid clams occur in a great variety of habitats: from large rivers and lakes to springs, peatbogs and temporary pools. The highest species diversity is characteristic of lakes, ponds and small rivers. Springs are usually colonized by one species — *Pisidium casertanum* (in Europe *P. personatum* Malm, 1855²⁰ may be also found) which is usually quite abundant. Some species show clear preference to particular habitats (e. g. *P. idahoense*, *P. liljeborgi* Clessin, 1886²¹ and *P. conventus* — to lakes, *P. supinum* — to rivers), while others may live in different types of habitats. The latter species seem to be less sensitive to variations in oxygen and calcium content in the water. However, they apparently cannot live in anaerobic conditions and therefore avoid pools with deep layer of liquid ooze or decaying debris. Some species, e. g. *Sphaerium occidentale* Prime, 1853²², *M. lacustre* and *P. casertanum* can survive temporary drying up in thin layer of water or even in wet soil or leaves. As a rule, sphaeriids does not tolerate salinity higher than 0.03% Cl, and only a few species can withstand higher salinity: *P. casertanum*, *P. henslowanum*, *P. nitidum* Jenyns, 1832²³ and

²⁰ *Euglesa (Euglesa) personata* in Korniushev, 1996.

²¹ *Henslowiana liljeborgi* in Korniushev, 1996 and *Euglesa liljeborgi* in Korniushev's list.

²² *Horringtonium occidentale* in Korniushev's list.

²³ *Cingulipisidium nitidum* in Korniushev, 1996 and *Euglesa nitida* in Korniushev's list.

P. subtruncatum Malm, 1855 are the most tolerant in Europe and may live in the lowest courses of rivers (Kuiper, Wolf, 1970).

Being burrowers, most sphaeriids avoid coarse sediments (rocks and gravel), as well as hard sand, preferring fine sand, muddy sand and mud. Some amount of detritus seems to be necessary for them, probably because of their feeding on saprotrophic bacteria (Lopez, Holopainen, 1987). Therefore, they are usually rare in the main stream of rivers or along the beaches exposed to waves and numerous in more quiet places, where some mud or debris can be accumulated. Species such as *Sphaerium occidentale*, *Musculium lacustre*, *Pisidium casertanum* and *P. ventricosum* Prime, 1851²⁴ (in Europe *P. obtusale* (Lamarck, 1818)²⁵ are often abundant in small forest lakes or streams with bottoms covered with dead tree leaves. Only several species (*Sphaerium striatinum* and *P. dubium* (Say, 1822), in Europe *S. rivicola*, *S. solidum* (Normand, 1844) and *P. amnicum* (Müller) show clear preference to lotic environments and coarser sediments (sand or even gravel). Despite their ability for dispersal by birds and water insects (Mackie, 1979), sphaeriids are rarely found in artificial pools not connected with natural streams (personal observation).

Practical applications. Until now, the sphaeriids did not seem to be of any practical importance. While many of them contain trematode larvae (personal observations), none were reported to be intermediate hosts of human parasites. Being small and having a short life span, they are not as suitable for environmental monitoring as unionids. Apparently, some species may be indicators of good (or bad) water quality (for example in Europe, *P. amnicum* and *P. pulchellum* Jenyns, 1832²⁶ while in America they are yet to be determined). It is also necessary to include this group in current ecological surveys, since some species are apparently vulnerable because of their limited distribution and specific ecological demands. They may suffer from water pollution, change of habitats and other negative consequences of human activity.

Addendum: the list of North American sphaeriids that were absent in the manuscript

Euglesa aequilateralis (Prime, 1851)

E. compressa (Prime, 1851)

E. fallax (Sterki, 1896)

E. ferruginea (Prime, 1851)

E. insignis (Gabb, 1888)

E. milia (Held, 1836)

E. rotundata (Prime, 1865)

E. variabilis (Prime, 1851)

E. walkeri (Sterki, 1895)

E. adamsi (Prime, 1851)

Musculium partumeium (Say, 1822)

M. secures (Prime, 1851)

Neopisidium simplex (Sterki, 1895)

N. cruciatum (Sterki, 1895)

Sphaerium rhomboideum (Say, 1822)

Family Corbiculidae – Asiatic Clams

Only one species of this family, *Corbicula fluminea* (Müller, 1774), is reliably identified in North America as being introduced before 1938 (Britton, Morton, 1979). The presence of a second, not yet identified species is possible (Morton, 1986; Siripattawan et al., 2000). The type locality of *C. fluminea* is Canton, China (Araujo et al., 1993), and the species is considered to be widely distributed in South East Asia (Morton, 1986).

²⁴ *Euglesa ventricosa* in Korniusshin's list.

²⁵ *Euglesa obtusalis* in Korniusshin, 1996.

²⁶ *Pseudeuopera pulchella* in Korniusshin, 1996.

Many other *Corbicula* Megerle von Muhl Feld, 1811 species were described from different Asian countries, Africa and Australia; their taxonomic status is still disputable, and some modern reviewers (Morton, 1986) recognize only two species, namely *C. fluminea* and *C. fluminalis* (Müller, 1774) (type locality – Euphrat River in Mesopotamia). Introduced populations of *C. fluminea* were found also in South America (Buenos Aires), and both above mentioned species were introduced to West Europe (see Morton, 1986 and Araujo et al., 1993 for reviews). *Corbicula* is reported to be a serious pest in its introduced range (Morton, 1979 after: Morton, 1986).

The morphology and biology of *Corbicula* was extensively described by Britton and Morton (1979), and only the most remarkable characters are presented here. They differ from sphaeriids in their much larger size (normally up to 35 mm long, but in some populations up to 60 mm). The sculpture is much coarser, and arrangement of ribs may be a taxonomic character (about 10 pronounced ribs per 10 mm in *C. fluminea*, and more than 15 in *C. fluminalis*). The hinge of each valve includes 3 cardinal teeth, and long lateral teeth (the same set as in *Sphaerium*) that bear small denticles. Pores similar to that of sphaeriids are noticeable on the inner surface. The mantle line is clear and smooth (without any extending muscle scars), and a small pallial sinus is usually noticeable; in some other corbiculid genera, e. g. in the South American *Neocorbicula* Fischer, 1887, the mantle sinus is pronounced.

The siphons of *Corbicula* are relatively short and their openings are fringed with papillae. Form and pigmentation of siphons, as well as number and arrangement of papillae were also suggested as species diagnostic characters (Britton, Morton, 1979; Harada, Nishino, 1995), but many Asian species and forms are not yet studied in this respect. The siphonal muscles form two broad bands, as in marine venerid bivalves. Each gill consists of two almost equally developed demibranchs (outer one somewhat lower). The gonad is big and branched, and produces a great number of oocytes. *Corbicula fluminea* is proterandric or simultaneous hermaphrodite with a triploid chromosome set based on $n = 18$ (Okamoto, Arimoto, 1986). The fertilized eggs are incubated within the inner demibranch without any brood pouches. The larvae are released with a straight-hinged (D-shaped) shell, but an already well developed creeping foot. Even longer incubation of young takes place in *Neocorbicula limosa* (Maton, 1809); the larvae of this species reach in gills apparently rather advanced stage of development, and several broods may develop in one parent animal simultaneously (Ituarte, 1994; Dreher Mansur, Meier-Brook, 2000). The other mode of reproduction (dioecious, releasing free-swimming larvae without incubation) was reported for some Asian taxa. Modern Japanese authors (Harada, Nishino, 1995) recognize one of them as a distinct species *Corbicula japonica* (Prime, 1864), but Morton (1986) assign all non-incubating forms to *C. fluminalis*. An intermediate mode (release of creeping larvae without incubation) is known in *C. sandai* Reinhardt, 1878, restricted to the Japanese lake Biwa (Harada and Nishino, 1995). Both *C. japonica* and *C. sandai* are diploid ($2n = 19$ and 18 , respectively, see Okamoto, Arimoto, 1986 for details). *C. fluminea* lives 3 years, and *C. japonica* – up to 9 years (Morton, 1986, a review).

In America, *Corbicula* can be found in rivers, including the low courses and reservoirs, but generally not in estuaries. It occurs both in lotic and lentic conditions, mainly embedded in coarse sediments (sand and gravel). In contrast, the non-incubating Asian forms, are estuarine (brackish water). The broad ecological range correlated with a variety of reproduction modes makes Corbiculidae (and the genus *Corbicula* in particular) the good model for studying the evolutionary adaptation of bivalves for freshwater environments.

The methods and equipment for collecting *Corbicula* are basically the same as suggested for sphaeriids. Handling them is definitely simpler because of their larger size. Special methods for the chromosome study are described in A. Okamoto and

B. Arimoto (1986), and the DNA sequencing data are summarized by S. Siripattawan et al. (2000). Given the on-going dispute on the taxonomy of various *Corbicula* forms, the further studies on their morphology (including anatomy and the chromosomes), DNA sequences and biology are of great importance.

Family Dreissenidae – Zebra Mussels

Dreissena polymorpha (Pallas, 1771) appeared in North America in 1988 (Hebert et al., 1989; Ludyanskiy et al., 1993). A second European species, *D. bugensis* (Andrusov, 1897) (sometimes called quagga mussel), was also reported (Mills et al., 1996). *Dreissena* Beneden, 1835 can be immediately recognized by their triangular shell, somewhat similar to that of *Mytilus* Linnaeus, 1758 and attached mode of life. The byssus is very well developed, and the foot in the adult specimens is rudimentary. The anterior adductor muscles are reduced; the poster adductor and the pedal muscle are strong and form big scars. Two siphons are present, and both demibranchs of each gill are almost equally developed. A big massive gonad is placed at the base of the foot. In contrast to other freshwater bivalves, *Dreissena* releases free swimming veligers. Further information on distribution, habitats and life cycles of American populations can be obtained from the above mentioned papers.

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