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NOTES ON OLDHAMINID BRACHIOPODS*

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ABSTRACT—The aberrant brachiopod genera included in the family Oldhaminidae possess a peculiar brachial valve which has been thought to be an immobile internal plate. Detailed study of excellently preserved material suggests that the brachial valve was functional and served for protection and lophophore support. A ptycholophus lophophore was characteristic of the family and incurrent waters probably entered the shell via the distal ends of the lateral lobes while excurrent waters left it via the median incision. Two groups, one characterized by symmetrical and the other by asymmetrical musculature may be distinguished and do not coincide with the groups previously separated on the basis of symmetry or asymmetry of the brachial valve. Two new genera *Rigbyella* and *Pseudoleptodus* are described. A new species is questionably referred to *Adriana*. The Triassic genus *Pterophloios* is figured and discussed and is referred to the Oldhaminidae. Such ecologic data as exist are presented for each of the species considered.

INTRODUCTION

NOT uncommonly, an aberrant group arouses more interest and receives more study than is accorded important but commonplace relatives, and yet remains imperfectly understood. Among Upper Paleozoic brachiopods this has been the case with the unusual and highly specialized oldhaminids, for though they have received a disproportionately large amount of study they are still poorly known. Many investigations of the group have been based on imperfect material as witnessed by the fact that various representatives were placed first as fish and later as gastropods prior to their recognition as brachiopods. Recent studies of silicified Permian faunas from the Guadalupe Mountains of West Texas, based on nearly perfect specimens, have added many details to our knowledge of the group and so justify further discussion.

Many of the specimens examined reveal evidence of the nature and position of the soft parts, and this makes possible what are at least probable reconstructions of some gross aspects of the soft anatomy. Recovery of many specimens either in position of growth or clearly showing attachment scars permits some conclusions as to living habits. Good control on Permian water depth is possible in the collecting area and some indication of habitat preferences can be gained.

Since Waagen's (1882) recognition of the

oldhaminids as brachiopods, important studies of the group have been made by Noetling (1905), Watson (1917), Fredericks (1926), Wanner & Sieverts (1935) and by Williams (1953). The recent study by Williams is a comprehensive one which includes discussion of the shell structure, gross morphology and classification. He presents the arresting and original idea that the brachial valve in this group was an internal plate and the animal functionally univalved. It was in part to test this hypothesis that the present investigation was undertaken, and evidence bearing on this point is set forth below.

The brachial valve and associated structures.—The brachial valve in advanced oldhaminids is a highly complex structure which in outline more nearly resembles a fern frond than the typical brachiopod valve. It generally consists of a more or less massive posterior plate from which two main trunks, often posteriorly united, run forward giving off lateral branches. It has been shown by Williams (1953) that with the exception of a very small triangular area near the hinge the valve consists of only a single shell layer. This was determined by the study of sections but is also apparent from observation of the shell surface which exhibits numerous pseudopunctae (a feature of the inner shell layer of typical strophomenids) except in a small triangular area near the hinge, where they are hidden by the lamellar layer.

In Recent terebratuloid brachiopods Wil-

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liams has observed that the inner shell layer is secreted only by the surface of the mantle and that internal structures composed only of the inner layer are formed in invaginations of the mantle. From this evidence he reasons that the brachial valve of the oldhaminids, consisting almost exclusively of this shell layer, must have been internal.

The unusual shape of the brachial valve has excited the curiosity of many investigators and has evoked much speculation. If viewed in other than functional morphologic terms, its shape seems inexplicable. So considered, however, it becomes apparent that the peculiar shape must bear an intimate relationship to the lophophore. In all Recent articulate brachiopods the lophophore occupies most of the area between the valves while the remaining viscera are limited to a small posterior space. Fossil articulates giving evidence on this point also suggest that the lophophore generally occupied not only the anterior portions of the valves, but a majority of the enclosed space. It seems beyond doubt that a similar situation existed in the oldhaminids.

One of the prime functions of the brachial valve is the support of the lophophore and reduction of the valve may logically be supposed never to have proceeded to such a stage that efficiency as a lophophore support was lessened. This being the case, and the oldhaminid brachial valve being as drastically reduced as it is, it seems probable that its shape was closely related to that of the lophophore itself. A careful examination of the interior of the brachial valve in well preserved specimens reveals a slight ridge close to and paralleling the margin throughout the extent of the valve (Pl. 41, fig. 3). This ridge was probably the site of attachment of what can only have been a complexly ptycholophus lophophore.

Recent work on the feeding mechanisms of brachiopods by Richards (1952) suggests that feeding is accomplished by the forcing, under differential pressure, of the food bearing water currents past the filaments of the lophophore. Unfortunately, the observations leading to this conclusion were limited to one species, with a plectolophus lophophore, and were not complete. Such mechanical data as are now available indicate that the probable distribution of currents was as

Williams (1953, p. 284) has suggested, with incurrent waters entering the distal ends of the lateral lobes and excurrent waters leaving by way of the median incision. However, until a comprehensive study of the water current system of some living ptycholophus form such as *Lacazella* is carried out, it is impossible to do more than speculate about water currents in the oldhaminids.

Interpretation of the morphology and function of the oldhaminids depends considerably on the nature of the brachial valve. If, as Williams contends, the valve was an immobile internal plate, then function must be analyzed within the rather narrow parameters possible in such an animal. If, on the other hand the brachial valve was functional, the animals were less specialized than Williams suggests, and more like normal brachiopods. It is necessary therefore at this point to investigate evidence bearing on the function of the brachial valve.

The oldhaminid hinge is very short and in this respect quite unlike that of most related groups. Despite this peculiarity, the brachial valve rests freely in the articular area of the pedicle valve and was, when normally developed, structurally capable of considerable movement. Striated surfaces of the pedicle articular area suggest movement. The articulation is somewhat different in principle from that in most strophomenids for the two valves were not in contact throughout the extent of a long hinge but at two points only, one on either side of the hinge. This system had the advantage of continuously increasing the leverage of the diductor muscles as the valves became longer and heavier, for the point of articulation continued to migrate upward with growth. If the brachial valve were an immobile, internal plate such an adaption seems in-



TEXT-FIG. 1—Longitudinal section of part of an oldhaminid shell showing the relationships of the brachial valve to the pedicle valve and the seating notches in the latter in which the brachial valve snugly fits.

explicable as does the persistence of articulation itself.

Interpretation and even discovery of the muscle patterns in oldhaminids is often difficult because poor impression of the scars seems to be the rule. A careful examination of a large number of specimens and most published illustrations indicates that the group is divisible into two large sections on the basis of the muscle pattern. One group retains the essentially symmetrical musculature characteristic of brachiopods in general. The other possesses a peculiar and highly specialized asymmetrical musculature.

In the first group the musculature is basically symmetrical although individual variation due to asymmetry of the shell as a result of crowding or peculiarities of the attachment surface is high. The muscle pattern is fairly well known for at least some members of this group. *Coscinophora* Cooper & Stehli may be cited as an example. In the pedicle valve a pair of large elongate, medially located adductors are bordered by the much smaller, elongate diductors—such a size relationship is unlike that of other brachiopod groups, and the extreme development of the adductors was probably necessitated by the difficulties of holding a valve of such large surface area in place in agitated water. In the brachial valve the cardinal process is reduced in the fashion characteristic for oldhaminids. This was apparently required by the extreme shallowness of the body chamber and was not, as Williams implies (1953, p. 284), due to degeneracy. The feature can be seen, in well preserved specimens, to bear distinct scars for diductor attachment. Anterior to the cardinal process are the insertions of adductors, which can be seen only on exceptional material and then, poorly. If the size of the muscle scars is any indication of functionality, as indeed it must be, then the musculature of these animals was functional and not as Williams suggests "degenerate to a degree of almost total atrophy." It is interesting that *Coscinophora* which possesses well developed muscle scars also had a massive, brachial valve. This may account for their strong impression in this genus as contrasted to the weak impression in most others.

Among the asymmetrically muscled group

of oldhaminids, impression of muscle scars is very poor. Typically, only the very large right diductor muscle (interpretation of this large right muscle as having a diductor rather than adductor function as supposed by Watson (1917) is discussed under the description of *Adriana? guadalupensis*) scar can be noted, and this only because it was characteristically housed in a more or less calcified sheath. Such other muscle impressions as we have observed are discussed by Watson (1917) in his description of *Poikilosakos*. In this genus the brachial interior, insofar as the writer is aware, is almost completely unknown. In spite of very incomplete knowledge, it is apparent that the right diductor at least was large and presumably functional.

In summary, it may be said of such oldhaminids as preserve well impressed muscle scars, that the musculature is well developed and presumably powerful. As this is the case where the evidence is clear, it seems unnecessary to assume atrophy in those forms in which muscular impression is poor or in which the details of the musculature are simply unknown. The presence of well developed muscles seems to indicate that they were functional. Functional adductor and diductor muscles can only mean mobility of the brachial valve, unless the muscles had become modified to serve some other purpose, and of this there is no evidence whatever.

Williams believed that the oldhaminids could not move the brachial valve and suggests that this immobility was not detrimental to the animal. He suggests further that the brachial valve was elevated above the pedicle valve by the septal apparatus of the latter so that a steady current of nutrient and oxygen-bearing waters could enter the lophophore cavity by way of the distal ends of the lateral lobes and leave by the median incision. Careful examination of complete, and undamaged specimens indicates, however, that the edges of the brachial valve rested everywhere in contact with a receiving notch in the pedicle valve so that the brachial valve, at rest, was nowhere elevated above the pedicle (Pl. 42, fig. 3). It is apparent, then, that in order to introduce nutrient currents into the lophophore cavity, the brachial valve had to be

elevated, even if only slightly. Examination of a large series of oldhaminids indicates that where movement of the brachial valve of the animal was hampered by asymmetry of one or both valves, sufficient mobility was always maintained to allow slight anterior gape of the valves. Study of damaged Recent brachiopods which were dredged alive in apparent good health, indicates that the animals can continue to exist even with gape of the valves reduced to a very slight amount.

While the specific ancestors of the oldhaminids are not yet known, it is nevertheless true that all candidates for the position possess a normal entire and protective brachial valve. This is borne out also by the ontogeny of *Poikilosakos* in which the pinnate valve develops from an initially simple one. If the deductions of Williams are valid, then at some point both in phylogeny and ontogeny the brachial valve no longer was needed to serve a protective function. This suggestion does not clash with the known increase in the complexity of lobation of the brachial valve with time, for the valve freed of its former protective function could develop almost without regard for reduction in strength. The idea does seem to be at variance, however, with the trend toward secondary strengthening which is manifest in several later stocks. *Coscinophora* shows one modification in the direction of increasing strength. Here the posterior plate-like

portion of the brachial valve has become extremely massive and has incorporated a considerable portion of the valve. In addition dissepiments have developed between the lateral lobes uniting them at regular intervals. As has been pointed out above, the brachial valve of the oldhaminids can be interpreted meaningfully only by relating it to a ptycholophus lophophore. The dissepiments of *Coscinophora* do not bear any conceivable relationship to the lophophore and seem meaningful only if interpreted as an adaptation toward strengthening, a feature of doubtful value in an immobile internal plate. This conclusion is supported by the concomitant increase in the thickness of the pedicle valve, and may be related to a change in niche occupation such as invasion of a very rough water habitat.

The trend toward strengthening is also manifest in the last known member of the oldhaminid stock, the Upper Triassic genus, *Pterophloios*. In this form the brachial valve has become completely altered so as to present a secondarily smooth margin. It was definitely protective in function and covered the entire pedicle valve. This type of development is difficult to reconcile with the concept of an immobile, internal lophophore support.

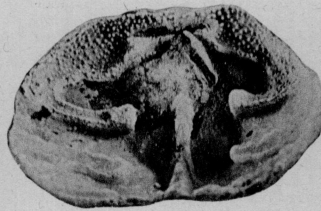
A final, though indirect, bit of evidence may be of interest here. Contrary to the assertion made by Williams (1953, p. 280), in discussing oldhaminid shell micro-struct-

EXPLANATION OF PLATE 41

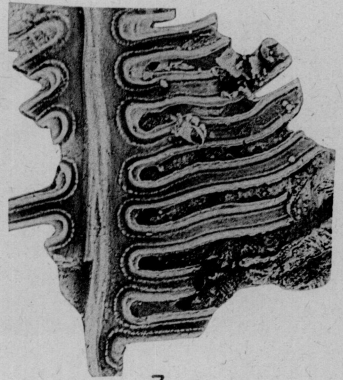
- FIG. 1,4,6,8—*Adriana? guadalupensis* Stehli, n. sp. 1, interior of pedicle valve (A.M.N.H. 27935:1) attached to a brachial valve of *Pylonotus* sp. and showing the two main trunks, $\times 3$. 4, profile of same specimen in assumed growth position showing the characteristic conical form of the pedicle valve, $\times 2$. 6, pedicle interior of same specimen showing the calcareous sheath which surrounded the large diductor muscle, $\times 3$. 8, pedicle interior (A.M.N.H. 27935:2) showing the septal apparatus and calcareous muscle sheath, $\times 3$.
- 3—*Leptodus* sp. (C.I.T. 5949). Interior of a fragmentary brachial valve showing the ridge believed to have been the site of lophophore attachment, $\times 1$.
- 2,5—*Pseudoleptodus getawayensis* Stehli, n. gen., n. sp. 2, hinge region of pedicle interior showing the asymmetrical musculature as indicated by the calcareous sheath of the right diductor (A.M.N.H. 27934:1), $\times 2$. 5, profile (A.M.N.H. 27934:2) showing the assumed growth habit and the conical form, $\times 2$.
- 7,9-13—*Rigbyella girtyi* (Wanner & Sieverts). 7, pedicle interior showing symmetrical adductor scars. (A.M.N.H. 27933:1), $\times 2.5$; 9, pedicle interior same specimen showing straight edged medial grooves and lobate lateral lobes, $\times 2$. 10, complete specimen (A.M.N.H. 27933:2) showing the brachial valve in place, $\times 4$. 11, pedicle valve still attached to a specimen of *Stenosisma* (A.M.N.H. 27933:3), $\times 3$. 12, pedicle exterior (A.M.N.H. 27933:2), note attached bryozoan, $\times 3$. 13, pedicle exterior (A.M.N.H. 27933:3) in position of growth, $\times 3$.



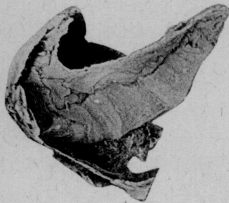
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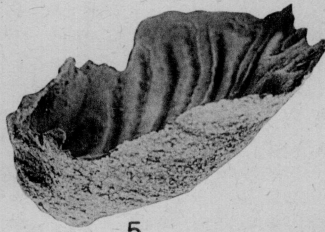
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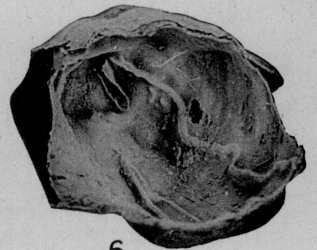
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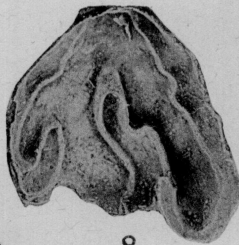
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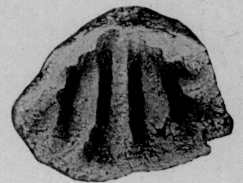
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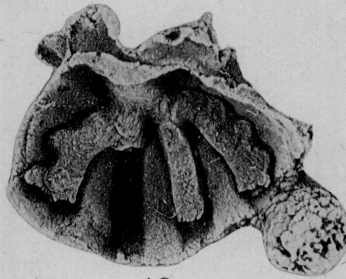
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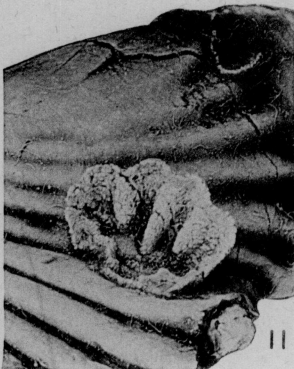
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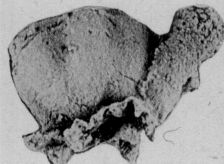
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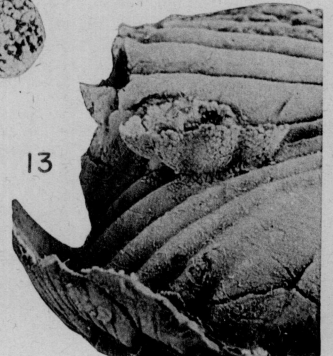
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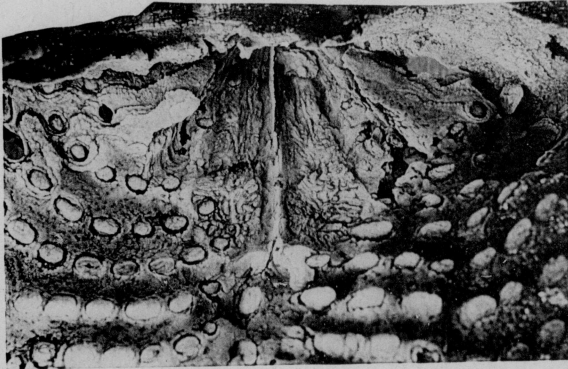
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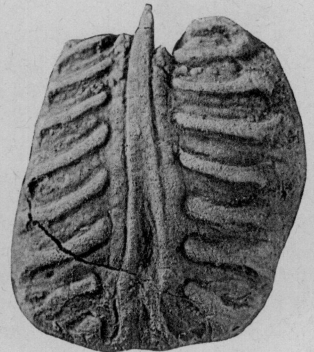
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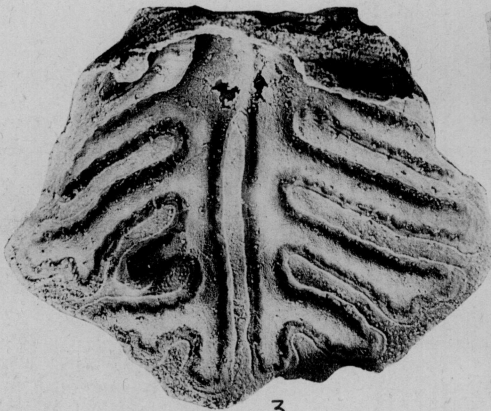
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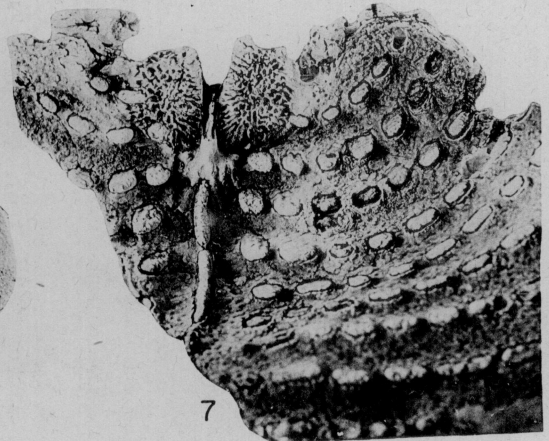
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ture, that "the absence of the lamellar layer for so large an area is not known in any other brachiopod," the lamellar layer is completely lacking in the brachial valve of brachiopods belonging to the productaceid family Richthofenidae. The strong articulation of the richthofenid brachial valve and its undoubted complete closure of the pedicle cone, leave little doubt that it was entirely functional. It seems hardly necessary to point out that the richthofenids are a great deal closer in relationship to the oldhaminids than are the terebratuloids. A more reasonable homology may thus be drawn between the two former than the two latter groups.

In the opinion of the writer the evidence brought forward above, both direct and indirect, tends to make the hypothesis of an internal brachial valve untenable. It appears far more likely that the cells at the tip of the mantle lobe of the oldhaminids and richthofenids either did not function as a depositional tissue beyond early ontogeny, or that at some point in the maturation of the animal, the metabolism and/or physiology of these cells was so altered that they like the rest of the mantle cells produced fibrous shell.

Remarks on soft part anatomy, growth habit and preferred habitat.—If, as the writer believes, the brachial valve of oldhaminids was external and functioned in part for protection, then the line along which closure took place (Pl. 42, fig. 3) marks a position to which the mantle of the pedicle valve had to be withdrawn during closure. The pedicle mantle must therefore have

been remarkably retractile. One is reminded of such modern gastropods as the various species of *Cyphoma* in which a thin, film-like mantle can be extended to cover the entire outer surface of the shell.

In general, the soft part anatomy of the oldhaminids of the symmetrically muscled group seem to have closely followed the basic plan for articulate brachiopods, except for the unusually large size of the adductors in the pedicle valve and the complexly ptycholophus lophophore in the brachial valve. Among the asymmetrically muscled forms, poor impression of muscle scars leaves considerable doubt as to the mechanics of valve articulation and deviation from the normal articulate brachiopod plan is extreme.

Apparently all oldhaminids with the exception of *Oldhamina* itself, were attached throughout life by the pedicle umbo, and even this genus was attached in early ontogeny. The exact mode of attachment is rather variable, and the pedicle valve may be entirely cemented or only attached apically. The larvae seem to have settled on suitable attachment sites and then initiated cemented shell growth. In many forms secretion of the initial cementation disc was followed by an abrupt turning away from the substratum. When found attached to objects which can be confidently restored to their life position, the oldhaminids are found to live in the positions shown in Plate 41, figures 4, 5, 13. Forms living attached to crinoid stems probably hung downward.

In the Guadalupe Mountains and the

EXPLANATION OF PLATE 42

- FIG. 1,3—*Pseudoleptodus getawayensis* Stehli, n. gen., n. sp. 1, hinge region (A.M.N.H. 27934:1) showing calcareous muscle sheath; note papillae which are in reality pseudopunctae, $\times 4.5$. 3, pedicle interior (A.M.N.H. 27934:2) showing the ridges indicating the seat of the brachial valve, $\times 2$.
- 2,7—*Coscinophora* sp. 2, hinge region showing large adductor scars at either side of the median septum and the laterally placed diductors, $\times 1.5$. Note also the characteristic beaded ridges of the genus. (C.I.T. 5950:1) 7, posterior of a partial pedicle valve showing the anterior ends of the adductor scars, $\times 2$. Note also the initiation of the pallial trunks between the muscle scars. (C.I.T. 5950:2)
- 4-6—*Pterophloios* sp., $\times 4$. 4, profile of brachial valve showing the calcareous shell material filling the inter-pinnal spaces (U.S.N.M. 108873); 5, posterior same specimen showing geniculation of valve indicating cementation of umbo of pedicle valve. 6, interior of brachial valve showing the characteristic pinnate structure of the oldhaminids with the secondary infilling characteristic of the genus.

Sierra Diablo where water depth can be rather closely estimated by reference to the tops of reefs on the assumption that they represent sea level, the oldhaminids prove to prefer shallow water. Scattered and probably transported shells are sometimes found in deep water areas, but large concentrations of shells essentially in place are shallow water deposits. With the exception of *Oldhamina* and those forms attaching to crinoid stems, most oldhaminids and all of the larger forms required hard bottoms. This requirement seems to have been equally well satisfied by reefs, rocky bottoms or accumulations of larger invertebrate skeletal debris. The water depth of the deposits in which oldhaminids are plentifully found suggests that they preferred to live in the illuminated zone.

Oldhaminoid classification.—The proper classification of the oldhaminid brachiopods has long been and still remains a perplexing question. The group has most frequently been assigned a place either among the Productacea or the Strophomenoidea. The complete absence of spines, a persistent productaceid character in any known species, seems to bar the group from a place among productaceids and by elimination strongly suggests that they are strophomenoids. No other group of brachiopods morphologically and temporally acceptable as ancestral to the oldhaminids is known, and it seems probable that they can be securely placed among the Strophomenoidea.

Williams (1953) believes that the oldhaminids can be divided into two distinct groups based on symmetry or asymmetry of the brachial valve. The results of the present study also suggest that a two-fold division can be made, but on the basis of symmetry or asymmetry of the musculature. Genera having both symmetrical and asymmetrical musculature fall within the group characterized by Williams as having symmetrical valve development. It is quite apparent that evidence afforded by valve symmetry and that afforded by muscle symmetry are not in accord, and the classification of the oldhaminids can not yet be regarded as stabilized.

The writer believes that a natural classification can be achieved only by considering all available characters and that tax-

onomy based on a single character must be suspect. In view of the obvious confusion still existing concerning the group, it is felt that its elevation to subordinal rank by Williams and his use of two family divisions, was unwise. Elevation of a group to higher taxonomic rank does not aid in discovering its relationships and merely serves to complicate the literature. For this reason, the writer prefers to retain the more conservative but also less misleading classification of the group into a single admittedly heterogeneous family within the Strophomenoidea pending some conclusive demonstration of lower rank relationships.

SYSTEMATICS

RIGBYELLA Stehli, n. gen.

Diganosis.—Small cup-shaped oldhaminids attached by cementation of the pedicle beak. Brachial valve symmetrical and consisting of few anteriorly directed lobes. Pedicle interior sometimes with three short myophragms immediately anterior to the hinge; musculature symmetrical.

Genotype: *Paralyttonia girtyi* Wanner & Sieverts, 1935.

RIGBYELLA GIRTYI (Wanner & Sieverts) Pl. 41, fig. 7,9-13

Leptodus americanus GIRTY, 1908, (considered *Rigbyella girtyi* to be the young of *L. americanus*), U. S. Geol. Survey, Prof. Paper 58, pl. 4, fig. 8-8b.

Paralyttonia girtyi WANNER & SIEVERTS, 1935, N. Jahrb. für Min., etc., Beilage Band 74, Abt. B, p. 209-210.

Diganosis.—Minute, cup-like *Rigbyella* cemented to a foreign object. Pedicle exterior with faint, irregular growth lines; attached by the beak and by a small wash of adventitious shell material; valve roughly cup-shaped, wider than long. Brachial valve symmetrical, very much reduced and consisting of four, or very rarely six, anteriorly directed lobes (when six lobes are present there are four primary lobes and each of the lateral primary lobes gives rise near the front to a smaller lobe); outer lobes bearing on their lateral margins several small irregular extensions while the median edge is straight; inner lobes straight on both edges; the four main lobes united posteriorly and terminated in a narrow hinge which is

slightly expanded at its articular edge; surface ornament destroyed by silicification in the specimens examined but probably consisting of fine papillae.

Pedicle interior with four deep troughs, corresponding to the lobes of the brachial valve, which are separated by ridges; troughs uniting posteriorly and bordered by a low ridge reaching the hinge; hinge with a triangular articular surface at either side; three low myophragms are sometimes present, parallel to one another and just anterior to the hinge, between them, or in this position when they are absent are elongate, symmetrical adductor muscle scars; diductor scars not impressed. Interior of the brachial valve unknown.

Discussion.—Girty (1908, pl. 4, fig. 8–8b) in his pioneer studies of the West Texas Permian figured a specimen of this species but incorrectly assigned it to *Leptodus americanus* of which he believed it to be a juvenile. This error has been pointed out by Wanner & Sieverts (1935) who place the species in the genus *Paralyttonia* under the name *P. girtyi*. Examination of a number of excellent silicified specimens from the Guadalupe Mountains of West Texas has shown that the species differs from *Paralyttonia* in many important respects. The growth habit is entirely different, *Rigbyella* being cup-like and free of the substratum except at the beak, while *Paralyttonia* is cemented by the entire outside of the pedicle valve. It further differs from *Paralyttonia* in the symmetrical development of the brachial valve and in the occasional presence of the three small myophragms in the pedicle valve.

It is quite clear from the specimens at hand that the brachial valve closely apposed the pedicle valve when closed and was completely free to articulate. The presence of symmetrically developed muscle scars in the pedicle valve suggests that it did in fact open and close.

In one specimen the pedicle valve is attached to a large specimen of *Stenosiscisma*. The shell of the host shows little evidence of wear, retaining much of the recurved skirt characteristic of the genus and was almost certainly not subject to much transport. If the host shell rested on the bottom, in what would seem the only likely position, with the pedicle valve down, then the attached

Rigbyella lived with the pedicle cup so oriented that the brachial valve was in a nearly horizontal plane.

R. girtyi is found in deposits which accumulated at the foot of the great Capitan reef during the latest phase of its existence. It can not be definitely ascertained whether the species lived here, where the water was between 1500 to 2000 feet deep, or whether it was a reef dweller which reached the deeper water after death, but the latter seems highly probable. Collections made in the reef, including portions of the same age as the beds containing *R. girtyi* have not revealed the species. As a statistical sample, however, the small collections hammered out of the reef are less satisfying than those obtained by acid etching of many cubic feet of the forereef limestones. Even in the silicified collections *R. girtyi* is very rare.

Range.—During the present investigations *R. girtyi* has been found only in the Lamar limestone member of the Bell Canyon formation. Girty (1908, p. 212) cites the species from the "Capitan formation, hill southwest of Guadalupe Point (station 2906)." Girty's stations have proved very difficult to locate as his usage of the term Capitan was not by any means the current one. His locality map indicates that station 2906 is in an area of fault blocks and his material may have come from any Leonardian or Guadalupian horizon.

Genus PSEUDOLEPTODUS Stehli, n. gen.

Genotype: *P. getawayensis*, n. sp.

Diagnosis.—Moderate sized, heavy shelled oldhaminoids. Pedical valve a squat cone. Brachial valve more or less symmetrically developed. Musculature asymmetrical.

Discussion.—This genus differs from the superficially similar group of genera closely related to *Leptodus* in the asymmetrical development of the musculature. From other asymmetrically muscled forms it differs in its heavy shell and in its symmetrical brachial valve. It might most easily be confused with *Keyserlingina* Tschernyschew which is a rather similar cup-shaped form. *Keyserlingina*, however, as shown by Tschernyschew (1902, pl. 42, fig. 15a and text-fig. 16) in *K. schellweini*, the genotype, does not possess the calcareous sheath for housing of the right diductor muscles

which characterizes asymmetrically muscled forms. The genus thus belongs to the symmetrically muscled group and is distinctly different from *Pseudoleptodus*. This conclusion is supported also by a figure given by Fredericks (1916, pl. 4, fig. 10) which shows an internal mold of *Keyserlingina* clearly showing the absence of the muscle sheath.

PSEUDOLEPTODUS GETAWAYENSIS

Stehli, n. sp.

Pl. 41, fig. 2,5; Pl. 42, fig. 1,3

Diagnosis.—Moderate sized oldhaminoids. Pedicle valve heavy shelled, forming a low cone, highest at the anterior margin; growth initiated as a flat plate on the object of attachment, in subsequent growth the margins become geniculated upwards to form the adult cone; valve marked only by irregular growth wrinkles. Brachial valve unknown except insofar as its shape is reflected by the pedicle valve. Pedicle interior with a short ridge-like hinge from which two ridges diverge indicating the form of the brachial valve, except posteriorly where the ridge excludes the articular areas at the hinge; lateral ridges of the "septal apparatus" usually single and massive; median ridge beginning at some distance in front of the hinge; lateral ridges inclined at about 45 degrees to the median ridge and numbering five or more on each side; interior of the cone especially the area not covered by the brachial valve, papillose; a single large diductor muscle scar is present on the right side, inside a calcareous sheath.

Material.—Two nearly perfect pedicle valves. A.M.N.H. 27934:2, holotype; 27934:1, paratype.

Discussion.—This species may be recognized by its thick shell, symmetrical brachial valve, moderate size and asymmetrical musculature. It seems to represent a branch of the stock which apparently originated with *Poikilosakos* that has converged with the "*Leptodus*" group in its external morphology. The species is found in association with symmetrically muscled, "*Leptodus*" forms of several types, but no other asymmetrically muscled species are found in the association. *P. getawayensis* is known only from one locality and here it occurs in what are believed to be detrital accumulations from a small reef which represented an area

of firm bottom on an otherwise muddy sea floor. No specimens have yet been found in position of growth; they presumably, because of their attached habit, grew on the reef or its flanks. All the known specimens came from distinctly detrital deposits where they were found disarticulated.

Range.—Known only from the lower part of the Getaway limestone member of the Cherry Canyon formation in the Guadalupe Mountains of West Texas. The specimens studied were collected at American Museum of Natural History locality 512 (Newell, et al., 1953, p. 223).

Genus ADRIANA de Gregorio, 1930

ADRIANA? GUADALUPENSIS

Stehli, n. sp.

Pl. 41, fig. 1,4,6,8

Diagnosis.—Small, Guadalupian oldhaminoids. Pedicle valve thin-shelled and forming a deep cone, highest at its anterior margin; growth initiated as a flat plate on the object of attachment; margins geniculated abruptly upwards as larger size is reached to form the adult cone; ornament consisting only of irregular growth wrinkles; shell very thin. Pedicle interior with a short ridge-like hinge at either side of which is a small, striated, triangular area for the articulation of the brachial valve; two diverging ridges run forward from the hinge ridge and, excluding the articular areas, outline the brachial valve; lateral and median ridges usually conspicuously double walled; median ridge arising a short distance anterior to the hinge; lateral ridges normally present and inclined at a low angle to the median ridge or sometimes subparallel to it, or more rarely scarcely developed; a single large diductor muscle scar is present on the right side where it is housed in an elongate shell-walled trough. Brachial valve pinnate and asymmetrical but otherwise unknown.

Material.—A.M.N.H. 27935; holotype A.M.N.H. 27935:1.

Discussion.—The reference of this species to *Adriana* must be considered, I believe, highly doubtful. Because of the inadequacy of de Gregorio's (1930) figures and description, it is thought better to make a tentative assignment to *Adriana*, rather than to propose a new generic category which may be synonymous.

The musculature of this species is similar to that of *Poikilosakos* as described by Watson (1917). That author believed that the large right muscle served an adductor function. The specimens of *Adriana? guadalupensis* examined in this study exhibit an extended calcareous sheath about this muscle which reaches almost to the position of the cardinal process. This is interpreted here to mean that the muscle served a diductor function.

Adriana? guadalupensis is known only from the Pinery limestone member of the Bell Canyon formation where it occurs in what are believed to be turbidity current deposits (Am. Mus. Nat. Hist. loc. 635).

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