Revista Mexicana de Ciencias Geológicas, volumen 12, número 2,
1995, p. 211-223.
Universidad Nacional Autónoma de México, Instituto de Geología,
México, D.F.

THE MEANING OF "INVERSION" IN CHAMIDS AND RUDISTS (BIVALVIA) REVIEWED AND AN UNBIASSED THEORETICAL APPROACH TO LATE JURASSIC-EARLY CRETACEOUS RUDIST PHYLOGENY

*Nikolaus Malchus**

ABSTRACT

Older phylogenetic studies of Late Jurassic to Early Cretaceous rudists tend to refer to the Recent bivalve family Chamidae as a model, especially if the "inversion" of the hinge dentition and of fixation are concerned. Although today works generally avoid direct comparison as well as the use of related terms like "normal", "inverse", or α valve, β valve, there exists no modern summary and discussion on the possible underlying processes of "inversions" and of the different meanings of the terms. The present theoretical approach tries to close this gap by reviewing the different types of "inversion" in chamids and rudists, by discussing possible genetic underlying processes, and by examining the consequences of "inversion" for the homologation of the valves. These results serve as a base for assumptions which are needed for a basic theoretical analysis of the phyletic state of various higher rudist taxa.

The only acceptable type of "inversion" in bivalves seems to affect only the hinge teeth whereas the whole animal-"inversion" of Munier-Chalmas's and Yonge's mantle/shell-"inversion" is unlikely. Three types of genetically controlled teeth reversals are discussed. Their effects for homologation depend on the frequency of their occurrence within a species (or genus) and within the Heterodonta, but, in general, it is rather safe to compare right valves, and left valves respectively, of different species. It will be seen that true hinge teeth reversals did probably occur neither in the Chamidae nor in the rudists. This had already been stated earlier but partly based on wrong arguments. A model is presented of how the teeth transformation in rudists could have evolved. It is postulated the hypothesis that apart from growth economy simple mechanical constrictions and the availability of space were responsible for the gradual changes of the hinge including the invagination of the ligament. The ideas complement previous interpretations of the functional design in rudists. On the basis of mainly two characters—attachment and hinge transformation—and on assumptions related to the previous discussions, a very simple phylogenetic analysis is carried out for the Late Jurassic-Early Cretaceous rudists. The arguments are based on cladistic reasoning. In three of four cases the Hippuritacea remain monophyletic, in the fourth diphyletic. The stem species is most likely to be found either within the Diceratinae, or within the group of Heterodiceratinae, Plesiodiceratinae, and Epidiceratinae. Reasons are presented in which cases and why the "Diceratinae", "Diceratidae", "Dextrodonta" and "Sinistrodonta" are paraphyletic and why there is no need for the taxon "Dicerasodonta". These results still hold in the case that most of the higher taxa within the Hippuritacea are para- or polyphyletic.

Key words: Chamidae, Hippuritacea, Bivalvia, inversion, Late Jurassic, Cretaceous, theoretical approach, phylogenetic analysis.

RESUMEN

Los primeros estudios sobre la filogenia de los rudistas del Jurásico Tardío y del Cretácico Temprano, tomaban como modelo a la familia Chamidae de bivalvos recientes, especialmente cuando se referían a la inversión de la dentición de la charnela y de la fijación de las valvas. Los trabajos recientes generalmente evitan la comparación directa de Chamidae y rudistas, así como el uso de los términos "inversa" o "normal" o alfa y beta para designar las valvas. Actualmente no existe un compendio moderno sobre los posibles procesos responsables de las "inversiones" y sobre los diferentes significados de los términos. El presente enfoque teórico trata de llenar ese vacío, revisando los diversos tipos de "inversión" en rudistas y en Chamidae, discutiendo los posibles procesos genéticos implicados y examinando las consecuencias de la "inversión" para la homologación de las valvas. Los resultados son tomados como base para proponer suposiciones necesarias para un análisis teórico básico de la filogenia de taxa superior de rudistas.

El único tipo aceptable de "inversión" en los bivalvos es el que afecta solamente los dientes de la charnela, en tanto que la inversión total del animal de Munier Chalmas y la inversión manto-concha de Yonge son improbables. Se discute tres tipos de inversiones de los dientes, controladas genéticamente. Sus efectos para la homologación de las valvas dependen de la frecuencia de su ocurrencia en una especie (o género) y en los Heterodonta, pero en general es acertado comparar valvas derechas y valvas izquierdas respectivamente, de diferentes especies. Se verá que verdadera "inversión" de los dientes probablemente no ocurrió ni en Chamidae ni en rudistas. Esta idea ya había sido planteada pero se basaba parcialmente en argumentos equivocados. Se presenta un modeló de cómo pudo haber evolucionado la transformación de los dientes en los rudistas. Se emite la hipótesis de que además de la economía en el crecimiento, simples constricciones mecánicas y la disponibilidad de espacio, fueron responsables del cambio gradual de la charnela y de la invaginación del ligamento. Estas ideas complementan interpretaciones previas sobre el diseño funcional de los rudistas. Con base principalmente en dos caracteres, fijación y transformación de la charnela, y en ideas relacionadas con discusiones previas, se realizó un análisis filogenético muy simple para los rudistas del Jurásico Tardío-Cretácico Temprano. Los argumentos están basados en el razonamiento cladístico. En tres de

**Departament de Geologia, Unitat de Paleontologia, Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain.*

cuatro casos, los Hippuritacea son monofiléticos y el cuarto es difilético. El tronco de las especies es más probable que se encuentre dentro de Diceratinae, o dentro del grupo de Heterodiceratinae, Plesiodiceratinae y Epidiceratinae. Se presenta razones que explican en qué casos y porqué los "Diceratinae", "Diceratidae", "Dextrodonta" y "Sinistrodonta" son parafiléticos y porqué no es necesaria la existencia del taxon "Dicerasodonta". Estos resultados se mantienen aun en el caso de que la mayor parte de los taxa superiores de Hippuritacea sea parafilética o polifilética.

Palabras clave: Chamidae, Hippuritacea, Bivalvia, inversión, Jurásico Tardío, Cretácico Temprano, enfoque teórico, análisis filogenético.

INTRODUCTION

The study of the phylogeny of Late Jurassic-Early Cretaceous rudistid bivalves reveals three important points: First, there is nearly no discussion about this matter without explicit reference to the Chamidae. This is understandable since the two groups are strikingly similar through their attachment by either valve, their spiral shell growth, cup shaped lower valve, hinge dentition, and existence of two adductor muscles (Yonge 1967; Kennedy *et al.,* 1970). In fact, Munier-Chalmas (1882), Douvillé (1886), Bernard (1895, 1897), Yonge (1967) and recent Russian authors (*fide* Boss, 1982, p. 1128; see *e. g.*, Scarlato and Starobogatov, 1979) considered the two groups to be close relatives, while these similarities have been regarded as convergences by the late Douvillé (1935), Cox (*in* Yonge 1967, p. 86), Dechaseaux and coworkers (1969), Kennedy and coworkers (1970), and most of the more recent rudistologists. Second, the comparison with the Chamidae has led to much confusion with respect to rudist shell terminology and hinge dentition (Dechaseaux, 1943), with important effects for phylogenetic interpretations. And third, nearly all diverging ideas circle around two unsolved problems: that of homology of right/left, versus attached/free, versus α/β valves, and, the homology of their respective hinge dentitions (Munier Chalmas, 1882; Douvillé, 1886; Dechaseaux, 1941; Yonge, 1967; Perkins, 1969; for a brief summary, and Kennedy *et al.*, 1970). It is, therefore, almost inevitable to begin with an analysis of the Chamidae. Nevertheless, their special situation is only used to search for more general mechanisms that may control attachment and "inversion" of hinge dentitions (including genetic and functional explanations). Several realistic scenarios are described that could lead to "inversion", but it is also shown that inversion is not necessary to explain the situation found in chamids or rudists.

It can hardly be avoided that most of the ideas discussed below have already been expressed by earlier rudist workers (see also Karczewski, 1969). A summarising discussion, however, has not been found in the literature. In addition, the reviewed ideas were generally based on other (and in part false) arguments than the ones presented here, and they have normally been stated as firm facts which they are not.

It will be seen that the Chamidae represent a model of limited value for rudist evolution notwithstanding that the more general ideas are well applicable to the rudists (third chapter). Finally, based on conclusions drawn from the previous chapters, a very simple phylogenetic analysis will serve to explore the usefulness of some higher taxonomic categories that have been proposed for groups within the rudist bivalves.

For the discussion, the following rudist taxa (as recognized in the "Treatise") will be provisionally differentiated: "Diceratinae" Dall, the group of Heterodiceratinae Pchelintsev, 1959, Plesiodiceratinae Pchelintsev, 1959, and Epidiceratinae Pchelintsev, 1959 (="HPE-group" here) ("Diceratinae" and "HPE-group" together = "Diceratidae" Dall), the Requieniidae Douvillé, 1914, and the group of Monopleuridae Munier-Chalmas, 1873, "Caprotinidae" Gray, 1848, and "Caprinidae" d'Orbigny, 1850 (here referred to as "MCC-group") (quotation marks indicate probable para- or polyphyletic states). Comparison of these groups focuses on the attached valve (left or right) in connection with the hinge dentition, *i.e.*, "Diceratinae": RV attached, with two teeth, free LV with one tooth. "HPE-group": LV attached, with one tooth, free RV with two teeth. Requieniidae: LV attached, with one tooth, free RV with two teeth. "MCC-group": RV attached, with one tooth, free LV with two teeth.

THE MEANING OF "NORMAL" AND "INVERSE" IN CHAMID BIVALVES

The chamids were brought into the discussion by Munier-Chalmas's (1882) comparative study about their shell morphology and hinge dentition—the "Études critiques sur les Rudistes, pt. II". For convenience, the critical passages from the first paragraph (p. 472f)—"Valves dextres et sénestres"—are cited below (underlining added for later discussion):

"Lorsque l'on étudie les différentes espèces du genre *Chama*, on remarque avec tous les auteurs qui se sont occupés de leur organisation, que quelques-unes d'entre elles sont **sénestres**. Mais on ne peut démontrer la sénestrosité d'un mollusque acéphalé qu'en le comparant à un autre type du même groupe, dont **tous les organes sont symétriquement disposés dans un ordre inverse**, et que l'on sera convenu d'appeler **dextre**. Or, comme les *Chama calcarata, lamellosa, gigas*, etc., ont été considérées commes **dextres**, il en résulte que les *Chama Janus, fimbriata*, etc., sont **sénestres**.

Ce fait est très important car il démontre que les noms de **valve droite** et de **valve gauche** sont des termes qui ne peuvent indiquer que des rapports de position et qu'on ne doit y attacher aucun sens qui entraîne avec lui des caractères d'ordre zoologique, puisque la **valve droite** d'une **Chame sénestre**, est bien incontestablement l'homologue de la **valve gauche** d'une **espèce dextre.**

Il s'ensuit que les mots de **valve droite** et de **valve gauche**, sans être suivis d'un autre terme qui indique leur relation d'homologie, ne peuvent être utilisés dans un travail où l'on s'occupe de la morphologie générale des Rudistes."

Munier-Chalmas concluded, in analogy to the chamids, that the right side of a "dextre" rudist species corresponds to the left of a "sénestre" species and provisionally designated the supposed homologues as α and β valves. As type for the first (α) he chose the free valve of chamids which, he continued, is the valve that remains free in the majority of the rudists (*i. e.*, the left valve). Consequently, the attached valve was given the letter β. According to the examples Munier-Chalmas cited, "dextre" and "sénestre" refer to the coiling direction of the umbo and would thus correspond to the anticlockwise rotation of the attached left valve of a "normal" chamid and clockwise rotation of the attached right valve of an "inverse" species (Yonge, 1967). Nevertheless, Munier-Chalmas's interpretation of "dextre" and "sénestre" remains somewhat dubious, since he described *Chama fimbriata* as "sénestre", which, at least according to material borrowed from the Musée Royal des Sciences Naturelles de Belgique, is not correct.

The situation in the Chamidae represents a special case of homologation problem in bivalves since comparisons among shell characteristics require the ability to identify correctly homologous shell halves, unless one uses the method of numerical taxonomy. With the realisation of "inversion" (see above) in the Chamidae, which was later also found in other bivalves, there are, theoretically, three possibly homologous combinations: (a) Right valves and left valves respectively are homologous. This is the usual assumption for bivalves. Odhner (1919) defended this view also for the chamids, but he also denied the existence of inversion. (b) Free valves (α) and attached valves (β) respectively are homologous (Munier-Chalmas's assumption for the chamids and rudists). (c) Right valves and left valves are homologous (Dechaseaux, 1943, 1952 in comparing the two rudistid genera *Diceras* Lamarck, and *Valletia* Munier-Chalmas) (see chapter: "Inversion in rudist bivalves").

Superficially, the choice among possibilities a, b, and c seems to depend on the taxon one considers. But, comparison between, say taxon A (right/left) and taxon B (α/β) requires a more general answer which can be related to a series of questions: Does inversion occur at all? What types of inversion exist? Does it affect the whole animal? Are inversion of cementation and inversion of the hinge dentition independent processes? Are there alternative explanations for the situation found in the chamids? Do all inversions have the same effects on phylogenetic interpretations, or, in which cases and to what extent can shells be compared? And finally, what would be the effect of undetected inversions on our phylogenetic reconstructions?

It is desirable in the following analysis to keep the discussion of the homology of valves separate from the one of the homology of the hinge dentition. Unfortunately, this is not strictly possible because the latter forms part of the evidence that inversion indeed occurred. One should thus be aware of the danger of circular reasoning concerning the homology between valves.

"INVERSION" IN THE SENSE OF MUNIER-CHALMAS AND YONGE

Munier-Chalmas (1882) based his assumption about the consequences of "inversion" on the statement that the whole animal occurs in an inverse state (see underlined phrase above). In this case. indeed, the free right valve of a "normal" individual is homologous to the free left valve of an "inverse" animal. Nevertheless, Yonge's (1967) examination of normal and inverse chamids—"*Chama*" *pellucida* Broderip and "*Pseudochama*" *exogyra* (Conrad) respectively—revealed that the viscero-pedal mass is not inversed (evidenced by the position of the unpair stomach). But he concluded from the mirror images of the hinge dentition and from the bilateral asymmetry (*i. e.*, internal cavity, see p. 55 there) that the mantle/shell is inversed. In fact, Yonge regarded the inversion to be a mutation "which made it possible for species of the Chamidae to attach by either valve with dentition associated with attached and free, *not* left and right, valves" (Yonge, 1967, p. 86). He thus postulated a genetic link between inversion of hinge teeth and inversion of attachment (this aspect will be discussed further in the following section: "Other types of inversion").

The independent torsion of mantle/shell and body is well known from gastropods (Bandel, personal communication, 1991) and according to Yonge (1967) also occurs in other molluscs. It appears therefore as a realistic scenario for the Chamidae. But, the fact that *Arcinella* Schumacher, which is only attached in early life stages, and possesses subequal body cavities, contradicts the idea that the mantle is involved in the "inversion" (see also below: "Other types of "inversion"). Also, the disposition for both right and left valve attachment needs not be a mutation within a single species but may be as well based on an underlying synapomorphy (Saether, 1979) inherited from the common ancestor of the different chamid genera.

Whatever the reasons for the supposed mantle/shell inversion may be, Munier-Chalmas's argumentation would still hold for the comparison between valves, while it would not for the viscero-pedal mass. Two consequences should be faced: First, one would have difficulties to homologise a chamid valve with the right and left valves of other bivalves. And second, inversions may have occurred convergently in different bivalve lineages, but could not be detected by shell comparisons because of the bilateral symmetry of most bivalves; then no shells could be safely homologised.

INVERSIONS OF HINGE TEETH EXCLUDING THE MANTLE

What consequences would have to be faced, if inversion affected the hinge teeth without involving inversion of the

mantle? (Such inversions have generally been called "transpositions". The term "reversal" is preferred here as "transposition" may also refer to chromosomal changes). Examples of tooth reversals are known from various independent lineages of non cemented lamellibranchs, *e.g.*, Astartidae, Crassatellidae, Unionidae, Sphaeriidae, a.o. (for summaries see: Dechaseaux, 1941, p. 350f; and Cox 1969, p. N 56f). In addition, the example of the Sphaeriidae reveals that reversals may affect either anterior cardinals and laterals alone, or the posterior laterals alone, or the complete hinge dentition (Eggleton and Davis, 1962). This independence casts even more doubt on the idea of a complete mantle/shell inversion (see above).

Three possible cases of tooth reversals may be distinguished: (a) Reversal of hinge teeth occurs at a low but constant level within a species. This possibility refers to the above mentioned examples of uncemented heterodonts. It may be interpreted as non lethal accidents, such as chromosomal inversions, which sometimes have phenotypic effects (Maynard Smith, 1989). Or it may originate in genetical polymorphism—controlled only by intrinsic factors—or polyphenism—controlled by extrinsic factors.

(b) Reversal occurs as above, but is, in addition, genetically related to the attachment with the "wrong" valve. This is similar to the hypothesis of Yonge (1967) for the Chamidae, but differs in that mantle inversion is excluded (see above and previous chapter). In general, the controlling factors may be the same as above. Nevertheless, the example of the "diceratid" rudists themselves demonstrates that the link between attachment and hinge inversion is no universally applicable rule (Yonge, 1967; see also chapter: "Inversion in rudist bivalves").

(c) Reversal occurs once as a mutation and is part of a speciation event. Here, two scenarios may be distinguished: First, the mutation also affected the attachment and is not perfect, *i. e.*, the genetic information of the stem species is not lost, but persists as a (now) normally suppressed character, which may occasionally become functional. Such situations have been called "latente Potenzen" and "Kryptotypus" (Osche, 1965) and could well describe what can be observed in "*Chama*" Linné and "*Pseudochama*" Odhner. Second, the mutation of the hinge reversal is not genetically linked to a reversal of attachment. Apparently, this is the case in the "Diceratidae", Requieniidae, and "MCC-group" (see rudist chapter).

For the above examples, it can be concluded that, in general, reversals of hinge teeth do not affect the general homology of right valves, and left valves respectively. Thus, in cases (a) and (b), where the hinge dentition is reversed within a species, doubtful interspecific homologation can be avoided by excluding the reversed types (see also Cox, 1969, p. N 57). If the reversal evolves into a character of a new species there is, at least from an ancestor-descendant question, no need for further homologation because the statement as such already requires that it is known which of the species is ancestral. In other cases, right and left valves with the right and left valves respectively of other species may be compared, because there is still the possibility that reversals are only apparent and go back to phylogenetic tooth transformations (or reductions) as is probably the case in the Chamidae (and rudists, see chapter: "Inversion in rudist bivalves"). Possible effects of undetected—or ignored—tooth reversals on phylogenetic assumptions are discussed in the following section: "Frequency of reversals". Whether reversal of dentition and of attachment are genetically linked or not has no effect on the just drawn conclusions.

FREQUENCY OF REVERSALS

The applicability of the above drawn conclusions depends largely on the frequency with which reversals occur. Here, two hierarchical levels must be differentiated: (a) frequency within species or genera, and (b) within bivalves (here only heterodonts) in general.

(a) It was assumed before (cases a, b above) that reversal—whether connected to attachment or not—is a rare accident, which affects less than 1% of a population of a species. Eggleton and Davis (1962) on the other hand found a reversal rate of 12% for the Sphaeriidae. Clearly, if the percentage of reversed hinges is that high, it can hardly be spoken of a genetic accident. It is more likely based on genetic polymorphy and is thus a syn- or autapomorph character of the species or a symplesiomorphy. To evaluate the character, both hinge versions must be considered (and the reverse state of course indicated). Comparison with other—closely related—species should (a) involve all ontogenetic stages and (b) should be based on both comparison of right valves and left valves respectively, and on right and left valves. The outcome should reveal what actually happened.

(b) Analogous to case (a), the discussion in the previous paragraphs assumed—for heuristic reasons—a rather limited occurrence of hinge teeth reversals among heterodont bivalves. None the less, the quite large number of examples cited in Dechaseaux (1941) may signal that hinge teeth reversals are a general and widespread feature. If complete reversals, *i. e.*, without accidental re-reversals, occur as part of speciation events, there would be no shell morphological evidence of their existence. In this case, phylogenetical interpretations based on hinge structures were impossible and phyla based on, say corbiculoid and lucinoid, hinge types would probably be polyphyletic groups. Nevertheless, this should become obvious through unsolvable contradictions with the evidence from other independent sets of characters, as *e. g.*, anatomy, shell microstructures, larval characters, and more recently, also genetic information.

THE NON-REVERSAL ALTERNATIVE

Besides the two possibilities—mantle/shell inversion and hinge teeth reversal—there is a third one which assumes

that no reversal of the hinge teeth occurred. This conclusion can be drawn from Bernard's studies on the ontogenetic development of the dentition of both "normal" (Bernard, 1895, p. 140f) and "inverse" chamids (Bernard, 1897, p. 563f) (Figure 1, a-d).

VD	LA (I) 3a - 3b L - LP(I)	
VG	0 LA - 2 - 4b - L - LP- (II)	
(a)		
VD	LA - 3 - L	
VG	LA - 2 - L	
(b)		
VD	LA III -- L - LP I -- III	
VG	LA --(IV) - 2 - 4b - L - LP - II	
(c)		
VD	LA 1 - 3b - L - LP -- III	
VG	LA II - - L - LP -II ---	
(d)		

Figure 1. *a,* Complete formula of a "normal" *Chama*, about 5 mm large (copied from Bernard, 1895); *b,* reduced formula of a "normal" *Chama* (copied from Bernard, 1895); *c,* hinge dentition of a normal chamid (recent, from the Red Sea), about 400 mm large. The formula is extracted from the text of Bernard (1897); *d,* formula of an inverse chamid (extracted from the text of Bernard, 1897).

From his observations, Bernard inferred three important aspects. First, in species which are attached by their left valves (*i. e.*, "normal"), the large anterior tooth is the second cardinal, while in attached right valves of "inverse" species this position is occupied by the cardinal 1. Thus, there is no need for complicated mutations or reversals, and right (and left valves respectively) are readily homologised. It may be concluded that, in either case, the genetic programme provides the information for a full set of teeth; just which will be suppressed and which more pronounced is a question of mechanical necessities and space (see also chapter: "Processes for gradual change" in the rudist part). And this is actually what changes if a normal upper valve becomes the inverted lower valve. The process may be compared with the suppression of plication in *Lopha* Röding along the whole attachment area, or suppression of ribs in other oysters.

Second, he noted that in the right valve of some "normal" chamids, and especially in the right valve of some "inverse" *Echinochama*, a rudimentary tooth 1 exists below 3b, of which no equivalent is developed in the left valve of the "inverse" types. Bernard (*op. cit.*) assumed that the existence of this tooth 1 establishes a connection between "normal" chamids on one side and the "inverse" forms and the "Diceratidae" on the other. Following the generally accepted view that the Chamidae are no descendants of rudists, Bernard's statement must be restricted to "normal" and "inverse" chamids.

Third, Bernard stated that the hinge of a "normal" chamid has greatest resemblance to the lucinoid hinge type, while the hinge of an "inverse" chamid would be, without knowledge of the normal type, doubtlessly homologised with the cyrenoid (now corbiculoid) type, such as represented by *Cypricardia* Lamarck (= *Trapezium* Megerle von Mühlfeld) or *Isocardia* Lamarck (= *Glossus* Poli). The question arises (but will not be discussed further), whether one of the two hinge types could not have developed from the other by reversal or by reduction? (see previous chapter).

Though Bernard's interpretations seems sound, other workers—using his method of indicating homologous teeth—offered different conclusions, *i. e.*, formulas (Lamy 1927, for an overview), and even Bernard's first article from 1895 is not completely consistent with his second one from 1897. Kennedy and others (1970) wanted to avoid the implications of the Bernard formula and used instead a modified Steinmann notation from Boyd and Newell (1968), which is merely descriptive and thus more objective. However, one should be aware of the fact that also comparisons among Steinmann notations require a background hypothesis about the homology between the compared teeth. Otherwise similarities cannot be interpreted phylogenetically, or else one uses the method of numerical taxonomy. Thus, "objectivity" only applies insofar as references to the ontogenetic hinge development of non-rudist bivalves are excluded (except for the megalodontids).

It is obvious from the foregoing discussion, that the whole matter is not yet settled. Certainly, not much has changed since Yonge (1967) stated that more detailed studies of the hinge of nepionic shell stages would be most illuminating. As reversals of hinge teeth (if they occurred) must have a genetic origin even better answers might be provided through studies of the genome. Recent advances in this field at least revealed that the genetic polymorphism of bivalves is still underestimated (*e. g.*, Boyer, 1974; Koehn, 1991, on *Mytilus*; or Reeb and Avise, 1989; Karl and Avise, 1992, on oysters; for references to other examples, see Avise and Ball, 1990, p. 47).

APPLICABILITY TO RUDISTS

Do chamid bivalves present a good model with respect to the analysis of rudist shells? Doubtlessly, the comparison between the two groups had been fruitful, especially concerning the ideas about general shell growth and designs of rudist anatomy (Yonge, 1967; Skelton, 1978). But, the previous chapters also reveal that we have no safe idea about which of the interpretations displays the correct explanation for the chamid "inversion". It is the author's personal guess that chamids possess a genetically not completely fixed option for cementation with either valve (as *e. g.*, the edentulous Etheriidae; perhaps via a dominant/recessive allele pair). And the actual position, of the left or right valves being attached, triggers the phenotypical tooth development and the concave shape of the attached valve (as well in the Etheriidae, which exhibit an even greater bilateral asymmetry; see Yonge, 1962). Thus, there is no mantle/shell inversion and no reversal. There are, however, several other realistic scenarios (discussed

above) that could apply to the situation found in chamids and, consequently, also to the rudists.

Despite this ambiguity, "inversion" or reversal does not inhibit in general the comparison, *i. e.*, homologising, of right and left valves respectively, of course, on the condition that right and left can be determined by other means than the hinge dentition. This presents no problem within the groups discussed here. As a result, the distinction of right and left valves makes the following terms unnecessary: (a) "dextre"/"sénestre" (Munier-Chalmas, 1882) and anticlockwise/clockwise (Yonge, 1967). They can be substituted by the term "prosogyrate"; (b) "normal"/"inverse" and α/β; they do not need any substitute. These terms had already been abandoned by Dechaseaux (1943; but see below: "Inversion in rudist bivalves"), Dechaseaux and coworkers (1969), Skelton (1978), Masse (1994), and others. Nevertheless, the old concepts are still in use in the classification schemes of higher taxa (Pchelintsev, 1959; Masse and Philip, 1986; Masse, 1994; Mainelli, 1992).

"INVERSION" IN RUDIST BIVALVES

According to Dechaseaux (1941) the term "inversion" could be applied to three (independent) shell characters: coiling direction of the umbo, fixation, and hinge dentition. The first relates to Douvillé's episodic comparison between diceratids and exogyrinids (Ostreoidea) (Douvillé 1887). But, clearly, the term does not apply to the situation: rudists are prosogyrate—as far as right and left valves can be determined—and oysters are opisthogyrate (with accidental exceptions among ostreid species). Furthermore, they are no closely related groups. In fact, Douvillé did not use the term "inversion" but only noted that they coil in a contrary sense. Thus, the two original meanings are left.

"INVERSION" OF FIXATION

Whether a real inversion, *i. e.*, of the mantle/shell, took place must be strongly doubted in the light of the earlier discussions; thus the term "reversal of fixation" or "cementation" is used instead. It is on the other hand clear that reversals occurred within the rudist groups under consideration. But, just how often this happened and on which taxonomic levels is not really known. Answers to these questions have a great bearing on the phylogenetic outcome. This will be discussed further in the following chapter.

"INVERSION" OF HINGE DENTITION

For the same reasons as above, the term "reversal" is preferred here. But, whether reversals really occurred is difficult to say, although the answer is (probably) already given by earlier workers on this subject (see Perkins, 1969, for an overview). It is surprising that Bernard (1895) is not cited in table E1 of Perkins (*op. cit.*, p. N 756) because he was the first to translate Douvillé's hinge teeth notation into his own notation, thus providing a hypothesis about their homology (Figure 2). (It may be noted that normally reference is also made to Munier-Chalmas [1895]; see references). The present author was unable to detect this article and it appears that the original is Bernard (1895).

Authors	LV, β				RV, α			
Douvillé, Fischer	b'	N	b	M	B'	n	B	m
Minuer-Chalmas, Bernard	1'	2	3'	4b	1	2'	3	4b'

Figure 2. Correlation between the notations from Douvillé and Bernard (reproduced from Bernard, 1895, p. 141).

Douvillé (1896) supported Bernard's principle interpretation. In addition, he observed that in the Cretaceous a new "inverse" group (attached by the right valve), develops, in which the ligamental nymph shortens step by step until the ligament becomes internal. In this series—*Valletia* Munier-Chalmas, *Gyropleura* Douvillé, *Monopleura* Matheron—the posterior tooth progressively develops until finally P II becomes as important as A II. Only A II, 3b, and P II become true teeth while the other lamellae border the cardinal grooves (Figure 3). He concluded that one must renounce the idea of the rudists being mirror forms ("forme symetrique") of *Diceras* (*i. e.*, "Diceratidae" of today).

RV	AI		III	**3b**		L P I		III
LV	A	**II**				L P	**II**	

Figure 3. Generalized dentition of "inverse" rudists, extracted from the description of Douvillé (1896). Bold typed symbols refer to true teeth.

Bernard (1897) again accepted this view of Douvillé (1896) and added some more details. All together, these observations are well expressed in the notations given by Douvillé (1918, 1935, *fide* Perkins, 1969, table E1). In principle, the two authors agree in two important observations: (a) the anterior lamella A I (or tooth 1) becomes reduced, and thus only one tooth remains in the right valve, and (b) P II of the opposite (left) valve develops until it represents a true tooth. This observation, if correct, proves that no inversion and no tooth reversal took place! Bernard and Douvillé continued to use the term "inversion", but it should be realised that the meaning was different from that of Munier-Chalmas (1882) and Yonge (1967).

Dechaseaux (1943, 1952) principally made the same observations. Only her lines of evidence and conclusions are confusing. In her first article (1943) she stated that "l'inversion ne modifie donc pas la 'valeur' des dents" [this is correct]. But then she went on: "On a vu que la valve gauche des Rudistes dits inverses avait deux dents qui devraient résulter, s'il y a bien inversion, de la transposition des deux dents de la valve droite des Rudistes dits normaux." This is wrong, because she is going to compare a right valve with a left valve. As repre-

sentatives of a normal and inverse rudist she chose *Diceras* ("Diceratidae") and *Valletia* (as the earliest representative of the Monopleuridae).

Dechaseaux noted about the dentitions that A I of *Diceras* is weakly and the cardinal 3 strongly developed, and furthermore, that A I of *Valletia* is atrophied (the notion was taken from Douvillé) and its P II appears as a rudimentary lamella (Figure 4).

	Diceras	*Valletia*
RV	AI **3**	(AI) **3**
LV	AII	**AII** PIV

Figure 4. Generalized hinge dentitions of a "normal" (*Diceras*) and an "inverse" rudist (*Valletia*), extracted from text of Dechaseaux (1943, p. 68). Well developed teeth are here shown in bold type. (A II of *Diceras* was not mentioned in her text).

In comparing the reciprocal dentition of both genera, Dechaseaux concluded that no inversion occurred between *Diceras* (or more general "normal" forms) and *Valletia*. Otherwise A II should be small and P IV large in *Valletia*, or as she said before they should have the same "valeur" (see above). Dechaseaux's statement as such, *i. e.*, that no inversion of hinge teeth occurred, matches Douvillé's (1896) interpretation. Nevertheless, this is lucky because her conclusion is based on the comparison of non-homologous valves and hinge dentitions (see also Dechaseaux, 1952, p. 324).

It should be briefly noted here why tooth transformation and fixation in rudists are supposed to be independent processes. Originally, the main argument was that the hinge dentition in the "Diceratidae" does not change whether attachment occurred with the right or the left valves. The same argument could not serve for the step from the "Diceratidae" to the Monopleuridae as long as tooth reversal was a reasonable possibility. Now, a genetic link between both processes appears very unlikely because the hinge teeth of the Monopleuridae most probably experienced a slow phylogenetic transformation.

Based on the arguments just put forward, there is now a relatively safe hypothesis about what happened during this tooth transformation. But the question remains why it happened. Some possible underlying processes will be discussed in the following chapter.

PROCESSES FOR GRADUAL CHANGES

It may be assumed from the previous discussions that the tooth transformations had been gradual which, in turn, suggests that the underlying processes are of functional rather than genetic origin. Recently, the functional design of Late Jurassic to Early Cretaceous rudists has been studied by Skelton (1978, 1985). According to him, the first important evolutionary step—from megalodontids to "diceratids"—was attachment (by either valve), which allowed the "diceratids" to grow away from the substrate. But upward growth of the dorsal side was constricted by the external ligament forcing the shell to grow in a spiral. With the invention of invagination of the ligament this handicap was overcome and the shell could grow conically upwards, *i. e.*, secondarily uncoiled (this stage is reached in the Monopleuridae, except for *Valletia*). Apparently, conical growth (away from the substrate) was more efficient and needed less shell material than growth in a helicoidal spiral. Another effect of the invagination was that the anterior and posterior teeth approached the dorsal ligament. This site of the commissure possesses the smallest growth potential and thus the complete hinge construction afforded much less shell material than in earlier rudists. In consequence, Skelton (*op. cit.*) interpreted the evolutionary changes in terms of improved growth economy.

The economical aspect is certainly an important driving force in evolution. Nevertheless, the model provides no answer to the question why the anterior tooth of the right valve in "diceratids" should be reduced and the posterior one grow continuously larger in the monopleurids. Obviously, the hinge complex—ligament and cardinal area—rotates posteriorly in a helicoidal spiral. And thus, it is unavoidable that the former site of the anterior tooth (here A I) will be overgrown by new shell material. Furthermore, to remain an effective triangle with the ligament also the anterior and posterior adductors must rotate and thus the anterior adductor comes to sit on the overgrown site of the anterior tooth. This process could go on in an endless spiral, unless the anterior tooth is reduced to leave space for the anterior adductor. As two teeth alone are hardly effective as a hinge, the small posterior tooth rudiment of the opposite valve becomes continuously more important. Invagination and the change from helicoidal to conical growth occurred in a further step (see below).

The above scenario combines a functional aspect with the availability of space. The suggestion that space may indeed be an important factor is supported by examinations of larval shells of oysters which possess a kind of taxodont hinge dentition (with two known exceptions). In nearly all recent Crassostreinae and a number of fossil ostreids, the left valve umbo is quite strongly opisthogyrate. It can be demonstrated that in late veliger phases the posterior teeth are reduced and smoothed out by shell material while at the same time growth of new teeth continues anteriorly. During this phase, the direction of maximal growth is antero-ventral. In contrast, in recent Ostreinae, where the umbo is much less opisthogyrate or nearly orthogyrate, and the area of maximal growth is along the ventral margin, anterior teeth are reduced prior to the posterior ones (Hu *et al.*, 1993; Malchus, 1995). Although the time and place of these reductions are certainly mainly under genetic control, the considerable dissymmetry between anterior and posterior teeth in the Crassostreinae suggests that the availability of space had an additional effect. Thus, a posteriorly coiled specimen with an anteriorly directed maximum growth direction leaves more space for anterior teeth to grow,

while the space is reduced posteriorly. In a prosogyrate shell type, one could expect the opposite effect. This interpretation would be consistent with the tooth development seen in rudists.

The invagination of the ligament in the monopleurids can as well be related to spatial effects. Posterior shell structures (radial bands, pillars) suggest that the posterior part of the mantle was considerably more complex than the anterior one. Thus, the posterior tooth (here posterior of the ligament!) might not have been as free to proceed on its helicoidal growth track. This, in turn, may have lead to differential growth velocities, with the anterior tooth moving faster posteriorwards. As the ligament sits between the anterior and posterior teeth, continuous shortening and finally invagination could have been a logical consequence of differential helicoidal growth.

The hypothetic mechanism would also indirectly explain why the "HPE-group" did not show a parallel evolution. The fact seems somewhat enigmatic since, at least from a morphological point of view, the only significant difference between the "Diceratinae" and "HPE-group" is their right and left attachment respectively. Three possible reasons might be imagined. First, because the posterior tooth of the right valve occupies a position still anterior of the ligament, it could not serve as an abutment against which the ligament was to "subduct". Second, species of the "HPE-group" had a less complicated posterior body plan. The third possibility would be a combination of both. Though the scenario is highly speculative, there is at least a theoretical possibility to check it. If the distances between the posterior tooth and the ligament, and respectively between the anterior tooth and ligament, are measured of successive growth stages the difference should show whether differential growth really occurred or not.

PHYLOGENETIC CONSEQUENCES

We are not yet in a state to unravel the phylogenetic history of the Late Jurassic-Early Cretaceous rudists. But enough is known to express some reasonable phylogenetic scenarios which allow the discussion about the monophyletic, paraphyletic or polyphyletic states of some higher rudist taxa (as used in the "Treatise", or by Pchelintsev, 1959; Masse and Philip, 1986; and Mainelli, 1992, respectively): "Diceratinae", "Diceratidae", Hippuritacea, and "Dextrodonta", "Sinistrodonta", and "Dicerasodonta". The "HPE-group" is added here. The analysis is naturally based on a number of assumptions which in part follow from the discussion of the previous chapters. Consequences of the case that the assumptions are wrong will be considered in the last section (see "Consequences of incorrect assumptions"):

1—The following groups are regarded monophyletic in the sense that each has its own stem species (proposed autapomorphic characters are added in brackets): "Diceratinae" (attached by right valve), "HPE-group" (attached by left valve), Requieniidae (attached by left valve, shell shape varied, but not *Diceras*-like; better autapomorphies are restricted to genera), and "MCC-group" (attached by right valve, transformed hinge structures) (Radiolitidae and Hippuritidae, momentarily excluded). The proposition of monophyly is chosen here for reasons of convenience. It is certainly incorrect for a number of taxa (see last section).

2—The origin of the rudists is to be found within the Megalodontidae. This hypothesis is currently accepted by most rudist workers (see e. g., Dechaseaux *et al.*, 1969; Skelton, 1978).

3—Tooth transformation (no reversal) occurred only once within the rudists and was independent of attachment by either valve (proposed for parsimonious reasons).

4—Attachment was exclusively either with the right or the left valves within a species and a genus (proposed for parsimonious reasons).

5—The switch from right to left valve attachment (or vice versa) occurred only once, or not at all (proposed for parsimonious reasons).

PHYLETIC STATE OF THE HIPPURITACEA

The oldest representatives of the superfamily Hippuritacea are the left attached "diceratids" (here "HPE-group") and the right attached "Diceratinae" (together "Diceratidae"). Both make their appearence in the Oxfordian, *i. e.*, more or less time equivalent (if one ignores minor stratigraphic differences). Now four theoretical cases of ancestry and descent which could have given rise to the Hippuritoidea can be distinguished.

Case 1 (Figure 5)—The oldest species of *Diceras* and of the "HPE-group" have the same stem species (being an unattached megalodontid species). Thus, *Diceras* sp. 1 (D.1) and HPE sp. 1 (HPE.1) are sister species. Together, they constitute the true monophylum Hippuritoidea. "Attachment" itself could be regarded as the synapomorphy of D.1 and HPE.1, while attachment by the right and left valves respectively are the autapomorph characters.

Case 2 (Figure 6)—The oldest species of *Diceras* and of the "HPE-group" have both their origin in the Megalodontidae but in different species. In this case, two possibilities are to be discussed.

Case 2a. The two megalodontid species (M.1 and M.2) are sister species, *i. e.*, they have a common direct ancestor. This would be similar to the first case, but the Hippuritacea had to include also M.1 and M.2 to be a monophylum. In addition, "attachment" would be no synapomorph but only an apomorph character of *Diceras* sp. 1 and HPE sp. 1.

Case 2b. The two species M.1 and M.2 are not sister species. Then, indeed, *Diceras* sp. 1 and HPE sp. 1 would not be sister species, and thus the Hippuritacea diphyletic.

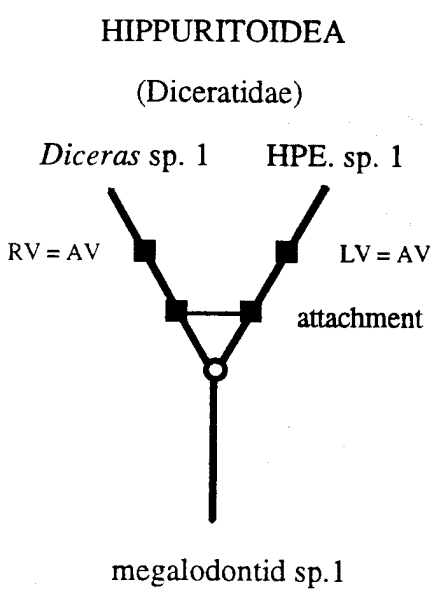

Figure 5. Hypothetical dichotomy which assumes that the oldest species of *Diceras* and of the "HPE-group" have the same megalodontid stem species. Black squares with a connecting line symbolise a synapomorphy, single black squares are autapomorphies (see text for explanations: "case 1").

Case 3 (Figures 7, a; 8, a)—A megalodontid species gave rise to a right attached *Diceras* (D.1) and "diceratinids" contain the stem for the "HPE-group". Again there are two possibilities to continue the story.

Case 3a (Figure 7, a). D.1 is the stem for both the right attached *Diceras* sp. 2 and the left attached HPE sp. 1.

Case 3b (Figure 8, a). The right attached *Diceras* sp. 2 (D.2) which gave rise to the left attached HPE sp. 1 is not member of what is here provisionally called "stem line of other *Diceras* species".

In both cases, the Hippuritacea would be monophyletic. Right valve attachment would be the autapomorph character of *Diceras* sp. 1, but plesiomorph for all other *Diceras* species (Figures 7, a, 8, a), and left valve attachment would be the autapomorph character for HPE sp. 1 (Figure 7, a) or synapomorph for HPE sp. 1 and its (theoretical) sister species (Figure 8, a).

Case 4 (Figures 7, b; 8, b)—The first rudist is a left attached HPE species (HPE.1). The argumentation is analogous to case 3, only that HPE-species and species of *Diceras* are exchanged (compare Figures 7, a, 8, a).

The four scenarios reveal that the Hippuritacea are diphyletic only in case 2b. In all other situations they are monophyletic (as long as they comprise all ancestors and descendants of the group). But, it is presently impossible to offer good criteria to choose among cases 1 to 4. Nevertheless,

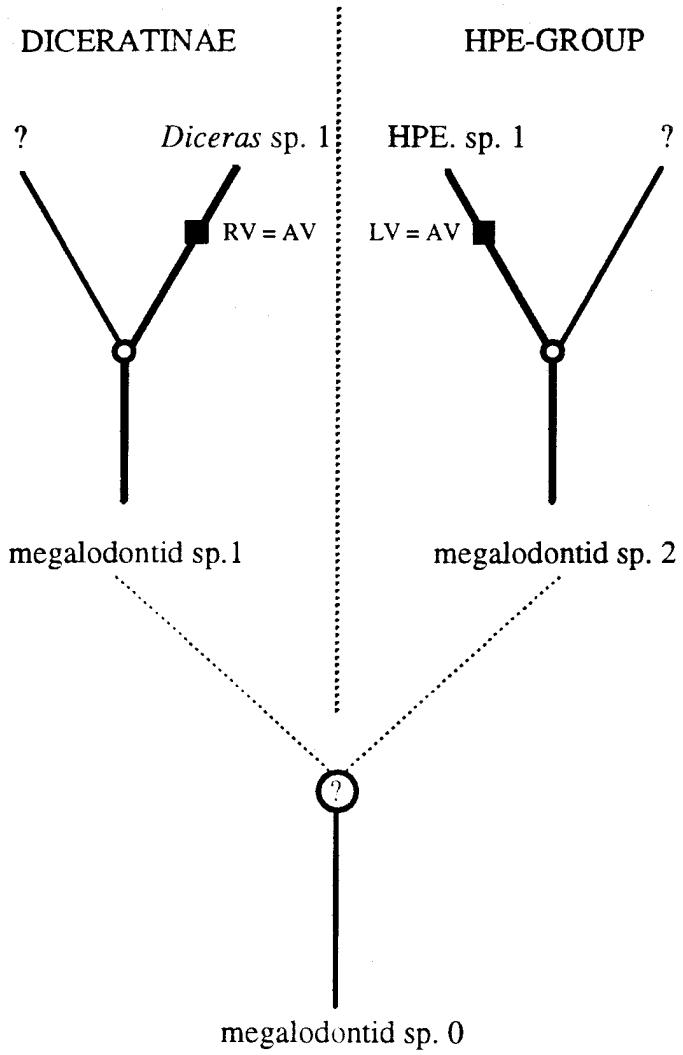

Figure 6. Hypothetical phylogram based on the assumption that the oldest species of the "Diceratinae" and "HPE-group" descended from two megalodontid species. Whether the two groups are sister taxa or not depends on whether the two megalodontid species are sister species or not (see text for explanations: "case 2 with 2a, 2b").

some will be offered now. Perhaps cases 3 or 4 are more likely than case 1, which affords the occurrence of the autapomorphic character "attachment by right valve" and "by left valve" at the same time, or case 2a, because this involves more evolutionary steps. The diphyly hypothesis may be rejected for two reasons. First, it seems unlikely that two different megalodontid species gave rise to two nearly identical species. Second, the (assumed) megalodontid stem species was probably bilaterally symmetric. Thus, during early generations of the new species (*Diceras* sp. 1 or HPE sp. 1) there may have been no preferential side for attachment. Besides, quantum speciation—*i. e.*, a daughter species arises from a small peripheral isolate of an ancestral species—is a speciation process which allows for a large number of phenodeviants (Grant, 1991, p. 243). This may as well include the potential to attach with both valves. Thus, for the following discussion monophyly is assumed for the Hippuritacea.

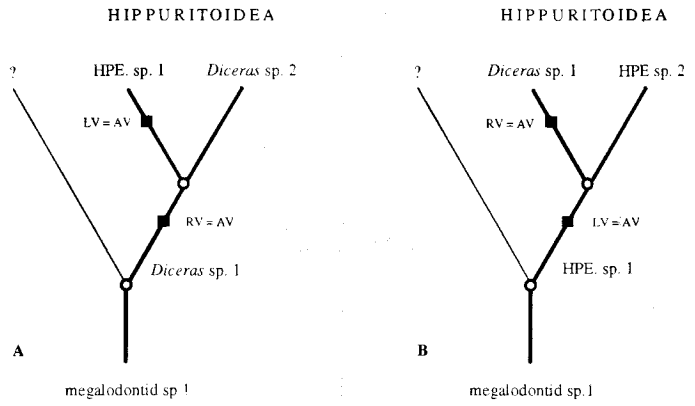

Figure 7. *a,* Hypothetical phylogram assuming that the oldest *Diceras* species 1 descended from a megalodontid species and is itself the stem species of both the "HPE-group" and of all other "Diceratinae" (further explanations see case 3a); *b,* Hypothetical phylogram assuming that the oldest HPE sp. 1 descended from a megalodontid species and is itself the stem species of both the "Diceratinae" and of all other species of the "HPE-group". Black squares represent autapomorphies (further explanations see case 4a).

PHYLETIC STATES OF THE "DICERATINAE" AND "HPE-GROUP"

The value of the subfamily divisions Heterodiceratinae, Plesiodiceratinae and Epidiceratinae as used in the "Treatise"—"HPE-group" here—have already been questioned by Dechaseaux and others (1969), while the "Diceratinae" are normally considered to represent a monophylum. This interpretation is probably shared by most current rudist workers although reasons have never been explicitly mentioned.

Referring to the discussion of the previous section, it can be seen that in cases 1, 3a and 4a (Figures 5, 7) the taxa "Diceratinae" and "HPE-group" would only be monophyletic if they were used as synonyms of the Hippuritacea. These taxa are then unnecessary.

In case 2 (Figure 6), both "Diceratinae" and "HPE-group" appear to be monophyletic if they also comprise their respective (unspecified) sister taxon, but only in case 2a they would define the higher taxon Hippuritacea. In case 3b (Figure 8, a) the "HPE-group" appears to be monophyletic and the sister group of the "stem line of other *Diceras* species" which were paraphyletic; in case 4b (Figure 8, b) the "Diceratinae" appear to be monophyletic with the "stem line of other HPE-species" being paraphyletic.

In the last cases 2, 3b and 4b monophyly is only apparent. On the above assumptions that attachment by either valve and transformation of the hinge dentition only occurred once in rudist evolution, it must be concluded that the "HPE-group" gave rise to the Requieniidae, while the "Diceratinae" include the stem species of the "MCC-group" (+ Radiolitidae, Hippuritidae). Thus, there are three monophyletic outcomes. In case 2, both "Diceratinae" and "HPE-group" are valid monophyla provided they include all species following megalodontid sp. 1 and megalodontid sp. 2, respectively. In the remaining two cases, either the "HPE-group" + Requieniidae (case 3b; Figures 8, a; 9; 11) are monophyletic or the "Diceratinae" +

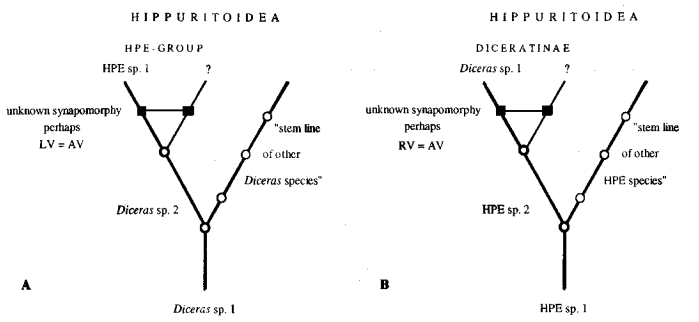

Figure 8. *a,* Hypothetical phylogram assuming that the "HPE-group" descended from a *Diceras* species (sp. 2) which is not member of the stem line of all other Diceratinae (further explanations see case 3b); *b,* hypothetical phylogram assuming that the "Diceratinae" descended from a HPE species 2 which is not member of the stem line of all other species of the "HPE-group" (further explanations see case 4b).

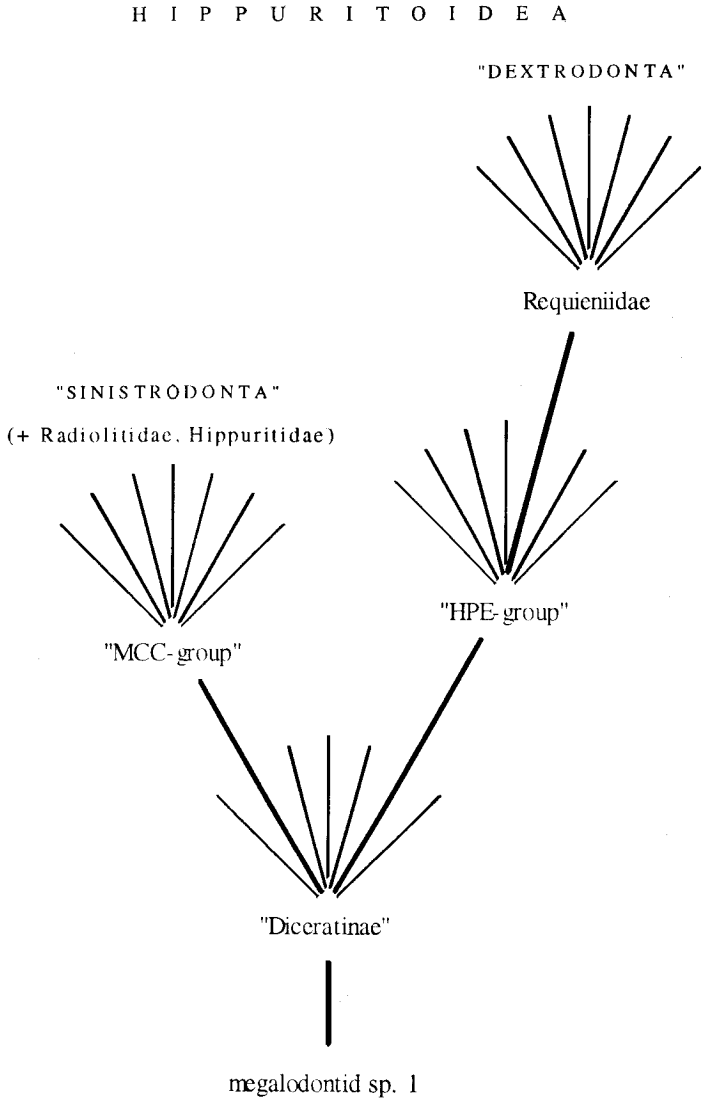

Figure 9. Highly abstracted phylogram assuming that two species of the "Diceratinae" gave rise to the "MCC-group" and "HPE-group", respectively. The latter contains the stem species of the Requieniidae. Each line of a bush symbolizes a species (the number of lines is fictive) and each bush represents a pseudo-polytomy (see text for further explanations).

"MCC-group" (+ Radiolitidae, + Hippuritidae) (case 4b; Figures 8, b; 10). It will be seen that these monophyla may correspond to the "Sinistrodonta" and "Dextrodonta" as discussed below.

PHYLETIC STATE OF THE "DICERATIDAE"

The taxon "Diceratidae" has been recently considered a "paraphylum" (Skelton, 1991) but without further explanations. According to the "Treatise", the "Diceratidae" comprise the "Diceratinae" and "HPE-group". Thus, they are defined by the plesiomorph characters *"Diceras* shape" and *"Diceras* hinge dentition" which exclude members of the above recognized two monophyla—the Requieniidae, and the "MCC-group" (and Radiolitidae, Hippuritidae). It is therefore in each case paraphyletic. The "Diceratidae" would only be monophyletic if they were used synonymously with the Hippuritacea in cases 1, 2a, 3 and 4. The taxon is then unnecessary.

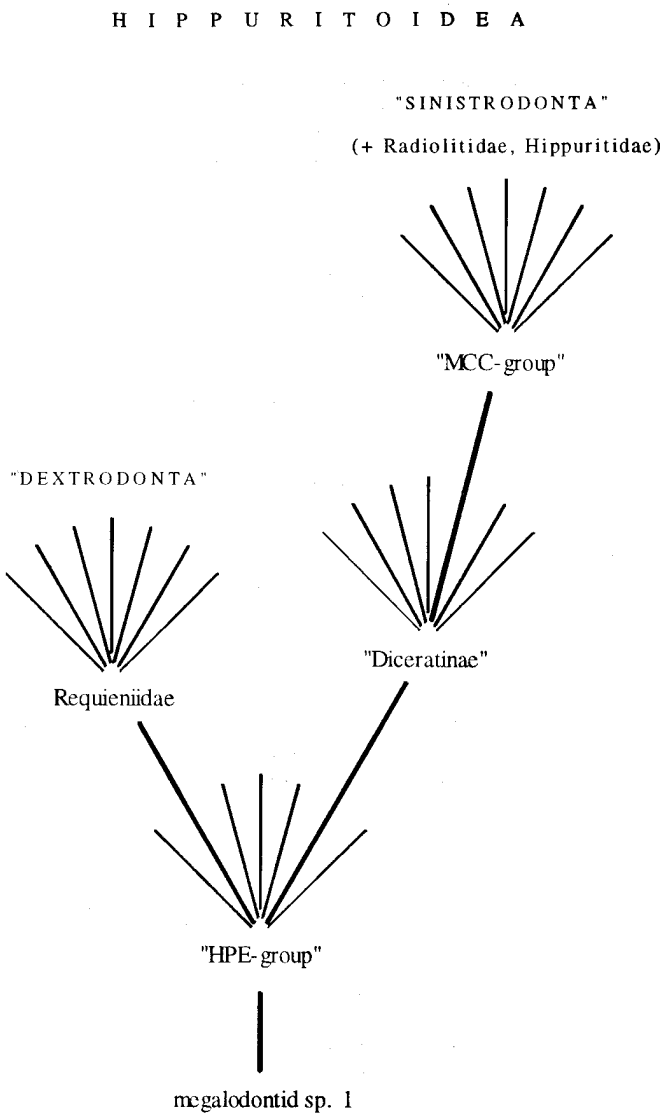

Figure 10. Highly abstracted phylogram assuming that a species of the "HPE-group" gave rise to the Requienidae and another to the "Diceratinae" which themselves contain the stem species of all other rudist families (for explanations see Figure 9 and text).

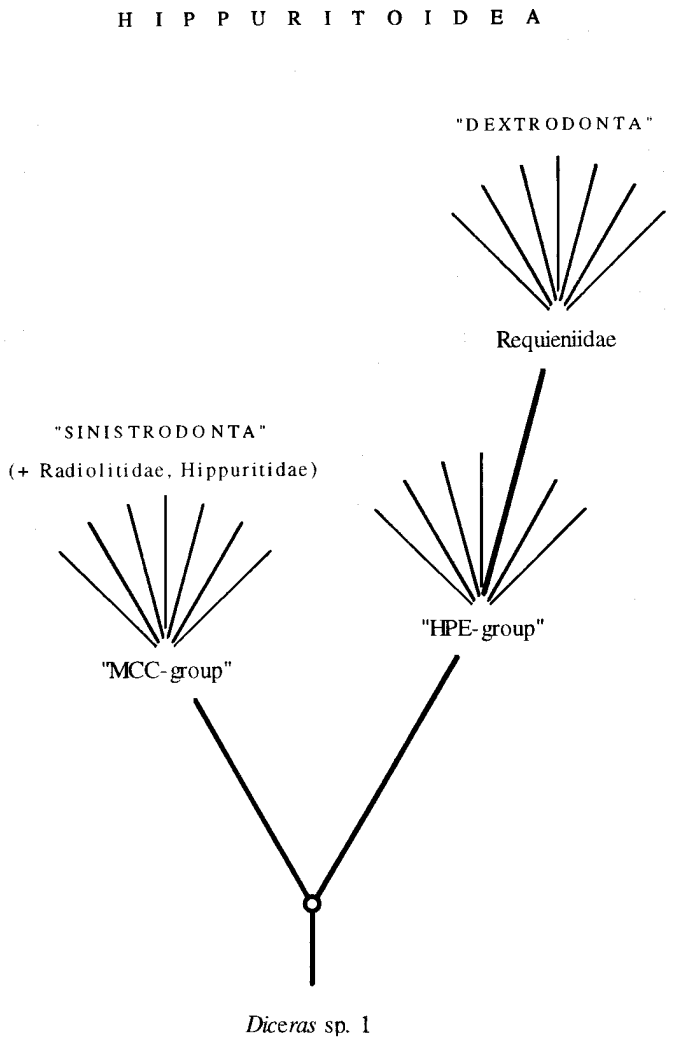

Figure 11. Highly abstracted phylogram assuming that only one *Diceras* species existed and that this was the stem species of all other rudists (for explanations see Figure 9 and text).

PHYLETIC STATES OF THE "DICERASODONTA", "SINISTRODONTA", AND "DEXTRODONTA"

Similar problems as before can be quoted for the phyletic states of the "Dicerasodonta", "Sinistrodonta", and "Dextrodonta". As the suborder "Dicerasodonta" (Mainelli, 1992) contains only the "Diceratinae", it is unnecessary.

The "Sinistrodonta" originally comprised only the Monopleuridae, later also the "Caprotinidae", "Caprinidae", Radiolitidae and Hippuritidae, thus, all groups attached by the right valve except for the "Diceratinae" (see Masse and Philip, 1986; Mainelli, 1992). The taxon may indeed be a monophylum if the oldest monopleurid species (*e. g.*, *Valletia*) proves to be the stem species of the whole group. Nevertheless, its sister group remains unknown (Figures 9, 10).

The "Dextrodonta" originally comprised the paraphyletic "Diceratidae" and (perhaps) monophyletic Requieniidae (Pchelintsev, 1959). In the sense of Masse and Philip (1986), it was identical to the Requieniidae (and would thus be superfluous), and Mainelli (1992) restricted the taxon to the paraphyletic "HPE-group". Again, the sister group is not known (Figures 9, 10).

If, as might be suspected, the "Diceratinae" contain only a single species and this were the oldest representative of the superfamily Hippuritacea—as indicated in Figures 7, a and 8, a, then the "Sinistrodonta" and "Dextrodonta" could be sister taxa. This hypothesis is shown in Figure 11 (see also Figures 5; 7, a).

CONSEQUENCES OF INCORRECT ASSUMPTIONS

The most serious false assumption put foward at the beginning of the chapter was that of monophyly. Reasons have just been discussed for the paraphyletic state of the "Diceratinae" and "HPE-group".

The "Caprotinidae" (of the MCC-group here) may be added as defined in the "Treatise". According to Skelton (1978), they comprise a polyphyletic group of monopleurid species which independently developed accessory cavities. Skelton proposed to unite the two groups under the older name Caprotinidae Gray, 1848. It may be noted here that the "Caprotinidae" emend. Skelton, 1978, remain paraphyletic because they give rise to at least four independent groups (Caprinidae, Radiolitidae, Hippuritidae, Antillocaprinidae; Skelton and Gili, 1991, fig. 6). Also the "Caprinidae" (of the MCC-group) have long been known to include several lineages (Douvillé, 1887, 1935; MacGillavry, 1937; Damestoy, 1971; Dechaseaux *et al.*, 1969, p. N789) and have been recently termed polyphyletic by Skelton (1978). Even the Requieniidae may be paraphyletic; at least they are not characterized by a common autapomorphy (*cf.* Masse, 1994). In addition, the subfamily within the HPE-group which contains its stem species is not known. It seems therefore that the Radiolitidae and Hippuritidae are the only quite reliable monophyla among higher rudist taxa. The pseudo-polytomic structure of Figures 9 to 11 tries to account for these uncertainties. But even these figures could not be constructed if we allowed for multiple (parallel) changes in attachment or tooth transformation, or if we assumed a link between the two characters. In particular, attachment by right or left valves may have been controlled by a dominant/recessive allele pair early in "diceratid" evolution (see Karczewski's [1969] data on the percentages of right and left attachment in different populations [or species assemblages] from different regions in Europe and the Crimea). But this can only be revealed by a revision of the group. None the less, these wrong assumptions have no effect on the monophyletic state of the Hippuritacea as long as one of the cases 1, 2a, 3 or 4 of above is correct.

ACKNOWLEDGEMENTS

The author is greatly indebted to J.M. Pons (Universitat Autonoma Barcelona) for taking the time to read the various drafts of the manuscript and for his constructive criticism and advice. He also wants to thank all specialists who most kindly reviewed the final manuscript. The author takes, of course, full responsibility for the published version. The work was financially supported through a fellowship (ERBCHBICT 93.07.93) of the European Communities (programme "Human Capital and Mobility", 1992-1994, of the Commission of the European Communities).

BIBLIOGRAPHICAL REFERENCES

Avise, J.C., and Ball, R.M., 1990, Principles of genealogical concordance in species concepts and biological taxonomy: Oxford Surveys in evolutionary Biology, v. 7, p. 45-67.

Bernard, Felix, 1895, Première note sur le developpement et la morphologie de la coquille chez les lamellibranches: Bulletin de la Société Géologique de France, v. 23, no. 3, p. 104-154.

———1897, Quatrième et dernière note sur le developpement et la morphologie de la coquille chez les lamellibranches: Bulletin de la Société Géologique de France, v. 25, no. 3, p. 559-566.

Boss, K.J., 1982, Bivalvia, *in* Parker, S.P., ed., Synopsis and classification of living organisms, v. 1, p. 1103-1163.

Boyd, D.W., and Newell, N.D., 1968, Hinge grades in the evolution of crassatellacean bivalves as revealed by Permian genera: American Museum Novitates, v. 2328, 52 p..

Boyer, J.F., 1974, Clinal and size-dependent variation at the LAP locus in *Mytilus edulis:* Biological Bulletin, v. 147, p. 535-549.

Cox, L.R., 1969, General features of Bivalvia, *in* Moore, R.C., ed., Treatise on invertebrate paleontology: Geological Society of America and University of Kansas Press, Mollusca 6, Bivalvia, Part N, v. 1 (of 3), p. N2-N129.

Damestoy, G , 1971, Essai de classification phylogénique des Caprinidés: Bulletin du Muséum d'Histoire Naturelle, ser. 2, v. 42, no. 5, p. 1003-1008.

Dechaseaux, Collette, 1941, L'inversion chez les lamellibranches: Bulletin de la Société Géologique de France, ser. 5, v. 11, p. 343-355.

———1943, La notion d'inversion ne peut s'appliquer aux rudistes: Bulletin de la Société Géologique de France, Compte Rendus des Séances, ser. 5, t. 13, p. 67-69.

———1952, Classe des lamellibranches, *in* Piveteau, J., ed., Traité de Paléontologie: Paris, Ed. Mason, v. 2, p. 323-364 (rudist part).

Dechaseaux, Collette; Coogan, A.H.; Cox, L.R.; and Perkins, B.F., 1969, Hippuritacea, Systematic descriptions, *in* Moore, R.C., ed., Treatise on invertebrate paleontology: Geological Society of America and University of Kansas Press, Mollusca 6,Bivalvia, Part N, v. 2 (of 3), p. N 776-817.

Douvillé, Henry, 1886, Essai sur la morphologie des rudistes: Bulletin de la Société Géologique de France, ser. 3, v. 14, p. 389-404.

———1887, Sur quelques formes peu connues de la famille des chamidés: Bulletin de la Société Géologique de France, ser. 3, v. 15, p. 756-802.

———1896, Observations sur la charnière des lamellibranches hétérodontes: Bulletin de la Société Géologique de France, ser. 3, v. 24, p. 26-28.

———1914, Les Requiénides et leur évolution: Bulletin de la Société géologique de France, ser. 4, v. 14, p. 383-389.

———1918, Le Barrémien supérieur de Brouzet. Part 3. Les rudistes: Mémoire de la Société Géologique de France (Paléontologie), Mémoire 52, v. 22, no. 1, p. 1-20.

———1935, Les rudistes et leur évolution: Bulletin de la Société Géologique de France, ser. 5, v. 5, p. 319-358.

Eggleton, F.E., and Davis, G.M., 1962, Hinge tooth reversal in populations of Ohio Sphaeriidae: American Malacological Union, Pacific Division, report 28, p. 19-20 (abstract).

Grant, V., 1991, The evolutionary process—A critical study of evolutionary theory: Columbia University Press, New York, Oxford, 487 p., 2nd edition.

Gray, J.E., 1848, On the arrangement of the Brachiopoda: Magazine Natural History, Annals, v. 2, p. 435-440.

Hu, Ya-Ping; Fuller-S., Cynthia; Castagna, M.; Vrijenhoek, R.C.; and Lutz, R.C., 1993, Shell morphology and identification of early life history stages of congeneric species of *Crassostrea* and *Ostrea*: Journal of the marine biological Association of the United Kingdom, v. 73, p. 471-496.

Karczewski, L , 1969, Upper Jurassic Rudistae of the margin of the Holy Cross Mountains, Poland: Acta Palaeontologica Polonica, v. 14, no. 3, p. 395-465.

Karl, S.A., and Avise, J.C., 1992, Balancing selection at allozyme loci in oysters—Implications from nuclear RFLPs: Science, v. 256, p. 100-102.

Kennedy, W.J.; Morris, N.J.; and Taylor, J.D., 1970, The shell structure, mineralogy, and relationships of the Chamacea (Bivalvia): Palaeontology, v. 13, no. 3, p. 379-413.

Koehn, R.K., 1991, The genetics and taxonomy of species in the genus *Mytilus*: Aquaculture, v. 94, p. 125-145.

Lamy, E., 1927, Révision des Chama vivants du Museúm National d'Histoire Naturelle de Paris: Journal de Cochyliogie, v. 71, no. 4, p. 293-283.

MacGillavry, H.J., 1937, Geology of the province of Camagüey, Cuba—with revisional studies in rudist paleontology (mainly based upon collections from Cuba): Holland, University Utrecht, Ph. D. dissertation, 168 p. (unpublished).

Mainelli, Michele, 1992, Rudists classification—A new proposal: Geologica Romana, numero speciale dedicato alla The second international Conference on Rudists, v. 28, p. 261-265.

Malchus, Nikolaus, 1995, Larval shells of Tertiary *Cubitostrea* SACCO, 1897, with a review of larval shell characters in the subfamilies Ostreinae and Crassostreinae (Ostreoidea, Bivalvia): Bulletin de l'Institut des Sciences Naturelles de Belgique, v. 65, p. 187-239.

Masse, J.P., 1994, L'évolution des Requieniidae (rudistes) du Crétacé Inférieur. Charactères, signification fonctionelle, adaptative et relations avec les modifications des paleoenvironnements: Geobios, v. 27, no. 3, p. 321-333.

Masse, J.P., and Philip, J., 1986, L'évolution des rudistes au regard des principaux événements géologiques du Crétacé: Bulletin du Centre de Recherche de Exploration et Production de Elf Aquitaine, v. 10, no. 2, p. 437-456.

Maynard-Smith, J., 1989, Evolutionary genetics: Oxford, Oxford University Press, 325 p.

Munier-Chalmas, H.,1873, Prodrôme d'une classification des Rudistes: Journal of Conchyliologie, v. 3, p. 71.

———1882, Études critiques sur les rudistes: Bulletin de la Société Géologique de France, ser. 3, v. 10, p. 472-492.

———1895, Note préliminaire sur le developpement de la charnière chez les mollusques acéphales: Bulletin de la Société Géologique de France, ser. 3, v. 33, p. 53-70.

Odhner, N.H., 1919, Studies on the morphology, the taxonomy and the relations of recent Chamidae: Handl.K. svenska Vetenskapsakad., v. 59, no. 3, 102 p.

Orbigny, Alcide d', 1850, Prodrôme de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés: Paris, v. 2, 427 p.

Osche, G., 1965, Über latente Potenzen und ihre Rolle im Evolutionsgeschehen: Zoologischer Anzeiger, v. 174, p. 411-440.

Pchelintsev, V.F., 1959, Rudisty mezozoya gornogo Kryma (Mesozoic rudistids of the Crimean Range): Geologicheskiy Muzei A.P. Karpinskii, Akademiya Nauk SSR, Seriya Geologicheskaya, 178 p.

Perkins, B.F., 1969, Rudist morphology, *in* Moore, R.C., ed., Treatise on invertebrate Paleontology: Geological Society of America and University of Kansas Press, Mollusca 6, Bivalvia, Part N, v. 2 (of 3), p. N 751-764.

Reeb, C.A., and Avise, J.C., 1989, A genetic discontinuity in a continuously distributed species. Mitochondrial DNA in the American oyster, *Crassostrea virginica*: Genetics, v. 124, p. 397-406.

Saether, O.A., 1979, Underlying synapomorphies and anagenetic analysis: Zoologica Scripta, v. 8, p. 305-312.

Scarlato, O.A., and Starobogatov, Y.I., 1979, Morphology, systematics and phylogeny of molluscs: Proceedings of the Zoological Institute, Academy of Sciences of the USSR, v. 80, p. 5-38 (in Russian).

Skelton, P.W., 1978, The evolution of functional design in rudists (Hippuritacea) and its taxonomic implications: Philosophical Transactions of the Royal Society of London, ser. B, v. 284, p. 305-318.

———1985, Preadaptation and evolutionary innovation in rudist bivalves: Special Papers in Palaeontology, v. 33, p. 159-173.

———1991, Morphogenetic versus environmental cues for adaptive radiations, *in* Schmidt-Kittler, N., and Vogel, K., eds., Constructional Morphology and Evolution, p. 375-388.

Skelton, P.W., and Gili, E., 1991, Palaeocological classification of rudist morphotypes, *in* Proceedings of the First International Conference on Rudists, Beograd, 1988, Serbian Geological Society, Special Publications, v. 2, p. 265-287 (it will probably be published in Palaios, 1996).

Yonge, C.M., 1962, On *Etheria elliptica* Lam. and the course of evolution, including assumption of monomyarianism, in the family Etheriidae (Bivalvia. Unionacea): Philosophical Transactions of the Royal Society of London, ser. B, v. 244, p. 423-458.

———1967, Form, habit and evolution in the Chamidae (Bivalvia) with reference to conditions in the rudists (Hippuritacea): Philosophical Transactions of the Royal Society of London, ser. B, v. 252, p. 49-105.

Manuscript received: August 16, 1994.
Corrected manuscript received: June 21, 1995.
Manuscript accepted: July 6, 1995.