NOTES ON THE BRACHIOPOD GENUS CARDINOCRANIA.

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ABSTRACT. Study of the only complete specimen known of the curious brachiopod described by Waagen in 1885 as *Cardinocrania* shows that it can not belong in the inarticulate family Craniidae, where Waagen placed it, but that it is in all probability the young of the genus *Richthofenia*, with which it is associated.

A FEW years ago the Geological Survey of India did the writer the great favor of permitting Mr. Austin M. N. Ghosh of its staff to make for him a large collection of the well preserved Permian fossils of the Salt Range. In this collection there were numerous specimens of *Cardinocrania indica*, among them a unique individual having the dorsal valve articulated with the lower or cemented valve. This, the only complete individual known, was found by Dr. H. de Terra, then connected with Yale University and in the field at the time with Mr. Ghosh. With this valuable specimen at hand, it at once became clear to the writer that *Cardinocrania* is not an inarticulate brachiopod, but that it belongs to the Protremata, and that it probably represents the young of the highly specialized genus *Richthofenia*.

Waagen found *Richthofenia* so strange that he felt himself obliged to erect for it the new brachiopod suborder Coralliopsidae. Since then we have learned much about what shell cementation does to inherited characters, not only in brachiopods but likewise in bivalves (rudistids) and in gastropods. The writer said, in his "Synopsis of American Fossil Brachiopoda" (1897): "In *Richthofenia* calcareous cementation is complete, and the modifications resulting therefrom have so changed the shell that the lower or fixed valve is very suggestive of a cyathophylloid coral, not only in form but even in shell structure" (p. 84). The coral-like features, other than the septa, are also seen in the cystiferous shell layers and in the tabulae in the posterior side which develop beneath the soft parts as the animal rises in its growing shell.

With regard to *Cardinocrania*, Waagen was very doubtful about its systematic position. He considered the possibility of its being "the juvenile state of *Richthofenia*," but gave up the idea because, so far as he could see, it does not have the "least traces of the vertical septa and of the pseudodeltidium" such as are possessed by *Richthofenia*. The rudiments of the delthyrium and deltidium are, however, present in *Cardinocrania*,

but are too small and obscure to have been fully appreciated by Waagen.

It is interesting to note, further, that Waagen also compared *Cardinocrania* with *Lyttonia* [=*Leptodus*], a genus which has a cardinal area and in addition has the posterior part of the dorsal valve much like that in *Richthofenia*. But here again he gave up the hint of genetic relationship, and he finally placed *Cardinocrania* in the inarticulate family Craniidae.

The most characteristic feature of *Cardinocrania*, Waagen took to be the cardinal area. The time was not then at hand to evaluate the presence of this structure, but we now know that no inarticulate brachiopod possesses a true cardinal area, and therefore *Cardinocrania* can not be referred to the family Craniidae, or, for that matter, to either of the orders of inarticulate brachiopods. Again, *Cardinocrania* has in the dorsal valve an enlarged but modified cardinal process—a structure unknown in any craniid—and this feature lends additional support to the conclusion that it is the young of some strophomenid.

The "elevated muscular platform" of the ventral valve described by Waagen is not seen in any of the Yale specimens, nor is there any homologous structure in *Richthofenia*. Evidently here he was misled by something extraneous in his material.

In *Cardinocrania*, the anterior margin is always more or less indented (a feature due to an inherited ventral sinus), and inside of the indentation there is a depressed septum directed posteriorly (see Pl. I, figs. 1-3, 5). This blunt septum develops into what Waagen called the saddle in the body chamber of *Richthofenia*.

Waagen held that the family Richthofeniidae should be placed "in the vicinity of the Productidae." Evidently he believed that the genus arose out of some form of the Productinae, a subfamily to which he also referred *Aulosteges*, although, curiously, he put the closely related *Strophalosia* in the Chonetinae. The progenitor of the coralliform *Richthofenia* must be sought, however, in a cemented ancestor. *Aulosteges* is not of this type, but all the species of *Strophalosia* are so fixed to foreign bodies. The last-named genus in all probability arose in *Productella*, a form that has (1) a narrow but distinct cardinal area transected by a narrow delthyrium, which is covered by a full-length deltidium, and (2) functional cardinal teeth. In Middle Devonian time the members of *Produc-*

tella evolved along two main lines. One, retaining the characters of *Chonetes* and the spinosity of *Productella*, became cemented by the ventral umbo, thus giving rise to the *Strophalosia* line. The other branch did not become cemented by the umbo, and, changing greatly, lost its peduncle, its cardinal area, and its hinge-teeth, and gave rise to the specialized, prolific, and highly variable productids. Cementation took place, beginning in the Middle Devonian *Strophalosia truncata* (Hall), because the peduncle was delicate and short, and, issuing through the apex of the ventral valve, presumably held the shell close to the object of attachment and thus caused the mantle around the peduncle to spread and deposit calcium carbonate.

Dunbar and Condra (1932) say that the typical productid shell has no hinge-teeth and no cardinal area, but, they add, "Several productid genera, on the other hand, possess a distinct cardinal area. We have become convinced that it is not in all cases a primitive character and has no more than generic value among the productids." Narrow cardinal areas, they state, appear "in certain of the Pennsylvanian species of *Dictyoclostus* and *Linoproductus*, though their Lower Carboniferous ancestors apparently had no area. A small area is

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LEGEND FOR PLATE.

Figs. 1-5. *Cardinocrania indica* Waagen.

1. A cluster of about fifteen ventral valves (not all shown in the photograph) on a *Linoproductus*. All the individuals are oriented in the same direction, i.e., with the anterior margin toward the ground. In other clusters, the individuals may be oriented differently, but within each group they are directed the same way. Nat. size. 2. Ventral shell, on *Meekella*. 3. Another, on *Linoproductus*. 4. The only known specimen with both valves in position, on *Spiriferella*; note the pustules on the dorsal valve, which are like those of *Richthofenia*. 5. Deformed specimen, on *Spiriferella*, which appears to have on the left side a sprawling spine like those in adult shells. All x 3.

Schuchert collection, Yale Peabody Museum.

Figs. 6-10. *Richthofenia lawrenciana* (Koninck).

6. Dorsal valve in place, showing faintly the minute pustules. Nat. size. 7. Partially exfoliated shell, with pustules. x 1.5. 8. Waagen's Fig. 15a, Pl. 83, of an exfoliated shell, showing greatly reduced cardinal area with modified deltidium and covered delthyrium. About nat. size. 9. Waagen's Fig. 3, Pl. 82A, showing dorsal valve with pustules surrounded by margin of ventral shell (= vestibule). x 2. 10. Waagen's Fig. 2, Pl. 83, another dorsal valve. Note the nature of the ventral cardinal area in all these figures, and the modified dorsal cardinal area including the outer surface of the cardinal process, together making the posterior portion of the upper valve.

Figs. 6 and 7 from Schuchert collection, Yale Peabody Museum.

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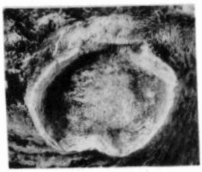

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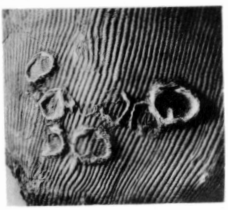

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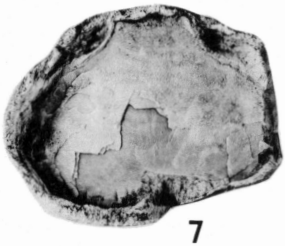

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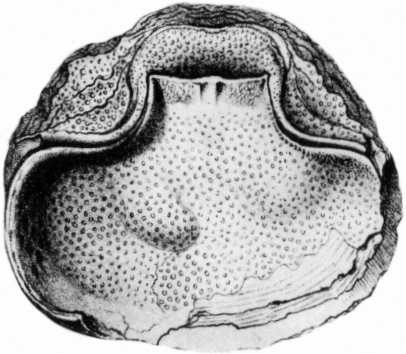

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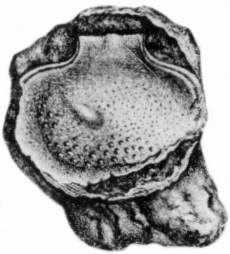

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Cardinocrania and Richthofenia

normally present also in the genus *Juresania*" (p. 183). These observations indicate that a narrow cardinal area may redevelop sporadically among the productids but that in none is it so striking a structure as in *Aulosteges.*

It is difficult to see in what kind of a productid *Richthofenia* could have arisen, since the former shells as a rule have no cardinal area with its associated structures. Genuine cardinal areas are, however, always present in *Strophalosia* and *Aulosteges.* If Waagen's Plate 62 illustrating the last-named genus is examined, and his figures compared with those of *Richthofenia* on his Plate 83, it will be seen that the characters of the latter are very much like those of *Aulosteges*, which is said to be one of the Strophalosiinae, but that they are modified in *Richthofenia* by the coral-like growth due to complete apical cementation. In *Strophalosia* we have all the characters of *Aulosteges* and, in addition, apical cementation. Accordingly, the writer holds that it was some form of *Strophalosia* that gave rise to *Richthofenia.* We now know that this transition took place at least as early as middle Upper Carboniferous time in *Teguliferina. T. armata* (Girty) is fully described by Dunbar and Condra (1932). These authors, however, do not believe that *Teguliferina* arose in some form of *Strophalosia*, but that it represents, more probably, "an independent development of the sessile habit out of *Marginifera*" (p. 277). This last productid genus, however, is an uncemented one, without cardinal areas and with a peculiar internal structure, and, as indicated above, can not have given rise to the Richthofeniidae, a family that seemingly must have arisen out of ancestors with functional cardinal areas.

As a result of cementation, the ventral cardinal area and its allied structures became obscured through burial in the much thickened coral-like growth of the shell, as shown in Fig. 8 of Plate I. On the other hand, ventral cementation did not much modify the inherited structures of the free dorsal valve, and here the cardinal process, and the vertical walls of the notothyrium and its chilidial covering, were flattened down into the articulating rectangular posterior hinge portion so conspicuous in youthful "*Cardinocrania*" and in adult *Richthofenia* (Pl. I, figs. 4, 6, 7, 9, 10).

The writer will not attempt to go further into the genetic relationships of the highly specialized brachiopods of the Richthofeniinae and the Scacchinellinae, but will refer those who wish to do so to Licharev's excellent study of 1928.

Looking now into the time range of these fossils, *Richthofenia* is unknown in the Upper Carboniferous, but appears early in the Lower Productus limestone and continues through the Middle and into the older part of the Upper Productus limestone. *Cardinocrania* is known in the upper part of the Lower Productus limestone and has the same upward range as *Richthofenia*, a fact noted by Waagen. In the collections at Yale, *Richthofenia* is present in thirty-one different lots, from different beds at four collecting grounds, and *Cardinocrania* in seventeen lots, most of which also include *Richthofenia.*

Probably the largest and best preserved Permian fauna known, with more than six hundred species, occurs on the island of Timor in the East Indies, to the north of Australia, and here *Cardinocrania* and *Richthofenia* are also found. Wanner and Sieverts (1935), in their excellent study of the Timor Lyttoniidae [= Leptodidae], describe *Cardinocrania waageni*, but regard the genus as an articulate brachiopod and as the most primitive adult stage in the evolution of the family. However, the species mentioned does not have the multilobed lophophore seen in all stages of growth in the Leptodidae, but, instead, the lophophore remains in the bilobed or schizolophus stage of development. It does not appear that these authors ever thought that their *C. waageni* might be the young of *Richthofenia*, a genus sparingly present in the Timor Permian, as we learned long ago from Broili (1916). They were possibly led to their opinion regarding the relationships of their species by Waagen's remark that *Cardinocrania* might be related to *Lyttonia.* The present writer suggests that *C. waageni* is but a young stage of *Richthofenia lawrenciana*, which, according to Broili, is found at Besleo, the type locality of *C. waageni.*

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