

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/283437520>

"History of Limnocardiinae (Bivalvia, Cardiidae)"

Article in *Paleontological Journal* · January 2001

CITATIONS

52

READS

218

3 authors, including:



[Sergey Popov](#)

Russian Academy of Sciences

27 PUBLICATIONS 372 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



History of Paratethys [View project](#)



Fundamentals of the natural environment history of the south of Western Siberia and Turgai in the Cenozoic: sequence sedimentology, abiotic geological events and the evolution of the Paleobiosphere [View project](#)

10

Shevch

Paleontological Institute, Russian Academy of Sciences

L. A. Nevesskaja, N. P. Paramonova, and S. V. Popov

History of Lymnocardinae (Bivalvia, Cardiidae)

Responsible editor
A.A. Shevyrev, Dr. Sci. (Biol.)

MOSCOW
2001

Contents

Vol. 35, Suppl. 3, 2001

The supplement is published only in English by MAIK "Nauka/Interperiodica" (Russia).
Paleontological Journal ISSN 0031-0301.

INTRODUCTION	S147
SYSTEM OF THE SUBFAMILY LYMNOCARDIINAE	S147
GEOLOGICAL HISTORY AND PHYLOGENY OF LYMNOCARDIINAE	S149
<i>Oligocene</i>	S150
<i>Early Miocene</i>	S150
<i>Middle Miocene</i>	S152
<i>Late Miocene</i>	S154
<i>Pliocene–Early Pleistocene</i>	S163
ECOLOGY OF LYMNOCARDIINAE	S170
MAIN FEATURES OF LYMNOCARDIINAE EVOLUTION	S171
ISSUES OF LYMNOCARDIINAE SYSTEMATICS	S173
SYSTEMATIC PALEONTOLOGY	S174
Tribe <i>Cerastodermatini</i> Nordsieck, 1969	S175
Tribe <i>Merklinicardiini</i> Popov, tribus nov.	S176
Tribe <i>Limnopappiini</i> Schlickum, 1962	S177
Tribe <i>Chokrakiini</i> Popov, tribus nov.	S178
Tribe <i>Plicatiformini</i> Paramonova, tribus nov.	S179
Tribe <i>Obsoletiformini</i> Paramonova, tribus nov.	S179
Tribe <i>Planacardiini</i> Paramonova, tribus nov.	S181
Tribe <i>Aviculocardiini</i> Paramonova, tribus nov.	S181
Tribe <i>Lymnocardiini</i> Stoliczka, 1870–1871	S182
Tribe <i>Paradacnini</i> Ebersin, 1965	S189
Tribe <i>Phyllocardiini</i> Nevesskaja, 1986	S190
Tribe <i>Pontalmyrini</i> Taktakischvili, 1987	S191
Tribe <i>Arcicardiini</i> Nevesskaja, 1986	S198
Tribe <i>Prosodacnini</i> Andreescu, 1974	S199
Tribe <i>Pachydacnini</i> Andreescu, 1975	S204
Tribe <i>Avicardiini</i> Popov, 1977	S205
Tribe <i>Acobaecardiini</i> Paramonova, 1986	S207
Tribe <i>Adacnini</i> Vest, 1875	S207
CONCLUSIONS	S212
REFERENCES	S213

INTRODUCTION

The study of the phylogeny and system of the subfamily Lymnocardinae (family Cardiidae) is of special interest, because its history may provide an example of repeated events of adaptive radiation and appearance of numerous homeomorphic taxa due to reduced competition when most of the biota went extinct.

Such phenomena occurred in the Oligocene–Pliocene epicontinental basins of the Paratethys. The term was introduced by Laskarev (1924) to refer to intracontinental basins at the northern margin of the ancient Tethys Ocean. Low salinity and modified composition of salts in these basins were caused by their partial or complete isolation from the World Ocean. Kolesnikov (1949, p. 14) wrote about one of these basins: "We can call the Sarmatian Basin a natural laboratory where faunal development proceeded at a much faster rate than in the open seas." The same is true of all the above-mentioned basins.

In terms of salinity and dominating type of fauna, the Oligocene–Pliocene Paratethys fluctuated from the almost normal marine to mixohaline regime, thus resulting in the formation of varying types of basins: semimarine half-closed basins (salinity 18–25‰); semimarine basins episodically connected to the open sea (salinity 5–18‰); and brackish basins with an ion composition characteristic of the Caspian type. Such semimarine basins that were only episodically connected to the open sea, and brackish basins repeatedly emerged in the Paratethys area, and the history of Lymnocardinae is chiefly connected with them.

Stratigraphy of the Oligocene–Pliocene Paratethys, the paleogeography of the basins, and history of their malacofaunas were treated in detail in the monographs "History of the Neogene Molluscs of Paratethys" (Neveeskaja *et al.*, 1986) and "Stratigraphy and Bivalves of the Oligocene–Lower Miocene of Eastern Paratethys" (Popov *et al.*, 1993). Some questions concerning the phylogeny and ecology of the Neogene bivalves (including lymnocardines) were discussed by Neveeskaja *et al.* (1987, 1989); descriptions of lymnocardine species are given in "Atlas of the Miocene Bivalves of Southwestern Eurasia" (Neveeskaja *et al.*, 1993) and "Atlas of the Pliocene Bivalves..." (Neveeskaja *et al.*, 1997).

In this monograph, the systematics, phylogeny, ecology, and zoogeography of Cerastodermatini, Merklincardiini tribus nov., Lymnopappiini (Oligocene, Kozahurian), and Chokrakiini tribus nov. (Chokrakian) are treated by S.V. Popov; Obsoletiformini tribus nov., Aviculocardiini tribus nov., Plicatiformini tribus nov., Planacardiini tribus nov. (Sarmatian), Cerastodermatini, Avicardiini and Acobaecardiini (Akchagilian) by

N.P. Paramonova; and Lymnocardini, Paradacnini, Phyllocardiini, Arcicardiini, Pontalmirini, Prosodacnini, Pachydermini, and Adacnini (Pontian–Kujalnician and Apsheronian) by L.A. Neveeskaja.

SYSTEM OF THE SUBFAMILY LYMNOCARDINAE

The subfamily Lymnocardinae was created by Stoliczka (1870–1871) to include the genera *Lymnocardium* Stoliczka, 1870–1871 and *Didacna* Eichwald, 1838. During the same years, Vest (1875) established the family Adacnidae, comprising the genera *Adacna* Eichwald, 1838; *Monodacna* Eichwald, 1838; and *Myocardia* Vest, 1875 (= *Lymnocardium* Stol.).

Thus, these students believe that the brackish-water cardiids from the Cenozoic of Europe and western Asia and those from the modern Caspian Sea differ from the marine representatives of Cardiidae so markedly that they should be raised to the subfamily or even family level.

Subsequent development of the system of Cardiidae as a whole and that of the brackish-water cardiids was long and quite complicated. Andrussov (Andrussoff, 1903, 1910; Andrussov, 1923) contributed much towards the solution of this problem; he characterized the genera known before (*Adacna*, *Didacna*, *Arcicardium*, *Hypanis*, *Phyllocardium*, *Monodacna*, *Lymnocardium*, and *Prosodacna*) and added new genera (*Plagiodacna*, *Apsheronia*, *Pteradacna*, and *Stenodacna*). As for the systematic relationships between the marine and brackish-water cardiids, he regarded the latter as independent genera and placed them and their marine relatives into the same family, Cardiidae (Andrussoff, 1903).

Ebersin (1947, 1951, 1959, 1962, 1967) wrote a five-volume monograph on the Pliocene brackish-water cardiids of the southern USSR (excluding those from the Akchagilian and Apsheronian), assigned all of the genera studied to the family Cardiidae, and divided them between five subfamilies (Ebersin, 1965a, 1967): Lymnocardinae Stoliczka, 1870–1871; Didacninae Ebersin, 1962; Paradacninae Ebersin, 1965; Adacninae Vest, 1875; and Pseudocarditinae Ebersin, 1965.

This subdivision was accepted by Keen (1969) in "Treatise on Invertebrate Palaeontology," but she lumped these subfamilies together as a separate family, Lymnocardidae, thus contrasting the brackish-water and marine forms (retained in Cardiidae).

Earlier, both Andrussoff (1903) and Ebersin (1947) argued against this opposition, pointing to the intimate relationships of marine and brackish-water forms. This was confirmed by detailed studies of the morphology, including shell microstructure, in marine and brackish-

water cardiids performed by Popov (1977) and Kafanov and Popov (1977). Popov demonstrated the transitional character of the genus *Cerastoderma*, which is closely related both to the members of Fraginae and to brackish-water cardiids, most of which evolved from this genus. Based on this fact, he quite reasonably united all brackish-water cardiids and *Cerastoderma* into the subfamily Lymnocardinae (in a broader sense than used before).

Kafanov and Popov (1977) divided the subfamily Lymnocardinae into nine tribes. In addition to the tribes Didacnini, Lymnardiini, Hypanini (=Adacnini), and Paradacnini that were treated as subfamilies by Ebersin, five more tribes were included: (1) Cerastodermatini Nordsieck, 1969, in addition to *Cerastoderma* containing the Oligocene genus *Korobkoviella* and Sarmatian genera *Plicatiformes* and *Planacardium*; (2) Limnopappiini Schlickum, 1962, comprising the Kozahurian–Otrrangian genera *Limnopappia*, *Limnopageta*, *Succuridacna*, and provisionally *Eoprosodacna*; (3) Prosodacnini Andreescu, 1974, uniting the Pliocene genera *Prosodacna*, *Dacicardium*, *Fischeridacna*, and others; and two newly established tribes, (4) Avicardiini Popov, 1977 for the Akchagilian genus *Avicardium* and (5) Hyrcaniini Kafanov et Starobogatov, 1977 for several Apsheronian genera (*Hyrcania*, *Didacnoides*, *Hyrcanomya*, and *Turkmena*).

Before turning to the system of Lymnocardinae accepted in this paper, let us consider the difficulties of constructing such a system, resulting mainly from the broad distribution of homeomorphy and parallel evolution in many semimarine and brackish-water molluscs. These phenomena were discussed in detail in a monograph entitled "History of the Neogene Molluscs of Paratethys" (Nevesskaja *et al.*, 1986). The system of the subfamily Lymnocardinae is a compromise combining the elements of both vertical (phylogenetic) and horizontal (morphological) classifications.

Our study demonstrated that the subfamily in question is endemic to the Oligocene–Neogene Paratethys (except for *Cerastoderma* and the Mediterranean Messinian species), the Ponto–Caspian region, and comprises 73 genera with more than 700 species. The genera are separated into 18 tribes. We tried to rank the individual phyletic lineages of lymnocardines as tribes. This causes many problems, because attempts to define taxa morphologically are often hampered by the repeated development of similar character sets in different lineages and by difficulties in recognizing these parallelisms. Sometimes (e.g., for the tribe Limnopappiini), this results in the lack of diagnostic characters and the separation of taxa according to their stratigraphic distribution and reconstructed phylogeny rather than morphology.

The systematic position of the genus *Cerastoderma* (ancestral to most of the lymnocardines as mentioned above) is still controversial. In the shell morphology and microstructure, living *Cerastoderma* species inhabiting shallow waters both of the open sea basins and of

lagoons with abnormal salinity (from 5 to 70‰) have no essential differences from the representatives of the subfamily Fraginae, being especially similar to the genus *Parvicardium*. At the same time, they form continuous phyletic lineages towards many undoubtedly lymnocardines with modified hinges, two-layered shells, and retarded ontogeny of the ornamentation. Moreover, these characters sometimes appear within a single species at the level of individual or group variability (e.g., in the modern *Cerastoderma glaucum* from the Caspian Sea). To assign cerastoderms to the subfamily Fraginae means to divide numerous, continuous phyletic lineages (even at the level of infraspecific categories) between different subfamilies. Therefore, as in the earlier papers (Kafanov and Popov, 1977; Nevesskaja *et al.*, 1997), we somewhat artificially place *Cerastoderma* in the subfamily Lymnocardinae.

The subfamily Lymnocardinae includes tribes that arose from different representatives of the tribe Cerastodermatini (and from *Parvicardium*) in different time intervals (Fig. 1) and thus cannot be considered strictly monophyletic. The same is true of some tribes (Lymnardiini, Pontalmyrini, Adacnini, etc.) and many genera and subgenera of this subfamily. Thus, the tribe Pontalmyrini and its oldest genus, *Pseudocatillus*, evidently originated from different *Obsoletiformes* species that inhabited different adjacent basins. The tribe Lymnardiini, comprising more than ten genera, probably arose from two or three lineages and diverged from one or several *Plicatiformes* species in different basins of the Paratethys. In the tribe Adacnini, most of the genera descended from different *Cerastoderma* species, whereas some other genera are derivatives of *Avicardium* and *Acobaecardium* (belonging to other tribes; see the next section). Therefore, most of the lymnocardine tribes, genera, and subgenera are not strictly monophyletic. Adhering to the principle of strict monophyly in the classification of these forms, one will receive several taxa that are indistinguishable morphologically and have identical diagnoses. At the same time, quite similar species and genera of lymnocardines, which existed in periods separated by considerable time intervals, are assigned to different taxa (genera and tribes). These are *Merklinicardium acanthoides* (Oligocene) and *Lymnocardium* (?*Euxinocardium*) *kalidjanicum* (Uppermost Miocene–?Lowermost Pliocene), *Eoprosodacna* (upper Lower Miocene) and *Eupatorina* (uppermost Miocene), *Pseudocatillus* (uppermost Miocene–Lower Pliocene), *Monodacna* (uppermost Pliocene), etc.

Thus, within the subfamily Lymnocardinae, 18 tribes comprising 73 genera are recognized:

Subfamily Lymnocardinae Stoliczka, 1870–1871

Tribe Cerastodermatini Nordsieck, 1969

Cerastoderma Poli, 1795

Korobkoviella Merklin, 1974

Raricardium Paramonova, 1986

Tribe Merkliniardiini Popov, tribus nov.*Merklinicardium* Popov, 1982**Tribe Limnopappiini Schlickum, 1962***Limnopappia* Schlickum, 1962*Limnopagetia* Schlickum, 1963*Eoprosodacna* Davidaschvili, 1934**Tribe Chokrakiini Popov, tribus nov.***Chokrakia* Popov, gen. nov.**Tribe Obsoletiformini Paramonova, tribus nov.***Obsoletiformes* Kojumdgieva, 1969*Inaequicostates* Kojumdgieva, 1969**Tribe Aviculocardiini Paramonova, tribus nov.***Aviculocardium* Bagdasarian, 1978*Kubanocardium* Muschelischvili, 1965**Tribe Plicatiformini Paramonova, tribus nov.***Plicatiformes* Kojumdgieva, 1969**Tribe Planacardiini Paramonova, tribus nov.***Planacardium* Paramonova, 1971**Tribe Lymnocardiini Stoliczka, 1870-1871***Lymnocardium* Stoliczka, 1870-1871*Arpadicardium* Ebersin, 1947*Pannonicardium* Stevanović, 1951*Bosphoricardium* Ebersin, 1947*Hellenicardium* Neveeskaja, 2000*Euxinicardium* Ebersin, 1947*Tauricardium* Ebersin, 1947*Budmania* Brusina, 1897*Dacicardium* Papaianopol, 1975*Schirvanocardium* Andreescu, 1974*Nargicardium* Ebersin, 1947*Moquicardium* Ebersin, 1947*Limnodacna* Ebersin, 1936*Ecericardium* Ebersin, 1947**Tribe Paradacnini Ebersin, 1964***Paradacna* Andrussov, 1909**Tribe Phyllocardiini Neveeskaja, 1986***Phyllocardium* Fischer, 1887*Parvidacna* Stevanović, 1951**Tribe Pontalmyrini Taktakischvili, 1987***Pontalmyra* Stefanescu, 1896*Pseudocatillus* Andrussov, 1903*Chartoconcha* Andrussov, 1907-1908*Pteradacna* Andrussov, 1907-1908*Oraphocardium* Ebersin, 1949*Stenodacna* Andrussov, 1923*Panticapaea* Andrussov, 1923*Macradacna* Ebersin, 1967*Oxydacna* Davidaschvili, 1930*Luxuridacna* Papaianopol, 1980*Submonodacna* Livalent, 1931*Tschaudia* Davidaschvili, 1956*?Caladacna* Andrussov, 1917*?Pseudocardita* Oppenheim, 1918**Tribe Prosodacnini Andreescu, 1974***Eupatorina* Achvlediani, 1970*Prosodacnomya* Ebersin, 1959*Prosochiasta* Ebersin, 1959*Prosodacna* Tournouer, 1882*Zamphiridacna* Motaş in Andreescu, 1974*Metadacna* Ebersin, 1959*Stylodacna* Stefanescu, 1896*Psilodon* Cobalcescu, 1883*Prionopleura* Ebersin, 1949*Horiocardna* Stefanescu, 1896**Tribe Arcicardiini Neveeskaja, 1986***Arcicardium* Fischer, 1887*?Protoplagiodacna* Stevanović, 1978*?Plagiodacna* Andrussov, 1903**Tribe Pachydacnini Andreescu, 1975***Pachydacna* Ebersin, 1955**Tribe Acobaecardiini Paramonova, 1986***Acobaecardium* Paramonova, 1986**Tribe Avicardiini Popov, 1977***Avicardium* Kolesnikov, 1950*Miricardium* Paramonova, 1986*Andrusovicardium* Paramonova, 1986**Tribe Adacnini Vest, 1875***Monodacna* Eichwald, 1838*Hyrcania* Kolesnikov, 1950*Plagiodacnopsis* Andrussov, 1923*Apscheronia* Andrussov, 1903*Parapscheronia* Ebersin, 1955*Caspicardium* Astafieva, 1955*Didacnoides* Astafieva, 1960*Hypanis* Ménériés, 1832*Adacna* Eichwald, 1838*Didacna* Eichwald, 1838**GEOLOGICAL HISTORY AND PHYLOGENY
OF LYMNOCARDIINAE**

Although the history and phylogenetic relationships of selected representatives of Lymnocardiinae were studied by many authors, i.e., Andrussov (1903, 1910), Kolesnikov (1935), Ebersin (1965a, 1967), Popov (1977), Andreescu (1977), Papaianopol (1977, 1981, 1989) and others, the phylogeny of this subfamily as a whole was not considered in these papers.

Oligocene

The first representatives of the subfamily belonging to the genus *Cerastoderma* (tribe Cerastodermatini) are known from the Early Oligocene (Pscchekian) of the Eastern Paratethys: one species (*C. karaschokense*) is described by Merklin (1974) from the Ashcheairyk Formation of the northern Ustyurt plateau.

Cerastoderms became widespread throughout the Paratethys in the next time interval, the Solenovian (Late Rupelian, level of the base of nannoplankton zone NP23), when the Paratethys lost an open connection to the ocean for the first time and became less saline (Fig. 1). Being eurytopic, the members of the genus *Cerastoderma* were able to colonize the freshened waters that were unfavorable for most of the marine forms. Some of these cerastoderm species remained similar to their marine congeners in their fully developed hinges and three-layered shells [*C. mutabile* Pop., *C. chersonense* (Nossov.), *C. serogosicum* (Nossov.), and *C. concameratum* (Hözl)], whereas others (*C. anadariformicum* Pop. and *C. zhuzhunae* Pop.) differed from them in the reduction of the hinge and outer shell layer, thus approaching typical lymnocardines in these characters. Two other genera, which occurred there and descended from *Cerastoderma*, differed still more widely from the marine cardiids. The genus *Korobkoviella* is characterized by a two-layered shell, poorly developed teeth, a thickened anterior part of the hinge plate, and poorly developed ribs. In the shell shape and ribbing pattern, it is similar to cerastoderms of the *C. serogosicum* type and probably descended from them. This genus, comprising two species [*K. kiktenkoi* (Merkl.) and *K. ahalcikhensis* Pop.], still could be included in the tribe Cerastodermatini.

Even more deviated from the marine cardiids were the members of the genus *Merklinicardium* [*M. apostolovense* (Merkl.), *M. acanthoides* Pop., and ?*M. chvintense* Pop.], separated hereafter into the tribe **Merklinicardiini**, characterized by a two-layered shell, poorly developed hinge, and ornamentation consisting of high, widely spaced ribs, triangular in cross section and sometimes subdivided into the primaries and intercalaries.

Lymnocardines were less common in the mid-Oligocene of the Western Paratethys, which in Solenovian time was quite closely connected with the Eastern Paratethys. At present, this area is represented only by finds of *Cerastoderma* cf. *serogosicum* from Transylvania and Austria, *Korobkoviella* cf. *kiktenkoi* from Austria (Ottenthal section, determined in the collection of F. Steininger, University of Vienna), and "*Cardium*" *lipoldi* Rolle (described from the Hungarian Paleogene basin). The shells of the latter species are so poorly preserved that they cannot be reliably assigned to any genus, although they undoubtedly belong to the Lymnocardinae.

Thus, Solenovian time marks the first stage of divergence in lymnocardines, which deviated considerably from their marine ancestors. These species and genera,

endemic to the Paratethys, went extinct when the Paratethys became increasingly saline due to its connection to the open sea in the terminal Rupelian or early Chattian.

In the Late Oligocene, the salinity of the Eastern Paratethys probably decreased slightly, and cerastoderms (four species) were quite widespread there. In the second half of the Late Oligocene (Late Kalmykian), one of them, *Cerastoderma prigorovskii* (Bog.), became the dominant species along the entire northern edge of the Eastern Paratethys, from the Black Sea region to the Kyzylkum Desert. However, the morphology of these species did not deviate from that of their marine congeners: they had fully developed hinges, three-layered shells, and the ornamentation typical of cerastoderms.

Early Miocene

Normal marine conditions of the earliest Miocene were unfavorable for lymnocardines, and only in marginal parts of the basin, three or four cerastoderm species inherited from the Oligocene occasionally occurred (Popov *et al.*, 1993).

The next (second) stage of widespread occurrence and diversification in lymnocardines was the Kozahurian-Late Ottnangian (second half of the Early Miocene), characterized by the closure and freshening of the entire Paratethys (Popov and Voronina, 1983). At that time, the Eastern Paratethys was inhabited by both the species of *Cerastoderma* (*C. ivericum* Pop. and *C. lacustre* Pop.) and the endemic genera descending from this genus and belonging to the tribe **Limnopappiini**: *Eoproso-dacna* (with the subgenus *Kozahuria*) and *Limnopappia* (Popov, 1983) (Fig. 1). The members of these genera differed from the ancestral *Cerastoderma* species in the hinge structure (cardinal and posterolateral teeth are weak and anterior laterals are well developed); two-layered shell; and weak, poorly developed ribs (up to complete reduction of the radial ribs in the subgenus *Kozahuria*). In the Eastern Paratethys, these cardiids are presently known mainly from the Georgian and Kopetdag sections (Popov *et al.*, 1993).

Lymnocardines were no less widespread and diverse in the Western Paratethys, being known from the Upper Ottnangian of northern Hungary, Moravia, and Bavaria. In contrast to the fully formed brackish-water Kozahurian fauna of Georgia that lacks transitional forms, the Bavarian material (collections of W.R. Schlickum, Senckenberg Museum, Frankfurt am Main, and of F. Steininger, University of Vienna) contains a quite complete transitional series from the typical *Cerastoderma* to undoubted lymnocardines separated into the genera *Limnopageta* and *Limnopappia* (Schlickum, 1971).

The Kirchberg beds of Swabia and Upper Bavaria unquestionably contain members of the genus *Parvicardium* ("*Cerastoderma*" *traubi* Schlickum); cerastoderms with almost fully developed hinges, typical ornamentation, and three-layered shells (*Cerastoderma ganssi* Schl.); cerastoderms retaining the characteristic

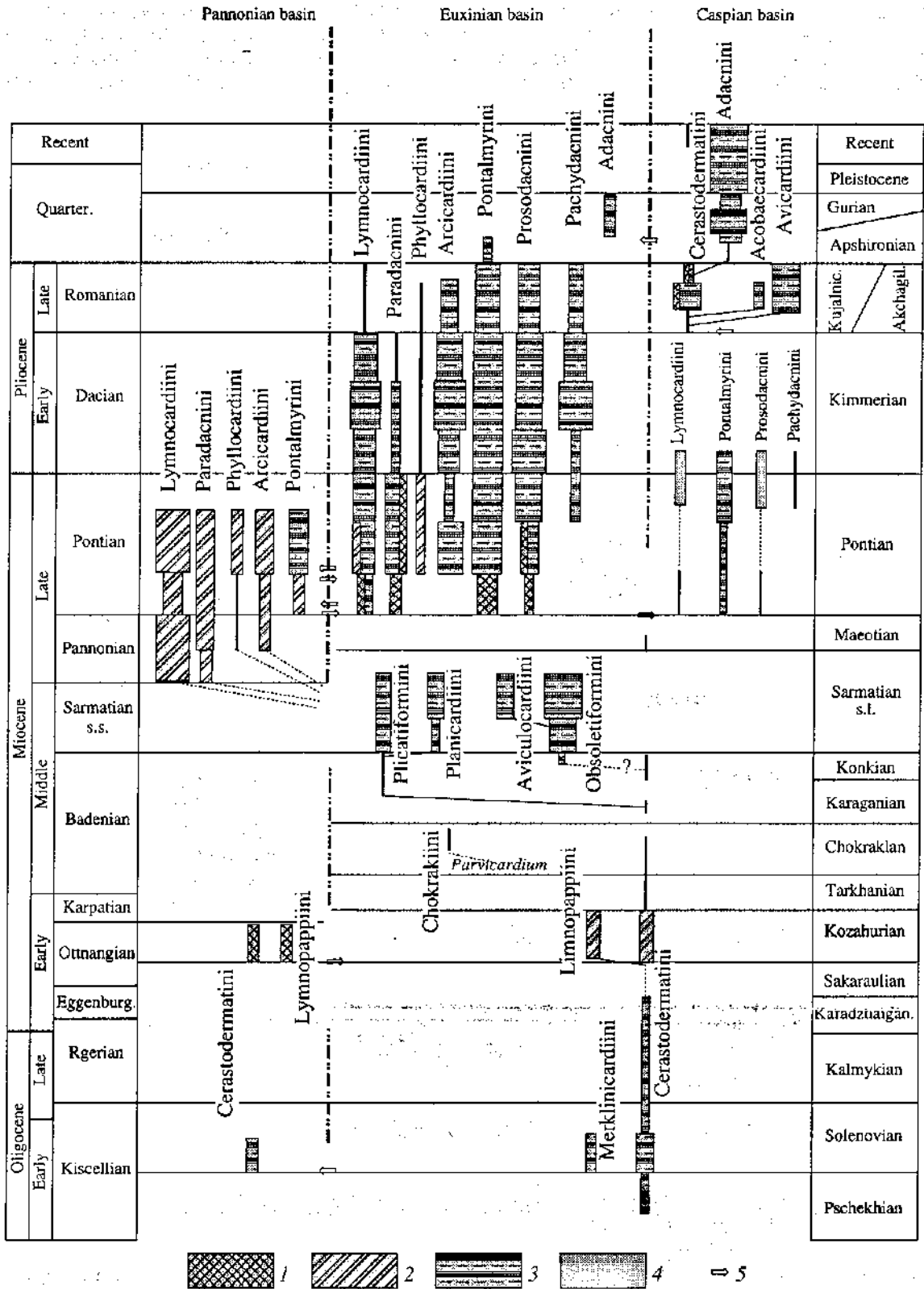


Fig. 1. Phylogeny and distribution of the tribes of the subfamily Lymnocardiinae. The proces of origin of members of the tribes are shown by shading: (1) Mediterranean (Messinian) basin; (2) Western Paratethys; (3) Eastern Paratethys; (4) grey shading denotes that the place of origin is uncertain; (5) arrows denote migrations to the adjacent basin.

morphology and structure of the ribs but differing in having retarded ontogeny of ornamentation, reduced outer shell layer, and weak cardinal teeth [*C. bavarica* (Ammon), *C. sociale* (Krauss), and *C. stefani* Schl.]; and typical lymnocardiines having a reduced outer shell layer and scales along both the anterior ribs and the posterior rib of the posterior area [*"Cerastoderma" solitarium* (Krauss), which in Popov's opinion, is best placed in *Limnopageta*]. This type of ornamentation with scales on the ribs formed by the remnants of the outer shell layer was characteristic of comparatively early stages of phylogenetic development in lymnocardiines and was observed later in the Middle Miocene cardiids (Chokrakian *Chokrakia* and Sarmatian *Obsoletiformes*). These beds also contain *Limnopageta friabilis* (Krauss) with two-layered shells and moderately reduced hinges and *Limnopappia shuetti* Schl. with even more reduced cardinal teeth.

The Lower Bavarian beds with *Rzehakia*, deposited in an isolated basin (Schlickum and Strauch, 1968), contain other species of the same lymnocardiine genera. In the series assigned by Schlickum (1971) to a single species, "*Limnopageta" schmieri* Schl., a gradual transition is observed from the cerastoderms with a normally developed hinge to typical lymnocardiines with a poorly developed hinge, inclined teeth, and scales along the ribs, similar to the ornamentation in some Sarmatian *Obsoletiformes*; the holotype of this species (as well as the species "*Limnopageta" modelli* Schl.) more likely belongs to *Cerastoderma*. These beds yielded also *Limnopappia kuiperi* Schl. with a single cardinal tooth, reduced posteriolateral teeth, and two-layered shell with scales along the anterior ribs.

By the end of the Kozahurian-Late Ottnangian, the members of the tribe Limnopappiini went extinct because of the next transgression; thus, in subsequent marine basins, Tarkhanian and Carpathian, the only species of *Cerastoderma*, i.e., *C. arcella* (Duj.), represented by an endemic subspecies, was confined to the most freshened parts of these basins.

Middle Miocene

In the Chokrakian Basin, only the same cerastoderm subspecies endemic to the Paratethys persisted, i.e., *C. arcella bogatschevi* (Kol.), inherited from the Tarkhanian. However, the history of Chokrakian lymnocardiines is especially interesting in that the features characteristic of lymnocardiines appeared in the descendants of the genus *Parvicardium*, in the series *Parvicardium kubanicum*-"*P.*" *brykense* Zhgenti et Gontcharova, 1989 (Gontcharova, 1989). The latter species is assigned herein to a separate genus *Chokrakia* and separate tribe Chokrakiini in the subfamily Lymnocardiinae.

In the Early Karaganian of the Eastern Paratethys, cardiids (including lymnocardiines) were absent. Only about the mid-Karaganian during the short connection

to the open sea (Varna episode) did the species *Plicatiformes praeplicatus* (Hilb.) (tribe Plicatiformini) distributed this basin along with some other marine fauna.

In the Badenian of the Western Paratethys, cerastoderms were very rare and were represented by a single species *C. arcella* (type subspecies). However, already in the Late Badenian basin, as well as in the Konkian, the members of the genera typical for the Sarmatian were quite common: *Plicatiformes* and *Obsoletiformes* (*P. praeplicatus* and *O. lithopodolicus*). It is quite possible that the latter species gave rise to members of the genus *Inaequicostates* as early as the Konkian. These three genera became dominant in the Sarmatian semimarine basin, which replaced the Konkian-Badenian basin and was only episodically connected to the open Mediterranean Sea. In response to the Early Sarmatian closure and freshening, most of the marine taxa went extinct and few surviving species (including lymnocardiines) gave rise to numerous (especially in the Middle Sarmatian) species and genera. It was a further, third stage of the explosive diversification and broad distribution of lymnocardiines belonging to four tribes endemic to the Sarmatian.

A peculiarity of the Sarmatian cardiids is that their intraspecific variability affects both specific and generic characters; thus, it is often easier to trace out the phyletic lineages than to divide them into taxa. So, within the variability limits of the species *Inaequicostates politioanei* Jekelius (Jekelius, 1944, pls. 34, 35), one can observe a gradual transition from the specimens similar to *Cerastoderma* to quite peculiar forms with inequally developed ribs, spinules at the strongest ribs, and poorly developed hinges, i.e., characters typical for *Inaequicostates*. The identification of these forms as species and genera is often subjective and requires studying quite considerable material from many localities. For example, the forms that we included (Neveesskaja *et al.*, 1993) in the species *Plicatiformes plicatus* (Eichw.) as subspecies, i.e., *P. p. plicatus* (Eichw.), *P. p. jammensis* (Hilber), *P. p. latusulcus* (Munster in Goldfuss), and *P. p. plicatofittoni* (Sinz.), were raised to the species rank by most other authors.

Sarmatian lymnocardiines were classified into several groups (Kolesnikov, 1948; Kojumdgieva, 1969) and regarded either as subgenera of the genus *Cerastoderma* [*Plicatiformes*, *Obsoletiformes*, *Inaequicostates*, and *Planacardium* (Paramonova, 1971; Iljina *et al.*, 1976)] or as separate genera (Bagdasarian, 1978). Our revision of all Neogene cardiids of the Eastern Paratethys shows that it is more expedient to regard these taxa as genera. In addition to them, two more genera characterized by a considerably modified shell shape and somewhat weakened hinge merit separation from *Obsoletiformes* (*Kubanocardium* Muskhel. and *Aviculocardium* Bagd.). The subgenus "*Cardium*" (*Replidacna*) described by Jekelius (1944) and recorded by other authors both in the Western (*Sarmatien...*, 1974) and Eastern Paratethys (Ali-Zade, 1974) is possibly syn-

onymous with *Inaequicostates*. This subgenus was described from the small fragments of the beak area of valves, giving the false appearance of hypertrophied teeth. The holotype of the type species *Replidacna carasi* Jekelius (Paramonova, 1977) is probably a fragment of the beak area of the shell of *Inaequicostates politioanei* (Jekelius).

The largest of these genera was *Obsoletiformes*, as its species was especially numerous in the Middle Sarmatian. Within this genus, several species groups occurred, more or less differing in shell form, degree of rib development, and carination. However, these groups are insufficiently separated and too closely interconnected by transitional series; therefore, they probably do not merit any taxonomic rank. So, it appears unjustified to rank the species groups *protractum* and *fischerianum* as the genus *Protractiforma* Koles. (emend. Bagd.) with the subgenus *Fischericardium* Bagd. The group *protractum* is morphologically close to the group *obsoletum*, differing only in having a less inclined, often straightened posterior branch of the hinge margin, as noted already by Laskarev (1903) when establishing these groups. The sharp carination of the shell, taken as a diagnostic character of the subgenus *Fischericardium*, appeared independently at the beginning of the Early Sarmatian (in *Obsoletiformes kaundensis volhynicus*) and at the end of the Middle Sarmatian (in the species assigned to this subgenus). It also seems unjustified to rank the species group *desperatum* (differing from the *obsoletum* group only in having less developed ribs) as the genus *Sarmaticardium* Bagd.

As for the origin of the above genera, *Plicatiformes*, as already mentioned, appeared in the mid-Karaganian and descended from *Cerastoderma* (Nevesskaja, 1950; Bagdasarian, 1970, 1974; Paramonova, 1971), most probably from *C. arcella*. The earliest species *P. praeplicatus* (Hilb.) already differed from *Cerastoderma* in the ornamentation (relatively wide and flattened interspaces), reduction of the outer shell layer, and weakening of the hinge, and its descendants deviated even more from the ancestral form.

The origin of the genus *Obsoletiformes* is a more complicated problem. Most authors accepted its relationship to *Cerastoderma* (Kojumdieva, 1969; Paramonova, 1971; see also Iljina *et al.*, 1976). However, Bagdasarian (1970, 1974, 1978) suggested that *Obsoletiformes* descended from members of *Parvicardium*. Popov (1977) also noted the similarity of at least some species of *Obsoletiformes* to *Parvicardium*. Paramonova (1994) argued against this opinion, insisting on the monophyletic origin of *Obsoletiformes*, most probably from *Cerastoderma*.

The genus *Inaequicostates* obviously descended from *Obsoletiformes* in the Konkian. Phylogenetic relationships of the species of this genus, which inhabited different bottom types and different depths, are still unclear in many respects. The species that lived on the muddy sediments of relatively deep (or in shallow but

calm) waters had usually thin-walled shells and weakened lateral hinge teeth. The species that lived on the sandy and muddy sediments of shallow waters had more thick-walled shells and well-developed hinges, like in *Obsoletiformes*. Within the genus *Inaequicostates*, Muskhelishvili (1965) established a subgenus *Chartocardium* to comprise two species, i.e., *I. barboti* and *I. lessitchinensis*, which lived on muddy sediments (in the opinion of Paramonova, these are two subspecies of *I. barboti*). This subgenus has no definite ecological characteristics and does not represent any separate lineage within *Inaequicostates*; thus, its separation seems unjustified.

The genera *Kubanocardium* and *Aviculocardium* descended from *Obsoletiformes* at the beginning of the Middle Sarmatian, and the genus *Planacardium* originated from *Plicatiformes* in the middle of the Early Sarmatian.

According to their development and morphology, Sarmatian lymnocardiines could be divided into four tribes. The genus *Plicatiformes* assigned to **Plicatiformini** contains four species, which changed with time in one direction: the average value of the total number of ribs decreased from 24 to 9; in the posterior area, from 7 to 3; and the width of interspaces increased in the adcarinal part of the anterior area. The genera *Obsoletiformes* (34 species) and *Inaequicostates* (11 species) constitute the tribe **Obsoletiformini**. The members of these genera, which often occurred in the same communities as *Plicatiformes* species, show no trends in the evolution of characters. The genus *Planacardium* (four species), possessing very peculiar features (elongate flattened shell and weakened hinge), is separated as the tribe **Planacardiini**; and the genera *Kubanocardium* (three species) and *Aviculocardium* (two species) characterized by a wing-shaped posterior part of the shell and weakened hinge, into the tribe **Aviculocardiini**.

As noted above, the maximum number of new lymnocardiine species appeared in the Middle Sarmatian. It should be noted that in the Early and early Middle Sarmatian the Paratethys was a single basin, consisting of (from west to east) the Pannonian, Dacian, and Euxinian-Caspian basins, which were connected to each other at that time. In the late Middle Sarmatian, it became divided into the western (Pannonian Basin) and eastern (Dacian and Euxinian-Caspian basins) parts with different histories; thus, their lymnocardiine faunas evolved differently.

In the Early Sarmatian, three lymnocardiine species (*Plicatiformes praeplicatus*, *Obsoletiformes lithopodolicus* and *Inaequicostates elegantis*) gave rise to no less than 17 new species, mostly those of Obsoletiformini (13). An even greater number of new species (up to 40) appeared in the Middle Sarmatian (about 30 species in Obsoletiformini) when the water salinity decreased to leave more ecological niches vacant. The systematic diversity of lymnocardiines reached a maximum in the Euxinian-Caspian Basin (with the lowest salinity) and a minimum in the Pannonian Basin (with the highest

salinity), where Obsoletoformini were represented by only a few taxa, and Aviculocardiini were not represented at all. Thus, during the Early–Middle Sarmatian, three Lymnocardiine species gave rise to 56 new species, 3 genera, and 2 tribes.

Late Miocene

In the Eastern Paratethys, the genera that lived there in the early Middle Sarmatian survived until the end of the Middle Sarmatian and went extinct at the beginning of the Late Sarmatian due to a considerable decrease in salinity.

The subsequent Early Maeotian basin contained only one cardiid species of the genus *Cerastoderma*. *C. arcella*, represented by an endemic subspecies. The latter went extinct in the Late Maeotian brackish-water basin, which contained only one rare endemic species *Cerastoderma galidzense* of limited occurrence.

In the Western Paratethys, which became disconnected from the Eastern Paratethys in the mid-Sarmatian, the brackish-water Pannonian Basin of the Caspian type emerged, where bivalves were represented only by dreissenids and lymnocardiines. These latter were probably descendants of the Sarmatian forms, as noted by many authors (Andrussov, 1888; Gillet, 1943; Ebersin, 1947; Papp, 1953; Taktakischvili, 1987). However, as pointed out by Taktakischvili, this is as yet an inadequately studied question. Indeed, students cannot as yet trace Pannonian lymnocardiines to their direct ancestors. In the Early Pannonian, sarmatian lymnocardiines apparently gave rise to several new genera constituting new separate tribes: Lymnocardiini (genus *Lymnocardium*), Paradacnini (genus *Paradacna*), Pontalmyrini (genus *Pseudocatillus*), and possibly Phyllocardiini (?genus *Parvidacna*). It was a beginning of the next, fourth stage of explosive diversification in lymnocardiines. In the Early Pannonian basin, the species of the genus *Lymnocardium* (~25 species) dominated, whereas the other genera were represented by only a few species.

In the Late Pannonian, the generic composition of Lymnocardiinae was supplemented by several genera: *Arpadiocardium*, *Pannonocardium*, and *Bosphoricardium* (tribe Lymnocardiini); *Phyllocardium* (tribe Phyllocardiini); *Protoplagiodacna* (?tribe Arcicardiini); and possibly *Caladacna* (?tribe Pontalmyrini). As a rule, all these genera were represented by one to three species, whereas an intensive speciation occurred only in *Lymnocardium* (~40 species, according to the literature).

Therefore, the Pannonian lymnocardiines included members of the tribes Lymnocardiini, Pontalmyrini, Phyllocardiini, Paradacnini, and possibly Arcicardiini.

Probably at the same time, several lymnocardiine taxa emerged in the northern freshened parts of the Messinian Mediterranean Sea, including the members of the tribes Lymnocardiini (genera *Euxinocardium* and *Helenocardium*), Pontalmyrini (species of *Pontalmyra*

and *Pseudocatillus*), Prosodacnini (genera *Eupatorina* and *Prosodacnomya*), and Paradacnini (*Paradacna abichi*).

In the subsequent, Pontian interval, the entire Paratethys became a brackish-water basin, but in the Early Pontian, there was no direct connection between its western (Pannonian Basin) and eastern parts (Dacian–Euxinian–Caspian Basin), so the generic composition of Lymnocardiinae differed markedly in these two basins.

In the Western Paratethys, the members of the same Pannonian genera persisted into the Early Pontian, with *Lymnocardium* (~10 species) still dominating, whereas *Arpadiocardium* and *Pannonocardium* were represented by one species each (Figs. 2, 3). *Caladacna* (tribe Pontalmyrini), the genus that apparently evolved from Sarmatian Plicatiformini already in the Pannonian, and of *Pseudocatillus* (see below) were recorded for the first time.

Concurrently, the Eastern Paratethys was invaded as a result of the Early Pontian transgression by the forms that were mentioned above as those originated in the northern freshened parts of the Messinian Mediterranean Sea: members of *Euxinocardium*, *Pseudocatillus*, *Pontalmyra*, *Prosodacnomya*, *Eupatorina*, and *Paradacna* (Figs. 3–5, 7). Generic composition of this assemblage was elucidated by Ebersin (1949). Some of these genera do not occur in the Western Paratethys (Pannonian Basin); they were undoubtedly of Mediterranean origin ("Aegean," after Ebersin, 1949; Andreev, 1977; Popov and Neveeskaja, 2000) and most probably descended from members of the genus *Cerastoderma*. The origin of other genera raises some questions. These are *Pontalmyra*, *Pseudocatillus*, and *Paradacna*, the species of which were recorded from the Pannonian (i.e., from the beds deposited earlier than the Lower Pontian). Let us consider each of them separately.

Many authors believe that *Pontalmyra* includes five Pannonian species. However, *Lymnocardium viquesneli* Pavl. was transferred by Stevanović (1978) to the genus *Protoplagiodacna* Stevanović; *L. danicici* Pavl., *L. promultistriatum* Jek., and *Adacna ottophora* Brus. most probably belong to the genus *Lymnocardium* (Lueger, 1980; Taktakischvili, 1987); and the generic position of *L. desertum* Stol. is unclear. Therefore, there were no true *Pontalmyra* in the Pannonian Basin during the Pannonian; thus, the genus is undoubtedly of Mediterranean origin.

Two other genera are a more complicated problem. About ten species from the Pannonian deposits were assigned to *Pseudocatillus*. Although most of them [*P. ducici* (Brus.), *P. loerentheyi* (Pavl.), *P. petkovici* (Pavl.), *P. stojadinovici* (Pavl.), *P. stoosi* (Brus.), *P. voesendorfensis* (Papp), and *P. viennensis* (Papp)] were never revised in detail; this assignment raised doubts in subsequent students. The species *P. simplex* (Fuchs) most probably belongs to *Pseudocatillus*; this species is

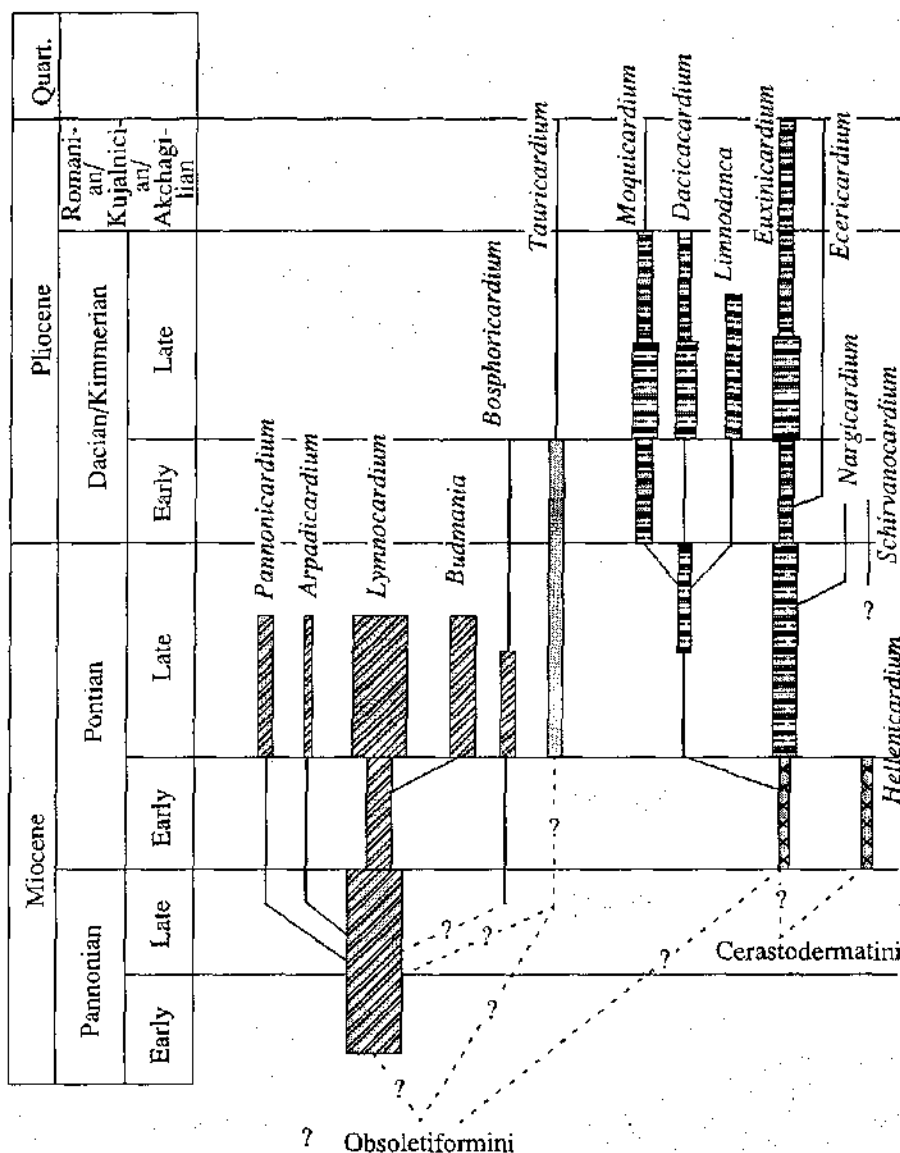


Fig. 2. Phylogeny and stratigraphic range of the genera of the tribe Lymnocardiini.

known, in addition to the Pannonian, from the Pontian (Lower and Upper) of Austria, Serbia, Romania, Bosnia, Slovenia, Croatia, i.e., from both the Western and Eastern Paratethys. This species is very similar to *P. pseudocatillus* (Barb.), the type species of the genus, found in abundance in the Lower Pontian deposits from the Aegean region to Transcaspia. Ebersin (1967) considered *P. simplex* an ancestral form to all other *Pseudocatillus*, whereas Gillet and Marinescu (1971) supposed that this is only a form of *P. pseudocatillus*, appearing in parallel in different basins (Pannonian and Euxinian races).

The species *Paradacna abichi* shows a similar distribution that is characteristic of both the Pannonian and Pontian beds. In this case, one can likewise propose different hypotheses: parallel developments of the same species from a single or several closely related

species in different basins and at different times; emergence of *Paradacna* and *Pseudocatillus* in the freshened gulfs of the pre-Messinian (Late Tortonian) Sea and their penetration into the Pannonian Basin during the Pannonian time; or just the opposite, evolution of these genera from Sarmatian ancestors in the Pannonian Basin and their subsequent migration to the northern parts of the Messinian Sea through a hypothetical strait that connected the Pannonian Basin with the Late Miocene Mediterranean Sea.

Anyway, the question cannot be solved at present, because the direct ancestors of both genera remain to be found both in the Messinian and Pannonian basins.

Thus, of six lymnocardiine tribes that existed in the Early Pontian Paratethys, Prosodacnini were of Mediterranean origin; Paradacnini, Phyllocardiini, and pos-

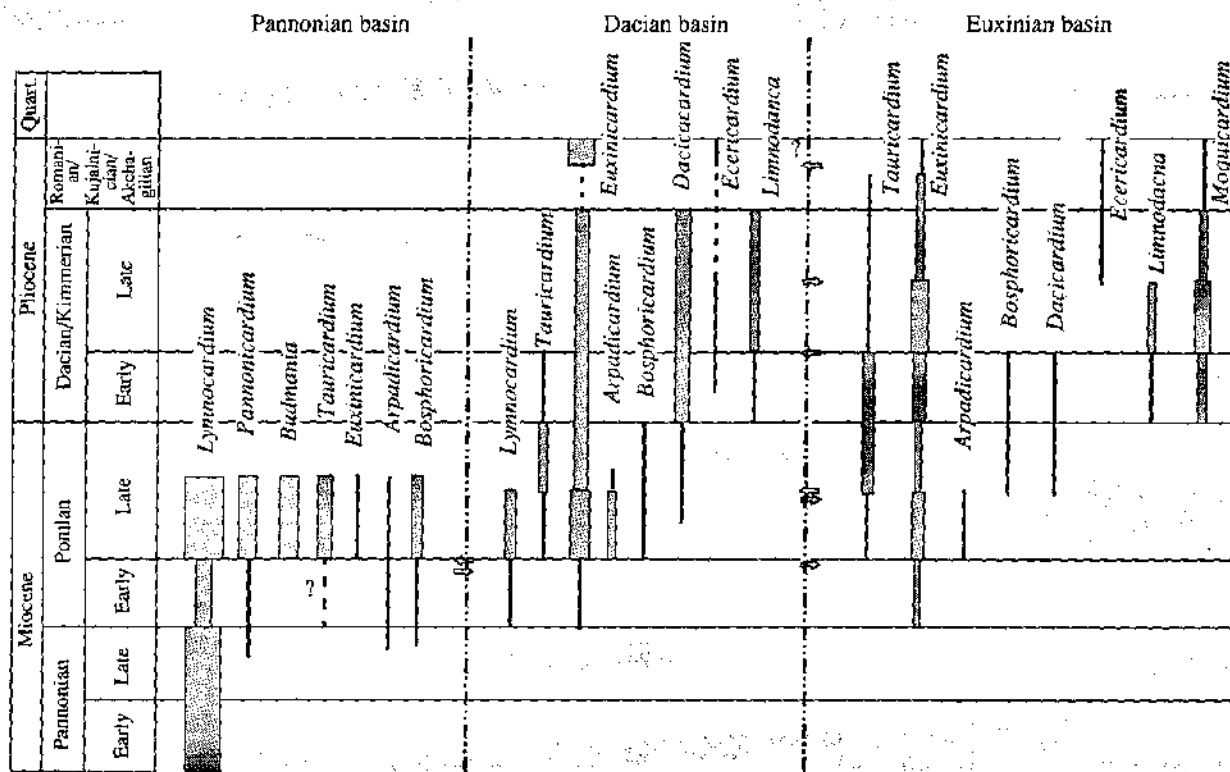


Fig. 3. Distribution of the genera of the tribe Lymnocardiini in the basins of the Paratethys.

sibly Arcicardiini were of Pannonian origin; and Lymnocardiini and Pontalmyrini were partly of Aegean (*Euxinicardium*, some species of *Pseudocatillus*) and partly of Pannonian origin.

It is only at the beginning of the Late Pontian (Portaferrian) that the Western and Eastern Paratethys became closely connected through the Dacian Basin, which in the Early Pontian, was connected only with the Euxinian-Caspian Basin. At that time, lymnocardiines migrated both eastward and westward. Simultaneously, an event of explosive diversification (at the generic and subgeneric level) took place, mainly in the Eastern Paratethys (fifth stage of the divergence in Lymnocardiinae).

The number of tribes remained constant throughout the Portaferrian. Members of the seventh tribe, Pachydacnini, appeared in the latest Pontian.

In the Western Paratethys, one or two new genera originated in the tribe Lymnocardiini (Fig. 2): *Budmania* and possibly *Tauricardium* (origin uncertain). Events of intensive speciation occurred in *Lymnocardium* (~30 species) and *Budmania* (7 species); the remaining genera were represented by two to four species (*Arpadicardium*, *Bosphoricardium*, *Pannonicardium*, and *Tauricardium*). All of the genera (except for *Euxinicardium*, which came from the east) were of Pannonian origin. *Budmania* and *Pannonicardium* were endemic to the Pannonian Basin; *Arpadicardium*, *Lymnocardium*, and *Tauricardium* migrated to the Dacian-

Euxinian Basin at the beginning of the Late Pontian (Fig. 3). Although species of *Euxinicardium* migrated from the Dacian-Euxinian to Pannonian Basin, they remained uncommon there. As for species diversity, in the Late Pontian Pannonian Basin, species of the genus *Lymnocardium* were the most numerous; *Budmania*, *Pannonicardium*, and *Tauricardium* were less numerous; and *Arpadicardium* and *Euxinicardium* were represented by a single species each.

In the Eastern Paratethys, during the early Late Pontian, only a single genus, *Dacicardium*, originated, most probably in the Dacian Basin (Fig. 3). Subsequently, it penetrated into the Euxinian Basin. The species of *Euxinicardium* dominated there, especially in the Dacian Basin. Three species were common in these basins, *E. subodessae*, *E. nobile*, and *E. amicorum*, with the first occurring at that time in the Pannonian Basin as well. The remaining genera were represented by one or two species each; of these genera, the species common in the Dacian and Euxinian basins were *Tauricardium petersi*, *Bosphoricardium emarginatum*, and *Arpadicardium peregrinum*; the first was also recorded in the Pannonian Basin.

In the latest Pontian in the Caspian Basin, which became isolated from the Euxinian one, the genus *Nargicardium* originated (probably from *Euxinicardium*) and the genus *Schirvanocardium* appeared. The origin of the latter remains uncertain; it was descended either from *Bosphoricardium*, being similar to it in the proso-

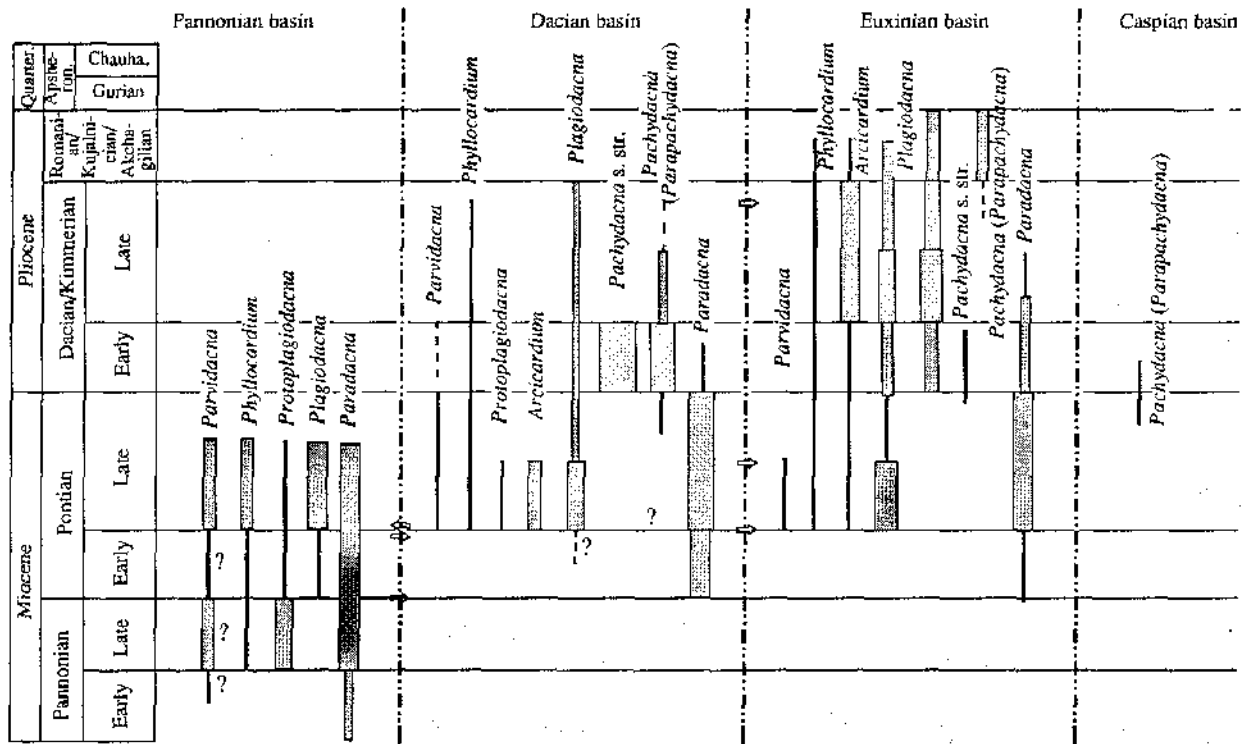


Fig. 4. Distribution of the genera of the tribes Phyllocardiini, Arcicardiini, Pachydacnini, and Paradacnini in the basins of the Paratethys.

dacnoid shell and rib pattern, through fetalization (the hinge is well developed only in young *Bosphoricardium*), or from *Lymnocardium*, being similar to it in teeth development, through the development of the prosodacnoid shell and loss of the shell gape and the sinus. In the latter case, *Schirvanocardium* should be regarded as a colonizer from the west.

At that time, the generic composition of Lymnocardiini remained in the Dacian–Euxinian Basin the same as in the early Late Pontian. As for species composition, several new species appeared and others went extinct, but the dominance structure remained nearly the same as in the previous time interval: the species of *Euxinocardium* prevailed, although their number and the abundance of individual species sharply decreased; *Tauricardium* was represented by two species common in both basins; the remaining genera, by one species each. Five species were common to the Dacian and Euxinian basins: *Euxinocardium amicorum*, *E. inlongaezum*, *Bosphoricardium emarginatum*, *Tauricardium petersi*, and *T. squamulosum*.

The other tribes known in the Pannonian Basin from the Pannonian and later beds changed their composition only slightly; this change was caused mainly by the immigration from the east of several genera new to this basin.

The tribe Paradacnini was represented by five species of the genus *Paradacna* in the Early and early Late Pontian of the Pannonian Basin and by five species in

the Early Pontian of the Dacian Basin, whereas in the Euxinian–Caspian Basin only one species, *P. abichi*, occurred at that time in abundance in the silty facies. In the early Late Pontian of the Euxinian Basin, this genus became more diverse to include, in addition to *P. abichi*, five species, three of which were local endemics (*P. huoti* known only from the Kerch Peninsula and *P. substratonis* and *P. urthensis* from western Georgia) and the fourth, *P. retowskii*, was mentioned by Taktakishvili (1977) as being from Georgia only. In the latest Pontian of the Dacian Basin, four new species appeared, while *P. abichi* and *P. retowskii* persisted. Coeval beds of the Euxinian Basin contained, besides *P. abichi*, also *P. retowskii*, *P. andrussowi*, and *P. huoti*, of which the last two were local, rather rare endemics (Fig. 4).

The tribe Phyllocardiini was represented by two genera differing in distribution. The genus *Phyllocardium*, which appeared in the Pannonian, persisted into the Pontian of the Pannonian Basin up to its complete freshening, migrated eastward in the middle Late Pontian, and lived there until the early Late Pliocene. The genus *Parvidacna*, which likewise migrated from the Pannonian Basin, was restricted in the Dacian–Euxinian Basin to the Late Pontian; in the Euxinian Basin, it was recorded only from the early Late Pontian (Porterian) of the Rioni Gulf (Fig. 4).

The tribe Pontalmyrini is one of the largest (12–14 genera). As noted above, its origin is disputable (Figs. 5, 6). Among *Pontalmyra* species of Mediterra-

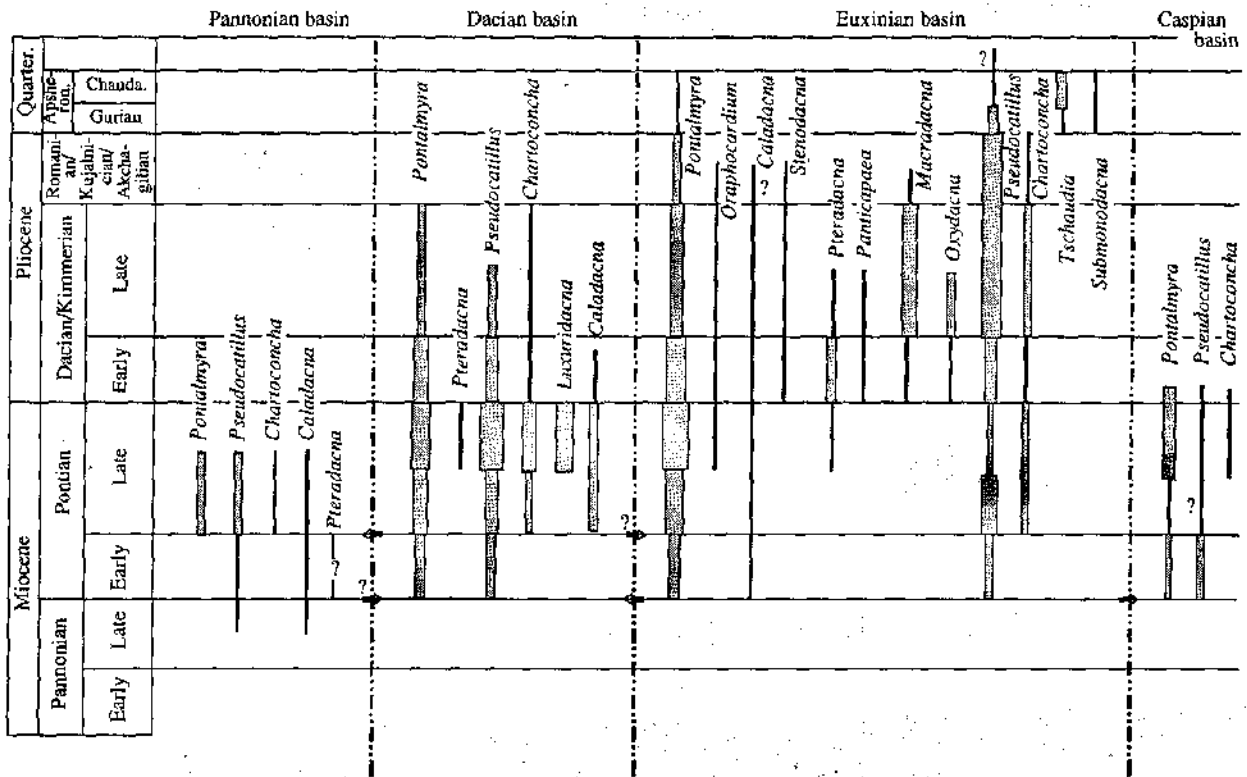


Fig. 5. Distribution of the genera of the tribe Pontalmyrini in the basins of the Paratethys.

nean (Aegean) origin, the most widespread in the Early Pontian was *P. novarossica* known in the Aegean Gulf of the Messinian Sea, as well as throughout the Dacian–Euxinian–Caspian Basin. It was probably ancestral to many subsequent species of *Pontalmyra*. The Aegean Gulf was also inhabited by the species *P. incerta* (Popov and Neveßskaja, 2000), which later extended its range into the Euxinian Basin and gave rise to several other species. Besides *P. novarossica*, the Early Pontian Euxinian–Caspian Basin contained three more rare species provisionally assigned to *Pontalmyra*: *P. (?) kubanica*, *P. (?) transcaspica*, and *P. (?) infrapontica*. As noted above, the Pannonian Basin had no species that may be reliably assigned to this genus.

In the early Late Pontian (Portaferrian) of the Pannonian Basin, only a few *Pontalmyra* species occurred, including *P. rarissima* and *P. budmani*, which probably came from the Dacian Basin, contrary to Papaianopol's opinion (1981) that these species were of Pannonian origin (no ancestral species have been proposed). At that time, the Dacian Basin provided a habitat for about ten species of *Pontalmyra*, including two species occurring in the Pannonian Basin and four in the Euxinian Basin. In the early Late Pontian of the Euxinian part of the Eastern Paratethys, 7–11 species occurred, of which 4 species occurred also in the Dacian Basin: *P. subincerta*, *P. subcarinata* (Taktakischvili, 1977), *P. dacica*, and *P. otiothora*. The latter species, recorded

by Taktakischvili (1977) from the Portaferrian of Georgia, was the only one that also occurred in the Pannonian Basin. Only three species were quite abundant: *P. subincerta*, *P. novarossica*, and *P. megrelica*. The latter species was locally distributed (Rioni Gulf) and the remaining species were rare.

In the latest Pontian (Bosphorian), the genus *Pontalmyra* flourished (Fig. 5). The Dacian Basin was at that time inhabited by 14 *Pontalmyra* species (Papaianopol, 1981; Taktakischvili, 1987), including 4 species occurring also in the Euxinian Basin, among which *P. subcrenulata* and *P. subincerta* were immigrants from the Euxinian Basin. The Euxinian Basin was populated by more than 30 species (Ebersin, 1962), among which *P. planicostata*, *P. paucicostata*, and *P. sulcatina* were abundant and widespread, and *P. incerta*, *P. subcarinata*, *P. crenulata*, and *P. repens* were locally distributed. Of ten species occurring in the Caspian Basin (Shemaha and Babadzhan beds), nine species were endemic, *P. laskerevi* was found in abundance, *P. pirsagatica* and *P. depereti* were quite abundant, and only a single species occurred also in the Euxinian (*P. mutabilis*).

As for the origin of the Late Pontian species of the Euxinian and Caspian basins, some of them descended from *P. novarossica* (*P. subincerta* and *P. dacica*) or similar species (*P. sulcatina* and *P. subcarinata*) in the Euxinian or Dacian basins (*P. subcarinata* most likely in the Dacian), and most of them from *P. incerta*

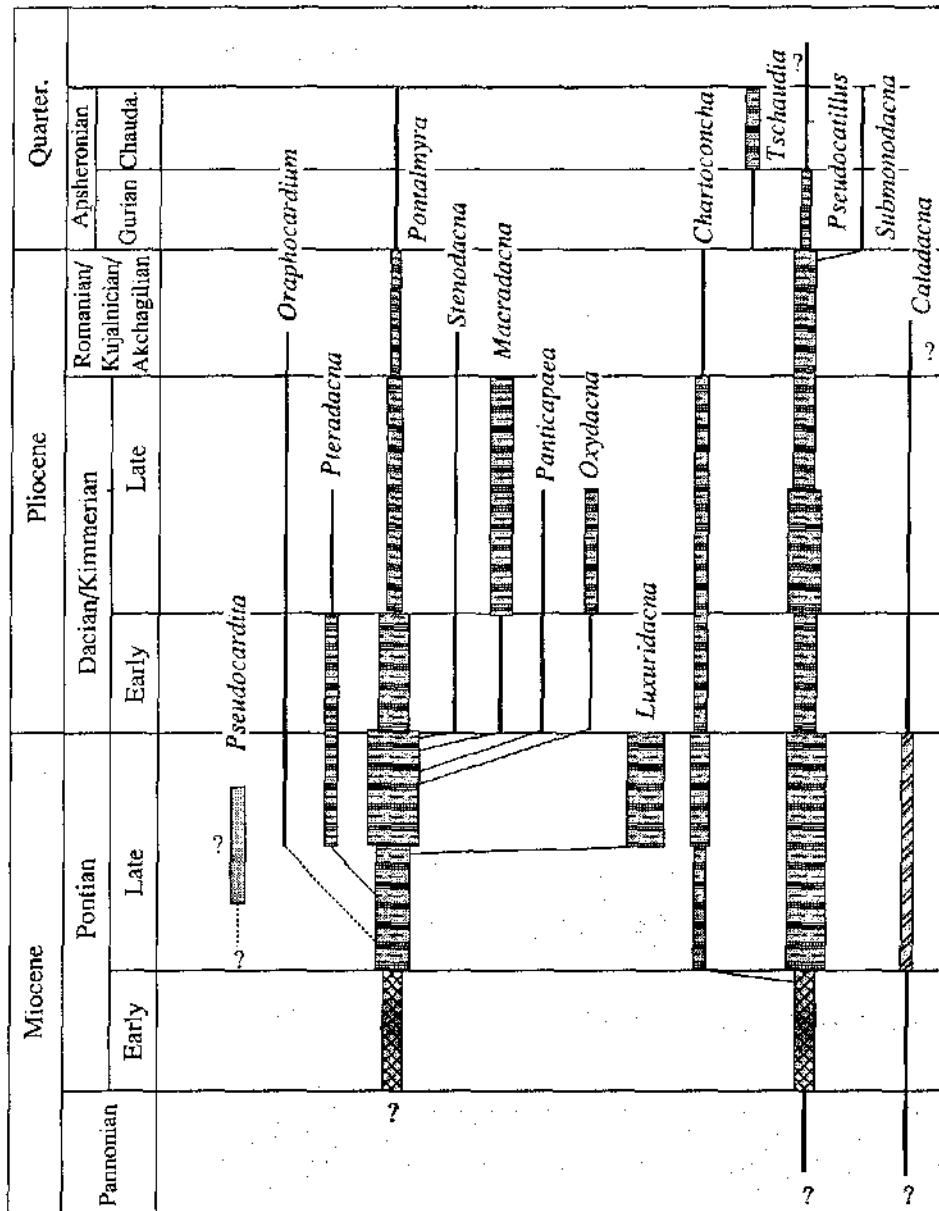


Fig. 6. Phylogeny and stratigraphic range of the genera of the tribe Pontalmyrini.

(*P. planicostata*, *P. perfecta*, *P. caucasica*, *P. annosa*, *P. gourieffi*, *P. crenulata*, *P. subcrenulata*, and possibly *P. praecrenulata*) and from *P. subincerta* (*P. repens*, *P. megrelica*, and *P. subdepressa*). *P. azovica* originated from *P. subincerta* or from its descendant, *P. subdepressa*, while *P. paucicostata* and *P. zuzica* separated from *P. planicostata*. *P. multistriata* descended either from *P. sulcatina* in the Euxinian Basin or, according to Papaianopol (1981) and Akhvediani (1984), from *P. otiofhora* in the Dacian Basin to enter later the Euxinian Basin. The origin of *P. georgiana* remains uncertain. Most pontalmyras of the Late Pontian Caspian probably originated from *P. incerta*, while *P. schemachinica* obviously originated from *P. sulcatina* and *P. crassatellatoides* possibly originated from *P. subcras-*

satellata or *P. crassatellata*; the origin of *P. (?) squamosa* is unclear.

Similar to *Pontalmyra*, the genus *Pseudocatillus* was represented by many species, some of which were index fossils for respective assemblages. The genus *Pseudocatillus* is diphyletic, as noted above (Figs. 5, 6). Among the *Pseudocatillus* species of Mediterranean (Aegean) origin, the most widespread and abundant was *P. pseudocatillus*, known in the Ponto-Caspian, Aegean, and Dacian basins and ancestral to most of its congeners. In the Ponto-Caspian Basin, this species coexisted in the Early Pontian with four more rare and locally distributed species, one of which, *P. (?) beslachubae*, was of uncertain origin and only provisionally

assigned to the genus *Pseudocatillus*. Other species of unclear origin were *P. balatonicus*, *P. cisaralensis*, and *P. omnivagus*. The latter form was homeomorphic relative to *Pseudocatillus* (?) *subcoloratus*. In the Dacian Basin, *P. pseudocatillus* coexisted with another species that is likely to belong to *Pseudocatillus*, "*Pontalmyra* (*Sinupontalmyra*)" *barbata*, and in the Aegean Gulf, this species coexisted with *P. submedius* and *P. multicostratus* (Popov and Neveesskaja, 2000).

In the Pannonian Basin, the first finds of *Pseudocatillus* were dated to the Pannonian (Fig. 5), but it is likely that (similar to Pannonian *Pontalmyra*) some of these are homeomorphic forms; thus, "*P.*" *stojadinovici* (Brus.) and "*Didacnomya*" *bosniaca* Stev. do not belong to *Pseudocatillus*, and only *P. simplex* should be included in this genus.

In the early Late Pontian (Portaferrian) of the Pannonian Basin, the members of the genus remained rare (*P. pseudocatillus* and *P. balatonicus*). In the Dacian Basin, ten species existed at that time (Papaianopol and Pavnotescu, 1981), of which only two also occurred in the Euxinian Basin (*P. pseudocatillus* and *P. subdentatus*). In the Euxinian Basin, of six or seven species that occurred in the early Late Pontian, *P. pseudocatillus* and *P. corbuloides* were abundant and widespread, and *P. medius* and *P. subdentatus* were locally distributed. The latter two species descended directly from *P. pseudocatillus* (Ebersin, 1967); *P. corbuloides* descended from *P. subdentatus*; and the local rare species, *P. guriensis*, is of uncertain origin.

In the latest Pontian (Bosphorian), 14 species inhabited the Dacian Basin, and only 2 species persisted in the Euxinian Basin (both of them inhabited also the Dacian Basin): *P. corbuloides* was abundant, and *P. subdentatus* was locally distributed. In the Caspian Basin (Shemaha and Babadzhan beds), the only endemic, rare species, *P.* (?) *babadjanicus*, was recorded, which possibly descended from *P. subdentatus*.

In the early Late Pontian (Portaferrian), apparently from some *Pseudocatillus* species probably in the Dacian Basin, the genus *Chartoconcha* originated (Fig. 6) and colonized all the basins of the Paratethys (Fig. 5). At that time, one species of this genus existed in the Pannonian Basin and two species inhabited both the Dacian (Papaianopol, 1975b) and the Euxinian basins (*Ch. bayerni* and *Ch. candida*, which apparently came to the Euxinian Basin from the west). It is worth mentioning that *Chartoconcha*, including both smooth (*Ch. bayerni*) and distinctly ribbed (*Ch. candida*) forms, appeared in all these basins simultaneously, thus implying that the smooth and ribbed species originated from different *Pseudocatillus* species concurrently. In the Bosphorian, *Chartoconcha* species increased in number up to four in the Dacian Basin, whereas in the Euxinian Basin, they were represented by the same two species that survived from the Portaferrian; one of them (*Ch. candida*) penetrated also into the Caspian Basin.

In the latest Pontian (Bosphorian), the genera *Oraphocardium* and *Pteradacna* evolved from the genus

Pontalmyra (Fig. 6). *Oraphocardium* was represented at that time by a single species of local distribution, endemic to the Euxinian Basin. *Pteradacna* possibly penetrated into the Dacian Basin as well (Fig. 5). *Oraphocardium* probably originated from *Pontalmyra subdepressa* through fetalization, i.e., development of lateral teeth in the left valve; these teeth were lacking in the adult forms of *Pontalmyra* (Ebersin, 1962). *Pteradacna* most probably descended from the species *Pontalmyra gourieffi*, which gave rise to *Pteradacna bosporana*, which has a shell similar to that of young *P. gourieffi*, i.e., again through fetalization. According to an alternative opinion (Papaianopol, 1974), *Pteradacna* is of Pannonian origin, i.e., *P. pterophora* (Portaferrian of the Pannonian Basin) and gave rise to all the other species, including *P. tochanensis* (latest Pontian of the Dacian Basin), which in turn gave rise to the Euxinian species. In our opinion, both of the latter species possibly belong elsewhere and, therefore, are assigned only provisionally to *Pteradacna*.

In the Bosphorian of the Dacian Basin, an endemic genus *Luxuridacna*, characterized by a weakened hinge, evolved probably from *Pontalmyra* (Fig. 6). This genus was represented by several species that existed only in the Bosphorian and went extinct by the beginning of the Pliocene (Papaianopol, 1980).

It is possible that *Pontalmyra* also gave rise to the genus *Pseudocardita*, the representatives of which were found in the ?Pontian deposits of Turkey (Oppenheim, 1918).

The genus *Caladacna* stands somewhat by itself and is known as early as the Late Pannonian and Early Pontian of the Pannonian Basin (Figs. 5, 6). As suggested by Taktakisvili (1977), this genus apparently originated from descendants of the Sarmatian *Plicatiformes*, possibly via the Pannonian species "*Limnocardium*" *ornatum* Pavl., assigned to *Caladacna* by Stevanović (1953, 1957). In this case, the genus possibly merits to rank as a separate tribe. In the Pannonian and Dacian basins, there was a widespread species, *C. steindachneri*, that entered during the Portaferrian from the Pannonian Basin into the Dacian and Euxinian basins and persisted there into the Early Pliocene and in the Euxinian Basin probably into the Middle Pliocene (Fig. 5).

The tribe *Arcicardiini* was represented by the genus *Arcicardium*, first recorded from the Portaferrian beds (early Late Pontian) of the Dacian Basin. This genus was absent from the Pannonian Basin to appear only in the Bosphorian in the Euxinian Basin (Fig. 4). The genera *Protoplagiodacna* and *Plagiodacna* were also provisionally assigned to this tribe. The former is of Pannonian origin; i.e., it existed in the Pannonian Basin during the Pannonian and Pontian to migrate to the Dacian Basin in the early Late Pontian and go extinct at the end of the Portaferrian (Fig. 4). This genus probably descended from some Sarmatian forms (?*Obsoletiformes*) and, in turn, could give rise first, in the Early Pontian, to *Plagiodacna* (in the Pannonian Basin) and subsequently, in the late Early Pontian–early Late Pon-

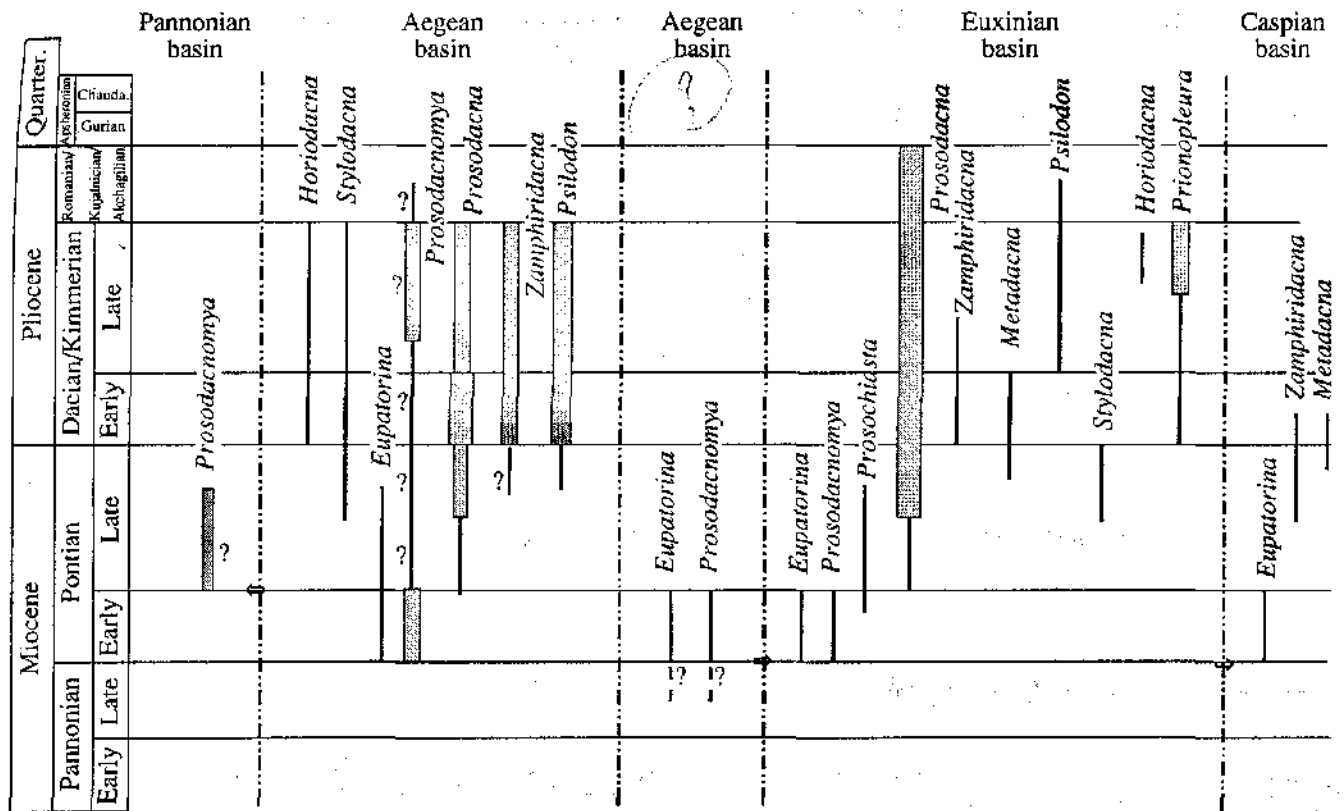


Fig. 7. Distribution of the genera of the tribe Prosodacnini in the basins of the Paratethys.

tian, to *Arcicardium*. At the beginning of the Late Pontian, *Plagiodacna* migrated from the Pannonian Basin to the Dacian–Euxinian Basin (Fig. 4).

The tribe **Prosodacnini** comprises ten genera, seven or eight of which were recorded from the Late Miocene (Figs. 7, 8). The earliest members of this tribe, the genera *Eupatorina* and *Prosodacnomya*, were found in the Early Pontian of the Aegean Gulf and of the Dacian and Euxinian basins. *Eupatorina* was also found in the Caspian Basin. The genus *Eupatorina* apparently originated in the pre-Pontian Aegean Gulf of the Messinian Sea, possibly from some *Cerastoderma* species, and migrated in the Early Pontian to the Euxinian–Caspian and Dacian parts of the Paratethys but not to the Pannonian Basin (Figs. 7, 8).

The genus *Eupatorina* was restricted to the Pontian time and comprises a single species, *E. littoralis*, which was abundant and widespread throughout the Paratethys, except for the Pannonian Basin. In the Late Pontian, this genus disappeared from the Euxinian and Caspian basins and persisted until the early Bosphorian (two species) in the Dacian Basin.

The genus *Prosodacnomya* is probably also of Mediterranean origin, but Müller and Magyar (1992) believed that it originated from the Pannonian *Lymnocardium* (*L. decorum*). One cannot exclude that the type species of *Prosodacnomya*, i.e., *P. rostrata*, evolved

from *Cerastoderma* in the Messinian Aegean Gulf, whereas the species assigned to *Prosodacnomya* from the Pannonian and Dacian basins (*P. sturi*, *P. dainelli*, and *P. stenopleura*) are of different origin and should be transferred to a separate genus, dated to the Late Pontian or even the Pliocene (Figs. 7, 8). *P. rostrata* had limited distributional ranges both in time (Early Pontian) and in space (South Ukraine, Romania; Ebersin, 1959).

The most widespread genus of the tribe, *Prosodacna*, evolved in the early Late Pontian from *Eupatorina* (Ebersin, 1959; Akhvlediani, 1984), most probably in the Dacian Basin (*P. semisulcata portaferrica* Pap.), and then it penetrated into the Euxinian Basin, where it was represented by a single rare species *P. fischeri* during the Portaferrian and by four species during the Bosphorian: abundant and widespread *P. semisulcata*, quite common *P. macrodon*, and rare *P. fischeri* and *P. duabica*. In the Bosphorian, the Dacian Basin was inhabited, in addition to *P. fischeri*, *P. semisulcata semisulcata*, and *P. macrodon*, by the species *P. stolitzkai* (Taktakischvili, 1987).

The genera *Prosochiasta*, *Zamphiridacna*, and *Metadacna* most probably also evolved from *Eupatorina*: *Prosochiasta*, in the Early or Late Pontian; *Zamphiridacna*, in the Late Pontian; and *Metadacna*, in the latest Pontian or Early Kimmerian.

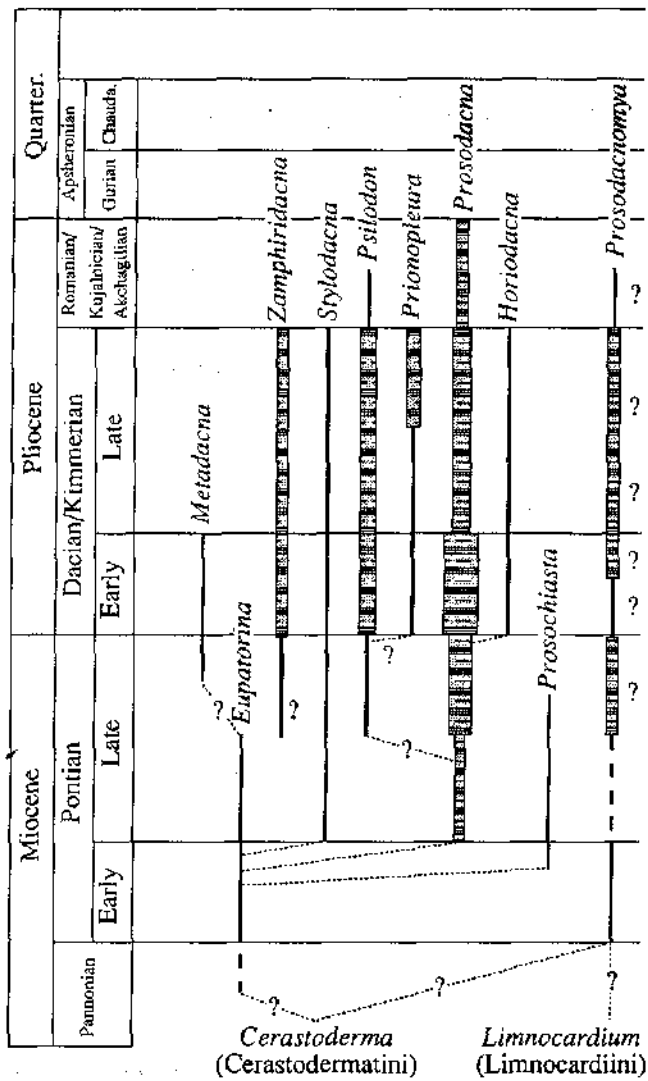


Fig. 8. Phylogeny and stratigraphic range of the genera of the tribe Prosodacnini.

The genus *Prososchiasta*, endemic to the Euxinian Basin and represented only by *P. prososchiasta*, was restricted to the Pontian Rioni Gulf (Abkhazia). The genus *Zamphiridacna* was characteristic of the Pliocene of the Dacian Basin (Portaferrian–Dacian; Papaianopol, 1976; Andreescu, 1977); in the Euxinian and Caspian basins, it was very uncommon; and in the Pontian time, it possibly disappeared completely. As for the genus *Psilodon*, it possibly descended from *Prosodacna* through the development of ribbing or, according to Papaianopol (1978b), from *Eupatorina*; this genus first appeared in the Bosphorian of the Dacian Basin and migrated subsequently to the Eastern Paratethys only in the Pliocene.

The monotypic genus *Styloacna* originated in the Dacian Basin, probably from the genus *Zamphiridacna* in the Early Bosphorian (Fig. 8) and persisted there into

the Early Pliocene; only a few representatives of this genus penetrated into the Euxinian Basin (one specimen from the Bosphorian of the Kerch Peninsula was provisionally assigned to the genus).

The tribe **Pachydacnini** consists of a single genus, *Pachydacna*, with two subgenera. The subgenus that appeared earlier, i.e., *Parapachydacna*, probably descended from the genus *Dacicardium* (tribe Lymnocardiini), most probably in the Dacian Basin (Fig. 4) during the Bosphorian (Papaianopol and Motaş, 1978). There were no pachydacnas in the Pontian of the Euxinian Basin.

It is noteworthy that the species of this genus in the Caspian Basin, *P. (P.) marasinica*, was found in younger strata, in the Babadzhan beds (Late Pontian–?Early Kimmerian), thus indicating that the species from the Dacian Basin apparently migrated to the Caspian somewhere along the southern coast of the Eastern Paratethys, passing over the main part of the Euxinian Basin.

Summing up the Pontian stage of lymnocardiine evolution, one should note that there were no significant changes in the generic composition in the Late Pannonian and Early Pontian of the Paratethys. The fifth stage of the explosive evolution in lymnocardiines began in the early Late Pontian (Portaferrian) and was confined mainly to the Eastern Paratethys, namely, to the Dacian–Euxinian part. Seven genera (*Arcicardium*, *Plagiodacna*, *Chartoconcha*, *Dacicardium*, *Oraphocardium*, *Prosodacna*, and *Zamphiridacna*) originated there. It should be stressed that all of these newly appeared genera belonged to already existing tribes. The species of *Euxinocardium*, *Pontalmyra*, *Pseudocatillus*, and *Paradacna* dominated in the Dacian–Euxinian Basin at that time.

In the latest Pontian, the Western Paratethys gradually diminished and eventually ceased to exist as a brackish-water basin changing into a series of freshwater lakes. Within the Eastern Paratethys, the brackish-water basin persisted and the lymnocardiine evolution continued. In the Caspian Basin, which separated from the Dacian–Euxinian Basin and thus maintained its brackish water for some time, only the genus *Pontalmyra* speciated intensively, whereas the remaining genera were represented by a few species.

The generic composition in the latest Pontian of the Euxinian and Dacian basins was similar to (and mainly inherited from) that of the preceding Portaferrian basin: both basins were inhabited by species of *Pontalmyra*, *Pseudocatillus*, *Chartoconcha*, *Caladacna*, *Phyllocardium*, *Plagiodacna*, *Paradacna*, *Tauricardium*, *Euxinocardium*, *Dacicardium*, and *Prosodacna*. The Dacian Basin was inhabited by *Parvidacna* and *Arpadicardium*, which came earlier from the Pannonian Basin. Only three new genera appeared in this basin, i.e., *Pachydacna*, *Luxuridacna*, and *Styloacna*, of which *Pachydacna* belonged to a new tribe Pachydacnini and was represented by the subgenus *Parapachydacna*. In the Euxinian Basin, only one new genus, *Ptera-*

Styloacna, apper-
Basin.
Chart-
dac-
L.

dacna, appeared, while *Arcicardium*, *Dacicardium*, and *Stylodacna* migrated to this basin from the Dacian Basin. The species of *Pontalmyra*, *Pseudocatillus*, *Chartoconcha*, *Euxinocardium*, *Paradacna*, and *Proso-dacna* dominated in both basins, whereas species of *Luxuridacna* dominated only in the Dacian Basin. During the Bosphorion, the fifth stage of the explosive diversification in the lymnocardiine history continued, but it was less pronounced.

Pliocene–Early Pleistocene

In the Pliocene, the lymnocardiine evolution proceeded after the same scenario as in the Late Miocene, namely, within the same seven tribes. In the Early Pliocene (Kimmerian–Dacian), the Dacian and Euxinian basins began to separate and their lymnocardiine faunas became increasingly divergent; some forms went extinct and others appeared. The diversification in the Euxinian Basin was more intensive than that in the Dacian Basin. Eight new genera originated there (*Stenodacna*, *Macradacna*, *Panticapaea*, *Oxydacna*, *Moquicardium*, *Limnodacna*, *Metadacna*, and *Prionopleura*), in contrast to only three in the Dacian Basin (*Ecericardium*, *Horiocardna*, and *Pachydacna*).

The mutual prochoreses also became restricted and transformed into unidirectional eastward migration: the species of *Horiocardna*, *Pachydacna* s. str., *Zamphiridacna*, *Ecericardium*, and *Parapachydacna* came to the Euxinian Basin; the latter two genera penetrated into the basin only very late in the Kimmerian.

In the Middle–Late Pliocene, only the Euxinian Basin retained its brackish-water character; the Dacian Basin turned into a freshwater basin; whereas the Caspian, on the contrary, became semimarine and was colonized by a new fauna. The Kujalnician Euxinian Basin, which replaced that of the Kimmerian, was restricted in area to the northern part of the modern Black Sea and the Sea of Azov and included only minor parts of the modern main land (western Georgia, the Taman and Kerch peninsulas, the northern coast of the Sea of Azov, and the northwestern coast of the Black Sea). This basin was inhabited by 18 genera and subgenera, all of which were inherited from the Kimmerian basin. The species of *Pontalmyra*, *Pseudocatillus*, *Pachydacna* s. str., and *P. (Parapachydacna)*, *Proso-dacna*, and *Euxinocardium* dominated. Most of these taxa went extinct during the Kujalnician, and only four genera survived in the subsequent Early Pleistocene (=Eopleistocene) Gurian Basin, where two new genera originated: *Tschaudia* and *Submonodacna*.

These events mark the end of the fifth stage in lymnocardiine history, which was confined mainly to the Euxinian–Dacian Basin of the Eastern Paratethys. Let us consider the development of individual tribes during this interval in more detail.

In the tribe **Lymnocardiini**, three genera appeared, of which *Ecericardium* originated in the Dacian Basin

from *Euxinocardium* (Ebersin, 1965b), whereas *Moquicardium* and *Limnodacna* apparently descended from *Dacicardium* in the Euxinian Basin (Figs. 2, 3). *Ecericardium* came from the Dacian Basin to the Euxinian Basin in the late Kimmerian, and *Limnodacna* probably migrated from the Euxinian to the Dacian Basin about mid-Kimmerian time (Motaş *et al.*, 1976). *Moquicardium* was an endemic of the Euxinian Basin. In the Dacian Basin, *Euxinocardium* and *Dacicardium* were the most species-rich genera, especially in the Late Dacian, with equal numbers of species (Papaianopol and Popescu, 1978; Papaianopol, 1983b). In the Euxinian Basin (Ebersin, 1947), the most species-rich genera were the same *Euxinocardium* (four species in the Early and seven in the Late Kimmerian) and *Moquicardium* (two or three species in the Early and six in the Late Kimmerian). Only two of these *Euxinocardium* species also occurred in the Dacian Basin (Papaianopol, 1983a). The remaining genera of this tribe were poor in species. *Tauricardium* disappeared from the Dacian Basin in the middle of the Early Dacian and was represented in the Euxinian Basin by two species in the Early Kimmerian and by a single species in the Late Kimmerian–Early Kujalnician. During the Early Kimmerian, rare *Bosphoricardium* and *Dacicardium* still occurred in the Euxinian Basin (Fig. 3).

In the Kujalnician Basin, a few species of the genera *Tauricardium*, *Moquicardium*, *Euxinocardium*, and *Ecericardium* persisted, the members of the latter two genera possibly penetrated into the Dacian Basin at the end of the Romanian (Papaianopol and Motaş, 1978), but they survived there for a very short time. By the end of the Pliocene all Lymnocardiini went extinct to leave no descendants (Figs. 2, 3).

The tribe **Paradacnini** with its only genus *Paradacna* disappeared from the Dacian Basin in the Pliocene, whereas in the Euxinian Basin, it was represented by two species in the Early and one in the early Late Kimmerian and became extinct thereafter (Fig. 4).

The only species of the genus *Phyllocardium* (tribe **Phyllocardiini**) occurred in the Early Pliocene in both the Dacian and Euxinian basins, but it disappeared from the former in the Late Dacian to persist in the Euxinian Basin at the beginning of the Middle Pliocene (early Kujalnician) and to go extinct thereafter (Fig. 4).

In the Pliocene, the **Pontalmyrini** remained the most diverse and numerous tribe, although the shares of its individual genera changed. In particular, in the Kimmerian–Dacian, the number of *Pontalmyra* species decreased a lot in both the Dacian and Euxinian basins. In the Dacian Basin, six species were recorded from the Early and two from the Late Dacian (Papaianopol, 1981); all of them were endemic. By the end of the Early Pliocene, *Pontalmyra* went extinct in the Dacian Basin. In the Euxinian Basin, 11 species of this genus occurred in the Early Kimmerian and 6–7 in the Late Kimmerian. Of these species, *P. gourieffi* and *P. crassatellata* were abundant and widespread and *P. occi-*

dentalis and *P. kiptschakensis* were locally distributed. Six species were inherited from the preceding Late Pontian basin, and five more originated in the Early Kimmerian: *P. crassatellata* from *P. subcrassatellata*, *P. occidentalis* from *P. paucicostata*, *P. kiptschakensis* and possibly *P. oxypleura* from *P. planicostata*, and *P. karpinskyi* from *P. subcarinata*. Of the three species that appeared in the Late Kimmerian, *P. tamanensis* descended from *P. planicostata*, *P. voskobojnikovi* probably evolved from *P. sulcatina* (although the latter species was not recorded from the Early and early Middle Kimmerian), and *P. postoxypleura* possibly evolved from *P. oxypleura* (Akhvlediani, 1984).

In the Kujalnician basin (Middle-Late Pliocene), only four species were recorded, of which one species (*P. medeae*) was locally distributed and the other three were rare. Two species were inherited from the Kimmerian basin (*P. crassatellata* and *P. oxypleura*), and the other two evolved in the Kujalnician basin: *P. medeae* from *P. multistriata* (Ebersin, 1962) and *P. phasiaca* probably from *P. tamanensis*. Each of the Gurian and Chaudian Eopleistocene basins contains only one species of very low abundance. The species *P. plesiochora*, which originated in the Chaudian Basin, possibly descended from *P. medeae*. By the end of the Eopleistocene, all *Pontalmyra* went extinct and left no descendants (Figs. 5, 6).

Outside the main basins of the Paratethys, some species apparently belonging to *Pontalmyra* are known from the Pontian deposits of southern Turkey (Taner, 1974). It is quite possible that the endemic genus *Pseudocardita* originated from one of these species (Fig. 6).

The genus *Oraphocardium* (endemic of the Euxinian Basin), which descended from *Pontalmyra* in the Pontian, was represented in the Early Kimmerian by only one widespread species *O. alatoplanum*, which persisted into the Kujalnician (Figs. 5, 6).

In the Early Kimmerian, the genus *Pteradacna* was comprised of two species that originated from the Late Pontian *P. bosphorana*: *P. praeedentula*, extinct by the end of the Early Kimmerian, and *P. edentula*, which survived into the early Late Kimmerian; the extinction of the latter closed the record of this genus (Figs. 5, 6).

At the beginning of the Kimmerian, *Pontalmyra* gave rise to the genera *Stenodacna*, *Macradacna*, *Panticapaea*, and *Oxydacna* (Fig. 6). All these genera included a few species and were endemic to the Euxinian Basin (Fig. 5). Of these species, *Stenodacna angusticostata* was abundant and widespread during the second half of the Kimmerian and *Macradacna meridionalis* and *M. schakonensis* were locally distributed. The genus *Stenodacna* (*S. praeangusticostata*) probably evolved from the species *Pontalmyra subcrenulata*, as suggested by Ebersin (1951) and Akhvlediani (1962, 1984). Akhvlediani even included the latter species in *Stenodacna*. The Early Kimmerian *S. praeangusticos-*

tata gave rise to *S. angusticostata* (Ebersin, 1951; Akhvlediani, 1962), which survived until the mid-Kujalnician.

Macradacna, *Panticapaea*, and *Oxydacna* probably originated from *Pontalmyra incerta* (Ebersin, 1951, 1967). The earliest species of *Macradacna*, *M. ukrainica*, is known from the Early Kimmerian. At the beginning of the Late Kimmerian, this species gave rise to three species, i.e., *M. maxima*, *M. schakonensis*, and *M. commilitans* (the latter possibly descended from *M. schakonensis*). The former species survived until the mid-Kujalnician, and the other two (as well as *M. subschakonensis*) were restricted to the early Late Kimmerian. In the latest Kimmerian, two more species originated, *M. pseudoesperanzae* (probably from *M. schakonensis*) and *M. meridionalis*. The origin of the latter is uncertain (from *M. maxima* or from *M. schakonensis*), but in any case, fetalization took place: *M. meridionalis* possessed well-developed teeth, whereas in the adults of both possible ancestral species, the hinge was weak. The same is true of the evolution of *M. commilitans* and *M. pseudoesperanzae*.

The monotypic genus *Panticapaea* was restricted to the Early-early Late Kimmerian (Figs. 5, 6).

The genus *Oxydacna* entered the record in the Early Kimmerian, with the species *O. ambrae*, which still retained well-developed cardinal teeth but already formed the sinus. This species gave rise to the species *O. tertiana* and *O. tenericardo*, which had weak hinges and occurred in the early Late Kimmerian (Fig. 6).

As mentioned above, the genus *Caladacna* passed from the Miocene Pontian Basin to the Early Pliocene Dacian-Euxinian Basin. It survived in the Dacian Basin until the middle Early Dacian and in the Euxinian until the mid-Kimmerian, being the most abundant and common in the Early Kimmerian. In the second half of the Kimmerian (Kamyshburunian), this species gave rise to *C. escheri*, which was an endemic of the Euxinian Basin and possibly survived there until the mid-Kujalnician (Figs. 5, 6).

The genus *Pseudocatillus* was widespread in the Pliocene Euxinian Basin, especially from the second half of the Kimmerian to the Kujalnician, but it went extinct in the Dacian Basin in the early Late Dacian (Papaianopol and Motaş, 1978) (Fig. 5).

At the beginning of the Kimmerian, the number of species of this genus in the Euxinian Basin was somewhat higher than in the Late Pontian; the only widespread and abundant species was *P. corbuloides*; the species *P. sokolovi* was locally distributed and possibly migrated from the Dacian Basin, where it presumably originated from ancestors similar to *P. securus*. The same is true of *P. tschelidzei*, which was infrequent in the Euxinian Basin. *P. azovicus* first recorded at that stage probably descended from *P. subdentatus* (Akhvlediani, 1984), as well as *P. polemontis*.

In the early Late Kimmerian (Kamyshburunian), the number of *Pseudocatillus* species was doubled mainly

due to new
situation chr
also occ
widesp
Late
war
ar

due to newly-appearing endemics. The species composition changed significantly (of ten species, only three also occurred in the Early Kimmerian). No abundant or widespread species were recorded among members of Late Kimmerian *Pseudocatillus*. The species *P. sokolovi* was locally distributed in the early Late Kimmerian, and *P. polemonis*, *P. lebedinzevi*, *P. donacoides*, *P. zlatarskii*, and *P. pleonexia* were quite common throughout the Late Kimmerian. Among the newly appearing species, *P. zlatarskii* probably descended from *P. dentatus* (Ebersin, 1967) and *P. kubanicus* descended from one of these two species. *P. pharnaci*, *P. donacoides*, and *P. lebedinzevi* most probably originated from *P. polemonis*, although Ebersin (1967) considered *P. lebedinzevi* a descendant of *P. azovicus*. It is probably premature to create a separate subgenus *Pseudocatillus*, *Donaciatillus* Akhvlediani comprising *P. (D.) donacoides*, *P. (D.) postdonacoides*, *P. (D.) pharnaci*, *P. (D.) polemonis*, and *P. (D.) septemputeanus* (Akhvlediani, 1984), because this means that some other groups (subgenera?) should be established within *Pseudocatillus*. If established, *Donaciatillus* should include *P. lebedinzevi* as well. *P. pleonexia* probably descended from *P. azovicus* directly rather than via *P. lebedinzevi*, as suggested by Ebersin (1967); the origin of *P. monachorum* is uncertain; it is quite possible that it migrated from the west (Ebersin, 1967).

In the latest Kimmerian, the number of species became as low as seven; five of them were inherited from the preceding basin and the other two were newly appeared species: *P. praecoloratus*, which possibly descended from *P. sokolovi*; and *P. vulgaris*, which is of uncertain origin.

In the subsequent Kujalnician basin, the number of *Pseudocatillus* species increased up to ten, of which only four species were inherited from the Late Kimmerian basin, and the other were recorded there for the first time. Of these latter, some descended from the Late Kimmerian forms (*P. postdonacoides* probably from *P. lebedinzevi* and *P. subriegeli* from *P. sokolovi*) and most of the others are of uncertain origin. *P. wassovitschi*, *P. tanaicus*, *P. dalii*, and also *P. vulgaris*, recorded already from the Late Kimmerian, are possible descendants of the Dacian species that migrated into the Euxinian Basin, but this suggestion remains unproven. The origin of *P. hypaniformis* is uncertain as well. At the beginning of the Quaternary, *Pseudocatillus* became rare: two species are known in the Gurian Basin, and one or two are known in the Chaudian Basin. The Gurian species *P. kitovaniae* and *P. praehellesspenticus* probably descended from *P. sokolovi* or *P. subriegeli* and from *P. pleonexia*, respectively. The origin of the Chaudian species *P. cazecae* is uncertain, as well as that of *P. (?) subcoloratus*. It is quite possible that the last species descended from *P. praecoloratus* or from an as yet unknown similar species from the Kujalnician-Gurian deposits. In this case, the species *P. (?) subcoloratus*, which was found in abundance in freshened parts of the Chaudian Basin and recorded as a rare species

already in the Paleoeuxinian Basin, was the latest species of the genus *Pseudocatillus* (Figs. 5, 6).

The genus *Chartoconcha* was represented in the Pliocene of the Dacian-Euxinian Basin by a few species. From the Early Pliocene of the Dacian Basin, one Early Dacian and one Late Dacian species were recorded (Fig. 5). In the Kimmerian basin, throughout its lifetime, the species *Ch. bayerni* persisted, and from the Late Kimmerian of this basin, one more, very rare endemic species *Ch. laevis* was recorded. From the Middle-Late Pliocene (Kujalnician) of the Euxinian Basin, only one species, *Ch. postkimmeria*, is known. This species went extinct and left no descendants. In that time, the long-lived species *Ch. bayerni* (early Late Pontian-Kimmerian) was most widespread. The species *Ch. postkimmeria*, endemic to the Kujalnician Rioni Gulf, was a quite distinctive form there. The remaining species were local and rare (Figs. 5, 6).

Two more genera originated from *Pseudocatillus* in the Early Quaternary of the Gurian Basin: *Tschaudia* most probably evolved from *Pseudocatillus vulgaris*, and *Submonodacna*, probably from a species similar to *P. pleonexia* (Davidaschvili and Kitovani, 1964). Both of them were short-lived genera, which after the Late Chaudian, went extinct to leave no descendants. *Tschaudia* were abundant and widespread forms in Gurian and Chaudian mollusc communities (*T. digressa* in the Gurian and *T. tschaudae* in the Chaudian), and the genus *Submonodacna* was represented by a single, rather rare species.

The members of the tribe *Arcicardiini*, the genus *Arcicardium* and provisionally assigned genus *Plagiadacna*, were characteristic of the Early Pliocene of the Dacian-Euxinian Basin. The first genus intensively speciated in the Late Kimmerian Euxinian and persisted there until the mid-Kujalnician, but it was absent from the Dacian Basin in the Pliocene. *Plagiadacna* was widespread in both basins, especially in the Early Pliocene; in the Euxinian Basin, species of this genus persisted until the Early Kujalnician (Taktakisvili, 1970a; Akhvlediani, 1966, 1984) (Fig. 4).

The tribe *Prosodacnini* comprised in the Pliocene ten genera, of which the most diverse and widespread genus was *Prosodacna*. This genus included *P. semisulcata*, *P. macrodon*, and *P. duabica*, which passed from the Pontian to the Kimmerian basin. The first two species were abundant and widespread. Locally distributed *P. longiuscula* migrated from the Dacian Basin; *P. inflatissima*, which probably descended from the previous species, was rare. *P. callopiestes*, endemic to the Rioni Basin (Duabian Beds), most probably originated from *P. longiuscula*. In the Kujalnician basin (Middle-Late Pliocene), four species were recorded, of which only *P. misera* was quite common, whereas *P. semisulcata*, *P. macrodon*, and *P. duabica* were rare and locally distributed. The species *P. misera*, specific to the Kujalnician, probably originated from *P. semisulcata* and was, as well as *P. callopiestes*, *P. duabica*, and

P. inflatissima, endemic to the Euxinian Basin. A half of the *Prosodacna* species of the Euxinian-Caspian Basin (four of eight) also occurred in the Dacian Basin (Andreescu, 1977; Papaianopol, 1977), but went extinct by the end of the Early Pliocene (Figs. 7, 8).

The genus *Zamphiridacna* passed into the Early Pliocene Dacian-Euxinian Basin from the preceding Pontian Basin and persisted until the end of the Early Pliocene in the Dacian Basin (Papaianopol, 1976; Andreescu, 1977) and for a rather short interval (Early-early Late Kimmerian), in the Euxinian Basin. Rare finds were reported from the Babadzhan beds of Azerbaijan (Neveesskaja *et al.*, 1986).

The genus *Psilodon*, showing a similar distribution, originated in the Dacian Basin in the Late Pontian, was widespread there throughout the Dacian (Motaş *et al.*, 1973), migrated to the Euxinian Basin in the early Late Kimmerian, and existed there until the mid-Kujalnician (early Middle Pliocene). These two genera were represented by a few species each (Figs. 7, 8).

The members of the two-species genus *Metadacna*, endemic to the Euxinian-Caspian Basin, were recorded in the earliest Kimmerian of western Georgia (Ebersin, 1959) and in the Babadzhan beds of Azerbaijan.

The monotypic genera *Stylodacna* and *Horiodacna* were mainly limited to the Dacian Basin. Although *Horiodacna*, which originated in the earliest Pliocene (apparently from *Prosodacna*), penetrated into the Euxinian Basin during the Late Kimmerian, this genus was restricted to the northwestern part of the basin (the Sea of Azov region; Ebersin and Semenenko, 1966b).

The endemic genus of this tribe, *Prionopleura*, presumably originated in the Euxinian Basin from the genus *Psilodon*, several members of which migrated (as mentioned above) to the Euxinian Basin in the Kimmerian. The genus *Prionopleura* was comprised of three or four rare species.

As already mentioned, the species from the Upper Pontian and Kimmerian deposits of the Dacian Basin that were assigned to the genus *Prosodacnomya* possibly do not belong to it and merit separation into another genus.

The tribe Prosodacnini ended its existence in the Late Kujalnician (Akchagilian) to leave no descendants (Fig. 8).

The tribe Pachydacnini, represented by a single genus with two subgenera, was characteristic of the Dacian and Euxinian Early Pliocene Basins and of the Middle-Late Pliocene Euxinian basins (Fig. 4).

The species of the subgenus *Parapachydacna* occurred in the Dacian Basin during the Early Pliocene and Early-early Late Dacian, whereas in the Euxinian Basin, their finds (two species) are known only from the Kujalnician (Middle-Late Pliocene); i.e., their migration to the Euxinian Basin probably took place at the end of the Early Pliocene and left no evidence in the record.

The subgenus *Pachydacna* descended from *Parapachydacna* in the earliest Pliocene of the Dacian Basin, migrated during that interval to the Euxinian Basin to become widespread there during the entire Middle-Late Pliocene whereas in the Dacian Basin (Papaianopol and Motaş, 1978), it went extinct by the mid-Dacian (Fig. 4). Quite widespread and abundant in the Kimmerian basin were the species *P. (P.) azovica* (in the Early Kimmerian) and *P. (P.) cimmerica* (in the Late Kimmerian). The species *P. (P.) duabica* occurred in abundance in the Duabian facies developed in the Rioni Gulf. The remaining five species of the nominal subgenus found in the Kimmerian were rare and usually locally distributed. Only one species, *P. (P.) suchumica*, passed to the Kujalnician basin, where it was locally distributed. Of the other two Kujalnician species, *P. (P.) kujalnicensis* was quite abundant, but restricted to regions in southern Ukraine, and *P. (P.) postduabica* was represented by a few specimens from the Rioni Gulf region.

In the Caspian Basin, the latest species of the tribes Pontalmyrini, Prosodacnini, and Lymnocardiini persistent through the Late Miocene and possibly the earliest Pliocene to go extinct because of the freshening of the basin, where lymnocardiines reappeared only in the Akchagilian.

The fifth stage of lymnocardiine diversification, which began in the Late Miocene (early Late Pontian), ended in the earliest Quaternary when the latest member of the tribe Pontalmyrini became extinct.

The subsequent history of lymnocardiines is associated with the Caspian rather than the Euxinian Basin. After the Balakhanian interval (when lymnocardiines were completely absent there), the Akchagilian semimarine basin appeared to receive one species of the genus *Cerastoderma* (*C. dombra*) that migrated to this basin (probably from the Mediterranean region) with the Early Akchagilian transgression and gave rise to numerous species, some of which differ from the ancestral forms to an extent that they deserve to be recognized as separate genera.

Akchagilian cardiids were previously assigned to the genera *Cardium* (s. l.) and *Avicardium* (Kolesnikov, 1950). Within the latter genus established by Kolesnikov and characterized by the peculiar shell shape, straightened hinge margin, posterior alation, and very weak hinge (Ebersin and Chei'tsov, 1966), several species groups were distinguished (Uspenskaya, 1931; Kolesnikov, 1950; Alizade, 1954). When revising brackish-water cardiids, Ebersin (1965a) properly noted that the group ancestral to the Akchagilian cardiids included several (or one) species of the genus *Cerastoderma* that migrated to this basin from some sea basin. Popov (1977) studied the shell microstructure in many species of Akchagilian cardiids and confirmed their assignment to *Cerastoderma*; in addition (accepting the descent of *Avicardium* from *Cerastoderma*), he established a separate tribe for this genus, *Avicardiini*.

The revision of Akchagilian lymnocardiines demonstrated that in addition to the considerable similarity between them and the Sarmatian lymnocardiines, they were even more diverse in shell shape (some species resemble mytilids and pholadids); in the presence of a shell gape in some species; and in the structure of the hinge, which was more complete (posteriolateral tooth present in the left valve) in some species or markedly weakened (up to the total absence of teeth) in others. Akchagilian lymnocardiines are classified into six genera (Paramonova, 1994) belonging to three tribes: **Cerastodermatini** with genera *Cerastoderma* (eight species) and *Raricardium* (four species), **Acobaecardiini** with genus *Acobaecardium* (two species), and **Avicardiini** with the genera *Avicardium* (ten species), *Miricardium* (six species), and *Andrusovicardium* (six species).

The species *Cerastoderma dombra*, which extended its range in the Early Akchagilian, probably migrated from the eastern Mediterranean region, where it apparently originated from some species of the *Cerastoderma glaucum* group. In the mid-Akchagilian, it gave rise to a considerable number of new species, more or less differing in the shell form, the shape and development of ribs, carination, and the presence or absence of a posterior gape. The species of *Cerastoderma* could be divided into several groups, some of which are similar in appearance to the species groups placed into the Sarmatian genus *Obsoletiformes*, but differ from them in having a more developed hinge (usually, in the presence of the posteriolateral tooth in the left valve) and ribs with fine longitudinal grooves. In the mid-Akchagilian, the genus *Cerastoderma* gave rise to five endemic genera. Of these genera, only *Raricardium*, which resembles the Sarmatian genus *Plicatiformes* in shell shape and ribbing pattern, possessed a mostly fully developed hinge. In the other genera, either the teeth were completely lacking or the hinge was markedly weakened (sometimes only rudiments of the cardinal or lateral teeth were present). Nearly toothless species of the genus *Acobaecardium* (tribe **Acobaecardiini**) were cerastoderm-shaped, whereas the genera of the tribe Avicardiini were characterized by a straightened hinge margin, a shell elongated towards the posteroventral angle, and an alate posterior area. Some genera of the tribe differed in the carination, shell convexity, and beak development. Thus, the species of the genus *Miricardium* possessed a convex, carinate, triangular-trapezoidal shell; those of the genus *Andrusovicardium* had a flattened, sharply carinate, elongate triangular shell; and those of the genus *Avicardium* were characterized by a moderately to weakly convex, bluntly carinate, and aviculoid (sometimes orbicular) shell. Some species of the genus *Avicardium* were similar in appearance to those of the Sarmatian genera *Aviculocardium* and *Kubanocardium* (tribe **Aviculocardiini**), differing in having a much more reduced hinge (mainly in the lack of cardinal teeth).

In the mid-Akchagilian, the average size of lymnocardiines increased, especially, in avicardiines. In many phyletic lineages, the ribs became smoother.

In the earliest Akchagilian, only the species *Cerastoderma dombra* occurred in abundance throughout the basin. In the mid-Akchagilian, it remained widespread, although in the areas with well-developed muddy bottom sediments, it was replaced by avicardiines. These were broadly (but usually locally) distributed in the southern part of the basin (Azerbaijani-Turkmenian): *Andrusovicardium radiiferum*, *Miricardium dahestanicum*, *Avicardium kamischense*, *A. nikitini*, etc. Local distribution was also characteristic of *Cerastoderma konschini*, *C. siphonophorum*, *Raricardium konjushevskii*, *Acobaecardium acobae*, etc. Most species were rare, e.g., *Cerastoderma altum*, *C. sanani*, *Andrusovicardium tshandyricum*, etc.

Thus, a single Early Akchagilian species, *Cerastoderma dombra*, gave rise in the Middle Akchagilian to 36 new lymnocardiine species, 5 genera, and 2 tribes. As a consequence, in the first half of the Akchagilian, the sixth stage of lymnocardiine diversification took place (Fig. 9).

In the Late Akchagilian, the species *Cerastoderma dombra* (usually represented by the individuals of small size) spread again over the whole basin. Few other species that passed to the Late Akchagilian basin became rare and seem to be stunted, apparently due to reduced salinity. By the end of the Akchagilian, Cerastodermatini went extinct.

The beginning of the Apsheronian time (Eopleistocene) was accompanied by the significant freshening of the basin, where rare lymnocardiines were represented by small forms with thin-walled shells. The origin of diverse and numerous lymnocardiines of the Late Apsheronian (including "the Middle Apsheronian" of some authors) cannot be determined directly from the available material. From the mid-Apsheronian, the last (seventh) explosive diversification began, when the members of the youngest lymnocardiine tribe, **Adacnini**, appeared and became widespread. This tribe originated either from Akchagilian *Cerastoderma* or from the other Akchagilian genera that evolved from *Cerastoderma* (*Avicardium* and *Acobaecardium*). The tribe comprises ten genera (Fig. 9), four of which survived into the Present in the Caspian Sea (*Didacna*, *Monodacna*, *Adacna*, and *Hypanis*); in addition, *Hypanis* and *Monodacna* live in the estuaries and deltas of the Black Sea and the Sea of Azov, and *Adacna* live in the Aral Sea.

In the Early Apsheronian basin, the members of six genera already appeared: *Apscheronia* most probably descended from *Cerastoderma* of the *konschini* group, which is marked by poorly developed ribs, rather than from *Cerastoderma sanani* as suggested by Ali-Zade (1973); *Monodacna* apparently originated from *Cerastoderma konschini* (*Cardium balchanicum* after Ali-Zade, 1967, 1973); *Parapscheronia* was either derived

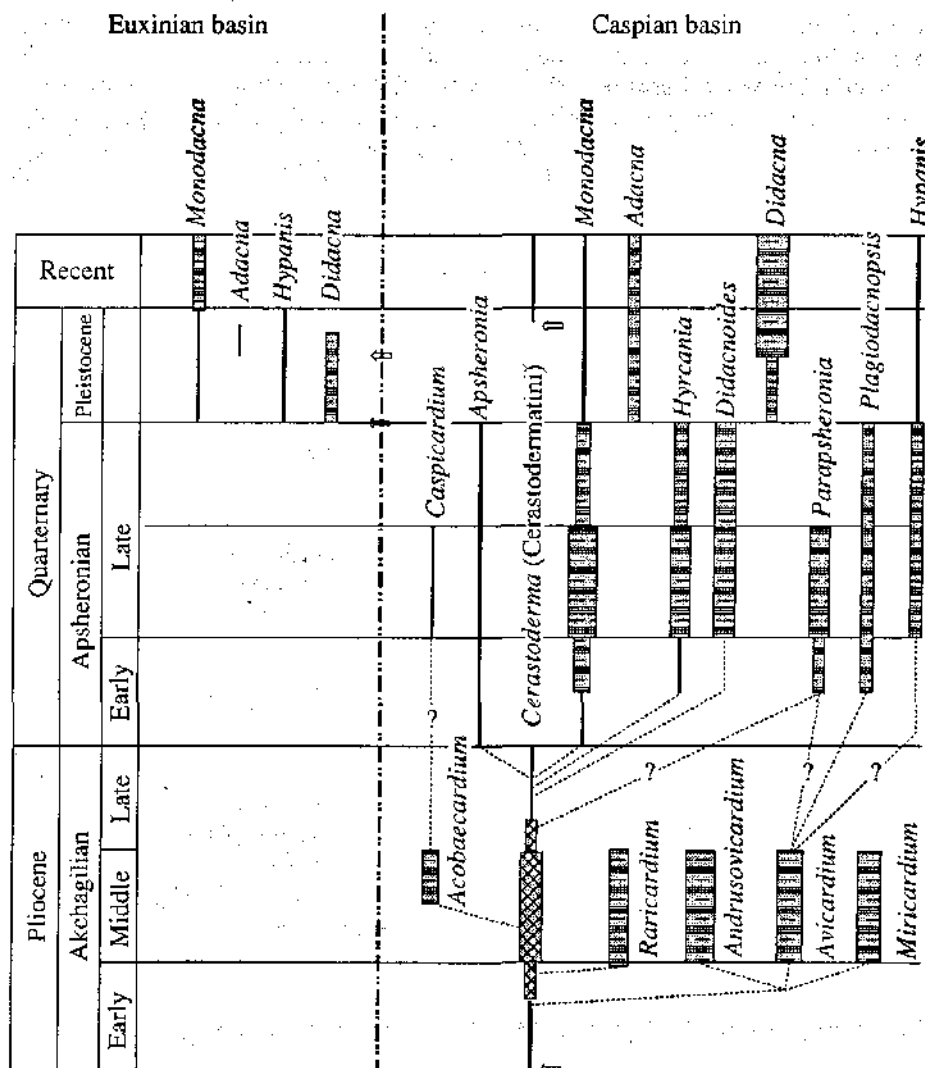


Fig. 9. Phylogeny and distribution of the genera of the tribe Adacnini.

from *Acobaecardium acobae* (= *Cerastoderma toronglynicum* after Ali-Zade, 1967, 1973) or polyphyletic (see below); *Hyrcania* probably descended from an ancestor common to *Monodacna* and *Didacnoides*, because *Hyrcania* and *Didacnoides* are quite similar. Astafieva (1955a) even regarded them as subgenera of the same genus. The origin of *Hyrcania* from *Raricardium konjuschevskii*, suggested by Ali-Zade (1967), is less probable.

Two more genera appearing in the Early Apsheronian were possibly related to *Avicardium* rather than to *Cerastoderma*. These are *Hypanis*, which possibly descended from a species similar to *Avicardium kazanbulangense* (Ali-Zade, 1973), and *Plagiodacnopsis*, presumably related to the Akchagilian species *Avicardium subleve* (= *Cardium tantali* after Ali-Zade, 1967). All the genera mentioned, except for *Monodacna* and *Hypanis*, were endemic to the Caspian Basin and specific to the Apsheronian interval (they became extinct by the Late Apsheronian).

The genus *Apscheronia* was monotypic with a single species abundant and widespread in the early Late Apsheronian and persisting throughout the Apsheronian.

The genus *Monodacna* was quite diverse and comprised up to 15 species. In the Early Apsheronian, four species existed. In the early Late Apsheronian, ten new species appeared, most of which descended from *M. sjoegreni* (*M. beibatica*, *M. porsugelica*, *M. nitida*, *M. kabristanica*, *M. azerbajanica*, and possibly *M. praelaeviuscula*). *M. dubia* and *M. incipiens* most probably originated from *M. laevigata*. The last species apparently gave rise to *M. monoapteris*, and the origin of *M. goesdekiana* remains uncertain. Three species were inherited from the Early Apsheronian basin; 13 species thus existed in the early Late Apsheronian. Only two of them survived into the latest Apsheronian, and a newly appeared species, *M. (?) alizadei*, was provisionally assigned to the genus. Among monodacnas, only the

species *M. sjoegreni* was abundant and widespread in the Late Apsheronian and *M. porsugelica* was locally abundant (early Late Apsheronian, Cheleken region). All of the Apsheronian *Monodacna* species, except for *M. sjoegreni*, went extinct by the end of the Apsheronian to leave no descendants. *M. sjoegreni* gave rise to the species *M. caspia*, which became widespread in the Quaternary in the Caspian and Black seas and lives now in the estuaries and deltas of the Black Sea and the Sea of Azov, as well as in the Caspian Sea. At present, one more species, *M. colorata*, which probably descended from *M. caspia*, inhabits the estuaries of the Black Sea (Neveeskaja, 1965).

The genus *Hyrkania* was represented in the Early Apsheronian by a single species, *H. intermedia*. In the early Late Apsheronian, this species gave rise to the species *H. turkmena*; *H. kolesnikovi*; *H. major*; and, probably, *H. loerentheyi*. These the ancestral species, *H. intermedia*, also persisted. In the latest Apsheronian, only two species persisted, *H. intermedia* and *H. loerentheyi*. The species *H. intermedia* was abundant and widespread (in the Late Apsheronian), and *H. kolesnikovi*, *H. major*, and *H. turkmena* were locally distributed (early Late Apsheronian, Cheleken region).

The genus *Parapscheronia* comprised only four species, two of which were recorded in the Early Apsheronian: *P. raricostata* and *P. volarovici*. These species presumably originated from different species: *P. raricostata* from *Acobaecardium acobae* (= *Cerastoderma toronglynicum* after Ali-Zade, 1967, 1973), and *P. volarovici* from *Avicardium subleve* Tschel. (= *Cardium veneratum* Ali-Zade). In the early Late Apsheronian, these species persisted and gave rise to two other species: *P. eurydesma* (from *P. raricostata*) and *P. calvescens* (from *P. volarovici*). All species of the genus were rare and became extinct by the middle Late Apsheronian.

The genera *Hypanis* and *Plagiocardnopsis* were represented in the Apsheronian by two rare species. *Plagiocardnopsis carinifera* existed in the Early Apsheronian to give rise in the early Late Apsheronian to *P. isseli*. The species of *Hypanis* appeared in the early Late Apsheronian. The species of *Plagiocardnopsis* along with *Hypanis andrussovi* became extinct in the Late Apsheronian, and *H. plicatus*, which survived into the Quaternary Caspian, repeatedly migrated to colonize the Black Sea Basin in the periods of its freshening.

Two more endemic Apsheronian genera, *Didacnoides* and *Caspicardium*, are known only since the early Late Apsheronian, but they both most probably directly descended from the Akchagilian species and merely remain to be found yet in the Early Apsheronian. The genus *Didacnoides* probably originated from an ancestral species common to *Monodacna*, *Cerastoderma konchimi* (= *Cardium balchanicum* after Ali-Zade, 1967). The monotypic genus *Caspicardium* possibly descended from *Acobaecardium conspectum* (= *Cardium*

veneratum after Ali-Zade, 1967) and had a restricted range, being known only from the early Late Apsheronian.

Similar to other genera, the genus *Didacnoides* was best represented in the early Late Apsheronian (five species). It is quite possible that species of this genus originated synchronously in different regions from different populations of the same species: *D. caucasica* and *D. bakuana* in the western Caspian (Azerbaijan), whereas *D. didacnoides* ancestral to *D. delto curta* and *D. transcaspica* in the eastern regions (Cheleken). All five species occurred in abundance in respective regions: *D. didacnoides*, *D. delto curta*, *D. transcaspica* along the eastern coast of the Caspian (Cheleken), *D. bakuana* and *D. caucasica* along the western coast (Azerbaijan). *Didacnoides* survived until the end of the Apsheronian.

In the Late Apsheronian, *D. didacnoides* apparently gave rise to the genus *Didacna*. Subsequently, its members became widespread in both the Caspian and Black Sea basins and still persist in the Caspian Sea. The origin of *Didacna* from Apsheronian "*Didacnomya*" and "*Pseudocatillus*" was suggested in the last papers of Fedorov (1979). However, this opinion was not supported by some other authors (see Neveeskaja *et al.*, 1986).

It should be stressed that in the Black Sea *Didacna* appeared earlier than in the Caspian Basin, i.e., in the Chaudian (Late Apsheronian). Most probably, the members of *Didacnoides* (some of them were hardly distinguishable from the true *Didacna*) migrated to the Black Sea Basin to evolve there further under new environmental conditions: the lateral teeth were lost in adult but retained in juvenile forms and the ribs became even more flat to merge with the interspaces and differ from them only in color. Later (in the Bakuan), *Didacna* (*D. crassa*) migrated to the Caspian Basin already as a fully formed genus to dominate the mollusc assemblages. Only in the Holocene, when *Cerastoderma glaucum* (= "*Cardium edule*") penetrated into the Caspian, the members of *Didacna* were partly ousted by this extremely eurytopic species.

The youngest genus of the tribe, *Adacna*, probably descended from *Monodacna* and possibly even from the different species: *Adacna vitrea* descended from *Monodacna laevigata*, and *A. laeviuscula* descended from *M. praeleviuscula*. The transition from *Monodacna* to *Adacna* was marked by the development of a deep sinus, a diagnostic feature of the genus *Adacna*. Both of the *Adacna* species are known since the earliest Pleistocene and still persist in the modern Caspian Sea. *A. vitrea* penetrated into the Black Sea Basin during the period of its freshening, and now, besides the Caspian it lives (or lived?) in the Aral Sea.

There were also different opinions about the Apsheronian genera constituting the tribe Adacnini. Thus, Andrussov (1923) considered some of these genera to be of Euxinian origin, closely related to the Pontian-

Kujalnician forms (*Monodacna*, "*Didacnomya*" = *Didacnoides*, etc.), and the remaining genera to be of uncertain origin (*Apscheronia*, *Parapscheronia*). Alizade (1945), Kolesnikov (1950), and Georgii Popov (1970) suggested that some Apsheronian molluscs could be of Euxinian origin and the others were descended from the Akchagilian forms.

Astafieva (1960) and Ali-Zade (1961, 1967, 1973) strongly argued that all of the Apsheronian molluscs originated from the Akchagilian species, the opinion first suggested by Davidaschvili (1933). This opinion was supported in the monograph on the Apsheronian of Turkmenia (Gennadii Popov, 1961). The hypothesis that the Apsheronian lymnocardiines originated from Akchagilian *Cerastoderma* was confirmed by S. Popov (1973, 1977) in the study of the shell microstructure in the Akchagilian, Apsheronian, and Pontian-Kujalnician Lymnocardiinae. He demonstrated that the species of Apsheronian genera were much closer in shell structure to the Akchagilian *Cerastoderma* than to the Pliocene lymnocardiines of the Euxinian Basin.

At present, the view that all of the Apsheronian lymnocardiines originated from the Akchagilian members of *Cerastoderma* and possibly from those of other genera (*Avicardium* and *Acobaecardium*) is well founded.

In the post-Apsheronian (Pleistocene to Present) Caspian Basin, only a few members of the tribe Adacnini (*Didacna*, *Adacna*, *Monodacna*, and *Hypanis*) persisted, and a member of the tribe Cerastodermatini, *Cerastoderma glaucum* (= "*Cardium edule*"), appeared in the Late Holocene to penetrate also into the Aral Sea, where the genus *Adacna* occurred as well.

In the Pleistocene Azovian-Black Sea Basin, the members of Adacnini (*Didacna*, *Monodacna*, *Adacna*, and *Hypanis*) dominated lymnocardiines during the periods of freshening (Paleoeuxinian and Neoeuxinian times), whereas in the periods when this basin was connected with the Mediterranean Sea, lymnocardiines were dominated by a member of the tribe Cerastodermatini, *Cerastoderma glaucum*. At present, Adacnini (*Monodacna*) are restricted to the freshened estuaries, whereas *C. glaucum* dominates the benthic ecosystems of the Black Sea estuaries (except for those much to freshened) and the northwestern part of this sea, as well as the shallow waters of the Sea of Azov; this species also occurs as a rare form in open shallow waters of the Black Sea (Fig. 9).

Thus, the history of the subfamily Lymnocardiinae indicates that its members were the most successful group of molluscs in semimarine, i.e., only episodically connected with the open sea and brackish-water basins (Solenovian, Kozahurian, Sarmatian, Pontian and several Pliocene basins of the Eastern Paratethys), but they underwent mass extinctions because of environmental changes, especially, in salinity.

Of all the numerous lymnocardiine tribes, only two, Cerastodermatini (genus *Cerastoderma*) and Adacnini

(genera *Didacna*, *Adacna*, *Monodacna*, and *Hypanis*), persisted to the present.

ECOLOGY OF LYMNOCARDIINAE

The most eurytopic of all the cardiids, representatives of this subfamily occupied various ecological niches and, thus, acquired diverse adaptations, affecting their shell morphology.

The ancestral tribe Cerastodermatini dominated in the semimarine basins (Late Konkian, Sarmatian, Early Maeotian, and Akchagilian) and in the earlier brackish-water basins (Solenovian and Kozahurian).

Most of Sarmatian and Akchagilian lymnocardiines belonged, like nearly all members of the marine cardiid subfamilies, to infaunal suspension feeders with well-developed siphons (*Cerastoderma*, *Plicatiformes*, *Obsoletiformes*, and *Raricardium*). However, some species and genera modified their ecology and partly adopted the epifaunal mode of life. Among Sarmatian lymnocardiines, very few species of the genera *Aviculocardium* and *Kubanocardium* were apparently capable (like living *Parvicardium*) of fixing itself by the byssus to the algae or branched bryozoan colonies. This life habit was especially common in areas where bioherms developed (Bagdasarian, 1978). At the same time, when these species lived on sandy-muddy or muddy bottom sediments outside bioherms, they obviously retained the ability to burrow into the sediment. It is quite possible that some thin-walled *Inaequicostates* species with ribs provided with long, slender, tubular, clawlike spines (e.g., *I. subfitoni*, *I. pius*, and *I. inopinatus*) were able to live on the surface of muddy sediments.

Some species of the genus *Planacardium* could probably burrow deeper than the other Sarmatian lymnocardiines, whereas some other could possibly fix itself by the byssus to bryozoan colonies (Bagdasarian, 1978).

The genera of the other tribes were even more ecologically diverse. Many of them retained the same life mode and feeding type as the members of the ancestral tribe Cerastodermatini; i.e., they were infaunal suspension feeders with well developed siphons. These are *Lymnocardium*, *Pontalmyra*, *Pseudocatillus*, *Macradacna*, *Tschaudia*, *Monodacna*, *Hyrcania*, *Didacnoides*, *Adacna*, etc. Some infaunal forms burrowed less deep than Cerastodermatini (*Paradacna*, *Apscheronia*, some *Pontalmyra*, etc.), and others, on the contrary, burrowed much deeper (*Hypanis*, *Adacna*, *Proso-dacnomya*, and some *Pseudocatillus*); these different life habits differently changed the shape and structure of the mollusc body.

Some other genera and species, chiefly suspension feeders, changed their ecology to occupy some niches equivalent to those held in marine basins by members of other families. Thus, several lymnocardiines came to live on the bottom (i.e., became epifaunal); some of

them apparently rested upon either of two valves (*Phyllocardium*, *Parvidacna*, and *Oraphocardium*), and others (recliners) leaned the anterior part of their valves on the substrate at an angle (most of *Prosodacna* species and also *Arcicardium*, *Plagiodacna*, and *Pachydacna*).

In the opinion of Akhvediani (1984), the representatives of the genus *Prosochiasta* possessed a powerful foot and were capable of active and rapid movement over hard substrate (coarse-grained sands and gravel).

The substrates and depths occupied by lymnocardiines varied with their modes of life. The shallow-water forms that lived on shelly-detritus, sandy, muddy-shelly, and muddy-sandy bottom sediments were represented by *Cerastoderma*, nearly all *Plicatiformes*, many of *Obsoletiformes*, and also *Phyllocardium*, *Caladacna*, *Oraphocardium*, *Stenodacna*, *Tschaudia*, *Eupatorina*, *Prosodacna*, *Plagiodacna*, *Pachydacna*, *Raricardium*, *Monodacna*, *Hyrkania*, *Didacnoides*, *Didacna*, most of *Lymnocardium* and *Pontalmyra*, etc. Confined to shallow but calm waters were *Planacardium*, *Pteradacna*, *Panticapaea*, *Macradacna*, *Prionopleura*, *Arcicardium*, *Acobaecardium*, and some *Plicatiformes* and *Obsoletiformes*. *Inaequicostates*, *Paradacna*, *Chartoconcha*, *Avicardiini*, some *Lymnocardium*, *Pontalmyra*, and *Pseudocatillus* lived at considerable depths on muddy bottom sediments. *Aviculocardium* and *Kubanocardium* were chiefly confined to biherms, which, in addition, were inhabited by many *Obsoletiformes* and some *Planacardium* species.

Lymnocardiines lived mainly in low-salinity waters. Only the genus *Cerastoderma* was able to survive in waters with salinity ranging from 5 to 70‰. The other genera were much less euryhaline. Sarmatian and Akchagilian lymnocardiines probably lived in water with a salinity of 10–18‰ and an ionic composition characteristic of seawater, whereas the Kozahurian and Pliocene (except for Akchagilian) genera were brackish-water, stenohaline forms living in low-salinity water the salt composition of which probably differed from normal seawater. Some members of the subfamily were able to live in nearly fresh water along with the euryhaline freshwater forms: *Macradacna*, *Eupatorina*, *Prosodacna*, *Prionopleura*, *Pachydacna*, *Apscheronia*, *Hypanis*, *Adacna*, some *Lymnocardium*, *Pontalmyra*, and *Pseudocatillus*.

Most lymnocardiines apparently lived, like the modern species, under the normal oxygen regime. Only the members of *Paradacna*, *Avicardiini*, and possibly *Chartoconcha* and some *Inaequicostates*, *Obsoletiformes*, and *Pseudocatillus* could tolerate a degree of oxygen deficit. It is difficult to judge the thermal preferences of lymnocardiines; most of them were probably eurythermal, and only some of the specific Kimmerian genera (*Panticapaea*, *Oxydacna*, *Macradacna*, *Prionopleura*, *Arcicardium*, and *Pachydacna*) and some Kimmerian species of the other genera might be thermophilic. The Akchagilian genera (except for *Cerastoderma*), which

inhabited only the southern part of the, apparently were to a certain degree thermophilic.

In the brackish-water and semimarine basins episodically connected to the open sea, lymnocardiines formed the main nucleus of benthic ecosystems confined to the zone of mobile suspension feeders, which in these basins often included the zone of sorting deposit feeders.

MAIN FEATURES OF LYMNOCARDIINAE EVOLUTION

Members of the subfamily Lymnocardiinae were the most flourishing group of Paratethyan bivalves during the periods of existence of semimarine (Sarmatian and Akchagilian) and brackish-water (Early Solenovian and Late Ottnangian–Kozahurian) basins that were episodically connected with the ocean and of nearly closed basins (Pannonian, Pontian–Kujalnician, and several Pleistocene ones). The character and rates of lymnocardiine evolution in the basins of the first two and of the third type differed essentially, and eventually, when the water salinity in these basins became either too high or too low, their lymnocardiine faunas went extinct.

The genus *Cerastoderma* or its direct descendants gave rise to numerous lymnocardiine genera (less often, similar forms evolved from *Parvicardium* ancestors). These new forms originated within several independent periods. There were at least seven such diversification events during the Oligocene–Pleistocene.

The fact that evolutionary rates considerably increased under conditions of periodic closure of the basins and rapid changes in their hydrological regime, which caused partial or complete elimination of the former malacofauna, was noted by many authors, including (in chronological order) N.I. Andrussov, V.P. Kolesnikov, L.Sh. Davitashvili, R.L. Merklin, and others (for references, see Neveeskaja *et al.*, 1986; Goncharova, 1989; Paramonova, 1994).

Such accelerated diversification at the species and higher levels was caused first of all by the disturbance of biocenotic relationships and subsequent forced reorganization of benthic ecosystems. Extinction of the majority of stenotopic species resulted in elimination of several ecological types characteristic of the normal marine basins (borers, free-living epifaunal forms, infaunal deposit feeders, etc.) and in modification of the trophic zonality typical of marine basins (Neveeskaja *et al.*, 1986). As a result, few progressive eurytopic forms (Merklin, 1966), which survived these sudden environmental changes, underwent rapid diversification, trying to occupy the ecological niches left vacant. The members of the genus *Cerastoderma*, ancestral to other lymnocardiines, were (like *Parvicardium*) shallow-burrowing and capable of moving along the bottom and provided with short siphons; well-developed hinges; and three-layered shells ornamented by closely-

spaced, rounded, or flattened radial ribs with tubercular ornamentation or scales. The periods of explosive endemic evolution give rise to genera that markedly deviated from the ancestral forms. Most of these genera were endemic and often specific (occurring only in a certain time interval). Lymnocardiines appearing in different time intervals are readily divided into parallel ecological groups that evolved through an adaptation to similar niches left vacant.

Most lymnocardiines (similar to nearly all marine cardiids) were shallow-burrowing infaunal suspension feeders (*Cerastoderma*, *Plicatiformes*, *Obsoletiformes*, *Raricardium*, etc.). In addition to them, different lymnocardiine lineages gave rise to both epifaunal forms and infaunal suspension feeders. Appearance of such adaptations (not characteristic of the other members of this family) in the closed basins was termed by Kafanov (1991) as "specialization beyond the limit."

The epifaunal suspension feeders included lymnocardiines lying on the substrate with a beak (markedly displaced anteriorly) directed downwards, having a thickened shell in the anterior part, and the anterior lateral teeth hypertrophied or a poorly developed hinge: *Eoprosodacna* (Late Ottnangian–Kozahurian), *Eupatorina* (Early Pontian), *Prosodacna* and *Prionopleura* (Late Pontian–Kimmerian), *Apscheronia* (Apscheronian), etc. Alate forms with thin-walled shells probably floated on liquid muddy sediment, possibly at quite great depths: *Andrusovicardium* and *Avicardium* (Akchagilian). Some suspension feeding species possibly used the method of deposit feeding as well after stirring the silt up with their siphons, like modern *Didacna* (Romanova, 1963).

The appearance of forms with flattened and oblong shells being a weakly projecting beak, weakened ribs, and reduced hinges (*Limnopappia* in the Late Ottnangian, *Planacardium* in the Sarmatian, and *Phyllocardium* in the Late Pontian–Kujalnician) and forms with a deep pallial sinus (*Adacna* and *Hypanis* in the Pleistocene and now) indicates the deep-burrowing infaunal life mode.

Phylogenetically diverse species with similar life habits evolved similar morphologies in different basins. Thus, eight pairs of homeomorphic forms are evident among Sarmatian and Akchagilian lymnocardiines (Paramonova, 1994). However, many examples of such heterochronous homeomorphy in unrelated taxa cannot be explained by their ecological peculiarities alone, thus demonstrating the morphological limits of evolution. It was noted that the transformation of the hinge, ornamentation (Neveeskaja, 1967), microstructure of the outer shell layer, and inner structure of ribs (Popov, 1977) evolved in the lymnocardiine lineages in the opposite direction of the ontogenetic development of these characters in both cerastoderms and parvicardiines: adult forms retain the characters observed only at the early ontogenetic stages in their ancestors.

Such fetalization phenomena were noted in the development of ornamentation in Sarmatian *Plicatiformes* (Neveeskaja, 1950, 1967); microstructure of the outer shell layer and inner structure of ribs in several Solenovian, Kozahurian–Ottangian, Akchagilian species of *Cerastoderma* (Popov, 1977); and the ontogenetic transformation of the hinge in the Pontian *Ora-phocardium* (Ebersin, 1962) and the species of *Cerastoderma* and *Parvicardium*.

In the detailed study of shell ontogeny in *Cerastoderma* spp. by Popov, it was shown that in water of normal salinity, the shell in this genus is three-layered and has a fully developed hinge. In ontogeny, the posterior cardinal tooth and posterolateral teeth of the left valve and the upper posterolateral tooth of the right valve appeared later than the others. In the species living in low-salinity waters, the teeth were reduced; in this case, teeth equivalent to those that appeared last in the forms with a fully developed hinge disappeared (i.e., ceased to develop) first. The outer shell layer in the species that lived in low-salinity water appeared later than in those that lived in normal marine environments.

Subsequent transformations resulted in the morphological separation significant enough to rank these derived taxa as endemic genera. At this stage, the shell is usually two-layered, but it still retains the pattern of composite internal ribs. The intercalary ribs (appearing 0.5–0.6 mm away from the beak of *Cerastoderma glaucum*) occur only on shells with a size as large as several millimeters and often remain less developed than the primary ribs. Remnants of the reduced outer layer often form a peculiar ornamentation consisting of scales, which are better developed on the anterior area on the carinal rib or the posteriormost rib of the posterior area. This structure is characteristic of the members of *Limnopagetia*, *Chokrakia brykense*, many of Sarmatian cardiids, and some *Lymnocardium* and *Didacnoides*.

At the next stage of the lymnocardiine evolution, the reduction involved the anterior cardinal tooth in the right valve and the anterior lateral tooth in the left valve. These teeth appeared in the ontogeny of *Cerastoderma glaucum* when the size of the shell reached 0.4–0.8 mm. The intercalary ribs did not develop at all; the primary ones remained widely spaced and triangular in cross section or poorly developed with a simple inner structure (growth lines parallel to the outer surface). These characters (or some of them) are found in Solenovian *Merklincardium*, Kozahurian–Ottangian *Limnopappia*, and Miocene–Pliocene *Pseudocatillus*, *Pontalmyra*, and *Oxydacna*.

Finally, the most modified lymnocardiines in this direction [*Eoprosodacna* (Kozahuria), *Planacardium*, *Aviculocardium*, *Apscheronia*, *Adacna*, *Paradacna*, *Arcicardium*, *Chartoconcha*, *Avicardium*, *Andrusovicardium*, and *Acobaecardium*] are characterized by a completely reduced hinge (or at most with only poorly-developed cardinal teeth present) and a smooth shell or by widely spaced triangular ribs.

This type of evolution based on fetalization probably played an important role in lymnocardiine history. This evolutionary mode possibly allowed more rapid morphological despecialization and the development of innovations beyond the cardiid limit, such as long siphons (as indicated by the presence of the pallial sinus and shell gape), alate (pteroid) shell, epifaunal forms leaning their beaks on the substrate (recliners), etc.

This development was doubtlessly canalized, forced, and brought about by the environmental changes. This is evident from the fact that, in similar conditions, the directions of development were similar in every instance when marine cerastoderms found themselves in a brackish-water basin.

In semimarine and brackish-water basins episodically connected to the open sea, the patterns of lymnocardiine evolution and their diversification rates differed considerably from those in the nearly closed basins of the Paratethys.

Semimarine and brackish-water basins episodically connected to the open sea. These basins may show the earliest stages in the formation of endemic genera and often also the coexistence of these endemics with their marine ancestors. Each disturbance of the normal marine regime that caused the extinction of stenotopic forms and even of entire ecosystems resulted in an abrupt increase in the variability and in the rate of diversification. New taxa sympatrically appeared through occupation of vacated ecological niches; the extent of such diversification depended on the duration and character of basin isolation from the open sea and on the taxonomic diversity of survivors of the former marine fauna. Diversification was usually gradual, often through fetalization. Transitional, less advanced forms sometimes persisted, making taxonomic considerations difficult and subdivision of the phyletic lineages into species very subjective. Such evolutionary patterns are observable in the Oligocene Solenovian basin, Late Ottnangian (Bavarian material) and Kozahurian basins, at the end of the Early Chokrakian, and in the Early-Middle Sarmatian and in the Akchagilian.

In addition to some common features, these basins show specificity in lymnocardiine development. Thus, the early developmental stages of the Kozahurian fauna remains unknown. It is possible that this was a fully formed faunal group when it came from the Ottnangian basin. The early developmental stages of the Solenovian and Sarmatian fauna probably took place in the lagoons of the pre-existing Pschekhian and Badenian-Konkian basins.

In such basins, the evolution proceeded at a moderate rate, the number of supraspecific taxa increased slowly, and the characters of specialization beyond the limit were uncommon.

Brackish-water, nearly closed basins. As a rule, basins of this type (Pannonian, Pontian-Kujalnician, and Apscheronian-Pleistocene Caspian Sea) signify a further stage of basin closure and therefore their fauna

developed from the fauna endemic to the basins discussed in the previous section. In the nearly closed basins, the rate of diversification; number of endemic species, genera, and tribes; and the importance of cardiids in the communities increased. So, the Portaferrian-Kimmerian basin, the lifespan of which approximates that of the Early-Middle Sarmatian basin (2.5-3 Ma), gave rise to more than 20 genera, whereas the Sarmatian basin only gave rise to 5 genera. Ancestral cerastoderms usually went extinct in these basins.

In addition to the characters formed through fetalization (reduction of the hinge and outer shell layer, simplification of the rib structure, etc.), some new features not typical of marine cardiids were acquired: the disproportional development or hypertrophy of some hinge elements, alate shell, and formation of the pallial sinus. The gradual formation of these atypical characters was not really unusual even when associated with the formation of new genera (Ebersin, 1959, 1962, 1967; Neveeskaja *et al.*, 1987). In this case, the early stages of evolution of a supraspecific taxon often gave rise to quite diverse forms, the variability of which exceeded that of later members of this taxon. Such an archaic diversity occurred in the Early Pontian *Pseudocatillus*, *Pontalmyra*, *Euxinocardium*, Apscheronian *Monodacna*, etc. (Neveeskaja *et al.*, 1987).

Less often, new taxa appeared suddenly, and their ancestry can only tentatively be decided (*Prionopleura* in the Kimmerian, *Caspicardium* in the Apscheronian, etc.). In two instances, a cryptogenic phase at the beginning of development of a new lymnocardiine assemblage can be identified (Pannonian and Apscheronian stages): the intermediate beds contain rare, small forms with thin-walled shells, which cannot be assigned to any genus without doubt. Subsequently, a burst of diversification took place, including the appearance of new genera and subgenera of uncertain origin (their immigration from another basin was impossible).

ISSUES OF LYMNOCARDIINAE SYSTEMATICS

The extensive fossil material, often containing complete phyletic series, allows one to reconstruct the course of lymnocardiine evolution in much detail, and, on the other hand, obstructs attempts to fix this dynamic pattern in a static framework of the system of this group. As demonstrated above, the subfamily Lymnocardiinae (in which we and our predecessors include the whole diversity of brackish-water cardiids) is neither mono- nor even paraphyletic: its members originated repeatedly from different ancestors and in different basins. The somewhat artificial assignment of the genus *Cerastoderma* to Lymnocardiinae cannot change the situation, because the features characteristic of the subfamily could be attributed to *Parvicardium* ancestors. Although the members of Lymnocardiinae could be, for all practical purposes, rather easily and reliably distinguished from marine cardiids (and much more easily from the members of the other bivalve families)

owing to their unique combination of characters, it is extremely difficult to diagnose this subfamily formally. The characters beyond the limit make this diagnosis very broad.

The same difficulties appear when discriminating between tribes and genera. Strict adherence to the principle of grouping individual lineages into taxa based solely on a common origin will result in the failure to determine such taxa and to find differences between them, in an overly divided, extremely unstable, and subjective system. Thus, the proposed system of lymnocardiines is constructed on the basis of similarity and differences, but the phylogenetic data are also taken into account. It is on the basis of phylogeny that the tribes (Fig. 1) were separated, although due to numerous cases of homeomorphy, it is quite difficult to trace individual lineages unless separated by considerable time intervals.

The first tribe distinct from Cerastodermatini originated from *Cerastoderma* in the Solenovian (tribe Merkliniardiini). In the Ottnangian-Kozahurian, the tribe Linnopappiini also descended directly from *Cerastoderma*. The third tribe, Plicatiformini, probably descended in the Karagantian from the genus *Cerastoderma* that inhabited the Middle Miocene seas of the Paratethys. As mentioned above, the tribe Obsoletiformini, which originated in the Konkian, is possibly polyphyletic. In the Sarmatian, this tribe gave rise to the genera *Kubanocardium* and *Aviculocardium*, which was separated into the tribe Aviculocardiini. Tribe Plicatiformini gave rise in the Sarmatian to the genus *Planacardium*, which was separated into the tribe Planacardiini.

The tribe Lymnocardiini, which appeared in Pannonian-Messinian time, most probably descended from the Sarmatian Plicatiformini and Obsoletiformini, although its origin is impossible to trace. Most genera of this tribe are phylogenetically related to each other, but the origin of some of them remains uncertain; however, the genera *Euxinocardium* and *Helenicardium* undoubtedly descended directly from *Cerastoderma* in the northern regions of the Messinian Sea. Nevertheless, these genera should be included in the same tribe because of their structural similarity.

The tribes Phyllocardiini, Paradacnini, and possibly Arcicardiini, as well as Lymnocardiini, probably originated from different species of the tribe Plicatiformini; the tribe Prosodacnini, from *Cerastoderma* in the freshened parts of the Messinian Sea; and the tribe Pachydacnini, from Lymnocardiini.

As for the tribe Pontalmyrini, the region of its origin is disputable (see the above discussion about the genus *Pseudocatillus*). It is quite possible that this tribe is polyphyletic, but it should remain undivided, because its earliest genera, which originated in separate regions, were too morphologically similar.

The tribes Acobaecardiini and Avicardiini originated in the Akchagilian Caspian Basin from *Cerasto-*

derma; the youngest tribe, Adacnini, probably likewise originated from the Akchagilian *Cerastoderma*, although it may turn out to be polyphyletic.

Thus, the morphological and phylogenetic approaches are combined in the practice of classifying the taxa at the tribal and (sub)generic level. Even so, considerable difficulties remain in diagnosing the taxa, because different diagnoses often include the same homeomorphically similar characters appear. Following the principle of strict monophyly will make it impossible to classify (i.e., discriminate) individual taxa, since their diagnoses absolutely coincide in many instances. It is especially true of synchronously occurring taxa that probably descended from the same ancestors but in the separate basins. On the other hand, very similar heterochronous taxa, the appearances of which were separated by a considerable time interval, are treated as independent (e.g., tribes Linnopappiini and Prosodacnini).

SYSTEMATIC PALEONTOLOGY

CLASS BIVALVIA

Order Venerida

Suborder Venerina

Superfamily Cardioidea

Family Cardiidae Lamarck, 1809

Subfamily Lymnocardiinae Stoliczka, 1870-1871

Lymnocardiinae: Stoliczka, 1870-1871, p. 205; Popov, 1977, p. 67; Kafanov and Popov, 1977, p. 60.

Lymnocardiidae: Keen, 1969, p. 590.

Lymnocardiinae: Ebersin, 1965a, p. 12, 1967, p. 11; Taktakishvili, 1987, p. 11.

Diagnosis. Shell equivalve, of various shape, radially ribbed, rarely smooth, closed or gaping, with prosogyrate beak. Ribs smooth, rarely scaly, from prominent to obsolete. Fully developed hinge with cardinal teeth in each valve, duplicate anterior and posterolateral in right valve, and single anterior and posterior in left valve. Usually, some teeth reduced, sometimes lacking at all; some teeth hypertrophied. Ligament external, opisthodontic, on nymph behind beak. Adductor scars subequal. Pallial line entire or with sinus. Inner surface usually radially sulcate, rarely smooth. Shell usually two-layered due to outer layer of composite prismatic structure reduced, sometimes three-layered.

Composition. Tribes: Acobaecardiini Paramonova, 1986; Adacnini Vest, 1875; Arcicardiini Neveesskaja, 1986; Avicardiini Popov, 1977; Aviculocardiini Paramonova, tribus nov.; Cerastodermatini Nordsieck, 1969; Linnopappiini Schlickum, 1962; Lymnocardiini Stoliczka, 1870-1871; Merkliniardiini Popov, tribus nov.; Obsoletiformini Paramonova, tribus nov.; Pachydacnini Andreescu, 1975; Paradacnini Ebersin, 1965; Phyllocardiini Neveesskaja, 1986; Planacardiini Paramonova, tribus nov.; Plicatiformini Paramonova, tribus nov.; Pontalmyrini Taktakishvili, 1987; Prosodacnini Andreescu, 1974; and Pseudocardiini Ebersin, 1965.

Comparison. From the other subfamilies, differs mainly in the reduction or hypertrophy of some teeth; usually, in the absence of ornamentation on the ribs and in the reduction of the outer shell layer; and, in several cases, in the presence of a more or less developed pallial sinus.

Occurrence. Oligocene–Recent. Europe, Asia. Recent representatives, in the Atlantic Ocean and the North, Baltic, White, Barents, Mediterranean, and Black seas, the Sea of Azov, Caspian, and Aral seas.

Tribe Cerastodermatini Nordsieck, 1969

Cerastodermatini: Nordsieck, 1969, p. 98; Kafanov and Popov, 1977, p. 60.

Diagnosis. Shell orbicular, ovate, orbicular- or ovate-triangular, quadrangular, or trapezoidal, more or less convex, weakly to considerably inequilateral, closed. Outer surface radially ribbed (rarely anterior ribs poorly developed), ribs smooth or scaly. Hinge with two cardinal, one or two anterior and posterolateral teeth in right valve, and one or two cardinal and single anterior and single posterolateral teeth (the posterior one sometimes absent) in left valve. Pallial line entire. Shell usually three-layered.

Composition. *Cerastoderma* Poli, 1795; *Korobkoviella* Merklin, 1974; and *Raricardium* Paramonova, 1986.

Comparison. From all other tribes, differs in having almost equally developed cardinal and lateral teeth; from some tribes, in the absence of pallial sinus.

Occurrence. Same as for the subfamily.

Genus *Cerastoderma* Poli, 1795

Cerastoderma: Poli, 1795, p. 252.

Cardium (*Cerastoderma*): Mörch, 1853, p. 34; Korobkov, 1954, p. 118; Neveeskaja, 1963, p. 59.

Cerastoderma: Cossmann and Peyrot, 1911, p. 476; Keen, 1969, p. 590; Merklin and Neveeskaja, 1974, punchcard 32; Popov, 1977, p. 68; Neveeskaja *et al.*, 1997, p. 141.

Type species. *Cardium edule* Linné, 1758; Recent, northeastern Atlantic Ocean.

Diagnosis (Fig. 10). Shell orbicular- to ovate-triangular, ovate, or ovate-trapezoidal; moderately to considerably convex; more or less inequilateral; closed; very rarely gaping; with a more or less projecting beak and variably developed posterior ridge. Outer surface radially ribbed (rarely, ribs weakly raised anteriorly). Ribs rounded convex, rarely angulate in cross section or flattened, usually scaly, sometimes with closely spaced longitudinal grooves. Hinge with two cardinal, two anterior lateral, and one or two posterolateral teeth in right valve, and one or two cardinal and single anterior and single posterolateral teeth (the posterior one sometimes absent) in left valve.

Composition. *C. altum* (Tscheltzov, 1965); *C. ammoni* (Rzehak); *C. andariformicum* Popov, 1982; *C. arcella* (Dujardin, 1837); *C. azerbaijanicum* (Alizade,

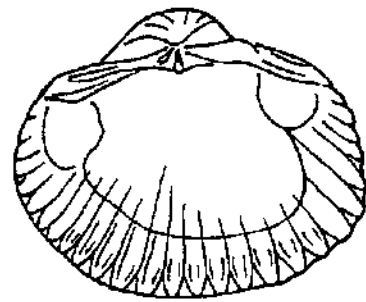


Fig. 10. *Cerastoderma* (beginning with this figure, figures represent, unless specified otherwise, schemes of the inner surface of valve).

1932); *C. arcaense* (Bel.); *C. bavarica* (Ammon); *C. chersonense* (Nossovsky, 1962); *C. concameratum* (Hözl, 1957); *C. davidaschvili* (Kolesnikov, 1950); *C. dombra* (Andrussoff, 1902); *C. edule* (Linné, 1758); *C. galidzgenense* Neveeskaja, 1976; *C. ganssi* Schlickum, 1970; *C. glaucum* (Poiret, 1789); *C. ivericum* Popov, 1983; *C. karaschokense* Merklin, 1974; *C. karelini* (Andrussoff, 1902); *C. konschini* (Andrussoff, 1902); *C. lacustre* Popov, 1983; *C. macedonicum* Neveeskaja, 2000; *C. modelli* (Schlickum, 1970); *C. mutabile* Popov, 1982; *C. prigorovskii* (Bogachev, 1959); *C. samodurovi* Merklin, 1974; *C. sanani* (Ali-Zade, 1967); *C. schmiereri* Schlickum, 1970; *C. serogosicum* (Nossovsky, 1962); *C. siphonophorum* (Andrussoff, 1902); *C. sociale* (Krauss, 1852); *C. stephani* Schlickum, 1966; and *C. zhuzhunae* Popov, 1982.

Comparison and remarks. Differs from *Raricardium* in having a greater number of closely spaced ribs, from *Korobkoviella*, in having well-developed posterolateral teeth and both the anterior part of the hinge plate and the anterior lateral teeth not thickened. In shell form and ribbing pattern, resembles members of other tribes, in particular *Obsoletiformes* (tribe *Obsoletiformini*) but differs from them in having a more fully developed hinge and, usually, a three-layered shell. From *Bosphoricardium* (tribe *Lymnocardiini*), differs in having less developed anterior lateral teeth and, usually, a three-layered shell.

Occurrence. Same as for the subfamily.

Genus *Korobkoviella* Merklin, 1974

Cerastoderma (*Korobkoviella*): Merklin, 1974, p. 97.

Korobkoviella: Popov and Titova, 1982, p. 43.

Type species. *Cerastoderma* (*Korobkoviella*) *kiktenkoi* Merklin, 1974; Oligocene, Serogozky Beds, Dnepropetrovsk Region, Southern Ukraine.

Diagnosis (Fig. 11). Shell orbicular, orbicular-triangular, ovate, trapezoidal, weakly convex, weakly to moderately inequilateral, closed, with slightly projecting beak and distinct (but not sharp) posterior ridge. Ribs numerous (30 or more), poorly developed, weakly raised anteriorly, adcarinal ones asymmetrical and ridge-like. Hinge with two cardinal teeth in each valve,