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A TENTATIVE CLASSIFICATION OF THE
PALEARCTIC UNIONIDS

BY FRITZ HAAS
CURATOR OF LOWER INVERTEBRATES

INTRODUCTION

The arrangement which is to follow is based upon more than thirty years' experience in work on unionids in general and on the palearctic ones in particular; it aims to place the pearly fresh-water mussels of the palearctic region within the general system of the unionids, and to show the natural inter-relationships of the forms. This requires some mention of earlier taxonomic essays on the subject.

Until the middle of the last century, that is to say, until the time of Rossmassler in Germany and Dupuy in France, Linnaean methods prevailed; every animal believed to be unknown to science was described as a new species and nobody worried about the natural relations of the "species" thus originated. This being so, it is not surprising to find that many phaenotypic features were mistaken for specific ones and that many forms which had nothing to do with each other were thrown together. It seems that Rossmassler was the first to recognize clearly the transformation of the unionid shell by environmental conditions; he, at least, knew about the shaping influence of lacustrine life, which manifests itself in the larvation of the still specifically characteristic juvenile shell, or in that of the fluviatile phase of unionids.

The following era may be characterized by the methods of J. R. Bourguignat and his pupils—Locard, Servain, Coutagne, and many others. This *nouvelle école* attributed specific value to all the differences of shape in fresh-water mussels, which may have originated through environmental influences as well as through geographic isolation. Under this school, discrimination went far more into detail than under the Linnaean method: each shell which differed from an already known mussel in three dimensions, or by the indices calculated from them, was a new species. It is obvious that such a

method, because of the impossibility of securing exact measurements in the always somewhat ventricose unionid shell, could afford approximate figures only; it led inevitably to the description of every individual examined as a new species. Umbonal sculpture and details of the hinge composition were not considered at all. Thus, convergencies due merely to similarity of measurements in the three dimensions, often led to unwarranted inferences with regard to natural relations. The placing of *Margaritifera margaritifera* and of *Psilunio littoralis* close to certain elongated forms of crassoid unios affords an example.

Truth compels us to admit that, leaving aside slips of judgment due to deficiencies of the method, the natural arrangement of the many described "species" was not spoiled; on the contrary, they generally were united into groups, which correspond to a certain degree to our modern racial groups. The geographical factor, however, without which a natural taxonomic arrangement can not now be imagined, does not play any rôle in the Bourguignatian method, nor was the anatomy of the soft parts considered.

Another Frenchman, H. Drouët, stands quite alone among his contemporaries, by reason of the emphasis he placed upon the connection between the shape of his new unionids and the life conditions of their respective habitats. Drouët was, indeed, a pioneer, but he knew too little about the ecology of fresh-water mussels and was therefore often deceived by convergent shapes.

After Rossmäessler's death, at a time when descriptions of new unionids were produced by the hundreds in France, in Italy, and in other countries, work on fresh-water mussels lagged in Germany. The German malacologists (especially Kobelt, who continued Rossmäessler's incomplete *Iconographie*) did not agree with Bourguignat's views, which were also in disfavor with some of the French specialists; for example, with the editors and collaborators of the *Journal de Conchyliologie*. Kobelt's disapproving attitude had won him Bourguignat's intense hatred, but he kept to his own ideas on unionids, which he did not publish until after Bourguignat's death.

The list of the Unionidae in C. A. Westerlund's *Fauna der in der paläarktischen Region lebenden Binnenconchylien* (7, 1890) shows how Bourguignat and his school, to which Westerlund belonged, believed the fauna of palearctic fresh-water mussels to be composed.

More modern ideas on this subject originated with Kobelt, who, in various publications, pointed out the isolating effect of hydrographic frontiers. By many examples he tried to prove the theory,

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PALEARCTIC UNIONIDS—HAAS

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upon which his principal conclusion was based, that a natural arrangement of the unionids had to take into consideration their distribution in the different hydrographic systems. When this view was accepted, and it was understood that the overwhelming number of described palearctic unionids must be reduced to a very limited number of "fundamental" species, there was the unfortunate circumstance that nobody knew which these fundamental species might be.

Everyone agreed, at least, that these fundamental species, whichever they might be, had given origin to local races in the different parts of the river systems inhabited by them. Collectors and scientists—among them, thirty years ago, even the writer of these lines—began to prove the existence of these local races and to describe them wherever necessary. In Germany, where the Bourguignat method had not been so popular as it had been in France, Italy, and the lower Danube Basin, comparatively few unionids had been described, aside from the fundamental ones, so that there were few names available for such new races as seemed to be worth describing. New names were invented, and I plead guilty to having encumbered nomenclature with not less than fifteen new denominations, bestowed mostly on mussels from western Germany.

Looking backward, I can not wholly disapprove of my course at that time. I have come to realize that the differences mistaken by me for racial features were phaenotypic, due to environmental factors; furthermore, I have learned that the limited geographic areas inhabited by such uniformly characterized fresh-water mussels, were nothing but areas of uniform conditions of life. But even if such distinct local forms, for instance, those of the *Unio crassus* group, are not worth retaining as trinomially named races, they are nevertheless somewhat more than mere variations. They can be considered to be incipient races, having a mutative basis. That such slight differences, which are nevertheless distinguishable to an experienced eye, can not be made the basis of named forms, is due to our present system of nomenclature, which does not go beyond a third name. I have been greatly pleased to learn from modern herpetologists and ornithologists that they have found similar conditions and feel some need for a method of designation for the above-mentioned "subraces," which we may call incipient ones. I can not but agree that this would be desirable.¹

¹ William Morton Wheeler, in his work on ants, consistently employs a quadrenomial nomenclature; cf., for example, his *Ants* (1910).

We shall leave aside, as being far from our present object, the merely geographical part of the unionid problem, which, following Kobelt's ideas, involved the tracing of old and bygone connections between now separated river systems, and other related subjects.

The arrangement of the palearctic unionids which follows rests mostly on Kobelt's ideology. It is backed by long experience in field observation and indoor study and by personal knowledge of many types of unionids contained in the extremely rich collection of the Senckenberg Museum in Frankfort-on-the-Main or entrusted to me for study by other museums; for example, that of Geneva, Switzerland, which possesses Bourguignat's types, and the United States National Museum, where I have had the privilege of studying Lea's types of unionids from Asia Minor. The investigation of such authentic material often gave results quite different from those derived from the study of descriptions and figures; the attributions to synonymy to be found in my arrangement, therefore, often differ from those customary, and are the immediate consequence of personal acquaintance with the respective "species."

As to the position of the palearctic unionids within the general system of the family, my arrangement also differs from that of other writers, and even from that of Thiele in his *Handbuch der systematischen Weichtierkunde*. In many cases I have no anatomical evidence, and I trust that my system may be attributed to special acquaintance with the subject; paleontological data have frequently influenced my ideas upon the relationships between palearctic and exotic genera.

The following arrangement is only a tentative one. In France, where Bourguignat's influence prevailed up to the beginning of this century, Germain in his *Mollusques terrestres et fluviatiles de la France* (22, Part 2: Faune de France, Paris, 1931) reduces the number of French unionids to a very few fundamental species. It is thus evident that the endeavor to simplify and to concentrate the system is everywhere obvious. Since others have ideas similar to mine, they may perhaps welcome my arrangement as a basis for future and more extensive research.

Finally, I must try to explain my concept of a "subspecies" or a "local race," in order to justify my arrangement. I realize that, in many cases, it is very difficult to distinguish two neighboring local races, as they seemingly are linked by intermediate forms. The impossibility of a sharp separation may be due to overlappings at the borders of distribution or, possibly, to hybridizations; but in all

such cases, the respective subspecies are more easily distinguishable at the centers than at the borders of their areas. Something of the same kind, only on a much smaller scale, also happens to adjacent full species; for instance, to *Unio pictorum* Linnaeus and *Unio elongatulus* C. Pfeiffer, which can scarcely be distinguished in eastern France, where there are certainly hybridizations between them.

In cases such as these, the distinction between species or subspecies is very difficult, and I have usually based my decisions upon the shape of the shells found in the centers of the areas of distribution in question. I am well aware of the tentative character of such an arrangement; larger series of material from new localities may necessitate much revision of the system set forth in this paper.

The present paper recognizes 9 genera, 19 species, and 61 subspecies of palearctic unionids.

TENTATIVE ARRANGEMENT OF THE PALEARCTIC UNIONIDS INTO NATURAL GROUPS

Family Margaritiferidae

The palearctic margaritiferids all belong to the genus *Margaritifera* Schumacher; the following species or specific groups are known:

Genus *Margaritifera* Schumacher, 1816

Margaritana Schumacher, 1817

Pseudunio Haas, 1910

Potamida Swainson, 1840

Margaritana syriaca Pallary, 1929, is clearly a *Psilunio*. See under *Psilunio littoralis homsensis* Lea, page 135.

***Margaritifera auricularia* Spengler, 1793**

***Margaritifera auricularia auricularia* Spengler, 1793**

Unio sinuatus Lamarck, 1819

Unio margaritanopsis Locard, 1889

Iberian Peninsula; France; Po basin in North Italy. Subfossil in England (Thames); Germany (Thuringia, Rhine basin); central Italy.

***Margaritifera auricularia maroccana* Pallary, 1920**

Margaritana redomica Pallary, 1927

Margaritana dernaica Pallary, 1928

Very closely related to typical *auricularia*, but probably distinguishable as a local race.

Morocco.

Margaritifera margaritifera Linnaeus, 1758

A holarctic species, represented in the palearctic region by the following four subspecies:

Margaritifera margaritifera margaritifera Linnaeus, 1758

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|--|---|
| <i>Unio elongata</i> Lamarck, 1819 | <i>Margaritana pyrenaica</i> Bourguignonat, 1889 |
| <i>Unio roissyi</i> Michaud, 1831 | <i>Margaritana alleni</i> Castro in Locard, 1889 |
| <i>Unio margaritifera</i> var. <i>minor</i> Rossmuessler, 1835 | <i>Margaritana margaritifera parvula</i> Haas, 1908 |
| <i>Unio brunneus</i> Bonhomme, 1840 | <i>Margaritana durrowensis</i> Phillips, 1928 |
| <i>Unio tristis</i> Morelet, 1845 | |
| <i>Margaritana freytagi</i> Kobelt, 1886 | |
| <i>Margaritana michaudi</i> Locard, 1889 | |

Part of the names quoted in the synonymy designate incipient races which have no status in modern nomenclature.

Extra-mediterranean Europe.

Margaritifera margaritifera dahurica Middendorff, 1851

Eastern Siberia.

Margaritifera margaritifera middendorffi Rosen, 1926

Unio complanatus Middendorff (not Solander) 1851

Kamchatka.

Margaritifera margaritifera laevis Haas, 1910

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|--|---|
| <i>Margaritana dahurica</i> Kobelt (not Middendorff), 1879 | <i>Margaritana sachalinensis</i> Shadin, 1938 |
| <i>Ptychorhynchus laevis</i> Haas, 1910 | |

Saghalin; northern Japan.

Family **Unionidae**

Subfamily **Unioninae**

Some of the genera grouped here, such as *Leguminaria*, *Pseudodontopsis* and *Microcondylaea*, the anatomy of which is entirely unknown or only partly known, may not belong to this subfamily at all.

Genus **Unio** Retzius, 1788

Palearctic, entering into the Oriental region just in the East and the Southeast; closely related to the nearctic genus *Elliptio* Rafinesque.

Unio pictorum Group

Very similar and probably related to the East-Asiatic *Unio douglasiae* Griffith and Pidgeon and its group.

Unio pictorum Linnaeus, 1758

Palaearctic region, except the Mediterranean basin, where it is found only in the Rhone system, in North Africa and in the rivers flowing into the Black Sea. In the parts of the Mediterranean basin where it is absent, it is represented by the races of *Unio elongatulus* C. Pfeiffer. In the Rhone system as well as in North Africa, both species occur side by side; in central France (Rhone basin and rivers of the central plain) they apparently hybridize, for the unios of the *pictorum* group are intermediate between these two forms and are distinguished by extreme variability.

Unio pictorum pictorum Linnaeus, 1757

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| <i>Unio limosus</i> Nilsson, 1882 | <i>Unio torsatellus</i> Berthier, 1882 |
| <i>Unio deshayesi</i> Michaud, 1832 | <i>Unio hollandrei</i> Bourguignat, 1882 |
| <i>Unio pictorum</i> var. <i>grandis</i> Rossmaessler, 1842 | <i>Unio fascellinus</i> Servain, 1882 |
| <i>Unio maltzani</i> Küster, 1854 | <i>Unio falsus</i> Bourguignat, 1882 |
| <i>Unio pictorum</i> var. <i>niger</i> Joannis, 1858 | <i>Unio strigatus</i> Servain, 1886 |
| <i>Unio platyodon</i> Jordan, 1879 | <i>Unio caravellus</i> Servain, 1887 |
| <i>Unio jousseaumi</i> Bourguignat, 1882 | <i>Unio lesumicus</i> Bourguignat, 1888 |
| <i>Unio pincianus</i> Bourguignat, 1882 | <i>Unio subbalatonicus</i> Servain, 1888 |
| <i>Unio dolfussianus</i> Bourguignat, 1882 | <i>Unio brebissoni</i> Locard, 1889 |
| <i>Unio joannisi</i> Bourguignat, 1882 | <i>Unio campylus</i> Locard, 1889 |
| <i>Unio gallicus</i> Bourguignat, 1882 | <i>Unio siliquiformis</i> Locard, 1889 |
| <i>Unio cancrorum</i> Bourguignat, 1882 | <i>Unio macropisthus</i> Bourguignat, 1889 |
| <i>Unio rhynchelinus</i> Letourneux, 1882 | <i>Unio hospitali</i> Locard, 1889 |
| <i>Unio rostratellus</i> Bourguignat, 1882 | <i>Unio oesiacus</i> Locard, 1889 |
| | <i>Unio rectus</i> Locard, 1890 |
| | <i>Unio battonensis</i> Kobelt, 1896 |

The synonymy of this and the following races is still very much confused, especially for the French forms. It was due to their variability that so many "species" and "varieties" were described in France. They could not be interpreted by Germain (1931). Hence the list of synonyms is neither correct nor complete.

Atlantic northern and central and northwestern Europe; apparently hybridizing with *Unio elongatulus* C. Pfeiffer in eastern France.

Unio pictorum praeposterus Küster, 1854

Naab; Regen; Thaya (Danube system).

Unio pictorum latirostris Küster, 1854

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|--|---------------------------------------|
| <i>Unio concinnus</i> Küster, 1840 (nomen nudum) | <i>Unio baletonicus</i> Küster, 1861 |
| <i>Unio quinqueannulatus</i> Küster, 1854 | <i>Unio balatonicus</i> Servain, 1881 |
| <i>Unio arca</i> Held in Küster, 1854 | <i>Unio dubreuwili</i> Servain, 1881 |
| <i>Unio decollatus</i> Held in Küster, 1854 | <i>Unio eucallistus</i> Kobelt, 1915 |

Haas and Schwarz (1913) regard *U. quinqueannulatus* as a hybrid between *U. pictorum latirostris* and its northern neighbor *U. pictorum pictorum*.

German Danube; Hungary; entering into the Save system.

Unio pictorum platyrhynchus Rossmäessler, 1835*Unio longirostris* Rossmäessler, 1836*Unio ponderosus* Spitz in Rossmäessler, 1842*Unio graniger* J. F. Schmidt, 1847

Styria; Carinthia; Carniolia (Danube system).

Unio pictorum middendorffii Westerlund, 1890

Eastern Siberia, still in the Amur River.

Unio pictorum schrenckianus Clessin, 1880*Unio pictorum* var. *okae* Kobelt, 1911*Unio annulatus* Kobelt, 1912*Unio pictorum schrenckianus* var. *dicki* Modell, 1930*Unio lindholmi* Shadin, 1938*Unio pictorum* var. *okensis* Shadin, 1938*Unio pictorum* var. *pygmaeus* Shadin, 1938*Unio pictorum* var. *defectivus* Shadin, 1938

Pontic Russia.

Unio pictorum ascanius Kobelt, 1913

Northern Asia Minor.

Unio pictorum proëchistus Bourguignat, 1870

Rumanian Danube; Vardar River(?)

Unio pictorum gaudioni Drouët, 1881*Unio gentilis* Haas, 1911

Doiran Lake, Macedonia; Maritza River; Varna, Bulgaria; vicinity of Istanbul.

(?)Unio pictorum proëchus Bourguignat, 1862*Unio actephilus* Bourguignat, 1862

Lake Lucerne, Switzerland.

(?)Unio pictorum moussonianus Clessin, 1887

Lake Zug, Switzerland.

Unio pictorum rostratus Lamarck, 1819

The synonymy still being unsettled, the compilation is tentative:

Unio pictorum var. *vinceus* Joannis, 1858*Unio pictorum* var. *tumens* Joannis, 1858*Unio gestroianus* Bourguignat, 1882*Unio charpyi* Drouët, 1888*Unio lugdunicus* Coutagne, 1889*Unio cristulatus* Drouët, 1889*Unio perroudi* Locard, 1889*Unio hydrellus* Locard, 1889*Unio bramicus* Baichère, 1890Occasionally hybridizing with *Unio elongatulus* C. Pfeiffer, where they occur together.

Rhone system, France.

Unio pictorum platyrhynchoideus Dupuy, 1849

- (?) *Unio michaudiana* Des Moulins, 1833
Unio requienii var. *crassidens* Rossmessler, 1844 (not Lamarck, 1819)
Unio philippeii Dupuy, 1849
Unio danielis Gassies, 1867
Unio moreletii Folin and Berillon, 1874 (not Deshayes, 1848)
Unio brindosianus Folin and Berillon, 1874
Unio baudoni Folin, 1874
- Unio moreletianus* Folin and Berillon, 1877
Unio moriscottei Folin, 1877
Unio bayonnensis Folin and Berillon, 1877
Unio berilloni Locard, 1882
Unio hauterivianus Bourguignat, 1882
Unio corbini Bourguignat, 1882
Unio milne-edwardsi Bourguignat, 1882
Unio fagoti Bourguignat, 1883

Southwestern Atlantic France, including the Garonne River.

Unio pictorum mucidus Morelet, 1845

- Unio nevesi* Castro, 1885
Unio simoesi Castro, 1885
Unio cameratus Drouët, 1893
Unio limosellus Drouët, 1893
Unio decurtatus Drouët, 1893
Unio callipygus Drouët, 1893
Unio aeschrus Locard, 1899
Unio tameganus Locard, 1899
Unio onconensis Locard, 1899
Unio hypoxanthus Locard, 1899
Unio chorellus Locard, 1899
Unio chorellinus Locard, 1899
Unio submucidus Locard, 1899
Unio barbosanus Locard, 1899
Unio castroi Locard, 1899
Unio silvai Locard, 1899
- Unio ocesanus* Locard, 1899
Unio paulinoi Locard, 1899
Unio subhispanus Locard, 1899
Unio hyperephanus Locard, 1899
Unio chasmirhynchus Locard, 1899
Unio mundanus Locard, 1899
Unio euchasmus Locard, 1899
Unio schousboei Locard, 1899
Unio taganus Locard, 1899
Unio abranestianus Locard, 1899
Unio scalabisianus Locard, 1899
Unio allenianus Locard, 1899
Unio cyrtus Locard, 1899
Unio sousanus Locard, 1899
Unio novus Locard, 1899
Unio neolthausmus Locard, 1899

Northwestern part of Atlantic Iberian Peninsula.

Unio pictorum delphinus Spengler, 1793

- Unio gibbus* Spengler, 1793
Unio hispanus Rossmessler, 1844
Unio dactylus Morelet, 1845
Unio lusitanus Drouët, 1879
Unio (*hispanus* var.?) *sevillensis* Kobelt, 1887
- Unio hispanus* var. *sphenoides* Westerland, 1892
(?) *Unio gravatus* Drouët, 1893
Unio turdetanus Drouët, 1893
Unio taginus Kobelt, 1903

Southwestern part of Atlantic Iberian Peninsula.

Unio pictorum ravoisieri Deshayes, 1848

- Unio atharsus* Bourguignat, 1889

Mediterranean North Africa, including Tunisia in the east.

Further synonymy still unsettled.

Unio tigridis Bourguignat, 1852

Southwestern Asia.

Unio tigridis tigridis Bourguignat, 1852

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| <i>Unio truncatus</i> Swainson, 1829 (not Spengler, 1793) | <i>Unio jouberti</i> Locard, 1883 |
| <i>Unio hueti</i> Bourguignat, 1855 | <i>Unio antiochianus</i> Locard, 1883 |
| <i>Unio natolicus</i> Küster, 1856 | <i>Unio kobelti</i> Rolle, 1895 |
| <i>Unio mussolianus</i> Küster, 1861 | <i>Unio tigridis</i> var. <i>harunis</i> Kobelt, 1912 |
| <i>Unio rasmus</i> Lea, 1863 | <i>Unio dignatus semiramidis</i> Kobelt, 1913 |
| <i>Unio mosulensis</i> Lea, 1863 | <i>Unio dignatus assuricus</i> Kobelt, 1913 |
| <i>Unio bourguignatianus</i> Lea, 1863 | <i>Unio dignatus ninusi</i> Kobelt, 1913 |
| <i>Unio dignatus</i> Lea, 1863 | <i>Unio hyperamblius</i> Kobelt, 1913 |
| <i>Unio delicatus</i> Lea, 1863 | <i>Unio calliopsis</i> Kobelt, 1913 |
| <i>Unio tigris</i> Lea, 1870 | <i>Unio siouffi</i> Kobelt, 1913 |
| <i>Unio anemprosthus</i> Locard, 1883 | <i>Unio schwarzi</i> Kobelt, 1915 |
| <i>Unio subtigridis</i> Locard, 1883 | |
| <i>Unio aziacus</i> Locard, 1883 | |
| <i>Unio chantrei</i> Locard, 1883 | |

Syria, in the Orontes basin; Iraq; Lake Urmiah.

Unio tigridis terminalis Bourguignat, 1852

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| <i>Unio grelloisianus</i> Bourguignat, 1856 | <i>Unio tristrami</i> Locard, 1883 |
| <i>Unio grelloisianus</i> var. <i>giganteus</i> Bourguignat, 1856 | <i>Unio ellipsoideus</i> Locard, 1883 |
| <i>Unio lunulifer</i> Bourguignat, 1856 | <i>Unio genezarethanus</i> Locard, 1883 |
| <i>Unio jordanicus</i> Bourguignat, 1865 | <i>Unio tiberiadensis</i> Locard, 1883 |
| <i>Unio pietri</i> Locard, 1880 | <i>Unio prosacrus</i> Locard, 1883 |
| <i>Unio lorteti</i> Locard, 1880 | <i>Unio zabulonicus</i> Locard, 1883 |
| | <i>Unio herodes</i> Kobelt, 1895 |
| | <i>Unio kisonis</i> Kobelt and Rolle, 1895 |

For this subspecies, Prashad (1919) has introduced the sub-generic name of *Eolymnium*, apparently without sufficient reason.

Littoral rivers of Cilicia, Syria and Palestine; Jordan River.

Unio abyssinicus von Martens, 1866

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| † <i>Unio willcocksii</i> Newton, 1899 | † <i>Unio fayumensis</i> Pilsbry and Bequaert, 1927 |
| † <i>Unio vignardi</i> Pallary, 1924 | |

Abyssinia; the subfossil forms (†) in the basin of the Lower Nile.

Unio elongatulus Group**Unio elongatulus** C. Pfeiffer, 1825

Mediterranean region; Asia Minor.

Unio elongatulus elongatulus C. Pfeiffer, 1825

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| <i>Unio lijacensis</i> Kobelt, 1890 | <i>Unio lijacensis</i> var. <i>gallensteini</i> Kobelt, 1890 |
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Area north of the Adriatic Sea: Tagliamento River(?); basin of Isonzo River; northern Dalmatia(?)

Unio elongatulus pallens Rossmassler, 1842

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| <i>Unio viridiflavus</i> Küster, 1854 | <i>Unio petrovichi</i> Küster, 1854 |
| <i>Unio petterdianus</i> Küster, 1854 | <i>Unio nitidosus</i> Drouët, 1879 |

Central and southern Dalmatia (Narenta, Imoshi); north Greece; River Save in Croatia(?)

Unio elongatulus fiscallianus Kleciach, 1872

Imoshi, Dalmatia; may turn out to be only a lacustrine form of *U. elongatulus pallens* Rosσμαessler.

Unio elongatulus sandrii Rosσμαessler, 1844

Unio nuperus Ziegler, in litt.

Unio sandrii var. *sericatus* Rosσμαessler, 1844

Unio ceratinus Drouët, 1879

Unio dalmaticus Drouët, 1879

Unio succineus Drouët, 1881

Unio morlachicus Kobelt, 1915

Northern Dalmatia; may be identical with *Unio elongatulus pallens* Rosσμαessler.

Unio elongatulus decipiens Drouët, 1881

Dalmatia; Montenegro. Possibly a lacustrine form of *Unio elongatulus pallens* Rosσμαessler.

Unio elongatulus krüperi Drouët, 1879

Unio destructilis Villa in Kobelt, 1915

Montenegro; Lake Vrachori in Aetolia, Greece. This race may be only a degenerate form of *Unio elongatulus pallens* Rosσμαessler.

Unio elongatulus quelleneci Drouët, 1895

Unio copaisanus Drouët, 1895

Lake Kopais, Aetolia, Greece; possibly a lacustrine form of *Unio elongatulus pallens* Rosσμαessler.

Unio elongatulus bourgeticus Bourguignat, 1882

Unio sabaudianus Bourguignat, 1882

Unio riciacensis Bourguignat, 1882

Unio orthus Coutagne, 1882

Unio occidaneus Drouët, 1888

Unio mucidellus Bourguignat, 1889

Unio voltzii Kobelt, 1911

Unio voltzii var. *ursannensis* Kobelt, 1911

Basin of River Saone in western France; Swiss Jura; Savoy; introduced into the Rhine system (Mühlhausen) by means of the Rhine-Rhone Canal.

A very difficult and until recently little understood race, often confounded with forms of *Unio crassus* Retzius on account of its oval shape and wavy umbonal sculpture. The above list of synonyms is provisional.

Unio elongatulus turtoni Payraudeau, 1826

Unio capigliolo Payraudeau, 1826

Unio bandini Küster, 1837

Unio exauratus Locard, 1889

Corsica, Sardinia.

Unio elongatulus moquinianus Dupuy, 1843

Unio antimoquinianus Locard, 1889 *Unio consentaneus* var. *moquini*
 Germain, 1931

Hautes-Pyrénées; Basses-Pyrénées; southern France.

This race has also often been confounded with forms of *crassus*. The synonymy will certainly prove to be more extensive.

Unio elongatulus aleroni Companyó and Massot, 1865

Central southern France (Hérault, Aude, Pyrénées-Orientales, Tarn, Haute-Garonne, Ariège).

Unio elongatulus rousii Dupuy, 1849

Unio thermalis Dupuy, in litt. *Unio malafossianus* Bourguignat,
 1882

Southern France (Garonne, Gers). Often confounded with *Unio tumidus* Retzius; synonymy still incompletely known.

Unio elongatulus mancus Lamarck, 1819

Unio arduasianus Reyniès, 1843 *Unio eutrapelus* Servain, 1887
Unio condatinus Letourneux, 1882 *Unio oberthurianus* Bourguignat,
 1889
Unio mucidulus Bourguignat, 1882
Unio gobionum Bourguignat, 1882 *Unio arcuatulus* Bourguignat, 1889
Unio mongazonae Servain, 1887 *Unio amblyus* Castro, 1889
Unio asticus Servain, 1887

A very variable, difficult form, often confounded with forms of *crassus*; occasionally hybridizes with *Unio pictorum* Linnaeus.

Central France, mainly basins of rivers Seine and Marne.

Unio elongatulus requienii Michaud, 1831

Unio jacquemini Dupuy, 1849 *Unio aramonensis* Locard, 1889
Unio saintsimonianus Fagot, 1882 *Unio vardonicus* Locard, 1889
Unio veillanensis Blanc, 1882 *Unio talus* Bourguignat, 1889
Unio orthellus Bérenguier, 1882 *Unio souzanus* Castro, 1889
Unio jourdheului Ray, 1882 *Unio royanus* Locard, 1889
Unio forojuliensis Bérenguier, 1882 *Unio aegericus* Locard, 1889
Unio triffoiricus Bourguignat, 1885 *Unio mucidulinus* Locard, 1889
Unio fabaeformis Bourguignat, 1889 *Unio baicheri* Locard, 1890
Unio frayssianus Bourguignat, 1889 *Unio arelatus* Bourguignat, 1892
Unio meyrannicus Bourguignat,
 1889

Further synonymy still unsettled, the above list not final.

Southeastern part of France, the Rhone, and east of the Rhone.

Unio elongatulus penchinatianus Bourguignat, 1865

Rivers of Mediterranean coast of northeastern Spain, to and including the Ebro.

Unio elongatulus valentinus Rossmäessler, 1854*Unio graëllsianus* Bourguignat,
1865*Unio courquinianus* Bourguignat,
1865*Unio almenarensis* Drouët, 1893

Rivers of Mediterranean coast of Spain, south of the Ebro;
southern border unknown.

Unio elongatulus gargottae Philippi, 1836*(?)Unio lobata* Jan, 1832*Unio biformis* Monterosato, 1896*Unio aradae* Philippi, 1844*Unio bitortus* Monterosato, 1896*Unio aradasii* Kobelt, 1876*Unio bipartitus* Monterosato, 1896*Unio benoiti* Bourguignat, 1883*Unio ricconianus* Monterosato, 1896*Unio monterosati* Bourguignat, 1883*Unio cuspidatus* Monterosato, 1896*Unio bivonianus* Bourguignat, 1883*Unio subindentatus* Adami in Mon-
terosato, 1896*Unio caficianus* Bourguignat, 1883

Sicily.

Unio elongatulus lawleyanus Gentiluomo, 1868*Unio larderehianus* Pecchioli, 1869*Unio meridionalis* Drouët, 1883*Unio romanus* Kobelt, 1875*Unio latinus* Bourguignat, 1883*Unio cumensis* Kobelt, 1880*Unio campsus* Bourguignat, 1883*Unio cumanus* Kobelt, 1880*Unio uziellii* Bourguignat, 1883*Unio pornae* Bourguignat in Lo-
card, 1880*Unio pisanus* Bourguignat, 1883*Unio meretricis* Bourguignat in
Locard, 1880*Unio gentiluomoi* Bourguignat,
1883*Unio moltenii* Adami, 1882*Unio pecchiolii* Bourguignat, 1883*Unio umbricus* Adami, 1882*Unio polii* Drouët, 1883*Unio etruscus* Drouët, 1883*Unio planci* Drouët, 1883*Unio campanus* Drouët, 1883*Unio isseli* Bourguignat, 1883*Unio d'Anconae* Bourguignat, 1883

Peninsular Italy.

Unio elongatulus glaucinus Porro, 1838*Unio corrosus* Villa, 1841*Unio eucallistellus* Bourguignat,
1883*Unio spinellii* Villa, 1852*Unio callichrous* Bourguignat, 1883*Unio requienii* var. *vulgaris* Stabile,
1859*Unio padanus* Bourguignat, 1883*Unio requienii* var. *oriliensis* Stabile,
1859*Unio strobili* Bourguignat, 1883*Unio requienii* var. *blaureri* Stabile,
1859*Unio pedemontanus* Bourguignat,
1883*Unio gestroianus* Bourguignat, 1871*Unio longobardus* Drouët, 1883*Unio villae* Issel, 1871*Unio brianteus* Drouët, 1883*Unio larius* Drouët, 1879*Unio sabintensis* Bourguignat, 1883*Unio gurkensis* Bourguignat, 1881*Unio verbanicus* Bourguignat, 1883*Unio brachyrhynchus* Drouët, 1881*Unio athesinus* Adams, 1885*Unio opisdartos* Adami, 1882*Unio ruffonii* Kobelt, 1886*Unio stephaninii* Adami, 1882*Unio humerosus* var. *costanus* Tie-
senhausen, 1894*Unio subcylindricus* Drouët, 1883*Unio directus* Drouët, 1895*Unio fluminalis* Drouët, 1883*Unio palustris* Drouët, 1895*Unio delpretei* Bourguignat, 1883*Unio humerosus* var. *elongata* Ko-
belt, 1915*Unio gredleri* Drouët, 1883*Unio minusculus* Drouët, 1883*Unio humerosus* var. *roboretana*
Kobelt, 1915*Unio benactinus* Drouët, 1883*Unio siliquatus* Drouët, 1883*Unio destructilis* Villa in Kobelt, 1915*Unio nitidus* Drouët, 1883

Basin of the Po, and Adige, continental Italy.

Unio elongatulus eucirrus Bourguignat, 1857

- | | |
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| <i>Unio raymondi</i> Locard, 1883 | <i>Unio cilicicus</i> var. <i>subsaccatus</i> Kobelt and Rolle, 1895 |
| <i>Unio alexandri</i> Kobelt and Rolle, 1895 | <i>Unio berythensis</i> Kobelt and Rolle, 1895 |
| <i>Unio cilicicus</i> Kobelt and Rolle, 1895 | <i>Unio raymondopsis</i> Kobelt, 1913 |
| <i>Unio cilicicus</i> var. <i>adanensis</i> Rolle, 1895 | <i>Unio kuweikensis</i> Kobelt, 1913 |
| <i>Unio cilicicus</i> var. <i>jenemterensis</i> Kobelt and Rolle, 1895 | <i>Unio sesirmensis</i> Kobelt, 1913 |
| | <i>Unio (cilicicus</i> var.) <i>anceyi</i> Kobelt, 1913 |

Littoral rivers of Cilicia, Syria, and Palestine.

Unio elongatulus dembeae Sowerby, 1865

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|---|--|
| <i>Unio aeneus</i> Jickeli, 1874 | <i>Unio meneliki</i> Bourguignat, 1885 |
| <i>Unio jickelii</i> Bourguignat, 1883 | <i>Unio soleilleti</i> Bourguignat, 1885 |
| <i>Unio alfierianus</i> Bourguignat, 1885 | <i>Unio traversii</i> Pollonera, 1888 |
| <i>Unio hamyanus</i> Bourguignat, 1885 | <i>Unio erlangeri</i> Kobelt, 1909 |
| <i>Unio ilqi</i> Bourguignat, 1885 | |

Abyssinia.

Unio elongatulus durieui Deshayes, 1847

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|---------------------------------------|--|
| (?) <i>Unio emarginatus</i> Lea, 1834 | <i>Unio medjerdae</i> Kobelt, 1886 |
| <i>Unio tafnanus</i> Kobelt, 1884 | <i>Unio micelii</i> Kobelt, 1886 |
| <i>Unio silifensis</i> Kobelt, 1884 | <i>Unio deleveleusae</i> Hagenmüller, 1887 |
| <i>Unio issericus</i> Kobelt, 1884 | |
| <i>Unio tetuanensis</i> Kobelt, 1884 | |

After studying the type of *Unio emarginatus* Lea (U. S. Nat. Mus. No. 86159) I can not decide whether this form, known only by this type, is identical with *durieui* or not; the type specimen is composed of two odd valves.

Mediterranean North Africa.

Unio tumidus Group**Unio tumidus** Retzius, 1788

Atlantic and Pontic parts of Europe.

Unio tumidus tumidus Retzius, 1788

- | | |
|--|--|
| <i>Unio conus</i> Spengler, 1793 | <i>Unio tumidus</i> var. <i>maxima</i> Moersch, 1864 |
| <i>Mya depressa</i> Donovan, 1802 | <i>Unio tumidus</i> var. <i>limicola</i> Moersch, 1864 |
| <i>Mya ovata</i> Donovan, 1802 | <i>Unio batavus</i> var. <i>incurvatus</i> Colbeau, 1868 |
| <i>Mya oralis</i> Montagu, 1803 | <i>Unio tumidus</i> var. <i>heckingi</i> Colbeau, 1868 |
| <i>Mysca solida</i> Turton, 1822 | <i>Unio tumidus</i> var. <i>rohrmanni</i> Kobelt, 1880 |
| <i>Unio inflata</i> Hecart, 1833 | <i>Unio bardus</i> Bourguignat, 1881 |
| <i>Unio mülleri</i> Rossmäessler, 1838 | <i>Unio edyus</i> Bourguignat, 1882 |
| <i>Unio tumidus</i> var. <i>saccatus</i> Rossmäessler, 1854 | <i>Unio alpecanus</i> Bourguignat, 1882 |
| <i>Unio pictorum</i> var. <i>niger</i> Joannis, 1859 | |
| <i>Unio tumidus</i> var. <i>pictus</i> Beck in Moersch, 1864 | |

Unioourneli Bourguignat, 1882
Unio mulierum Servain, 1882
Unio schroederi Bourguignat, 1885
Unio rhenanus Kobelt, 1886
Unio tumidus var. *godetiana* Clessin, 1887
Unio tumidulus Locard, 1889

Unio aldemericus Bourguignat, 1889
Unio giberti Locard, 1889
Unio rothomagensis Locard, 1890
Unio albovicensis Locard, 1893
Unio lacrymiformis Locard, 1893
Unio levoturieri Locard, 1893
Unio lauterborni Haas, 1909

Even the brief synonymy of this widespread form is still unsettled, since it is known that it has often been confounded with short, stout forms of *Unio pictorum* Linnaeus.

Atlantic western and central Europe.

Unio tumidus borysthenensis Kobelt, 1880

Unio gerstfeldtianus Clessin, 1880
Unio tumidus var. *falcatulus* Drouët, 1881
Unio tumidus ilekensis Kobelt, 1912
Unio tumidus var. *natermanni* Honigmann, 1914
Unio tumidus var. *bashkiricus* Shadin, 1938

Unio tumidus var. *moltshanovi* Shadin, 1938
Unio tumidus var. *fridmani* Shadin, 1938
Unio kobeltianus Shadin, 1938 (not Haas, 1913)

European streams draining into the Black Sea: lower part of Danube system; southern Russia.

Unio crassus Group

The members of this group have often been confounded with elongated forms of *Psilunio* and with round forms of *Unio elongatulus*.

Unio crassus Retzius, 1788

Unio crassus crassus Retzius, 1788

Unio musivus Spengler, 1793
Unio ater Nilsson, 1822
Unio rubens Menke, 1828
Unio rugatus Menke, 1828
Unio crassus var. *maximus* Kobelt, 1872
Unio pseudolittoralis Clessin, 1875
Unio kochi Kobelt, 1886
Unio hamburgiensis Servain, 1888

Unio pseudolittoralis var. *curonicus* Riemenschneider, 1907
Unio crassus heimbürgi Haas, 1911
Unio crassus thuringiacus Israel, 1917
Unio crassus polonicus Polinski, 1917
Unio crassus ornatus Polinski, 1917
Unio crassus var. *ishnensis* Shadin, 1938

North Europe; Atlantic Central Europe, in the west to the Rhine, but not in it; Atlantic and boreal Russia.

Unio crassus cytharea Küster, 1833

(?) *Unio planus* Studer, 1820; unidentifiable
Unio sinuatus Studer, 1820 (nomen nudum)
Unio dilatatus Studer, 1820 (nomen nudum)

Unio ovatus Studer, 1820 (nomen nudum)
Unio sinuolata Küster, 1833
Unio dubius Fitzinger, 1833 (nomen nudum)

- Unio nigricans* Fitzinger, 1833
 (nomen nudum)
Unio castaneus Fitzinger, 1833
 (nomen nudum)
Unio decurvatus Rossmmaessler, 1835
Unio labacensis Rossmmaessler, 1835
Unio vitreus Rossmmaessler, 1835
Unio atrovirens Rossmmaessler, 1836
Unio amnicus Rossmmaessler, 1836
Unio piscinalis Rossmmaessler, 1836
Unio reniformis Rossmmaessler, 1836
Unio consentaneus Rossmmaessler, 1836
 (?) *Unio retusa* Held, 1836
Unio batavus var. *gibbosus* Held, 1836
Unio batavus var. *elongatus* Held, 1836
Unio carinthiacus Rossmmaessler, 1836
Unio fuscus Rossmmaessler, 1836
Unio squamosus Charpentier, 1837
Unio gangraenosus J. F. Schmidt, 1840
Unio pruinosis J. F. Schmidt, 1840
Unio nessorhynchus Küster, 1854
Unio heldii Küster, 1854
Unio bosnensis von Moellendorff, 1873
Unio phaseolus Held in Kobelt, 1879
Unio neocomensis Drouët, 1881
Unio croaticus Drouët, 1881
Unio striatulus Drouët, 1882
Unio truncatulus Drouët, 1883
Unio rivalis Drouët, 1884
Unio serbicus Drouët, 1884
Unio savensis Drouët, 1884
Unio dokiçi Drouët, 1884
Unio ondovensis Hazay, 1885
Unio albensis Hazay, 1885
Unio subrobustus Servain, 1885
Unio duregicus Servain, 1885
Unio sandriopsis Servain, 1885
Unio ostiorum Servain, 1885
Unio turicus Servain, 1885
Unio tiguricus Servain, 1885
Unio travnicensis Kobelt, 1910
Unio brandisi Kobelt, 1910
Unio consentaneus hohenwarti Kobelt, 1910
Unio langi Kobelt, 1910
Unio (consentaneus var.?) gallensteini Kobelt, 1910
Unio consentaneus subterminalis Kobelt, 1910
Unio batavus elongatus Clessin, 1910
Unio consentaneus thayacus Kobelt, 1910
Unio consentaneus biaudeti Kobelt, 1911
Unio consentaneus bodamicus Kobelt, 1911
Unio consentaneus dilatatus Kobelt, 1911
Unio consentaneus abnobae Kobelt, 1911

May hybridize with the Atlantic *U. c. batavus*.

Rhone basin to and inclusive of Lake Geneva; Swiss Rhine and tributaries; Danube system; Galicia; Wardar River.

Unio crassus batavus Maton and Rackett, 1807

- Unio nana* Lamarck, 1819
Unio riparia C. Pfeiffer, 1821
Unio arcuatus Bouch.-Chant., 1838
Unio droueti Dupuy, 1849
Unio courtillieri Hatteman, 1859
Unio batavus var. *minimus* Joannis, 1859
Unio batavus var. *baraceus* Joannis, 1859
Unio lamboltei Malzine, 1867
Unio subtilis Drouët, 1879
Unio ligericus Bourguignat, 1882
Unio dubisianus Coutagne, 1882
Unio sequanicus Coutagne, 1882
Unio rayi Bourguignat, 1882
Unio pilloti Bourguignat, 1882
Unio crassatellus Bourguignat in Locard, 1882
Unio socardianus Bourguignat in Locard, 1882
Unio locardianus Bourguignat in Locard, 1882
Unio lagnysiacus Locard, 1882
Unio macrorhynchus Bourguignat, 1882
Unio melas Coutagne, 1882
Unio dubisianopsis Locard, 1882
Unio carantoni Coutagne, 1882
Unio minutulus Ray, 1882
Unio berthellini Bourguignat, 1882
Unio andegavensis Servain, 1882
Unio cyprinorum Berthier, 1882
Unio matronicus Bourguignat, 1882
Unio septentrionalis Bourguignat, 1882
Unio oxyrhynchus Brevière, 1882
Unio marcellinus Berthier, 1882
Unio potamius Bourguignat, 1882
Unio feliciani Bourguignat, 1882
Unio arenarum Bourguignat, 1882
Unio danemora Bourguignat, 1882
Unio brevieri Bourguignat, 1882
Unio tumidiformis Castro, 1885
Unio sadoicus Castro, 1885

- Unio macropygus* Castro, 1885
Unio eupygus Castro, 1885
Unio batavellus Letourneux, 1885
Unio batavus var. *taunica* Kobelt, 1886
Unio baeticus Kobelt, 1887
Unio carcasinus Souverbie, 1887
Unio besnardianus Servain, 1888
Unio baudoni Folin, 1888
Unio crassulus Drouët, 1888
Unio vegeackensis Servain, 1888
Unio visurgisus Servain, 1888
Unio badiellus Drouët, 1888
Unio catalaunicus Coutagne, 1889
Unio zoasthenicus Locard, 1889
Unio jurianus Locard, 1889
Unio subamnicus Locard, 1889
Unio aturicus Locard, 1889
Unio lemoheuxi Servain, 1889
Unio orbis Locard, 1889
Unio andeliacus Bourguignat, 1889
Unio vallieriacus Bourguignat, 1889
Unio nubilus Locard, 1889
Unio diptychus Surrault, 1889
Unio ingradiensis Surrault, 1889
Unio materniacus Locard, 1889
Unio melantatus Bourguignat, 1889
Unio balbignyanus Bourguignat, 1889
Unio occidentalis Bourguignat, 1889
Unio stygnus Locard, 1889
Unio bouchardi Bourguignat, 1889
Unio passavanti Bourguignat, 1889
Unio surraulli Servain, 1889
Unio adonus Servain, 1889
Unio camonti Bourguignat, 1889
Unio hattmanni Bourguignat, 1889
Unio seneauxi Bourguignat, 1889
Unio visurgicus Servain, 1889
Unio carioliensis Pacôme, 1889
Unio mariae Pacôme, 1889
Unio nicolloni Locard, 1889
Unio euthymeanus Locard, 1889
Unio ignarifformis Bourguignat, 1889
Unio ignari Bourguignat, 1889
Unio manculus Locard, 1889
Unio perroudi Locard, 1889
Unio scotinus Locard, 1889
Unio redactus Locard, 1889
Unio conimbricus Kobelt, 1893
Unio gliscerus Locard, 1893
Unio ampullaceus Locard, 1893
Unio chardonii Bourguignat in Locard, 1893
Unio lancelevei Locard, 1893
Unio hassiae Haas, 1908
Unio pseudocrassus Haas, 1909
Unio batavus sabulosus Haas, 1910
Unio batavus badensis Haas, 1910
Unio batavus palatinus Haas, 1911
Unio batavus hexameri Haas, 1911
Unio batavus probavaricus Haas, 1911
Unio batavus distinguendus C. Boettger, 1912
Unio batavus navensis C. Boettger, 1912
Unio batavus kobeltianus Haas, 1913
†*Unio cantharus* Kennard and Woodward, 1924

This list is a first and incomplete attempt to gather the synonyms of this highly variable race.

Atlantic Iberian Peninsula; Atlantic France; western Germany, not including the Weser; subfossil in England.

Unio crassus carneus Küster, 1848

- Unio luxurians* Küster, 1848
Unio brevirostris Küster, 1848
 Montenegro; Albania.

Unio crassus jonicus Drouët, 1879

- Unio helenae* Kobelt, 1893
 Western Greece; isles of Corfu and Levkas.

Unio crassus gontieri Bourguignat, 1856

- Unio colchicus* Drouët, 1881
Unio sieversi Drouët, 1881
Unio steventianus Drouët, 1881
Unio mingrelicus Drouët, 1881
Unio raddei Drouët, 1881
Unio araxenus Drouët, 1881
Unio stepanovi Drouët, 1881
Unio raddei var. *kutaisanus* Kobelt, 1886
Unio crassus okae Kobelt, 1911
Unio kungurensis Kobelt, 1912

<i>Unio kungurensis</i> var. <i>irenjensis</i> Kobelt, 1912	<i>Unio armeniacus</i> Kobelt, 1912
<i>Unio kungurensis</i> var. <i>sylvensis</i> Kobelt, 1912	<i>Unio roseni</i> Kobelt, 1912
<i>Unio kungurensis</i> var. <i>chlebnikowi</i> Kobelt, 1912	<i>Unio gregorii</i> Kobelt, 1912
	<i>Unio subbataricus</i> Kobelt, 1913
	<i>Unio mingrelicus</i> var. <i>stevonianiformis</i> Shadin, 1938

This subspecies has been cited as *stevonianus* Krynicki, 1837, but this name remained a nomen nudum until 1881, and *gontieri*, dating from 1856, has priority.¹

Caucasus; Basin of River Kama; White Russia.

Unio crassus bruguierianus Bourguignat, 1853

<i>Unio orientalis</i> Bourguignat, 1852 (not Lea, 1840)	<i>Unio thiesseae</i> Drouët, 1892
<i>Unio prusii</i> Bourguignat, 1853	<i>Unio scissus</i> Drouët, 1893
<i>Unio vescoi</i> Bourguignat, 1856	<i>Unio pseudonymus</i> Simpson, 1900
<i>Unio schwerzenbachi</i> Bourguignat, 1856	(?) <i>Unio modiola</i> Preston, 1912
<i>Unio turcicus</i> Küster, 1862	<i>Unio specialis</i> Kobelt, 1913
<i>Unio kolschyi</i> Küster, 1862	<i>Unio ancyrensis</i> Kobelt, 1913
<i>Unio damascensis</i> Lea, 1863	<i>Unio ancyrensis</i> var. <i>louisei</i> Kobelt, 1913
<i>Unio orontesensis</i> Lea, 1863	<i>Unio orphaensis</i> var. <i>ehrmanni</i> Kobelt, 1913
<i>Unio syriacus</i> Lea, 1863	<i>Unio diarbekrianus</i> Kobelt, 1913
<i>Unio orphaensis</i> Lea, 1864	<i>Unio billisensis</i> Kobelt, 1913
<i>Unio mardinensis</i> Lea, 1864	<i>Unio ciconius</i> Kobelt, 1913
<i>Unio kullethensis</i> Lea, 1864	<i>Unio medicus</i> Kobelt, 1913
<i>Unio vicarius</i> Westerlund, 1879	<i>Unio thospiensis</i> Kobelt, 1915
<i>Unio desectus</i> Westerlund, 1879	<i>Unio (Rhombunio) wenzii</i> Kobelt, 1915
<i>Unio heldreichi</i> O. Boettger, 1886	

Eastern Greece; Asia Minor.

Unio crassus mongolicus Middendorff, 1851

Known only from Middendorff's original description. Preston (1912) cited it from the upper Indus River, but this information does not seem to be reliable.

Amur River System, northeastern Asia.

The three genera which now follow, i.e. *Leguminaia*, *Pseudodontopsis* and *Microcondylaea*, are only intuitively grouped with the Unionines, since anatomical evidence is not yet available. The three genera cited above are close relatives of the genus *Pseudodon* Gould, which is now restricted to southeastern Asia, though it ranged much farther westward in late Tertiary time.

¹ *Unio steveniana* Krynicki, Bull. soc. imp. nat. Moscou, 10, p. 59, 1837 (nomen nudum); Siemaschko, Bull. soc. imp. nat. Moscou, 22, p. 126, 1847 (nomen nudum); *Unio gontieri* Bourguignat, Aménités Malacologiques, 2, p. 33, pl. 4, figs. 1-4, 1856; *Unio stevenianus* Drouët, Union. Russie Europ., p. 14, 1881 (first description of species).

Genus *Leguminaia* Conrad, 1865*Leguminaia wheatleyi* Lea, 1862*Monocondylaea mardinensis* Lea,
1864*Leguminaia chantrei* Locard, 1883*Leguminaia bourguignati* Locard,
1883*Leguminaia naegelei* Kobelt, 1913*Leguminaia graeteri* Kobelt, 1913*Leguminaia nisibina* Kobelt, 1913*Leguminaia haasi* Kobelt, 1915

Iraq; Kara-su in Syria; Lake Antioch, Syria.

Leguminaia saulcyi Bourguignat, 1852*Unio michonii* Bourguignat, 1852*Unio tripolitanus* Bourguignat, 1852*Pseudodon chantrei* Locard, 1883*Leguminaia locardi* Simpson, 1900

Germain (1911) has created a new subgenus *Pseudoleguminaia* for this species, which is characterized by oval shape, but I am unwilling to recognize it.

Lake Antioch; rivers of Syrian littoral to the Nahr-el-Audja near Jaffa in the south.

Genus *Pseudodontopsis* Kobelt, 1913*Pseudodontopsis euphraticus* Bourguignat, 1852*Unio opperti* Bourguignat, 1856*Pseudodon churchillianus* Bourgui-
gnat, 1857*Monocondylaea rhomboidea* Lea,
1859*Pseudodon pachyolenus* Bourgui-
gnat, 1881 (nomen nudum)*Pseudodontopsis piestius* Kobelt,
1913*Pseudodontopsis babylonicus* Kobelt,
1913Iraq; *churchillianus* is said to come from Konieh.Genus *Microcondylaea* von Vest, 1866*Microcondylaea compressa* Menke, 1830*(?)Anodonta uniopsis* Lamarck,
1819; unidentifiable*Unio depressa* C. Pfeiffer, 1825 (not
Lamarck, 1819)*Unio bonellii* Férussac in Ross-
maessler, 1835*Unio bonellii* var. *curvata* Ross-
maessler, 1835*Unio moreleti* Drouët, 1879*Microcondylus crassus* Drouët, 1879*Microcondylus gibbosus* Drouët,
1879*Microcondylus squamosus* Drouët,
1879*Microcondylus truncatus* Drouët,
1879*Microcondylaea servaini* Bourgui-
gnat, 1883*Microcondylaea doriae* Bourgui-
gnat, 1883*Microcondylaea gestroi* Bourguignat,
1883*Leguminaia pedemontana* Pollonera,
1889*Leguminaia craverii* Pollonera,
1889*Microcondylaea bonellii* f. *parisii*
Kobelt, 1913*Microcondylaea bonellii* f. *levicensis*
Kobelt, 1913*Pseudanodonta depressa* var. *augusti*
Graziadei, 1933

Po basin; Adige basin; littoral rivers east of Adige to and comprising the Isonzo.

Subfamily **Quadrulinae**

This holarctic subfamily has only one representative in the palearctic region at the present time, *Psilunio* Stefanescu; but in the Pliocene there were more quadruline genera in Europe, which were closely related to the modern east-Asiatic genera *Cuneopsis* Simpson and *Lamprotula* Simpson. The center of distribution of the quadrulines is North America.

The quadruline nature of *Psilunio* was proved by the study of its anatomy (Haas, 1920, 1924).

Genus **Psilunio** Stefanescu, 1896*Rhytia* Stefanescu, 1896*Rhombunio* Germain, 1911**Psilunio acarnanicus** Kobelt, 1879*Unio acarnanicus* var. *messenicus*
Westerlund, 1879*Unio pamisinus* Drouët, 1894

Western Greece, in Lake Vrachori; in Messenia and in the Eurotas River.

Psilunio littoralis Lamarck, 1801**Psilunio littoralis littoralis** Lamarck, 1801

Unio brevalis Lamarck, 1819
Unio subletragonus Michaud, 1831
Unio draparnaldii Deshayes, 1831
Unio pianensis Farines, 1833
Unio cuneatus Jacquemin, 1835
Unio rotundatus Mauduyt, 1839
Unio barraudi Bonhomme, 1840
Unio bigerrensis Millet, 1843
Unio moulinianus Dupuy, 1850
Unio astierianus Dupuy, 1850
Unio rhomboideus Moquin-Tandon,
 1855
Unio unduliferus Küster, 1861
Unio subreniformis Bourguignat,
 1863
 †*Unio hippopotami* Bourguignat,
 1869

Unio rathymus Bourguignat in
 Locard, 1882
Unio gaudiensis Drouët, 1888
Unio pacomei Bourguignat in
 Locard, 1889
Unio circulus Bourguignat in
 Locard, 1893
Unio sphaericus Bourguignat in
 Locard, 1893
Unio ovuliformis Locard, 1893
Unio rhysopterus Drouët, 1894
Unio circinatus Drouët, 1894
Unio mauduyti Germain, 1897
Unio littoralis var. *taginus* Kobelt,
 1903
 †*Unio kinkelini* Haas, 1910
Unio batavus catalonicus Haas, 1921

Subfossil in the Rhine basin and in South England; recent in France, Iberian Peninsula with the exception of the southern part.

Psilunio littoralis umbonatus Rossmäessler, 1844

(?)*Unio incurvus* Lea, 1831; said to
 have come from Gibraltar, un-
 identifiable
Unio hispalensis Kobelt, 1887

Unio calderoni Kobelt, 1887
Unio calderoni var. *salvadori* Wes-
 terlund, 1892

Southern part of Iberian Peninsula.

Psilunio littoralis komarowi O. Boettger, 1880

Armenia.

Psilunio littoralis semirugatus Lamarek, 1819*Unio rothi* Bourguignat, 1863*Unio emesaensis* Lea, 1864*Unio simonis* Tristram, 1865*Unio timius* Bourguignat in Locard, 1883*Unio galilaei* Locard, 1883*Unio luynesi* Locard, 1883*Unio rhomboidopsis* Locard, 1883*Unio tinctus* Drouët, 1893*Unio rollei* Kobelt, 1895*Unio graeteri* Kobelt, 1913*Unio babensis* Kobelt, 1913*Unio naegelei* Kobelt, 1913*Unio berocus* Kobelt, 1913*Unio halepensis* Kobelt, 1913*Unio halepensis* var. *cazioti* Kobelt, 1913*Unio corbiculiformis* Kobelt, 1913*Unio chinnerethensis* Preston, 1913*Unio salamboana* Pallary, 1929

Syria; Jordan basin in Palestine.

Psilunio littoralis homsensis Lea, 1864*Unio episcopalis* Tristram, 1865*Unio barroisi* Drouët, 1893*Margaritana syriaca* Pallary, 1929

"*Margaritana*" *syriaca* is an unmistakable *Psilunio*, in spite of its elongated, ear-shaped shell; this becomes evident by the umbonal sculpture, the hinge, the roundish juvenile shell, the deep umbonal cavity, and other characters, and Pallary (1929) quite inadequately arranged it with *Margaritana* (= *Margaritifera*). It is by no means impossible that *homsensis* Lea can not be retained as a separate subspecies, but has to be united with *semirugatus*, of which it may be a rather extraordinarily elongated form. *Unio tinctus* Drouët, living together with *homsensis* in the Orontes River, combines a rounded, typical *Psilunio* shape of the shell with the purple nacre, by which *homsensis* is characterized. *Unio modiola* Preston, 1912, which I place with *Unio crassus bruguierianus* Bourguignat, may as well belong to *homsensis*; its description is too poor to make possible a decision on this point.

Orontes River, Syria.

Psilunio littoralis delesserti Bourguignat, 1853*Unio ferussacianus* Lea, 1868*Unio wagneri* Kobelt, 1895*Unio tracheae* Kobelt, 1895*Unio lycicus* Kobelt, 1895*Unio deschampsi* Kobelt, 1913*Unio langloisi* Kobelt, 1913*Unio abrus* Kobelt, 1913*Unio blanchianus* Kobelt, 1913

Littoral rivers of Palestine.

Psilunio littoralis fellmanni Deshayes, 1847*Unio ravoisieri* Deshayes, 1847*Unio moreleti* Deshayes, 1847*Unio unduliferus* Küster, 1861*Unio maccarthyanus* Bourguignat, 1866*Unio mauritanicus* Bourguignat, 1868*Unio ksibianus* Mousson, 1873*Unio jolyanus* Bourguignat in Kobelt, 1886

Unio zenaticus Letourneux in Bourguignat, 1887

Unio rouirei Bourguignat, 1887

Unio marteli Pallary, 1918

Unio rhomboideus var. *bucheti* Pallary, 1921

Unio tiffeticus Pallary, 1927

Rhombunio asananus Pallary, 1928

Unio unduliferus Küster (Martini-Chemnitz, 9, pt. 2, Unio, p. 162, pl. 46, fig. 4, 1861) described as probably of South American origin, certainly belongs here.

North Africa.

Subfamily Anodontinae

Contains the holarctic genus *Anodonta*; also *Pseudanodonta*, which is a close relative of the Asiatic genus *Pilsbryconcha*, and *Gabillotia*, a European endemism.

Genus *Anodonta* Lamarck, 1799

Anodonta cygnea Group

Anodonta cygnea Linnaeus, 1758

Under this name I combine all the palearctic anodontas, with one exception, which will be mentioned below. The enormous plasticity and variability of the *Anodonta* shell have led to the proposal of many hundreds of specific names, in which not only Bourguignat and his school have shared; for even conscientious scientists of the other camp have again and again been induced by apparently characteristically shaped pond-mussels, to propose new names, being convinced of having separable species or, at least, local races before them.

There is only one—or, according to the most modern researches, two—fundamental species of *Anodonta* in the palearctic region, to which all the many different-looking “species” that have been described can be reduced. I myself, when beginning my studies on unionids in 1910, was inclined to recognize two such fundamental species, the broader *Anodonta cygnea* and the more elongated *Anodonta cellensis* Schroeter. This point of view I have meantime abandoned; it is at present maintained by Franz in Jena, and by his school, who recognize *Anodonta cygnea* and *Anodonta piscinalis* Nilsson as fundamental species. I am of the opinion that all the palearctic anodontas belong to one unique species, with the exception above indicated. It is worth mentioning that Clessin also arrived at the same conviction; he described an *Anodonta mutabilis* which was to comprise all the palearctic pond-mussels, including even their typical Linnaean species, *cygnea*.

Anodonta cygnea, as it is here understood, lives throughout the palearctic region. In northern and central Europe, it is a relatively common species, but becomes less so in the Mediterranean basin, is scarce in North Africa and in Asia Minor, and is only locally known from central Asia; for instance, from Samarkand (*samarkandensis* Kobelt), Buchara (*sogdiana* Kobelt, *bactriana* Rolle), the Seisan-Nor (*seisanensis* Kobelt), the Lena River (*lenae* Shadin), Lake Baikal (*sorensiana* Dybowsky, *sorica* Dybowsky) and its tributary, the Selenga River (*nova* Dybowsky, *selengensis* Dybowsky).

Pallary has described (1933) a subgenus *Euphrata*, based upon *Anodonta bahlikiana* (nomen nudum) from Mesopotamia, and Bédé has created (1932) another subgenus, *Liouvillea*, which rests on his Moroccan species *pallaryi* and *théryi*. Not having seen them, I cannot form a judgment of them; but knowing Pallary's tendency to publish new names for merely phaenotypic mutations, I rather strongly suspect that both subgenera are founded upon environmentally shaped and only apparently separable forms of *Anodonta cygnea*.

As I am unwilling to give up this point of view, it is unnecessary for me to give a complete synonymic list of *Anodonta cygnea*. The anodontas contained in Westerlund's *Fauna* constitute such a list up to 1890, and the following enumeration includes only such "species" as have been described since that date.

Anodonta ataxia Baichère, 1891
Anodonta culoziana Nicolas, 1891
Anodonta suevica Kobelt, 1891
Anodonta borealis Kobelt, 1891
Anodonta recurvirostris Kobelt, 1892
Anodonta gallensteini Kobelt, 1892
Anodonta graeca Drouët, 1892
Anodonta quelleneci Drouët, 1892
Anodonta lepida Drouët, 1892
Anodonta lhotellerii Drouët, 1892
Anodonta discoidea Drouët, 1893
Anodonta baudoniana Drouët, 1893
Anodonta planulata Drouët, 1893
Anodonta viridiflava Drouët, 1893
Anodonta macella Drouët, 1893
Anodonta lanceolata Drouët, 1893
Anodonta limbata Drouët, 1893
Anodonta laevigata Drouët, 1893
Anodonta retziana Drouët, 1893
Anodonta gregalis Drouët, 1893
Anodonta aeneolina Drouët, 1893
Anodonta pulchella Drouët, 1893
Anodonta fuliginea Drouët, 1893
Anodonta errica Kobelt, 1894
Anodonta latirostris Drouët, 1894
Anodonta mollis Drouët, 1894
Anodonta adusta Drouët, 1894

Anodonta glaucina Drouët, 1894
Anodonta prasina Drouët, 1894
Anodonta nobilis Drouët, 1894
Anodonta bicolor Drouët, 1894
Anodonta valentina Drouët, 1894
Anodonta emacerata Drouët, 1894
Anodonta cilicica Kobelt, 1895
Anodonta simulans Drouët, 1895
Anodonta sogdiana Kobelt, 1896
Anodonta bactriana Rolle, 1897
Anodonta fedderseni Westerlund, 1898
Anodonta goesi Westerlund, 1898
Anodonta anura Westerlund, 1898
Anodonta apala Locard, 1899
Anodonta pelophila Locard, 1899
Anodonta simoesi Locard, 1899
Anodonta portensis Locard, 1899
Anodonta leprosa Locard, 1899
Anodonta retteri Drouët, 1899
Anodonta chivoti Germain, 1904
Anodonta bourrieri Rochebrune, 1904
Anodonta falcata var. *fluviatica* Rosen, 1905
Anodonta (piscinalis var.) *portulana* Kobelt, 1908

- | | |
|---|--|
| <i>Anodonta piscinalis transsylvanica</i>
Haas, 1911 | <i>Anodonta jesseni</i> Schlesch, 1926 |
| <i>Anodonta seisanensis</i> Kobelt, 1912 | <i>Anodonta (Liouvillea) pallaryi</i> Bédé,
1932 |
| <i>Anodonta anatina</i> var. <i>circularis</i>
Hilbert, 1912 | <i>Anodonta (Liouvillea) théryi</i> Bédé,
1932 |
| <i>Anodonta (cyrea</i> var.) <i>samarkandensis</i>
Kobelt, 1913 | <i>Anodonta (Euphrata) bahlikiana</i>
Pallary, 1933 (nomen nudum) |
| <i>Anodonta piscinalis</i> var. <i>sorica</i>
Dybowsky, 1913 | <i>Anodonta cygnea</i> var. <i>armenica</i>
Ovtshinnikov, 1935 |
| <i>Anodonta complanata</i> var. <i>sorensiana</i>
Dybowsky, 1913 | <i>Anodonta anatina</i> var. <i>petshorica</i>
Shadin, 1938 |
| <i>Anodonta nova</i> Dybowsky, 1913 | <i>Anodonta anatina</i> var. <i>lenae</i> Shadin,
1938 |
| <i>Anodonta cellensis</i> var. <i>selengensis</i>
Dybowsky, 1913 | <i>Anodonta piscinalis</i> var. <i>volgensis</i>
Shadin, 1938 |
| <i>Anodonta waterstoni</i> Tomlin, 1923 | |

The genus *Cristaria* Schumacher, so widely distributed in eastern Asia, does not form part of the actual palearctic fauna. Nevertheless, some lacustrine European *Anodonta cygnea* which have acquired the characteristic shell features of *Cristaria*, i.e., a symphynote shell and a kind of hinge composed of claustra, may be considered as convergent forms; so the Danubian *Anodonta cygnea*, upon which Bourguignat (1881) based his genus *Colleopterum*, those from Lake Balaton (Hungary), Lake Doiran (Macedonia), and from the Albufera de Valencia (Spain). But it must be emphasized that the shell features we just mentioned are genotypically anchored in *Cristaria* and only phenotypically developed in lacustrine European *Anodonta cygnea*.

Anodonta woodiana Group

With this East-Asiatic species, to which the group of the North American *Anodonta grandis* Say, 1829, belongs, I place the following palearctic species:

Anodonta vescoiana Bourguignat, 1857

Anodonta vescoiana var. *mesopotamica* Mousson, 1874

Anodonta schlaeflii Mousson, 1874

Iraq. If Bourguignat's information, that his *Anodonta vescoiana* originated from Konieh, Asia Minor, is correct, then his *Anodonta apollonica* and *Anodonta taurica*, both coming from the Lake of Apollonia, Asia Minor, may belong to the *woodiana* group.

Genus Pseudanodonta Bourguignat, 1877

Upon this genus opinions still differ widely. While some scientists do not regard it even as a subgenus of *Anodonta*, I consider it as a separable genus, well characterized by its peculiar shape and by the features of its glochidium; it is most closely related to the genus *Pilsbryconcha* Simpson of southeastern Asia. Quite in con-

trast with *Anodonta*, *Pseudanodonta* forms local races, but it is so variable that there is as yet no agreement about these local races or even about its fundamental species. Thus the arrangement given below will soon need amendment.

Pseudanodonta elongata Holandre, 1836

- | | |
|---|---|
| <i>Anodonta grateloupiana</i> Gassies, 1849 | <i>Pseudanodonta isarana</i> Bourguignat, 1890 |
| <i>Anodonta grateloupiana</i> var. <i>globosa</i> Gassies, 1849 | <i>Pseudanodonta mongazonae</i> Bourguignat, 1890 |
| <i>Anodonta normandi</i> Dupuy, 1849 | <i>Pseudanodonta lacustris</i> Servain, 1890 |
| <i>Anodonta jobae</i> Dupuy, 1849 | <i>Pseudanodonta rivalis</i> Bourguignat, 1890 |
| <i>Anodonta siliqua</i> Küster, 1852 | <i>Pseudanodonta septentrionalis</i> Locard, 1890 |
| <i>Pseudanodonta rayi</i> Bourguignat, 1881 | <i>Pseudanodonta aploa</i> Bourguignat, 1890 |
| <i>Pseudanodonta ligurica</i> Bourguignat, 1881 | <i>Pseudanodonta euthymei</i> Pacôme, 1890 |
| <i>Anodonta dorsuosa</i> Drouët, 1881 | <i>Pseudanodonta morini</i> Locard, 1890 |
| <i>Pseudanodonta locardi</i> Locard, 1882 | <i>Pseudanodonta cazioti</i> Bourguignat, 1890 |
| <i>Pseudanodonta ararisana</i> Locard, 1882 | <i>Pseudanodonta pacomei</i> Bourguignat, 1890 |
| <i>Pseudanodonta servaini</i> Bocard, 1885 | <i>Pseudanodonta trivurtina</i> Bourguignat, 1890 |
| <i>Anodonta pachyproktus</i> Borchherding, 1889 | <i>Pseudanodonta brebissoni</i> Locard, 1890 |
| <i>Anodonta fusiformis</i> Borchherding, 1889 | <i>Anodonta albica</i> Drouët, 1893 |
| <i>Anodonta microptera</i> Borchherding, 1889 | <i>Anodonta</i> (<i>Pseudanodonta</i>) <i>acutalis</i> Drouët in Westerlund, 1894 |
| <i>Pseudanodonta rothomagensis</i> Locard, 1890 | <i>Pseudanodonta dumasi</i> Locard, 1894 |
| <i>Pseudanodonta nantelica</i> Bourguignat, 1890 | <i>Pseudanodonta beryacensis</i> Dumas, 1894 |
| <i>Pseudanodonta pechaudi</i> Bourguignat, 1890 | <i>Pseudanodonta limosina</i> Dumas, 1895 |
| <i>Pseudanodonta imperialis</i> Servain, 1890 | <i>Pseudanodonta occidentalis</i> Coutagne, 1895 |
| <i>Pseudanodonta arnouldi</i> Pacôme, 1890 | <i>Pseudanodonta nicarica</i> Haas, 1908 |

Atlantic western Europe to and comprising the Weser in the East; England; France approximately to the Garonne in the south.

Pseudanodonta complanata Rossmäessler, 1835

- | | |
|---|--|
| <i>Anodonta klettii</i> Rossmäessler, 1835 | <i>Pseudanodonta complanata silesiaca</i> Kobelt, 1911 |
| <i>Pseudanodonta nordenskiöldii</i> Bourguignat, 1881 | <i>Pseudanodonta maelarensis</i> Kobelt, 1911 |

Pseudanodonta borealis Kobelt, 1890, from Newa River, Russia, which occasionally is cited as belonging here, is based upon a misunderstood long and slender form of *Anodonta cygnea* Linnaeus.

Sweden; Atlantic Central Europe from the Elbe in the west to Finland in the east.

Pseudanodonta middendorffi Siemaschko, 1848

Pseudanodonta middendorffi middendorffi Siemaschko, 1848

Anodonta complanata jijiana Nico-
dim, 1909

Pseudanodonta euzina Rossmas-
sler in Kobelt, 1911

Anodonta complanata sobriewskii
Rosen, 1925

Tributaries of the Black Sea, east of the Danube.

Pseudanodonta middendorffi compacta Zeebor, 1851

Alasmodonta penchinati Bourgui-
gnat, 1870

Alasmodonta berlandi Bourguignat,
1870

Pseudanodonta praeclara Bourgui-
gnat, 1881

Pseudanodonta letourneuxi Bour-
guignat, 1881

Pseudanodonta danubialis Bourgui-
gnat, 1881

Pseudanodonta mecyna Bourgui-
gnat, 1881

Pseudanodonta pančiči Bourgui-
gnat, 1881

Pseudanodonta scrupea Bourgui-
gnat, 1881

Pseudanodonta rosmaessleri Bour-
guignat, 1881

Pseudanodonta ellipsiformis Bour-
guignat, 1881

Pseudanodonta savensis Kobelt,
1911

Pseudanodonta compacta küsteri
Haas, 1913

Pseudanodonta compacta küsteri apparently hybridizes with the Atlantic *P. elongata* where their ranges overlap in the Regnitz basin, tributary to the Rhine via the Main (Haas and Schwarz, 1913).

Basin of the Danube.

Genus **Gabillotia** Servain, 1890

This genus is endemic in the palearctic region and is most closely related to *Anodonta*.

Gabillotia pseudodopsis Locard, 1883

Gabillotia locardi Servain, 1890

Known only from Lake Antioch in Syria.

APPENDIX

Unionids which have erroneously been attributed to the palearctic region:

Unio bagdadensis Bourguignat, 1852.—Said to come from Baghdad, but is a synonym of *Caelatura egyptiaca* Caillaud from the Nile.

Unio eucyphus Bourguignat, 1857.—Believed to have been found in the Skamander River, northern Asia Minor, but equally identical with *Caelatura egyptiaca* Caillaud from the Nile.

Unio bythinicus Kobelt, 1893.—Not from Asia Minor, as believed by Kobelt, being nothing but *Elongaria orientalis* Lea from Java.

Unio lapidosus Kobelt, 1893.—Supposed to be from the Euphrates River; it is *Lampsilis (Disconaias) discus* Lea from North Mexico.

Unio wolwichi Morelet, 1845.—This species, which was said to have been found at the banks of the River Tajo in Portugal, has been proved to be a synonym of *Diplodon parallelipipedon* Lea from the Río de la Plata.

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