THE CLASSIFICATION AND GEOGRAPHICAL DISTRIBUTION OF THE PEARLY FRESH-WATER MUSSELS.

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The naiades, or pearly fresh-water mussels, have a universal distribution throughout the ponds, lakes, and streams of the world, not only on the continents, but on most of the larger and some of the smaller islands. Some of the genera have probably extended back with but little change to the beginning of Mesozoic or possibly well into Paleozoic time; hence their study is an extremely interesting one, which may help us in obtaining a knowledge of the distribution of other life, and the mutations of land and sea in time past.

I. CLASSIFICATION OF THE NAIADES.

In 1806[1] and 1812[2] Lamarck established the family of Nayades, which he afterwards changed to Naiades,[3] and in which he placed two genera, *Unio* and *Anodonta*. In 1819 he added the genera *Hyria* and *Iridina*, but placed *Castalia* wrongly in the family Trigoniacea, an error which was rectified by Ferussac in 1822, by Latrielle in 1825, by Blainville in the same year, and by Menke in 1828. In 1820 Rafinesque[4] created the family Pediferia for *Unio*, *Anodonta*, and several related genera, including *Cyclas*.

Blainville in 1825[5] refused to accept the classification of Lamarck, and made a family Submytilacea, with the genera *Anodonta*, *Unio*, and *Cardita*, thus returning to the errors of Poli, who in 1795[6] gave the name *Limnæa* to animals inhabiting the shells belonging to the genera *Unio*, *Anodonta*, and *Cardita*.

The name Unionidæ was created in 1828 by Fleming,[7] and adopted afterwards by Gray,[8] Swainson,[9] and other modern authors.[10]

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[1] Philosophie Zoologique, p. 328, 1805.

[2] Extrait du Cours de Zool., p. 106, 1812.

[3] Phil. Zoologique, I, p. 318, 1830.

[4] Ann. Génér. Sciences Physiques, p. 290, 1820.

[5] Man. de Malacol. et Conchyliol., p. 537, 1825.

[6] Testacea Utriusque Siciliæ, II, p. 253, 1795.

[7] Hist. British Animals, p. 408, 1828.

[8] In Turton, A Manual of the Land and Fresh-water Shells, p. 288, 1840.

[9] Treatise on Malacology, p. 259, 1840.

[10] The names of Lamarck, Rafinesque and Blainville can not be considered, since it is a rule in nomenclature that a family or subfamily name must be founded on one of its principal genera. Hence *Unionidæ* must take precedence.

Swainson in 1840[1] divided the Unionidæ into five subfamilies, from a study of the shell: First, Unioninæ (*Unio*, Lamarck; *Æglia*, Swainson; *Mysca*, Turton); Second, Hyrianæ (*Iridea*, Swainson; *Castalia*, Lamarck; *Hyria*, Lamarck; *Hyridella*, Swainson); Third, Iridininæ (*Iridina*, Lamarck; *Calliscapha*, Swainson; *Mycetopus*, A. d'Orbigny); Fourth, Anodontinæ (subgenera *Anodon*, Lamarck, etc.); Fifth, Alasmodontinæ (*Alasmodon*, Say).

Gray in 1847,[2] following the anatomical papers of A. d'Orbigny and other authors, proposed to form a new family, Mutelidæ, with the genera *Mutela*, *Leila*, *Pleiodon*, and a part of *Paxyodon* of Schumacher. These genera differ from *Unio* by the presence of two distinct siphons, and were separated from the Unionidæ for that reason. Previously Gray, in 1842,[3] had made a family Mycetopodidæ for the genus *Mycetopoda*, d'Orbigny, on account of the foot presenting a remarkable conformation.

The views of Gray have been adopted by many authors, who have admitted among the Naiades of Lamarck two or three families; others an equal number of subfamilies. Thus H. and A. Adams[4] admit two families: Unionidæ (subfamilies Unioninæ and Mycetopinæ) and Mutelidæ. Chenu[5] enumerates three subfamilies: Unioninæ, Mycetopinæ, and Iridinæ; Gill,[6] three families: Unionidæ, Iridinidæ, and Mycetopodidæ; Clessin,[7] two subfamilies, to which he gave the names generally adopted for the families—Unionidæ and Mutelidæ; Tryon,[8] three families: Unionidæ, Iridinidæ, and Mycetopodidæ; and Fischer,[9] two subfamilies: Unioninæ and Mutelinæ.

We see, then, that all the authors agree to make two grand divisions among the Naiades of Lamarck, based upon the fact of the siphons being more or less complete. The other organs of the animals, which to a lesser extent serve for purposes of classification, have been examined by Troschel[10] and characterize the nine genera which are known in the family Unionidæ. The anatomical classification of Agassiz[11] is not applicable to these mollusks in North America. Isaac Lea[12] attempted to classify the Unionidæ by the external characters of the shell, the hinge (dorsal border symphynote or non-symphynote), the sculpture and the form. This classification is, of course, largely artificial,

[1] Treatise on Malacology, p. 377, 1840.

[2] Proc. Zool. Soc. London, p. 197, 1847.

[3] Syn. Brit. Mus., pp. 81, 92, 1842.

[4] The Genera of Recent Mollusks, II, p. 505, 1857.

[5] Manuel Conchyl. et Paléont. Conch., II, pp. 136, 147, 1862.

[6] Arrang. Families of Mollusks, p. 20, 1871.

[7] Malakozool. Blatt, XXII, p. 12, 1875.

[8] Struc. and Syst. Conch., III, p. 237, 1884.

[9] Manuel de Conchyliol., p. 998.

[10] Wiegmann's Archiv, XII, 1847.

[11] In W. Stimpson, The Shells of New England, 1851. See also Archiv für Naturg., 1852, p. 41.

[12] A Synopsis of the Family Unionidæ, pp. xxiv, xxv, 1870, and in earlier editions.

since it brings together many unrelated species and widely separates others that have strong affinities. In justice to Dr. Lea it should be said that he regarded it as merely a temporary expedient, to be superseded by a more natural method when a better knowledge of the soft parts could be obtained.

H. von Ihering has recently proposed a new classification[1] of the Naiades, taking the form of their larvæ as a distinctive character. While the species of Europe and North America have a larva (Glochidium) furnished with a bivalve shell, which can completely inclose it, a certain number of forms of South America pass through a peculiar stage, named *Lasidium* by v. Ihering, in which the larva is formed of three segments, carrying only a small single shell on the middle part. The same stage is probably passed through by the young of several African genera. In consequence he divides the Naiades into two families—the Mutelidæ (genera *Leila*, Gray; *Fossula*, Lea; *Mycetopus*, A. d'Orbigny; *Glabaris*, Gray; *Aplodon*, Spix; *Plagiodon*, Lea; *Solenaia*, Conrad; *Mutela*, Scopoli; *Iridina*, Lamarck; *Spatha*, Lea) and the Unionidæ (genera *Hyria*, Lamarck; *Castalia*, Lamarck; *Castalina*, v. Ihering; *Unio*, Philipsson; *Margaritana*, Schumacher; *Cristaria*, Schumacher; *Pseudodon*, Gould, and *Anodonta*, Lamarck).

The foregoing sketch of the classification of the Naiades is taken in part from the admirable work of Fischer and Crosse on Mexican and Central American mollusks.[2]

In the present state of our limited, and in some cases total lack of knowledge of the anatomy of several of the genera of Naiades, any classification must be more or less tentative. The division of these mollusks by most authors into two families, Unionidæ and Mutelidæ, or two subfamilies, Unioninæ and Mutelinæ, founded upon the incompleteness or completeness of the development of siphons, can not stand. This has been shown by the researches of Lea and d'Orbigny into the anatomy of *Glabaris* many years ago; for while some species of this genus have the mantle closed posteriorly so as to form siphons, in others, which are evidently closely related, the mantle is free. More recently v. Ihering has shown[3] that a given species of his genus *Castalina* may have an animal which has the two siphons completely developed, thus placing it with the Mutelidæ, or it may be that of a perfect *Unio*, having no siphons at all, thus belonging with the Unionidæ. The same thing is true to some extent in the well-known genus *Castalia*, and it is quite probable that this character will be found to vary in other genera of Naiades.

So far as conchological characters are concerned, *Castalia* (and with it *Castalina*, which has been separated from it) and *Hyria*, though hitherto placed with the Mutelidæ, are evidently members of the

[1] Archiv für Naturgeschichte, p. 52, 1893.

[2] Mission Scientifique au Mexique et dans l'Amerique Centrale, 7th part, II, p. 505, 1894.

[3] Zool. Anzeiger, Nos. 386 and 381, 1891–92, pp. 1–14.

Unionidæ.[1] The Castalias, Castalinas and Hyrias have the radial beak sculpture which is found on every species of South American *Unio*, but on none of the other Naiades. The hinge teeth consist of cardinals and laterals, the former being more divided than is usual in *Unio*, though there are some species in the latter genus which have the cardinals separated into several parts. The laterals are Unionoid, but are more or less vertically striated in *Castalia* and *Castalina*, and sometimes, to a certain extent, in *Hyria*. This latter character, however, is not generic or even specific. The hinge teeth in the bivalves were undoubtedly developed in order to lock the valves of such species as were subject to shock, and prevent them from being twisted out of place. I believe it will be found that in most, if not all cases where they are needed, the shell never opens so far but what they lock one valve with the other. The mantle is carried as a thin, tough, elastic sheet between the hinge plates and over the teeth in the Naiades, and it will be readily seen that any unusual roughening, such as the development of granules or vertical striation, would render them much less liable to slip than if they were smooth. Hence, in many solid-shelled Unionids, especially in elongated species, the character of vertical teeth striation will be found. It is especially developed in many of the heavy Chinese Unios, and I have noticed it in *Unio parallelopipedon* of South America, in *Unio shepardianus*, *ligamentinus*, *crassus*, *luteolus*, *anodontoides*, and others, of the United States.[2]

Unio kraussi, Lea, of Surinam, of which the type is in the National Museum (No. 84379), seems to stand about midway, conchologically, between *Unio* and *Castalia*, but in a different direction from *Castalina*. It has the strong radial beak sculpture of *Castalia*, especially near the posterior ridge, where it extends more than one-third of the distance from the beaks to the periphery. It is much inflated, and has a form more circular than that of *Castalia*, a brown epidermis and strong concentric sculpture. The teeth stand about midway between those of

[1]Ihering believes that *Hyria* will be found to vary in the character of its mantle openings in the same way that *Castalina* and *Castalia* do. (Zool. Anzeiger, Nos. 380 and 381, 1891-92, p. 5.)

[2]The characters of the teeth of the four genera *Unio*, *Hyria*, *Castalia* and *Castalina*, are very variable. *Unio charruanus*, d'Orbigny, has about 4 strong cardinals and several minor teeth in each valve, besides the ordinary laterals, which, with quite a number of not closely related species from Brazil, show traces of vertical striation. *Unio acutirostris*, Lea, from southern South America, has about 12 denticles in the cardinal area of each valve. In the younger shells there are usually the ordinary compressed cardinals, one in the left valve and two in the right, and as the specimens become adult they split up and assume a very different appearance. *Unio patagonicus*, d'Orbigny, shows this transition finely. In *Unio gibbosus*, Barnes, of the United States, the laterals are quite often somewhat vertically striated, and sometimes have oblique striæ pointing anteriorly or posteriorly. Specimens of *Castalina martensi*, v. Ihering, in the National Museum (No. 125736), plainly show both vertical and oblique striæ on the laterals in the same hinge, the oblique lines being finer and partly laid over the vertical ridges.

Unio and *Castalia*, the cardinals being somewhat elongated and broken; and these, with the laterals, are more or less corrugated, and show traces of vertical striation. It was named *Castalia sulcata* by Krauss, but was placed in *Unio* by Lea, and as its specific name was preoccupied in the latter genus, he changed it to *kraussi*.

Castalia duprei, Lea, shows characters in the teeth which approach *Hyria*. It is a smooth, light yellowish green shell of thin texture, triangular in outline, and much inflated, with an excessively high, sharp keel running from the beaks to the posterior basal margin. The cardinals are much elongated and sometimes broken, as in *Hyria*. The arch of the hinge plate under the beaks is high and sharp. There is no radiating sculpture, and there appears to be none of any kind on the beaks. I agree with von Ihering that this should quite probably be placed in a new genus.

Hyria, on the other hand, seems to be equally connected with *Unio*. In *U. stevensi*, Lea, from northern South America, the form, sculpture, and external appearance are decidedly like that of *Hyria corrugata*, it being furnished with quite a distinct anterior dorsal wing and a slight hint at one posteriorly. This species of *Hyria* is sometimes destitute of a wing behind, and this part of the shell occasionally ends in a somewhat obtuse angle. The hinge teeth of *Unio stevensi* partake, to some extent, of the characters of both genera, though they are more Unionoid than Hyrioid. The species should probably, however, be placed in *Hyria*.

Unio ortoni, Lea, of which the type—a single left valve, and the only specimen I have seen—is in the Museum collection (No. 25430, U. S. N. M.), approaches the form of *Unio* somewhat, but its sculpture is very much like that of *Hyria*, and its cardinals are multifid. It is very doubtful which genus should receive it, and it quite probably should have a new generic name.

I think there can be little doubt that the relation between these four genera, *Unio*, *Hyria*, *Castalia* and *Castalina*, is a close one anatomically and conchologically, and that they must all be placed in one family in any natural arrangement. Yet in a classification based upon the development or want of development of the siphons, the former has been made the type of one family, the Unionidæ, and the other three have been placed in another, the Mutelidæ. *Glabaris*, which, as I have shown, may have either perfect siphons or an open mantle, has generally been placed in the genus *Anodonta*, in the Unionidæ, though some authors give it a place in the other family. *Mycetopus*, which has an open mantle, has generally been put in the Unionidæ, but it is, as I expect to show farther on, more likely a member of the Mutelidæ.

So far as I am aware, nothing is known of the larval state of any of the African Naiades, so that the character of the embryo, on which von Ihering bases his classification, can not yet be used in determining the relationships of the peculiarly African genera.

Genus UNIO, Retzius.

It seems to be impossible to ascertain with certainty who is the author of this genus. In 1788 Laurentius Münter Philipsson described it in a thesis delivered under the presidency of his master, Retzius,[1] at the University of Lund, in Sweden, at a public examination for a doctor's degree. Whether Philipsson or Retzius should be credited with the genus can not be positively known, as it is believed by some that the master was the author of the dissertation, which the student merely defended. I am inclined to take this view of the matter, for the reason that Retzius was an author of repute, while it is not known that Philipsson ever gave any attention to natural history or was the author of any genera or species before or since. There was no special designation of any type, but the species were mentioned in the following order: *Unio margaritiferus*, *U. crassus*, *U. tumidus*, *U. pictorum*, *U. ovalis*, *and U. corrugatus*.

We can not consider the genus *Margaritana*, founded on the absence of lateral teeth, a valid one, because the first species which is mentioned in this list is the type of the genus *Unio* (and also of *Margaritana*, founded many years later), and this is placed by itself in a section which is designated as lacking lamellar teeth,[2] while the other five species are put in a second section, characterized by lateral teeth. Therefore, in case of a generic separation, founded on the presence or absence of lamellar teeth, the species wanting them would have to be placed in the genus *Unio*, and another name given to the forms having both sets of teeth. But, as I shall show farther on—I think satisfactorily—that the different species usually placed in *Margaritana* are merely Unios with ordinarily imperfect teeth, we can use Retzius' generic name to include all the forms that are commonly placed in the two genera.

The genus *Unio* is by far the most numerous in species, and is the most widely distributed of any of the Naiades, as well as the most variable in its characters. It is found in the fresh waters of all the continents, especially in the rivers and streams, while the nearly related *Anodonta* is more commonly an inhabitant of lakes and ponds.

In the East Indian Archipelago it is met with in perhaps all the larger islands, extending east into the Solomon group; it is abundant in Australia, New Zealand, Tasmania, the Philippines and Japan. It is found in Ceylon, Madagascar, the British Isles, and in Cuba. The only considerable continental areas in which it is believed not to occur are that part of North America lying south of the fortieth parallel of north latitude, having a drainage into the Pacific; the extreme arctic regions, and a considerable area of the Sahara and Gobi deserts.

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[1] Dissertatio historico-naturalis, sistens nova testaceorum genera, p. 16. The following is the original diagnosis: "Unio.—Animal ascidia. Testa bivalvis, æquivalvis, æquilatera.—Cardo. Dens ani in valvula dextra solidus, subintrusus, in sinistra duplex; omnes crenulati. In plurimus dens vulvæ longitudinalis lamellaris intra sinistræ valvulæ bilamellarem.

[2] Dente vulvæ nullo, sed margo horizontalis.

On account of the great variability of characters of the shell and animal of many of the different species, a number of conchologists, among whom are Rafinesque,[1] Swainson,[2] Agassiz[3] and others, have attempted to divide the genus into other genera and subgenera. These groups are, I believe, unworthy of any scientific standing on account of the absolute blending of conchological characters in many cases and the great variability of the soft parts.

Ihering has stated[4] that the South American Unios, so far as his knowledge goes, develop the embryos in the inner branchiæ and not in the outer. Sutor has examined a number of the New Zealand Unios in order to determine whether they were closely related anatomically to those of South America, and he states[5] that he found nearly all the embryos in the inner branchiæ. Conchologically there is a very close relation between the Unios of New Zealand, Australia, Tasmania and South America, and there can be little doubt that the species throughout have this anatomical peculiarity. In addition to this, the embryos of the austral species seem to be mostly destitute of hooks, and von Ihering believes that they do not pass a part of their larval stage encysted on the fins and gills of fishes, as do many of those of the northern hemisphere.[6]

On the other hand, the Unios of the northern hemisphere, so far as is known, bear their embryos in the outer gills, and a considerable proportion of them have hooks. Lea found these appendages in a large number of embryos of Unios and Anodontas, but absent in others. In those of *U. luteolus* he found no hooks, but the nearly related *U. radiatus* was furnished with four small ones, while in some specimens of *Anodonta ovata*, Lea, they were present and in others absent.[7]

It is possible that hooks may be in some cases developed on the embryo at one stage of its existence, and become broken off or obsolete at another, as Lea found some examples in which they were imperfectly developed. Some of the species of Europe have been actually observed attached to the gills and fins of fishes by these hooks, and it is quite probable that many of those of North America have similar habits. During this period of attachment, which occupies two months or more, the larvæ become encysted, and the organs develop, though the shell does not increase greatly in size

So far as I know, all the Unios of South America, south of the Isth-

[1] Mon. des Coq. Biv. Fluv. de la Riv. Ohio, 1820. Ann. Gén. des Sci. Phys., Brux., p. 291.

[2] A Treatise on Malacology, 1840, p. 266.

[3] Archiv für Nat., 1852, p. 42.

[4] New Zealand Journal of Science, I, No. 4 (n. s.), p. 152, 1891.

[5] New Zealand Journal of Science, I, No. 6 (n. s.), p. 250, 1891.

[6] Lea found hooks on the embryos of *Unio peculiaris* and *U. firmus*, two well-known South American species. (Obs., XII, pp. 26, 28.) He also states that *Unio multiplicatus*, Lea, *U. rubiginosus*, Lea, *U. kleiniauus*, Lea, and *U. subrotundus*, Lea, bear the embryos in all four leaves of the branchiæ.

[7] Obs. on the Genus Unio, VI, p. 49, X, p. 89.

mus of Panama, have radial beak sculpture, which sometimes extends well over the body of the shell. I know of no others having this character except *Unio rotundatus*, Lamarck, of Texas and Louisiana, which occasionally exhibits this peculiarity in a slight degree, and which, singularly enough, by its form resembles many of those of South America. The Unios of New Zealand and Australia have, so far as I have been able to observe, curved or imperfectly radial beak sculpture, approaching somewhat that of several of the species of South America. Nearly all the austral forms (excepting those of Africa) have peculiarly compressed cardinal teeth, there being a single one in the right and two in the left valve, sometimes slightly multifid, and between those of the latter valve there is a parallel-sided pit, into which the cardinal of the right valve fits.

I believe that these characters of the shell and embryo, which seem to be reasonably constant, will justify the separation of the Unios of South America, Australia, New Zealand and Tasmania into a subgenus, for which may be used the name *Diplodon*, applied by Spix to *Unio ellipticus* and *U. rotundus* of Brazil.[1] There can be but little doubt that these belong to a different and perhaps older phylum than the species of Europe, Asia, Africa and North America.[2]

The writer has proposed for the American species[3] a subdivision into groups, which should contain species evidently allied by conchological, anatomical and embryological characters. Each group he proposed to call after some widely distributed, abundant and characteristic species belonging to it. Thus an assemblage of solid, oval forms with radiating stripes, common in the Mississippi Valley, is fairly typified by the well-known *Unio ligamentinus* of Lamarck; another of large, rather light, inflated forms from the same region, is represented by *U. rentricosus*, Barnes; a third, consisting of compressed, rhomboid species of the Atlantic drainage, by *U. complanatus;* and to speak of these different divisions as the group of *Unio ligamentinus*, *U. occidens*, or *U. complanatus* group, at once conveys to the mind of the merest novice just what is meant.

The arrangement is not at all a new one, having been used more or less by Lea, Lewis, Call, Marsh, and other conchologists. Recently Fischer and Crosse[4] in monographing the Mexican and Central American Anodontas and Unios, group them in the same way, but apply special names to the sections. It seems to me that such names merely tend to cumber the literature, and uselessly add to the labor of the conchologist in committing them to memory.

In arranging the Naiades of the National Museum, I have become convinced that this system of grouping, as I have outlined it, is practi-

[1] Test, Fluv. Bras., p. 33, 1827.

[2] Lea believed that a natural classification would be founded on the development of the embryos in the internal or external branchiae.

[3] Proc. U. S. Nat. Mus., XV, 1892, p. 405, and Amer. Nat., XXVII, No. 316, p. 353.

[4] Miss. Sci. aux Mex. dans l'Am. Cent., 7th part, II, pp. 517, 555, 1894.

cal, and may be applied to every genus, and that we may thus refer to certain species as belonging to the group of *Unio littoralis*, the group of *Anodonta cygnea*, the group of *Spatha rubens*, and the like.

In 1817 Schumacher[1] subdivided *Unio*, and established the genus *Margaritana* for the *U.* (*Mya*) *margaritiferus* of Linnæus, on account of the fact that it lacked the lateral teeth of the other species. Since that time a number of North American forms have been added to this genus, which has been quite generally accepted as such by modern authors, among whom is Tryon;[2] and as a subgenus by Lea[3] and Fischer.[4]

After a good deal of study of the animal and shell, I am forced to the belief that the different Margaritanas are merely a number of generally not at all closely related species of Unios, in which the lateral teeth—perhaps from various causes to be mentioned hereafter—have become either more or less blurred or depauperated. Some of these, by the characters of the shell and soft parts, evidently group with species of Unios in which the teeth are nearly or quite perfect. In such species as *Margaritana rugosa*, Barnes, *M. confragosa*, Say, *M. complanata*, Barnes, and *M. calceola*, Lea, there are almost always more or less perfectly developed laterals which look as though they were diseased, and have a blurred appearance, the normally single or double lamellæ being divided into several irregularly developed, elongated ridges. Nearly all the species occasionally have as perfect teeth as any Unio. The National Museum possesses a series of young shells of *M. margaritifera* (No. 60878) from the State of Washington, in which most of the specimens have fairly good laterals, and another specimen (No. 86286, U. S. N. M.) in the Lea collection from Massachusetts has cardinals and laterals as perfect as those of any Unio. The same is true of many specimens of this species from Europe and northern Asia. The group which this species typifies is a remarkable one, not only because it shows great variation in the development of the hinge teeth, but for its wide and somewhat peculiar geographical distribution. I place in it the following species, beginning with those which have the laterals least developed and proceeding to forms in which they are perfect:

UNIO MARGARITIFERUS, Linnæus.

All Europe; all northern Asia, including Japan; northwestern North America south to latitude 40° north; Upper Missouri River; Canada and eastern United States south to latitude 40° north, in streams draining into the Atlantic. Cardinals sometimes stump-like and imperfect; laterals generally wanting.

[1] Essai d'un nouveau syst. des habit. des vers testacés, p. 137, 1817.

[2] Structural and Systematic Conchology, p. 240.

[3] Synopsis of the Unionidæ, p. 67 et seq.

[4] Manuel de Conchyliologie, p. 1001.

UNIO MONODONTUS, Say.

Central part of the Mississippi Valley. The teeth are very variable. Cardinals usually quite imperfect, or even rudimentary, though sometimes well developed. Laterals present or absent, and showing every possible degree of development. On account of this great variation the species has been placed about as often in *Unio* as *Margaritana*.

UNIO DECUMBENS, Lea.

Northern Alabama and possibly adjoining States. Shell somewhat resembling *U. monodontus*, but shorter, wider, and with rather better developed teeth.

UNIO HEMBELI, Conrad.

Louisiana. Very closely resembles *Unio margaritiferus*, but is occasionally slightly plicate on the posterior slope. The hinge is very much like that of the latter species, but in all the specimens I have seen the somewhat feeble laterals are always present.

UNIO LAOSENSIS, Lea.

Southeastern Asia. A somewhat smaller species than *U. margaritiferus*, but closely resembling it. The teeth are generally quite well developed.

UNIO CRASSUS, Retzius.

Southern Europe. A large, very heavy species, often becoming arcuate when old, with very strong, well-developed cardinals and laterals.

Conchologically and anatomically, so far as is known, the above species form a very natural group. All the shells are elongated, rounded before and behind; arcuate when old, without angles or sculpture, except in the case of *U. hembeli;* with uniform, rayless, thick, dark epidermis; a curved hinge line, and a hinge plate which is narrowed and rounded just back of the cardinals.

The fact of the presence or absence of lateral or cardinal teeth in certain of the Naiades can not be taken as a proof of generic distinction. In Java, the Philippines, and perhaps certain other islands of the East Indian Archipelago, there is found a group of Naiades having moderate sized, thin shells, of a peculiar lurid purplish or reddish texture, in which the prismatic layer forms a rather wide border.[1]

These species, all of which have greatly compressed teeth, exhibit the most remarkable variation in the degree of their development. Some of them have perfect cardinals and laterals, others to the naked eye are destitute of either, but with a glass show traces of one or both, and

[1]The group is typified by *Unio bengalensis*, Lea, but it is doubtful whether any of the species are found on the continent. According to Hanley and Theobald (Conch. Indica, p. 62), *U. bengalensis* does not come from India, but from the Philippines.

these edentulous forms have been generally called Anodontas. But it often happens that in a lot of individuals of a single species taken from one locality, there will be found every variation from perfect teeth to the merest vestiges. For this reason, and on account of the fact that most of the shells of the group have beautiful, delicate, chevron-shaped beak sculpture, which often extends well on to the body of the shell, of a form quite characteristic of many Oriental Unios, I have no doubt, although we know nothing of the soft parts of the members of this group, that they must be placed with *Unio*. Some of the Margaritanas evidently belong with well-known groups of Unios. In the group of *U. margaritiferus*, I have given examples. *Margaritana rugosa*, Barnes, sometimes approaches so closely in external appearance to *Unio pressus*, Lea, that one is labeled with the name of the other by competent students. It has the same compressed, elongate-rhomboid form, and both are rayed alike; the only essential difference in appearance being that the former is usually somewhat corrugated on the posterior slope, while the latter is without sculpture. Immediately under the beak in the right valve in either species, the hinge plate is almost or entirely cut away. Just before this is a single cardinal, usually somewhat compressed, and on the posterior part of the hinge plate is a more or less perfectly developed lateral. It is usually considerably blurred, even in the *Unio*.

In the left valve there is a triangular, compressed tooth directly opposite the missing portion of the hinge plate in the left valve, which is generally curved backward, and fits into the gap almost perfectly. Just before this is a slightly developed, compressed cardinal, and behind it in the *Unio* two not very perfect, elongated laterals. In the *Margaritana* the laterals of the left valve are generally blurred; sometimes in old shells they are shown as a sort of rounded ridge, but frequently they run more or less diagonally across the hinge plate and point downward posteriorly, as they do in other species of the genus.

In a specimen of *Unio pressus* before me, from White River, Indiana, the same direction is taken by the laterals of the left valve: the lower one running out and ending at the ventral edge of the plate, attaining only a little more than half the length of the other. In rare instances the laterals of the *Margaritana* are nearly perfect, and those of the *Unio* quite blurred. The sculpture of the beaks in both species is much alike, that of the *Unio* being finer. In both, it has a tendency to fall in two loops from points on either side of the beaks. The soft parts of these species are singularly alike.

COMPARISON OF DESCRIPTIONS OF UNIO PRESSUS AND MARGARITANA RUGOSA.

Unio pressus, LEA.	*Margaritana rugosa*, BARNES.
Branchiæ large, rounded below, free nearly the whole length of the abdominal sac.	Branchiæ very large, rounded below, the inner ones much the larger, free the whole length of the abdominal sac.
Palpi small, subangular, united halfway down the posterior edges.	Palpi rather small, subangular, united nearly halfway down the posterior edges.
Mantle thin, slightly thickened on the margins.	Mantle rather thin, much thicker on the margins, blackish on posterior, basal edge.
Branchial opening large, blackish on the edge, and with numerous papillæ.	Branchial opening rather large, with small brown papillæ.
Anal opening rather small, blackish, and without papillæ.	Anal opening rather large, without papillæ.
Superanal opening rather large, united for some distance below, blackish on the edges.	Superanal opening very large, with a dark brown line within, united below.
Color of the mass, dirty white.	Color of the mass, salmon.
Embryonic shell subtriangular, light brown; with hooks.	Embryonic shell triangular, brown; with hooks.

In *Margaritana complanata*, Barnes, which has a beak sculpture quite like that of *Unio pressus*, but coarser, a similar arrangement of teeth is seen, though the shell is heavier, more rounded, and the hinge plate is broader. In many specimens the hinge of the right valve is completely cut away at the beaks, and the cavity is filled by a corresponding tooth in the left valve. *Unio charlottensis*, Lea, from North Carolina, an undoubted member of this group, has a form approaching that of *Margaritana complanata*, but it is rather more elongated.

Margaritana holstonia sometimes exhibits laterals, and in general form, size and texture so closely resembles some of the species of the group of *Unio nashvillensis*, that even Dr. Lea occasionally labeled them wrongly. *M. confragosa*, Say, resembles no other *Margaritana* at all, but approaches more nearly in form to the Unios of the *Lachrymosus* group, and the animal is remarkably close to those of that assemblage. *Unio biesianus*, Heude, of China, has the same kind of blurred laterals as the American Margaritanas, but it appears from conchological characters to be a member of the group of Unios typified by *U. sinensis*, Lea. I have dwelt at length on this part of the subject because the partial or total want of lateral teeth in the species of *Margaritana* is a very curious feature. I can only believe that they are all true Unios whose teeth have been modified or injured by conditions of water, food, bottom, or some other element of environment. In some of them, where the laterals have merely become obsolete, such as those of the *Margaritifera* group, I think the explanation is easy. *M. monodonta* and *hildrethiana* are found in running water under stones, buried slightly in the mud, and *U. hembeli* lives in the nearly stagnant bayous of Louisiana, so that a strong, toothed hinge is not required to hold the valves in place. The heavy-shelled species that live in running water have blurred laterals which appear as if diseased, and it seems not improbable that they may

have been subjected to injurious influences in the matter of food, deleterious water, or the like, until these characters have become more or less fixed. In every group of Unios to which these Margaritanas seem to belong, there are species in which the lateral teeth are more or less imperfect, which seems to show that they have been somewhat susceptible to these injurious influences.

In view of the facts I have presented, and many others that might be brought forward, I am forced to the conclusion that the so-called genus *Margaritana* consists of a number of species of Unios with depauperate cardinal or lateral teeth, or both, and that they will have to be placed in the genus *Unio*.

In southeastern Asia and some of the islands of the East Indian Archipelago there is a peculiar group of Naiades with greatly compressed, somewhat elongated shells, having slightly concentric sculpture, the species of which are almost or quite destitute of teeth, and have wonderfully brilliant, silvery, soft-tinted nacre. This group consists of probably but two or three species, though they have received a large number of names, and is fairly typified by a form which Deshayes and Julien called *Anodonta semperrivens*. Nearly all the specimens of the different species show, when examined with a glass, long, delicate, rudimentary laterals, and often vestiges of cardinals in the shape of a smooth, compressed elevation. One of these Lea named *Monocondylæa compressa*. They do not in any way approach any *Anodonta* I know of, though most of the so-called species have been placed in that genus. Deshayes and Julien[1] state that the animal is pure, milky white, but that they "cannot give a detailed description of it, though it resembles in its characters generally that of the species (of *Anodonta*) common in streams and ponds." They appear to be most nearly related to *Unio semialatus*, Deshayes, and others of the *Marginalis* group.

Rochebrune in 1882[2] gave the generic name *Harmandia* to *Unio somboriensis*, Rochebrune. It is merely a peculiar *Unio*, having the surface covered with somewhat radiating, sometimes slightly zigzag ribs, those of the posterior running nearly horizontal, the remainder more or less radiant from the umbonal region. Near the center of the disk, two or three of these irregular ribs before, and as many behind, curve toward each other and join, somewhat after the manner of several South American species. Sculpture approaching this, but not so strongly developed, is often found in *U. cæruleus* and other Indian Unios. The laterals are double in each valve, and a small, thin lamella curves upward from the upper lateral near its posterior end. A vestige of this third, upper, curving tooth is found in *U. fluctiger*, Lea, said to come from Guiana, but undoubtedly an East Indian species, and the same character is found in *U. crispatus* of Gould.

[1] Mollusques Nouveaux du Cambodge. Nouv. Arch. du Muséum, Bull. IX, pp. 122, 123.

[2] Bull. Soc. Philom. (7), VI, pp. 45, 46, pl. 1, 1882.

Grandidieria, Bourguignat, erected by that author into a genus, and placed by him in the family Corbiculidæ,[1] is merely a section of small, rather solid, inflated Central African Unios, often having compressed, reflected, dentate cardinal teeth, much like those of *Unio parvus* and its allies of the United States. In 1888 Bourguignat claimed to know twenty-five species of this genus in Lake Tanganyika, and believed that if its waters were to be fully explored the number would be increased to one hundred. No further comment is needed on the work of the great master of the new school of French conchologists.

Pharaonia, Bourguignat,[2] is another of this author's African genera, which includes a few thin-shelled Unios, with compressed, elongated cardinals and laterals.

Reneus, Jousseaume,[3] is still another so-called genus, consisting of a few small, thin-shelled, concentrically-striated tropical African Unios.

Microdontia, Tapperone Canefri,[4] was established for *Unio anodontiformis*, Tapperone Canefri, from the Fly River, New Guinea, and is probably only a section of *Unio*. The very brief Latin description is wholly inadequate for its proper determination.

The characters of the shell and soft parts of the genus *Unio* may be summed up as follows:

Shell variable in form, usually equivalve and inequilateral, rounded, elongated, angular or symphynote; with tubercular, zigzag, or concentric sculpture; beaks variously sculptured or smooth, and occasionally showing vestiges of a glochidium; epidermis thick, hinge line incurved in front of the beaks; hinge having normally one cardinal and one lateral tooth in the right valve, and two cardinals and two laterals in the left, or they may be almost wholly lacking or greatly varied in arrangement; pallial line entire; interior nacreous. Animal dioecious; mantle open; branchial opening oblong, fringed with numerous papillæ; anal opening with or without papillæ, usually separated from the superanal opening; labial palpi generally wider than long, with free points, more or less united posteriorly; branchiæ large, the embryos being borne in the outer or inner pair, or rarely in all four of them.

Genus BURTONIA, Bourguignat.[5]

I am inclined to believe that the species of this genus, of whose anatomy nothing whatever is known, are merely peculiar, compressed, somewhat symphynote Unios. In such species as I have been able to examine, there are vestiges of cardinal and lateral teeth; the anterior cicatrices are united, and the nacre is of a peculiarly rich, usually reddish tint.

[1] Bull. Soc. Malac. France, II, pp. 1–12, 1885.
[2] Bull. Soc. Zool. France, XI, pp. 471–502, pl. XII–XIV, 1894.
[3] Bull. Soc. Zool. France, XI, pp. 481, 482, pl. XII, fig. 4, 1894.
[4] Ann. Mus. Genova, XIV, p. 229, pl. XI, figs. 3–5, 1883.
[5] Moll. Fluv. Nyanza, pp. 20–23, 1883.

From the region of the beaks in the interior, there springs a series of slight, radiating, irregular ridges, and between the outer ends of these are three curious dorsal cicatrices. These are like the posterior cicatrices of an ordinary *Unio*, being rounded or semicircular, and not impressed. The posterior muscle scars are very indistinct.

The beaks are sculptured with somewhat scattered nodules, which are seen very plainly in *B. tanganyicensis*, Smith, but not so clearly in *B. elongata*, Bourguignat. Two specimens of the latter in the National Museum collection (No. 127190), seem to show the remains of a glochidium quite distinctly; and this character, the beak sculpture, and the rudimentary cardinal and lateral teeth, induce me to place the group in the Unionidæ instead of the Mutelidæ, to which it has been assigned. The shells frequently have the posterior end turned to the left or right like those of *Tellina*.

Genus ANODONTA, (Bruguière *em.*) Lamarck.[1]

In 1792 Bruguiere[2] applied the name *Anodontites* to certain edentulous mollusks, properly describing the genus, mentioning *Mytilus cygneus* and *M. anatinus* of Linnæus, as belonging to it, and describing a new species, *A. crispata* of Guiana, which is now believed to have no generic relation to either of the other species. In 1797 he figured, without text, a large number of species.[3] This generic name was adopted by Cuvier, Poiret, Deshayes and others.

In 1799 Lamarck changed the name to *Anodonta*,[4] describing the genus, and citing *A. cygnea*, Linnæus, as the type. In 1805 Roissy[5] explained that the genus was due to Bruguière, but that Lamarck changed the termination, because in the nomenclature as then regulated, the termination *ites* indicated that the genus included only extinct species. Dr. Dall has worked out the above puzzling synonymy with a great deal of care, and believes that under the rules of nomenclature as they then existed Lamarck was justified in making the change in termination—that *Anodonta* is synonymous with *Anodontites*, and that the former should be retained.

The *Anodontites crispata* of Bruguière, from northern South America, is fairly typical of a large group of the genus *Glabaris* of Gray, which is now placed by v. Ihering and others in the family Mutelidæ.

The genus *Anodonta*, as now restricted, consists of Naiades with generally thin, inflated shells, for the most part without sharp angles, and free from sculpture except on the region of the beaks. The hinge line is a regular curve and is not indented in front of the beaks as is that of *Unio*, and this seems to be about the best distinguishing character

[1] Prodrome Class. Coq., p. 87, 1799.
[2] Journ. Hist. Nat., I, p. 131, 1792.
[3] Encycl. Meth., pls. 201–205, 1797.
[4] Prodrome Class. Coq., p. 87, 1799.
[5] Hist. Nat. Moll., VI, p. 312, 1805.

between the two genera. The hinge is either destitute of teeth or exhibits them only in a rudimentary condition, and the nacre is less brilliant, as a rule, than it is in the Unios. *Anodonta implicata*, Say, and *A. fenoulli*, Heude, are greatly thickened usually in the anterior region, often becoming as solid as some of the heavier Unios. *A. angulata*, Lea, is also quite a solid shell, and is generally strongly inflated and sharply angled on the posterior slope. According to Hemphill,[1] it was found in hard, clayey gravel, in the Snake River, burrowing so that only the solid, angled posterior end came to a level with the surface. This is no doubt a modification of the shell in order to enable it to resist the shock of the currents, as specimens of the same species taken from still waters are thinner, more compressed, and almost entirely destitute of the posterior angle. This species has usually rudimentary teeth, and in the young both cardinals and laterals are often perfect. The shell is incurved in front of the beaks and it may be a true *Unio*.

The animal of *Anodonta* is essentially the same as that of *Unio*, and there can be but little doubt that the two genera are very closely related. Whether *Anodonta* or *Unio* is the older it is impossible in the present state of our knowledge to tell, as it is quite probable that some of the more ancient forms referred to the former genus are not Anodontas at all. There can be, I think, little doubt that the thick shells and hinge teeth of the Unios were developed in order to enable them to live in currents, as they are generally inhabitants of streams; while the thin, edentulous shell of *Anodonta* is caused by its living in still water; the genus belonging, for the most part, to ponds, lakes, and canals.

The distribution of the true Anodontas is confined to the northern hemisphere—for the most part north of the Tropic of Cancer, the so-called species of South America being *Glabaris*, and those of tropical Africa belonging to *Spatha* and *Mutela*, all genera of the family Mutelidæ. The Anodontas are found throughout North America as far south as southern Mexico; in northeastern Asia; in Japan and China, and in the great region north and west of the Himalayas; also throughout all Europe and northern Africa to the Desert of Sahara, excepting in the Nile, which is peopled with Spathas and Mutelas. The embryo is a glochidium, and probably attaches itself to fishes as does that of *Unio*. It is very difficult to draw the line between the genera *Unio* and *Anodonta*. In the United States there occurs a small group of species, some of which have been placed with *Margaritana*, such as *M. elliotti*, Lea, *M. tombigbeensis*, Lea, and *M. elliptica*, Lea; and others with *Anodonta*, such as *A. edentula*, Say. These species are, with some others, closely related by characters of the shell and soft parts, and all undoubtedly belong to a single group of one genus. In many cases in this group, even in *A. edentula*, there are fairly developed cardinals and even rudimentary laterals, and this, with the general character of the shells, leads me to place the species in *Unio*. *Anodonta ferussaciana*, Lea, and

[1] Zoe, I, No. II, p. 326.

a few forms grouping with it, appear to be nearly allied and to stand on the borderland between the two genera. In these species the hinge line is generally incurved at or near the beaks, and quite a distinct vestige of a cardinal is often found, and occasionally rudimentary laterals.

LEPIDODESMA, new genus.

In China there are found a couple of species of remarkable fresh-water bivalves of large size, thin structure, and greatly inflated form, with slightly nacreous interiors and triangular outlines. These mollusks were placed by Heude in the genus *Unio*, and by him were named *U. languilati* and *U. aligerus*, the latter of which he makes a variety of the former, but which seems to me quite distinct. The shell has a strong, elevated, sharp ridge running from the beaks to the posterior ventral portion, and another more faintly developed behind this, which ends on the edge of the dorsal slope, thus making it strongly biangulate behind. The young shell, until it is half grown, is sculptured into exceedingly strong, concentric ridges, which follow the growth lines, and which, in the later growth, become more crowded and less elevated, and are covered with a thick lamellar epidermis.

The ligament is enormous; wide, elevated, and rather short, dark brown and shining, and composed of concentric scales, which lap over each other in a posterior direction, the whole looking like the back of a short, stout myriapod. The hinge line in a general way makes a rounded sweep, conforming to the high arch of the beaks, but directly under them it is incurved.

In the left valve are two elevations which probably stand for cardinals, the anterior being elongated, running inwardly in a diagonal manner across the narrow hinge plate, and ending abruptly at the anterior muscle scar. Behind this is a vestige of another, much shorter and fainter, but running parallel with the first, this being on the incurved part of the hinge plate, and just forward of the beaks.

Beneath the ligament are two strong lamellar laterals, the inner much the higher, and with its upper portion strongly curved outward. Just beneath the posterior part of the ligament this tooth is suddenly truncated, but the base extends some distance farther on. Rising from the dorsal slope of this large tooth, and growing partly out of it, is a smaller, lamellar tooth, truncated abruptly behind, and having its upper edge curved outward.

In the right valve there is a single large lateral, truncated behind, curving out at its upper edge, and fitting between the two laterals of the left valve. Anteriorly its hinge plate slopes inward, and bears at its inner edge a low, somewhat elongated cardinal, running nearly parallel with the outer edge of the shell. From the beaks to a considerable distance in front of them is a kind of scaly, folded growth, of modified epidermis perhaps, which extends from the outside of the shell halfway across the hinge plate, which, in life, no doubt, keeps the dorsal

part of the valves a little way apart, and this probably prevents the teeth from coming in contact. A single dorsal scar can be made out on the inner part of each hinge plate in front of the beaks; the posterior muscle scars are united, as are the anterior ones, and the palleal line is distinct. Nothing is known of the soft parts of this mollusk, but it probably belongs to the Unionidæ, as the teeth, nacre, and muscle scars agree with those of that family. *Unio languilati*, Heude, may be considered the type of the genus.

Genus CRISTARIA, Schumacher.

In 1814 Leach[1] bestowed the generic name *Dipsas* on *Anodonta plicata* (Humphrey), Solander. This name had been used by Laur in 1768, and for that reason could not stand. *Barbula*, frequently applied to this and allied species, is an anonymous catalogue name, attributed to Humphrey. *Cristaria*, bestowed by Schumacher in 1817,[2] will have to be applied to the group. It consists of a few species of large, thin, usually more or less symphynote Naiades, inhabiting Chinese and Japanese waters. Usually there is, especially in younger shells, a fair development of lateral teeth, which, however, are often entirely wanting in old specimens, and occasionally there are rudimentary lamellar cardinals. Some of the species have a row of peculiar, small corrugations or plications running from the beaks to the outer edge of the dorsal slope.

I know nothing of the anatomy of this genus,[3] but from a careful comparison of the shells of several of the species with those of various Chinese Unios, I think it probable that they are depauperate forms, which have descended from the group typified by *U. cumingi*, Lea. This species often shows plainly a row of plications on the dorsal slope, as do *C. plicatus* and *C. spatiosa*. In the Unios of the *Cumingi* group the cardinals are often more or less blurred, or nearly wanting in such species as *U. delaporti*, Crosse and Fischer, *U. myersianus*, Lea, and *U. delphinus*, Lea. Their teeth are sometimes broken up into small denticles or nodules, after the manner of those of certain Hyrias. The suppression of the teeth in the Cristarias is probably caused by the fact that they are inhabitants of muddy places and still water, and they do not therefore need teeth, as do the Unios which inhabit streams. Many of these are abundant in the rice fields of China and Japan. As the group seems to be a tolerably natural one, it perhaps may stand as a genus. *Unio swinhoi*, Adams, of which a shell in the National Museum collection (No. 85069) is said to have come from Formosa, is a thin, somewhat inflated shell, with greatly compressed, feeble cardinals and laterals, and the specimen examined seems very near to *Cristaria discoidea*, Lea,

[1] Zool. Miscell., I, p. 119, 1814.

[2] Essai d'un nouv. syst., p. 107, 1817.

[3] The anatomy of the species *Cristaria plicata* has been worked up, I believe, under the title of *Dipsas plicata*, Lea, by Ishkewara in his "Introduction to the Anatomy of Animals," published in Japanese at Tokio. The paper is not accessible to me.

which, when young, has usually well-developed cardinals. I believe both should be placed in the genus *Unio*. *Craspedodonta* (Kuster, MS.) differs from *Anodonta* by a peculiar thin lamella at the hinge of the left valve, and is founded on *Anodonta smaragdina*, Anton.[1]

The locality given is uncertain, but Clessin thinks it may be America. The figure represents what is probably an immature shell, of a species unknown to me, and is, I think, a young *Cristaria* with a rather high dorsal ridge, which may be *C. herculea*, Middendorf.

Genus ARCONAIA, Conrad.[2]

In the rivers of China and southeastern Asia certain peculiarities of environment seem to exist, which, in some cases, wonderfully modify the teeth of bivalves, and in others produce curious distortion. Mention has been made in this paper of the remarkable vertical striation of the teeth of some of the Chinese Unios, a character which is not confined to this region, and may be a mechanical development to strengthen the shell. A large number of these Unios are strangely distorted, of which an account will be given later under the heading "Oriental Region," in the discussion of geographical distribution.

In the Arconaias the twisting is both axial and lateral, and I have no means of knowing whether or not this contortion is always in the one direction. However, in certain species of Unios in the groups typified by *U. pisciculus*, Heude, and *U. triformis*, Heude, the shells may be turned sharply at the posterior end either to the right or the left. It is doubtful whether *Arconaia* is generically distinct from *Unio*, but as the anterior part of the shell is always developed into a little wing, and the cardinals differ somewhat from those of any *Unio* I know of, it is perhaps best to let it stand as a genus. According to Deshayes,[3] *A. contorta* has the mantle lobes separable as in *Unio*.

Genus PSEUDODON, Gould.[4]

The species which are now generally included under this generic name were placed by Lea and other authors in *Monocondylæa*—an unrelated South American genus—on account of the similarity of the hinge characters. In most of them a single rounded cardinal tooth or tubercle is found in each valve, and there are no laterals present. *Leguminaia*, Conrad, consisting of a few species of compressed Naiades from southern Europe and western Asia, with vestiges of cardinals, which genus was included by Dr. Lea in *Monocondylæa*, is now generally regarded as a valid genus, so that all the species I should place in *Pseudodon* are confined to southern and eastern Asia, and a few of the islands of the Malay Archipelago.

The group, even when separated from *Monocondylæa* and *Leguminaia*,

[1] Clessin, in Mart. Chem. Conch. Cab. (Anodonta), p. 93. 1876.

[2] Amer. Journ. Conchology, I, p. 234, 1865.

[3] Journ. de Conch., XXII, p. 85.

[4] Proc. Bost. Soc. Nat. Hist., p. 161, 1844.

is not a natural one, and is made up of what are probably depauperate Unios of different groups. Deshayes and Julien[1] state that the animal of *Monocondylæa* (*Pseudodon*) *tumida*, Morelet, is identical in character with that of *Unio* and *Anodonta*. This is corroborated by Fischer,[2] who probably based his statement on that made by Deshayes and Julien.

There seems to be a peculiar tendency on the part of many of the Naiades of southern and southeastern Asia to develop aborted or imperfect teeth. This is shown in *Cristaria;* in the groups of Unios typified by *U. bengalensis* and *U. sempervivens*, and in *Unio biasianus*, in which, as has been heretofore mentioned, the laterals are blurred, much as in some of the North American Margaritanas. Many of these Pseudodons seem by the form of the shell and its general appearance to be closely allied to certain groups of Unios; thus *P. planulata*, Lea, which has defective laterals and cardinals, is very near in form, texture and nacre to *Unio marginalis*, Lamarck. However, since so little is known of the anatomy of these Oriental forms, it is perhaps best for the present to let the genus stand.

Genus LEGUMINAIA, Conrad.[3]

In 1865 Conrad applied the above generic name to the *Monocondylæa mardinensis* of Lea. In the following year Vest[4] gave the name *Microcondylæa* to *Alasmodonta bonelli* of Ferussac. From a study of the shells I believe the two species, together with a few others in southwestern Asia that seem to be nearly related, should be placed in one genus, and in that case the name *Microcondylæa*, which has generally been applied to Ferussac's species, must be placed in the synonymy. The shells, for the most part, are elongated and compressed, smooth, with slightly corrugated beaks, and have somewhat the appearance of Spathas. The hinge is without laterals, and in place of the cardinals there is in each valve a single, low, compressed tubercle or hook. According to Drouet,[5] the branchial lamellæ of *L. bonelli* are joined on the back; the internal are not adherent to the abdominal sac; the external are united to the mantle throughout their whole length; and Clessin states[6] that the mantle is open the whole length, and in this respect the animal is like that of *Unio*. Nothing definite is known of the soft parts of the Asiatic forms. *Pseudanodonta*, Bourguignat, is no doubt a synonym.

Genus TETRAPLODON, Spix.[7]

The above name was applied by Spix to *Unio pectinatus*, Wagner, which is believed by Lea to be the equivalent of *Castalia truncatus* of authors. The name *Castalia* commonly applied to this genus can

[1] Nouv. Arch. Mus. d'Hist. Nat. Paris, X (1874), p. 118.
[2] Man. de Conchyl., p. 1001.
[3] Amer. Journ. Conch., I, p. 233, 1865.
[4] Verh. u. Mitth. d. Sieben. Ver. f. Natur., 1866, p. 201.
[5] Bull. Soc. Philomathique, 7th Serie, VII, p. 1.
[6] Mal. Blätt., XXII, p. 129.
[7] Testacea Fluviatilia Braziliana, 1827, p. 32, pl. XXV, figs. 3, 4.

not stand, as it was preoccupied in Vermes by Savigny in 1817. The name *Prisodon* of Schumacher, which is sometimes given to this genus, will have to be used, I think, for the symphynote forms belonging to the group commonly called *Hyria*. The systematic position and relationships of this group have been discussed in this paper under the head of general classification, and the genus undoubtedly should be placed with the Unionidæ. According to Orbigny,[1] the animals examined by him had the mantle free the whole length, except in the anal region, where it was developed into two short distinct tubes, of which the branchial was the larger and furnished with cirri. The branchiæ were large and slightly unequal, and the rounded palpi were very large.

The Adams Brothers state that the outer gill is united to the mantle as far as its extremity, which does not agree with the observations of v. Ihering. According to this observer, *Tetraplodon quadrilatera* has a rounded triangular glochidium without hooks, the embryos being developed in the inner gills.

Genus CASTALINA, v. Ihering.[2]

This genus, of which certain characters have already been discussed, was founded by its author for a few species of South American Naiades which have a somewhat triangular outline and appear to stand about midway between *Unio* and *Tetraplodon*. The fact, as v. Ihering declares, that shells of certain species of the group may contain animals with an open mantle which are perfect Unios, and that others have soft parts with closed siphons, and are therefore *Tetraplodons*, shows that there is a very close relation between *Unio* and *Tetraplodon*, and that this is a transition group, which, from the characters of the animal alone, would not be worthy of generic rank; but the shells are sufficiently distinct from both the above genera to be separated without great difficulty.

Their cardinals are much like those of *Unio*, only more numerous, and the laterals often have traces of vertical or oblique striation, while the posterior ridge is less strong than it is in *Castalia*, and the shells are more compressed.

Genus PRISODON, Schumacher.[3]

The genus *Prisodon* included under Section A, *P. obliquus*, Schumacher, which is a species that has since been placed in Lamarck's genus *Hyria;* and under Section B, *P. truncatus*, Schumacher, a member of another genus, which is now more commonly put in Lamarck's *Castalia*. The excellent figures and descriptions of these species leave no doubt that the above conclusion is correct, while the generic description fairly covers the first species, and it seems to me, notwithstanding

[1] Voy. Am. Mér., p. 597.

[2] Zool. Anzeiger, 1891, p. 478.

[3] Essai Nouv. Système des Habit. vers Testacés, 1817, p. 138, pl. xi, fig. 2.

the fact that authors generally have based this genus on *P. truncatus*, it must be established on *P. obliquus*, the first-described species.[1]

The corrugated species of this genus have somewhat radiately sculptured beaks, while the smooth forms seem to be destitute of beak sculpture.

Genus SOLENAIA, Conrad.[2]

In southeastern Asia and possibly Australia there is a group of remarkable fresh-water bivalves, having a greatly elongated shell and foot, and bearing some resemblance to *Mycetopus* of South America. Lea placed these forms with this genus,[3] but in 1869 Conrad called attention to the fact that the shells had a long rudimentary lateral, and gave them a generic name, as above. Fischer, in a carefully written paper,[4] places the oriental forms in *Mycetopus*. The foot of the latter genus is enormously developed, cylindrical, and enlarged at its extremity like a mushroom. This remarkable configuration of the shell and foot are to enable the animal to burrow in the sand or mud, where it lives in a vertical position. Fischer communicated with Heude in China, who had described a large number of species, and at his request the latter gathered all the information possible concerning the species of that country. They, too, have a greatly elongated foot, enlarged into a button at its extremity, and burrow in the mud in shallow water. Fischer was no doubt deceived by the fact that similar environment had produced similar modifications in two unrelated groups. *Unio dehiscens*, Say, of the United States, has an elongated shell and a greatly lengthened club-shaped foot, and it also burrows; and I have mentioned the case of *Anodonta angulata*, Lea, which buries itself in the bottoms of rivers and closely resembles one of Heude's species. *Unio anodontoides*, Lea, a well-known form of the Mississippi Valley, was found by Mr. John B. Henderson, jr., in burrows from nine to twelve inches deep, in soft mud in the Maramec River, Missouri, with the foot greatly distended. Yet none of these are *Mycetopus*, or at all closely related to it.

The South American species differ considerably in form from those of Asia, being generally more rounded posteriorly, their shells smooth and of a delicate texture, and having interiorly a wonderfully soft, pearly nacre, while the oriental forms are rather rough, often concentrically sculptured, and covered with a heavy epidermis; the nacre,

[1] Lea applied Schumacher's name *Prisodon* to the *P. truncatus* of that author (Synopsis of the Unionidæ, p. 27, 1870), stating that this name (*Prisodon*) could not be used for his first species (*P. obliquus*) because Klein, in 1753, had given the name *Triquetra* to these symphynote Naiades. As Klein was not a binomial author, *Triquetra* can not stand, and the generic name *Prisodon* will have to be given to *P. obliquus* and the species of that group. Schumacher's *Paxyodon*, described on page 139 of the Essai, is also a *Prisodon*.

[2] Amer. Journ. Conch., IV, pt. 4, p. 249, 1869.

[3] Synopsis of the Unionidæ, p. 90.

[4] Journ. de Conch., XXXVIII, p. 93, 1890. (Observations on the genera *Mycetopus* and *Solenaia*. Second note.)

though slightly pearly, is dull, and their beaks are plicately sculptured so far as I have been able to observe, while those of *Mycetopus* are smooth. All of these Old World forms have a vestige of a lateral usually in each valve, while the South American species are either absolutely edentulous or present slight traces of taxodont teeth. These are sometimes so faint and so concealed under the external layers of nacre that they can only be seen with a strong glass and a good light, but I have observed them in several specimens. Besides this the two groups are separated by half the diameter of the globe, and I know of none found fossil at any intermediate points.

There is a shell described by Higgins as *Mycetopus falcatus*,[1] which he states came from the Upper Amazon, but which I am inclined to believe is oriental. It has the dull color of the recognized species of *Solenaia*, and the anterior basal portion of the shell is drawn down into a curious projecting lobe. *M. falcatus* might be almost taken for a diminutive form of *Solenaia soleniformis*, Lea, from Southeastern Asia.

Some of the species of *Solenaia* closely resemble *Anodonta angulata* of California, and it would not surprise me if the young of the former might sometimes be found with rudimentary cardinal teeth, or that this so-called *Anodonta*, which seems to be an aberrant form with a strongly developed foot, should prove to be a *Solenaia*.

Sowerby credits to Australia one species of the genus under consideration. This is the *Mycetopus rugatus* of Sowerby, described in the Conchologia Iconica.[2] It is irregularly, concentrically wrinkled, and the anterior basal portion is somewhat produced, like that of Lea's *M. emarginatus*, while the posterior part is wide and obliquely truncated, after the manner of Lea's species, to which it is no doubt closely related.

If these two genera are separated, *Solenaia*, which is oriental, being placed in the Unionidæ, and *Mycetopus*, a strictly occidental group, in the Mutelidæ, as I believe they must be, they do not support the theory of a connecting antarctic continent, or render it necessary to account for their distribution. Ihering has separated the genera as I do, but places them both in the Mutelidæ.[3]

The following genera have been referred to the Unionidæ, but their rank and position are extremely doubtful, or they belong elsewhere.

Australiella, Tennison Woods,[4] has concentrically sculptured valves, but is not nacreous and therefore not a Naiad.

Jolya, Bourguignat,[5] has been placed near *Mutela* by its author, but is probably a marine or brackish water form.

Byssanodonta, d'Orbigny,[6] of the Parana River, has been often put in the Unionidæ near *Anodonta*, but it belongs in the Mytilidæ.

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[1] Proc. Zool. Soc., London, 1869, p. 179.

[2] Volume XVI, *Mycetopus*, No. 7, 1868.

[3] Archiv für Naturg., 1893, p. 52.

[4] Trans. Roy. Soc. Vict., XVII, 1881, 1882, p. 82.

[5] Lettres Malacologiques, pp. 42–44, 1877.

[6] Voy. Am. Mér., p. 621, 1846.

Gabillotia, Servain,[1] is typified by *G. pseudopsis*, Locard, of Lake Antioch, Syria. I do not know its position.

Zairia, Rochebrune,[2] proposed for *Z. discrepans*, Rochebrune, etc., from the Congo.

Coltotopterum, Bourguignat,[3] proposed for *C. prælarum*, Bourguignat, is probably a form of *Anodonta cygnea*. The publications containing the last three genera are not accessible to me.

From the foregoing descriptions of genera, I am able to deduce a diagnosis of the family Unionidæ, which I think will contain all the valid genera heretofore described, and which will have to be, in our present state of knowledge of the anatomy, founded largely on shell characters. These, I think, when understood, are sufficiently distinct and constant for use in separating the two families Unionidæ and Mutelidæ. The force of this statement is added to when it is considered that the arrangement I propose, which is founded so largely on shell characters, fully agrees with what we know of the facts of geographical distribution, of the paleontology of the Naiades, and the classification of v. Ihering, based on the characters of the embryos.

Family UNIONIDÆ.

Shell usually equivalve and inequilateral, smooth or variously sculptured, angular or rounded, symphynote or non-symphynote, covered with a thick epidermis, which may be green, brown, yellowish, black, rayed, or variously painted; *beaks usually sculptured* with concentric ridges, corrugations, chevron-shaped or radial patterns, or pustules, *often showing remains of the nuclear shell;* ligament opisthodetic, well-developed, external except when the shell is symphynote. Interior nacreous; with or without hinge teeth, *but showing vestiges of them in every genus;* when present *always schizodont and arranged as cardinals, laterals* (pseudocardinals and pseudolaterals), *or both;* adductor scars generally distinct, the anterior commonly impressed; pallial line simple and generally well marked; *prismatic border usually narrow and not conspicuous.*

Animal: *Labial palpi almost always wider than long, having the upper parts of the posterior margins united; anal opening usually separated from the superanal.* Mantle either free or closed posteriorly to form a branchial opening. *Embryo a glochidium*, the soft parts being inclosed in a pouch-shaped bivalve shell, either with or without hooks, and borne in the inner or outer, or in all four leaves of the branchiæ, which are modified to form a marsupium.[4]

[1] Bull. Soc. Mal. France, VII, p. 296, 1890.

[2] Bull. Soc. Mal. France, III, pp. 1–14, pl. 1, 1886.

[3] Bourguignat, Lettres Malacologiques, pp. 45–48, 1882.

[4] In the above description I have italicized the most important characters, and those which contrast most strongly with the same in the Mutelidæ.

The following is a list of genera which I place in this family:

Unio, Retzius.
Anodonta, (Bruguiére *em.*) Lamarck.
Prisodon, Schumacher.
Tetraplodon, Spix.
Castalina, v. Ihering.
Burtonia, Bourguignat.
Arconaia, Conrad.
Cristaria, Schumacher.
Lepidodesma, Simpson.
Pseudodon, Gould.
Leguminaia, Conrad.
Solenaia, Conrad.

Family MUTELIDÆ.

Genus MUTELA, Scopoli.[1]

As yet, we know very little of the anatomy of this or several other groups of African Naiades, and upon shell characters alone it seems difficult to decide whether this should be united with *Spatha* or kept separate. Typically the shells are quite distinct; those of *Mutela* being thin, elongated, and often furnished with quite well-developed taxodont teeth; while those of *Spatha* are solid, oval or oblong in outline, and have only a low, compressed tubercle or short ridge on the hinge line. But there are species which are so completely intermediate that it is very difficult to say to which group they belong. Most of them have unusually soft, brilliant nacre, generally inclining to bluish in the characteristic Mutelas, and to coppery in the Spathas. According to Clessin,[2] the mantle lobe of *Mutela* is united as far as the middle of the ventral margin; the animal has two stout siphons, and the shell gapes in front. Fischer states[3] that the palpi are long, curved and rounded at their extremities, and that the external branchiæ are united to the mantle throughout. Adams Brothers[4] say that in *Mutela* the inner gill is entirely united to the foot, while in *Spatha* it is free. If this distinction could be proved to be good throughout, it would be a sufficient character on which to base the two genera, but in *Unio* it is well known that the union of the inner gill with, or its separation from the foot, or the connection of the outer gill with the mantle, is very variable.

Mutela dubia, Gmelin, shows two or more slightly compressed elevations on the hinge line, especially in the left valve, and sometimes smaller denticles, while in *M. exotica*, Lamarck, the whole hinge line is often strongly crenulated.

The name *Mutelina*, which was proposed by Bourguignat[5] as a genus to include *Anodonta senegalensis*, Lea, and *Mutela rostrata*, Rang, is synonymous with *Mutela* and *Spatha*.

[1] Intr. Hist. Nat., p. 397, 1777.
[2] Kuster, Conch. Cabinet, IX, 1. Abth., p. 191.
[3] Man. de Conch., p. 1004.
[4] The Genera of Recent Mollusca, II, pp. 505–507.
[5] Esp. nouv. et gen. nouv. des grands Lacs Africains, p. 188, 1885.

Genus CHELIDONOPSIS, Ancey.[1]

In 1886 Rochebrune[2] established the generic name *Chelidoneura* for *Mutela arietina*, Rochebrune. The name having been used previously for a mollusk of the family Philinidæ, Ancey changed it to that given above. I have not seen *C. arietina*, but a fine specimen of *C. hirundo*, v. Martens (which Rochebrune included in his genus), is in the National Museum collection, and is certainly a peculiar shell. It has the anterior dorsal part developed into a sharp point like a *Prisodon* or *Arconaia*, and a curious, elevated wing-like carina running from the beaks to about the middle of the posterior end, which most decidedly gapes, with a sort of diamond-shaped opening. Just in front of the posterior end each ridge is developed into a tubular spine, which, in the specimen I have seen, is nearly half an inch in height. One of these, in the shell examined, is closed by shelly matter; the other opens into the interior. The whole is covered with a thin, smooth epidermis, and in texture and color strongly recalls *Mutela*.

Genus SPATHA, Lea.[3]

This genus has been discussed under the head of *Mutela*. While most of the shells have a rich coppery nacre and are smooth externally, one species, which may perhaps be placed here, *Spatha rignoniana*, Bernardi, is of a greenish lurid texture throughout, and has the surface sculptured into a sort of reticulated and zigzag pattern, the only instance I know in which a Mutelid is truly sculptured. There is a low groove running down along the dorsal slope in this species, and the posterior end is somewhat angulated. I believe that the African Naiads, which were referred by the older authors to *Anodonta*, belong in this group or in *Mutela*, and that no true members of the former genus are found south of the Sahara. While most authors agree that *Spatha* has the mantle developed into siphons, yet in *S.* (*Anodonta*) *chaiziana*, Rang, the branchial opening is not closed.[4]

According to Clessin,[5] the laminæ of the gills are united in perpendicular rows.

The shell of *S. alata*, Lea, shows slight nodules in certain specimens embedded under the external nacre along the hinge line, which are no doubt vestiges of taxodont teeth.

Moncetia, Bourguignat,[6] is quite likely a group of compressed Spathas, which may possibly be worthy of subgeneric rank. Its author states that the beaks are smooth; that there is a tubercular eminence on the hinge line of the right valve in the cardinal region, without a cor-

[1] Conchologist's Exchange, II, p. 22. 1887.
[2] S. B. Nat. Fr., 1886, pp. 3–5, pl. 1. figs. 1–4.
[3] Trans. Phil. Soc., VI (n. s.), 1858, p. 141, footnote. Type, *S. rubens*, Lea.
[4] See Lea's Synopsis of the Unionidæ, p. 79, 1870.
[5] Kuster, Conch. Cab., part 234, p. 184.
[6] Esp. nouv. et gen. nouv. des Lacs Africains, pp. 34–36, 1885.

responding one in the left, and a smooth lateral lamella as in *Margaritana;* that it has two ligaments, both internal, and three groups of muscular impressions. The figures represent what seem to be diseased or stunted specimens, and I can not say where the group should be placed, never having seen shells of it. It may not be a Mutelid, or even a Naiad.

Genus PLEIODON, Conrad.[1]

This genus, consisting of a few African species, has been much confounded in time past. Conrad gave it the above name in 1834, and it seems to me to be perfectly distinct from all others. In 1871 Gill placed the species with the genus *Iridina* (which is synonymous with *Mutela*) in a separate family,[2] which he called Iridinidæ, while Fischer[3] makes *Pleiodon* a mere section of the genus *Mutela.* The shells are solid, ovate in outline and inflated, with smooth, shining, greenish epidermis, and the teeth, which are irregularly taxodont, are strong, usually somewhat oblique anteriorly, and more or less perfectly V-shaped posteriorly, their bases pointing forward. In the middle of the hinge they are often broken and blurred, sometimes crossing the hinge plate in zigzag lines. The teeth in young shells are often quite oblique.

Pelseneer,[4] in an able paper on the anatomy of *Pleiodon*, states that the labial palpi are semilunar, with a long, straight attachment; that the gills divide the pallial chamber into two quite distinct spaces, so that there are three openings into the mantle cavity—pedal, branchial, and anal. It has a closed branchial siphon, and the mantle border is united for some distance forward.

Cameronia of Bourguignat[5] is based on characters which, according to the above writer, vary much in different individuals, and I doubt whether it is a valid genus. The shells are solid, inflated, with a heavy hinge plate, in which the teeth are somewhat taxodont, as in *Pleiodon.* Bourguignat claims distinction on account of its having elongated anterior teeth, a character which is not shown in many of the specimens he figures. In the shells I have seen, the hinge seems to be diseased, the teeth are blurred, and the plate is somewhat split up anteriorly, but crenulated, and I should hesitate before calling these ridges lamellar teeth. I should not give the group, at most, more than subgeneric rank

Genus BRAZZÆA, Bourguignat.[6]

Inflated, thin, shining, toothless shells, with smooth beaks, having a purplish interior, and numerous (4 or more) deep dorsal cicatrices. There is a strong, triangular escutcheon at the end of the ligament, and

[1] Journ. Acad. Nat. Sci. Phila., VII, 1834, p. 178.

[2] Arrangement of the Families of Mollusks, Smith. Misc. Coll., 227, p. 20.

[3] Manuel de Conch., p. 1004.

[4] Bull. Mus. Belg., IV, pp. 116–128.

[5] Moll. Nyanza Ouk., p. 19, 1883.

[6] Esp. nouv. et gen. nouv. des Lacs Africains, pp. 32–34, 1885.

the left valve is dorsally winged, while the right is not. I have not seen any of these singular shells, but from the figures and descriptions I should think the genus was a valid one, and that it belonged with the Mutelidæ. It was proposed for *B. anceyi*, by Bourguignat.

Chambardia of Bourguignat, a new name for the Egyptian Iridinas,[1] probably contains nothing which can not be satisfactorily placed in other genera. The publication in which the genus is proposed is not accessible to me. All the foregoing genera of Mutelidæ are from Africa south of the Sahara desert, with the exception of the Nile, which is peopled with these forms to the Mediterranean. Some of the species extend south into the Cape region.

Genus GLABARIS, Gray.[2]

This generic name has been adopted by the Adams Brothers, von Ihering, and others, for South American Naiades with edentulous hinges, which had until 1847 been placed in *Anodonta*. So far as I know, no true Anodontas are found south of Mexico, all the Central and South American forms I have seen being undoubtedly members of the genus *Glabaris*. The shells of this group, though resembling those of *Anodonta* in the fact that they are without teeth, are really quite distinct, and when once the differences are understood, there need be no difficulty in distinguishing them.

The shells of *Glabaris* are usually of more solid structure than those of *Anodonta*, and some of them are covered with the peculiar clothlike epidermis which is found on a number of the Monocondylæas. The nacre is of a peculiarly soft, often brilliant and iridescent texture, in strong contrast to the lusterless interiors of most of the Anodontas. In a few of the species typified by *G. tenebricosa*, it is a sort of lurid greenish hue, but in these its tints are soft and rich. Frequently slightly elevated rays reach out from the cavity of the beaks, especially in those with the brightest nacre. There is in nearly all cases a well-defined and tolerably broad border of the prismatic layer shown around the inside of the shell, which is generally darker in tint than the nacre, and often semi-transparent. In the *G. lato-marginata* group this is especially dark and broad, being often as much as a quarter of an inch in width. It is caused by the fact that the mantle does not deposit nacre to the border of the shell. Traces of taxodont teeth have been noticed in some of the South American species by v. Ihering and the writer, and these are sometimes present in *G. granadensis* of Nicaragua.

According to d'Orbigny,[3] *Iridina* (*Glabaris*) *trapezialis*, Lamarck, and other allied species, are characterized by having distinct siphons, while in *G. membranacea*, Orbigny, which probably is the same as *G. lato-marginata*, Lea, the borders of the mantle are free at the siphonal

[1] Bourguignat, in Servain, Bull. Soc. Mal. France, VII, pp. 304–315, 1890.
[2] Proc. Zool. Soc., London, 1847, p. 197.
[3] Voy. Amer. Mérid., pp. 596, 617.

region. The embryo, as v. Ihering has shown, is a lasidium. By the characters of the shell most of the *Glabaris* are closely related, and v. Ihering has placed these two species in the same group. Here, then, in another genus, is an example of the great variation of siphonal development in closely related forms, which helps to prove that the character is not constant. Dr. Lea found that in *G. icymani*, Lea, and *G. lato-marginata*, Lea, the branchiæ were united their whole length to the abdominal sac, and the palpi of both were rounded, and he stated that in this latter respect they differed from all North American Anodontas he had examined. The superanal opening was not united below. And in *Glabaris strebeli*, Lea, of Mexico, which is closely allied to the South American forms, he found the same kind of rounded palpi which were united only above. The genus is distributed from central Mexico all through Central and South America to Patagonia, but has not been found west of the Andes, though a number of Unios are met with in that region.

Genus LEILA, Gray.[1]

Conchologically *Leila* is very close to *Glabaris*. The color, form and texture of the shells are the same as in species of the Trapezialis group of *Glabaris*, and, like most of those forms, they gape more or less in the anterior ventral region. According to von Ihering *Leila* has siphons,[2] and the pallial line in most specimens is quite deeply and broadly indented in the siphonal region. But the latter character is often found in a less degree in the shells of *Glabaris trapezialis* and its allies, especially *G. sinuata* and *G. anserina*. Both *Leila esula* and *L. blainvilleana* occasionally show vestiges of taxodont teeth near the beaks. The range of the genus is much the same as that of *Glabaris*, but I do not know of its having been found in North America.

Genus MONOCONDYLÆA, d'Orbigny.[3]

This group was first described as a subgenus of *Unio*, and was afterwards given generic rank in the author's great work on the mollusks of South America.

Spix's name, *Aplodon*,[4] was preoccupied by Rafinesque, in Heliacea in 1819, and therefore it must be relegated to the synonymy.

The shells of this group are generally solid, with a rather rough, brownish or greenish, cloth-like epidermis. The right valve has a large tooth opposite the beak, and a smaller one some distance forward of it. The large tooth of the left valve fits the space between, and there are occasionally small scattered denticles on the hinge plate. According to d'Orbigny,[5] *Monocondylæa guarayana*, d'Orbigny, has long, rounded

[1] Syn. Brit. Mus., 1840, p. 142.
[2] Zool. Anzeiger, Nos. 380, 381, p. 2, 1891. See also Fischer, Man. de Conch., p. 1005.
[3] Guer. Mag. Zool. Cl., V, No. 62, p. 37, 1835.
[4] Test. Fluv. Braz., pl. XXV, figs. 1, 2, 1827.
[5] Voy. Amer. Mér., pl. LXVIII, fig. 7.

labial palpi, which are attached in a curved line above, and which are not united posteriorly. Otherwise the animal does not seem to differ greatly from that of *Unio*.

Genus FOSSULA, Lea.[1]

In 1870, Lea separated *Monocondylæa fossiculifera*, d'Orbigny, from the genus in which it had been formerly placed, and gave it the above generic name. The shell is solid, and externally quite closely resembles that of *Glabaris lato-marginata*, Lea, but the hinge is peculiar. In that of the left valve there are two distinct humps, with a depression between, which latter is opposite the beak. In the right there is a large, blunt elevation which fits into this depression of the left valve; then behind this is a pit, and still behind it a smaller hump. Frequently a smaller set of denticles are seen above one or more of the pits, which project into a sort of ligament in the upper part of the hinge. This latter character is shown more plainly in a species recently named *F. balzani* by v. Ihering. The animal is said by this author to scarcely differ from that of *Glabaris*.[2]

Genus IHERINGELLA, Pilsbry.[3]

In 1859, Lea applied the name *Plagiodon*[4] to *Monocondylæa isocardioides*, Lea, but as that name had been preoccupied by Dumeril in reptilia (1835), Pilsbry proposed the name *Iheringella* for it, in honor of the eminent biologist von Ihering, who has done such excellent work among the Naiades. The type, *P. isocardioides*, Lea, resembles in form an *Isocardia*. The hinge appears as if injured, like that of a *Margaritana*. In the right valve are two irregular teeth under the beak, and a broken, saddle-shaped tooth in the left valve fits in between them. In each valve there are pseudolaterals which start under the beak and slope downward across the plate, and the whole surface of the hinge is covered—teeth and all—with irregular wrinkles and pustules. Conchologically it seems most closely related to *Monocondylæa*. The nacre has a peculiarly soft, greenish hue. The animal is unknown.

Genus MYCETOPODA, d'Orbigny.[5]

Orbigny first applied the above name to *M. Soleniformis*, Orbigny, and *M. Siliquosus*, Orbigny, characterizing the genus in a proper manner, and afterwards, in the "Voyage Amerique Méridionale," changed the name without explanation to *Mycetopus*, by which it is generally known. The former name will, I am sorry to say, have to supersede the latter.

[1] Synopsis of the Unionidæ, p. 72, 1870.
[2] Archiv für Naturgeschichte, I, pt. 1, p. 65, 1893.
[3] Nautilus, VII, No. 3, p. 30, 1893.
[4] Proc. Acad. Nat. Sci. Phila., VIII, p. 79.
[5] Guer. Mag. Zool. Cl., V, No. 62, p. 41, 1835.

I have discussed the genus somewhat at length under the head of *Solenaia* in this paper, and nothing more need be said regarding the shell.

The palpi, as in other genera of the Mutelidæ, are longer than wide. The mantle is open all around, there being no distinct branchial siphon. The anal siphon is only indicated by an oval aperture with a low border, and it is separated from the branchial opening by a sort of bridge. The branchiæ are very large, and the Adams Brothers state that the outer ones are entirely grown together.[1]

The foot is an enormous and greatly modified organ, very long and cylindrical, and near the lower part contracted like the neck of a bottle. From this the base swells out into a large button, which d'Orbigny, in the magnificent figure in his great work on South American mollusks, has represented as covered with low, rounded protuberances. The wall of the burrow corresponds to the shape of the animal, being narrowed in near the button and expanded above and below, and the foot could not be withdrawn unless its lower end was contracted. The unionoid characters of the animal have induced some authors to place it in the Unionidæ; by others it has been considered the type of a separate family, Mycetopodidæ.[2] But as it is known that other unrelated Naiades burrow in the same way, some of which have a strikingly similar foot, and that the shell has a wonderfully soft, silvery nacre, and that it never has a vestige of cardinal or lateral teeth, but sometimes faint traces of taxodont denticles, I think it may be safely placed in the Mutelidæ. The genus is found from southern Brazil northward to Central America. It may be here remarked that all the members of the Mutelidæ as herein classified are confined to Africa and South America, with the exception of a few *Glabaris*, which go up as far north as southern Mexico, and a single Central American *Mycetopoda*.

From the foregoing characters of the different genera placed in the Mutelidæ, we may deduce the following family description:

Shell generally without sculpture or angularities, smooth or rarely slightly sulcate, covered with a thick epidermis; *beaks nearly or quite destitute of sculpture, and never exhibiting the remains of an embryonic shell; nacre of a peculiarly soft, rich texture*, silvery, coppery, lurid or greenish, *generally surrounded by a wide, distinct prismatic border;* hinge with or without teeth, *which, when present, are always irregularly taxodont, and showing vestiges of this kind of dentition in occasional specimens in all the genera;* escutcheon large, triangular, and distinctly marked; muscular impressions variable; pallial line usually simple, but in some cases more or less inflected into a sinus posteriorly.

Animal: *Labial palpi large, oval or rounded below*, and usually *without free points, scarcely united posteriorly:* outer gills attached firmly on each side to the mantle and abdomen, so that the suprabranchial cham-

[1] Genera of Recent Mollusks, II, p. 501.

[2] Gray bestowed this name in the "Synopsis of the British Museum" in 1840.

ber ending in the anal siphon is completely separated from the mantle cavity; *anal and superanal cavity united, continuing backward over the adductor muscle into a superanal chamber.* Mantle open or closed into more or less perfect siphons, *sometimes united for some distance forward. Embryo a lasidium, composed of three segments*, the anterior head-like, the median bearing a single shell, the posterior tail-like.

It will be seen from the above that the characters of the soft parts are quite variable, and I have italicized those in both shell and animal which seem to most constantly differ from the same in the Unionidæ. It is very probable that with a more thorough anatomical knowledge of the Naiades the descriptions will have to be a good deal modified.[1]

The following is a list of the genera I place in this family:

Mutela, Scopoli.
Chelidonopsis, Ancey.
Spatha, Lea.
Pleiodon, Conrad.
Brazzaea, Bourguignat.
Glabaris, Gray.
Iheringella, Pilsbry.
Monocondylæa, d'Orbigny.
Fossula, Lea.
Mycetopoda, d'Orbigny.

Although in time past the Naiades or pearly fresh-water mussels have often been placed in a single family, and though even v. Ihering, whose recent classification of the genera is, I believe, a natural one, has placed the two groups, Unionidæ and Mutelidæ, in one superfamily, and notwithstanding the fact that there are a few genera whose position on account of our lack of knowledge is doubtful, yet I think it quite probable that the relationship between these two great groups is not a very close one.

It is true that the animals themselves do not seem to altogether bear out this assertion. The character of the presence or absence of siphons, on which the families have generally been founded is, as I think I have conclusively shown, utterly variable and worthless. There is usually some distinction in the form and the union or nonunion of the labial palps, but these characters are not perfectly constant, and even if they always held good, they would be of little importance. Ihering is authority for the statement that in all the South American and African Mutelidæ (and all the genera belong in these two continents) the outer gill-leaves on each side are firmly attached both to the mantle and abdomen, thus completely separating the suprabranchial cavity from that of the mantle back to the anal opening. This, however, according to that most excellent authority, occasionally occurs in the Unionidæ of the northern hemisphere.

[1]There will doubtless be found great variation in the matter of union of the mantle and gills in many other Pelecypods. Jackson observed in some specimens of *Perna ephippium* that the two pairs of gills were separated from one another throughout their length, whereas in other specimens the two median gills were connected by concrescence at their dorsal border, thus uniting the two pairs as in *Ostrea*. The degree of union varied in different specimens, the gills being united for their whole extent, or only posteriorly. (Phylogeny of the Pelecypoda. Mem. Bost. Soc. Nat. Hist., IV, No. VIII, p. 326, 1890.)

It is in the characters of the embryo and the shell that we find the great vital distinctions between these families. In the Unionidæ the embryo, perhaps without exception, is a *glochidium*, which is probably characteristic of the nepionic stage of all the genera in the family. The embryo of the South American Mutelidæ has, wherever examined by v. Ihering, proved to be a *lasidium*, and, although perhaps the relation of the African mutelid groups may not be so close to those of South America as is that of the latter among themselves, yet I have no doubt that their embryos will prove to be something very much like a lasidium. This peculiar stage is, so far as I know, entirely unique among Pelecypods, and though by the character of *taxodont* teeth the mutelids show affinities for *Nucula*, *Arca*, *Pectunculus*, and the like, yet by the evidence of their embryos they seem wholly unrelated to any other lamellibranchs.

The irregularly taxodont teeth which characterize the Mutelidæ are totally different from the schizodont teeth, which are found more or less developed in every genus of the Unionidæ. The peculiar cartilage pits of *Fossula* resemble to some extent those in *Perna*, and suggest a possible distant relationship with this and allied genera. On the other hand, it would seem reasonable to suppose that the unionids had their closest affinity with other schizodont families.

II. GEOGRAPHICAL DISTRIBUTION OF THE NAIADES.

In mapping out the general distribution of the Naiades, although they are all confined to the fresh waters of the globe, it will be found that they fall into provinces something in the same way as do the other members of the animal kingdom. So nearly do these areas coincide in a number of cases with those of generally recognized regions of animal life, that in several instances I have applied the same names to them. To a considerable extent, as would be expected, these divisions of Naiad life are bounded by the sea, by deserts, and mountain chains which act as watersheds for different river systems. Yet none of these in all cases effectually restrict the distribution of the fresh-water mussels; and it is true that in several instances the borders of a Naiad region are not marked by any tangible natural barriers.

The Palearctic Region.—This, the largest region of Naiad life, includes in a general way the whole of Europe, Africa (excepting the Nile), north of the Desert of Sahara; all of Asia north of the Stanovoi and Altai Mountains, including, probably, the greater part of Afghanistan and Beloochistan, Persia, Arabia, and Asia Minor; and all of North America that is drained into the Pacific. This vast region, covering an area of perhaps 16,000,000 square miles, is inhabited by a single and remarkably homogeneous Naiad fauna. One species characteristic of this province, *Unio margaritiferus*, Linnæus, is found in all parts of Europe except the region along the Mediterranean; also throughout Siberia; in northern Japan, which stands on the border between this and the Oriental region, and in that part of this province in North America

lying north of about 40°: occupying in all an area in the palearctic region of something like 9,000,000 square miles. The Amoor River, which takes its rise in Siberia and Mongolia south of the Stanovoi range, has a mixed Naiad fauna whose characters partake of the Palæarctic and Oriental provinces. *Unio pictorum*, a species common to all Europe and Siberia, is found at Khabarovka, in the Amoor Valley, as well as *Anodonta magnifica*, Lea, *A. cellensis*, Schroeter, and *A. plicata*, Solander, which is synonymous with *Cristaria discoideus* of Lea, the latter three being common to China.[1]

According to Middendorf,[2] *Anodonta herculea*, Middendorf, a Japanese species, which is a *Cristaria; Unio mongolicus*, Middendorf (=*Unio margaritiferus*, Linnæus?), and *Anodonta cellensis*, Schroeter, are found in the Amoor region. His *Unio complanatus*, Solander, a common New England species, which he credits to Siberia, is, according to his figures, without lateral teeth, and appears to be a stunted form of *Unio margaritiferus*.

Schrenck[3] gives the following list of species of the Amoor Valley:[4]

Unio grayanus, Lea.
* *U. pictorum*, Linnæus.
* *Unio (Marg.) margaritiferus*, Linnæus.
Anodonta plicata, Solander.
A. magnifica, Lea.
* *Unio mongolicus*, Middendorf.
* *U. (Marg.) dahuricus*, Middendorf.
* *Anodonta anatina*, Linnæus.
* *A. cellensis*, Schroeter.

His *Unio grayanus* is certainly not that species, but a shorter, heavier shell, belonging, however, to an Oriental group; and the *Unio mongolicus* is most likely a form of *Unio margaritiferus* with imperfect laterals.

The southern limit of the Palæarctic Region in North America can not be accurately given, but it probably extends to near the Isthmus of Tehuantepec, as one of the common Californian Anodontas has been found in Oaxaca.

In all this vast area there are perhaps not more than 50 valid species of Naiades, which belong to the genera *Unio*, *Leguminaia*, *Anodonta*, and the species of *Cristaria* alluded to, though the new school of conchologists have considerably multiplied the genera and have run the specific names up into the thousands. The species are, for the most part, small to medium in size, without conspicuous sculpture or angles, or, as a rule, any bright patterns of coloring.

The group of Anodontas typified by the well-known *A. cygnea*, Linnæus, *is distributed over this entire region*, all the forms found in the Pacific drainage of North America either belonging to it or being, I think, closely related. One species, *A. yukonensis*, Lea, from the Yukon River, Alaska, is absolutely identical with specimens of *Ano-*

[1] On the authority of Mousson (Journ. de Conch., XXVII, p. 26).
[2] Malacoz. Rossica, Sib. Reise, 1847–1851, p. 273.
[3] Reisen und Forsch. im Amur-Lande, 1854–1856, p. 694.
[4] Those belonging properly to the palearctic region I have characterized by an *; the others are Oriental species.

donta beringiana, Middendorf, collected by Dr. Dall at Petropaulovski, Kamchatka. This I have verified by comparing the types with Dr. Dall's shells.

Unio raristissus, Kobelt, of Afghanistan, appears to be a member of one of the great European groups. Two Unios have been credited to Oregon, *U. famelicus* of Gould, and *U. oregonensis* of Lea. The types of both of these species are in the National Museum collection, and I can say without hesitation that the former is a young shell of *U. multistriatus*, Lea, of Brazil, while the latter is only an old, rather large and solid *U. rowelli*, Lea, of Central America. *Unio margaritiferus*, Linnæus, is the only species of the genus known at present in the Pacific drainage of North America.

Although there is a slight mingling of the forms of this and the Oriental regions in the Amoor Valley and northern Japan, I only know of one group, represented by a single species, belonging to the Palæarctic province which is extralimital, this being *Unio margaritiferus*, Linnæus, which is found in the Upper Missouri of the Mississippi area, and in eastern Canada and New England of the Atlantic drainage. Of its distribution, more will hereafter be said. On the other hand, I do not know of a single Naiad belonging to any other province, which is found within this great region.

The Ethiopian Region.—All the continent of Africa lying south of the Desert of Sahara, including the Nile to its mouth, is peopled by a common assemblage of Naiad life. The only genera of the Unionidæ represented in this region are *Unio*, which is distributed over the whole territory, and *Burtonia* (if it be a valid genus), with a few species confined, so far as is known, to the region of the Great Lakes. All the Unios are small to medium in size, and are not particularly striking in any way. A large proportion of them are more or less covered with slight zigzag or reticulated delicate sculpture, and in this particular, as well as in form and texture, they recall the Unios of India. This is especially true of the forms known from the Cape region. A few species which I have not seen, have been reported on rather doubtful evidence from Madagascar.

Within this area are found five genera of the Mutelidæ: *Mutela*, *Spatha*, and *Pleiodon*, having a wide distribution, and *Brazzaa* and *Chelidonopsis*, which are probably more restricted. Little is known as yet of the Naiades of this great territory, but long ago it was remarked by Morelet that the fauna, including the land and fresh-water mollusks of this entire region, was remarkably homogeneous. Several of the groups of *Unio* and of the Mutelidæ appear to be distributed over the greater part of the province. So far as I know, no species or group of the Naiades belonging within it is found outside of the region, nor is there an immigrant from any other area within its borders. The ocean and the Desert of Sahara appear to be absolute barriers to the ingress or egress of Naiad life.

The Oriental Region.—All that part of Asia lying south of the great

Thibetan plateau, including, probably, the Indus on the west and the Hoang-Ho on the northeast, is inhabited by a peculiar Unione fauna. With this region must be included Japan, Korea, Manchooria, Formosa, the Philippines, and probably all the islands of the Malay Archipelago, which are peopled with Naiad life, to and including the Solomon group. The genus *Unio* is everywhere abundant throughout this area, and *Pseudodon* is common to nearly all of it. A magnificent set of Anodontas is developed in northern China, and in this region *Cristaria*, *Lepidodesma* and *Arconaia* are found. *Solenaia* inhabits the greater part of the area.

Dr. Lea was led to believe that two or three of the Unios of the southern part of this region were found in Australia, but later he was convinced that this was an error, and that no species of the two families is common to the Oriental and Australian regions. The Naiad fauna of this region is magnificent and diversified, and almost rivals that of the Mississippi Valley in vigor, size, solidity and variety of forms. Both Dr. C. A. White and von Ihering believe that the Unios and Anodontas of this area are closely related to those of the central part of North America. Not only does there seem to be a general relationship among a large number of the Naiads of this province with those of the Mississippi basin, but several Oriental groups are apparently so close to those of our own region that it is well-nigh impossible to separate them. Thus, the Asiatic Anodontas typified by *A. woodiana*, Lea, if found in the United States, would be placed by most students with *A. plana:* the Chinese Unios of the group of *U. housei*, Lea, and *myersianus*, Lea, are evidently quite near the *Alatus* assemblage; *Unio superbus*, Lea, is very much like our *U. capax*, Green, and a number of the tuberculate forms of China could almost be placed in the American groups of *U. lachrymosus* and *U. pustulosus*.

Certain peculiarities of shell growth are remarkable among the Naiades of this entire region. One of these is the loss or partial degeneration of the hinge teeth, and another is the remarkable development of vertical tooth striation, to both of which attention has already been called in this paper. The third is the singular contortion of many of the species, of which there are three varieties. The first and simplest is a mere bending of the posterior part of the shell, either to the left or right, something like that of a *Tellina*, which is seen in two or three groups of elongated Chinese species. Some of these forms are bent into a strong curve. The second is a twisting of the shell on its axis, which occurs in the Arconaias and some of the Unios.[1] These two forms of distortion may occur in the same species. The third and most strange form of irregular growth is seen in a number of very solid, oval and somewhat

[1] *Arconaia provancheriana*, Pilsbry, which is twisted on its axis like a *Parallelopipedon*, is no doubt a distorted form of *Unio complanatus*, Solander, from Canada, and does not come from China, as has been surmised. (See Naturaliste Canadien, XIX, p. 171, 1889.)

pustulous species, in which one valve appears as if it had been pushed downward when in a plastic state, and is always less inflated than the opposite one.

These peculiarities are not characteristic of entire groups, as they may be met with in one species and absent in closely related forms.

The Australian Region.—Australia, Tasmania and New Zealand are peopled with a very distinct set of Naiades, consisting, with the exception of the single *Solenaia* which has been referred to the former island, of Unios only. It may be possible that when New Guinea is thoroughly explored, some of the peculiar species of Unios found in Australia may be discovered, as it is believed that these two islands were connected during Tertiary time. Only a moderate number of species are found in this region, as Australia has few streams, and all, or nearly all, of them either go dry or are reduced to mere disconnected pools in time of drought. In general, the shells of this region are oval in outline, smooth, of a dull greenish olive or brownish tint, and without other patterns of color marking. Some of the forms have a slight development of concentric ridges, and only two species are known which have any other sculpture: *U. cucumoides*, Lea, which is somewhat tuberculous, and *U. napeanensis*, Conrad, which has rather sharp, pointed knobs or corrugations, extending out for some distance from the beaks. *Unio dorsuosus*, Gould, the type of which is in the Museum collection (No. 5925), is, I have no doubt, a young *U. napeanensis*, and is said to have come from the Fiji Islands.[1]

At the beaks of this shell the sculpture is imperfectly radial, much resembling that of the South American species. The very few perfect beaks of Unios of this region which I have seen, have a somewhat zigzag or curved radial sculpture, indicating, as do the form and color of the shells and the similarity of the soft parts, a close relationship with the South American species. The so-called *Alasmodonta stuarti*, from Australia, is merely a *Unio* with compressed, feebly developed teeth. No species of this region is known to be extralimital, and the *Solenaia*, if really from Australia, is the only member of a foreign group represented in this region.

The Mississippi Region.—All the waters that are carried to the Gulf of Mexico through the Mississippi River are filled with a common assemblage of Naiades, consisting of Unios and Anodontas. In fact, this fauna occupies almost exclusively all the streams emptying into the Gulf, from the Rio Grande on the west to the Chattahoochee River on the east, and beyond this either the species of this region or those belonging to its groups are scattered from Central America to North Carolina. To the northward, other species or members of groups belonging here have passed into New England and extended down to

[1] Gould says (U. S. Expl. Exp., XII, p. 431): "This shell was marked Fiji Islands, probably by some accident, as I doubt not that it came from eastern Asia." It is no doubt an Australian, and not an Asiatic or Polynesian species.

southern Virginia and even into Georgia. The Red River of the North, the Mackenzie, the Great Lakes, most of the lower peninsula of Michigan, and the southernmost portion of Canada are, for the most part, peopled with Mississippi Valley species.

No equal area on earth has such a diversity of Naiad life or such magnificent shells. Here are found the largest species in the world; here are forms with knobs, pustules, angles, lobes, and concentric sculpture. The nacre of many of them is wonderfully rich in tints of silver, pink, purple, salmon or red, and it is equaled in beauty by the elegant patterns of external painting, in stripes and mottlings and delicate hair lines. Perhaps twenty or more species of this region are extralimital, and about half as many from other areas occur within its borders.

The Atlantic Region.—East of the Appalachian chain, and occupying all the rivers and streams from Florida to Labrador that drain into the Atlantic, there is a set of Unionids, consisting of Unios and Anodontas, generally moderate in size, thin in structure, and for the most part without strong angles, sculpture, or brilliant coloring. Toward the southern part of this region the forms are immensely variable and puzzling, and I do not know of any other area in the world in which it is so difficult to satisfactorily separate species and groups. Although both in the southern and northern part of this province the forms of the Mississippi Valley have entered freely, until they have met and overlapped, yet there are perhaps not more than one or two species which belong in this region or members of any of its groups that appear in the waters of the Mississippi drainage proper. *Anodonta fragilis*, Lamarck, a form characteristic of the Atlantic province, is found in several places in the Mississippi area, notably in Minnesota; and *Unio radiatus*, Lamarck, is doubtfully reported from the St. Croix River, Wisconsin.

The specimens of *Anodonta footiana*, Lea (another northern form), said to come from the Illinois River, are no doubt *Anodonta orata*, Lea. There are scarcely a dozen Mississippi drainage species found within this region.

The Neotropical Region.—The entire continent of South America forms a single region of Naiad life, containing four genera of Unionidæ (*Unio*, *Prisodon*, *Tetraplodon* and *Castalina*) and six of Mutelidæ (*Glabaris*, *Leila*, *Monocondylæa*, *Fossula*, *Iheringella* and *Mycetopoda*).

The Unios are generally oval or rounded, moderate in size, usually slightly sulcate, and covered with a uniform brownish or greenish brown epidermis. All have radial beak sculpture, and very few have any other than what I have mentioned.

The genus *Unio* is represented throughout the entire area, and strangely enough the great Andean chain does not form a barrier between groups. The assemblage typified by the well-known oval, compressed *Unio ellipticus*, Spix, seems to be scattered over this whole area, and species belonging to this group in Peru and Chile on the Pacific Slope of the continent can scarcely be said to differ from forms

on the other side. I do not know that any other group of Unios is represented on the western slope, and so far as I am aware, none of the other genera have as yet been met with in the rather limited drainage of that region.

The great group of *Glabaris* typified by *G. trapezialis*, Lamarck, a very natural and closely related assemblage, is well represented, no doubt, throughout all the eastern and southeastern drainage of South America, from well down in Argentina to Central America and even southern Mexico. Indeed, the typical species is in the Museum collection from the streams of Argentina to Lake Maynos in the interior of Peru, the San Francisco River, Brazil, and the Rio Negro on the north. The group is well represented in Central America and southern Mexico by *G. bridgesi*, Lea, and allied forms. A single species, *G. leotandi*, Guppy, is found in Trinidad. No species and only three or four groups of this region are extralimital.[1]

The Central American Region.—All Central America, including, perhaps, the most of the Isthmus of Panama, and all of Mexico except the strip west of the Cordillera, together with Yucatan and the Island of Cuba, form a single Naiad province which is peopled with a large number of *Unios*, a fair representation of *Anodontas*, a single *Mycetopoda*, and a few *Glabaris*. The fauna consists really of three elements, which no doubt represent as many migrations.

First.—A large number of Unios, constituting the greater part of the fauna, which by their solid, sometimes angular and inflated forms and often pustulous or somewhat plicate sculpture, indicate evident relationship to groups in the Mississippi Valley. The groups showing these resemblances are placed opposite each other in the following table:

Relationship of Central American and Mississippi Valley Unios.

Central American region groups.	Mississippi Valley groups.	Central American region groups.	Mississippi Valley groups.
Unio pliciferus	U. crassidens.	Unio scutulatus	U. alatus.
Unio mexicanus	U. crassidens.	Unio popei	U. monodontus.
Unio rowelli	U. luteolus.	Unio usumasintæ	U. trigonus.
Unio cuprinus	U. alatus.	Unio usumasintæ	U. lachrymosus.

The group of Central American Unios, typified by *U. aratus*, does not seem to have a parallel in any assemblage of Mississippi Valley forms, but is undoubtedly related in a general way. The Unios of this region

[1]Attention may be called to the curious fact that a number of the South American species of Unios are imitated by certain *Glabaris* which very strongly resemble them externally. Thus the orbicular Unios typified by *U. nocturnus* have their parallel in *Glabaris* in a section typified by *G. lato-marginata*, and the elliptical Unios of the *Casablancæ* group are balanced by *G. puelchana*, etc. *Unio delodontus* and its allies are offset by *G. wymani* and others, and the elongated solid *U. parallelopipedon* and a few others have their counterpart in *G. ensiformis*, which sometimes so closely resembles the members of this group that anyone would at once place it with them unless the hinge was examined. There is no relation whatever between the genera. Their resemblances are probably adaptive.

below the Isthmus of Tehuantepec, as well as those of Cuba, are remarkable for their sulcate sculpture. This character is noticeable even in species which are pustulous or otherwise sculptured, and is seen in groups, the members of which in Mexico are smooth or nearly so.

Second.—A considerable number of Unios and Anodontas, some of which extend down into Central America, which are either absolutely identical with well-known forms in the Mississippi Valley or belong with the assemblages of that region. The following groups of the latter province are represented. The group of *Unio plicatus* is represented by *Unio eightsi*, Lea, which is found south to Vera Cruz, and is merely a synonym of *U. multiplicatus*, Lea, a common form in the central United States. There are one or two other species of this group which range south into Central America. Quite a number of species of the group of *Unio alatus*, such as *Unio tecomatensis*, Lea, *U. umbrosium*, Lea, *U. purpuratus*, Lamarck, and the like, are found in Mexico, and one species something like *Unio tenuissimus* (*U. delphinulus*, Morelet), is found in Honduras. The group of *Unio gibbosus* is represented by *Unio discus*, Lea, a compressed, ponderous species in Central America; that of *Unio lutcolus* by a nearly typical species *U. hydianus*, Lea, and that of *Unio anodontoides* by the form of the same name, all of which species extend across the Rio Grande River. *Unio couchianus*, Lea, of the *Lachrymosus* group, is a Mexican species, and it is probable that representatives of other northern groups will be found in this region. *Anodonta henryana*, Lea, of Mexico, is scarcely distinct from *A. imbecillis*, Say, of the Mississippi Valley; and the group of Anodontas, of which *A. grandis*, Say, may be considered the type, has several representatives in the northern part of the province.

Third.—The few *Glabaris* and the *Mycetopoda* heretofore mentioned, which are found in the southern part of this area. Only about a half dozen species of this region are found in the United States, and perhaps as many belonging to that country extend into Mexico, though these numbers will probably be increased with more thorough exploration.

DISTRIBUTION IN TIME AND GENERAL CONCLUSIONS.

Unio and *Anodonta* have been believed by some authors to extend well back into the Paleozoic, and, while this may quite probably be true, yet I do not think the evidence is sufficient to demonstrate it.

Two or three species of Unios were collected by Professor Cope in the valley of Gallinas Creek, New Mexico, from strata which he regarded as of Triassic age.[1]

These shells were so broken as to be hardly recognizable, though they are no doubt Unios. One of them, however, was described by Meek under the name of *Unio cristonensis*,[2] but it may be as well to state

[1] Ann. Rept. Expl. and Sur. west of the one-hundredth meridian, 1875, p. 81.

[2] Ann. Rept. Expl. and Sur. west of the one-hundredth meridian, 1875, p. 83.

that there is some little doubt as to whether the strata in which they were found is Triassic or Jurassic.

Something like a year ago a half dozen species of fossil Unios were sent to the writer by Mr. E. T. Dumble, of the Geological Survey of Texas, which came from what are believed to be fresh-water Triassic beds in that State. Numerous valves of one of the species show perfect cardinal and lateral teeth, which do not seem to differ from those of many recent species.[1] These six forms, though not particularly striking in outline or appearance, belong to at least as many different groups, and do not show any more relation to each other than a half dozen specimens would if taken at random from different parts of the world. One of them is somewhat triangular in outline and compressed, with cardinal teeth much like those of the South American forms; another has slight, radiating striæ on the posterior part, and a third species, which resembles some of the forms of *U. pictorum* of Europe, *has strongly developed, radial beak sculpture!* The fact of this diversity would go to show that the genus had been, in all probability, a long time established at the time these were living. A few species have been found in the Jurassic beds of the western United States, some of which seem to be prophetic of groups which are living to-day in the Mississippi Valley, and the forms which are known to be Cretaceous from that region bear out this prophecy. But when we come to the lacustrine or estuary strata of the Laramie group in this same territory, we find a most astonishing resemblance to forms now occupying the central United States. These beds are believed by some to be Upper Cretaceous; by others they are referred to the Lower Eocene, and Dr. White, whose labors in this field are so well known, believes that the waters in which they were deposited were slightly brackish; and in fact the Unios and other fresh-water shells of that region are often found associated with *Cyrena*, *Ostrea* and *Anomia*, genera which now live in estuaries.

In the Laramie beds, species are found evidently belonging to such groups as that of *Unio plicatus*, *U. perplexus*, *U. gibbosus*, *U. clavus*, *U. metanevra*, *U. securis*, *U. alatus*, and *Anodonta grandis*, and there are forms from these strata which could hardly be separated from living species if the latter were fossilized. Dr. White has called attention to the fact[2] that the anterior portion of many of the elongated species of these beds is greatly shortened, and this character is observable in a number of species in China. Whether the Naiades originated in North America or the Old World is not now known. At any rate, I do not think any careful student can examine a good series of species from the

[1] These species were sent to the writer to be named and described, and a paper was prepared with descriptions and figures, to be published in the report of the Geological Survey of Texas. On account of the lack of appropriations for continuing the work, the paper was not published by the Survey. The National Museum has undertaken its publication, and it will shortly appear in the present volume of Proceedings (pp. 379-383).

[2] Third Ann. Rept. U. S. Geol. Surv., p. 431.

Oriental region, without being convinced that the Unione fauna of that area is somewhat closely related to that of the Laramie beds and the Mississippi Valley, and the conclusion seems reasonable that a migration took place, perhaps during or shortly after the Laramie epoch, over an old, now submerged, landway, either from Asia to North America or *vice versa*. It is, I believe, more probable that this fauna developed in the western continent than the eastern, for, as we have seen, a few prophetic types of it appeared in the North American Jurassic, while the earliest recorded existence in the Old World of species which seem intimately related to it is in the later Cretaceous or earlier Tertiary. While some eight or ten groups of Unios and Anodontas now living in the Oriental region bear such a strong resemblance to similar assemblages in the United States that at first sight they seem to be the same, I believe every one of them to be distinct, and it seems probable, when it is taken into consideration how slowly the Naiades change, and the fact that the forms of the Laramie groups have scarcely altered specifically in our own country, that if any such migration and separation took place, it occurred a long time ago.

It is quite likely that about this time members of some of the Laramie groups found their way into Mexico, Central America and Cuba. It is very probable that this area was separated from South America at that time, and for a considerable period since, as no interchange of Naiades is known to have taken place between the continents until perhaps during the Pliocene, or at least since the last union of land areas took place. No North American form is found in South America, and the few *Glabaris* and the *Mycetopoda* that have entered the Central American province from the south, have scarcely changed specifically. This Laramie *Unio* fauna in Mexico and Central America has every appearance of having been in some way isolated from the rest of North America, as if it had developed under insular conditions. Almost all of the older groups of the Central American region have their analogues in the Mississippi Valley to-day, yet very few species of these Mexican groups come north of the Rio Grande River; and while there is a slight mingling of forms of the two provinces, yet the groups can be separated, and the southern Naiad fauna has a distinctive appearance, notably in the much softer, more silvery, nacre, and an indefinable difference in the epidermis. I should say that these older Central American fauna groups bore about the same relation to those of the Mississippi Valley as do many of those of the oriental region. Judging from the apparent evidence of the Naiades, one would suppose that after the migration of these old forms into Mexico and Central America, they were isolated from the rest of North America long enough to take on certain peculiarities, and that after this the two areas were connected again, and that since the connection a few species of Unios and Anodontas of the present Mississippi Valley groups had migrated southward. I am aware that what is known of the geology

of this region does not seem to support the idea of any separation of Mexico from the rest of North America during Tertiary time, but I simply give what appears to be the evidence of the Naiades.[1]

It is possible that at some time during the occupation of this region by the older Naiad fauna there may have been a strait through the present Isthmus of Tehuantepec, which separated Central America from Mexico. The strongly sulcate sculpture of most of the Unios of this lower region may have developed under insular conditions, or it is possible that it is wholly due to climate.

The Naiad fauna of the Atlantic area, while consisting generally of moderate-sized Unios and Anodontas, without, as a rule, any striking characters, was, I believe, developed from that of the Mississippi Valley, but it has long been separated by the Appalachian chain. *Unio* (*Anodonta*) *undulatus*, Say, of the Northeastern States, is only a mere variety at best of the *U.* (*Anodonta*) *edentulus*, Say, of the Mississippi drainage. *Unio* (*Margaritana*) *marginatus*, Say, found in the former region, though smaller and more delicate, is identical with the western species. *Unio radiatus* of New England belongs to the western *Luteolus* group, and in some cases approaches so close to the type that the two cannot be satisfactorily separated. *Unio ochraceus*, Say, and *U. cariosus*, Say, belong to the Mississippi group of *U. rentricosus*, while the groups of *Unio* (*Margaritana*) *calceolus* and *Unio pressus* are about equally developed in the two regions. The migration of these forms has no doubt been made around to the northward of the Appalachian chain, as the species belonging to these groups in the Atlantic drainage are abundant in New England, but gradually vanish as we go southward. South of the dividing range, the relationship is still more apparent. The great Mississippi Valley groups of *Unio tetralasmus*, *U. subrostratus*, *U. crassidens*, *U. parvus*, and *U. rentricosus* are all well represented in the Atlantic drainage of Georgia, Florida, and in some cases as far north as North Carolina, though there seems to be a slight separation of the two areas between the Ocmulgee River, which drains into the

[1] I quote from a letter received from Mr. H. A. Pilsbry, regarding the evidence of the land and fresh-water snails in this connection: "Now as to Mexico, we have there in the south a 'tincture' of South American types, evidently of recent origin. The *Solariopsis* and *Labyrinthus* very likely came north in or since the Pliocene elevation of the isthmus. The Melanians of Mexico are distinctly South American. Besides, Mexico has in the *Eucalodium*, *Holospira*, *Glandina*, etc., element a distinct fauna, *suggesting insular conditions both from the West Indies and North America*, but nearer the former. At all events, it looks as if the fauna of northern Texas and New Mexico is a recent mingling of the two faunas, the Polygyras moving south, and *Holospira*, *Bulimulus*, etc., moving north. How much this appearance is due to mere isotherms, I am not prepared to say; but still, without having any tabulation of the faunas before me, it looks as if to a peculiar nucleus of genera which evolved their differential features on Mexican soil had been added lately an element from South America, another from the West Indies, a third from the United States, these introduced factors being still far stronger toward their respective points of ingress."

Atlantic, and the Flint River, which empties into the Gulf. The great group of *Unio buckleyi*, which is so characteristic of Florida, the coast region of Georgia, and South Carolina, is so closely related to that of *Unio crassidens* on the one hand and *Unio complanatus* on the other, that the systematic position of many of their species is wholly uncertain. Again, the group of *Unio fisherianus*, also characteristic of the Atlantic region, almost insensibly merges into that of *U. buckleyi*, through such forms as *U. aheneus*, Lea, *U. oscari*, B. H. Wright, and *U. hazelhurstianus*, Lea; and the small group typified by *U. downiei*, Lea, inhabiting Georgia and Florida, shows about equal relationship to those of *U. crassidens*, *U. buckleyi*, and *U. complanatus*.

In 1868 Lea described a number of fossil Naiades[1] from a marl bed near Camden, New Jersey. He believed this bed to belong to the Greensand of the Cretaceous, and noticing the strong resemblance of the forms to many now living in the United States, gave them names indicating this resemblance. The age of these beds is uncertain, but is probably more recent than what Lea supposed. The fossils are all casts of a somewhat ferruginous marl, and are quite imperfect, but among them are forms strikingly like *Unio anodontoides*, *U. rectus*, *U. complanatus*, and *Anodonta corpulenta*, and I think it not unlikely that they are in most cases the remains of living species, and that the beds are not older than the Pliocene. At any rate, they seem to show a much more intimate mingling of Atlantic and Mississippi forms at the time they lived than is now known to exist anywhere in either of the two regions.

As I have shown before, many of the species of the Mississippi Valley extend into Canada; they occupy almost exclusively the southern peninsula of Michigan, the Great Lakes, the Red River of the North, and the drainage system of the Mackenzie. This migration, which is entirely distinct from the earlier mingling of eastern and western species, is due, no doubt, entirely to the influence of the Glacial epoch. It is now generally admitted that during this time a vast cap of ice covered a greater or less extent of the Arctic and North Temperate regions of North America, and that at the close of the Ice age the southern edge of this cap gradually melted back for some distance from its extreme limit. North of the Height of Land in British North America great lakes were formed, which could only drain into the Mississippi Valley, since the wall of ice on the north and east formed a barrier in that direction. Several of these ancient drainage beds have been discovered; one near Chicago, another at the western end of Lake Superior, by which the water flowed down the St. Croix River; a third down the Minnesota River by way of the Red River of the North, and still another along the Maumee across to the Wabash.[2] It is probable there was an overflow down the Missouri River, as *Unio margaritiferus* is found in the upper waters of this stream—the only point where it is known to occur in the Mississippi basin.

[1] Proc. Acad. Nat. Sci. Phila., XX, pp. 162–164, 1868.

[2] See Popular Science Monthly, XLVI, No. 2, p. 217.

Numerous species of Naiades no doubt pushed up from the Mississippi basin into these lakes, and when the ice cap finally melted they occupied much of the area of the Mackenzie and St. Lawrence systems. *Unio margaritiferus*, which is circumboreal, is not known to exist in the central British American region, but is found in eastern Canada and New England. It is quite probable, as has been suggested by Wetherby,[1] that this species may have extended across this whole area in pre-Glacial times; that the onward movement of the ice cap exterminated it in this central area, and that it was driven southward to the east of the Appalachian chain, where it still survives. This ice cap may have also driven out and destroyed much of the Atlantic drainage fauna, which was afterwards replaced by the more vigorous Mississippi Valley forms.[2] The Atlantic drainage group of Anodontas typified by *A. fluviatilis* seems to be closely related to the *Cygnea* group, and may have been separated from the latter by the ice sheet.

In the Old World, *Unio* and *Anodonta* are believed by Ludwig[3] to date back to the Carboniferous. The forms which he refers to these genera are from Rhenish Westphalia, and are small, oval, oblong shells, one of which has sulcations on the beaks. From the figures of the hinges, I greatly doubt whether the species referred to *Unio* belong to that genus. The few Unionidæ known from the Old World Jurassic and Cretaceous strata do not seem to show decided relationships with any other Naiad fauna. *Spatha galloprovincialis*, Matheron, which was described by its author as a *Unio*, is believed by Sandberger to belong to the former genus.[4]

In the figures of this species given by the author, the shell bears some resemblance to a *Spatha*, but is very different from any species I know of belonging to that genus, in the character of the beak sculpture. In *Spatha*, the umboes are smooth or nearly so, as are the shells of the Mutelidæ in general. This species has strongly concentrically sculptured beaks, the ridges ending in a very sharp angle posteriorly. It may possibly be a *Leguminaia*.

Several fossil Unios are known from Siberia and India, from what are believed to be Tertiary strata. These resemble the solid forms of China and the Mississippi Valley, and *Unio bituberculatus*, v. Martens, from the former country, is very much like *Unio perplexus*, Lea, from the Ohio River.[5]

In examining the fossil Tertiary Naiades of eastern Europe, one can not help noticing the wonderful resemblance of certain forms to well-known groups in the Mississippi Valley. Regarding these species and

[1] Journ. Cin. Soc. Nat. Hist., July, 1881, p. 7.

[2] See paper by the writer in Proc. U. S. Nat. Mus., XVI, pp. 991–995.

[3] Palæontogr., VIII. Die Najäden der Rheinisch-Westphalischen Steinkohlen-Formation.

[4] Land und Süsswasser Conch. der Vorwelt, p. 95.

[5] See Abdr. d. Zeitsch. deut. geol. Gesellschaft, 1871, p. 713.

their relationship to North American forms, I can not do better than to quote from Dr. C. A. White:[1]

It has already been shown that the living Unionidæ of all Europe depart comparatively little from the primary, typical, oval form, and smooth or plain surface. These are the characteristics, so far as I am aware, of all the fossil species, save one, that are found in the strata of western Europe, including those from the Wealden and Cretaceous rocks. The exception referred to is *Unio toulouzanii*, Matheron, from the Lignite strata of the department of the mouths of the Rhone, which, while differing but little in form from the other fossil and living Unionidæ of western Europe, is marked by small plications upon its postero-dorsal surface. In Slavonia, Croatia, Dalmatia, and other parts of southeastern Europe, however, the fossil Tertiary species of *Unio* are much more numerous than the living species of the family are in the whole continent. Furthermore a large proportion of the types of these fossil species of southeastern Europe are as distinctively "North American" in character as those are which now live in the Mississippi River and its tributaries.

From these facts the inference seems to be a natural one that the living Unionidæ of all Europe are descended from those which are represented by the Mesozoic and Cenozoic fossil species of the western part of that continent; while the line of descent of the fossil species of southeastern Europe has evidently been cut off by disastrous changes of the physical conditions necessary for its perpetuity. The fact that these last-mentioned fossil species are identical in type with those of North America presumably indicates, though it does not necessarily prove, a community of origin; in which case they must have reached their present separated regions by some ancient continental connection now destroyed.

Among the Pliocene Unios from Slavonia there are many which almost absolutely agree with species living in the United States, belonging to the groups of *U. clavus*, *U. trigonus*, *U. perplexus*, *U. pustulosus*, and other well-known Mississippi Valley assemblages; and *U. sibinensis*, Tenecke, is almost exactly like *U. houstonensis*, Lea, of Texas; *U. neumayri*, Tenecke, is the counterpart of *U. modicus*, Lea, of Alabama; *U. stolitzkai*, Neumayr, is a nearly perfect reproduction of *U. æsopus*, Green, from the Ohio River, and *U. novskalensis*, Tenecke, is like a slightly roughened *U. pyramidatus*, Lea, from the same stream. Other species from the Pliocene beds of Slavonia almost as closely resemble *U. leai*, Gray, and *U. osbecki*, Lea, of China.

It seems not unreasonable, no matter where these striking types of Unios and Anodontas may have originated, whether in North America or the Old World, that they afterwards spread so that they occupied the greater part of Asia, Europe, except its western part, and possibly Africa, whose Unione fauna is, by the characters of the shells, apparently closely related to the Tertiary fauna of Europe, and that of India at the present time. It may be that the extreme cold of the glaciers exterminated or drove these forms to the region south of the Himalayas in Asia, and that the simple and probably more hardy species of western Europe spread rapidly to the eastward and southward after the Glacial epoch until they peopled the vast Palearctic region. But it seems probable that the European and northern Asiatic Anodontas, whose descendants now inhabit North America west of the Rocky Mountains, crossed over during the late Tertiary, as some of the forms now found

[1] Bull. U. S. Geol. Surv., III, Art. 23, p. 621, 1877.

in the latter region have inhabited it long enough to change specifically from their oriental ancestors.

J. G. Cooper believes that he found a form of *Anodonta nuttaliana*, Lea, one of the *Cygnea* group, in the Pliocene beds of Kettleman Lake, California,[1] and in other localities, but these formations may be of more recent date.

It is probable that *Unio* (*Margaritana*) *margaritiferus*, Linnæus, is the type of a group which for a long time has been distributed around the boreal regions, as it seems to be very closely related to a number of widely scattered forms.

The theory of a comparatively recent land connection between northern Asia and North America is further confirmed by the fact that some fifteen species of land snails, and about five or six more fresh-water forms, are common to the entire boreal regions of the globe; and Dr. Asa Gray has shown[2] that there are very many species of plants belonging to China and Japan which are identical with those found in eastern North America, and for others there are exceedingly close representative species in the New World.

The Unione faunas of the Australian and Neotropical regions may be considered together, as they are evidently closely related. The theory of an antarctic land connection between these regions is not at all a new one, and recently Mr. Charles Hedley, in a paper on "The faunal regions of Australia,"[3] brings forward some strong arguments in favor of such a connection, as he believes it necessary in order to explain certain relationships between the life of the two regions. The Mutelid fauna of South America is also, no doubt, related more closely to that of Africa than to anything else at present existing, and von Ihering[4] suggests a probable land connection between South America and Africa across the Atlantic during the Mesozoic, to account for its present distribution.

It does not seem to me that it is necessary to bring in any such immense and violent changes of land and sea to account for the presence either of the Mutelidæ in Africa and South America or the nearly related Unios in the Australian and Neotropical regions. It must be remembered that changes take place in the fresh-water mussels very slowly; that species are living to-day that scarcely differ from those found at the close of the Cretaceous or the beginning of the Tertiary periods; and that the relation between the Mutelidæ of Africa and South America is not a very close one, so that it is not necessary in either case to prove any recent mingling of these faunas, either by a land way or other means. I believe it is far more probable that the Unios of South America and the Australian region are the remnants of earlier types that may have had a wide distribution throughout the northern hemi-

[1]Proc. Cal. Acad. Sci., 2d ser., IV, part 1, p. 168.

[2]Address before Am. Assn. Adv. Sci., August, 1872, p. 10.

[3]Read at the Adelaide meeting of the Australasian Assn. Adv. Sci., September, 1893.

[4]Zool. Anzeiger, Nos. 380 and 381, p. 11, 1891, 1892.

sphere. The presence of a species in what are probably Triassic strata in Texas, with strongly radial beak sculpture, a character now confined to the Unionids of the two areas in question, is evidence in this direction. The forms with variously sculptured beaks which bear the embryos in the outer gills may be a more recent, vigorous stock, and it is possible that they have taken possession of the lakes and streams of the northern hemisphere and driven these older types to the southward.

The same thing may be true with the Mutelidæ, whose northernmost limit in the Old World is the lower Nile, and in the New, southern Mexico. And if the Cretaceous fossil now known as *Spatha galloprovincialis*, Matheron, from the mouths of the Rhone, is really a member of that genus, it would give color to this theory, which necessitates no violent changes of land and sea to account for present Naiad distribution.

To briefly sum up: The old arrangement of the families Mutelidæ and Unionidæ based upon the presence of siphons in the former and their absence in the latter can not stand, as this character may be developed or wanting in a single genus or even species. Ihering's redefinition of the families, in which the former is founded on the fact that the embryo is a three-parted *lasidium*, and that of the latter a *glochidium*, with the animal inclosed in a bivalve shell, agrees essentially with the characters of the hinge and shell generally. Those forms which would seem to belong to the Mutelidæ have irregularly taxodont teeth or vestiges of them, while the Unionidæ have schizodont teeth, which are arranged as cardinals or laterals, or both, though they may be merely rudimentary or even sometimes absent. The Naiades seem to be capable of being grouped into assemblages of related forms which have a more immediate common ancestry, and on the basis of this grouping we find them distributed into eight provinces, four of which are in the Old World and essentially agree with the regions of animal life of Wallace and Sclater.

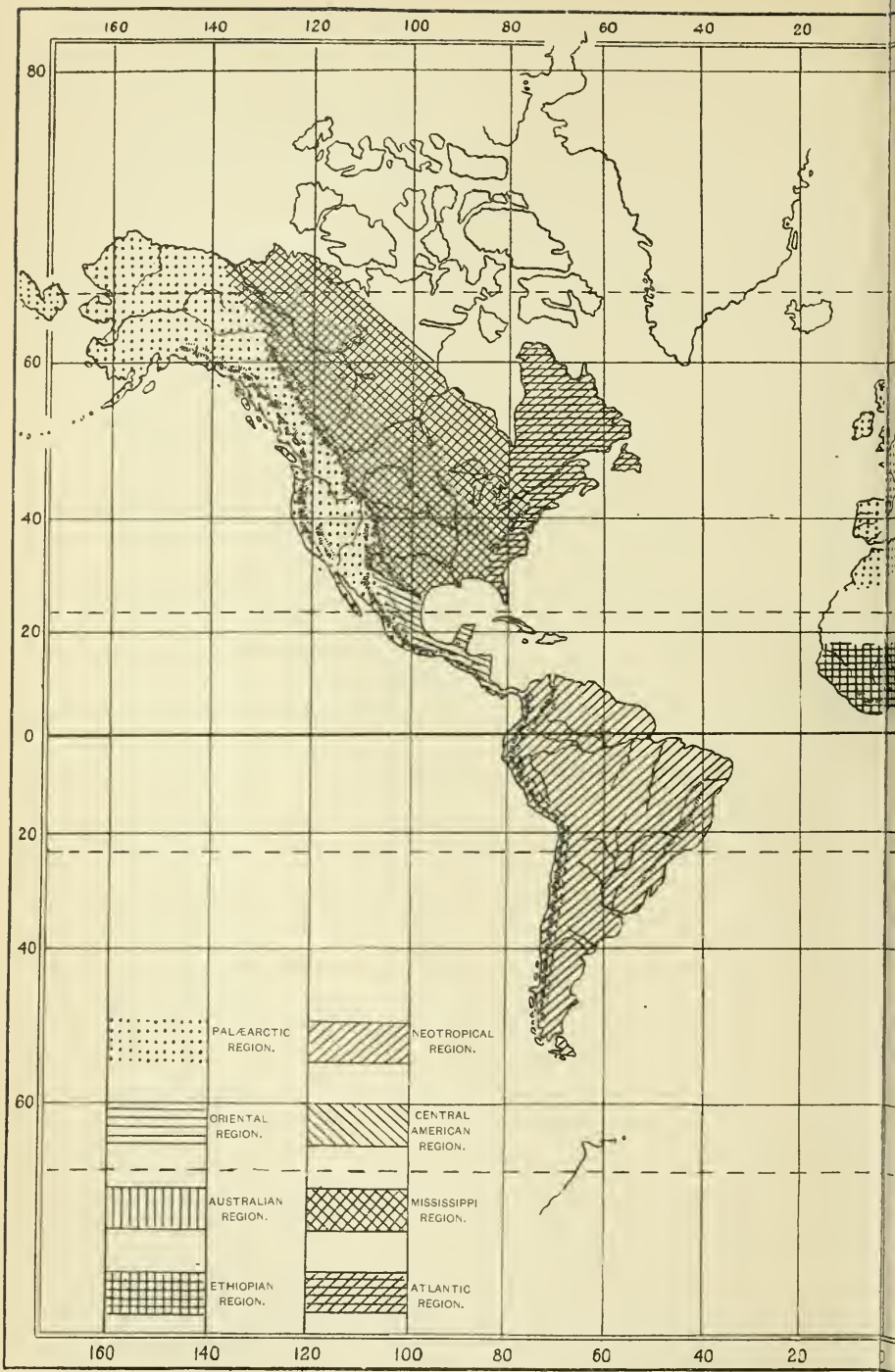
These may be tabulated as follows:

AREAS OF THE NAIAD REGIONS.[1]

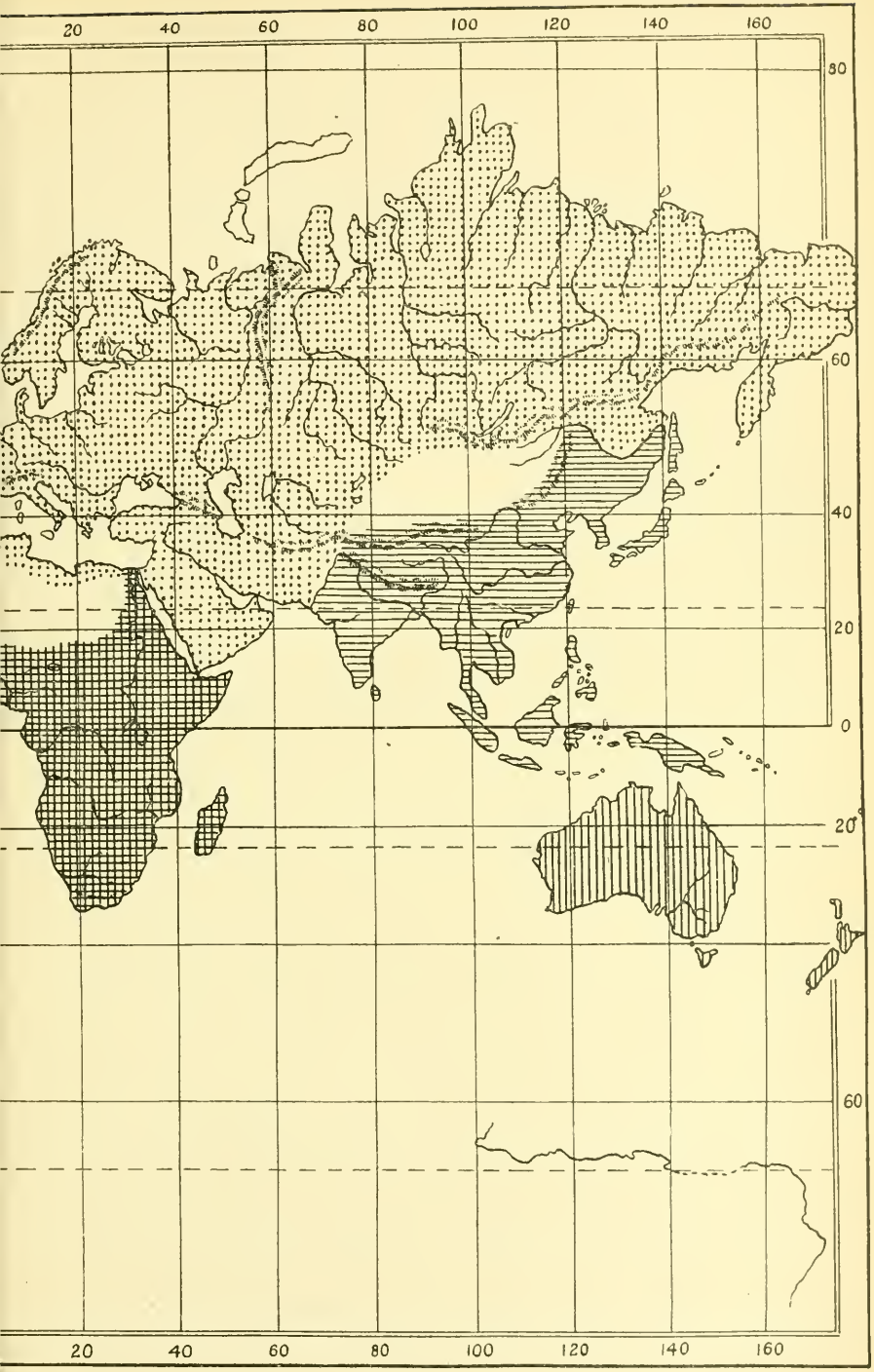
Palearctic	Europe. Northern and western Asia. North Africa to the Desert. Pacific drainage of North America.
Ethiopian	Africa south of the Sahara.
Oriental	Asia south of the Himalayas. East Indies to the Solomon Islands.
Australian	Australia. Tasmania. New Zealand.
Neotropical	South America.
Central American	Central America. Mexico east of the Cordillera. Cuba.
Mississippian	Entire Mississippi Valley and the Gulf drainage from west Florida to the Rio Grande. Mackenzie River system. Red River of the North. Great Lakes.
Atlantic	Lower St. Lawrence and rivers of eastern Canada. Atlantic drainage of the United States.

[1] For map of Naiad Regions see Plate IX.

The Unios undoubtedly date back well into the Jurassic; probably into the Triassic. The post-Cretaceous *Unio* fauna of the Northwestern States is evidently closely related to the fauna of the Mississippi Valley, and this seems to be related to that of Mexico, to the oriental fauna, and more distantly to that of tropical Africa, as well as to the Tertiary forms of eastern Europe and Siberia. The Unios of Australia and South America are apparently closely related to those of the Australian region. There seems to be, too, a general relationship between the Mutelidæ of Africa and South America. These Mutelids and the Unios which bear the embryos in the inner gills have perhaps formerly occupied extensive areas in the northern hemisphere, and may have been supplanted by more modern forms.



MAP SHOWING THE DISTRIBUTION



PEARLY FRESH-WATER MUSSELS