

THE NATURAL SYSTEM OF THE NAIADES

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PREFACE TO THE TRANSLATION

This paper, kindly translated by Professors David Stansbery and Ulf Soehngen, must be read with the understanding that it was written in 1942 during World War II. All museum specimens and literature were then preserved underground and wholly inaccessible.

It has been 22 years since this paper was written, and I have tried to continue this work. Meanwhile we have come to know the recent Australian and South American Naiades through the efforts of MacMichael and Bonetto respectively. The fossil forms of Siberia have been studied by Rammelmayer and Martinson; those of East Asia by Suzuki and Hoffert; those of the Sahara by Mongin; and the North American material by Russell, Yen, and others.

Consequently it is not strange that my inter-

pretations of 1942 are changed in many details. The basic outline, however, still stands.

Therefore I have no doubt that it is proper to reprint this old paper as a reference for all workers on Naiades who not only wish a system for use in classification, but for all questions confronting investigators in naiad phylogeny, their connections with climatology, paleogeography, and even geophysics.

I hope to publish a revised state of this system soon and also hope for the assistance of both authors of this translation.

Hans Modell
12 December 1963
Weiler am Allgäu
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THE NATURAL SYSTEM OF THE NAIADES

Since Simpson's great "Synopsis of the Naiades," of 1900 and its accompanying volumes, "The Descriptive Catalogue" of 1914, naiad research has not made very much progress. The main work of researchers has been directed towards the simplification of the species list which had become too lengthy, and toward the investigation of the anatomical relationships of individual species. In this regard in particular Ortmann's work "Notes Upon the Families and Genera of Naiades" of 1912 has been pioneering. Other works of Ortmann concerning the Naiades of Pennsylvania, the Tennessee and Cumberland systems, and those of South America have been additional contributions in anatomical as well as systematic fields.

The second part of the research, the arrangement of the species into natural groups, has also brought forth a series of important works. Several are: Frierson's "Checklist of the North American Naiades" of 1927; the revision of the Asiatic Naiades by F. Haas which was begun for the Conchyliencabinet in 1911, brought to a temporary halt in 1923, and was continued then in individual treatises. There are, in addition, the works on the inland Mollusca of Africa by the latter author in 1936 and a new revision of the Naiades of the Australian continent by T. Iredale in 1934.

Of the works listed, only those of Ortmann seemed to advance and support the system which Simpson had built to a great extent on inferences based upon analogies. Despite everything, our anatomical knowledge of the Naiades is not as general in all groups as might be desired. Furthermore, the anatomical structure varies in many cases so that we will not be able to clear up in this manner which are to be considered as species and generic characteristics and which are to be considered characteristics of the individual.

One thing, at any rate, is already certain today. The far-reaching conclusions made by Simpson, with regard to the use of the gills for incubation, were overextended and thereby his

theory of the close relationship of the four-gill breeders or the outside-gill breeders are to be rejected. Simpson has, as Ortmann emphasized in 1912, paid too little attention to the shell and especially to the sculpture of the beaks. The sculpture of the beak has, in particular, proven itself to be a most important characteristic.

All too much has been described in the field of naiad systematics even if one disregards the thoughtless species-making of Bourguignat and his school and the mass describing of *Lea* which does not stand too far behind this school. In all diagnoses it becomes obvious that time and again most authors had no idea at all of what is important and unimportant in the shell of the Naiades. Thus, on the basis of the most insignificant forms (or types) which appeared, genera were set up such that the diagnosis, in many cases, does not show a single important characteristic clearly enough that it can be recognized again. The end result was that the much-plagued museum man looked on the Naiades as being a small phantom of fright and that our museums, in too many cases, are supplied abundantly with incorrect determinations. Generic names have been through a marked inflation since Simpson (1900) began, in a greater measure, the division into sub-genera. Haas, Frierson, and Iredale have subsequently added their fair share so that soon each good species could insist on its own generic name. However, on the other hand, there is something to be said for such groupings since each natural species is usually based on a long phylogenetic history containing many geologic mutations.

Simpson has already said much (which could still be said) in the introductions of both works named above, so that I can point to them. I am sorry to say that introductions are seldom read.

The work of most researchers has been limited during recent years to the reduction of the number of species. This has been based upon literature research.

The most critical examination of the original description, if possible of the type specimen, followed by the removal of superfluous names

was the usual procedure. If there is sufficient participation, this process can bring us, in a hundred years, to a fairly usable and convenient system.

In order to arrive at a recognition of the species and higher categories which actually exist in nature, I have tried another approach. I have tried to view without bias the material which I have seen and worked over in our museums (i. e. Munich, Berlin, Stuttgart, and Frankfurt) together with that of my own collection and the material I have been able to obtain from the literature at my disposal. It is almost as if I had before me the material obtained on an expedition to an unexplored planet and I have used on it the experiences of a biological nature which I have obtained in better than 20 years of collecting.

I have come in this to surprising conclusions.

I emphasize emphatically that the present work is the first attempt to use equally and completely the possibilities of differentiation which have been given to us in the shell of the Naiades for the construction of a natural system. I am expecting the objection: What is a good species? and I have this answer: A good species is a community of individual animals of the naiad group which can be differentiated from every other community of equal standing by the form of the shell (the outline in the young specimens), the sculpture of the umbone (beak), and the structure of the hinge and - when it can be checked - of the soft body. This holds true only if the specimens are well preserved - and I believe the main importance should be placed on differentiability. With this concept I have arrived at a system of about 450 good species for the whole recent naiad fauna.

As important as the anatomy of the soft body has proven to be in many fields of molluscan research it may as easily be overestimated in its importance for the Naiades. If we disregard all "side work" there remain few points concerning the soft body which have value for systematics. These are mainly restricted to the true mutelids and their direct descendants, the North American elliptionids.

These are:

1. The position of the marsupium in the gills and the continuation of development up to the most complicated structure. In the latter case this can be known by the shell through difference of the sexes (Lampsilinae).

2. The growing together of the anal and supra-anal openings forming a distinct siphon can be seen at the shell through an indentation of the posterior margin of the mantle and occasionally also by the gaping of the shell. This development usually proceeds continuously to the enclosure of the body of the mussel through fusion of the lower mantle margins. Thus it is in part of the Mutelids.

3. The development of a long clinging foot with a sucking disc. This foot is especially strengthened with retractile muscles and the shell gapes at the rear end. So it is in the case of Mutelids and Elliptionids.

Most of the other anatomical characteristics go hand-in-hand with changes in shell form.

The shell itself gives us very few characteristics which are important for description and recognition except for following secondary anatomical characteristics:

1. The normal optimal form of the shell usually corresponding completely to the shell of the young.

2. The normal beak sculpture, varying biologically in swamp, stream, and lacustrine forms.

3. The normal structure of the hinge teeth of the species varying in the same manner.

The color of the mother of pearl can be used as an additional character in several North American, South American, and African species groups. However, it is assumed in this case that one is dealing with a character which has been acquired upon entering certain geologically homogeneous regions (orange and red coloration in tropical highlands, blue coloration in tropical lowlands, violet coloration in North America). Furthermore, in the hingeless African and South American mutelids the ligamental indentation, which very often has been lengthened into a hook, is a useful characteristic for differentiation.

For the fossil Naiades the conditions are more difficult since we usually have only incomplete remains. Thus most species in which one saw or suspected hinge teeth were placed in the Genus *Unio* and those lacking hinge teeth were placed into the Genus *Anodonta*. Henderson in 1935 still used both genera in this sense. He did this unjustly since today they correspond exactly to groups of species and are not a dumping ground for trash. As for the remainder, I have already tried, as far as is possible at this time, to build the fossil naiads into the system.

It is impossible to give exact descriptions of the individual parts of the naiad hinge and beak sculpture using current terms - which, in most cases, say almost nothing. I have redesignated these parts in a nonambiguous manner using several drawings. See table 6 and its explanation.

The hinge of the Naiades is very simple in its basic structure. It consists of two pairs of lamellae in the left shell and two single lamellae in the right shell. The attempt of Ihering, Stoliczka, and of others, to derive it from a taxodont hinge is mistaken and is based on an over-estimation of a single observation of the hinge of the African mutelid group *Iridina*. Its hinge, however, is not originally taxodont but is an auxiliary hinge which has been newly formed following the loss of the true hinge through cross-grooving of the still-present hinge plate according to the hypothesis of the non-reversal of evolution.

If a taxodont hinge were really the original hinge of the Naiades, more vestiges would still be present today. However, they are missing completely. Only the hinge of the left shell is important since it is somewhat more complicated and therefore gives greater possibility for description. In table 6 I give a scheme of the original naiad hinge. The figures signify: I = anterior cardinal tooth, II = posterior cardinal tooth, III = ventral lamellar tooth, IV = dorsal lamellar tooth. Regardless of whether the cardinal teeth are formed as lamellae or as thick teeth the above terminology holds. Their being named pseudo-cardinal teeth in the naiad group is misleading and worthless.

The sculpture of the umbone of the Naiades has behind it a rich developmental history. In the mutelids we still find the simplest stage - small, seemingly insignificant, irregular dots. The rest of the mutelid group has developed a regular sculpture which consists of two arches which meet at the umbone in a rather obtuse angle (Plate 6, fig. E). The Elliptionidae, direct descendants of the Mutelidae, have the same sculpture. The true unionids, (Plate 6, fig. C) however, have both arches of the mutelids subdivided again at the posterior ridge and on the anterior slope of the umbone so that 4 arches are formed. I have named them as follows: 1. the primary arch, 2. the anterior arch, 3. the posterior arch, and 4. the areal folds (Plate 6, fig. C, D). From this all such seemingly complicated naiad beak sculptures are formed. I shall discuss details when I come to the individual groups. I refer the reader to the illustration on plate 6.

The possibilities of naiad shell development go in three directions:

1. Standing-water forms having the greatest possible decrease in hinge development up to total disappearance (*Anodonta* forms).
2. Normally moving water forms which have the anterior lamellar arches of the hinge shortened to true cardinal teeth (*Unio* forms), (Plate 6, fig. G).
3. Fast-moving water forms with a strengthening of the hinge and a reformation of the shell in the direction of a high three cornered to high four cornered "rollingstone" shell form, (*Quadrula* form) (Plate 6, fig. H).

After these somewhat roundabout but necessary explanations I still have to dwell somewhat longer on the evolutionary history of the naiads for an understanding of the systematics based on it.

The whole group of the naiads presents in itself a complete entity, a group of the Lamelli-branchiata which is fitted, without exception, for life in fresh water. As far as it is possible for me to judge today the trigonids stand outside the naiad group and its progenitors. The Naiades are, however, more closely related to the Car-

dinids. This can be substantiated by a series of similar characteristics. It even seems probable that the Cardinids are a branch which has returned to the sea. This would not be surprising in view of the persistently fluctuating island-like nature of Mesozoic Europe.

Whether we can let the naiad stem begin with *Fordilla troyensis* Barrande from the middle Cambrian of New York or with the lower Devonian *Amnigenia catskillensis* Vanuxem is not yet clear. The first group we may definitely consider as Naiades is the Family Anthracosididae which were worldwide in distribution from the Carboniferous to the Triassic. Probably during the Permian, and at the same time on all continents, the stems of the Naiades developed from these dwarf-like forms. Nothing remains from this oldest development. We may however assume with certainty that the naiad type of this early fauna was fairly uniform. It, to a large degree, corresponded in shell structure and in its absence of sculpture to forms which we may consider to be the last remains of that fauna: in South America the Genus *Prisodon* Schum., in Africa *Pseudavicula* Sims., and in Australia *Velesunio* Ired.

The separation of the north continents from the south continents started at this time. This was followed by the division of the south continent itself, and these events determined the further direction of evolution. In South America, still very similar to Africa with respect to its original mutelid fauna, these forms continued to develop into almost or completely hingeless forms. They have probably also undergone great changes in anatomy. These are the subfamilies Anodontitinae, Glabarinae, Mycetopodinae, Monocondylaeinae and, a group having an atypical origin, that subfamily of freshwater clams which have sprung from the Anodontitinae, the Bartlettinae. Occasional later connections of shorter duration have also permitted the immigration of a species of the Spathopsinae and a species of the Iridininae from Africa. However, a connection with the North American continent, which probably had its origin before the Triassic, became more important. It brought to North America, in addition to the completely developed

Mycetopodinae with its reduced hinge, the basic form of the unionids of that time. These small naiads of the type of *Unio gallinensis* Meek, and *cristonensis* Meek probably became the progenitors of the North American Unios. Van der Schalie has placed them in the Genus *Trigonodus* Alb. Development continued rapidly from these forms to the Pleurobeminae which Ortmann has considered to be the progenitors of his *Elliptio*. These finally gave rise to the true Elliptioninae accompanied by a better development of the umbone sculpture, and finally to the Quadruline forms which are the Ambleminae of today. Already in earlier times a subfamily had begun with the reduction of the hinge. It had started in an unusual manner with total loss of the upper lateral tooth and the reduction of the lower to a large degree (Alasmi-dontinae). One species has even gone so far as to develop an anodontid form. An additional subfamily (the Lampsillinae) has evolved in different directions from true elliptionids. They have the marsupium limited to the posterior end of the outer gill and, through a folding or rolling up of the marsupium, have developed better water circulation. Whether this extreme specialization can be considered to be the highest development appears questionable to me. At any rate, it is the highest level the naiads have reached in the care of the young. In other respects this group in particular has remained very primitive. This is demonstrated by its glochidium and umbone sculpture which are directly related to the African mutelids. In the lower Cretaceous this development has, for the most part, already been completed. This group has apparently never spread beyond its present range.

The African mutelids have developed, with the exception of the original relic *Pseudavicula* which differs in its hinge teeth, a series constituting the subfamilies Mutelinae, Aspathariinae, and Spathopsinae, which find a parallel in the South American forms. Of the Spathopsinae, one species later migrated to South America. As a special development the Iridininae changed the hinge plate, after the loss of the

(TEXT CONTINUED ON PAGE 7)

EXPLANATION OF PLATES

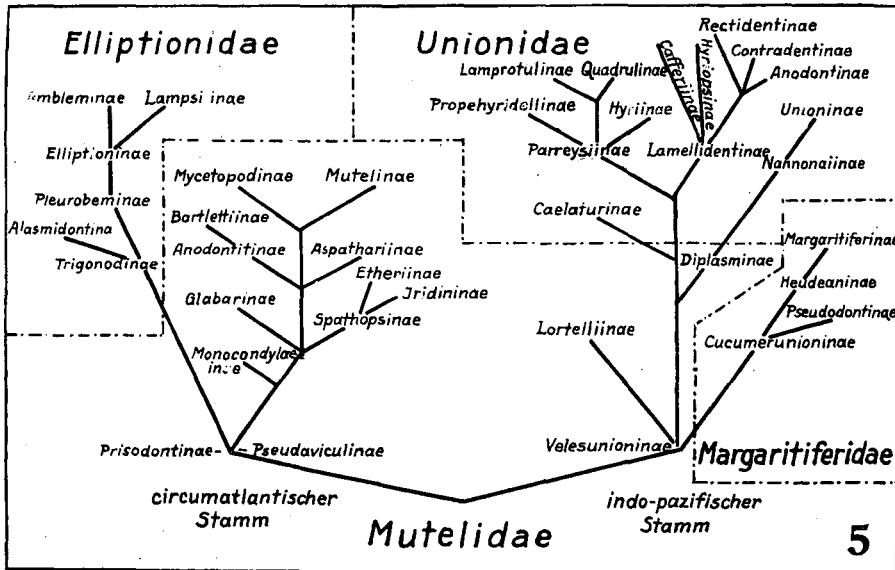
PLATE 5. Phylogenetic relationships of the Naiades.

PLATE 6. Fig. A, Outline of a Unio: I anterior margin, II umbone, III dorsal margin, IV ventral margin, V posterior margin (beak). Fig. B, View from above: I right valve, II left valve, III umbone. Fig. C, Unionid sculpture: I primary arch, II anterior arch, III posterior arch, IV areal fold. Fig. D, Parreysid or V-sculpture. Same terminology. Fig. E, Aspatharid sculpture. Same terminology. Fig. F, Lamellar hinge: I anterior cardinal tooth, II posterior cardinal tooth, III lower lamellar tooth, IV upper lamellar tooth. Fig. G, Unio-hinge. Fig. H, Quadrula-hinge.

Umbone sculptures: (slightly enlarged) Glabarinae: 1. *Glabaris trigonus* Spix, Spathopsinae: 2. *Spathopsis wahlbergi* Kr., Aspatharinae: 3. *Asp. rugifera* Dkr., 4. *Asp. pfeifferiana* Bern., 5. *Asp. rubens* Lam., Jridinae: 6. *Jrid. ovata* Sw., Pleurobemininae: 7. *Pleurob. mytiloides* Raf., Alasmidontinae: 8. *Alasm. undulata* Say, 9. *Pressodonta calceola* Lea, 10. *Pegias fabula* Lea, 11. *Platynaias viridis* Raf., 12. *Simpsoniconcha ambigua* Lea, 13.-15. *Strophitus undulatus* Say, 16. *Anodontoides ferussacianus* Lea, Elliptioninae: 18. *Ell. buckleyi* Lea, 19. *Ell. dilatatus* Raf., 20. *Uniomerus tetralasmus* Say, Ambleminae: 21. *Amblema plicata* Raf., Lampsilinae: 22. *Lamps. fasciata* Raf., 23. *Lamps. teres* Raf., 24. *Lamps. recta* Lam., 25. *Ptychobr. fasciolare* Raf., Cucumerunionae: 26. *Cuc. beccarianus* Tapp., Heudeaninae: 27. *Heud. murinum* Heude, Margaritiferinae: 28. *Marg. margaritifera* L., 29. *Cumberl. monodonta* Say, Pseudodontinae: 30. *Pseud. inoscularis* Gld., 31. *Monodontina vondembuschiana* Lea, 32. *Obovalis loomisi* Simps., 33. *Microcond. compressa* Mke., Hyriinae: 34. *Dipl. chilensis* Gray, 35. *Dipl. rhuacoicus* Orb., 36. *Hyria rugosissima* Sow., 37. *Dipl. fluctiger* Lea, 38. *Castalia quadrilatera* Orb., Prophehydellinae: 39. *Pr. nepeanensis* Conr., Parreysinae: 40. *Parr. corrugata* Müll., 41. *Acuticosta chinensis* Lea.

PLATE 7. 42. *Protunio messengeri* B. & Dautz., Lamprotulinae: 43. *Lampr. leai* Gray, 44. *Inversidens japonensis* Lea, Quadrulinae: 45. *Quadr. quadrula* Raf., 46. *Megalonaias gigantea* Barn., Lamellidentinae: 47. *Lam. marginalis* Lam., Hyriopsinae: 48. *Hyr. schlegeli* Marts., Cafferinae: 49. *Caff. caffra* Kr., Rectidentinae: 50. *Rect. orientalis* Lea, 51-52. *Physunio superbus* Lea, 53. *Pilsbr. exilis* Lea, 54-55. *Pyganodon grandis* Say, 56-57. *Lastena ohiensis* Raf., 58. *Last. suborbiculata* Say, Contradentinae: 59. *Contr. dimotus* Lea, 60. *Contr. (Sprickia) rusticus* Lea, 61. *Pressidens exanthematicus* Kstr., 62. *Caudiculatus caudiculatus* Marts., Anodontinae: 63. *Pletholophus discoideus* Lea, 65. *An. japonica* Cless., 66. *An. marginata* Say, Caelaurinae: 67. *Cael. aegyptiaca* Caill., 68. *C. bakeri* Ad., 69. *C. hauttecoeurii* Bourg., 70. *Grandid. burtoni* Woodw., 71. *Cael. gabunensis* Kstr., Nannonaiinae: 72. *Nann. caerulea* Lea, 73. *Nann. crispata* Gould, 74. *Trapezoideus foliaceus* Gould, 75. *Nann. mossambicensis* Marts., Unionae: 76. *Unio schödei* Haas, 77. *Cuneopsis pisciculus* Hde., 78. *Cun. celtiformis* Hde., 79. *U. douglasiae osbecki* Phil., 80. *U. dougl. dougl.* Gr. & Pidge., 81-87. *U. mancus glaucinus* Porro, Oberitalien, 88-92. *U. terminalis* Bourg., 93. *U. tigridis* Bourg.

(THE THREE PLATES OF THE ORIGINAL ARE HERE GROUPED INTO ONE)



original hinge (as in their ancestral group the Spathopsinae) into a new cross ribbed hinge.

The Etheriinae, coming from the Aspathariinae, reached the typical form of an oyster as did the South American Bartlettinae. The Indian fresh water oyster *Pseudomuleria* Anth. probably also belongs to this group. For the rest, Africa has seemingly added nothing directly to the further development.

The third large southern continent, Australia, compared to the Africa and South America of today, appears to be more ancient in its mutelid fauna in so far as all still have hinge teeth i. e. have not progressed very far in the reduction of these structures. The Subfamily Lorttiellinae Ir. forms a parallel with the Mycetopodinae and the Mutelinae of the other southern continents and has, in the case of one genus, spread as far as southeast Asia. The other Subfamily, the Veleunioninae Ir., still shows the steps of transition from the true lamellar hinge to the unionid hinge. They remain, however, without sculpture. It is probable that one must trace the development of the Family Margaritanae back to Australia. Their original sculpture consists only of the two middle arches which have small upswep lines on both sides. At any rate, Australia still has the most primitive subfamily of this family, the Cucumerunioninae Ir. The remaining subfamilies, the Heudeaninae, the Pseudontinae with the reduced hinge, and the true Margaritiferae are still found in nearby southeast Asia. The later expansion of the whole family occurred in the upper Cretaceous and Eocene. A further main migration of the Pseudodontinae to Europe and North America took place in late Miocene to Pliocene and the last circumpolar migration of *Margaritana margaritifera* L. in late Pliocene.

The most difficult problem is the nature of the connection of the true unionids to the mutelids. Following an intermediate stage, the Unionids appear to be connected with the Veleunionids of Australia. This stage corresponds to the American Trigonids and is represented by *Trigonodus* in the Raibler strata of the Triassic in Europe and by the living sculptureless

Diplasmids in India. This transition may have occurred at the time when Australia, according to Wegener's theory, was still located farther west. The fauna of the Indian continental block already represents a further developed stage. The structure of the hinge has developed slowly into the Unionid hinge and the sculpture is more primitive in-so-far as the rising arch and the areal folds are fully developed and separated. However, both middle arches, in complete contrast to the mutelid sculpture, form an acute angle pointing downward. Since a large number of the groups which have this sculpture soon develop the true Unionid sculpture, we can say, in the case of this Parreysien sculpture, that its appearance as a time-bound type-characteristic is to be understood in the sense of Daqué's theory of types. Probably in the Indian area where all basic forms are still living, there appeared in quick succession the three branches: the Parreysiinae, Lamellidentinae, and Nannonatinae.

The Parreysiinae, which have a definite "radial sculpture," continue to live in the main part of India and have continued to develop in eastern Asia and Europe into the Lamprotulinae which have the Unionid sculpture. In the Triassic of North America the subfamily Parreysiinae appears with the Hyriinae. The Parreysiinae of North America, however, change gradually in the Jurassic and Cretaceous into the Quadrulinae. The Hyriinae have today covered all of South America and have, in the Pliocene, advanced again toward North America together with the giant South American sloth. A last branch of the Parreysiinae, the Propehyridellinae Ir., still live in Australia.

The Lamellidentinae, which were also originally provided with V-sculpture, had also a complete lamellar hinge. They became, through scarcely noticeable, though not yet obliterated transitional characters, the progenitors of a series of subfamilies all of which, however, have Unionid sculpture. The first of the series is the subfamily Cafferinae which is limited to South Africa today. Secondly, the Hyriopsinae in the Tertiary exhibited a strong development of the shell and, today includes the largest living naiades,

Hyriopsis and Dipsas. On the other hand, this subfamily has the teeth and, in particular, the cardinal teeth reduced in part. They have also been represented in Europe from the Miocene to the end of the Pliocene. A further branch of the Lamellidentinae is split into the Contradentinae, Rectidentinae, and the Anodontinae. The former remain limited to southeast Asia, the Rectidentinae migrate, after the loss of their hinge, to Europe and North America. The Anodontinae also lose their hinge and spread over all of the north continents. A further subfamily, the Caelaturinae of Africa, forms the transition to the Nannonaiinae of East India. Also in this case the original sculpture is V-shaped. However, already within the stem group, the sculpture has changed to the Unionid type. This has a later throwback into an apparent V-sculpture in a single genus (*Cuneopsis*). For the rest, the development continues almost without deviation to the true Unioninae. These have occupied Europe and Asia since the Upper Cretaceous but have never reached North America.

Thus we see that the faunal pattern of today's Naiades has terminated, for the most part, at a geologically early time, i. e. the Upper Cretaceous. Only a few groups, which belong mostly to the higher developmental steps of the Unionids, made still further progress in the Tertiary. The last attempt to form new Quadruliné forms in the European Pliocene was by these young groups and this was disrupted by the onset of the ice age.

The over-all picture of the developmental history of the Naiades given here is probably as interesting as the development of the mammals. With "Altmeister" (old master) Boelsche one could write a volume titled "Wanderings of Naiades in Ancient Times."

I hope to be able to publish, within a short time, the bases for this paper. I am adding a compilation of the most important types of beak sculpture. They will give the reader a concept of the probability of what has been presented. The "family tree," which has also been added, is not, of course, meant to be a family tree in the sense of Haeckel's school but only a presentation of those transition lines which represent

the connection of relationships between the naiad groups. Despite its limited size, one may recognize in it several important points, which until now could not be discussed. One is the division of the originally uniform development into two lines. A circumatlantic branch, which has, in the southern portion of its range, already completed development to the Anodontid form and in its northern range, has reached its highest development in the Elliptionidae with the hinge retained. An Indopacific branch, whose mutelids have, for the most part, continued to develop into modern forms and brought forth the modern Unionids after having split off the older Margari-tiferidae. I consider these and not the one-sided highly-specialized Lampsilinae to be the only Naiades capable of further development.

In the following compilation I have assigned a series of Central American forms to the subfamilies Elliptioninae, Lampsilinae, and Quadrulinae, although this assignment is open to question. Frierson's compilation and assignments also have to be checked over critically. This was impossible for me to do because of the incompleteness and confusion of the literature and the sparse material present in German museums. I have also reserved a large part of the fossils for a later presentation.

I. Family Mutelidae (Gray) Ihering, 1893.

The lasidium of Ihering as the glochidial stage of the Mutelidae has not been found again since its discovery. Thus it remains questionable. If it should really exist, it would mean that this early stage of the mutelids has already gone through a far-reaching special development and reduction. It could possibly be identical with the original larval stage of the Naiades. Rather we are dealing with a form which presupposes the closing of the animal in a cylindrical shell which is approached in many cases in the mutelids today. In the concept of the family, I agree with v. Ihering and set aside the Hyriinae of Ortman as being totally heterogeneous. On the other hand, I include the primitive sculptureless forms of Australia.

The greater number of today's mutelids have become hingeless. There still remain, however, several groups in Australia and India which retain the lamellar hinge that was originally characteristic of all mutelids. Individual special developments, such as the apparently taxodont hinge of the Iridininae and the development of the Bartlettinae and Etherinae (which is similar to that of the oyster), can be explained by special adaptations during the infinitely long span of time of their existence. The definition of the family, therefore, has to be very broad:

Naiades, originally with no sculpture but later developing a punctiform sculpture, or double archs reaching from the anterior to the posterior margin with the tip at the umbone. Originally there was a lamellar hinge (left shell with two cardinal teeth and two lateral teeth; right shell with one cardinal and one lateral tooth), which later became completely reduced. It is often closed off by a triangular to hook formed ligamental indentation at the posterior margin. Anatomically there is a trend toward siphon formation of the anal and supra-anal openings, toward the fusion of the lower mantle margins, and toward the formation of a mushroom-shaped clinging foot.

Distribution today: South America to southern Middle America, Africa south of the Sahara, India, Australia, New Guinea, and New Zealand.

A. South American Developmental Series

1. Subfamily *Prisodontinae* n. subfam.

Type species: *Prisodon serratophorus* van Meuschen, 1781. Last remnant of originally fully-toothed mutelids of South America. Hinge consisting of teeth, umbone sculpture missing. Distribution: High land of Guiana (*Archigiana* v. Ihering) to the Amazon River. Single genus: *Prisodon* Schumacher, 1807.

2. Subfamily *Monocondylaeinae* n. subfam.

Type species: *Monocondylaea paraguayana* Orbigny, 1835. Umbone sculpture missing, hinge largely reduced in two phases. The first with a hinge plate still present and

with teeth on top. The second is without a hinge plate, with the teeth seemingly coming from the shell margin. Lateral teeth have completely disappeared; on the left a cardinal tooth is still present.

This group includes the genera: 1. Phase: *Iheringella* Pilsbry, 1893; *Marshalliella* Haas, 1931; *Diplodontites* Marshall, 1922; *Tamsiella* Haas, 1931. 2. Phase: *Monocondylaea* Orb., 1835; *Fossula* Lea, 1870. Distribution: Tropical South America east of the Andes.

3. Subfamily *Glabarinae* n. subfam.

Type species: *Glabarus exoticus* Lamarck, 1819 (= *Glabarus trapesialis* Lam., 1819). Anodontine development without hinge teeth, however with hinge plate still retained and triangular to hook-formed, ligamental indentation. Mother-of-pearl white, bluish to red. The development is parallel to the African *Aspathariinae*.

This group includes the genera: *Glabaris* Gray, 1847, with the species groups *mortoni* *Lea*, 1834, *patagonicus* Lam., 1819, *trigonus* Spix, 1827, *trapesialis* Lam., 1819, and *Leila* Gray, 1840.

I find myself forced to use the generic name *Glabaris* Gray which has been re-introduced by Simpson (1900) for the species groups which I have mentioned since the name *Anodontites* refers to another species group which is considerably further advanced in their anodontine change, thus probably having begun to change much earlier.

Distribution: Tropical South America and southern Central America.

4. Subfamily *Anodontinae* n. subfam.

Type species: *Anodontites crispatus* Bruguière, 1792. Umbone sculpture missing. The shell is elongate to knife-formed. Hinge-plate almost disappeared, ligamental indentation hook-formed. Mother-of-pearl blue-gray to blue-green. The shell sculpture appearing in tropical forms, and called "festoons" is not even useful as a species characteristic.

This group includes the genus: *Anodontites* Brug., 1792, with the species groups *crispatus* Brug., 1792, and *tenebricosus* Lea, 1843.

Distribution: Tropical South America.

5. Subfamily Bartlettinae n. subfam.

Type species: *Bartlettia stefaninii* Moricand. Oyster-shaped transformations of the Anodontitinae having pointed ligamental indentation hooks. They have a broad hinge plate and blue-green mother-of-pearl. Found living in the limestone debris below falls (*Bartlettia*) or attached to the sand bottom of rivers (*Acostaea*).

This group includes the genera: *Acostaea* Orbigny, 1835; *Bartlettia* H. Adams, 1870.

6. Subfamily Mycetopodinae n. subfam.

Type species: *Mycetopoda siliquosa* Spix, 1827. Umbone sculpture missing. Hinge-plate completely disappeared. Ligamental indentation long and flat. Mother-of-pearl bluish. Shell at the posterior margin gaping. "Sucking foot" well formed.

Into this group: *Lamproscapha* Swainson, 1840; *Mycetopoda* Orbigny, 1835; *Mycetopodella* Marshall, 1927.

Distribution: Tropics South to Central America. Known as a fossil since the Triassic from North America.

B. African Developmental Series

7. Subfamily Pseudaviculinae n. subfam.

Type species: *Pseudavicula johnstoni* Smith, 1893. Hinge with complete lamellae, umbone sculpture missing. A parallel to *Prisodon*. Into this group: *Pseudavicula* Simpson, 1900, Lake Mweru.

8. Subfamily Spathopsinae n. subfam.

Type species: *Spathopsis wahlbergi* Krauss, 1848. Elongate oval to rectangular species with hinge plate lacking teeth. Umbone sculpture single points. Mother-of-pearl reddish-orange. Ligamental indentation hook formed.

Into this group: *Spathopsis* Simpson, 1900 in Africa and with one species in the Guiana region of South America.

9. Subfamily Iridininae n. subfam.

Type species: *Iridina exotica* Lamarck, 1819. Continuation of development of the Spathopsinae by the re-introduction of an apparently taxodont hinge; originated in the great African lakes by grooving of the hinge plate. Point sculpture barely indicated.

Into this group: *Iridina* Lam., 1819; *Pleiodon* Conrad, 1834; *Cameronia* Bourg., 1879; a fossil species (upper Cretaceous or lower Eocene) in the state of Sao Paulo, Brazil; otherwise in Tropical Africa in the Tanganyika, Tschad, and West African rivers.

10. Subfamily Aspathariinae n. subfam.

Type species: *Aspatharia rugata* Dunker, 1848, (= *Asp. camerunensis* Ortm. & Walker). Short oval to elongate species with triangular ligamental indentation, hinge plate present, but without teeth. Mother-of-pearl white to bluish and red. Umbone sculpture double arches which meet below the umbone in an obtuse angle. Represents the South American Glabarinae and, in part, the Anodontitinae.

Into this group: *Aspatharia* Bourg., 1885, with *pfeifferiana* Bernardin; *rubens* Lam.; *Leptospatha* Roch. and Germain, 1904; *Arthropteron* Rochebrune, 1904, in which the *Asp. petersi* Martens forms a closer analog to the Anodontitinae.

Distribution: Tropical Africa.

11. Subfamily Etheriinae n. subfam.

Type species: *Etheria elliptica* Lamarck, 1807. Development similar to that of oysters with a hinge plate and ligamental indentation; probably evolved from the Aspathariinae of the *rubens* Lam. group.

Into this group: *Etheria* Lam., 1807, in Tropical Africa and North Madagascar; *Pseudomulleria* Anthony, 1907, in South India.

12. Subfamily Mutelinae Ortmann, 1911.

Type species: *Mutela dubia* Gmelin, 1791. In contrast to Ortmann, I am limiting the subfamily to the African relatives of *Mutela dubia* Gm.

Elongate thin-shelled forms; analogous to the Mycetopodinae; shell gaping at both ends. Mother-of-pearl bluish. No umbone sculpture; siphon development and probably clinging foot.

Into this group: *Mutela Scopoli*, 1777; *Chelidonopsis* Ancey, 1887; *Pseudospatha* Simpson, 1900; *Brazzaea* Bourg.; *Moncetia* Bourg., 1885.

Distribution: Tropical Africa.

C. INDIAN Developmental Series

13. Subfamily Diplasminae n. subfam.

Type species: *Diplasma vitrea* Raf. (= *Nodularia olivaria* Lea and author).

Small forms with a glossy shell structure, without sculpture, and with weak Unionid teeth. A remnant of a very old developmental step, which is represented in North America by *Trigonodinae*. Probably they are very close to the forerunner of the Unionidae.

Into this group: *Diplasma* Raf., 1831, in Assam, East India.

D. Australian Developmental Series

14. Subfamily Velesunioninae Iredale, 1934.

Type Species: *Velesunio balonnensis* Conrad, 1850. Umbone and shell smooth. Hinge completely lamellident, in part in the process of changing to the Unionid hinge. Umbone seldom "seemingly angled" (in *Hydrunio*).

Into this group: *Velesunio* Iredale, 1934; *Westralunio* Iredale, 1934; *Centralhyria* Iredale, 1934; *Hyridunio* Iredale, 1934; *Alathyria* Iredale, 1934.

Distribution: Australia, New Guinea, New Zealand.

This subfamily, or rather its geologic forerunners, has become the origin of all developmental series in the Indo-Pacific region. Also its forms today have not gone along with the

Atlantic series in their development to the anodontine form possibly as a result of the increasingly dryer condition of Australia.

15. Subfamily Lortellinae Iredale, 1934.

Type species: *Lortiella rugata* Sowerby, 1868. Elongate species, a younger parallel series to the Mycetopodinae and Mutelinae. In the oldest stages there is still a lamellar hinge, which later becomes rudimentary. Partially developed digging foot. Sculpture (in *Solenaia*) "weak concentric double arches."

Into this group: *Lortiella* Iredale, 1934; *Solenaia* Conrad, 1869.

II. Family Elliptionidae n. fam.

Starting with the South American forerunners of today's mutelids the elliptionids developed in North America at the latest since the Triassic. They have always remained limited to North America. The oldest known forms have an oval outline and no sculpture. They were followed by oval forms with a unionid hinge, the unionid-like forms immediately followed by quadruline forms, as a sideline a group with partially or totally reduced hinge, and, finally, as the highest developmental stage, the Lampsilinae with specialized marsupium. The primitiveness of the whole group is demonstrated by the umbonal sculpture which goes directly back to the aspartharid sculpture, as well as by the hookless glochidium which makes impossible a parasitic juvenile stage on the fishes. As a timewise and biological analog can be considered the family Margaritiferidae from the Indopacific developmental series. The definition of the family is as follows:

Naiades of North America with a complete to missing hinge, the umbone sculpture, as a rule, limited to the two inside arches whose posterior arch meets the anterior arch in an obtuse angle. The posterior arch can have, through a strong upward sweep, the character of a hook (*Alasmiodontinae*) or may, through a downward curve and an increase in thickness, form shell sculpture (*Ambleminae*). In the Lampsilinae, which

are characterized by a special brood chamber in the posterior part of the outer gills, the sculpture is the most primitive, being similar to that of the African *Aspatharia*. The shell surface often has radial green stripes (also inherited from the Mutelidae). Glochidium without hooks.

16. Subfamily Trigonodinae n. subfam.

Type species: *Trigonodus sandbergeri* v. Alberti, 1864. Shell short oval to short triangular, umbone without sculpture. Hinge unionid.

Into this group: *Trigonodus* v. Alberti, 1864; a series of so-called "Unio" species from the Triassic of southwest U. S. A. (*cristonensis* Meek; *gallinensis* Meek) which, for the first time, van der Schalie has placed in an equal footing with *Trigonodus* of the east-alpine Triassic.

17. Subfamily Pleurobeminae n. subfam.

Type species: *Pleurobema mytiloides* Rafinesque (= *Unio clavus* auct.)

Primitive forms with shortened oval to quadrate shell, umbone sculpture hardly noticeable (I only saw anterior end hooks in *P. mytiloides*) and a unionid hinge often of the thickened type. The type species itself is a special development with the umbone in a forward position. At times the shell sculpture occurs in a central row of knobs (*Plethobasis*).

Into this group: *Pleurobema* Raf., 1820; *Lexingtonia* Ortmann, 1914; *Plethobasis* Simpson, 1900; *Pleurobema* Frierson, 1927; *Fusconia* Simpson, 1900; *Obliquata* Frierson, 1927.

Distribution: North America, west of the Rocky Mountains, south probably to Central America.

18. Subfamily Alasmidontinae Frierson, 1927.

Type species: *Alasmidonta undulata* Say, 1817. Following Trigonodinae and Pleurobeminae, this group has begun very early with the reduction of the hinge teeth. At first the lower lamella disappeared (III) and in its place there occurred a thickening of the posterior

cardinal tooth through the interdental tooth, which for its part is connected to the remains of the lamella III. The upper lamella disappeared completely. The further development led to the complete loss of the hinge or the remaining of only a weakened posterior cardinal tooth (*Strophitus*). The sculpture is very uniform, short, flat, double arches, often protruding and, as often, with a strong upward arch at the end which can almost appear to be a radial sculpture.

Into this group: *Alasmidonta* Say, 1818; *Prolasmidonta* Ortmann, 1914; *Bullella* Simpson, 1900; *Pressodonta* Simpson, 1900; *Sulcularia* Raf., 1831; *Lasmigona* Raf., 1831; *Pterosyna* Raf., 1831; *Platynaias* Walker, 1918; *Decurambis* Raf., 1831; *Arcidens* Simpson, 1900; *Arkansia* Ortmann and Walker, 1912; *Pegias* Simpson, 1900; *Strophitus* Raf., 1820; *Pseudodontoideus* Frierson, 1927; *Jugosus* Simpson, 1914; *Simpsoniconcha* Frierson, 1927; *Hemistena* Raf., 1820; *Anodontoides* Simpson, 1898.

19. Subfamily Elliptioninae n. subfam.

Type species: *Elliptio niger* Raf., 1820 (= *U. crassidens* auct.). Unionid-like form which developed in North America. Umbone sculpture consisting of very flat double arches which scarcely arch up in the middle. Clinging muscles present at the posterior cardinal tooth. Found in North America at least since lower Cretaceous. There are several special developments in the southern states and in Central America.

Into this group: *Elliptio* Raf., 1819; *Elliptioideus* Frierson, 1927; *Uniomerus* Conrad, 1853; *Nephronaias* Crosse and Fischer, 1893; ? *Sphenonaias* Cr. & Fisch., 1893; ? *Pachynaias* Cr. & Fisch., 1893; ? *Reticulatus* Frierson, 1927; *Popenaias* Frierson, 1927; ? *Martensnaias* Frierson, 1927; *Micronaias* Simpson, 1900; ? *Canthyria* Swainson, 1840; *Plesielliptio* Russell, 1934; *Protelliptio* Russell, 1934; *Barynaias* Cr. and F. 1893; *Psoronaias* Cr. and Fisch., 1893.

20. Subfamily Ambleminae n. subfam.

Type species: *Amblema plicata* (Say, 1817). A further development of the Elliptionids in the lower Cretaceous to strongly sculptured quadruline forms with an elongation and enlargement of the posterior arch of the normal Elliptionid sculpture across the whole shell.

In this group: *Amblema* Raf., 1819; *Loxopleurus* Meek, 1870; *Plectomerus* Conrad, 1831.

Distribution: North America between the Alleghany and Rocky Mountains, south to Central America.

21. Subfamily Lampsillinae Ortmann, 1912.

Type species: *Lampsillis ovatus* Say, 1816. Similar in development of the shell to different groups of the Elliptionids. As the forms point out, they have in common the unique limitation of the marsupium to the posterior part of the outermost gill and the differentiation of the shell in both sexes. The rounded interdentum is considered to be a further characteristic. Concerning the sculpture see above. Known in North America since the Cretaceous, common since the upper Cretaceous.

Into this group: *Ptychobranthus* Simpson, 1900; *Subtentus* Frierson, 1927; *Obliquaria* Raf., 1820; *Cyprogenia* Agassiz, 1852; *Dromus* Simpson, 1900; *Friersonia* Ortm., 1912; *Lampsillis* Raf., 1820; *Ligumia* Swainson, 1840; *Ortmanniana* Frierson, 1927; *Villosa* Frierson, 1927; *Venustaconcha* Friers., 1927; *Leptodea* Raf., 1820; *Disconaias* Cr. & Fisch., 1893; *Proptera* Raf., 1819; *Carunculina* Simps., 1898; *Truncilla* Raf., 1819; *Plagiola* Raf., 1819; *Obovaria* Raf., 1819; *Pseudoon* Simps., 1900; *Glebulia* Conr., 1853; *Arotonaias* Martens, 1900?; *Medionidus* Simps., 1900; *Lemiox* Raf., 1831; *Dysnomia* Agassiz, 1852 with *Penita* Friers., 1927; *Torulosa* Friers., 1927; *Capsaeformis* Friers., 1927; *Pileo* Simps., 1900; *Epioblasma* Raf., 1831; *Actinonaias*, *Delphinonaias*, *Cyrtonaias* Cr. & Fisch., 1893; *Friersonia* Ortm.

III. Fam. Margaritiferidae Ortmann 1911.

The family of the Margaritanidae is (as I see it here, in contrast to Ortmann's view) very enlarged. Ortmann's view concerned only the closer group of the Margaritanidae. The apparently old and primitive structure of the body and especially of the gills caused him to separate them. However, more groups exist for which the same holds true. Perhaps we may see in its body structure really an older stage of the original Mutelid group, even if *Margaritifera* has brought forth here several special developments. In any case, the Margaritanidae are very old. Nevertheless, today's distribution is of fairly recent origin. Perhaps we may conclude from this that until their time of spread they had been limited to the isolated Australian continent where its most primitive group (to which Iredale has given the name *Cucumerunioninae*) is still found today. At least since the upper Cretaceous, and possibly earlier, active spread started. The subfamily of the Heudeaninae seems to have come up to Europe in the Upper Cretaceous. Today, however, it is limited to southeast Asia. The Margaritiferinae had also come as far as North America by the beginning of the Tertiary and have, at least since Oligocene, become an important part of the European Fauna. As a result of its last Pliocene migration, *Margaritifera* L. has become circumpolar. The Margaritiferinae already showed a tendency toward a reduction of the lamellar teeth. This was the case to a great degree in the *Pseudodontinae* which are mainly found today in Southeast Asia but which have come in the course of their migrations in the Pliocene and Miocene up to Europe and western North America where they still occur today. Their teeth, with the exception of one cardinal tooth in each shell, have disappeared.

The diagnosis of the Family is as follows: Primitive *Naiades* with crude gill structure; shell with complete unionid hinge having a continuation of reduction of the lamellae toward their total disappearance; cardinal teeth in a single group (*Pseudodontinae*) also in the process of

reduction; umbone sculpture consisting of two small curved nodules which are not connected in the center and with a tendency toward the formation of an extensive folding sculpture which extends from the dorsal margin out over the shell.

Distribution: All north continents and Australia.

22. Subfam. Cucumerunioninae Iredale, 1934.

Type species: *Cucumerunio novahollandiae* Gray, 1934. Elongate species with complete hinge which demonstrates the initial stage of lamellar reduction. A distinct shell sculpture with partially regular - partially irregular systems of folds which extend from the dorsal margin over the disc of the shell.

Distribution: Australia, New Guinea, and New Zealand.

Into this group: *Cucumerunio* Iredale, 1934; *Virgus* Simpson, 1900.

23. Subfam. Heudeaninae n. subfam.

Type species: *Heudeana murinum* Heude, 1883. Shell elongated rectangularly; hinge complete, unionid; sculpture consisting of an anterior arch and a posterior nodule; the dorsal fold sculpture of the other Margaritaniidae also occurs in this group.

Distribution: Borneo, South China. In the upper Cretaceous as far as Europe.

Into this group: *Heudeana* Frierson, 1922; *Schepmannia* Haas, 1910; *Ctenodesma* Simpson, 1900.

24. Subfam. Margaritiferinae n. subfam.

Type species: *Margaritifera margaritifera* L. Shell large, strong, with complete unionid hinge. In several species the hinge becomes reduced with increasing age through the shell material tending to grow over the lamellar teeth. In others the lamellar teeth disappear completely. Sculpture: 2 small hooked nodules set very close together (touching). In addition, at times numerous dorsal folds accompanied by shell sculpture.

Distribution: Europe, East Asia, North America.

Into this group: *Margaritifera* Schumacher, 1816; *Margaritanopsis* Haas, 1912; *Cumberlandia* Ortmann, 1912; *Ptychorhynchus* Simpson, 1900. This group definitely contains those which occur in calcium-poor water and those in calcium-rich waters. I have already mentioned above their distribution and wanderings in the European Tertiary.

25. Subfam. Pseudodontinae Frierson, 1927.

Type species: *Pseudodon inoscularis* Gould, 1844. Shell long to short oval, hinge reduced to cardinal teeth and these definitely very much worn off, button-form, and has a tendency toward a decrease to one in each shell. Sculpture has weak double arches, neither of which have an up or a down arch.

Distribution: Adriatic region, Syria, Mesopotamia, East Asia from Japan to Java, Pacific coast of U.S.A., center in back India.

Into this group: *Pseudodon* Gould, 1844; *Monodontina* Conrad, 1853; *Nasus* Simpson, 1900; *Cosmopseudodon* Haas, 1920; *Obovalis* Simpson, 1900 in Asia; *Pseudodontopsis* Kobelt 1912; *Leguminaia* Conrad, 1865; *Microcondylaea* v. Vest, 1866 in Europe; *Leptanodonta* Wenz, 1927 in the Pliocene of Rumania; *Gonidea* Conr., 1857 in California.

The group is especially interesting because of its Tertiary migrations.

IV. Family Unionidae (Adams) Ihering, 1893.

Contrary to the opinion of Ihering I have taken the genera *Margaritana* and *Pseudodon* out of this group and put them in the Margaritiferidae.

Most of the Naiades living today belong to the Family Unionidae.

Their independent development must have begun very early. I have already mentioned above the difficulty of determining their direct derivation. It is based largely on the fact that even today more and more variable connecting lines to forerunners can be established for the Unionidae than for any other family.

A. *Parreysia*

The umbone sculpture necessitates the subdivision of the family into two separate series which, however, are very close to each other in their origin. So it is not surprising that the individual characteristics of one series occur individually or as generic characteristics in other series.

The older developmental series (I shall call them the *Parreysiads* in the following) has, as a special characteristic, an unusual sculpture consisting of an upward arch and dorsal folds. Both arches in the middle go down in toward the center and meet in an acute angle. In this way the arches transect each other and form a complicated zig-zag sculpture (V-sculpture). We must consider the Indian *Parreysiinae* as the oldest form which is left to us. As early as the Triassic they occur in North America, while in east Asia, the *Parreysiinae* continued to develop into quadruline forms and thereby lose the old V sculpture in favor of the more modern double arch of the unionids. At the same time the American *Parreysiinae* continued their development in the old land locked lakes of the Rocky Mountains of today in the same direction and developed the true *Quadrulinae* which, in many cases, have the whole sculpture on the shell. An additional series comes from the oldest North American *Parreysiinae* and reaches an extensive distribution in South America as the *Hyriinae*, keeping the original sculpture. The last group, the *Propehyridellinae*, have remained in Australia as several relic populations.

Diagnosis of the *Parreysia* in the broad sense: Shell mostly shortened high quadratically to high triangularly, *Quadruline*, hinge strengthened often with heavy cardinal teeth. The sculpture consists of an upward curving arch, and two middle arches which have united into a V, and dorsal folds. In the higher developmental stages there is a double V in place of the single V, or double arches of the *Unioninae*.

26. *Hyriinae* Ortmann, 1911.

Type species: *Hyria corrugata* Lamarck, 1819. *Naiades* of America with definite V-sculp-

ture, unionid hinge structure with a tendency toward splitting into partial teeth; variable outline.

Into this group: *Diplodon* Spix, 1827; *Cyclomya* Simpson, 1900; *Bulloideus* Simpson, 1900; *Castalia* Lamarck, 1819; *Callonaia* Simpson, 1900; *Castalina* Ihering, 1891; *Castaliella* Simpson, 1900; *Hyria* Lamarck, 1819; fossil genera: *Antediplodon* Marshall, 1929; *Prodiplodon* Marshall, 1928; *Eodiplodon* Marshall, 1928; *Equadoria* Marshall and Bowles, 1932; *Castalioides* Marshall, 1934.

In North America it is known in the Triassic and again in the Pliocene; in South America it is known as a fossil since Pliocene, and is recently limited to South America.

27. Subfam. *Propehyridellinae* Iredale, 1934.

Type species: *Propehyridella nepeanensis* Conrad, 1850. The shell is unionid, hinge complete, having a V-sculpture from which develop the shell folds.

Into this group: *Propehyridella* Cotton and Gabriel, 1932; *Protohyridella* Cotton and Gabriel, 1932.

Isolated at least since Upper Cretaceous in Australia. It seems to me that in the case of *Naiades* that Ihering's hypothesis of the connection of his *Archiplata* with Australia cannot be proven.

28. Subfam. *Parreysiinae* n. subfam.

Type species: *Parreysia corrugata* Mueller, 1774. Shell short oval to high triangular; V-sculpture with upward growing arch, at times areal folds. In several cases the sculpture covers the whole shell. In the continuing development there is a change to unionid sculpture.

Into this group: *Parreysia* Conrad, 1853; *Radiatula* Simpson, 1900; *Unionella* Haas, 1912; *Acuticosta* Simpson, 1900; *Pseudobaphia* Simpson, 1900; *Protunio* Haas, 1912; *Chrysopseudodon* Haas, 1920; *Schistodesmus* Simpson, 1900.

Distribution from southern India to northern China, in the Pliocene to Siberia.

Chrysopseudodon Haas I have placed into this group because of the characteristics of its sculpture and in spite of the reduced hinge.

29. Subfam. Lamprotulinae n. subfam.

Type species: *Lamprotula nodulosa* Wood 1875. Shell unionid to quadruline. Sculpture double V to angular double arches with an upward and a downward bow. The beginning arch and the radial folds often pass over the whole shell and disintegrate into rows of nodules. Hinge completely unionid to thick.

Into this group: *Lamprotula* Simpson, 1900, (syn. *Gibbosula* Simpson, 1900), *Inversidens* Haas, 1911; *Psilunio* Sabba Stefanescu, 1896; *Discomya* Simpson, 1900.

Distribution: Southeastern and Southwestern Europe, Southern Asia, Morocco to Tunis, East Asia from Japan to Tonkin, Borneo. Known as a fossil since the Eocene in Europe and as a Tertiary developmental series in the Pliocene of Southeast Europe, Siberia, and China.

30. Subfam. Quadrulinae Haas, 1929.

Shell highly quadratic to high triangular, originally had V-sculpture, which later was transferred to the shell, and, in many cases, today leaves the umbone free of sculpture. The beginning arch and dorsal folds are still found in youthful specimens of richly sculptured species. The hinge is enlarged (strong) to thick, and quadruline.

Type species: *Quadrula quadrula* Rafinesque, 1820.

Into this group: *Quadrula* Raf., 1820; *Tritogonia* Agassiz 1852; *Pustulosa* Frierson, 1927; *Quincuncina* Ortmann, 1922; *Luteacarnea* Frierson, 1927; *Orthonymus* Agassiz, 1852; *Cyclonaias* Pilsbry, 1922; *Pachynaias* Crosse and Fischer, 1893; *Rotundaria* Raf., 1820; *Megalonaias* Utterback, 1918; *Psorula* Haas, 1929.

Fossil genus: *Proparreysia* Pilsbry, Upper Cretaceous.

Represented since the Triassic in North

America by the *Proparreysia* which are related and directly connected to the *Parreysia*. The change in the course of the Jurassic and Cretaceous is to the present forms, each of which goes back to a certain old lake region of the Rocky Mountain zone. Today's distribution: North America east of the Rockies south to Middle America.

B. Unionen

This second modern main group of the Unionidae also begins with a V-shaped sculpture with an upward arch and dorsal areal folds present in its first representatives. This sculpture, however, is soon replaced by a double V, that is, a double arched sculpture which is formed by a crossing of the V-arches. Thus the sculpture of the older forms is somewhat angular and the rounded sculptures of the younger forms are formed only later by the wearing off of the former. The shell is long oval to short oval, seldom changed to a quadruline form. The hinge is always complete with shortened cardinal teeth. The distribution today reaches over all of Africa, Europe, and Asia.

31. Subfam. Lamellidentinae n. subfam.

Type species: *Lamellidens marginalis* Lamarck, 1819. Shell elongated, unionid hinge, lamelliform laterals with a tendency toward the shortening of the cardinal teeth. Umbone sculpture very weak, V-formed.

Into this group: *Lamellidens* Simpson, 1900.

Distribution: India and Burma.

32. Subfam. Hyriopsinae n. subfam.

Type species: *Hyriopsis delphinus* Gruner, 1841. The development starts from the thin-shelled forms with lamellar teeth, which are closely related to the original Rectidentines and Contradentines. The sculpture is hardly noticeable. The first ones, which have a simple double arched sculpture, are the large and, in many cases, thick-shelled forms which developed from the former two groups. A special development has resulted in the loss of the cardinal teeth totally.

Into this group: *Hyriopsis* Conrad, 1853; *Lamproscapha* Lindholm, 1932; *Arconia* Conrad, 1865; *Lepidodesma* Simpson, 1896; *Chamberlainia* Simpson, 1900; *Cristaria* Schumacher, 1817.

Distribution: East Asia from the Amur to Malakka, Borneo, and Sumatra. Fossil in the Miocene and Pliocene of middle and east Europe and in Siberia.

33. Subfam. *Cafferinae* n. subfam.

Type species: *Cafferia caffra* Kraus, 1848. Mussel of the unionid type. Hinge teeth unionid, and powerful, umbone sculpture consisting of an anterior arch and a posterior sharply pointed triangle.

Into this group: *Cafferia* Simpson, 1900.

Distribution: South Africa.

This group, standing somewhat isolated, has its nearest relatives in the *Contradentinae* of Southeast Asia.

34. Subfam. *Rectidentinae* n. subfam.

Type species: *Rectidens orientalis* Lea, 1840. Shell long-ligulate to long-elliptical. Originally with lamellar hinge which, in most groups, disappeared very early. Umbone sculpture flat double arches without an upward or a downward arch, at times a double V with a long up and down arch.

Into this group: *Rectidens* Simpson, 1900; *Pilsbryconcha* Simpson, 1900; *Pseudodontia* Bourg., 1876; *Lastena* Raf., 1820; *Physunio* Simpson, 1900; *Ensidens* Frier-son, 1911; *Pyganodon* Crosse and Fischer, 1893.

Distribution: North Europe, Southeast Asia, North America east of the Rockies. This subfamily makes up a large part of the *Anodontinae* *Naiades* of the North Continents.

35. Subfam. *Contradentinae* n. subfam.

Type species: *Contradens contradens* Lea, 1848. Shell short to long oval, umbone sculpture consisting of double hooks, often largely dissolved and reaching far into the shell. Teeth regularly lamellar form, the cardinal teeth are seldom shortened as in the unionids.

Into this group: *Contradens* Haas, 1913; *Sprickia* n. subgen.; *Pressidens* Haas, 1911; *Simpsonella* Cockerell, 1903; ?*Caudiculatus* Simpson, 1900.

Distribution: Philippines, Java, Sumatra, Borneo, back part of India, possibly reaching into Middle China.

Caudiculatus Simpson is still doubtful to me even after a close study of the Berlin types. The preservation of the sculpture is not good enough for a sure grouping into the classification. I am assuming at present that I am dealing with a reduced *Contradens* sculpture.

Subgen. *Sprickia* n. subgen. I am proposing as a new name for the definite lake species, which are characterized as are *Sprickia verbeeki* von Martens and *Sprickia rusticus* Lea by the possession of an expanded shell sculpture with crosswise ridged folds.

Type species: *Contradens* (*Sprickia*) *verbeeki* von Martens.

Distribution: Singkarak Lake, Sumatra; Lake Tonle-Sap, Cambodia.

The new subgen. is dedicated to Mr. J. Sprick-Stralsund previously Oels, in grateful recognition for his many years of assistance in the field of the *Naiades*.

36. Subfam. *Anodontinae* Ortmann, 1910.

Contrary to the opinion of Ortmann the group is limited to a few species which belong together (as seen) on the basis of their sculpture. The original lamellar hinge has disappeared completely in most cases. The sculpture consists of double arches which may contain an upward arch and a downward arch.

Type species: *Anodonta cygnea* L., 1758.

Distribution: All of Europe, western part of North Africa, North and East Asia, is missing in India and the largest part of the back part of India, North America south to Mexico. Known as a fossil since the Eocene.

Into this group: *Anodonta* Lamarck, 1799; *Pletholophus* Simpson, 1900; *Haasiella* Lindholm, 1925; *Pteranodon* Fischer, 1893.

37. Subfam. *Caelaturinae* n. subfam.

Type species: *Caelatura aegyptiaca* Caillaud, 1827. Shell usually small, short to long oval, teeth lamellicent with many changes to the unionid hinge. Umbone sculpture a double V with upward arches and dorsal folds.

Distribution: Tropical Africa between Sahara and Kalahari, Nile.

This subfamily has a long independent development behind it, which places it somewhat aside of the related groups such as *Cafferiinae* and *Nannonaiinae*.

Into this group: *Caelatura* Conrad, 1853; *Mweruella*, *Kistinaia*, *Rhytidonaia*, *Kalliphenga*, all Haas, 1936; *Grandidieria* Bourg., 1855; *Zaitia* Rochebrune, 1886; *Laevirostris* Simpson, 1900; *Mesafra*, *Afroparreysia*, *Nyassunio* Haas, 1936.

38. Subfam. *Nannonaiinae* n. subfam.

Type species: *Nannonaiia caerulea* Lea, 1831. Mostly small species with long to tongue-shaped outline. Sculpture consisting originally of an upward arch, a V-angle and dorsal folds which is later changed to a double V-sculpture, which is further ground down into a flat double arched structure. Hinge unionid and, in individual cases, reduced.

Into this group: *Indonaia* Prashad, 1918; *Nitia* Pallary, 1924; *Trapezoideus* Simpson, 1900; *Nannonaiia* Haas, 1912.

Distribution: East Africa, Madagascar, Réunion, all of India, South China, Borneo.

This subfamily which perhaps follows directly the *Diplasminae* is connected through continuous transitions with the following *Unionae*.

39. Subfam. *Unioninae* Ortmann, 1910.

Contrary to the opinion of Ortmann, who unites in this place all species groups with a unionid hinge, my understanding of this subfamily is that it is very limited.

Type species: *Unio tumidus* Retz., 1788. Shell long-oval to long-lingulate form. Hinge with shortened cardinal teeth; umbone sculpture with upward arch and dorsal folds, two V V angles or double arches in the middle.

Into this group: *Scabies* Haas, 1911; *Unio* Retz., 1788; *Rhombuniopsis* Haas, 1920; *Oxynaia* Haas, 1912; *Cuneopsis* Simpson, 1900; *Lanceolaria* Conrad, 1853.

Distribution: All of Europe, western part of North Africa, East Asia to back part of India. Fossil in Europe known from the Eocene, perhaps going as far as the Jurassic.

I know that it was impossible to have hit the right thing on the first attempt in all cases and would appreciate technical corrections. It is different in the case of questions concerning nomenclature, especially in the North American *Naiades* where, after Simpson's divisions were not sufficient for these purposes, I had to go along completely with the uniform system of Frierson in order to give a better picture. With this however I also had to use Frierson's concepts of Rafinesque's names completely, although I know that these concepts are not shared by many North American researchers and are partially in contrast to the data of Ortmann, Pilsbry, and Walker.

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