MALACOLOGY.—*Trends and problems in pelecypod classification (the supergeneric categories)*. DAVID NICOL, U. S. National Museum.

Little has been written to guide workers in the various animal phyla in problems of classification in the supergeneric categories. Simpson (1945, pp. 20–24) and Mayr, Linsley, and Usinger (1953, pp. 46–59) have contributed valuable suggestions; but general principles of standardization that could be applied to the higher categories of all phyla are still lacking. The reason is that many of the classification problems of the entomologist or mammalogist, for example, are entirely different from those of the malacologist. From the standpoint of size alone, if not on a morphologic basis, a pelecypod family or other supergeneric category may not be comparable with a family of insects or mammals; this in itself would tend to create different problems in classification in the Insecta, the Pelecypoda, and the Mammalia. Other differences in higher categories of different classes of animals arise from the percentage of described species and the phylogenetic knowledge in the various groups. Hence, standardization at the level of the phylum would be virtually impossible; in fact, about all that can be hoped for in a large phylum is reasonable standardization within a class.

For the purposes of brevity and continuity in this paper, I have decided to treat the Pelecypoda as a class. This has been the most common treatment in the past, although I realize that at least some of our problems might be solved if the Pelecypoda were given the rank of, let us say, a subphylum.

It appears to me that the phylogenetic relationships of the Pelecypoda are not adequately or correctly shown by the present classifications; but, with the excellent fossil record of the pelecypods, these relationships *could* be shown and thus the usefulness of the classification could be improved.

The ideas and problems presented here are mainly those of a malacologist; however, many valuable suggestions and criticisms were given by Dr. R. E. Blackwelder, entomologist at the U. S. National Museum, and for these I am very grateful.

The purpose of this paper is to examine some recent examples of classification of pelecypods used by paleontologists and neontologists, to discuss present trends, and to offer possible solutions to some of the problems. A list of some important works on pelecypod classification is included.

THE SUBCLASS, SUPERORDER, ORDER, SUBORDER

The first example of classification is taken from the paleontology textbook *Invertebrate fossils* by Moore, Lalicker, and Fischer (1952). Moore, who wrote the chapter on the pelecypods, used a modified version of Dall's classification based on the hinge teeth. He divides the pelecypods (pp. 409–412) into two subclasses—Prionodesmacea and Teleodesmacea. In the first group Moore includes five orders and twelve suborders; in the second, in which he combines Dall's orders Anomalodesmacea and Teleodesmacea, he includes three orders and twelve suborders. According to Moore, the Paleoconcha are an order of the subclass Prionodesmacea; Dall, however, did not include them in any of his three orders in 1895 (p. 513) but set them aside as *incertae sedis*, although he later arbitrarily placed them in the Prionodesmacea.

Moore discusses the structure of the pelecypod ctenidia at considerable length but gives the ctenidia little importance in his classification—i.e., in the Prionodesmacea, Moore includes pelecypods with protobranch, filibranch, and eulamellibranch ctenidia. Furthermore, Moore places the anomiids and the spondylids together in the order Isodonta and places the nuculids and arcids together in the order Taxodonta; but on the basis of phylogeny and morphology it is difficult to see these relationships. In the order Dysodonta, Moore includes the mytilids, pectinids, pinnids, ostreids, limids, and dreissensiids—truly a heterogeneous assemblage.

The classification used by Shrock and Twenhofel in their book (1953, pp. 386–393) is that of Thiele, 1934, who divided the Pelecypoda into three orders, Taxodonta, Anisomyaria, and Eulamellibranchia, primarily on the basis of ctenidia, hinge teeth, and adductor muscles. In the order Taxodonta are included the nuculids and the arcids. However, in a footnote (p. 389) Shrock and Twenhofel make the following statement:

> The Arcacea are now regarded by some investigators (MacNeil, 1937; Nicol, 1950) as more closely related to certain groups of the Anisomyaria because the hinge structure is of a later type and may possibly be the result of convergence. It may well be, therefore, that this superfamily should be transferred to the order Anisomyaria or used as the basis for a new order.

Shrock and Twenhofel imply that the lack of close relationship between the arcids and the nuculids is a new idea, but if the authors had examined the writings of Pelseneer and Douvillé they would have found that the idea was presented much earlier than 1937. Furthermore, if my paper of 1950 had been carefully read (p. 89), the following statement would have been noted:

> Pelseneer, Douvillé, and others have pointed out the fact that the prionodonts are not closely related to the true taxodonts such as *Nucula*, *Nuculana*, and *Yoldia*.

This is but one example of the lack of knowledge of the basic works on pelecypod systematics.

A recent and much more comprehensive work is the *Traité de paléontologie* edited by Jean Piveteau, 1952. The major portion of the chapter on Pelecypoda was written by Colette Dechaseaux. The main divisions Dechaseaux uses are based on hinge characteristics, and she divides the pelecypods into four orders—Taxodonta (with three suborders), Dysodonta, Preheterodonta, and Heterodonta. Only the taxodonts are divided into suborders, one of which is the Paleoconcha. By far the largest order is the Heterodonta, which is comprised of more than half of the pelecypod families.

Dechaseaux's classification bears little resemblance to her schematic table on the evolution of the pelecypods (page 229). This is just one example of workers who, although cognizant of phylogenetic evidence, do not base their classification on phylogeny but, instead, follow the line of least resistance by using the outmoded classification of a predecessor. As long as this attitude occurs, little progress can be made in the classification of the pelecypods.

Another work worth analyzing is that of T. Habe (1951–1953), who uses Dall's classification with few modifications. Habe divides the Pelecypoda into three subclasses—Prionodesmacea, Teleodesmacea, and Anomalodesmacea. The first subclass is divided into four orders, and the Teleodesmacea is divided into two orders. Habe does not group the Anomalodesmacea above the level of superfamily. The categories superorder and suborder he does not use at all in his classification of the pelecypods.

Habe places the nuculids and arcids in the order Taxodonta, although, as has been pointed out before, they bear only a superficial resemblance to each other. Furthermore, although most of the Cenozoic arcids and nuculids do have similar hinges, the hinge teeth of the Mesozoic and Paleozoic arcids and their allies are generally quite unlike those of the nuculids. Thus, from the practical standpoint of classification, disregarding phylogeny, this grouping is not workable.

Little attempt is made by Habe to show relationships in the order Heterodonta, to which he assigns 14 superfamilies and 34 families.

The comprehensive treatment of the classification of the Pelecypoda by Cotton and Godfrey (*The molluscs of South Australia*, 1938) is also noteworthy. These authors subdivide the class into the three orders proposed by Dall. The order Prionodesmacea is subdivided into five suborders—Palaeoconcha, Taxodonta, Schizodonta, Isodonta, and Dysodonta—which are in turn divided into superfamilies and families. The order Anomalodesmacea is not grouped above the level of superfamily; however, the authors use the category "section" between the superfamily and family. Cotton and Godfrey subdivide the order Teleodesmacea into five suborders—Pantodonta, Diogenodonta, Cyclodonta, Teleodonta,

and Asthenodonta—and these suborders are further divided into numerous superfamilies.

Once again we find the unlike nuculids and arcids grouped together in the suborder Taxodonta. Cotton and Godfrey place the pteriids, ostreids, unionids, and trigoniids in the suborder Schizodonta; certainly the ostreids do not belong with such primitive nacreous groups. The grouping of the venerids, tellinids, solenids, and mactrids in the suborder Teleodonta seems arbitrary and appears to be based on little or no phylogenetic and morphologic evidence.

All the foregoing examples show certain common characteristics which are important as well as interesting. They are as follows:

1. In none of the treatments reviewed of the classification of the class Pelecypoda are all the common categories used, i.e., subclass, superorder, order, suborder, superfamily, family, and subfamily.

2. None of the classifications is basically new. With one exception, each author follows one authority almost exclusively with perhaps minor modifications; the one exception uses a combination of basic characters and classifications.

The fundamental concepts for classifying the Pelecypoda were mainly promulgated between the years 1889 and 1912. It was during this period that the morphologists, embryologists, and evolutionists were most intensively working on natural, or phylogenetic, classifications of the Pelecypoda. Since that time only a few details of classification have been added. Even thorough review and synthesis of the classifications have received little interest lately. This basic pattern of the development of classification may have counterparts in other groups of animals.

Indifference to the classification of the Pelecypoda began in 1913 and has continued for 40 years since. As a result, lack of knowledge of the basic works on the subject is continually being exhibited. One solution to our present state of stagnation is to reexamine the "classics" on pelecypod classification—papers by Neumayr, Dall, Pelseneer, Bernard, Jackson, and Douvillé. Each classification and set of facts on morphology, embryology (including growth stages of the shell), and paleontology should be thoroughly studied and the evidence evaluated. (Douvillé's classification might have been more widely accepted if he had assigned definite categories for his three-fold division of the Pelecypoda.) Incorrect data and conclusions should be deleted.

3. Little or no attention is paid to phylogeny in classification even when the evidence is clear and the author is aware of it.

This has led to serious errors in classification from the standpoint of practical morphology as well as phylogeny. For the past 40 years work on phylogeny has been considered relatively unimportant and unrewarding; however, at the ordinal level of pelecypod classification a careful analysis and synthesis of the classical work on pelecypods is our first need. Further work is needed on pelecypod morphology and shell structure, including more anatomical work on the soft parts. Further studies on the nepionic and later stages of the shell are also needed. The greatest lack, and probably the most fruitful line of investigation, is careful work on Triassic and Paleozoic pelecypods, for this work would lead to a better understanding of the relations of the various major groups of pelecypods.

THE SUPERFAMILY, FAMILY, SUBFAMILY

The superfamilies, families, and subfamilies have been undergoing some changes in number and scope within the past quarter of a century. The changes have been brought about slowly by the great increase in number of proposed genera and subgenera. The result has been for malacologists to group genera into new subfamilies, families, and superfamilies by redefining and restricting them. Two examples of this occurrence should show the involved problems.

Frizzell (1936) raised the family Veneridae to the rank of a superfamily and excluded the petricolaceans and glaucomyaceans from the Veneracea. The superfamily was then subdivided into nine families, and two of the families were further subdivided into subfamilies. Since 1936 other workers have erected more genera and subgenera of veneraceans, and the total is now about 200.

Recently Keen (1951) downgraded the Veneracea to the rank of a family, in which eleven subfamilies were included. In a more recent paper Tremlett (1953) followed Keen's classification and made the following comments (p. 1):

> D. L. Frizzell (1936), in one of the most recent works on this group, has suggested that they should be regarded as a superfamily Veneracea, with the same limits approximately as the family Veneridae as the term was used by Dall (1903), Jukes-Browne (1914), Palmer (1927), and others. I cannot see the advantage in raising the status of the group which is thereby separated from the closely related Petricolidae, and also from the Oncophoridae which are probably related to it; furthermore it unnecessarily increases the number of superfamilies. Even though the Veneridae are one of the largest families of pelecypods, the characters defining it are of about the same importance as those defining other families. Frizzell's families obviously have close similarities, and I prefer to regard them as subfamilies and retain the term Veneridae in its old sense.

The 11 subfamilies included by Keen in the Veneridae do not all have the same morphologic distinctness. How can these subfamilies be grouped to show the relationships? One solution that has been adopted is the one taken by Frizzell. Certainly the commonly used categories are available, and to raise the rank of several of the larger pelecypod families to the rank of superfamily would not create chaos in the classification. This course of action would probably be most acceptable to the malacologists and paleontologists. However, another solution is possible, if, as Tremlett claims, the morphologic characters defining the Veneridae are equal to, or of the same importance as, the morphologic characters defining other pelecypod families. This solution is to insert additional categories between the subfamily and the genus—for examples, the categories tribe and subtribe. The entomologists have done this for classifying many of the large families of insects.

Three ways of classifying a part of the veneraceans are shown on Table 1.

To add to the difficulties of an already large family, there are undoubtedly some aberrant groups which are venerids or veneraceans. I have considered the genus *Euloxa* a veneracean; but in order to fit it into the classification, I used Frizzell's arrangement, considered the Chionidae as a family, and subdivided the Chionidae into two subfamilies—the Chioninae and Euloxinae (Nicol, 1953, p. 60). This type of problem was also encountered in the genus *Pliocardia*. Once again I (1953a) used Frizzell's classification in order to show the systematic position of the genus. In each of these cases the only other reasonable solution would have been to create a category, such as tribe, between the subfamily and the genus.

It is true that some of the pelecypod genera and families have been split unreasonably (e.g., the genus *Inoceramus*); but the veneraceans do not appear to have received such disproportionate treatment, at least at the generic level, and Keen disagrees not with the number of groups designated by Frizzell, but with the rank to which he assigns them.

Furthermore, one of Tremlett's main objections to Frizzell's classification—namely that the morphologic characters defining the Veneridae are of about the same importance as those defining other families—apparently overlooks the fact that much of our classification of the pelecypods is based on the size of the group in question rather than on morphologic differentiation. For example, on the basis of morphologic characters the Cretaceous genera *Pseudocucullaea* and *Lopatinia* are quite distinct from all other prionodont genera; but, as they have few

TABLE 1.—THREE WAYS OF CLASSIFYING A PART OF THE VENERACEANS.

Frizzell, 1936	Keen, 1951	Another proposed solution
Superfamily Veneracea	Family Veneridae	Family Veneridae
Family Meretrecidae	Subfamily Meretrecinae	Subfamily Meretrecinae
Subfamily Meretrecinae	Subfamily Pitarinae	Tribe Meretrecini
Subfamily Pitarinae		Tribe Pitarini

species, they have not been placed in a separate subfamily or family. The Glycymeridae, on the other hand, although no more distinct morphologically than *Pseudocucullaea* or *Lopatinia*, have approximately 700 described species, ranging from the Cretaceous to the Recent, and have therefore been classified as a family. Although I do not assert that rank should be based upon size, it is nevertheless true that in many cases size has apparently been the decisive factor, and Tremlett's attitude is not realistic.

However, my objection to the ideas of Keen and Tremlett is not primarily that the rank should be Veneracea rather than Veneridae, but that their classification does not allow for enough categories to show adequately the relationships among the 200 genera and subgenera of the group.

A comparable situation is present in the arcaceans. The latest classification (Frizzell, 1946, p. 41) raises the rank of the family Arcidae to a superfamily, in which two families are included, the Arcidae and the Noetiidae. Of these, the first is subdivided into three subfamilies, and the second into two subfamilies. If Frizzell's arrangement is compared with the conservative arrangement of Reinhart (1935, pp. 11–12), one is astounded. Reinhart divides the Arcidae into three subfamilies—Arcinae, Anadarinae, and Noetiinae. The subfamily Litharcinae of Frizzell is relegated to the rank of a subgenus of *Arca* by Reinhart. Although I have found no published objection to Frizzell's arrangement of the Arcacea, objections similar to those of his classification of the Veneracea could, and probably will, be raised in the future. My preference for Frizzell's treatment of both the veneraceans and the arcaceans over more conservative classifications is that it has more categories in which to show more morphologic and phylogenetic relationships. Whether all the relationships as shown by Frizzell's classifications are correct or not is a matter to be investigated further.

Blackwelder (personal communication) has suggested to me the most objective and probably only satisfactory way of solving the type of problem exemplified by the Veneridae versus the Veneracea and the Arcidae versus the Arcacea. The genera of the family or superfamily being studied should be examined for morphologic similarities and inferred phylogenies. These genera can then be grouped, and the groups can likewise be grouped in a series of ascending categories. The number of categories necessary in order to show the relationships can then be ascertained. What category should be used for the group as a whole should be based primarily on what has been used in related groups; and when the rank of the group studied is decided, then the various subdivisions of the group should fall into place. In the case of the pelecypods this will not be easy because the entire classification at the familial levels is nebulous. However, much progress could be made if these problems were approached in as objective a manner as possible. Such studies would undoubtedly result in many major changes in the classification of the pelecypods above the generic level.

There has been a tendency to redefine, restrict, and propose more subfamilies, families, and superfamilies, apparently as a result of the rapid increase in the number of proposed genera and subgenera of pelecypods. This tendency has met with some opposition, but some of the objections to creating more families or raising the various groups to higher categories seem to be ill-founded. As MacNeil (1938, p. 1) stated:

> With our increasing knowledge of the structure and phylogeny of the Pelecypoda it becomes more and more obvious that their supergeneric classification is short of satisfaction, the principal defect being that not enough groups of high ordinal rank have been recognized.

Recognition of more groups of high ordinal rank would undoubtedly alleviate many of our present problems of pelecypod classification. Another solution might be to create categories for groups between the generic and subfamily levels as the entomologists, for example, have done.

To improve the classification more work is needed at the genus and family levels, and it should include a careful analysis of all morphologic, embryologic, chronogenetic, and geographic data. Many of the basic

data are in the literature—but careful analysis and synthesis of the data are needed to ascertain phylogenetic relationships.

SOME BASIC PELECYPOD LITERATURE

A thorough understanding of the following references is necessary as a starting point for a classification of the Pelecypoda. This list is not intended to be complete, but it should form a good basis for the student who is interested in this group of mollusks.

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