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Hinge Grades in the Evolution of Crassatellacean Bivalves as Revealed by Permian Genera

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ABSTRACT

The origin and affiliation of the conservative bivalve superfamily Crassatellacea Férussac, 1822 (=Astartacea d'Orbigny, 1844), have been uncertain. Some authors have regarded these mollusks as lucinoids. Others have placed them with the cyrenoids, or in a separate order of the Heterodonta, the "Astarte-donta."

Our discovery of numerous exceptionally well-preserved examples of the Crassatellacea of Permian age in Wyoming clarifies some problems of the early history of the group, showing how, by the acquisition of additional hinge teeth after Permian time, the hinge of living crassatellaceans became modified in separate lines from basically lucinoid to a more advanced hinge grade.

Representatives of post-Paleozoic Crassatellidae and Astartidae through convergent evolution resemble one another more closely than do their Paleozoic ancestors, the new subfamilies Oriocrassatellinae and Astartellinae. Members of these Paleozoic subfamilies are sufficiently dissimilar to suggest a diphyletic origin for the Crassatellacea.

The Bernard and Munier-Chalmas hinge formula and its implication of dental homologies are discussed, and a simplified, more objective hinge notation based on the Steinmann system is employed.

Two new species, *Oriocrassatella elongata* and *Astartella aueri*, are described.

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Examples of hinge transposition of cardinal and anterior lateral teeth, but not the posterior laterals, are recorded in both. This partial transposition of hinge teeth, recorded for the first time in Paleozoic bivalves, indicates that the posterior laterals are genetically independent of the other hinge teeth.

INTRODUCTION

A systematic search for Permian bivalves in the Rocky Mountains of the United States has extended over many decades. Following a discovery by Carl C. Branson (1930) of a diversified but poorly preserved pelecypod assemblage in the Park City (Phosphoria) Formation at Bull Lake, in the Wind River Mountains of Wyoming, one of the present authors (Newell) made several exploratory trips to that area in search of more satisfactory specimens of what appeared to be an unusually varied assemblage. His interest in this subject stimulated some of his students, notably A. G. Fischer and K. W. Ciriacks, to make additional exploration for well-preserved representatives of the Bivalvia in western Wyoming. Their work was rewarded by only limited success.

Ciriacks did, however, have access to extensive collections obtained during a large program of field research by the United States Geological Survey. Those collections were disappointing because of the imperfect preservation and the scarcity of instructive individuals showing critical morphological details. Ciriacks' (1963) outstanding research and publication on the available collections of Permian pelecypods from Wyoming and Idaho provided a tantalizing glimpse of a distinctive and varied fauna. Furthermore, he showed that the Park City sequence in the Wind River Mountains is mainly of early Guadalupian age, that is, more or less equivalent to the Word, Brushy Canyon, and Cherry Canyon formations of western Texas pertaining to the zone of advanced species of *Parafusulina*.

More recently, Benjamin Weichman, while a graduate student at the University of Wyoming, discovered exceptionally well-preserved silicified bivalves of limited diversity in the lower member of the Park City Formation along Beaver Creek Canyon, in the southeastern part of the Wind River Mountains. Boyd and Newell undertook extensive sampling from this locality, processing the fossils at the University of Wyoming and at the American Museum of Natural History. The resulting collection of bivalves, now divided between the University of Wyoming at Laramie, and the American Museum of Natural History, Department of Fossil Invertebrates, is the most remarkable thus far obtained from Permian rocks in the Rocky Mountains.

The present paper is the first of several contributions undertaken

jointly by us on the systematics of Permian bivalves. Faunal and ecological summaries necessarily must be deferred until the basic taxonomic-phylogenetic studies are well advanced.

The abbreviations used in this paper for various institutions are:

A.M.N.H., the American Museum of Natural History, specimens catalogued in the Department of Fossil Invertebrates

A.M.N.H.:F.I., used without the abbreviation "No." means a fossil locality, recorded by the Department of Fossil Invertebrates, the American Museum of Natural History

A.M.N.H.:L.I., the American Museum of Natural History, specimens catalogued in the Department of Living Invertebrates

U.I., the University of Indiana, Bloomington

U.W., the University of Wyoming, Laramie

ACKNOWLEDGMENTS

Mr. Benjamin Weichman, who discovered the fossil locality (A.M.N.H.: F.I. 2010) that has yielded our extraordinary collection, communicated his find to Boyd. Mr. and Mrs. John Auer, on whose ranch the discovery was made, have shown great interest in our work and have encouraged us in many ways. Dr. Heinrich Toots, then a graduate student at the University of Wyoming, aided in the arduous labor of collecting the samples, and Mr. G. Robert Adlington of the American Museum of Natural History prepared the outstanding photographs reproduced herein. Mrs. Margaret Boyd undertook the sorting of specimens and the compiling of biometrical data. Mr. and Mrs. Dan Steger of Tampa, Florida, and Mr. Thomas L. McGinty of Boynton Beach, Florida, contributed juvenile specimens of *Hybolophus speciosus* (Adams), a common living Caribbean crassatellid, for comparison with the Permian specimens of *Oriocrassatella*, and Dr. A. S. Horowitz, of the University of Indiana at Bloomington, lent us specimens of *Cypricardella subelliptica* Hall. To all these persons we extend our thanks. The studies of Australian and Kashmirian examples of *Procrassatella* by Newell were made possible by a grant from the National Science Foundation (Grant B-15567) to the American Museum of Natural History.

THE BEAVER CREEK MATERIAL

The Beaver Creek collection was obtained from a limestone ledge 64 feet above the Tensleep Sandstone in the northeast quarter of sect. 15, T. 30 N., R. 97 W. Approximately 2 tons of limestone was leached in muriatic acid, yielding predominantly bivalves and very few representatives of other groups (brachiopods, echinoderms, trilobites, bryo-

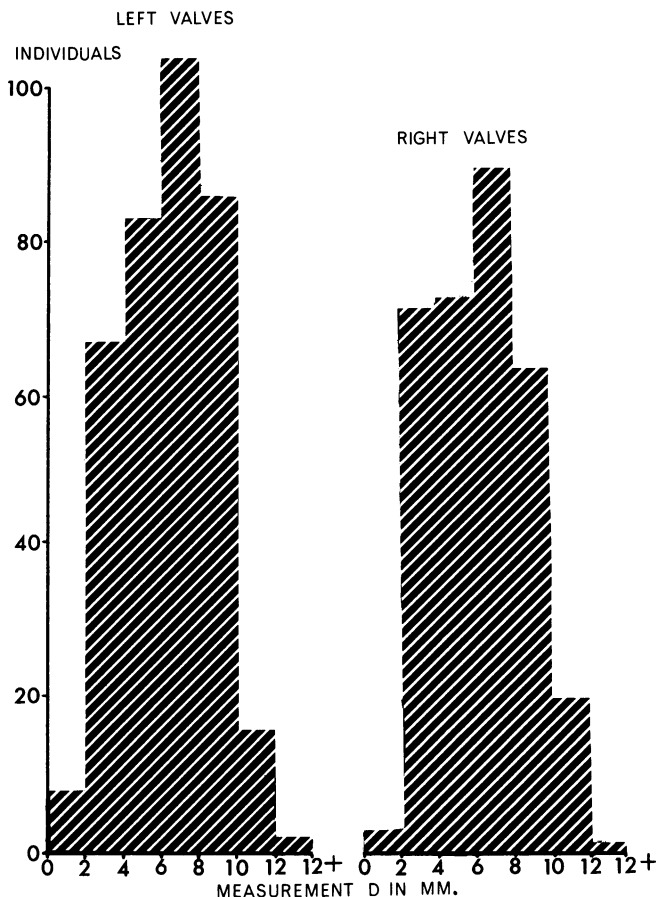


FIG. 1. Frequency histogram of length of cardinal armature, D, based on more than 700 specimens of *Oriocrassatella elongata*, new species, showing closely similar distribution of the two valves, with a suggestion of several age classes. Evidently there was very little postmortem sorting of the shells. See also figure 18 for the precise usage of variate D.

zoans, gastropods, nautiloids, and scaphopods). This assemblage suggests that the bivalve fauna lived under ecological conditions that were incompatible with the dominantly brachiopod-bryozoan association so characteristic of the Phosphoria-Park City formations in western Wyoming. Because these fossils were collected near the eastward transition from carbonate rocks to redbeds and gypsum (Maughan, 1964), it can

be assumed that deposition was at shallow depth near shore and that the waters may have been hypersaline or variable in salinity. Because right and left valves of the pelecypod species occur in approximately equal numbers and in various stages of growth (fig. 1), it is concluded that there was comparatively little sorting or movement of the material after death.

The Beaver Creek locality has provided thousands of silicified specimens of several pelecypod species. Unbroken valves are rare, but complete hinge plates are common. Of the several new pelecypod species in the collection, noteworthy are the crassatellaceans described herein.

It is generally agreed that the superfamily Crassatellacea of the subclass Heterodonta embraces two families, the Crassatellidae and the Astartidae. The pre-Cretaceous record of the Crassatellidae is very poor. Crassatellids reported in Permian strata of the Americas include only a single external mold from Greenland (Newell, 1955), two fragmental specimens from Wyoming (Ciriacks, 1963), and a few unpublished specimens from the Permo-Carboniferous of southern Brazil. Knowledge of Permian crassatellids has been based largely on Australian (e.g., Etheridge, 1907; Dickins, 1956; Newell, 1958) and Russian (Yakovlev, 1928) examples preserved as molds. The rarity of well-preserved specimens in the past has prevented a confident interpretation of hinge morphology. By contrast, we have assembled and studied more than 700 hinges of the new crassatellid species, from the Beaver Creek locality, a collection some 10 times greater than all the Permian specimens thus far reported over the world. The excellent Wyoming material thus has revealed certain fundamental differences between crassatellids of the Paleozoic and those of the post-Paleozoic.

The family Astartidae is represented in the Beaver Creek collections by a new species closely related to *Astartella subquadrata* Girty, a frequent component of Permian collections from the southwestern United States. Our silicified material has provided 268 specimens retaining the hinge. These reveal certain intriguing contrasts between astartid and crassatellid hinge patterns, and, as with the crassatellids, we find basic differences between Paleozoic and post-Paleozoic astartids.

The incentive for a detailed analysis of the hinge provided by our crassatellaceans has led us to review the conventional heterodont hinge notation. The current status of heterodont hinge analysis appears to be one of confusion and inconsistency. The following brief discussion of the heterodont hinge was deemed necessary, therefore, before the particular problem of crassatellacean dentition was discussed.

THE HETERODONT PELECYPOD HINGE

HETERODONT HINGE FORMULA OF BERNARD AND MUNIER-CHALMAS

A method of designating homologous bivalve hinge teeth was devised independently and synthesized late in the nineteenth century by Bernard and Munier-Chalmas. Their notation has been widely recommended, but it has not been universally adopted in practice. In many cases their method of naming teeth is difficult to apply because homologies among dissimilar bivalves commonly are not readily demonstrable; the homologous teeth must be recognized and correlated before the notation can be applied.

According to the original plan of Bernard and Munier-Chalmas (Bernard, 1895, 1896a, 1896b, 1897, 1898), cardinal teeth were assigned Arabic numbers and lateral teeth were given Roman numerals. These categories were numbered from a median position outward (cardinals) and from a ventral position upward (laterals). Growth studies of the hinges of various living species indicated to those investigators that a few primary lamellae along the anterodorsal margin became differentiated during growth into anterior laterals and cardinals in a characteristic manner. Bernard and Munier-Chalmas were not successful, however, in correlating anterior and posterior lateral teeth, and they were necessarily vague about the treatment of the posterior laterals.

Cardinal tooth 1 is a 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. On the other hand, 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 empirically determined, but they have never been well documented and need to be confirmed.

The notation of Bernard and Munier-Chalmas for cardinal teeth of the cyrenoid hinge grade

$$\begin{array}{l} \text{RV } 3a \text{ -- } 1 \text{ -- } 3b \\ \text{LV } \quad 2a \text{ -- } 2b \text{ -- } 4b \end{array}$$

specified three cardinals in each valve, whereas lucinoids characteristically possess only two

$$\begin{array}{l} \text{RV } 3a \text{ -- } 3b \\ \text{LV } \quad 2 \text{ -- } 4b \end{array}$$

But, if growth series are lacking, how can these teeth be identified?

Casey (1952, p. 123) has shown that a bifid, or chevron-shaped, tooth 2 may be produced in more than one way and that the limbs of the

chevron should be given a notation that reflects the origins of the resulting teeth. Such complications suggest that the system of Bernard and Munier-Chalmas, with its stress on homologies, may be misapplied when used for bivalve taxa in which ontogeny and phylogeny are poorly known.

The recognition of homologies and the tracing of phylogenetic trends in bivalve teeth are complicated by the fact that non-occluding, 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.

SIMPLIFIED PLAN FOR HINGE ILLUSTRATION AND NOTATION

In the present study, an effort is made to find a flexible, objective method of recording the morphological details of the hinge teeth that can be readily converted to a modified version of the Bernard system whenever homologies are secure.

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 (figs. 2A, B, 3B, C, 6A, 10B, D) in a manner that facilitates direct comparison with a simplified and objective notation. For use with poorly understood groups, our proposed method has the merit of being free from implications of uncertain homologies by the avoidance of speci-

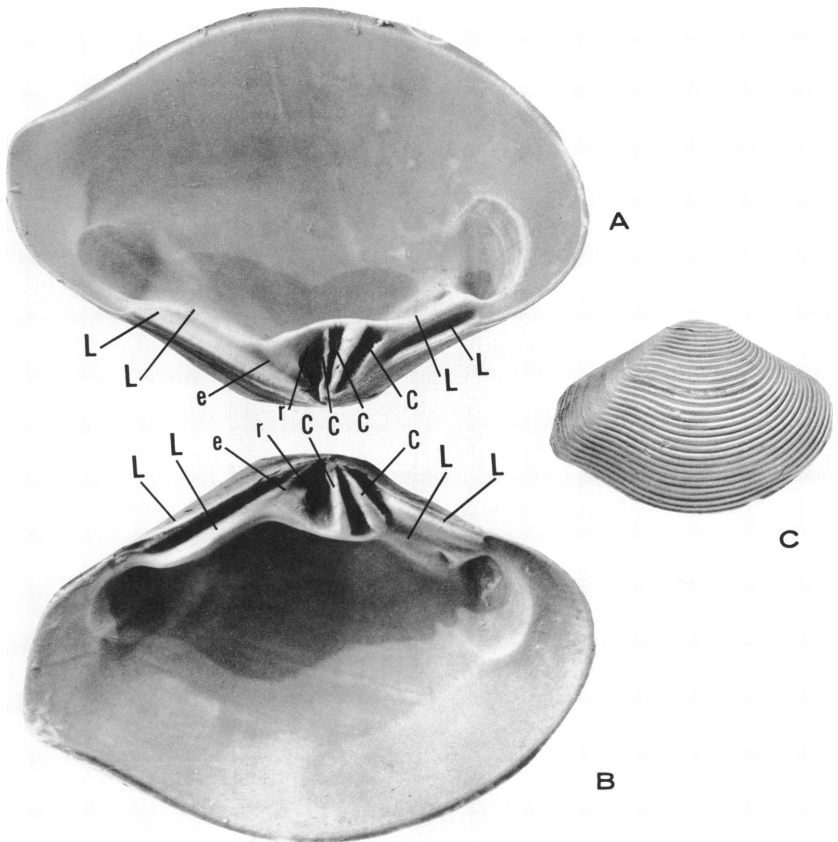


FIG. 2. *Hybolophus speciosus* (Adams), A.M.N.H. No. 28472, recent, dredged by T. L. McGinty at 20 fathoms, Gulf of Mexico, near Destin, Florida. Compare with *Oriocrassatella elongata*, new species (fig. 3B, C). A. Right valve. B. Left valve. Both $\times 2$. C. Right valve. $\times 1$.

Abbreviations: C, cardinals; e, elastic-ligament area; L, laterals; r, resilifer.

fication of homologues during preliminary studies. The two valves of a shell are illustrated beak to beak, with the right valve above the left valve (fig. 2A-C). Conventionally, the Bernard formula places the left valve 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 simplification of that of Steinmann as interpreted by Dall (1913), has been devised to be directly compared with such illustrations.

The right-valve hinge is expressed by the upper of two lines of sym-

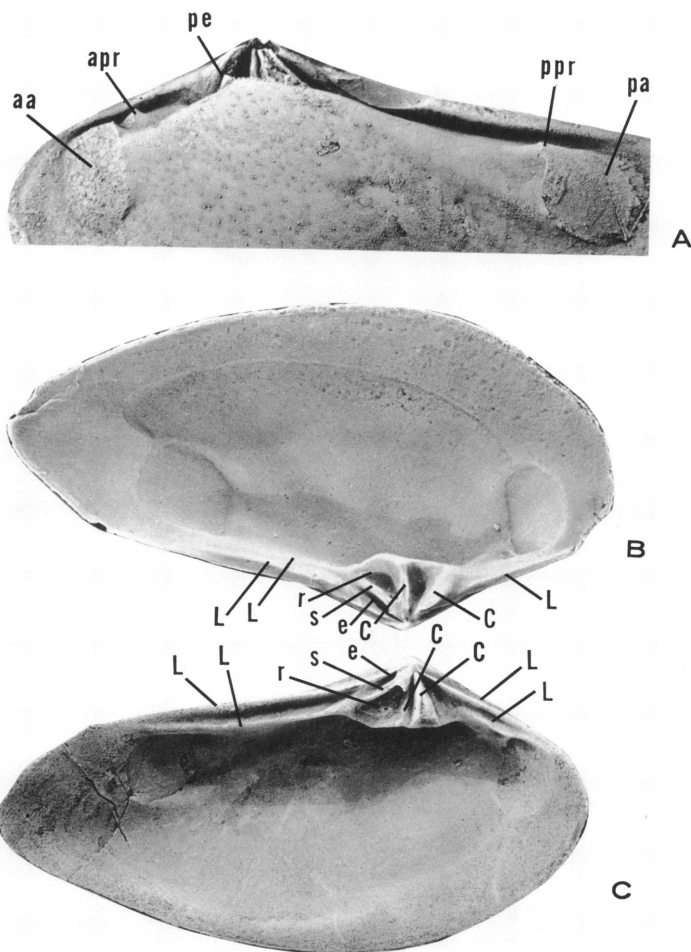


FIG. 3. *Oriocrassatella elongata*, new species, from A.M.N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. A. Latex impression of interior of left valve, the holotype, A.M.N.H. No. 28473, showing position of muscle insertions. We interpret numerous papilli over the umbonal region as borings of parasites. $\times 1.5$. B. Right valve, A.M.N.H. No. 28475. $\times 2$. C. Left valve, the holotype, A.M.N.H. No. 28473. $\times 1.5$.

Abbreviations: aa, anterior adductor; apr, anterior pedal retractor; C, cardinals; e, external ligament groove; L, laterals; pa, posterior adductor; pe, pedal elevator; ppr, posterior pedal retractor; r, resilifer; s, septum.

bols, 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. The arabic numeral (1) represents teeth or potentially articular ridges. 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. Vertical lines, discontinuous in case of doubt, 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, the septum, the nymph, and the elastic ligament, respectively.

THE CRASSATELLACEAN HINGE

CHARACTERISTICS OF THE HINGE

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 conclusions. 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 right valve.

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 would undesirably 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, indeed, 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 (see fig. 2), can be characterized as follows:

$$\begin{array}{rcccl} \text{Posterior RV} & 1 & 0 & (1) & | & e & r & 1 & 0 & 1 & 0 & 1 & | & 1 & 0 & 1 & \text{anterior} \\ & \text{LV} & 1 & 0 & 1 & & | & e & r & & 1 & 0 & 1 & 0 & & (1) & 0 & 1 \end{array}$$

Bernard and later students have supposed that the right-valve cardinals correspond to 5b, 3b, and 3a, and the two left-valve 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. Rearranged to correspond with the above scheme, the Bernard notation reads

$$\begin{array}{rcccl} \text{RV} & \text{PIII} & \text{---} & (\text{PI}) & | & e & r & 5b & \text{--} & 3b & \text{--} & 3a & | & \text{AIII} & \text{---} & \text{AV} \\ \text{LV} & \text{PIV} & \text{----} & \text{PII} & & | & e & r & \text{--} & 4b & \text{--} & 2 & \text{--} & | & (\text{AII}) & \text{----} & \text{AIV} \end{array}$$

There has been little agreement, however, about the lateral teeth. For example, Darragh (1956a, p. 98) cited only two laterals, AII and PI, in *Eucrassatella*, although he mentioned AI and PII (*ibid.*, pp. 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* (above). 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 the post-Paleozoic crassatellids known to us) possess more cardinals and laterals than does the Paleozoic *Oriocrassatella* (fig. 4). Furthermore, the strong septum that divides the resilium from the ligament in *Oriocrassatella* 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 antero-

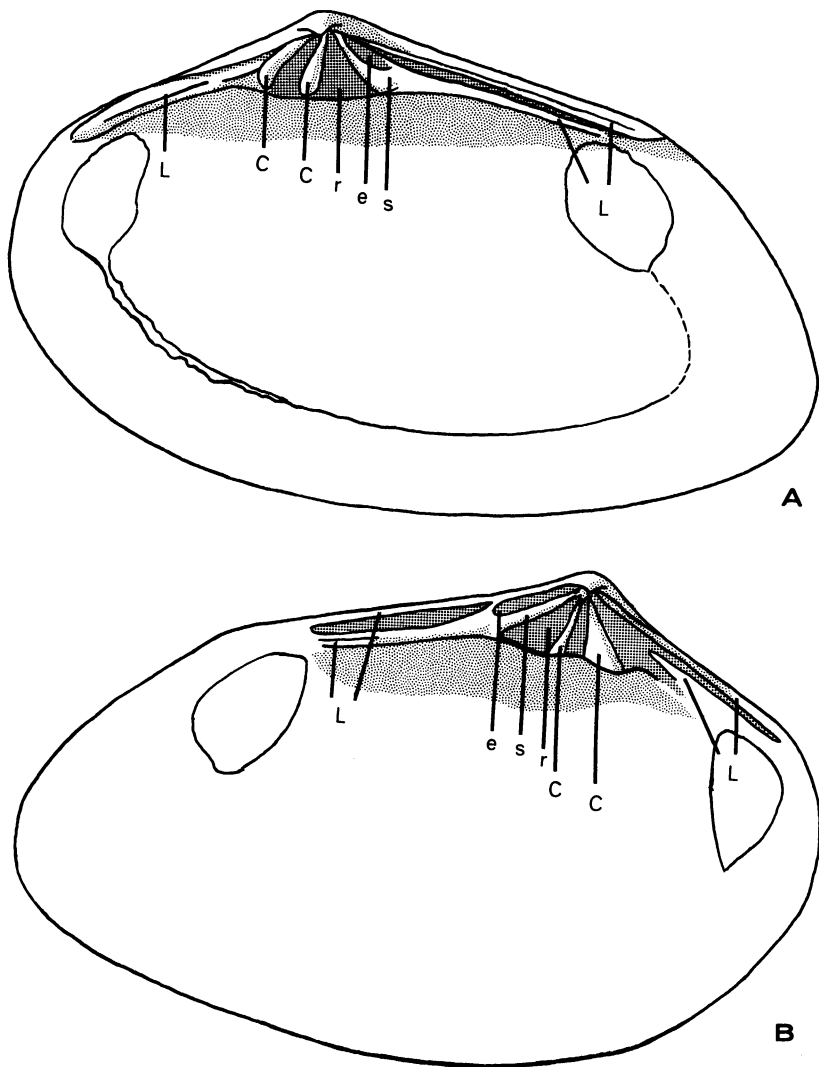


FIG. 4. Hinge features of *Oriocrassatella*. A. Right valve. B. Left valve.

Abbreviations: C, cardinal tooth; e, position of elastic ligament; L, lateral tooth; r, resilifer; s, septum.

dorsal margin of the right valves overlaps that of the left. 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.

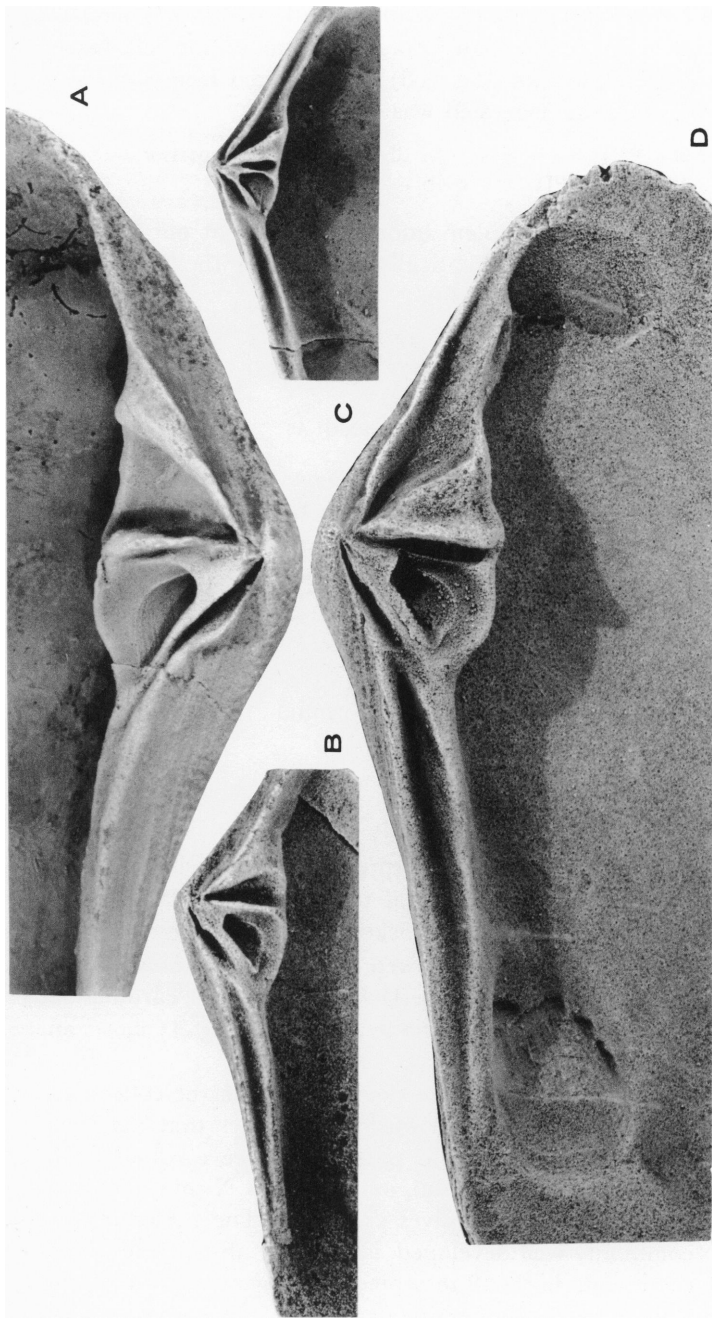


FIG. 5. *Oriocrassatella elongata*, new species, from A.M.N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. A. Right valve, A.M.N.H. No. 28484. Note resilial deck and small attachment area of the resilium, as indicated by growth lines; small vertical furrow in front of resilifer is socket for 4b of opposite valve. B. Left valve, with transposed anterior lateral and cardinal teeth, A.M.N.H. No. 28474. C. Normal left valve, A.M.N.H. No. 28477. D. Relatively large left valve, A.M.N.H. No. 28516. All $\times 3$.

In Newell's 1958 interpretation of the hinge of the tooth of *Oriocrassatella*, AII was taken to be the anterodorsal margin of the left valve; lateral AI and cardinal 3a (not observed) were inferred from sockets of the left valve. The formula suggested was

$$\begin{array}{rcll} \text{Posterior RV PIII} & \text{---} & \text{e s r} & 3b - 3a \text{ AI} & \text{anterior} \\ \text{LV} & \text{----} & \text{PII} & \text{e s r 4b -- 2 --} & \text{AII} \end{array}$$

In the light of the more complete information now at our disposal, we favor the following as diagrammatically representing the hinge structure of the Permian genus (fig. 5A, D):

$$\begin{array}{rcll} \text{Posterior RV} & 1 \ 0 \ (1) & \left| \begin{array}{l} \text{e s r} \quad 1 \ 0 \ 1 \\ \text{e s r} \ (1) \ 0 \ 1 \ 0 \end{array} \right| & \begin{array}{l} 1 \\ (1) \ 0 \ 1 \end{array} \text{ anterior} \\ \text{LV} & 1 \ 0 \ 1 & & \end{array}$$

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*; see fig. 6A) as

$$\begin{array}{rcll} \text{Posterior RV} & 1 \ 0 \ (1) & \left| \begin{array}{l} \text{n} \ 1 \ 0 \ 1 \ 0 \ (1) \\ \text{n} \ 0 \ 1 \ 0 \ 1 \ 0 \end{array} \right| & \begin{array}{l} 1 \ 0 \ 1 \\ (1) \ 0 \ 1 \end{array} \text{ anterior} \\ \text{LV} & 1 \ 0 \ 1 & & \end{array}$$

Davies (1935, p. 156), following Bernard's interpretation of the hinge in the Astartidae, derived the following formula, reversed here for convenience

$$\begin{array}{rcll} \text{Posterior RV PIII} & \text{---} & 5b \text{ -- } 3b - 3a \text{ AI} & \text{anterior} \\ \text{LV} & \text{----} & \text{PII -- 4b -- 2 --} & \text{AII} \end{array}$$

By contrast, Nicol (1955, p. 157) interpreted the hinge in *Astarte* as cyrenoid. He designated the large central tooth on the right valve as the pivotal tooth 1, and termed the bracketing teeth of the left valve 2b and 2a. He (*ibid.*, fig. 4, p. 157) showed a posterior cardinal on the right valve which he designated 3b. The lack of an anterior cardinal 3a in his diagram is perplexing, because the left valve (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 6A is characteristic in possessing three cardinal teeth in the right valve. The anterior cardinal, omitted from Nicol's diagram, is recognizable in nearly all right valves examined. The posterior cardinal, although commonly well developed, is virtually absent from three Eocene species examined. 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

$$\begin{array}{rcccl} \text{Posterior RV} & 1 & 0 & (1) & \left| \begin{array}{cccc} n & (1) & 0 & 1 & 0 \end{array} \right| \begin{array}{ccc} 1 & 0 & 1 \end{array} \text{ anterior} \\ & \text{LV} & 1 & 0 & 1 & \left| \begin{array}{cccc} n & 0 & 1 & 0 & (1) \end{array} \right| & (1) & 0 & 1 \end{array}$$

If this is interpreted as lucinoid, workers using Bernard's notation might express the cardinal arrangement as

$$\begin{array}{rcccl} \text{Posterior RV} & (5b) & \text{---} & 3b & \text{---} & \text{anterior} \\ & \text{LV} & \text{----} & 4b & \text{---} & (2) \end{array}$$

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

INTRODUCTION OF NEW TEETH IN THE 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 left valves of lucinoids gave rise to two teeth separated by a new socket. The latter receives a new pivotal cardinal tooth of the right valve. 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 left valve 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 right valves correspond to 5b, 3b, and 3a, whereas the two cardinal teeth of left valves were designated as 4b and 2. We have given thought to Nicol's (1955) view that the central cardinal on the right valve may be cyrenoid 1 rather than the lucinoid 3b, and we are unable, at this time, to resolve this problem. The Permian crassatellaceans here under consideration 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 right-valve series. This tooth is repre-

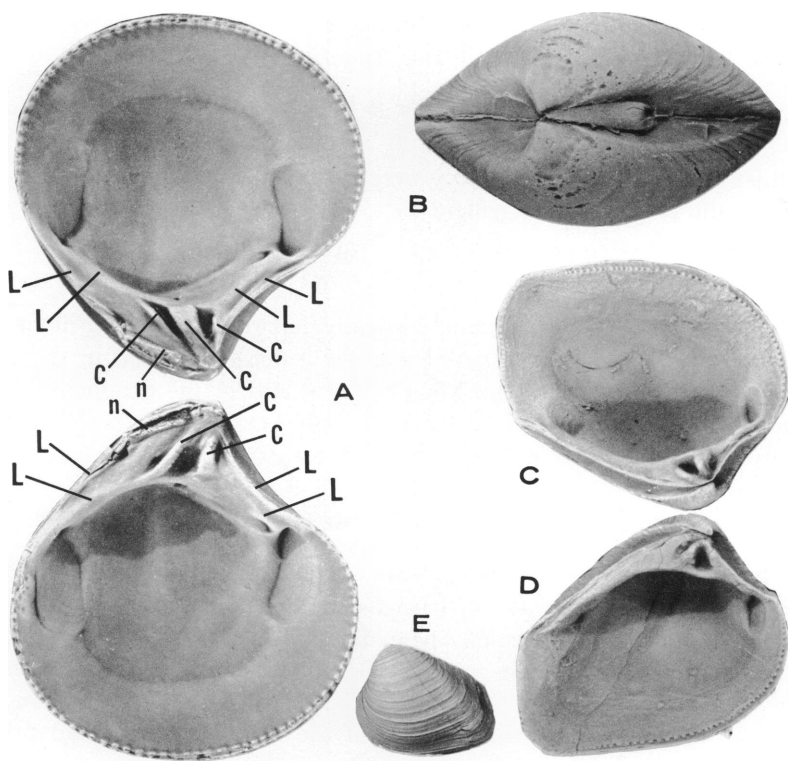


FIG. 6. A, B. *Astarte castanea* Say, A.M.N.H.:L.I. Nos. 29370a, 29370b, 29370c, shallow waters near Atlantic Highlands, New Jersey. Note crenulate cardinal teeth and inner margin and well-developed socket in left valve for 3a. $\times 2$. C-E. *Astartella vera* Hall, A.M.N.H. No. 28506, from A.M.N.H.:F.I. 18, Graford Shale, Pennsylvanian, near Martin's Lake, Bridgeport, Texas. C, D. $\times 2$. E. $\times 1$.

Abbreviations: C, cardinals; L, laterals; n, nymph.

sented 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 right valve. The pivotal tooth of the Paleozoic forms is perceptibly bifid in the genus *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 right valve in astartids but in the anterior cardinal socket in crassatellids. The two primary astartid teeth of the right valve 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 right valve (3a and 3b) would remain constant. Finally, the two teeth of the left valve 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 hypothesis is suspect, because both Paleozoic and post-Paleozoic left valves have only two cardinals. It 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 left valve to accommodate a new pivotal tooth in the right valve. However, this interpretation requires the disappearance of a pre-existing tooth, the left posterior cardinal. In the interest of simplicity, it would appear 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 left valve 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 right valves are homologous with the anterior and posterior elements of the three-toothed post-Paleozoic right valves, it appears 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. The preferred latter (but not necessarily correct) solution might be as follows in the Bernardian notation:

RIGHT VALVES

<i>Hybolophus</i>	PIII - (PI) e r	5b ---- 3b - 3a	AIII - AV
<i>Oriocrassatella</i>	PIII - (PI) e s r	---- 3b - 3a	AIII

LEFT VALVES

<i>Hybolophus</i>	PIV - PII e r	-- 4b -- 2 --	(AII) - AIV
<i>Oriocrassatella</i>	PIV - PII e s r	-- (4b) -- 2 --	(AII) - AIV

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 (fig. 5A). 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 left valves lack a corresponding socket in some species.

HINGE TRANSPOSITION IN *Oriocrassatella* AND *Astartella*

The phenomenon of hinge transposition involves an exchange of part or all of the dental elements by the two valves of a pelecypod shell. Thus teeth normally found in a left valve are found in the right, and so forth. Popenoe and Findlay (1933) have discussed the situation and have cited numerous examples.

The present study is the second in which transposed dentition has been recognized in Paleozoic pelecypods, and the first in which partial transposition has been recorded in Paleozoic material. Newell (1939) reported the correlated transposition of cardinals and posterior laterals in some imperfect valves of *Pleurophorus albequius* Beede from the Texas Permian. He noted that in other reported instances of transposition, all involving Tertiary and Recent heterodonts, the cardinals and anterior laterals are transposed independently of the posterior laterals. That is, in cases in which the posterior laterals were transposed, the other teeth were unchanged, and vice versa. He cited a previous suggestion (Popenoe and Findlay, 1933) that such incomplete transposition would be understandable in view of Bernard's observation that the heterodont cardinal and anterior lateral teeth develop from the same lamellae, whereas the posterior laterals develop from different lamellae. Presumably, the posterior laterals are governed by a separate genetic field from that of the other hinge teeth. Our present collections support such a hypothesis.

Three left valves of more than 700 specimens of *Oriocrassatella elongata* of Permian age from Beaver Creek, Wyoming, are abnormal in possessing a partially transposed dentition. They exhibit the two cardinal teeth and an anterior lateral tooth typical of right valves. The resilifer, septum, ligament furrow, and posterior lateral teeth and socket are identical with those of other left valves of the species (fig. 5B, C). Weaver (1963) reported the same type of transposition, affecting cardinals and anterior margin, in a left valve of *Crassatella collina* from the undifferentiated Sacate-Gaviota Formation of the California Tertiary.

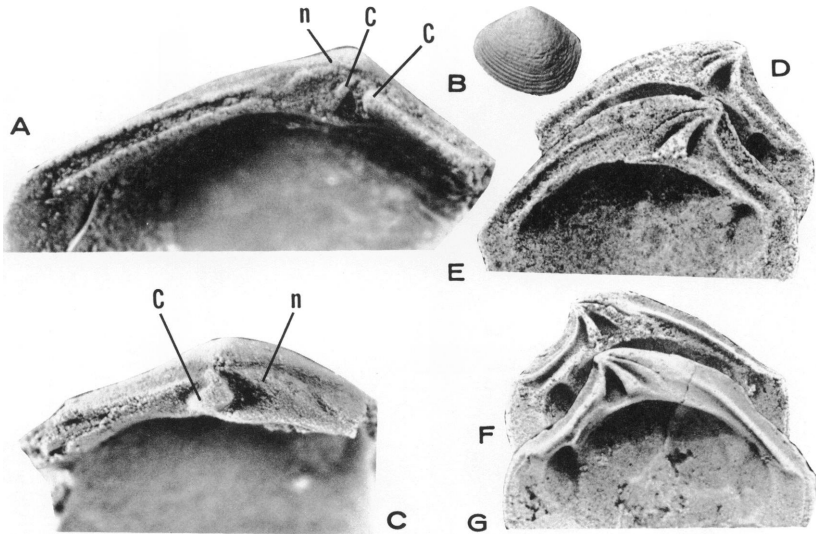


FIG. 7. A-C. *Cypricardella subelliptica* Hall, type species of *Cypricardella* Hall, Salem Limestone, Mississippian, Indiana; shown for comparison with *Astartella* Hall. A. Left valve, U.I. No. 8130, Salem Limestone, Mississippian, Cleveland Quarry, sect. 20, T. 7 N., R. 1 W., Monroe County, Indiana. $\times 20$. B. Left valve, A.M.N.H. No. 7641:1, one of Hall's syntypes, Salem Limestone at Spergen Hill, Indiana, showing close external similarity to *Astartella*. $\times 2$. C. Right valve. A.M.N.H. No. 7641:2, one of Hall's syntypes, Salem Limestone at Sperges Hill, Indiana. $\times 10$. D-G. *Astartella aueri*, new species, from A.M.-N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming, illustrating transposition of hinge teeth. D. Normal left valve, A.M.N.H. No. 28504. $\times 3$. E. Transposed left valve, A.M.N.H. No. 28509. $\times 3$. F. Normal right valve, A.M.N.H. No. 28497. $\times 4$. G. Transposed right valve, A.M.N.H. No. 28508. $\times 4$.

Abbreviations: C, cardinal teeth; n, nymph.

Darragh (1965b) observed the same phenomenon in two valves in a collection of 540 *Eucrassatella* specimens from the Tertiary of south-eastern Australia.

The Beaver Creek collection of *Astartella aueri* includes three valves with the same type of partial transposition described above. In one mature left valve, the anterior lateral teeth, anterior socket, and presumably the large cardinal tooth are those of a right valve, whereas the posterior lateral teeth are normal for a left valve (fig. 7D, E). In two right valves, the anterior laterals, anterior cardinal tooth, large socket, and large cardinal are those of a left valve, whereas the posterior hinge area is normal for a right valve (fig. 7F, G). The three astartid

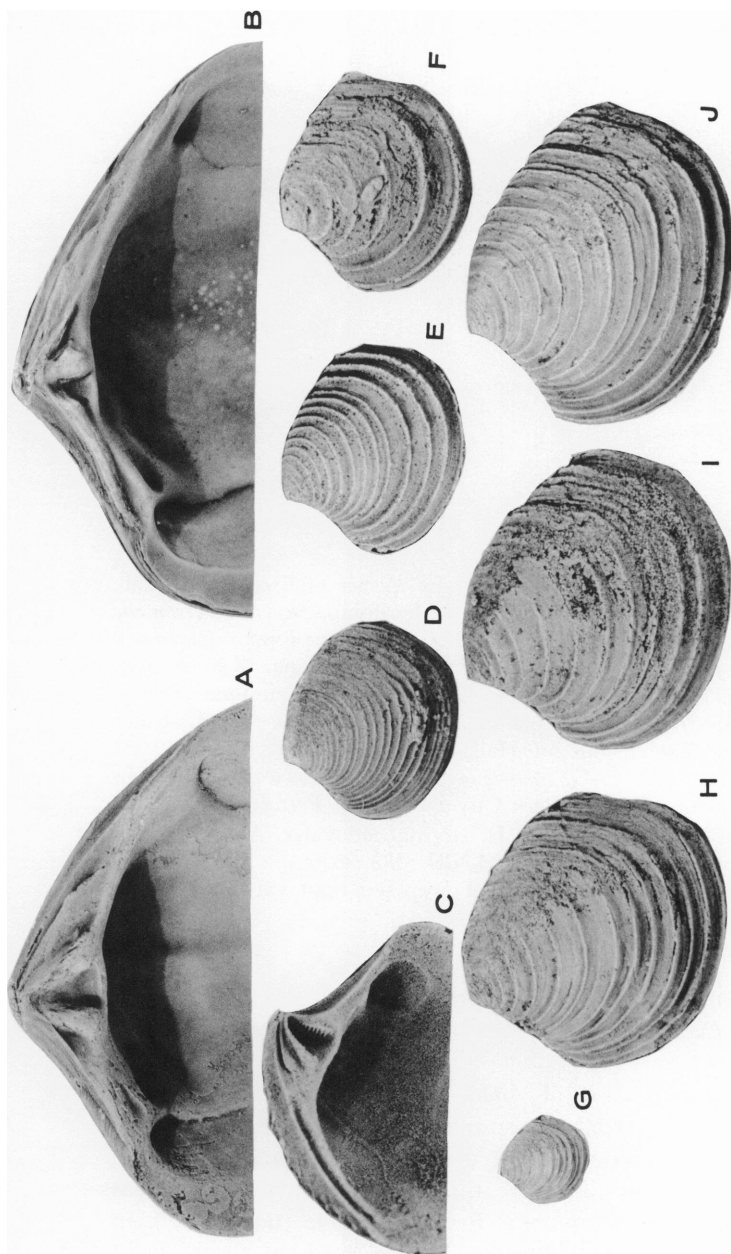


FIG. 8. A, B. *Astarte lens* Stimpson, Pleistocene, Woodford Corners, Deering, Maine. A. Right valve, A.M.N.H. No. 12602.1/1, showing transposed dentition. B. Normal right valve, A.M.N.H. No. 12602.1/2, showing normal dentition. Both $\times 2$. C-J. *Astartella ateri*, new species, from A.M.N.H.F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. C. Left valve, A.M.N.H. No. 28507, showing crenulated socket; note socket for 5b just below nymph. $\times 5$. D-F. A series of left valves, showing variation in spacing of concentric fila. D. A.M.N.H. No. 28510. E. A.M.N.H. No. 28511. F. A.M.N.H. No. 28512. All $\times 3$. G, H. A.M.N.H. No. 28513. G. $\times 1$. H. $\times 3$. I. A.M.N.H. No. 28514. $\times 3$. J. A.M.N.H. No. 28515. $\times 3$.

valves with transposed dentition were found in the course of an examination of 268 *Astartella* hinges from the Beaver Creek locality. Popenoe and Findlay (1933) reported the ratio of occurrence of transposition in astartids as 1/130 for *Astarte* and 1/3 for *Goodallia*. The transposition of the anterior lateral and cardinal dentition in a right valve of *Astarte lens* Stimpson is shown in figure 8A. A normal right valve of the same species is shown in figure 8B.

PRE-PENNSYLVANIAN CRASSATELLACEANS

The Crassatellidae are characterized in living species by a wholly internal alivincular ligament in adults, whereas the Astartidae retain the more primitive, external, opisthodetic, parivincular ligament. Both families may have been in existence in mid-Paleozoic times, since representatives have been reported from Mississippian and Devonian rocks. Although it is not our aim in this paper to undertake a thorough investigation of the pre-Permian members of these families, some comments are in order by way of placing the Permian material in perspective.

The name *Cypricardella* Hall (type *C. subelliptica* Hall, Salem Limestone, Mississippian, subsequent designation, S. A. Miller, 1889) is commonly applied to North American and European crassatellacean bivalves of Devonian and Mississippian age. Many of the species bear a close external resemblance to *Astartella* Hall, the latter name being conventionally used for Pennsylvanian and Permian astartids.¹

¹ The status of the two genera is complicated by the fact that both apparently were published in 1858, and we have been unable to determine which actually was released first. It appears, however, that there are adequate morphological grounds for distinguishing the two on hinge characteristics.

Diagnoses of *Cypricardella* and the two species *C. nucleata* and *C. subelliptica* were published in article 1, volume 4, of the *Transactions of the Albany Institute*. The volume in which this publication appears covers the work of the Institute for the period 1856-1863. Although the date 1858 is commonly attributed to article 1, the date of impression of the whole volume is 1864, and we are unable to confirm an earlier release of the section containing the publication of *Cypricardella*.

The date of the first use of the name *Astartella* Hall is clear. It was described as a new genus on page 715 of *Report on the Geological Survey of the State of Iowa*, volume 1, part 2. Two species of *Cypricardella*, *C. nucleata* and *C. subelliptica*, were described in the same volume on pages 663-664, but the genus *Cypricardella* was not described as new in this publication. In volume 1, part 1, there are three letters of transmittal from James Hall to the Governor of Iowa. The third and last of these is dated September, 1858. It is possible, but not probable, that *Cypricardella* as stemming from the Albany publication has a few weeks' or months' priority over *Astartella*. If the Iowa publication, on the other hand, was released before the Albany publication, then both genera would date from 1858, and we are adopting this conclusion.

The hinge characters of *Cypricardella* have not been well known, and we have attempted to investigate the type species, *C. subelliptica* Hall, with topotypes from the Salem Limestone of Indiana, lent to us by Dr. Alan Horowitz of the University of Indiana. The shells are quite small and were prepared mechanically for us by Mr. Frank Lombardi of the American Museum of Natural History (fig. 7A–C).

The cardinal teeth of the Indiana *Cypricardella* appear to us as

Posterior RV 0 1 0 anterior
LV 1 0 1

For comparison, *Astartella* is

Posterior RV (1) 0 1 0 anterior
LV 0 1 0 (1)

and the post-Paleozoic *Astarte* is

Posterior RV 1 0 1 0 (1) anterior
LV 0 1 0 1 0

All three genera have a lunule, escutcheon, external opisthodetic ligament, and concentric ornamentation. In all, the left valve overlaps the right behind the beaks, but the right overlaps the left in front of the beaks. Thus it is tempting to view the three genera as stages in a phylogeny independent of the crassatellid lineage and characterized by the addition of cardinal teeth in the right valve. Furthermore, the similarity of the Indiana *Cypricardella* and *Astartella* to the Myophoriidae in the location of the anteriormost cardinal tooth on the left valve is noteworthy.

Chavan (1952) thought that *Cypricardella* might be a crassatellid. He has pointed out to us (personal communication) that *C. subelliptica* resembles his *C. baudeti* from Visé, in Belgium, in the possession of a wide space between the principal cardinal tooth and the ligament nymph. Interpreting this to be a resilifer, he concludes that *Cypricardella* possessed both internal and external ligament elements. If so, the genus would be allied with the crassatellids, as indicated in his diagnosis of the hinge of *C. baudeti*. He recognized (1952, p. 119) two cardinals in each valve, the anteriormost of these being in the right valve. We have not recognized the anterior tooth in the Indiana material.

Haffer (1959) has discussed Devonian shells which he referred to *Cypricardella*. Although he regarded the genus as an astartid, his diagnosis of the teeth was similar to Chavan's in the recognition of an anterior cardinal on the right valve. He (1959, fig. 17) showed a socket in the left valve between the anterior cardinal and the margin, whereas in

left valves of the Indiana *Cypricardella* the anterior cardinal is the enlarged dorsal end of the anterior lateral (fig. 7A).

Another genus of interest in the early history of crassatellaceans is the Devonian *Crassatellopsis* of Europe. Beushausen's (1895) illustrations suggest cardinals like those of *Astartella*, with the anteriormost in the left valve. However, Haffer's diagrams (1959, fig. 16) indicate three cardinals, with the anteriormost on the right valve. Obviously, much more information is needed on these early forms.

CRASSATELLACEAN SUBFAMILIES

Although evidence at hand resolves neither the basic question of the phylogenetic relationship between the Astartidae and the Crassatellidae, nor the problem of recognizing homologous teeth in different genera, it does show that Paleozoic representatives of these two families differ in important ways from post-Paleozoic forms. We are emphasizing these differences by assigning the Paleozoic and post-Paleozoic species to separate subfamilies. Thus, the Oriocrassatellinae, new subfamily, and the Crassatellinae, include, respectively, the Paleozoic and the post-Paleozoic crassatellids, whereas the Astartellinae, new subfamily, and the Astartidae receive, respectively, the Paleozoic and the post-Paleozoic astartids.

ORIOCRASSATELLINAE AND CRASSATELLINAE

In order to gain an understanding of the family characteristics of the Crassatellidae, and to ascertain which features have been subjected to appreciable evolutionary changes subsequent to Permian time, we have studied some 26 post-Paleozoic species of the Crassatellidae in the collections at the American Museum of Natural History. We have not endeavored to confirm the specific identification or even generic assignments indicated on the museum labels, as we were interested primarily in general comparisons. The specimens examined include representatives of Cretaceous, Eocene, Oligocene, Miocene, Pliocene, and Recent age. The Recent specimens are from Australia, Tasmania, Timor, and the Gulf of Mexico; all are from low latitudes and warm waters. The fossil material is from Europe and North America. Useful data on Cenozoic members of the Crassatellidae also were gleaned from the publications of Lamy (1917), Darragh (1965a, 1965b), and Boreham (1965).

The 26 post-Permian species have several features in common which set them apart from those of Permian *Oriocrassatella*. Their external shape is variable, but all exhibit a lunule, escutcheon, and a third posterior cardinal tooth in the right valves; all these are lacking in the

Paleozoic forms. The lamellar ligament in the geologically younger species has become merged with the resilium as an essentially internal feature, with the corresponding disappearance of the septa. In most of the Crassatellinae the posterior cardinal of the right valve diverges at a low angle from the posterior side of the pivotal tooth near its ventral end, but in one species it projects anteriorly from that tooth almost parallel with the valve length. The posterior cardinal tooth in the right valve has a corresponding socket in the left valve in several Cretaceous and Eocene species, but this socket was not observed in the younger species studied. Another feature typical of post-Paleozoic crassatellids examined is the presence of transverse ridges and grooves (striae) on the sides of the cardinal teeth.

An easily recognizable and consistent characteristic of the Crassatellinae is a lateral socket of the right valve which embraces the antero-dorsal margin of the left valve. In *Oriocrassatella*, the anterodorsal margin of the left valve simply overlaps the margin of the right valve. Many, but by no means all, of the post-Paleozoic species possess concentric ridges over the umbonal area or over the entire shell, whereas most of the Paleozoic species are unornamented.

Several additional features not present in *Oriocrassatella* are found in post-Paleozoic crassatellids. The posterior cardinal of the left valve and the central cardinal of the right valve are inclined anteriorly in Miocene and Recent species studied, whereas in the pre-Miocene forms one or both of these teeth are inclined posteriorly. The ventral margin in most of the Cretaceous and Eocene species studied is crenulate, but crenulation was noted in only one of the post-Eocene species, a recent form from Ceylon. The inner margin of the valves and the teeth of all known species of *Oriocrassatella* are smooth.

In early ontogeny, recent crassatellids appear to have both external and internal ligament elements, but expansion of the ligament during growth is inward. Fresh or wet-preserved living crassatellids have not been available to us, but dry specimens show that the triangular fibrous resilium is bordered posteriorly by a band of uncalcified lamellar ligamental material evidently corresponding to the originally external lamellar ligament. Although a septum does not separate the two elements in living forms, the corresponding areas on the hinge plate are topographically distinct, and the resilifer is outlined as a depression in the ligamental area (fig. 2). In some, but not all, of the post-Paleozoic species, as well as in *Oriocrassatella*, the resilium does not extend to the ventral margin of the resilifer. The internal ligament somewhat resembles the internal ligaments of *Macra* or *Lutraria*. However, none of the mem-

bers of the Crassatellidae is known to be a deep burrower, and none is sinupalliate. Muscle scars, both adductor and pedal, are similar in position in all the crassatellids that we have examined (fig. 9). They consist of subequal adductors, one posterior and one anterior pedal retractor, and one pedal elevator.

ASTARTELLINAE AND ASTARTINAE

A survey was made by us of 16 Holocene species of *Astarte* from various localities of the British Isles, the Mediterranean, and the east and west coasts of North America in order to gain an understanding of modern representatives of the Astartinae. In addition, 13 Tertiary and

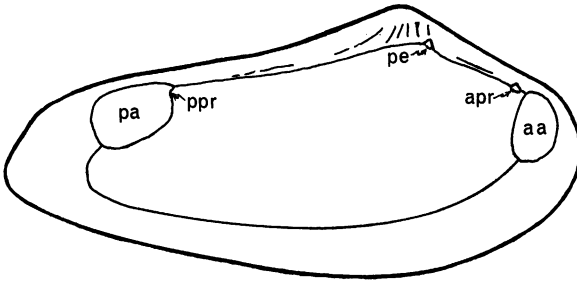


FIG. 9. Musculature in *Oriocrassatella elongata*, new species, as interpreted on latex internal mold of a right valve.

Abbreviations: aa, anterior adductor; apr, anterior pedal retractor; pa, posterior adductor; pe, pedal elevator; ppr, posterior pedal retractor. Approximately $\times 2$.

one Pleistocene species were examined. They represent localities in Europe and the east and Gulf coasts of North America. Specimens of five Mesozoic species were studied, although their hinges are too poorly preserved to permit an unequivocal determination of the presence or absence of minor teeth.

The right valves of post-Paleozoic species (Astartinae) are characterized by three cardinals (fig. 6A), whereas those of Paleozoic species (Astartellinae) have two (fig. 6C). In *Astartella* and, we believe, in the topotype material of *Cypricardella subelliptica* (fig. 7A), the anterior cardinal tooth is in the left valve at the anterior margin of the hinge plate. In *Astartella* this tooth is formed, rather inconspicuously, by an inward thickening of the valve edge (fig. 10D). A cardinal tooth is not present in this position in the Astartinae. In that group, the anterior cardinal is in the right valve, and its socket intervenes between the valve edge and the front cardinal of the left valve (fig. 6A).

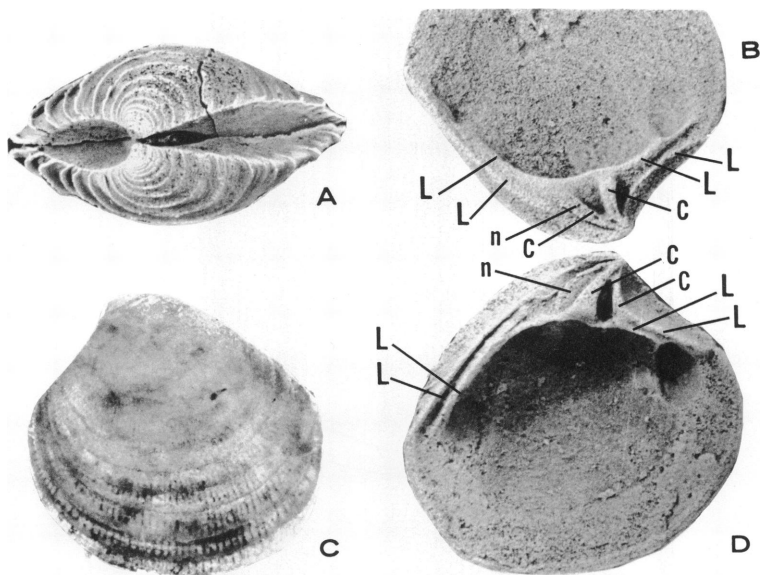


FIG. 10. *Astartella aueri*, new species, from A.M.N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. A. Beak view of articulated shell, A.M.N.H. No. 28483, showing lunule, escutcheon, and ligament cleft; right valve overlaps anteriorly and left valve overlaps posteriorly. $\times 4$. B. Right valve, A.M.N.H. No. 28482. $\times 3$. C. Left valve, A.M.N.H. No. 28486, photographed by transmitted light; the radial dark lines commonly are not visible on the surface. $\times 3$. D. Left valve, the holotype, A.M.N.H. No. 28479. $\times 3$.

Abbreviations: C, cardinal teeth; L, lateral teeth; n, nymph.

Dr. K. Nakazawa, of the University of Kyoto, Japan, has pointed out to us that this difference would be achieved if the anterodorsal marginal ridge of the left valve of *Astartella* migrated upward during evolution while the anterior cardinal lengthened ventrally. Support for this idea is found in the juvenile valve of a living species of *Astarte* figured by Haffer (1959, pl. 12, fig. 9). It appears to recapitulate the adult condition of *Astartella* in regard to the relationship of the anterior lateral and the anterior cardinal on the left valve. It is interesting to note that, if the postulated evolutionary modification is valid, the outer anterior lateral tooth on the left valve in the Astartinae is not homologous with that in the Astartellinae.

Two minor shell features known in both the Astartellinae and the Astartinae appear to be more frequent in the latter group. Minute crenulations on the inner ventral valve margin are present in the ma-

jority of Tertiary species and in about half of the Holocene species examined. One collection of modern specimens of *Astarte castanea* includes some valves with crenulations and some without. Prominent striations are common on the sides of the major cardinal teeth and sockets in Tertiary species studied and are somewhat less prominent in Holocene examples.

Both subfamilies have external, opisthodontic ligaments reflected by nymphs and adjacent narrow but sharply defined ligament grooves.

EVOLUTIONARY CONVERGENCE OF CRASSATELLIDAE AND ASTARTIDAE

The Beaver Creek Permian collection has provided the necessary quantity and quality of specimens for an ample understanding of the stage of evolution of Permian crassatellid and astartid hinges. The Astartidae and the Crassatellidae are represented by *Astartella* and *Oriocrassatella*, both of which probably lie in the lines of evolution culminating in living representatives of these families.

From the evidence cited above, it appears that hinge features of the two families converged after the Permian period. In fact, if only the Paleozoic record were available for consideration, the two families probably would never have been combined in the same superfamily. *Astartella* differs from *Oriocrassatella* in lacking an internal ligament and in possessing a lunule and escutcheon, in the overlap of the right valve on the left in front of the beaks, and the fact that the anteriormost cardinal is borne by the left valve.

The hinge of *Oriocrassatella* (figs. 3B, C, 4, 5A, D) may be diagrammed as

$$\begin{array}{rcccl} \text{Posterior RV} & 1 & 0 & (1) & \left| \begin{array}{ccc} e & s & r \end{array} \right. & 1 & 0 & 1 & \left| \begin{array}{c} 1 \end{array} \right. & \text{anterior} \\ \text{LV} & 1 & 0 & 1 & \left| \begin{array}{ccc} e & s & r \end{array} \right. & (1) & 0 & 1 & 0 & \left| \begin{array}{c} (1) & 0 & 1 \end{array} \right. \end{array}$$

whereas the hinge of *Astartella* (fig. 6C, D) is

$$\begin{array}{rcccl} \text{Posterior RV} & 1 & 0 & (1) & \left| \begin{array}{ccc} n & (1) & 0 & 1 & 0 \end{array} \right. & \left| \begin{array}{c} 1 & 0 & 1 \end{array} \right. & \text{anterior} \\ \text{LV} & 1 & 0 & 1 & \left| \begin{array}{ccc} n & 0 & 1 & 0 & (1) \end{array} \right. & \left| \begin{array}{c} (1) & 0 & 1 \end{array} \right. \end{array}$$

Our impression of the post-Paleozoic record of the two families is based largely on Tertiary and Recent collections. However, we also have examined excellent Cretaceous crassatellids as well as some inadequate Jurassic and Cretaceous astartids. The post-Paleozoic specimens of both families possess lunule and escutcheon, three cardinal teeth in the right valve, and two cardinals in the left; the anteriormost cardinal is borne by the right valve, and the right valve overlaps the left in front

of the beaks. The increased similarity of the hinges among the post-Paleozoic astartids and crassatellids is due mainly to the addition of many features in the crassatellids, whereas the main change in astartid hinge character was the addition of an anterior cardinal tooth on the right valve and a corresponding socket on the left valve. The astartids remained constant in ligament character, whereas the post-Paleozoic crassatellids lost the distinctive septum which separated the elastic and compressional ligament parts. Both the astartids and crassatellids added teeth during their evolution, producing modern representatives which display dentition not readily assignable to either the lucinoid or the cyrenoid heterodont hinges, the "astartedont" dentition. For convenience the formulas of *Hybolophus* and *Astarte* are repeated here

<i>Hybolophus</i>				
Posterior RV	1 0 (1)	e r 1 0 1 0 1		1 0 1 anterior
LV	1 0 1	e r 1 0 1 0		(1) 0 1

<i>Astarte</i>				
Posterior RV	1 0 (1)	n 1 0 1 0 (1)		1 0 1 anterior
LV	1 0 1	n 0 1 0 1 0 (1)		0 1

TAXONOMY

SUPERFAMILY CRASSATELLACEA FÉRUSSAC, 1822

FAMILY CRASSATELLIDAE FÉRUSSAC, 1822

ORIOCRASSATELLINAE BOYD AND NEWELL, NEW SUBFAMILY

DIAGNOSIS: Extinct Crassatellidae differing from Crassatellinae in absence of lunule and escutcheon, in possessing strong septate nymphs that intervene between resilium and parivincular (external), opisthodontic elastic ligament, in having only two cardinal teeth in each valve, with posteriormost cardinal in left valve, and in overlap of left valve on right valve in front of beaks.

HINGE FORMULA:

Posterior RV	1 0 (1)	e s r 1 0 1		1 anterior
LV	1 0 1	e s r (1) 0 1 0		(1) 0 1

RANGE: Mississippian-Permian, cosmopolitan.

GENUS *ORIOCRASSATELLA* ETHERIDGE, 1907

TYPE SPECIES: *Oriocrassatella stokesi* Etheridge, 1907, monotypic.

SUBJECTIVE SYNONYMY: *Procrassatella* Yakovlev, 1928; type species, *Schizodus planus* Golowinsky, 1868, monotypic.

DIAGNOSIS: Lenticular, ovoid, or elongate, with obliquely truncate

TABLE 1
DISTRIBUTION OF *Oriocrassatella*

Russian Permian Stages	Western Australia	Eastern Australia	Timor	Kashmir	Russia	Greenland	Wyoming	Brazil
Kazanian	<i>O. stokesi</i> ^a <i>O. sp.</i> ^b		<i>O. plana</i> ^{b, c}		<i>O. plana</i> ^d	<i>O. plana</i> ^e		
Kungurian	<i>O. stokesi</i> ^{b, f}		<i>O. plana</i> ^{b, c}				<i>O. elongata</i> , new species	
Artinskian	<i>O. stokesi</i> ^{b, f} <i>O. sp.</i> ^b <i>O. sp.</i> ^{b, g}	<i>O. queenslandica</i> ^g						
Sakmarian		<i>O. compressa</i> ^h		<i>O. lapidaria</i> ^{f, i} <i>O. intermedia</i> ^{f, i} <i>O. brenensis</i> ^{f, i}				<i>O. sp.</i> ^j
Upper Carboniferous		<i>O. compressa</i> ^h						
Lower Carboniferous		<i>O. compressa</i> ^h						

^a Thomas and Dickens (1954).

^b Dickens (1963).

^c Wanner (1940).

^d Newell (1958).

^e Newell (1955).

^f Dickens (1956).

^g Dickens (1961).

^h Maxwell (1964).

ⁱ Reed (1932).

^j Dr. A. C. Rocha-Campos, University of São Paulo, Brazil (personal communication).

^k Dr. K. S. W. Campbell, Australian National University (personal communication).

posterior margin, pedal and siphonal margins closed, beaks orthogyre to prosogyre; resilium (as inferred from growth lines) appreciably above ventral margin of resilifer, each half covered apically by a convex deck; arrangement and relative prominence of teeth as indicated in subfamily formula; left anterior (pivotal) cardinal tooth more or less bifid; left posterior cardinal bladelike, or obsolescent, forming anterior margin of resilium and commonly reflected by corresponding furrow upon or behind posterior cardinal of right valve.

RANGE: Mississippian-Permian, cosmopolitan. Table 1 shows the relative stratigraphic positions of species as interpreted from the literature. We have relied mainly on Dickins' (1963) correlation of Australian and Russian stages.

DISCUSSION: When Etheridge (1907) created the genus *Oriocrassatella* for Australian Permian shells, only imperfect right valves were available for study. Although he properly rejected the possibility that the resilifer might be a dental socket, it remained for Yakovlev, in 1928, to recognize that a septum separates a dorsal ligament groove from a triangular resilifer. These observations were made on late Permian (Kazanian) forms from the Russian platform. Etheridge had mistaken the septum of his specimens for a cardinal tooth, and he speculated that the furrow behind it might be a socket. He concluded that *Oriocrassatella* lacked lateral teeth, whereas Yakovlev recognized lateral teeth in his material of *Procrassatella* which was more complete and better preserved than the Australian specimens of *Oriocrassatella*. Noting apparent differences in hinge features in the Russian and Australian specimens, Yakovlev proposed a new genus, *Procrassatella*, for the former.

Dickins (1956) emended the diagnosis of *Oriocrassatella*, calling attention to a posterior lateral tooth in newly collected Australian material as well as a septum separating the ligament furrow from the resilifer. After studying good specimens of the type species of both *Procrassatella* and *Oriocrassatella*, Newell (1958) concluded that the Russian and Australian Permian crassatellids are too similar to be placed in separate genera. Consequently he regarded *Procrassatella* as a junior synonym of *Oriocrassatella*—a conclusion that is sustained here.

***Oriocrassatella elongata* Boyd and Newell, new species**

Figures 1, 3, 5, 9, 11-21

DIAGNOSIS: Elongate, on average about 1.7 times as long as high; ventral profile approximating equiangular spiral, with greatest convexity at anterior extremity; dorsal profile concave on both sides of beak except in juveniles, in which margins nearly straight, forming obtuse angle

at beak (figs. 11, 12); profile of posterior part of valve commonly obliquely truncate; surface with rounded siphonal ridge from umbo to posterior extremity of valve; ornamentation lacking; irregular growth varices prominent on peripheral parts of large valves; without pedal or siphonal gape; very short and narrow gape into ligament furrow behind beaks of articulated shell (fig. 13E).

Dental formula as given in discussion of subfamily Oriocrassatellinae.

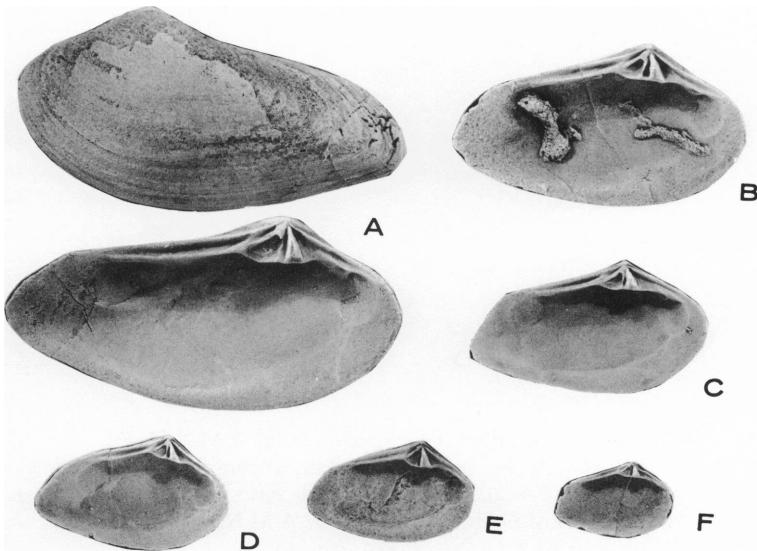


FIG. 11. *Oriocrassatella elongata*, new species, from A.M.N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. A. Two views of the holotype, A.M.N.H. No. 28473, a left valve. B-F. Growth series of left valves. B. A.M.N.H. No. 28518. C. A.M.N.H. No. 28491. D. A.M.N.H. No. 28477. E. A.M.N.H. No. 28490. F. A.M.N.H. No. 28489. All $\times 1$.

Left anterior cardinal sulcate and slightly bifid, projecting well beyond plane of commissure (figs. 5D, 13B); left posterior cardinal obsolescent, bladelike, and probably not preserved to full height in most specimens, extending slightly beyond plane of commissure in some specimens; right posterior cardinal (fig. 5A) narrow, and right anterior cardinal forming low, rounded ridge along anterior border of major socket.

In each valve, resilifer and cardinal teeth situated on ventrally projecting hinge plate, except for right anterior cardinal which rests on re-entrant at anterior extremity of hinge plate; resilifer separated from narrow ligament furrow by sharply defined but slender septum which

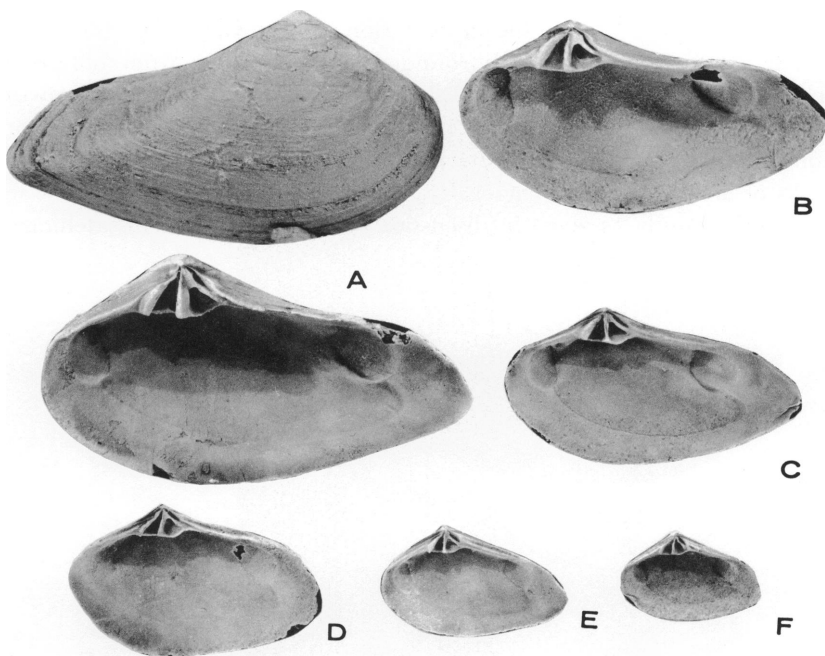


FIG. 12. *Oriocrassatella elongata*, new species, from A.M.N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. A. Two views of a right valve, A.M.N.H. No. 28517. B-F. Growth series of right valves. B. A.M.-N.H. No. 28481. C. A.M.N.H. No. 28475. D. A.M.N.H. No. 28487. E. A.M.-N.H. No. 28488. F. A.M.N.H. No. 28476. All $\times 1$.

originates apically in a vestigial nymph (fig. 13C-E) forming posterior wall of resilifer; anterior border of resilifer in right valves formed by posterior cardinal (fig. 5A). Anterior edge of resilifer in left valves delimited by posterior cardinal tooth; arched cover, or deck, over apex of resilifer in each valve connecting proximal ends of septum and adjacent cardinal tooth (fig. 5A, D); ligament furrow and posterior lateral socket of both valves separated by broad, low rise, and axially aligned parallel with posterodorsal margin.

Posterior and anterior adductor scars below distal ends of lateral teeth; anterior scar somewhat higher than long, whereas larger posterior scar slightly elongate; small, deep, pedal retractor scar adjacent to posterodorsal margin of anterior adductor scar; umbonal pedal elevator scar, just anterior to apex of umbonal cavity beneath large cardinal in left valve (fig. 3A) and beneath corresponding socket in right valve, varying in shape and clarity (fig. 9); pallial line, lacking sinus, faintly

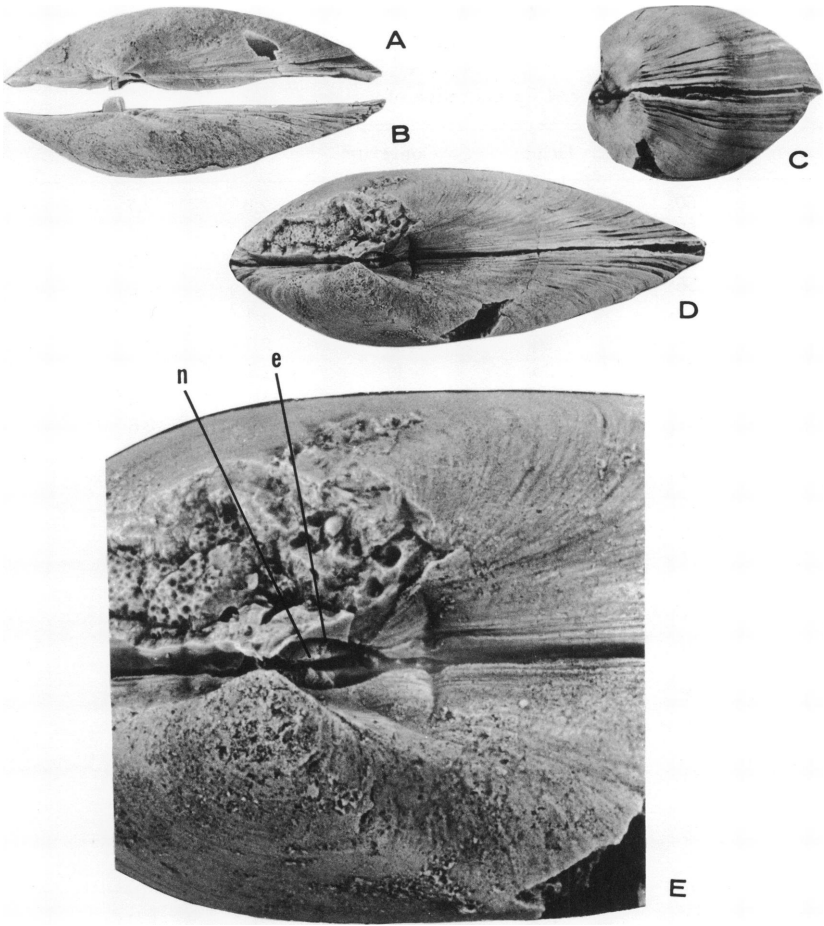


FIG. 13. *Oriocrassatella elongata*, new species, from A.M.N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. A. Right valve, A.M.N.H. No. 28481, showing prominent cardinal tooth; this is *not* the mate to B. B. Left valve, the holotype, A.M.N.H. No. 28473, showing prominent cardinal tooth. Both $\times 1$. C-E. Articulated specimen, A.M.N.H. No. 28480. C. Posterior aspect. D. Dorsal aspect. Both $\times 1$. E. External ligament region; nymphs (n) are visible within lanceolate ligament opening (e), $\times 3$.

defined in most valves and sharply defined in few; larger valves (e.g., greater than 20 mm. in height) thickened in anteroventral area.

VARIATION: More than 700 silicified specimens, about evenly divided between left and right valves, were studied. Most specimens consist only

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF RIGHT VALVES OF *Oriocrassatella elongata*,
NEW SPECIES
(See fig. 7 for indication of variates C and D.)

Length	Height	Convexity	C	D
60	31	13	2.8	7.7
58	30	13	4.2	11.4
58	30	13	3.7	9.3
56	28	15	3.9	10.2
55	29	14	3.4	10.9
53	26	12	2.3	7.7
51	30	11	2.7	9.3
51	27	12	3.1	7.6
51	27	11	3.2	8.6
51	26	11	2.9	8.1
51	26	11	2.2	7.4
49	26	11	2.3	7.8
48	25	10	2.7	6.8
44	25	10	2.1	7.5
43	26	9	3.0	7.2
41	21	8	1.7	5.1
40	24	9	1.9	7.4
40	21	7	1.5	5.3
38	23	8	1.7	5.9
38	21	11	1.3	6.5
37	25	8	2.3	6.7
33	20	7	1.3	5.3
29	17	5	1.0	4.9
28	16	6	0.5	3.8
27	16	6	1.0	3.3
26	16	5	1.0	4.0
25	15	6	0.8	3.7
25	15	5	0.9	3.5
24	15	5	1.0	3.6
24	14	6	1.1	3.2
24	14	5	1.0	3.5
23	15	5	0.9	3.5
23	14	5	0.9	2.8
23	14	5	0.8	3.3
23	13	5	0.8	3.2
23	13	5	0.8	3.0
23	13	4	0.7	3.2
22	13	5	0.6	3.1
22	13	4	0.9	3.3
21	14	5	0.9	3.6
21	12	5	0.6	2.9
20	14	4	0.6	3.1

TABLE 2—(Continued)

Length	Height	Convexity	C	D
20	13	4	0.9	2.6
18	12	4	0.7	3.0
18	12	4	0.7	2.8
18	11	4	0.9	3.0
17	11	4	0.7	2.4
15	11	4	0.8	2.6
12	8	2	0.4	1.8

of the sturdy hinge plate; approximately 20 specimens of each valve are essentially complete.

Measurements of the length, height, and convexity were made on all valves possible (figs. 15–17; tables 2, 3). The length and height were measured by placing the specimen on graph paper and reading the appropriate intervals to the nearest millimeter. The dorsal extremity was defined by the profile of the umbones. The measure of complexity from the plane of commissure was obtained with calipers after the valve convex was placed surface upward on a table. The interval measured was the maximum distance between the plane of commissure and the valve exterior, measured normal to the plane of commissure. Because the cardinal teeth of the right valve do not project significantly beyond the plane of commissure, the entire right valve was allowed to rest on the table. However, left valves were placed so that the anterior cardinal, a prominent projection in large valves, projected beyond the edge of the table and did not influence the measurement.

To determine the variability in the concavity of the posterodorsal shell profile, measurement C was made (figs. 18, 19). C is the greatest distance between the arc of the valve margin and a tangent drawn between the umbo and the posterodorsal extremity.

To determine the size distribution in the collection, measurement D was selected, as illustrated in figure 18. In right valves, this is the rectilinear distance along the hinge plate between the septum and the posterior distal corner of the anterior cardinal. On left valves, it is the rectilinear distance along the edge of the hinge plate between the septum and the anterior distal corner of the anterior cardinal. Dimension D was chosen because it can be measured on nearly every identifiable specimen in the collection (fig. 1). The observed range in D was 1.6 mm. to 12.0 mm. in right valves and 1.2 mm. to 13.1 mm. in left valves. The utility of D as an index of size is shown by a plot of D against

TABLE 3
MEASUREMENTS (IN MILLILETERS) OF LEFT VALVES OF *Oriocrassatella elongata*,
NEW SPECIES
(See fig. 7 for indication of variates C and D.)

Length	Height	Convexity	C	D
66	35	13	2.7	12.1
66	35	13	2.5	10.0
58	30	12	2.4	9.9
58	29	12	2.4	10.4
56	28	10	2.1	9.4
55	30	11	2.1	9.4
55	30	11	2.1	9.1
54	30	11	2.7	9.5
53	29	12	2.1	10.3
53	28	12	1.3	7.8
53	28	10	2.0	9.4
52	28	9	1.9	8.2
52	26	9	1.7	8.6
51	27	9	1.6	9.6
49	27	8	1.6	7.8
46	28	9	2.3	8.1
46	26	9	1.2	7.7
46	26	8	1.5	8.1
44	23	8	1.1	6.3
44	23	8	0.8	6.8
43	24	8	0.9	7.5
39	22	7	0.4	6.3
39	21	5	1.2	5.8
37	20	6	0.8	6.1
34	21	6	1.1	6.0
33	20	6	0.7	5.3
33	19	6	0.6	5.4
32	18	5	0.5	5.5
31	19	6	0.9	5.0
30	19	6	0.5	5.1
29	18	6	0.7	4.7
27	15	5	0.5	4.2
26	16	5	0.6	3.9
26	16	4	0.4	3.8
26	15	5	0.4	3.9
25	16	4	0.5	3.6
25	15	5	0.8	4.1
23	14	5	0.4	3.7
23	14	4	0.6	3.8
22	14	4	0.4	3.8
22	13	4	0.6	3.8
21	13	5	0.4	3.3

TABLE 3—(Continued)

Length	Height	Convexity	C	D
20	12	4	0.1	3.2
19	13	4	0.3	3.1
19	12	4	0.3	3.1
19	12	3	0.4	3.0
17	11	3	0.3	2.6
16	10	3	0.1	2.5
14	10	2	0.2	1.9

the length in complete valves (fig. 20). Nearly the same pattern was obtained when D was plotted against the height or convexity.

To express the position of the beak along the length of a valve, the partial length, PL, parallel to the shell length between the anterior extremity and the beak was measured on complete valves (figs. 18, 21).

One aspect of shape variability difficult to measure is the cross profile of the posterior part of a valve. This profile, although typically sub-angular, varies from arcuate to angular (fig. 13C-E).

Growth lines are prominent on large valves. The finest lines distinguishable average 0.1 mm. between crests. More prominent varices occur on peripheral parts of many large valves and are irregularly spaced on a single valve. For example, one valve exhibits seven such major growth lamellae, spaced as close as 1.5 mm. and as far apart as 7.1 mm. These marks represent changes in the rate of expansion of the valve margin, and they coincide with changes in the spiral angle of the surface profile. They are separated by sets of laminae representing an expansion of the valve convexity accompanied by relatively little increase in height and length. Major growth interruptions are especially prominent on peripheral parts of large valves, in which the successive margins of the shell cross the siphonal ridge. In such cases, the outer part of a lamina may not be in contact with the adjacent younger lamina. Several valves of similar size were compared in regard to the spacing and number of prominent growth lines, but no correlation was recognized. Consequently, growth interruptions may not be related to regular cycles.

Some variation of features of the hinge is apparent but is not extreme. One variable is the degree of furrowing of the large cardinal in the left valve. At most, the sulcus of the ventral part of the tooth produces a slightly bifid aspect. Australian specimens of the genus also have been described as having a bifid anterior cardinal in the left valve (Dickins, 1956, p. 33; 1961, p. 125). This tooth also varies in inclination, best

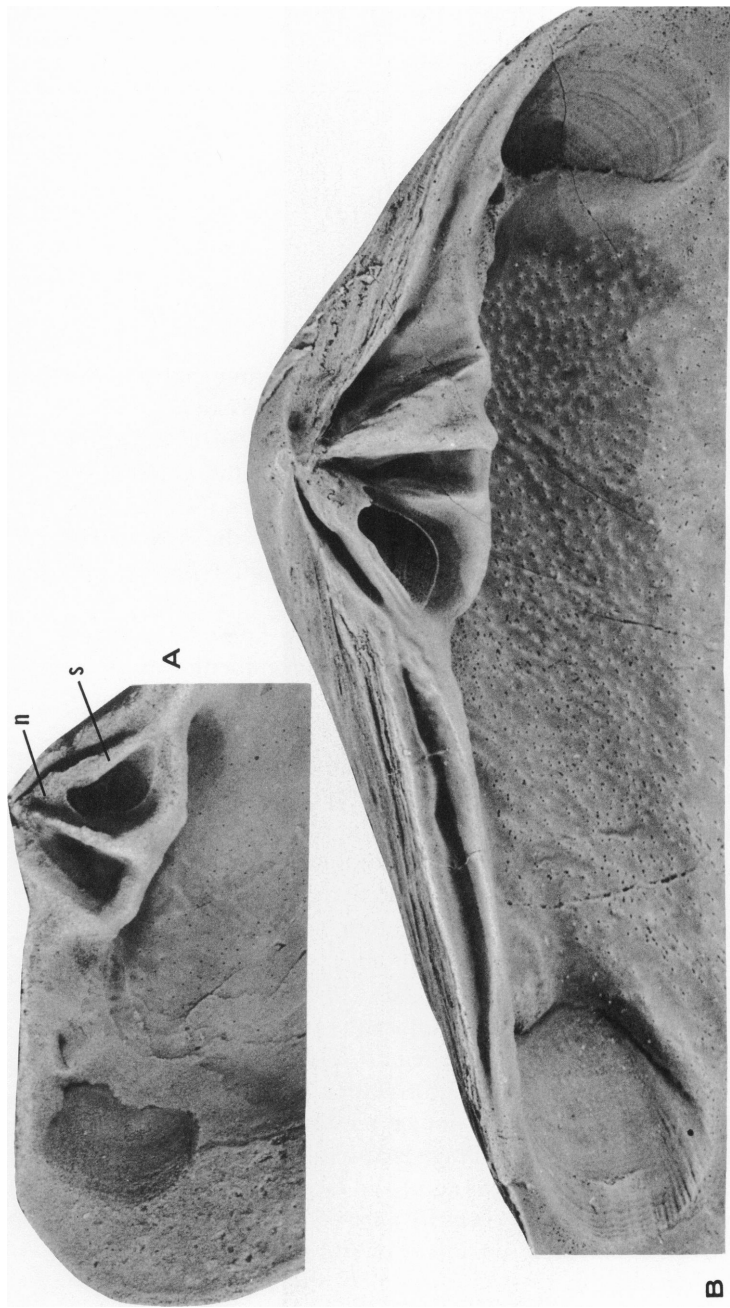


FIG. 14. *Oriocrassatella elongata*, new species, from A.M.N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. A. Right valve, A.M.N.H. No. 28485, tilted to show small nymph (n) and continuing septum (s). Approximately three-fourths of the ligament apparently was concealed from external view (see also figs. 13E and 14B). Note anterior pedal retractor immediately to right of adductor scar. B. Left valve, A.M.N.H. No. 28478; note crater-like blisters in umbonal cavity, interpreted here as apertures of parasites. Both $\times 3$.

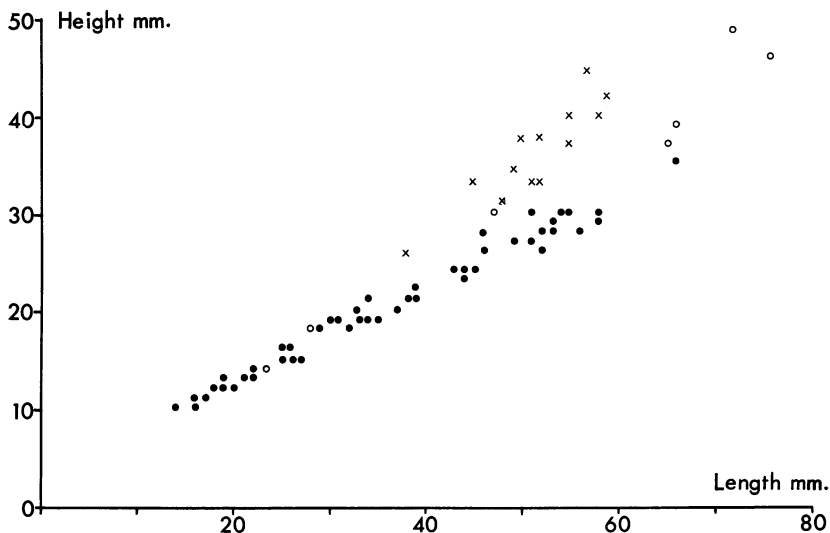


FIG. 15. Height/length variation in three species of *Oriocrassatella*. Solid circles: *Oriocrassatella elongata*, new species. Open circles: *Oriocrassatella plana* (Golowkinsky). Crosses: *Oriocrassatella stokesi* Etheridge. Data on *O. plana* and *O. stokesi* are from published tables and from measurements on latex replicas and published illustrations. For measurements of *O. elongata*, see tables 2 and 3.

expressed in terms of the position of the posteroventral corner of the tooth relative to the beak. In this sense, the corner of the tooth varies in position from anterior to the beak, directly beneath the beak, or posterior to the beak. In small valves, this point is most commonly anterior or ventral. Examples of all three conditions are found among larger valves.

The right posterior cardinal varies both in thickness and in inclination relative to the beak. The ventral end of this bladelike tooth ranges

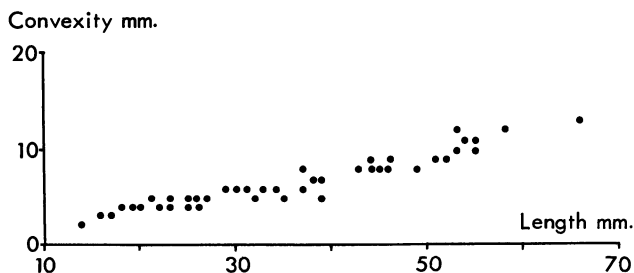


FIG. 16. Convexity/length variation of left valves of *Oriocrassatella elongata*, new species. Data are in table 3.

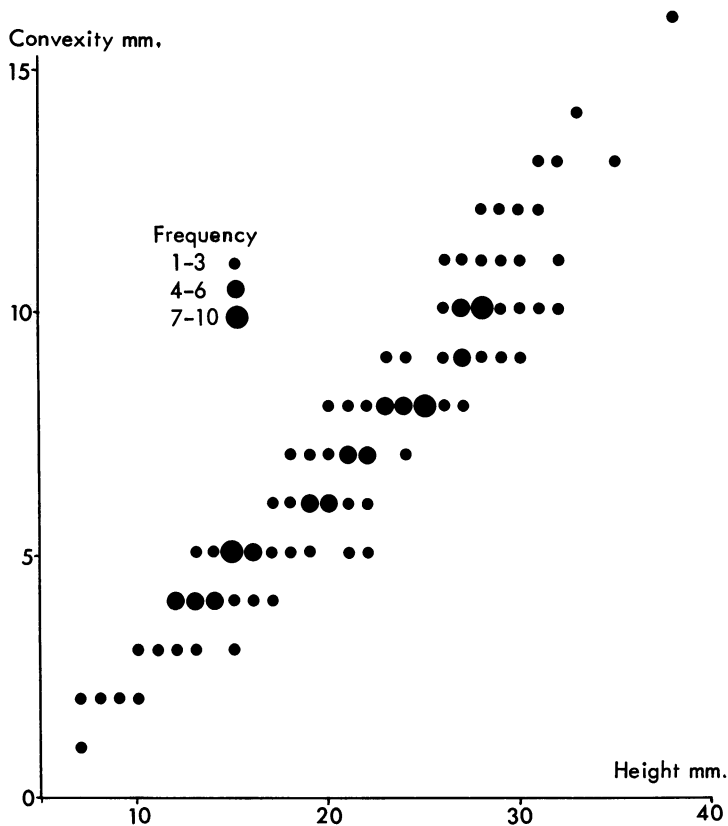


FIG. 17. Convexity/height variation in 181 left valves of *Oriocrassatella elongata*, new species. Measurements were rounded to the nearest millimeter.

from anterior, directly below, or slightly posterior to the beak. The posterior inclination is uncommon in small, but common in large, valves.

The upper end of the septum is commonly expanded in varying degrees at the expense of the ligament furrow, which narrows correspondingly (fig. 5A, D).

The relative lengths of the resilifer and the left anterior cardinal influence the configuration and orientation of the ventral margin of the shelflike hinge plate. The free margin varies from straight to irregularly convex, and its orientation varies with growth (figs. 11, 12). The large cardinal tends to lengthen faster in early growth than does the resilifer, so smaller valves (e.g., with height less than 20 mm.) have the ventral margin of the shelf inclined anteriorly. In later growth stages, the ven-

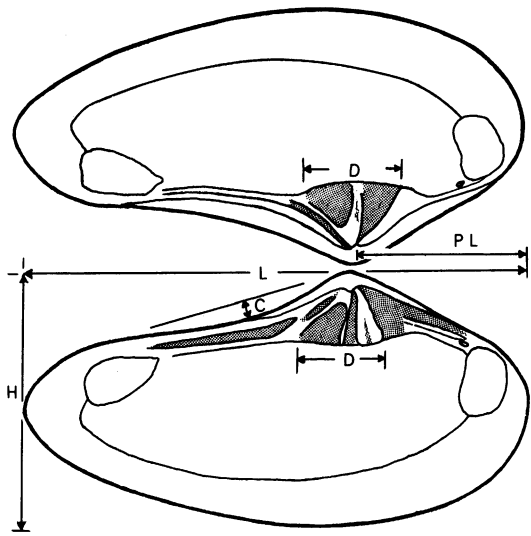


FIG. 18. Diagram of *Oriocrassatella elongata*, new species, indicating principal variates used for linear measurements.

Abbreviations: C, convexity of posterodorsal profile; D, arbitrary measure of cardinal armature; H, height; L, length; PL, anterior partial length.

tral expansion of the resilifer proceeds faster than the lengthening of the large cardinal, causing the ventral margin of the hinge plate to become parallel to valve length and, in some cases, to be convex outward below the resilifer.

COMPARISONS: Of the several described species of *Oriocrassatella*, *O. elongata*, new species, is most similar to *O. plana* (Golowkinsky) from the

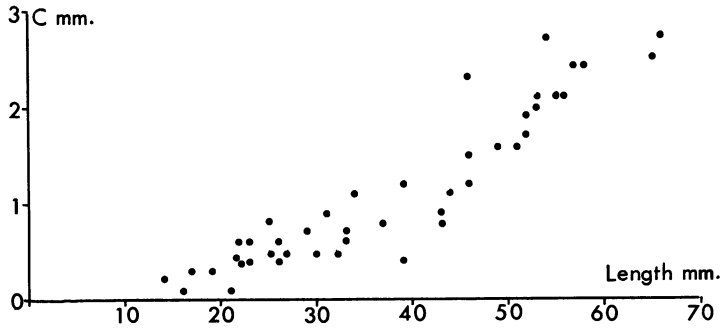


FIG. 19. Ratio of variate C to length in left valves of *Oriocrassatella elongata*, new species. Data are in table 3; for indication of C, see figure 18.

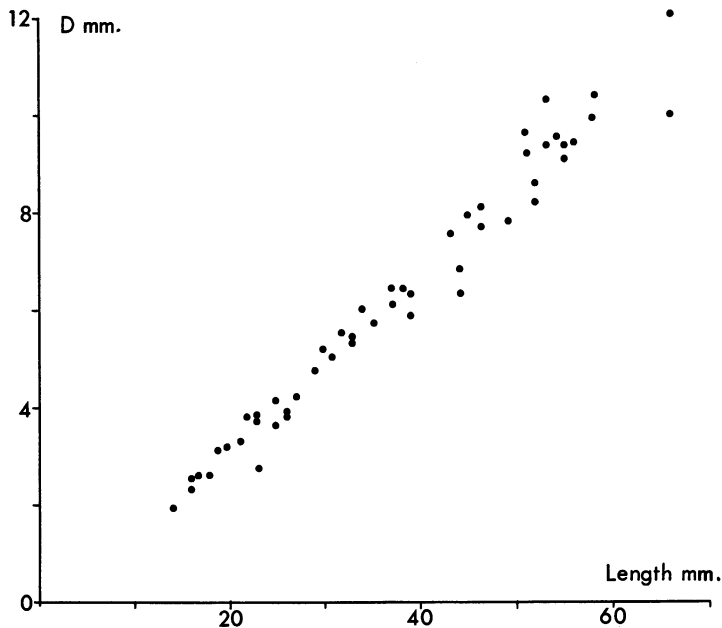


FIG. 20. Ratio of variate D to length in left valves of *Oriocrassatella elongata*, new species. Data are in table 3; for indication of D, see figure 18.

Russian Kazanian. The hinge features are notably similar, but *O. elongata* differs in its greater relative length of large valves (1.8/1 versus about 1.6/1), in having a marked concavity of the posterodorsal profile, and in having greater prominence of the beaks which are situated slightly closer to the anterior margin than in other species (figs. 15, 21). *Oriocrassatella plana* was assigned to *Schizodus* by its author (Golowkinsky, 1868), and Yakovlev (1928) used it as the type species for *Procrassatella*. Only one specimen outside Russia, an external mold of a right valve from Greenland, has been referred to the species (Newell, 1955).

Oriocrassatella elongata differs in the same respects noted above from the Australian mid-Permian and early Permian *O. stokesi* and *O. queenslandica*, and from Reed's (1932) early Permian *O. lapidaria*, *O. brenensis*, and *O. intermedia* from Kashmir. The specimen of *O. stokesi* illustrated by Newell (1958, fig. 2) has both the septum and the ligament furrow notably wider than the corresponding features on *O. elongata*, whereas *O. queenslandica* is distinguished by an exceptionally thick septum (Dickins, 1961). Reed's illustrations of the Kashmir species are not adequate for a comparison of hinge features, but photographs taken by Newell of

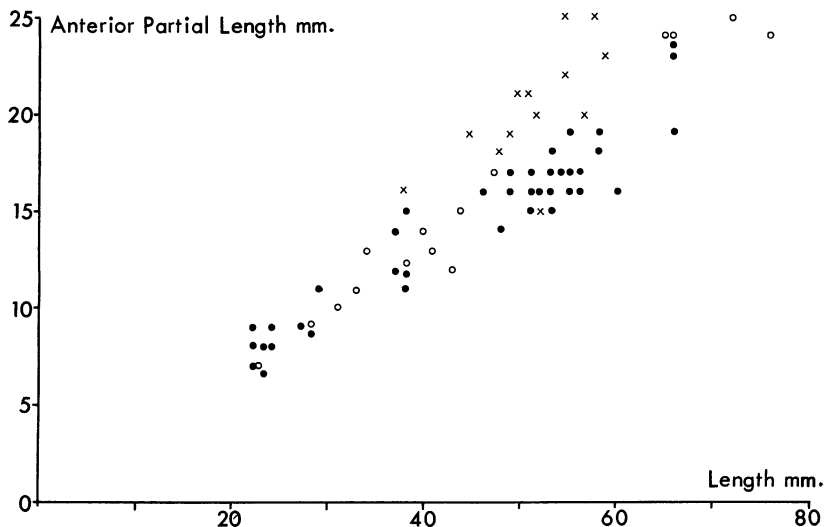


FIG. 21. Comparison of the placement of the beaks in three species of *Oriocrassatella*. Solid circles: *Oriocrassatella elongata*, new species. Open circles: *Oriocrassatella plana* (Golowinsky). Crosses: *Oriocrassatella stokesi* Etheridge. Data on *O. plana* and *O. stokesi* are from published tables and from measurements on latex replicas and published illustrations. For measurements on *O. elongata*, see tables 2 and 3. Anterior partial length is the dimension PL indicated in figure 18. Measurements were rounded to the nearest millimeter.

rubber casts of some of Reed's specimens have been examined. The cast from the specimen illustrated by Reed (1932, pl. 7, fig. 1) shows the right posterior cardinal not sharply separated from the anterior one. The septum is more robust and the resilifer is narrower than in *O. elongata*. Rubber casts from specimens of *Oriocrassatella intermedia* (Reed) illustrated in figures 3 and 4 of his plate 7 (Reed, *ibid.*) show several differences in comparison with *O. elongata*. The Kashmir specimens have a narrower left anterior cardinal, a wider right posterior cardinal, a more bladelike right anterior cardinal, and a more robust septum, than in *O. elongata*.

Oriocrassatella compressa Maxwell, another Australian species of upper Carboniferous and earliest Permian age, is characterized by slight shell biconvexity and by strong concentric lamellae. It was described (Maxwell, 1964, p. 13) as having only one cardinal tooth on each valve, but illustrations suggest that the species is based on imperfect molds, and the details of the hinge may not be fully known.

OCCURRENCE: A single right valve figured by Ciriacks (1963, pl. 12, figs. 1-3) is the only Permian crassatellid cited in the literature from the con-

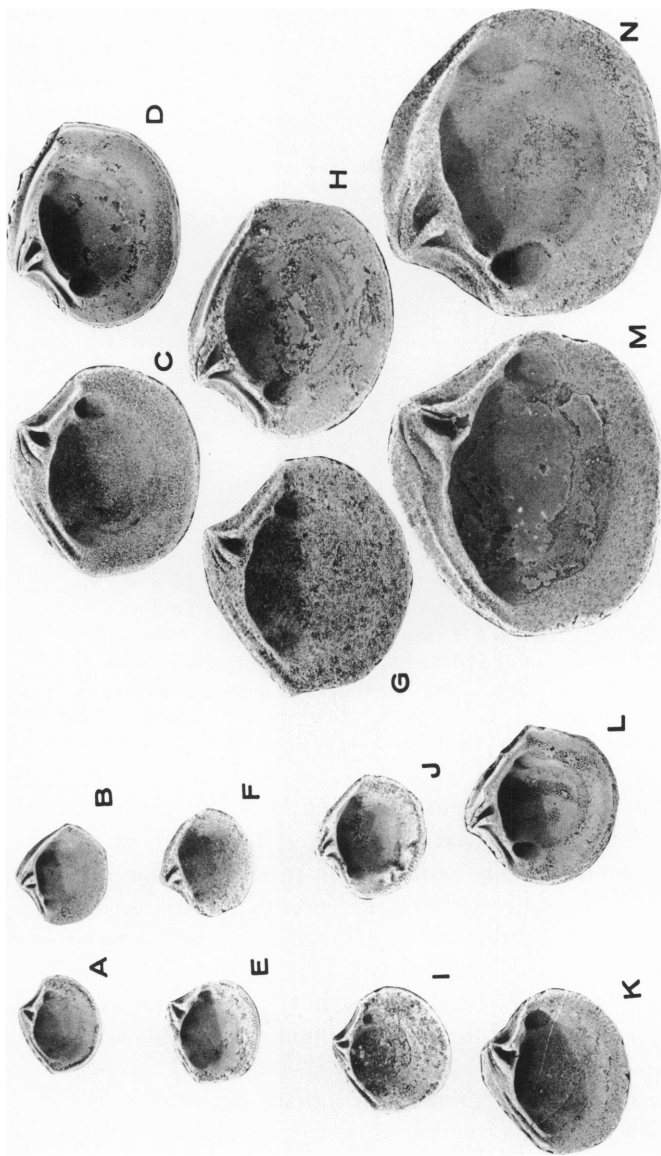


FIG. 22. *Astartella aueri*, new species, from A.M.N.H.:F.I. 2010, Grandeur Member, Park City Formation, Permian, Wyoming. A, C, E, G, I, K, M. Left valves. B, D, F, H, J, L, N. Right valves. A. A.M.N.H. No. 28499. B. A.M.N.H. No. 28492. C. A.M.N.H. No. 28503. D. A.M.N.H. No. 28496. E. A.M.N.H. No. 28500. F. A.M.N.H. No. 28493. G. A.M.N.H. No. 28504. H. A.M.N.H. No. 28497. I. A.M.N.H. No. 28501. J. A.M.N.H. No. 28494. K. A.M.N.H. No. 28592. L. A.M.N.H. No. 28495. M. A.M.N.H. No. 28505. N. A.M.N.H. No. 28498. E and J display crenulate inner margin. Crevice in tooth 2 of M is defect of preservation. Note occurrence of socket for 5b in front of nymph on most left valves but general lack of corresponding prominence on right valves. All $\times 2.5$.

tinental Americas prior to the present study. It was confidently referred to *O. elongata*. Ciriacks listed the specimen as from the Grandeur Member of the Park City Formation at Willow Creek, Wyoming. This locality is only a few miles north of Beaver Creek, where the present collection was obtained from the upper part of the Grandeur Member. The stratigraphic placement of our collection (A.M.N.H.:F.I. 2010) was made for us in the field by Mr. Edwin K. Maughan of the United States Geological Survey, an authority on the stratigraphy of the Park City Formation.

CATALOGUED SPECIMENS: Holotype, A.M.N.H. No. 28473; topotypes, A.M.N.H. Nos. 28474–28478, 28480, 28481, 28484, 28485, 28487–28491, 28516–28518, and U.W. Nos. A1582–A1585.

FAMILY ASTARTIDAE D'ORBIGNY, 1844

ASTARTELLINAE BOYD AND NEWELL, NEW SUBFAMILY

DIAGNOSIS: Extinct Astartidae differing from Astartinae in having only two cardinal teeth in each valve and in having anteriormost cardinal on left valve.

DENTAL FORMULA:

$$\begin{array}{c} \text{Posterior RV} \quad 1 \ 0 \ (1) \left| \begin{array}{c} n \ (1) \ 0 \ 1 \\ n \ 0 \ 1 \ 0 \ (1) \end{array} \right| \quad \begin{array}{c} 1 \ 0 \ 1 \ \text{anterior} \\ (1) \ 0 \ 1 \end{array} \\ \text{LV} \quad 1 \ 0 \ 1 \end{array}$$

RANGE: Devonian? Mississippian to Upper Permian, cosmopolitan.

ASTARTELLA HALL, 1858

TYPE SPECIES: *Astartella vera* Hall, 1858, monotypic.

Astartella aueri Boyd and Newell, new species

Figures 7D–G, 8C–J, 10, 22–24

DESCRIPTION: Laterally compressed shells, with beaks prominent and prosogyre; lunule and escutcheon prominent, essentially unornamented; beak near valve apex, not incurved; escutcheon steepening greatly toward beak, its anterior part apparently an extension of hinge plate; dorsal margin strongly concave in front of beaks and gently convex behind beaks; anterior and posterior extremities coinciding with points where posterodorsal and anterodorsal arcs intersect semicircular lower margin; ornamentation consisting of concentric ridges, with finer concentric lines in troughs; ridges of left valve crossing escutcheon border before dying out, ridges of right valve terminating abruptly at border, with situation reversed on lunule (fig. 10A); arrangement and relative

TABLE 4
 MEASUREMENTS (IN MILLIMETERS) OF RIGHT VALVES OF *Astartella aueri*,
 NEW SPECIES
 (Specimens were selected from a larger size-graded series by means of a table of
 random numbers.)

Length	Height	Convexity
15.2	14.2	4.9
14.3	13.3	4.0
14.1	12.9	3.4
13.8	12.5	3.3
13.7	12.7	4.0
12.7	11.8	3.8
12.7	11.8	3.7
12.7	11.8	3.2
10.7	9.3	2.6
9.8	8.6	1.9
8.8	7.8	2.4
8.8	7.3	2.1
8.6	7.5	2.1
8.4	7.5	2.0
8.3	8.1	2.1
7.4	6.6	2.3
6.9	6.2	1.8
6.9	6.0	2.0
6.4	5.6	1.8
6.4	5.6	1.6
5.8	4.9	1.5
5.4	4.7	1.7
5.3	4.7	1.4
4.4	3.9	1.2
4.1	3.8	1.1

prominence of teeth as indicated in subfamily formula; anterodorsal margin of left valve serving as lateral tooth, fitting into socket on right valve, posterodorsal margin of right valve received by socket on left valve; two cardinal teeth on left valve; left anterior cardinal formed by inward thickening of valve margin; left posterior cardinal triangular and inclined backward, with greatest relief near mid-length; on right valve, anterior cardinal narrow but well developed; obsolescent right posterior cardinal, formed by slight ridge along inner edge of nymph, typically less prominent than corresponding groove behind left posterior cardinal.

Narrow ligament nymphs separated from escutcheon by narrow ligament furrow; ligament opisthodontic, external, about one-third of length

TABLE 5
MEASUREMENTS (IN MILLIMETERS) OF LEFT VALVES OF *Astartella aueri*,
NEW SPECIES
(Specimens were selected from a larger size-graded series by means of a table of
random numbers.)

Length	Height	Convexity
15.7	15.0	4.0
15.3	14.5	5.0
13.9	12.7	3.0
13.9	11.8	3.5
13.6	12.2	4.7
13.2	12.3	3.5
13.1	12.1	3.4
13.0	12.1	4.5
12.4	10.9	2.7
12.1	11.8	3.6
10.9	10.1	2.8
10.9	9.9	3.0
9.4	8.0	2.7
9.1	7.8	2.6
8.5	7.7	1.8
7.9	7.7	1.8
7.7	7.0	2.2
7.6	6.6	1.5
7.4	6.5	2.1
7.1	6.7	1.4
6.9	6.1	1.6
6.5	6.3	1.5
6.4	5.8	1.3
6.0	4.9	1.6
5.1	4.3	1.2

of escutcheon; deep anterior adductor scar beneath lower end of lunule; posterior adductor scar faint, slightly larger than anterior scar; small, elongate, anterior pedal retractor scar behind and above anterior adductor; very faint posterior pedal retractor scar near dorsal margin of posterior adductor; pallial line faint, without sinus; umbonal cavity roofed by hinge plate; ventral edge of hinge plate declined forward.

VARIATION: The size distribution in 25 right and 25 left valves, chosen by a table of random numbers, is shown in tables 4 and 5. The variation in height relative to length is shown in figures 8G-J and 23. The spacing of concentric ridges varies greatly and erratically (fig. 8D-F).

Valve convexity is variable, although the species is notably compressed compared with other Paleozoic astartids (fig. 24). A very shallow sulcus

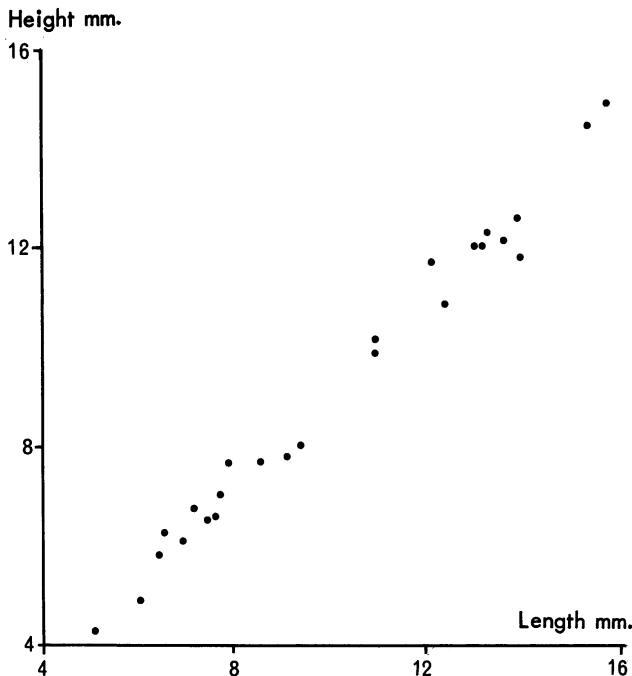


FIG. 23. Height/length ratio in left valves of *Astartella aueri*, new species. Data are in table 5.

is commonly present parallel to the posterodorsal margin and near it, but in some valves this is represented only by a slight flattening of the surface.

The left anterior cardinal varies in prominence with the degree of thickening of the valve edge in the critical area. The degree of thickening varies from prominent to imperceptible. The curvature of the major cardinal on the left valve increases as the tooth lengthens because the ventral component of inclination increases during growth. In a number of valves the sides of the major cardinal teeth and sockets are striated (fig. 8C). Incomplete transposition of the dentition is illustrated by one left valve and two right valves (fig. 7E, G). In each case, transposition has not affected the posterior laterals.

Several valves exhibit vestiges of minute crenulations on their inner ventral margins (fig. 22J). This feature is common in astartids from the post-Paleozoic but rare in those from the Paleozoic. In a few valves, a radial pattern is faintly visible as closely spaced black lines. These are found in translucent areas and appear to be opaque features beneath the

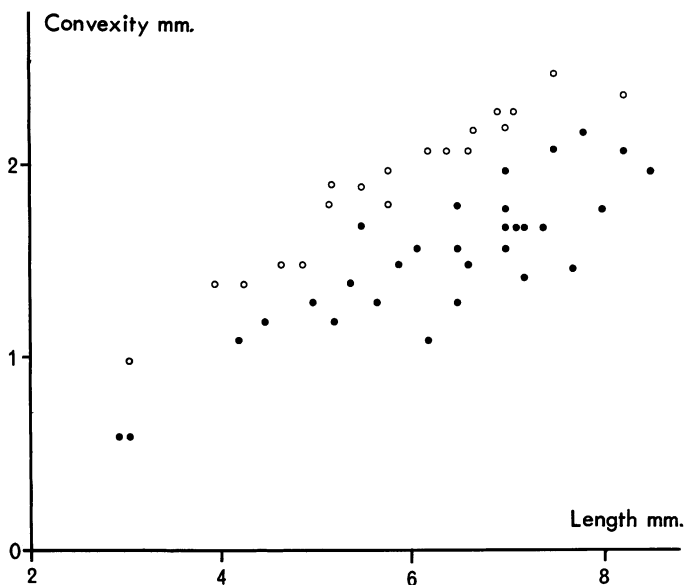


FIG. 24. Comparison of convexity/length ratio. Closed circles: *Astartella aueri*, new species. Open circles: *Astartella subquadrata* Girty. The samples include numerous specimens from the Kaibab Limestone of central Arizona and the Park City Formation of Beaver Creek, Wyoming.

valve surface (fig. 10C). Typical spacing of the lines is represented by one valve 8 mm. in height in which the black lines are five per 1 mm. in the ventral area and eight per 1 mm. in the posteroventral area. A similar pattern was illustrated by Girty (1915, pl. 18, fig. 9) on a specimen of *Astartella concentrica* (=vera) from the Wewoka Formation of Oklahoma which has three or four costae per 1 mm. in the depressed bands between concentric ridges. Girty (p. 143) wrote that, in some cases and perhaps in all, "this appearance is due to exfoliation and is probably to be connected with the rows of granules with which the margin is progressively marked." Girty (1915) reported that the valves show around their free edges a row of beading or dentition (fig. 6C, D).

COMPARISONS: *Astartella vallisneriana* (King), common in the Zechstein of Europe, has the ornamentation more prominent and more closely spaced, greater length relative to height, and a less concave and less steep anterior slope from the beak, than the Wyoming specimens. *Astartella subquadrata* Girty, of the Kaibab, San Andres, Yeso, Phosphoria, and equivalent formations in the western United States is more convex

and has a lower cardinal area (escutcheon) than does the new species. When convexity is plotted against length, the two species form adjacent but distinct patterns on a scatter diagram (fig. 24). Another distinctive difference between the two is that the beak in the new species is at the apex of the valve, whereas in *A. subquadrata* the beak is downcurved over the cardinal area. Girty's description did not mention dentition, but silicified specimens from the Kaibab Formation at the American Museum were compared by us with the Wyoming specimens, and we found that the dentition is essentially the same. *Astartella nasuta* Girty from the Permian of the southwestern United States has a notably truncate posterior.

OCCURRENCE: Phosphoria Formation (Grandeur Member), Beaver Creek, Wyoming. The new species is also represented in American Museum collections from the San Andres and Yeso formations and the Road Canyon Formation ("Word No. 1" limestone). In all three cases, *A. subquadrata* is also present. Ciriacks (1963) reported two specimens of *A. subquadrata* in the Grandeur Member of the Phosphoria Formation, but none was encountered in the present collection.

CATALOGUED SPECIMENS: Holotype, A.M.N.H. No. 28479; topotypes, A.M.N.H. Nos. 28482, 28483, 28486, 28492-28505, 28507-28515; and U.W. Nos. A1586, A1587.

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