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The Ventral Armor and Feeding Biomechanics of *Glyptaspis verrucosa* Newberry, a Placoderm From the Fammenian Cleveland Shale

JOHN C. BOYLAN¹ AND PAULA A. MURPHY²

ABSTRACT

The four plates that constitute the sole known remains of *Glyptaspis verrucosa* Newberry are identified and described. The identification of these elements allows them to be properly placed and fitted relative to one another and permits a complete reconstruction and restoration of the ventral thoracic armor. On the basis of the detailed anatomical study of

these plates it is possible to rule out speculations of previous authors that the ventral armor plates of *Glyptaspis verrucosa* might actually be the ventral plates of *Mylostoma* or *Diplognathus*. The present study also serves as a foundation for speculation on the biomechanics of feeding in *Glyptaspis*.

INTRODUCTION

Glyptaspis verrucosa Newberry is known solely from four ventral plates. These thoracic elements have, for the most part, been misidentified or not identified. Neither the elements themselves nor their relationships to one another have ever been adequately described. With little or no firm factual foundation, previous authors have suggested that these thoracic plates may actually have been the ventral armor of *Mylostoma* or *Diplognathus*.

and Mr. Walter Sorensen of the American Museum and Dr. David H. Dunkle of the Cleveland Museum of Natural History for their help and encouragement. Our gratitude is also extended to Mr. Michael Kossman, Hunter College, the City University of New York, who translated several portions of Russian text for us. One of us (Boylan) wishes to acknowledge a very special debt of gratitude to Dr. William L. Donn of the City College of the City University of New York and Lamont-Doherty Geological Observatory for his help and encouragement over the years.

ACKNOWLEDGMENTS

We thank the Department of Vertebrate Paleontology of the American Museum of Natural History for the use of its facilities and for specimens used in this study. We especially thank Dr. Bobb Schaeffer, Mr. Earl Manning,

PREVIOUS WORK

The genus *Glyptaspis* with *G. verrucosa* as the type species was erected by Newberry

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(1889, pp. 157-159). It is known only from four ventral plates from the Cleveland Shale (see Claypole, 1896, p. 351; 1903, p. 320) that were discovered by Terrell. Newberry (1889, p. 158) correctly identified one of these elements (AMNH 94G) as a "ventromedian" [postero-ventromedian] plate. He believed that the remaining three elements were part of a series of nonimbricating scutes situated along the flanks "like the scutes of the sturgeons."

Eastman (1907, pp. 147-149, pl. 13) erected the new species, *G. abbreviata*, on the basis of a single plate that he believed to be "identifiable as the right antero-ventrolateral of a form closely resembling the type species of *Glyptaspis*." He also referred "a few fragmentary plates" from the "Black slate of Kentucky (Genesee)" and from the Portage Shale of Seneca County, New York, to this species. He noted that the right anteroventrolateral plate had a significantly different length to width ratio from that of *G. verrucosa*. He stated that "actual specimens are wanting of the corresponding plate in *G. verrucosa*," but that a general idea of its configuration could be obtained by examining the overlap areas that accommodated it on the posteroventromedian and antero-ventromedian plates. The "ventromedian plate" figured by Newberry (1889, pl. XIII, fig. 1) was correctly identified by Eastman as a posteroventromedian element. Newberry (1889, pl. XIII, fig. 2) identified another element as a "lateral plate from the dorsal? surface." Eastman (1907, p. 148), attempting to correct Newberry, incorrectly identified this plate as an "anterior ventromedian." It was on this element that the supposed overlap areas for the anteroventrolateral plate were, according to Eastman, to be found. Such overlap areas are nonexistent. This specimen (AMNH 93G) is an anteroventrolateral plate.

On the basis of a comparison of its ornamentation and general configuration with those of *G. verrucosa*, Hussakof and Bryant (1918, pp. 102-104) stated that Eastman's "type of *G. abbreviata* belongs properly in the genus *Holonema* of Newberry" and erected the species *H. abbreviatum* with Eastman's specimens as the type.

Wells (1942, p. 655) removed Eastman's *G.*

abbreviata from the genus *Holonema* and erected the genus *Deirosteus* with *D. abbreviata* (Eastman) as the genotype. Into this new genus Wells placed three specimens from the Lower Enfield Formation on Tompkins County, New York, and the type specimen of *Holoptychius omaliusii* (Agassiz, 1844, p. 75, pl. 24, fig. 11; Woodward 1891, p. 331). Wells also referred two Buffalo Museum of Science specimens, BMS E 2008, catalogued by Hussakof and Bryant (1918, p. 60, fig. 18; pl. 19, fig. 2) as a "median occipital" of *Dinichthys* sp. and BMS E 2025 (*ibid.*, pp. 103-104; pl. 31) to the genus *Deirosteus*.

Obruchev and Sergienko (1961, p. 562) referred some material from the Saian-Altai Mountain Region of the Soviet Union to the genus *Deirosteus* and on the basis of these remains erected the species *D. angustatus*.

Clarke and Swartz (1913, p. 700, pl. LXX-III, figs. 1-3) erected a new genus, *G. eastmani*, on the basis of three specimens from two different locations in the Parkhead member of the Jennings Formation of Maryland. Hussakof and Bryant (1918, p. 104), however, suggested that these three specimens belong in the genus *Holonema* and possibly in the species *H. rugosum*.

Branson (1922, p. 128; pl. 31, fig. 3) referred a dermal plate from the Snyder Creek Shale of Callaway County, Missouri, to the genus *Glyptaspis*. The ornamentation on this element is wholly unlike that found on any of the specimens that Newberry (1889, pp. 157-159) referred to *G. verrucosa*. It is, in our opinion, not congeneric.

CLASS PLACODERMI McCoy, 1848

SUBCLASS ARTHRODIRA Gross, 1932

SUPERORDER EUARTHRODIRA Gross, 1932

EUARTHRODIRA *INCERTAE SEDIS*

Glyptaspis verrucosa Newberry, 1889

REFERRED SPECIMENS: AMNH 92G, left PVL plate; AMNH 93G, left AVL plate; AMNH 94G, PMV plate; AMNH 95G, (?) right PVL plate. All from Fammenian Cleveland Shale of Ohio.

DIAGNOSIS: Member of the Euarthrodira

known only from four ventral thoracic armor plates. Typical euarthrodiran ventral armor plate arrangement. Distinctive tubercular ornamentation concentrated in large sharply defined, concentrically located areas on all known elements. Overlap areas composed of smooth, dense bone. Overlap relationships extremely loose and no apparent fusion between elements. Unornamented overlap areas separated from central ornamented regions by broad, low-lying unornamented ridge. Distinctive shape of central ornamented area of PMV plate consists of larger, anterior, triangular area confluent, base-to-base, with smaller, posterior, similarly shaped area. PMV plate relatively larger than PMV of any described cocosteomorph (*sensu* Stensio, 1959; 1963) and pachyosteomorph (*ibid.*) euarthrodirans. No postpectoral connection between PVL and PL plates.

DISCUSSION: The left anteroventrolateral (AVL) plate (AMNH 93G) is roughly triangular (fig. 1). The anterior border is lost except for its anteromedial corner. From this remnant, however, it is possible to reconstruct the anterior border. The central, ornamented portion of this plate is paralleled by a peripheral unornamented area of reasonably uniform width. The preserved anteromedial corner indicates the direction and orientation of the anterior margin of the ornamented region. From the foregoing it appears that the anterior border was reasonably regular and fairly straight. It extended in a posterolateral direction.

The lateral border of this plate is more convexly arcuate than the medial border.

The medial margin of the AVL element appears to be composed of two subequal parts. The slightly larger posterior part extends in an anteromedial direction. The anterior segment extends in an anterior direction.

The lateral and medial borders of the AVL plate meet in a posteriorly projecting point that overlaps the anterior end of the PVL element (fig. 1).

The internal surface of the AVL element is relatively featureless. Along the medial bordering region there is a distinct break in slope that marks the lateral limit of the area that overlaps the PMV plate.

The outline of the central ornamented region

is generally concentric with the outline of the entire AVL element. The ornamentation consists of numerous tubercles varying noticeably in size. They show some evidence of alignment. In many places the tubercles have fused, forming elongate, ornamental ridges of various lengths. In such regions of fusion the evidence for alignment is more persuasive. The lineation seems to parallel, to some extent, the border of the ornamented region, and because of the aforementioned concentricity, to be roughly parallel to the border of the AVL plate itself (fig. 1).

The alignment of the minute bone trabeculae in the unornamented portions of the plate indicates peripheral accretionary growth similar to that in *Eastmanosteus* (Boylan MS).

Most of the left posteroventrolateral (PVL) plate (AMNH 92G) of *Glyptaspis verrucosa* is preserved. It is roughly elliptical. The posterior end is missing but a good estimate of its shape can be obtained from the direction and degree of convergence of the lateral and medial borders. This element probably terminated posteriorly in a slightly blunted point. In contrast the anterior end is almost complete and is arcuate in outline (fig. 2).

The lateral border is smoothly arcuate. The medial border consists of two subequal portions. The anterior portion extends in a slightly anterolateral direction, whereas the posterior portion extends in a posterolateral direction. The medial border thus has a slightly angular appearance. The two portions of this border meet about midway along the length of the bone forming an extremely obtuse angle.

The ornamented portion of the PVL plate accounts for most of the external surface. A more or less concentric unornamented region borders the central ornamented area. It is about the same width throughout.

The anterior overlap area for the posterior end of the AVL element is set off from the remainder of the PVL plate by a low, broad, unornamented ridge. The overlap area is triangular and sharply pointed posteriorly.

The ornamentation on the external surface of the PVL plate is similar to that on the AVL element. It consists of tubercles of various sizes. Some degree of alignment is exhibited in certain areas. The alignment tends to parallel

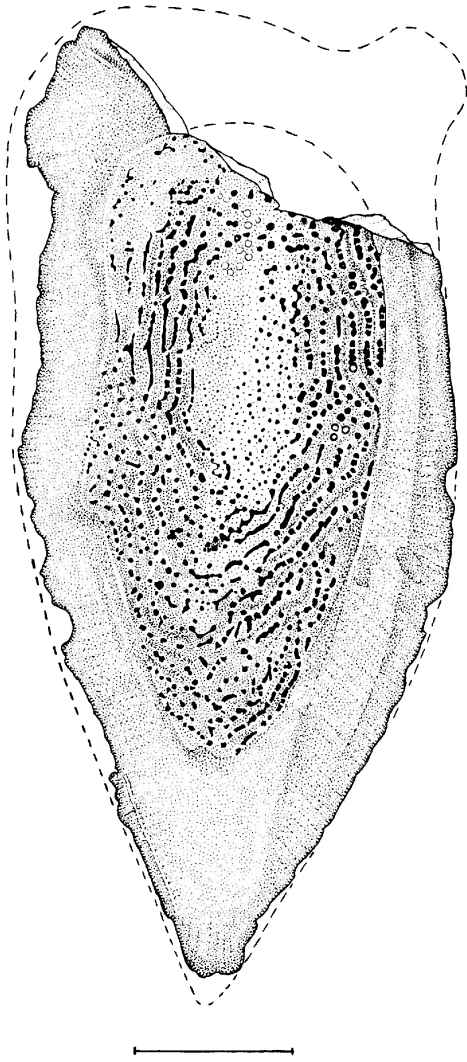


FIG 1. Anteroventrrolateral plate of *Glyptaspis verrucosa*. Scale line equals 50 mm. and refers to figures 1, 2, and 3.

the border of the ornamented area and, therefore, the border of the element itself. The tubercles occasionally merge into elongate, knobby ridges with a similar alignment. The arrangement probably indicates growth by peripheral accretion.

The posteromedianventral (PMV) plate (AMNH 94G) is roughly diamond-shaped. It reaches its maximum width (approximately 175

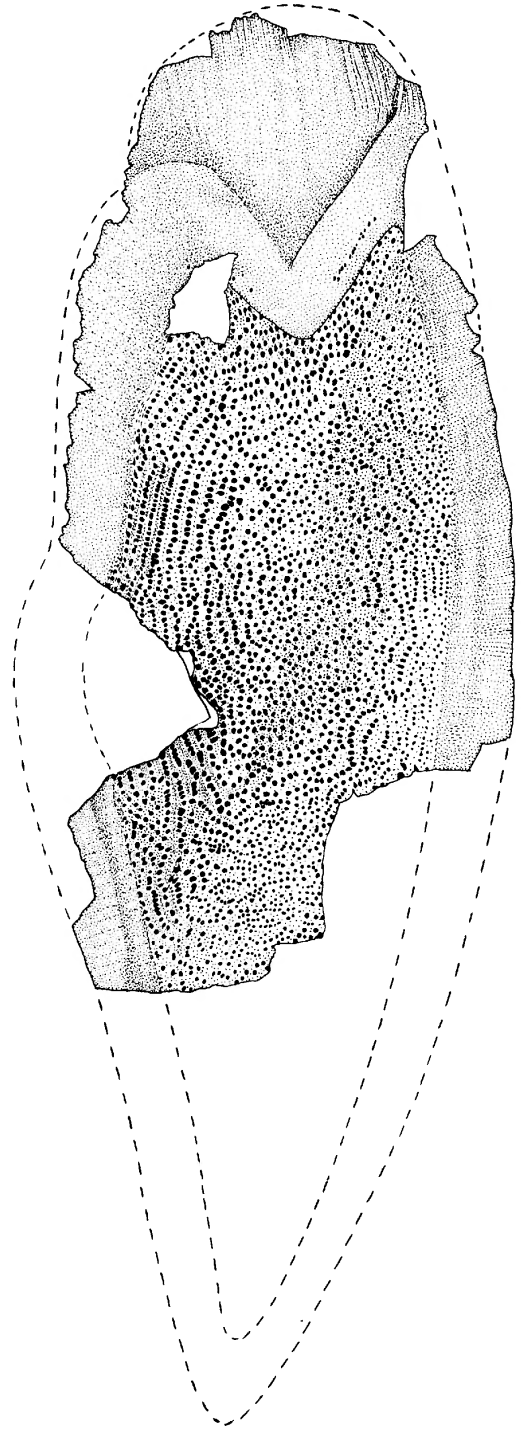


FIG 2. Posteroventrolateral plate of *Glyptaspis verrucosa*.

mm.) just posterior to the midpoint of its anteroposterior axis (fig. 3).

The central ornamented portion of the PMV plate is also diamond-shaped but this shape is, to some extent, modified. It is composed of two triangles resting base-to-base. The base of the anterior triangle is appreciably wider. The bases of these triangles coincide with the line of maximum width of the PMV element. The central ornamented region thus resembles an arrowhead.

The central ornamented area is separated from a bordering unornamented region by a broad, low, unornamented ridge. In places this ridge merges almost imperceptibly with the unornamented overlap regions. In other places it is sharply set off from these overlap areas. The overlap areas completely surround the central ornamented area.

Overlap areas for the left and right AVL plates are situated anterior to the line of maximum width of the PMV element. These areas reach their maximum width near the blunted apex of the anterior triangular portion of the ornamented region. Anterior to this apical region these AVL overlap areas do not merge but are separated by an elongate low-lying ridge. This ridge extends anteriorly from the anterior apex of the central ornamented area. It becomes less pronounced anteriorly. The right and left AVL overlap areas may have been separated at their anterior extremities by a small centrally located overlap area for the reception of the posterior extremity of the AMV plate as in *Dunkleosteus* (Heintz, 1932, p. 173, fig. 59A,B) and *Coccosteus* (Miles and Westoll, 1968, p. 434, fig. 37; p. 436, fig. 39d,f). Because this region is broken, the presence or absence of such an overlap area is problematical.

Posterior to its line of maximum width the PMV element is bounded by overlap areas for the PVL plates. These areas are of lesser rostrocaudal extent than the AVL overlap areas. Their maximum width lies near the region where the broader anterior triangular portion of the ornamented region merges with the posterior part.

The ornamentation of the PMV element is

like that on the other plates. There is some indication of alignment of the tubercles in rows that roughly parallel the borders of both the ornamented area and the plate itself. In places the tubercles merge into ridges similar to those on the AVL and PVL elements. A small central

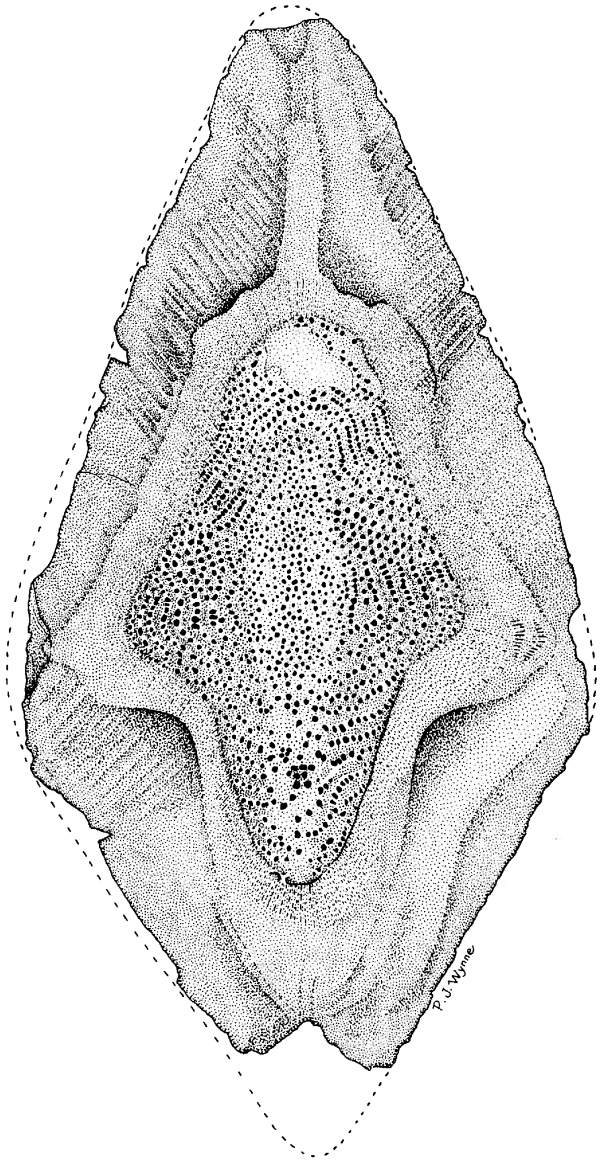


FIG. 3. Posteromedianventrolateral plate of *Glyptaspis verrucosa*.

area of ornamentation contains smaller, more randomly arranged, and more densely packed tubercles. We believe that this represents the original ornamented surface of the PMV plate at the initial stage of postnatal ontogeny and that the areas showing a tendency toward alignment were added subsequently by peripheral accretionary growth.

The lineation that can be observed in the minute bone trabeculae in the unornamented regions of the PMV plate, such as the overlap areas and the internal surface, seems to converge toward a center of ossification that coincides with the central region of randomly oriented tubercles. This lends support to our belief that this region is the primordial nucleus of subsequent marginal accretionary bone growth.

No anteromedianventral (AMV) plate of *Glyptaspis verrucosa* is known. It can, however, be reconstructed. It must fill the space bounded laterally by the left and right AVL plates and posteriorly by the PMV plate. It would therefore have a triangular shape. Its anterior border would, in all probability, continue the line established by anterior margins of the AVL plates. As noted in the description of the PMV plate, it is possible that the AMV element overlapped the anterior end of the PMV plate. The AMV plate was probably overlapped laterally by the AVL elements.

Since all the other known plates of *Glyptaspis verrucosa* are heavily ornamented, it seems likely that similar tuberculation would be present on the AMV element. It is just as probable that the external ornamentation was concentrated in the central region of the external surface and that it was separated from the overlap areas and the bone margins by a band-like unornamented area.

We have based our restoration of the AMV element of *Glyptaspis verrucosa* on the limits and probabilities considered in the preceding two paragraphs.

An additional fragmentary specimen (AMNH 95G) completes the array of dermal plates that can be referred to *G. verrucosa* with any degree of certainty. It appears to be the anterior end of the right PVL plate but is so

fragmentary that a definite identification is hardly possible.

COMPARATIVE MORPHOLOGY, RELATIONSHIPS, AND BIOMECHANICS OF FEEDING

The only elements that can be referred definitely to *Glyptaspis verrucosa* are the four ventral elements mentioned in the descriptive section of this study. As a result, the comparative and relational statements that can be made concerning *G. verrucosa* are stringently limited.

Newberry (1889, p. 158) suggested the possibility that the gnathal elements of *Mylostoma* (Newberry, 1883, pp. 144-147) may be found in association with the plates of *Glyptaspis* and that such an association would demonstrate that the ventral plates upon which the genus *Glyptaspis* is based are, in reality, part of the thoracic shield of *Mylostoma*. Subsequent discoveries have, however, ruled out this possibility (see, *inter alia*: Dean, 1901, pp. 101-109; pls. VII, VIII; Eastman, 1906, pp. 21-22; Hlavin and Boreske, 1973, p. 11, pls. IA,B). The gnathal elements of *Mylostoma* have been found in intimate association with other plates of the dermal armor. It is evident that none of the plates associated with the gnathal elements of *Mylostoma* are those of *Glyptaspis*.

More interesting from a speculative point of view is Newberry's (1889, p. 158) suggestion that the gnathal elements that have been given the specific designation *Diplognathus mirabilis* (Newberry, 1878, pp. 188-189) may be part of the same placoderm to which this ventral armor belongs. Eastman (1908, footnote on p. 181) believed that "as suggested by Newberry, there is considerable reason to suppose that the mandibles known under this name [*Diplognathus*] and the detached abdominal plates assigned to the provisional genus *Glyptaspis*, belonged in reality to the same kind of fish." Eastman's statement is misleading. Newberry's suggestion was merely that, and was not couched in terms as strong as those employed by Eastman. Newberry (1889, p. 158) merely stated that such

anatomical discoveries are "quite possible" but "not certain" and stressed the indications that the fish fauna of the Cleveland Shale was more diverse than was then known and contained "other genera and species than those already described."

No further remains have been discovered that can definitely be said to be the gnathal elements of *Glyptaspis*. Only the suborbital (SO) plate of *Diplognathus* has definitely been identified in addition to the gnathal elements (infragnathal, anteroinfragnathal, posterosupragnathal). Dunkle and Bungart (1943, p. 73) noted that although many other dermal plates of *Diplognathus mirabilis* are present in the same concretion with the suborbital, infragnathal, anteroinfragnathal, and posterosupragnathal elements, these other plates are fragmented and unidentifiable. The SO plate of *Diplognathus* does not display the highly developed, elaborate ornamentation seen on the ventral elements of *Glyptaspis*. This in itself, although not entirely conclusive, would tend to rule out Newberry's (1889, p. 158) conjecture that the ventral plates referred to *Glyptaspis* were in reality those of *Diplognathus*.

Newberry (1878, p. 188) believed that the gnathal plates of *Diplognathus mirabilis* "would form a very effective instrument for catching slender slippery fishes . . ." and even a most perfunctory examination of these infragnathal rami tends to bear this out. Newberry (1889, p. 159) later restated the case in somewhat stronger terms. Dunkle and Bungart (1943, p. 83) agreed with Newberry. If we use this consensus as a point of departure, the acceptance of the function suggested by Newberry (1878, p. 188; 1889, p. 159) leads to certain conclusions concerning *Diplognathus mirabilis*. With such prey as its staple diet, a predator would seemingly have to be fairly agile. *Diplognathus* must have been designed for quickness and reasonably high mobility. The ventral armor of *Glyptaspis* is of relatively great thickness. If the remaining, so far undiscovered, plates of *Glyptaspis* are of similar thickness then the probability of its being a fleet and agile predator seems remote.

The dimensions of the PMV plate of *Glyp-*

taspis are interesting. It is approximately 325 mm. long and about 175 mm. in maximum width. Some degree of breakage is present and these figures can probably be increased by 10 percent for the width and 5 to 10 percent for the length. The PMV plate of *G. verrucosa* makes a much greater contribution to the ventral armor than does its homolog in either *Dunkleosteus* (Heintz, 1932, p. 175, fig. 61), or *Coccoosteus cuspidatus* (see, *inter alia*, Dean, 1909, p. 283, fig. 62; Heintz, 1929, p. 13, fig. 1; Miles and Westoll, 1968, p. 434, fig. 37; p. 444, fig. 45, p. 455, fig. 49; pl. IV).

In *Glyptaspis* the ratio between the exposed length of the PMV plate and the length of the entire ventral thoracic armor is about 0.50, whereas in *Dunkleosteus* this ratio is about 0.35. The ratio between the exposed width of the PMV element and the total width of the ventral armor in *Glyptaspis* is also about 0.50. In *Dunkleosteus* this ratio is only approximately 0.20. The comparative magnitude of the contribution made by the PMV plate to the ventral thoracic armor of *Glyptaspis* is apparent in these ratios (see figs. 4, 5).

We believe that the accentuated importance of the PMV plate in *Glyptaspis verrucosa* is a character state that it shares with such primitive members of the Euarthrodira as *Jaekelaspis decipiens* (Heintz, 1929a, p. 37, fig. 10B; p. 39, fig. 12A; pl. I; pl. IV, fig. 1); *Monaspis acuticornis* (*ibid.*, p. 64, fig. 29); *Acanthaspis prümensis* (*ibid.*, p. 71, fig. 34); *Acanthaspis arcticus* (*ibid.*, p. 73); *Arctaspis holtedahli* (*ibid.*, pl. IX, fig. 2); *Arctaspis hoeli* (*ibid.*, pl. X, fig. 1); *Plataspis brevicornis* (*ibid.*, pl. XIII, fig. 2); *Huginaspis vogti* (*ibid.*, pl. XX, fig. 1); and *Huginaspis bröggeri* (Heintz, 1929b, p. 15, fig. 5A; pl. II, fig. 2; pl. III). This primitive character state persisted in *Glyptaspis verrucosa* despite the fact this species shares with many of the advanced Euarthrodira such derived character states as the lack of any postpectoral connection between the PVL and posterolateral (PL) plates and, apparently, extreme reduction or elimination of the spinal (SP) plate.

The extreme smoothness of the overlap areas on the PMV plate of *Glyptaspis* is striking. These dense, shiny areas show little or no ir-

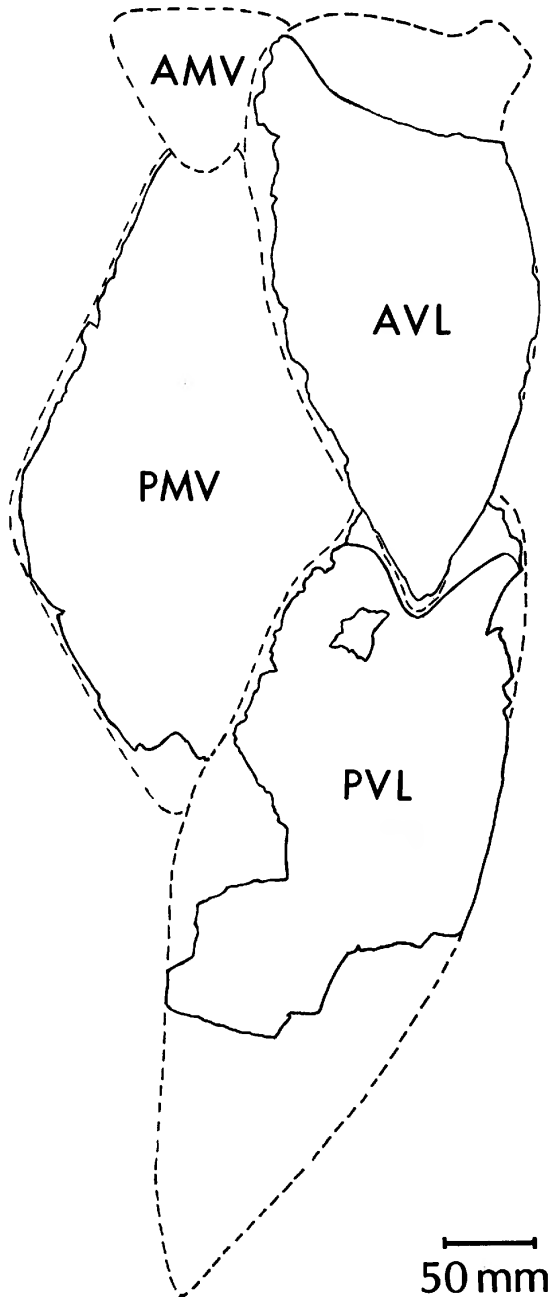


FIG 4. Elements of the ventral armor of *Glyptaspis verrucosa* arranged as in life. 50 mm. scale refers to figures 4 and 5.

regularity and no sponginess or rugosity (Newberry, 1889, pp. 158-159). This indicates that the overlapping relation with neighboring plates

was no more than a loose, and probably expandable or sliding, imbrication. There was, in effect, no strong, tightly knit suture between the PMV plate and the AVL and PVL elements. A similar overlapping relationship seems to have existed between the posterior end of the AVL plate and the anterior end of the PVL element.

The essentially flat-based, triangular, transverse section of the thoracic armor of many primitive euarthrodires (Heintz, 1929a, 1929b) indicates that they were undoubtedly bottom-dwelling forms. We agree with Heintz (1929a, pp. 72-73) that the flatness of the ventral thoracic armor and the outward projection of the enlarged SP plates in the same plane as the ventral thoracic plates indicate that these primitive euarthrodires were benthonic.

The relative thickness of the ventral plates indicates that *Glyptaspis verrucosa* was, in all probability, a benthonic form. Slightly less convincing, but certainly supportive of this bottom-dwelling hypothesis, is the elaborate ornamentation on these ventral elements. The analogy with living fishes is apparent. Elaborate surficial ornamentation is typical of bottom-dwelling fishes. Among living chondrichthyans and osteichthyans, the strong pelagic swimmers are almost invariably smoothly surfaced.

All available anatomical evidence indicates that both *G. verrucosa* and the primitive euarthrodires were bottom dwellers. As has been pointed out, the relative size and importance of the PMV plate is a primitive character state shared by *Glyptaspis* and the primitive Euarthrodira. It is therefore speculative, but justifiable, to suppose that *Glyptaspis* filled an ecological niche similar to the earlier niche occupied by the phlyctaenaspid euarthrodires. Many of the phlyctaenaspids probably grubbed in bottom sediments, feeding on small arthropods, molluscs, and other invertebrates. The ingestion of such small organisms probably involved little more than grabbing and gulping, strikingly similar to the mode of feeding of living codfish. Examination of codfish entrails reveals that little or no comminution or crushing is involved when feeding on small crabs or clams. It is safe to assume that *Glyptaspis* fed in the same way. If the gnathal elements of

Glyptaspis are ever found, it is probable that they will resemble the relatively unspecialized jaw ossifications of the phyllyctenaspids (Miles, 1969, p. 146).

The loosely articulated nature of the ventral

thoracic plates of *Glyptaspis verrucosa* would allow expansion of the body wall of the trunk. Miles (1969, p. 146) mentioned the development of a postbranchial lamina in the phyllyctenaspids. In coccosteomorphs and pachyoste-

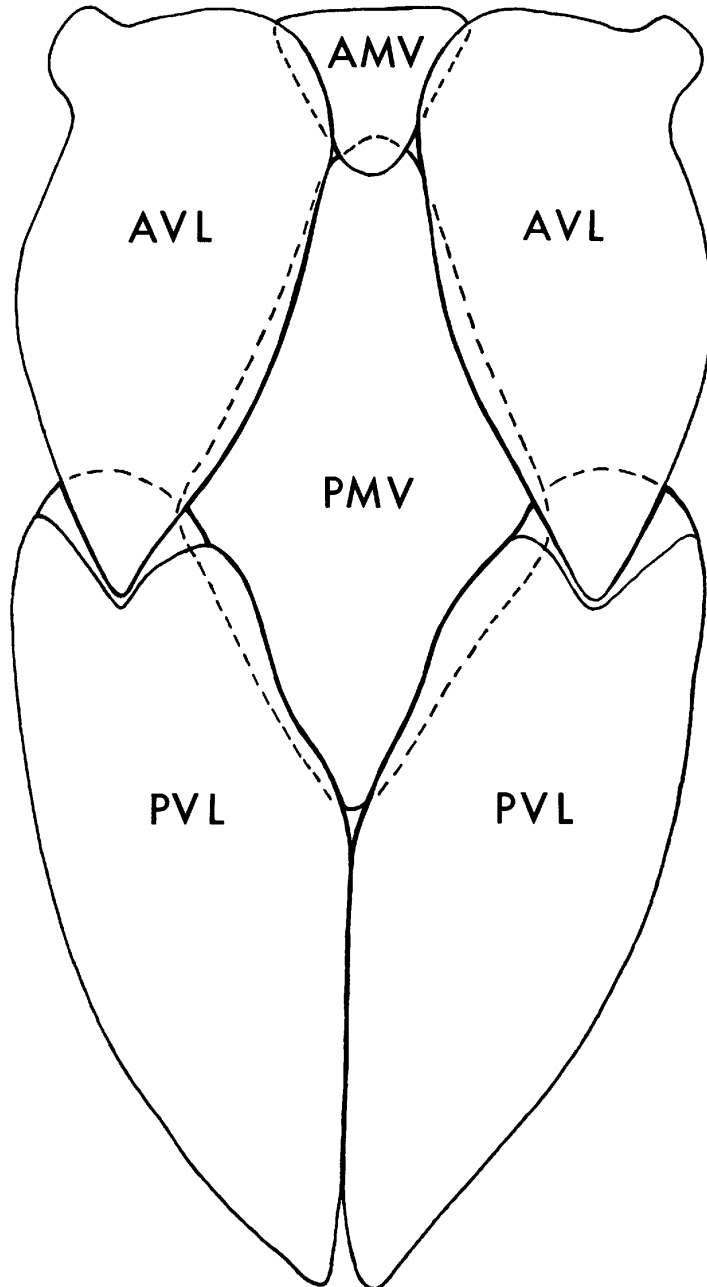


FIG 5. Reconstruction of complete ventral armor of *Glyptaspis verrucosa* showing overlap relations among the plates.

omorphs this bony wall is composed of contributions from the anterolateral (AL) and interolateral (IL) plates (see, *inter alia*, Miles, *ibid.*, p. 135, fig. 6b; Miles and Westoll, 1968, p. 443, fig. 44; Heintz, 1932, p. 180, fig. 68). It is probable that this osseous postbranchial lamina was continued as a fleshy, muscular, diaphragm-like structure, forming a transverse posterior wall for the orobranchial chamber. We believe that such a muscular, diaphragm-like posterior wall was present in *Glyptaspis*. Expansion of the trunk, increasing the volume of the thoracic space bounded by the body wall, would cause a positive pressure differential anterior to the diaphragm-like posterior wall of the orobranchial chamber. Reduction of the pressure posterior to this fleshy wall would cause it to bulge posteriorly. This would increase the volume of the orobranchial chamber and reduce the pressure within this cavity. A negative pressure differential relative to the surrounding water would then exist. Such an anatomical arrangement would cause a considerable inrush of water when the jaws were opened during the initial stages of prey prehension. Miles (1969, p. 142) stated that it is "unlikely that suction played a significant role" in the feeding behavior of arthrodires. This was true of many Euarthrodira such as *Coccoosteus* (Miles and Westoll, 1968), *Eastmanosteus* (Boylan, MS), *Dunkleosteus* (Heintz, 1932), and *Gorgonichthys* (Dunkle and Bungart, 1940, 1946). These genera, however, had forsaken the feeding methods of the primitive phlyctaenaspids and fed upon more active prey either from ambush or through active pursuit. *Mylostoma* (Hlavín and Boreske, 1973) probably preyed upon the same sort of benthonic invertebrates that phlyctaenaspids fed on, but its feeding apparatus was modified into flat, crushing bony elements. Again, we believe that Miles (1969, p. 142) is correct and that suction played no significant role in the ingestion of prey in *Mylostoma*. We believe, however, that *Glyptaspis* represents the culmination of a phylogenetic trend toward refinement of a feeding mechanism whose osseous components differed very little from those of the phlyctaenaspids. It is our opinion that suction through reduced pressure in the orobranchial chamber may well have played a key role in the ingestive apparatus of *Glyptaspis*.

SUMMARY AND CONCLUSIONS

Identification of the elements that comprise the remains of *Glyptaspis* has enabled us to reconstruct the ventral armor. Although *G. verrucosa* is known only from these four ventral plates, it has been possible to reconstruct this portion of the anatomy completely. The reconstruction has permitted us to demonstrate the unlikelihood of the affinities suggested by previous authors for these plates. Our study of this material leads us to conclude that these plates are not the ventral armor plates of *Mylostoma* or *Diplognathus*.

Examination of these specimens, their overlap surfaces, and overlapping relationships has allowed us to speculate on the biomechanics of the thoracic armor of *Glyptaspis*. The overlap surfaces on these plates are extremely smooth and shiny, indicating that the articulations involved were loose, probably sliding, articulations. This, we believe, would allow the expansion of that part of the body cavity enclosed by the thoracic armor. This, in turn, would provide the pressure differential necessary for expansion of the orobranchial chamber through rearward movement of a muscular, diaphragm-like posterior wall. A negative pressure gradient would then be produced between the orobranchial chamber and the external watery environment. Through such an anatomical arrangement, suction and a concomitant inrush of water would play a key role in the prehension and ingestion of prey. Other Fammenian arthrodires modified the bony elements of the gnathal apparatus. *Glyptaspis*, however, seems likely to have retained the relatively unspecialized gnathal elements typical of the phlyctaenaspids. It is probable that improvement was nevertheless achieved through the anatomical changes outlined above that allowed suction to become an important factor in the feeding behavior of *Glyptaspis*.

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