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(Gastropoda Pectinibranchia Viviparitormes)

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GENERIC COMPOSITION OF THE FAMILY VIVIPARIDAE

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The cosmopolitan freshwater molluscan family Viviparidae is usually considered to be widespread on all of the continents (except South America) and is known from paleontological studies to be from the Carboniferous period. In the last century the majority of Recent and extinct species of the family were attributed to the genera Viviparus or Paludina. Later, the living species, mainly Asian and African, were classified in a considerable number of genera (for a listing of these taxa and their distribution, see Starobogatov, 1970). Even several North American species were assigned to separate genera in the past. During the third decade of this century the division of the family into three subfamilies, Lioplacinae (= Campelominae), Viviparinae, and Bellamyinae, took place. Within this division, the majority of the genera of the family fall into the last subfamily - it includes all of the genera which are widespread in the east and south of Asia and in Africa; three genera from North America are in the subfamily Lioplacinae; and there are four from

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Europe and North America in the subfamily Viviparinae, while one of these genera (Scalez) is attributed to the viviparids with uncertainty. Until now the majority of the extinct forms from Europe and North America was included not only in the subfamily Viviparinae, but also, obviously, by tradition, in the genus Viviparus (see, for example, Wenz, 1928, 1938-1944; Franz, 1932). It was recently demonstrated (Sitnikova and Starobogatov, 1982) that the anatomical differences of representatives of these three subfamilies are so great that one is compelled to give to each of them the rank of an independent family; the family Bellamyidae is higher in the superfamily and more flourishing while the Viviparidae and Lioplacidae are sufficiently archaic in morphological features and obviously ancient. It was also made clear that both latter families possess such a set of archaic and progressive features that it may be concluded that their common ancestor cannot be attributed to either one or the other, but both undoubtedly belong to the superfamily Viviparoidea. This hypothetical progenitor like the Lioplacidae but in contrast to the Viviparidae particularly, did not have an ejaculatory chamber. Similarly, like the Viviparidae, but unlike the Lioplacidae, it did not have a prostate gland; the operculum like Lioplax but differing from the rest of the Viviparoidea, had a spiral nucleus - it was possibly even completely spiral; whereas the shell, like that of several Viviparidae, but in contrast to the Lioplacidae, was trochoidal in shape.

The considerable age of the family Viviparidae (here in the modern, more narrow sense) confirms that the diversity of extinct forms still exceeds that of contemporary forms by a good deal. This compels us to give a new survey of the generic composition of the family, taking into consideration both the extinct and modern-day forms. We do not make it our task to give here diagnoses of all the genera of the family, especially as many of them are well-known, but only to survey selected genera and subgenera, with an indication of their geographic and stratigraphic distribution, as well as with a basic synonymy and information regarding the type-species. We exclude from this survey only the genus Scalez Hanna and Gaylord, 1924, which on the basis of the presence of a calcified operculum we ascribe to the family Bithyniidae (Order Littoriniformes). Undoubtedly, this same superfamily Bithynioidea is related though it is not clear which of the families to the lower Carboniferous freshwater mollusk Bernicia praecursor Cox; evidence for this conclusion is based on its very small shell (height approximately 3 mm with 3.5 - 4 whorls), which is extremely similar to the shell of several amnicolids.

Information about the "viviparids" of Europe, which were discovered in deposits from the Carboniferous period through the lower Cretaceous (inclusive), is currently insufficient for generic, and even at times for familial evaluation. In particular, Viviparus carbonarius Garw., described from the lower

Carboniferous deposits of England, has a fairly small (up to 14 mm high) thin-walled form, which may be attributed in equal measure to both the superfamily Viviparoidea and to the superfamily Bithynioidea. It is more similar to the specimens of V. langtonensis (Hudlest.) from the Jurassic deposits of England; however it is now premature to consider even its systematic position. Other Jurassic species, like V. scoticus Tate from the Hebrides Islands and V. aurelianus (Cossm.) from France, more likely than all the others, do not belong to this superfamily. The former species is more plausibly considered to be a representative of the Valvatidae, and the latter, most likely, is related to the family Lymnaeidae, even to the genus Lymnaea. The lower Cretaceous V. fluviorum Mantel is very similar to V. carbonarius, and similarly may also be attributed to either the Viviparoidea and to the Bithynioidea. Finally, the upper Cretaceous V. novemcostatus (Math.) and related forms, such as V. cingulatus (Math.), V. subcingulatus (Sandb.), V. mazeli (Roule), and V. filicinctus Franz, in our view, judging by the features of the shape of the shell (on which we will briefly touch at the end of the article) belong to the family Lioplacidae in a special genus.

Scalipaludina Starobogatov gen. n.

(type-species Paludina novemcostata Matheron, 1842[1] - Fig. 1)

Diagnosis. Shell tall (so that [the ratio of] the width of the last whorl above the aperture consists of .65 - .75 parts of the

height from the aperture to the apex), subscalar with strongly protuberant whorls that have spiral ribs; the latter number 2 to 3 on the whorls of the spire, with the highest of these standing out the most, and number 9 to 11 on the body whorl. The aperture is of the narrow slit type.

Upper Cretaceous France and FRG [Federal Republic of Germany].

We first encounter authentic specimens of the Viviparidae only in upper Cretaceous deposits, although it is possible the family arose earlier. We take up the following genera of the membership of the family Viviparidae.

Paluditrochus Cossmann, 1921[2]

(type-species Paludina trochiformis Meek and Hayden, 1857[3] - Fig. 2)

Upper Cretaceous to Paleocene of North America. Species from the Triassic and Jurassic of North America are also included in this genus, but their generic membership is in need of more precise definition.

Tulotomops Wenz, 1939

(type-species Tulotoma thompsoni White, 1875[4] - Fig. 3)

Upper Cretaceous USA (states of Utah and Colorado).

Trochopaludina Starobogatov gen. n.

(type-species Phasianella angulosa Sowerby, 1818[5] - Fig. 4)

Diagnosis. A trochoidal or more highly conical shell with flat

whorls, which are separated by shallow sutures and with rounded corners on the periphery of the body whorl; the sculpturing is of spiral lines (about 7 on the penultimate whorl, that is, above the peripheral corner).

Eocene to Oligocene of England and France.

Viviparoides Starobogatov gen. n.

(type-species Helicites viviparoides Schlotheim, 1820 - Fig. 6)

Diagnosis. Shell from highly conical to turbinate, with moderately prominent whorls, sometimes shoulder sutured; sculpturing of thin spiral ribs (approximately 6 on the penultimate whorl), but sometimes not noticeable; umbilicus slit-shaped, aperture roundly quadrate.

Eocene to Miocene FRG [Federal Republic of Germany] and France.

Viviparus Montfort, 1810

(type-species Helix vivipara Linnaeus, 1758[6] - Fig. 7)

Synonymy:

Paludina Férussac, 1812 (type-species Helix vivipara Linnaeus, 1758[7]).

Vivipara Sowerby, 1813 (type-species Helix vivipara Linnaeus, 1758[8]).

Paludinum Jurine, 1817 (type-species Helix vivipara Linnaeus, 1758[9]).

Henterum Hübner in Menke, 1848 (nom. subst. pro Paludina (type-species Helix vivipara Linnaeus, 1758[10]).

Gallandiana Bourguignat, 1880 (type-species Paludina mamillata Küster, 1852 = Paludina atra Christophori and Jan, 1832[11]).

Acerosiana Bourguignat, 1880 (type-species Vivipara acerosa Bourguignat, 1862 = Paludina atra Christophori and Jan, 1832[12]).

Fasciatiana Bourguignat, 1880 (type-species Nerita fasciata Müller, 1774 = Helix vivipara Linnaeus, 1758[13]).

Duboisiana Bourguignat, 1880 (type-species Paludina duboisiana Mousson, 1863 = Helix vivipara Linnaeus, 1758 or an inland form of this species[14]).

Sphaeridiana Bourguignat, 1880 (type-species Vivipara sphaeridia Bourguignat, 1880 = Paludina atra Christophori and Jan, 1832[15]).

Subgenus Viviparus s. str.

Miocene FRG [Federal Republic of Germany] and France, Pliocene southern half of Europe; present - Europe (except the north), east and south Black Sea coast.

Subgenus Balcanipaludina Starobogatov subgen. n.

(type-species Paludina hellenica Clessin, 1879 - Fig. 8)

Diagnosis. Shell (in contrast to the nominate subgenus) always with strongly compressed or completely flat whorls and straight or nearly straight tangential lines (that is, touching the outside points of contour of all whorls with one of the sides of the shell).

Pliocene of southern Europe; Recent in western Balkan peninsula.

Subgenus Protulotoma Annandale, 1924[16]

(type-species Paludina dezmaniana Brusina, 1874 - Fig. 9)

Pliocene Danube-area countries.

Galizgia Michailowski, 1903[17]

(type-species Vivipara weberi Michailowski, 1903 - Fig. 10)

Synonymy:

Suchumica Seninski, 1905 (type-species Suchumica gracilis Seninski, 1905[18] = Vivipara weberi Michailowski, 1903).

Subgenus Galizgia s. str.

Pliocene eastern Black Sea coast.

Subgenus Palaeotaia Annandale, 1924

(type-species Paludina vukotinovici Frauenfeld, 1864[19] - Fig. 11)

Pliocene Danube-area countries.

Subgenus Semipaludina Starobogatov subgen. n.

(type-species Paludina ventricosa Sandberger, 1875 - Fig. 5)

Diagnosis. Turbiniform with very weakly protuberant whorls and fairly clear-cut, though roundly angled on the periphery of each whorl, while this angle is smoothed out as a measure of the growth of the whorls; if the lower side of each whorl presses against the previous one, the angulation is not noticeable; the

sculpture consists of the thinnest spiral lines.

Pliocene France.

Euxinomargarya Akhvledianai, 1957

(type-species Vivipara[20] mandarinica Seninski, 1905 - Fig. 12)

Synonymy:

Carinia Lörenthey, 1906[21] non Kieffer, 1905 (type-species Vivipara rothi Lörenthey, 1906[21]).

Pliocene of eastern Black Sea coast and Hungary.

Syriomargarya Starobogatov gen. n.

(type-species Vivipara syriaca Pallary, 1939[22] - Fig. 13)

Diagnosis. Shell turreted with three spiral knobby carinae on the periphery of the whorls; on the last whorl two more sub-basal and four to five basal carinae are added; the umbilicus is closed, the mouth has a rounded parietal-palatal angulation.

Pliocene of eastern Greece and Rhodes island(s), Pleistocene Syria.

Sculptopaludina Starobogatov gen. n.

(type-species Viviparus clairi Schlickum and Puisségur, 1977 - Fig. 14)

Diagnosis. Shell turbinate with a sharp apex, which is formed by the narrow first whorls; there are up to three sharp spiral carinae on the periphery of the whorls; the surface of the shell between them is compressed or concave.

Pliocene to Pleistocene of France and Italy.

Contectiana Bourguignat, 1880

(type-species Cyclostoma contectum Millet, 1813 - Fig. 15)

Synonomy:

Lacustriana Bourguignat, 1880 (type-species Vivipara lacustris Beck, 1846 = Cyclostoma contectum Millet, 1813).

Pliocene Europe; Recent - all Europe and southwestern Siberia (up to the Ob river bed in the East).

Tulotoma Haldeman, 1840

(type-species Paludina magnifica Conrad, 1834 - Fig. 16)

Recent Coosa River Basin (upper part of the Alabama River basin, U.S.A.).

Leapaludina Starobogatov gen. n.

(type-species Paludina georgiana Lea, 1834 - Fig. 17)

Diagnosis. Shell conical or highly conical, relatively small for a representative of the family, with moderately and uniformly protuberant whorls which are divided by fairly deep sutures; these same sutures divide the whorls of even the embryonic shell; the periphery of the last whorl is rounded; the sculpturing consists only of lines of growth and unclear spiral lines; the tangent-line of the shell is nearly straight; the aperture has a clearly expressed parietal-palatal angulation.

Cretaceous to Recent eastern U.S.A. and southern Canada.

Callinina Thiele, 1931

(type-species Paludina intertexta Say, 1829 - Fig. 18[23])

Synonymy:

Callina Hannibal, 1912 non Lowe, 1855 (type-species Paludina intertexta Say, 1829).

Recent eastern U.S.A.

In the course of the evolutionary development of the family Viviparidae the following transformations of the form of the shell may be revealed. One change is the gradual transformation of the shell from the initial trochoidal form into the "paludinal" shape characteristic of the modern-day viviparids. While this occurs the three principle spiral ribs are gradually smoothed out (especially the two upper ones) and from these remain only the spiral lines, covered with periostracal small spikes on the embryonic shell. Even the peripheral carina separating the compressed basal surface smooths out as well, the basal surface meanwhile becoming rounded. All of these changes may be traced along the morphological lines Paluditrochus[2] - Trochopalùdina - Viviparoides and (the shorter line) Paluditrochus[2] - Leapaludina. It is difficult to discuss the reason for this transformation, but it is possible that it lies in the transition from life in oligotrophic lakes to life in the currents of rivers, which was characteristic of many freshwater groups during the period from the middle Cretaceous to the early Palaeogene. The second transformation is the increase in the prominence of the whorls and the further thinning of the walls of

the shell. This transformation is traced along the lines Viviparus (Balcanipaludina) - Viviparus (Viviparus) - Sculptopaludina - Contectiana and Leapaludina - Callinina. It is likely that even this transformation can be connected with the concurrent change to this tendency: the species of Viviparus are fluvial and in significant measure rheophylic forms; the more hard-walled species from the genus Contectiana such as C. turrita (Kob.) or C. fennica (Kob.), are already characteristic of lakes, while the thin-walled species, like C. contecta (Millet) or the well-known C. listeri (Forbes and Hanley) (= Viviparus contectus auct. non Millet), are characteristic of the smaller continual reservoir type of pond. The third transformation, the new reinforcement of two spiral carinae (the highest ones - under the suture and periphery) with the formation of a compressed or concave section between them, by now is characteristic of only the Pliocene viviparids of the Pannonia Basin and connected parts of the hydrographic system of southeast Europe. This transformation is expressed by the lines Viviparus (Balcanipaludina) - V. (Protulotoma). The strengthening of only the most peripheral carina found striking expression in the shell of Galizgia. The fourth transformation, again coming independently to the European and American genera, was the appearance of bumps on the carinae. This can be traced along the lines Paluditrochus[2] - Tulotomops - Tulotoma and with the bounds of the subgenus Protulotoma of the genus Viviparus. One should note that the characteristic sculpturing of Syriomargarya cannot

be drawn directly from the sculpturing of the representatives of the subgenus Protulotoma, and these groups, contrary to common opinion, are not directly related to one another. It is more plausible to take this genus from the Euxinomargarya, which is closer in the shape of the shell and in the number and sculpturing of the formation of the carinae. It was characteristic that the formation of the bumps on the carinae evolved in the European and American forms on a slightly different basis, and, undoubtedly, at a different time. At this time it is difficult to say which ecological causes brought about the last two transformations.

This survey allows one to compare the principle tendencies of change of the shells of the Viviparidae and Lioplacidae, which may help in the evaluation of the systematic position of extinct forms. If, as was said above, the basic direction of evolution of the Viviparidae is from a trochoidal shell to the "paludinal," the compression of the upper two spiral ribs and then of even the peripheral carina, and after this to the increased protuberance of the whorls, then the Lioplacidae shell (also, probably, from the trochoidal) became highly conical and oval-conical, retaining the subsutural rib in the earliest stages (and of the shoulder above it, or, at least, of only the shoulder) and retaining the early disappearance of the peripheral carina. In the future the whorls of the shell may become more pronounced, and all spiral sculpturing elements may disappear. These observations compel us to ascribe the genus Scalipaludina to the family Lioplacidae.

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EDITORIAL FOOTNOTES

[1]This is an error; the original binomen is Cyclostoma novemcostata; the correct date is 1832 (see Matheron, 1832; and Sherborn, 1922-1933: 4426); consulting the illustration and description given by Oppenheim (1895: 328, pl. 16, figs. 26-28), one would judge that the line-cut drawing by Starobogatov scarcely represents the type-species.

[2]The correct spelling is Paludotrochus; the type-species was by original designation (see Cossmann, 1921: 185).

[3]The correct date is 1856 (see Ruhoff, 1980: 75).

[4]The correct date is 1876 (see White, 1876: 104, 134); the type-species was by original designation (see Wenz, 1939: 491).

[5]The correct date is 1817 (see Sherborn, 1922-1933: 322); Wenz (1928: 2288) also gave the date 1818.

[6]The correct type-species is, by original designation (Montfort, 1810: 246-7) Viviparus fluviorum Montfort 1810 [= Helix vivipara Linnaeus 1758].

[7]Although Férussac (1812: 253) attributed the name Paludina to Lamarck, he himself is the author; he listed three species by

name; the type-species was given as P. vivipara (= Helix vivipara Linnaeus 1758) by Children (1823: 245); see also Kennard, Salisbury and Woodward (1931: 23).

[8]Vivipara J. Sowerby 1813 can be considered an error for or emendation for Viviparus Montfort 1810 and therefore doesn't have its own type-species, besides Sowerby (1813: 77) did not list H. vivipara Linnaeus 1758 by name.

[9]Jurine (1817: 34) simply listed four names under this spelling, the first being P. viviparum; thus, the generic name appears to be a modification in the spelling of Paludina Férussac 1812 and it can be considered as an emendation not needing its own type-species.

[10]Henterum (Hübner ms) was not described but is a name proposed as a synonym of Paludina (Menke 1848: 56) and therefore not in need of its own type-species.

[11]Gallandiana has as its type-species Vivipara gallandi Bourguignat 1880 by virtual tautonomy and Starobogatov's subsequent designation of mamillata is unncessary.

[12]Acerosiana has as its type-species Vivipara acerosa Bourguignat 1862 by virtual tautonomy.

[13]Fasciatiana has as its type-species, by virtual tautonomy, Nerita fasciata Müller 1774, which Bourguignat (1880: 36) listed as Vivipara fasciata.

[14]Duboisiana has as its type-species, by virtual tautonomy, Paludina duboisiana Mousson 1862 which Bourguignat (1880: 43) listed in Vivipara and gave the incorrect date of 1863 for Mousson.

[15]Bourguignat (1880: 46) appears to have spelled this nomen Sphoeridiana despite its type-species by virtual tautonomy, Vivipara sphaeridia Bourguignat 1880. All the Bourguignat names listed above have been over-looked until now.

[16]Annandale (1924: 64) gave as the type-species, by original designation T. dezmanniana (sic) [= Vivipara dezmaniana Brusina 1874].

[17]An alternate spelling is Mikhailovski and the date on the cover of the serial in which the paper appeared is 1902 (see citation in bibliography under Mikhailovski (1902).

[18]Seninski (1905: 51 and 52) listed two species in his Suchumica and Korobkov (1955: 167) noted gracilis as genotype, here interpreted as type-species by subsequent designation; Seninski himself says that his name is the same as Galizgia which he

misspelled as Galisgia.

[19]The correct type-species is Melania hellespontica Calvert and Neumayr 1880 by original designation of Annandale (1924: 73); Starobogatov (1970) did not treat this nomen in the Viviparidae.

[20]Akhvledianai (1957: 453) misspelled this as Viripara.

[21]The date of Lörenthey's publication is questionable; some authors (Neave, 1939: 587; Wenz, 1939: 490) concur with Starobogatov and use 1906; the date on the title page is 1911, so cited by Prashad (1928).

[22]The original binomen of the type-species is Viviparus syriacus; Tchernov (1973: 40; 1975: 14-15, pl. 1, fig. 3) indicated that this name is a synonym of Viviparus apameae Blanckenhorn 1897.

[23]Thiele (1931: 747) introduced this as a new name for Callina Hannibal 1912, non Lowe 1855 (see Boss and Bieler, 1991: 19). The type species for Callina Hannibal 1912, non Lowe 1855 was given by original designation, as Paludina intertexta Say 1829 (Hannibal 1912: 193) and thus the same for Thiele's replacement name.

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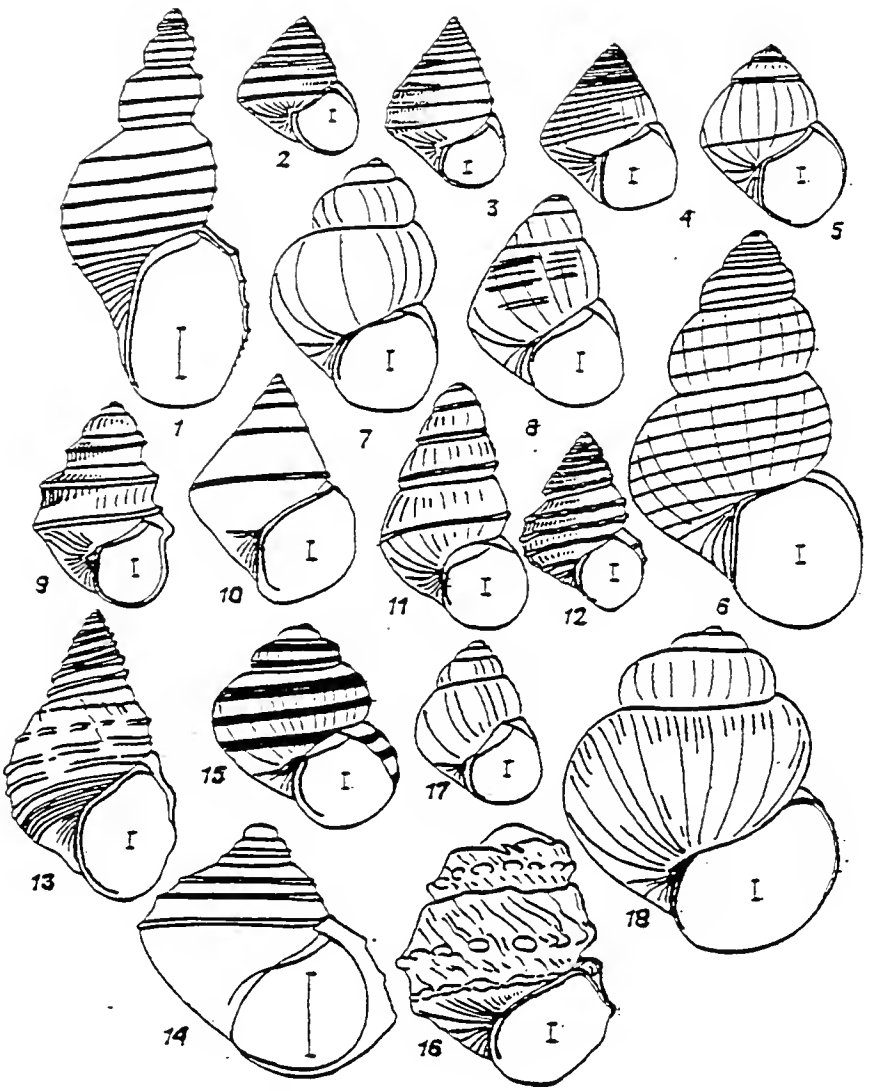

Figs. 1-18. Type-species of genus Scalipaludina (1) from the family Lioplacidae and genera and subgenera of the family Viviparidae (2-18).

Figs. 1, 3, 5, 6 - reconstructions; Figs. 1, 4-6, 9, 11 - after Franz, 1932; 2, 3 - after Wenz, 1938-1944; 10, 12 - after Seninski, 1905; 13 - after Pallary, 1939; 14 - after Schlickum and Puisségur, 1977; 18 - after Burch, 1982; 7, 8, 15-17-original. Scale lines on all drawings - 2 mm.