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ADDENDUM

LIMITATIONS OF BERNARD AND MUNIER-CHALMAS SYSTEM FOR BIVALVE HINGE NOTATION

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[Modified from D. W. Boyd and N. D. Newell, 1968; prepared under NSF Grant GB-6905X]

A method of designating homologous heterodont hinge teeth was devised independently and synthesized late in the 19th century by Bernard (1895-98) and Munier-Chalmas. It is described by Cox in a previous section (p. *N*53-55) of this *Treatise* Part. Their notation has been widely recommended, but it has not been accepted universally in practice. In many cases their method of naming teeth is difficult to apply because homologies among dissimilar bivalves commonly are not demonstrable readily; the homologous teeth must be recognized and correlated before the notation can be applied properly.

According to these workers, cardinal tooth *1* is an ontogenetically modified part of anterior lateral *AI, 2* of *AII,* and so on. Both *2* and *3* commonly divide to form *2a, 2b,* and *3a, 3b,* respectively. But, if growth series are lacking, how can these teeth be identified? Furthermore, tooth *4b,* although correlated with *AIV,* is not, in our experience, accompanied by *4a,* and *5b* apparently does not have a counterpart in *5a.* Details of these ontogenetic modifications presumably were determined empirically, but they have never been well documented and need to be confirmed.

The recognition of homologies and the tracing of phylogenetic trends in bivalve teeth are complicated by the fact that nonoccluding, or incompletely occluding, ridges and furrows along the hinge plate commonly are excluded from consideration in the dental notation by most investigators. An obsolescent or poorly developed tooth ridge, or the shell margin itself, commonly is not specified in the dental formula. Indeed, many students of heterodont bivalves designate as teeth only those that are completely embraced by a socket, or furrow, of the complementary valve. In this narrow definition, a weakly or incompletely occluding ridge may not be accepted as a hinge tooth. This is not only illogical but fails to provide for the recognition of newly appearing or obsolescent teeth.

Semantic difficulties aside, it is well established that teeth of the heterodonts are "variable" and that new elements may be added and old ones lost during evolution. It has not been demonstrated, however, that these historical events are recapitulatory in ontogenies of living bivalves, as supposed by Bernard. In fact, it may be that they are rarely recapitulatory.

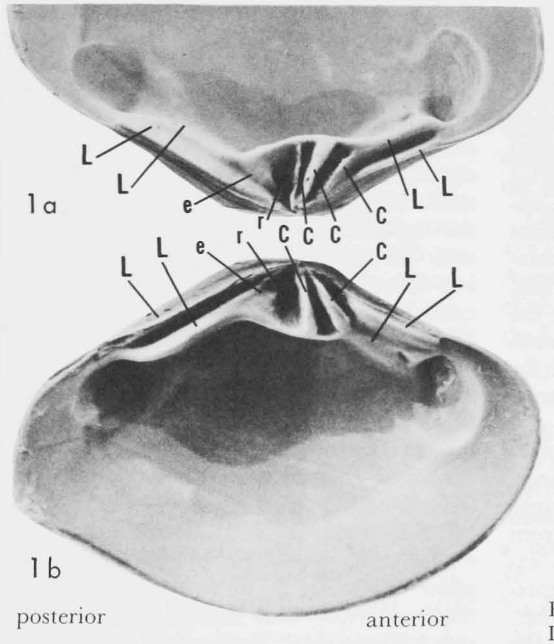
We believe the system of Bernard and Munier-Chalmas, with its stress on homologies, is misapplied commonly when used for bivalve taxa in which ontogeny and phylogeny are known poorly.

OBJECTIVE PLAN FOR HINGE ILLUSTRATION AND NOTATION

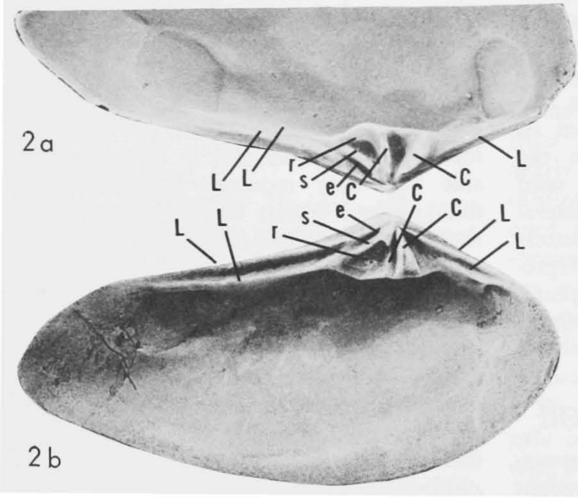
We propose a flexible, objective method of recording morphological details of the hinge teeth that can be converted readily to a modified version of the Bernard system whenever homologies are secure. The new system is equally applicable for both heterodont and nonheterodont hinges.

The conventional orientation in illustrating bivalve hinges and the arrangement of dental formulas are extremely confusing. Furthermore, the idea that dental homologies in related bivalves can be ascertained by matching hinge teeth in numerical sequence certainly is not warranted unless supported by independent evidence such as graded growth series or stratigraphic sequences.

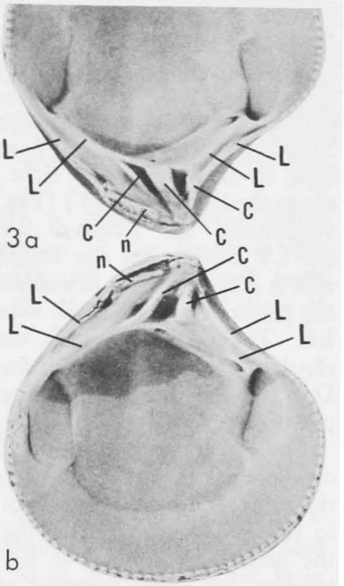
Consequently, we find merit in illustrating matched pairs of valves (Fig. BN1) in a manner that facilitates direct comparison with a simplified and objective nota-



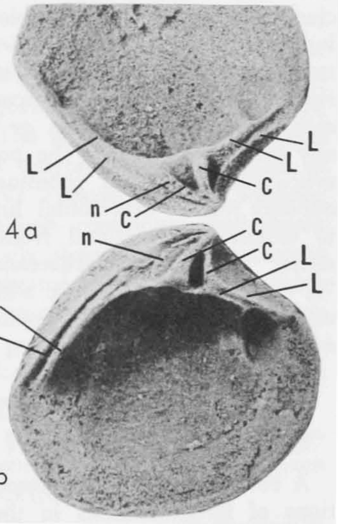
RV 1 0 (1)—e r 1 0 1 0 1———1 0 1
LV 1 0 1———e r 1 0 1 0—(1) 0 1



RV 1 0 (1)—e s r 1 0 1———1
LV 1 0 1———e s r (1) 0 1 0—(1) 0 1



RV 1 0 (1)—n 1 0 1 0 (1)———1 0 1
LV 1 0 1———n 0 1 0 1 0—(1) 0 1



RV 1 0 (1)—n (1) 0 1 0———1 0 1
LV 1 0 1———n 0 1 0 (1)—(1) 0 1

Fig. BN1. Crassatellacean hinges with notation of morphological elements and proposed formulas for them.

1. *Hybolophus speciosus* (Adams), Recent crassatellid from Florida; *1a,b,* RV and LV int., ×2, with formulas for hinges.
2. *Oriocrassatella elongata* Boyd & Newell, Permian crassatellid from Park City Formation, Wyoming; *2a,b,* RV and LV int., ×2, with formulas for hinges.
3. *Astarte castanea* Say, Recent astartid from shallow water off Atlantic Highlands, New Jersey; *3a,b,* RV and LV int., ×2, with formulas for hinges.
4. *Astartella aueri* Boyd & Newell, Permian astartid from Park City Formation, Wyoming; *4a,b,* RV and LV int., ×3, with formulas for hinges.

[Explanation: *C,* cardinal tooth; *e,* elastic-ligament area; *L,* lateral tooth; *n,* nymph; *r,* resilifer; *s,* septum; *0,* space between adjacent teeth or ridges; *1,* tooth or potential articular ridge; parentheses (), inconspicuous or doubtful tooth; horizontal line, boundary between lateral and cardinal teeth.]

tion. For use with poorly understood groups, our proposed method has the merit of being free from implications of uncertain homologies by avoiding specification of homologues during preliminary studies. The two valves of a shell are illustrated beak to beak, with the right valve (RV) above the left valve (LV) (Fig. BN1). Conventionally, the Bernard formula places the LV below, and our suggested orientation is a concession to this convention. Thus, the posterior parts of both valves lie on the left. The notation system, a modification of that of Steinmann as interpreted by Dall (1913), has been devised to be compared directly with such illustrations.

The RV hinge is expressed by the upper of two lines of symbols, and, in both lines, the symbols are arranged from left to right to reflect a traverse along the hinge from the posterior extremity to the anterior extremity. An arabic numeral one "1" represents each projection and ridge of an alternating series along the dorsal part of the shell. These alternate from one valve to the other but they do not necessarily occlude. Inconspicuous or dubious teeth are indicated between parentheses. A zero "0" represents a space between two teeth or ridges. Generally, but not invariably, these spaces function as sockets or grooves. In any case, they indicate the position of an articulating ridge or prominence on the opposite valve. Horizontal lines are used to delimit the cardinal from the lateral series. For the crassatellaceans, the letters "r," "s," "n," and "e" are added to represent the position of the resilium, septum, nymph, and elastic ligament, respectively.

CASE HISTORY: CRASSATELLACEAN HINGE

A review of past and present interpretations of hinge features in the heterodont superfamily Crassatellacea illustrates the limitations of the Bernard system of hinge notation, as well as the uncertain phyletic significance of grades of hinge complexity.

Bernard's research on the ontogeny and comparative morphology of the hinges of bivalve mollusks was cut short by his early death, and, to our knowledge, his work has not been subsequently brought under critical review. Essential documentation of his views about dental homologies among living crassatellaceans is lacking, so we are unable to confirm or deny his conclusion. However, we note that Bernard and many subsequent investigators have recognized certain peculiarities in the dentition of crassatellaceans. Some authors have placed the superfamily with the lucinoids, others with the cyrenoids. Davies (1935), following Bernard (1895) and Lamy (1917), considered the Crassatellacea Férussac, 1822 (=Astartacea d'Orbigny, 1844), to be of lucinoid derivation, superficially assuming a cyrenoid aspect as a result of evolutionary acquisition of an additional cardinal tooth in the RV.

Davies (op. cit.) segregated the Crassatellacea and Carditacea known to him from other lucinoids on the basis of their hinge characteristics and Korobkov (1954) applied the ordinal name "Astartedonta" to these bivalves. Our studies indicate, however, that this segregation undesirably would dismember the lines usually classed as Astartidae and Crassatellidae, and distribute them between two of Korobkov's orders, the Lucinodonta and the Astartedonta. Consequently, although we acknowledge the utility of "lucinoids" and "cyrenoids" as grades of hinge complexity, there is little to commend them as bases for separate taxa. It appears to us more probable that they represent iterative rather than phyletic grades of complexity. As is shown below, the characteristics of ancestral crassatellaceans do ally them with primitive lucinoids. But post-Paleozoic forms achieve a more advanced evolutionary status superficially similar to, but not quite like, the cyrenoid grade. Furthermore, the hinges of later members of the Crassatellidae and the Astartidae resemble one another more than they do those of their Paleozoic ancestors—an example, apparently, of evolutionary convergence. Thus, some doubt is cast on the integrity of the superfamily Crassatellacea as usually constituted.

CRASSATELLID DENTAL FORMULAS

In the notation suggested above, the hinge of *Hybolophus speciosus*, a living crassatellid, can be characterized as given in the two-line formulas accompanying Figure BN1,*1a,b*.

BERNARD and later students have supposed that the RV cardinals correspond to *5b, 3b,* and *3a,* and the two LV cardinals, to *4b* and *2*. We cannot find convincing documentation in the literature that this notation is firmly based on studies of ontogenetic development, or that these teeth are homologous with those of other heterodonts conventionally given the same numerals. Similarly, little agreement is found with respect to the lateral teeth. For example, DARRAGH (1965, p. 98) cited only two laterals, *AII* and *PI,* in *Eucrassatella,* although he mentioned *AI* and *PII* (*ibid.*, p. 100, 102), in comments on certain species of that genus. Authors using the BERNARD system have not specified as lateral teeth all the eight ridges indicated as such in our interpretation of *Hybolophus* (Fig. BN1,*1*). LAMY (1917, p. 200) utilized *AI, AII, AIII, PI, PII,* and *PIV*. In several diagrams he designated a strong posterior lateral between *PII* and *PIV* as *PI*. It is not clear whether he so intended, because, in the BERNARD system, the position between *PII* and *PIV* should be occupied by *PIII*. There is precedent, however, in one of BERNARD's diagrams (1895, p. 121) for the misplacement of a lateral tooth where he places *AII* above *AI*. We assume that this position was unintentional.

Recent crassatellids (indeed, all post-Paleozoic ones known to us), possess more cardinals and laterals than does the Paleozoic *Oriocrassatella* (Fig. BN1,*2*). Furthermore, the strong septum that divides the resilium from the ligament in this genus is obscure or lacking in post-Paleozoic crassatellids in which the ligament and the resilium are in contact.

In living crassatellids, as in all the astartids known to us, the anterodorsal margin of the RV overlaps that of the LV. The reverse situation exists in *Oriocrassatella.* The homologies of *Hybolophus* and *Oriocrassatella* are not at all evident and will remain uncertain until intermediate forms, if they exist, are discovered. We favor the hinge analysis of the Permian genus given with Figure BN1,*2a,b*.

ASTARTID DENTAL FORMULAS

Although astartids lack the internal ligament of crassatellids, the dentition of modern representatives of the two families is similar. We interpret the hinge of a Recent shell (*Astarte castanea*) as shown with Figure BN1,*3a,b*.

DAVIES (1935, p. 156), following BERNARD's interpretation of the hinge in the Astartidae, designated the cardinal teeth of the RV as *5b, 3b,* and *3a,* and those of the LV as *4b* and *2*.

By contrast, NICOL (1955, p. 157) interpreted the hinge in *Astarte* as cyrenoid. He designated the large central tooth on the RV as the pivotal tooth *1,* and termed the bracketing teeth of the LV *2b* and *2a.* He showed(*ibid.*, fig. 4, p. 157) on the RV a posterior cardinal which he designated *3b.* The lack of an anterior cardinal *3a* in his diagram is perplexing, because the LV (his fig. 1) shows an appropriate anterior socket.

In the present study, a survey of Cenozoic astartids in the collections of the American Museum of Natural History indicates that the shell shown in Figure BN1,*3,* is characteristic in possessing three cardinal teeth in the RV. The anterior cardinal, omitted from NICOL's diagram, is recognizable in nearly all RVs examined. The posterior cardinal, although commonly well developed, is virtually absent from three Eocene species investigated. Both of these teeth are generally small. In cases in which one is especially poorly developed, the corresponding socket is more conspicuous than the tooth.

The hinge of the Paleozoic genus *Astartella* is represented by the formulas given with Figure BN1,*4a,b*.

It appears that *Astarte* characteristically has the anterior cardinal in the RV, whereas *Astartella* has the anterior cardinal in the LV, as do members of the Myophoriidae and of the Scaphellinidae. The outer anterior lateral of the RV extends to the beak, an unusual and primitive feature in heterodonts.

INTRODUCTION OF NEW TEETH IN CRASSATELLACEAN HINGE

The lucinoid hinge grade appears at least as early as the Middle Ordovician (McAlester, 1965), whereas the cyrenoid hinge was rare or lacking before the Mesozoic. These differences in stratigraphic distribution lend support to the view of Bernard, Davies, and others that the cyrenoid hinge was derived by elaboration of the lucinoid hinge. Bernard concluded that the splitting of the pivotal (central and principal) cardinal tooth in LVs of lucinoids gave rise to two teeth separated by a new socket. The latter receives a new pivotal cardinal tooth of the RV. If this change has been a phyletic as well as an ontogenetic innovation, it may have been heralded by a broadening and bilobation of tooth *2* before actual bifurcation. Bilobation of the pivotal tooth of the LV is a characteristic feature of many late Paleozoic pelecypods (e.g., *Schizodus*) and suggests a possible pattern in a trend toward multiplication of hinge teeth.

Bernard, Davies, and others have supposed that the three cardinal teeth of living crassatellacean RVs correspond to *5b*, *3b*, and *3a*, whereas the two cardinal teeth of LVs were designated as *4b* and *2*. We have given thought to Nicol's (1955) view that the central cardinal on the RV may be cyrenoid *1*, rather than the lucinoid *3b*, and we are unable at present to resolve this problem. The Permian crassatellaceans clearly are similar to lucinoids in possessing two cardinal teeth in each valve, whereas the post-Paleozoic forms generally have a third tooth, commonly identified as *5b*, at the posterior end of the RV series. This tooth is represented in the Paleozoic in *Astartella* but not in *Oriocrassatella*. Although *Astartella* has the cardinal just cited, it has only two, not three, cardinals in the RV. The pivotal tooth of the Paleozoic forms is perceptibly bifid in *Oriocrassatella*. The evolutionary bifurcation of this tooth and the appearance of a new pivotal tooth, *1*, in the opposite valve conceivably could result in hinge development very similar to that which characterizes living crassatellaceans.

According to this interpretation, the crassatellaceans would consist of Paleozoic lucinoids, and post-Paleozoic forms of cyrenoid aspect lacking one tooth typical of the cyrenoid dentition. This suggestion is perhaps more attractive for the crassatellids than for the astartids, because the pivotal tooth in *Astartella* is not bifid.

In any case, the two families require a manipulation of different teeth, in order to derive for both a cyrenoid post-Paleozoic hinge from a Paleozoic lucinoid ancestor. The cyrenoid pivotal tooth would originate within the posterior cardinal socket of the RV in astartids but in the anterior cardinal socket in crassatellids. The two cardinal teeth of the astartid RV would then change numbers in transition from Paleozoic to post-Paleozoic (*5b* to *3b*, and *3b* to *3a*), whereas the enumeration of crassatellid cardinal teeth of the RV (*3a* and *3b*) would remain constant. Finally, the two teeth of the LV would originate from a splitting of the posterior cardinal (*4b*) of *Astartella*, but from the anterior cardinal (*2*) in *Oriocrassatella*.

Even for crassatellids, the preceding idea is suspect, because both Paleozoic and post-Paleozoic LVs have only two cardinals. The hypothesis recognizes an evolutionary trend toward an increase in the number of cardinal teeth and suggests that a shift in hinge symmetry is accomplished by a splitting of the Paleozoic pivotal tooth of the LV to accommodate a new pivotal tooth in the RV. However, this interpretation requires the disappearance of a pre-existing tooth, the LV posterior cardinal. In the interest of simplicity, it appears more likely that steps in the development of the cyrenoid hinge involved only the appearance of new teeth, rather than contemporaneous appearance and disappearance. In our present state of knowledge, it is more reasonable to suppose that the two cardinals of the LV in *Oriocrassatella* are homologous with those in modern crassatellids, than that the posterior one has disappeared while the anterior one evolved into two. Likewise, although it is possible that the two teeth of Paleozoic RVs are homologous with the anterior and posterior elements of the three-toothed post-Paleozoic RVs, it seems more likely that they are homologous with the anterior and central ones, leaving the posterior rather than the middle one as a post-Paleozoic innovation.

This alternative invites speculation that the posterior tooth in question, commonly designated as *5b,* developed as a wall related to the posterior margin of the resilifer. The border of the resilium in *Oriocrassatella* is reflected in a few valves by an obscure shelf along the anterior margin of the resilifer. This shelf occupies a position analogous to that of the posterior cardinal in post-Paleozoic specimens. Cardinal *5b* in living species is more variable in size and orientation than the other cardinals, and the LV lacks a corresponding socket in some species.

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INDEX

Italicized names in the following index are considered to be invalid; those printed in roman type, including morphological terms, are accepted as valid. Suprafamilial names are distinguished by the use of full capitals and author's names are set in small capitals with an initial large capital. Page references having chief importance are in boldface type (as **N327**). Some divergences in classification reflect differences of authors concerning validity of nomenclature.