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(Chelicerata, Merostomata), with Remarks
on Merostome Phylogeny

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ABSTRACT

A new genus and species of the merostome suborder Synziphosurina is described from the Lower Devonian of Bolivia. This new taxon has made possible a reinterpretation of other poorly understood genera commonly allocated to the Synziphosurina. *Weinbergina* Richter and Richter, *Bunodes* Eichwald, *Bunaia* Clarke, and *Pseudoniscus* Nieszkowski are re-examined in detail, based mainly on a study of the original material, as well as on collections of topotypical specimens of *Bunodes lunula* Eichwald and *Pseudoniscus aculeatus* Nieszkowski. Shorter discussions are presented for *Neolimulus* Woodward and *Limuloides* Salter in Woodward.

Weinbergina and the new Bolivian genus are monotypic. Each is known from only three specimens, and both occur in Lower Devonian marine rocks. *Bunodes* as presently understood is also monotypic: *B. lunula* from the Upper Silurian of Oesel; some British Silurian species described as *Limuloides* are probably referable to *Bunodes*. The three described species of *Pseudoniscus* (*P. aculeatus* Nieszkowski from Oesel; *P. roosevelti* Clarke, and *P. clarkei* Ruedemann from New York State), all Upper Silurian in age, are difficult to differentiate, and only the genus is rediagnosed. In addition, two specimens of *Pseudoniscus* are now known from the Silurian of Great Britain. *Neolimulus*, based on a single specimen from the Upper Silurian of England, is poorly known and apparently closely related to *Pseudoniscus*. *Bunaia* is based on four specimens (from the Upper Silurian of New York) and may be a junior synonym of *Pseudoniscus*.

The suborder Synziphosurina is rediagnosed and contains but four valid genera: *Weinbergina*, *Bunodes*, *Limuloides*, and the new Bolivian taxon. The families Weinberginidae (*Weinbergina* and the Bolivian genus) and Bunodidae (*Bunodes* and *Limuloides*) are recognized. The suborder Limulina is the sister group of the Synziphosurina, and in turn is comprised of the infraorders Pseudoniscina (diagnosed herein) and Limulicina. *Pseudoniscus*, *Bunaia*, and *Neolimulus* are referred to the Pseudoniscina, as is an unnamed family of primitive belinurid limulines in which the axis of the opisthosoma is broader than the prosomal cardiac lobe at the juncture of these two tagmata. A classification of the class Mero-

stomata is presented: the Aglaspida comprise the sister group of the Xiphosurida (i.e., Synziphosurina and Limulina) and the Eurypteridida and Chasmataspida are probable sister taxa. Two merostome subclasses, the Eurypterida and Xiphosura, are recognized. Finally, there is a brief discussion of evolutionary patterns within the Merostomata, with emphasis on the Xiphosurida.

INTRODUCTION

The present study was initiated in the summer of 1972, when Mr. LeGrand Smith, currently living in La Paz, Bolivia, visited the American Museum of Natural History and presented a specimen herein designated as the holotype of a new genus and species of a synziphosuran merostome from the Lower Devonian of Bolivia. Upon preparation, the specimen proved to be complete and one of the very best preserved Paleozoic xiphosurans yet known. In the course of preparing a description of this new taxon, I examined other synziphosuran and limuline xiphosurans, at first simply to shed light on some of the seemingly unique features of the Bolivian form. Instead, I eventually perceived that the morphology of the Bolivian species clarified many of the poorly understood points concerning the morphology of taxa conventionally considered as synziphosurans. Accordingly, formal revisions or detailed discussions are also included for the following taxa: *Weinbergina opitzi* Richter and Richter, 1929; *Bunaia woodwardi* Clarke, 1919; *Bunodes* Eichwald, 1854; and *Pseudoniscus* Nieszkowski, 1859. Shorter discussions are presented for *Neolimulus falcatus* Woodward, 1868, and *Limuloides* Salter in Woodward, 1865. Thus, Mr. Smith's discovery has prompted a reconsideration of all the apparently valid taxa classified together by Størmer (1955) as the suborder Synziphosurina.

ACKNOWLEDGMENTS

This study owes its genesis to the sharp eyes, generosity, and encouragement of Mr. LeGrand

Smith of La Paz, Bolivia. He graciously donated the holotype and one of the paratype specimens of the new taxon described below. I am also grateful to Prof. Leonardo Branisa, Geological Survey of Bolivia, who provided me with a latex mold and a cast of the other paratype specimen. I am further grateful to these gentlemen for their pains in describing details of the locality and its geological setting, including associated fauna.

I am grateful to the following persons and institutions for the loan of specimens: Ms. Katherine Krueger and Dr. Eugene Richardson, Field Museum of Natural History (FMNH) Chicago; Dr. Bruce Bell and Mr. Robert Conrad, New York State Museum (NYSM), Albany; Professor Wolfgang Struve, Natur-Museum und Forschungs-Institut Senckenberg (Senck. Mus.), Frankfurt am Main; Ms. Jann Miller and Mr. Frederick Collier, National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; Dr. Charles Waterston and Mr. William Baird, Royal Scottish Museum (RSM), Edinburgh; and Mr. Samuel Morris, British Museum (Natural History) (BMNH), London.

The photography was ably performed by Mr. G. Robert Adlington. Special thanks are due Mr. Frank Lombardi for his exceedingly painstaking work in preparing the holotype of the new Bolivian form, and for further help in preparing other material. Both Mr. Adlington and Mr. Lombardi are members of the Department of Invertebrate Paleontology, the American Museum of Natural History (AMNH).

I thank the following colleagues who examined either photographs or original specimens of the Bolivian taxon and gave freely of their opinions as to its identity and interpretation: Mr. Daniel Fisher; Drs. Jan Bergström, Ivo Chlupáč, Euan N. K. Clarkson, Frederick Schramm, Leif Størmer, Wolfgang Struve, and H. B. Whittington; I also acknowledge with thanks the many discussions I had with colleagues upon presenting the results of this study at the conference on Evolution and Morphology the Trilobita, Trilobitoidea, and Merostomata sponsored by NATO and convened by Dr. David L. Bruton in Oslo, Norway, on July 1-8, 1973. Finally, I acknowledge my deep appreciation of the practical help and timely, stimulating commentary from my very able assistant, Mr. Roy Plotnick.

SYSTEMATIC PALEONTOLOGY

LEGRANDELLA, NEW GENUS

Diagnosis. Large synziphosurans with highly vaulted prosoma roughly hemispherical in dorsal view. Cardiac lobe arising as high axial protuberance posteriorly, tapering and sloping downward anteriorly. Cardiac furrows and ridges present. Five pairs of ridges and furrows radiating from cardiac ridges, traversing interophthalmic areas and extending to ophthalmic ridges. Ophthalmic ridges large, crescentic, extending from near posterior margin of prosoma and running anteriorly approximately three-fourths the length of the prosoma. Median sensory areas (?ocelli) present at anterior margin of cardiac lobe near midline, set back just posterior to anterior margins of ophthalmic ridges.

Visual surface extending entire length of ophthalmic ridge, covered with corneal membrane. Large lensar structures present. Cheek regions inclined at steep angle, bearing small genal spinules. Prosoma with anterior median projection on anterior margin. Doublure reflected vertically around entire anterior and lateral prosomal margin. Prosomal surface pitted, with pits possibly serving as attachment bases for tubercles or short spines.

Opisthosoma with 11 segments, divided into preabdomen of eight free segments, and postabdomen of three free segments. Preabdomen about 95 percent prosomal length, distinctly vaulted, and with pronounced axial furrows. First anterior opisthosomal segment greatly reduced; third opisthosomal segment with greatest (sagittally [sag.]) length. Axial spines developed on segments 2-5 and 8. Pleura produced as spines on preabdominal segments 2-8. Postabdomen approximately 54 percent of prosomal length, consisting of three subcylindrical segments with axial spines. Pleura developed only as short ventrolateral projections. Telson triangular in cross section, of unknown length. Ornament of preabdomen obscure, possibly smooth, or as for prosoma. Postabdominal segments and telson covered with pits, possibly serving as bases for attachment of tubercles or spines.

Etymology. Named in honor of Mr. LeGrand Smith, discoverer of the holotype and one of the paratypes.

Referred Species. The type species, *Legrandella lombardii*, new species, is the only known species referable to this genus.

***Legrandella lombardii*, new species**

Figures 1-4

Diagnosis. As for genus.

Description. All measurements and descriptions of shape of the prosoma in the dorsal, lateral, and frontal views are made with the ophthalmic ridges oriented in the same horizontal plane.

Prosoma: In dorsal view, the general form of the prosoma is hemispherical, with the posterior margin approximating a straight line, the lateral margins curving gently anteroproximally approaching the anterior midline, which is deflected slightly by the anterior median projection. The curvature of the prosomal margin is roughly coincident with the curvature of the ophthalmic ridges except posteriorly, where the ophthalmic ridges are curved posterproximally. The posterior border, while approximating a straight line, actually is deflected slightly anteroproximally from the genal angle, curving posteriad near the posterior margin of the ophthalmic ridge; this "posterior marginal reflection" corresponds with the position of the posterolateral margin of the cardiac region (including the cardiac ridges) and with the anterior margin of the axial furrows of the opisthosoma. Axially, the posterior margin is slightly curved anteriorly.

The cardiac region is defined herein as the axial portion of the prosoma, consisting of the cardiac lobe proper, the cardiac furrows, and, distal to the furrows, the cardiac ridges. The cardiac region is not sharply demarcated from the interophthalmic areas by continuous furrows; the interophthalmic area is composed of a series of radiating furrows and broad ridges that become confluent with the cardiac ridges. Thus, the axial lobe of the prosoma at its posterior margin is composed of the cardiac lobe and, additionally, extends laterally as far as the posterior marginal reflection, i.e., includes the area occupied by the cardiac furrow, cardiac ridge, and the interophthalmic area.

The prosoma articulates with the first opisthosomal segment at the posterior marginal reflection

of the prosoma, which apparently act as fulcra; proximal to these articulations, the axial region of the prosoma receives the first opisthosomal segment that functions as an articulating half-ring. There are no marginal furrows on the prosoma, nor is an "occipital" furrow present. The posterior margin of the axial lobe is tall and sharply pointed; the cardiac lobe, defined by its bounding cardiac furrows, begins a short distance anterior to the posterior prosomal margin; the furrows run anteroproximally roughly 25 percent of the length of the prosoma, then diverge again to form a second, anterior lobate region of the cardiac lobe, which itself tapers and culminates in a depression in the midline just anterior to the anterior margin of the ophthalmic ridges.

The cardiac furrows are straight, shallow, and quite broad where the cardiac lobe becomes constricted. These and the flat, straight cardiac ridges, are inclined anteroproximally; both structures become indistinct near the anterior end of the cardiac lobe.

Five pairs of broad, conspicuous ridges radiate from each cardiac ridge and coalesce with the ophthalmic ridge, traversing the interophthalmic areas. These ridges separate six pairs of radiating furrows. The surface relief of these interophthalmic ridges and furrows, as well as of the cardiac ridges and furrows, have been affected by weathering on all available specimens. The furrows on the distal portions of the interophthalmic areas are shallow externally, but represent thickened portions of integument which, by analogy with *Limulus*, served as sites for appendage and other musculature. The posterior two pairs of radiating furrows are merged proximally, forming a V, and thus isolating the first (posterior) radiating ridge from the cardiac ridge. The fifth radiating furrow (counting from the rear) terminates near the anterior margin of the ophthalmic ridge; the sixth lies near the terminus of the cardiac lobe. In the holotype (AMNH 29273) these last two furrows are developed simply as rounded pits at some distance from the cardiac ridge, but as paratype AMNH 29274 clearly indicates, the furrows are developed completely and simply not completely weathered out on the holotype.

The median impression (median sensory organs or ?ocelli) just anterior to the anterior terminus of the cardiac lobe is also developed as a

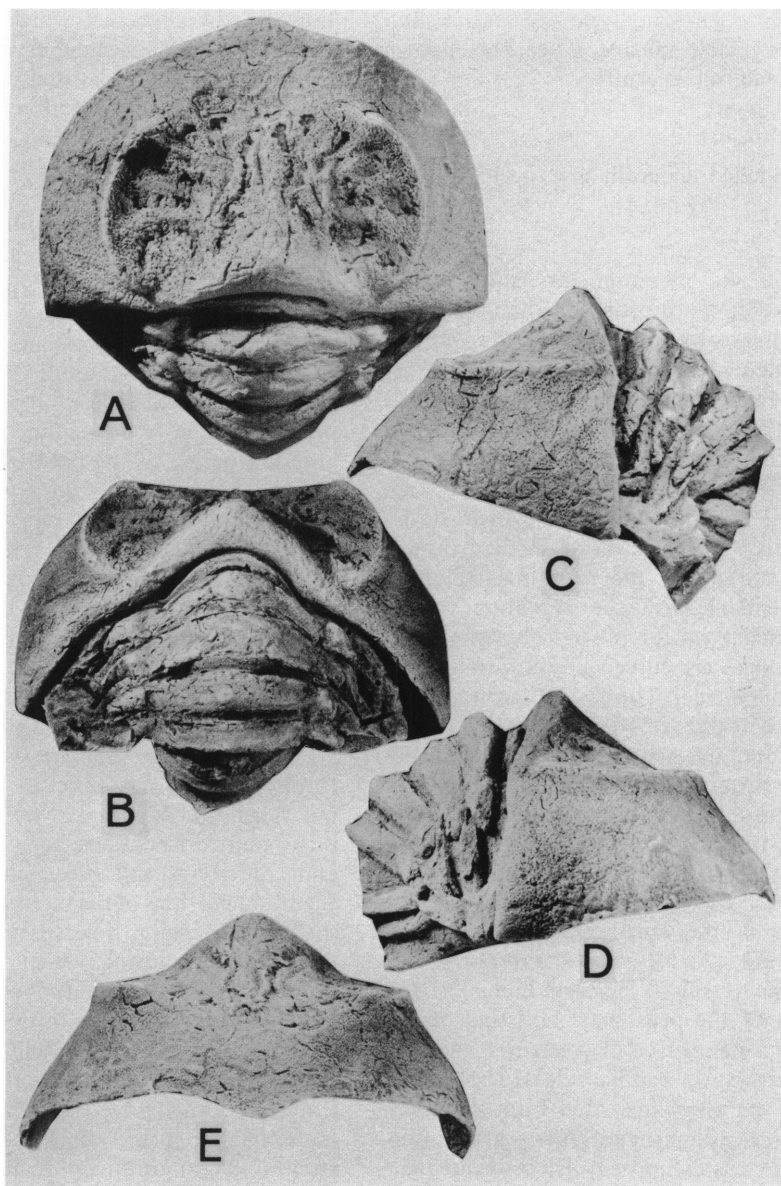


FIG. 1. *Legrandella lombardii*, new genus, new species. Holotype, AMNH 29273. A. Dorsal view of prosoma and opisthosomal segments 1-4. B. Oblique posterior view of prosoma and preabdominal segments 1-7. C, D. Left and right lateral views of prosoma and preabdominal segments. E. Frontal view of prosoma. All views $\times 1$.

thickened pad of integument. No lensar structures were observed in this area.

The ophthalmic ridges are narrow and crescentic. They arise just anterior to the posterior

marginal reflection of the prosoma and run approximately 57 percent of the length of the prosoma, terminating at a point approximately even with the anterior margin of the cardiac lobe.

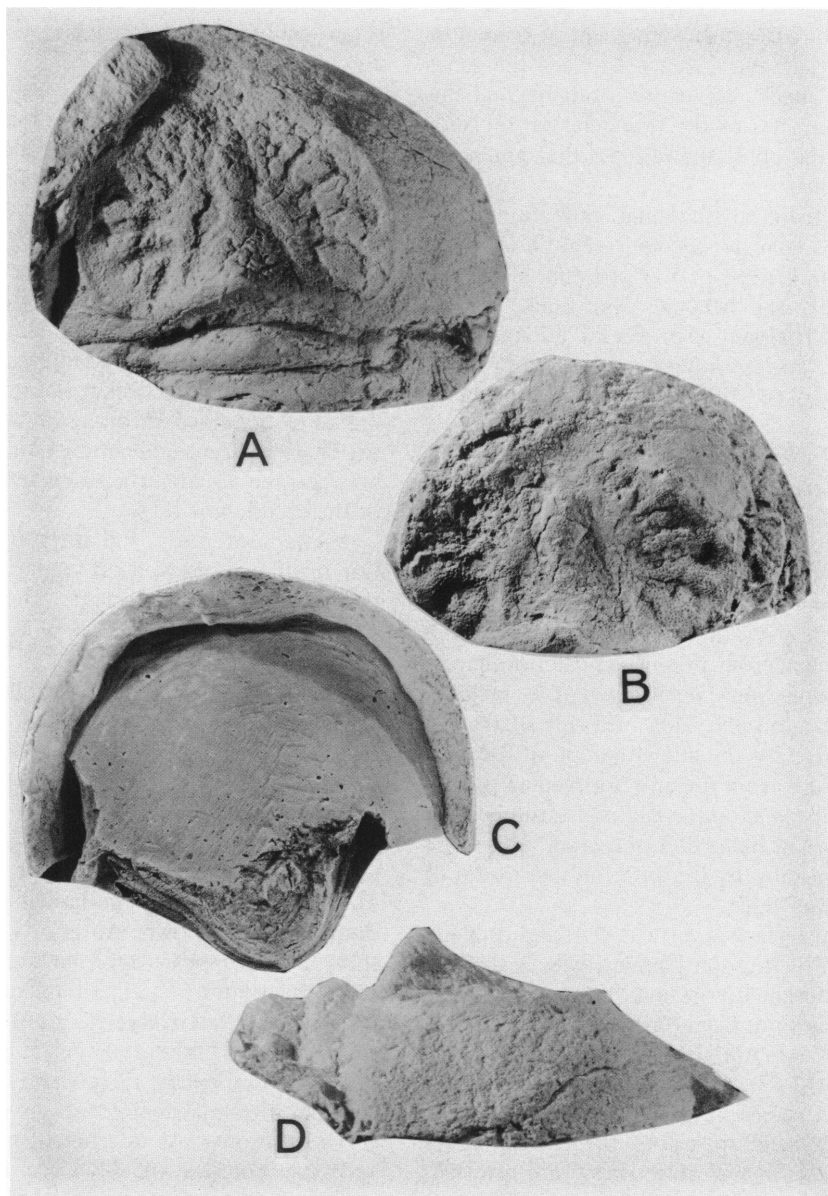


FIG. 2. *Legrandella lombardii*, new genus, new species, A, D. Dorsal and right lateral views of prosoma and anterior opisthosomal segments, cast of paratype, AMNH 29274. B. Dorsal view of prosoma, paratype, AMNH 29275. C. Ventral view of prosoma showing vertical doublure, holotype, AMNH 29273. All views $\times 1$.

Distal to the ophthalmic ridges the genal regions slope sharply ventrally. A minute genal spine was originally preserved on the left gena of the holotype (AMNH 29273). The region of the prosoma

anterior to the ophthalmic ridges and cardiac region slopes ventrally somewhat more gently.

In posterior view, the profile of the prosoma is triangular, the apex being formed by the axial

node of the posterior margin. The height of this triangle is approximately 56 percent of the width of the base (i.e., the distance between the genal angles). The cheek regions swell out beyond the ventral lateral sides of the triangular profile, culminating at the ophthalmic ridges that appear as flat projections.

At the posterior marginal reflections, the slope of the triangle becomes slightly steeper. The posterior margin of the prosoma along the genae is thick, and becomes even thicker in the axial region. The ventral profile of the axial ring is crescentic, corresponding to the shape of the axial region of the first (anterior) opisthosomal segment.

In lateral view, the prosoma appears asymmetrically triangular. The ventral margin describes a straight line, beginning at the genal angle and running anterodorsally to the anterior region at an angle of roughly 10 degrees in the holotype, defining an anterior arch. This profile is interrupted only by the ventral deflection of the anterior median projection. The posterior margin of the prosoma runs vertically and is inclined slightly anterodorsally. The third side of the triangle is formed by the straight slope of the midline, which runs from the anterior median projection smoothly posterodorsally and terminates at the axial node at the posterior margin. This slope is interrupted only by the anteriormost region of the ophthalmic ridge.

The visual surface is vertical, flat, and runs the entire length of the ophthalmic ridge. A smooth corneal membrane covers the "lensar structures" and facets have not been observed on the cornea. In the holotype (AMNH 29273) and one of the paratypes (AMNH 29274), the cornea is weathered away in places, revealing the internal structures of the visual apparatus. Structures, herein simply termed "lensar structures," are revealed, particularly along the anterior region of the left visual surface of the holotype. The lensar structures are large, circular, and closely packed although separated from one another by narrow walls presumably composed of thickened corneal tissue. The lensar structures are arranged into more or less orderly dorsoventral files of two or three lenses per file; it is not possible to estimate the number of such files or the total number of lensar structures on the visual surface. The

arrangement of the lensar structures is thus superficially reminiscent of the phacopid schizochroal eye.

The lensar structures consist of a small median spherical mound ("upper lensar structure") which, when absent, leaves a central depression on the remainder, or "lower lensar structure." The upper lensar structure appears to be solid; the lower lensar structure, which has a greater diameter than the upper, also seems to be solid and to taper conically proximally (i.e., toward the visceral surface). The solid material is dark brown, is not composed of mineral grains similar to those of the enclosing matrix, and is interpreted as preserved chitinous exoskeletal material. There is some indication of a "suture" line between the visual surface and the dorsal margin of the ophthalmic ridge.

Viewed anteriorly, the anterior arch and anterior median projection are apparent, as are portions of the ophthalmic ridges. The cardiac region slopes up to the axial peak at the posterior margin.

There is an apparent suture along the entire ventral margin of the prosoma. Although not unexpected, this "suture" may be an artifact of the loss of the extreme edge of the prosoma at the margin. The apparently thin prosomal doublure is everywhere reflected dorsally, parallel to, and closely associated with, the dorsal cuticle. The vertical extent of the lateral portions of the doublure is unknown. Anteriorly, the doublure thins and disappears approximately 12 mm. up from the ventral margin of the anterior median projection. Presumably, the doublure merged at this point with the softer ventral integument. No traces of the ventral integument, the chelicerae, or other prosomal appendages are known.

Opisthosoma: As interpreted herein, the opisthosoma consists of 11 free, articulated segments. A preabdomen of eight segments with pleura, and a postabdomen of three cylindrical segments with only short pleural spines, are clearly differentiated. The first (anterior) preabdominal segment is short (sag.) and consists of a highly arched axial ring closely appressed to the axial region of the prosoma. The axial ring of this segment does not project so high as the axial node of the prosoma or of the median region of the axial ring of the second opisthosomal seg-

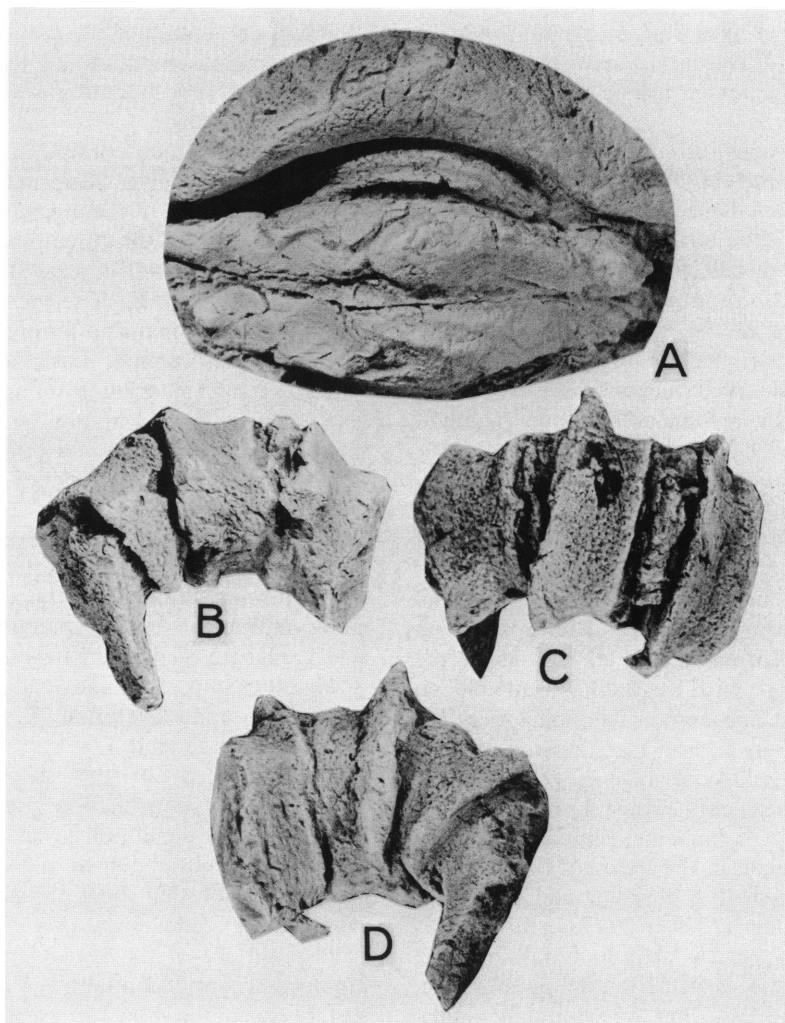


FIG. 3. *Legrandella lombardii*, new genus, new species. Holotype, AMNH 29273. A. Posterior region of prosoma and opisthosomal segments 1-3. $\times 2$. B-D. Postabdominal segments and telson. $\times 2$. B. Right lateral, slightly ventral view. C. Right lateral, slightly dorsal view. D. Left lateral, slightly ventral view.

ment. Thus the first opisthosomal segment is functionally an articulating ring acting as a juncture between the prosoma and the opisthosoma. The axial ring of this segment is tripartite (sagittal [sag.]), with a high median ridge which gradually slopes anteroventrally forming an articulating surface; posteriorly the axial ring slopes abruptly ventrally. The axial ring terminates laterally at a shallow axial furrow, distal to which the first opisthosomal segment is drawn out into

a short pleural spine, which extends as far distally as the point immediately posterior to the posterior margin of the ophthalmic ridge. Thus the pleura of the first opisthosomal segment is far shorter (trans.) than those of the seven succeeding preabdominal segments. The first two opisthosomal segments articulate along a short line running obliquely anteriorly across the axial furrow. Proximally, the short articulating half-ring of the second opisthosomal segment

runs beneath the axial ring of the first opisthosomal segment. (The interpretation of the first opisthosomal segment is moot, and is more fully discussed below.)

The second opisthosomal segment is strongly vaulted axially and produced into a tall median node. A stout apodeme is produced in the anterior portion of the axial furrow. The pleura are cylindrical and distally produced into large pleural spines, which do not extend distally so far as the genal angles of the prosoma. A pleural furrow, separating a small pleural ridge from the main body of the pleuron, runs obliquely posterodistally on the second opisthosomal segment only.

Opisthosomal segments 2-8 are much as described for opisthosomal segment 2. The axial furrows are well developed throughout the length of the preabdomen; the pleura are all developed as unfurrowed cylindrical spines, whose length and thickness decrease posteriorly. The proximal region of each pleuron is inflated high above the axial furrow, and, with weathering of the pleura, assume a nodal appearance. The axial rings become progressively shorter (sag.) posteriorly and less highly vaulted. Axial nodes are present on all preabdominal segments except 1, 6, and 7. No further evidence of apodemes is present. The segments all articulate in the region of the axial furrow. As shown by the holotype and only complete opisthosoma (AMNH 29273), this species could enroll in typical arthropod fashion, i.e., with the points of articulation acting as fulcra. The articulating half-rings of the preabdominal

segments are developed as smooth and flat, very thin and short extensions of the axial rings of each segment. Preabdominal sternites or appendages are unknown.

The postabdomen consists of three subcylindrical to subtriangular segments, corresponding to the axial region of the preabdomen; the integument on each of the three postabdominal segments is equally well developed dorsally, laterally, and ventrally. Each segment has stout median axial spines on the posterior margin, and very short "pleural" spines. Each segment is constricted (trans.) medially, forming a general hourglass shape. The articulation between each segment appears to consist of a thin circular articulating membrane, thus allowing lateral as well as dorsoventral flexion.

Telson: Incompletely preserved; it is triangular in profile, and apparently articulated in such a way with the third postabdominal segment to allow movement in all directions. Its reconstructed length is approximately 26 mm.

Measurements of some major linear dimensions of the exoskeleton in all available specimens are given in table 1.

The ornament of this species consists of densely packed, large shallow pits, especially well developed over the dorsal surface of the prosoma and over the postabdomen and telson. There is some indication that these pits supported spherical tubercles eroded away over most of the exoskeletal surface of the available specimens. This ornament covers essentially the entire prosomal surface except the visual surface of the ophthalmic

TABLE 1
COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF
LEGRANDELLA LOMBARDII AND *WEINBERGINA OPITZI*

	A	B	C	D	E	F
Prosomal length	39.8	—	—	37	42	43
Prosomal width	59.4	—	—	ca. 64	ca. 57	57
Length of cardiac lobe	22.7	24.2	24.7	—	—	—
Eye length	22.5	23.0	24.0	—	—	—
Maximum width between eyes	41.7	41.6	43.8	—	—	—
Maximum height of prosoma	32.7	—	—	—	—	—
Length of preabdomen	37.7	—	—	—	—	—
Length of postabdomen	21.3	—	—	—	—	—

Symbols: A-C, *Legrandella lombardii*, AMNH 29273 (holotype)-29275, respectively; D-F, *Weinbergina opitzi*, taken from Lehmann, 1956, page 77; D, holotype; E, Bonner specimen; F, second Frankfurt specimen.

ridge; the preabdominal segments, including pleura, appear to be smooth, but the ornament is heavily developed on all but the articulatory surfaces of the postabdomen and telson.

Material Examined. Holotype, AMNH 29273, a complete prosoma, opisthosoma, and telson. Cast of paratype, AMNH 29274, consisting of a somewhat flattened prosoma from which the left genal region is missing, and opisthosomal segments 2 and 3 (opisthosomal segment 1 is apparently buried under the prosoma; see discussion below). The original is in the collections of the Paleontological Laboratory, University of Bolivia, La Paz. Paratype (AMNH 29275), a highly weathered prosoma, also missing the left genal region. The right genal region has not been prepared, as the surrounding matrix contains fragile brachiopod fragments yielding important information on associated fauna.

Locality. The holotype (AMNH 29273) and paratype (AMNH 29275) come from Rumicorral, a small settlement 23 km. east of Aiquile on the old unpaved road between Cochabamba and Santa Cruz in the Cochabamba Department, Bolivia. The other paratype (AMNH 29274-cast) was collected a short distance north of Aiquile.

Associated Fauna and Geological Horizon: According to Leonardo Branisa and LeGrand Smith (personal commun.), the outcrops which produced the three specimens of *Legrandella lombardii* are associated with a typical "Icla" fauna. The following list of associated fauna at the outcrop was prepared by Smith. Brachiopods: *Australospirifer* and unidentified chonetids, abundant, as well as species of *Australocoelia*, *Meristella*, *Lingula*, *Orbiculoidea*, *Ambocoelia*, and *Cryptonella*. Conularids: *Conularia quichua*, *C. africana*, and *Mesoconularia* (all abundant). Gastropods: a bellerophonitid species and another unidentified species. Bivalves: a nuculoid "of the *Paleoneilo* type." Cephalopods: two unidentified species; one unidentified crinoid species. Trilobites: *Metacryphaeus giganteus*, *M. convexus*, *Acastoides verneuli*, *Phacopina* (Vogesina) sp., *Schizostylus brevicaudatus* and *Franchovichia* sp. To this list may be added the (?) fenestellid bryozoan encrusting a portion of paratype AMNH 29274, as well as another probable bryozoan species encrusting several preabdominal segments of the holotype (AMNH

29273). Furthermore, there is abundant evidence of borings or tubes created by another epizoite on the specimens of *Legrandella*.

The fauna is thus marine. The rock type is a well-indurated dark siltstone, weathering a light brown, with no carbonate present as mineral grains or cement. (These observations are based solely on the matrix adhering to AMNH specimens 29273 and 29275.) The associated fauna, furthermore, indicates the age to be either Emilian-*Franchovichia* zone (Ahlfeld and Branisa, 1960) or Middle or Upper Siegenian (*M. giganteus* or "*Odontochile*" *branisi* zones) (Wolfart, 1968).

Etymology. Named for Mr. Frank Lombardi in appreciation of his intense interest and diligence in the careful, painstaking task of freeing the holotype specimen from its surrounding matrix.

Discussion. Although the three specimens, and in particular the holotype, are in general well preserved, there are four major problems in the interpretation of the morphology of this species that merit discussion. These problems are: (1) the mode of preservation and its bearing on the interpretation of morphology in general; (2) the morphology of the structures associated with the visual surface; (3) the number of opisthosomal segments; and (4) the articulation of the opisthosoma with the prosoma with regard to the position of certain landmarks on the prosoma. This last problem bears directly on the correct interpretation of prosomal "cardiac" features and their homology with structures in *Limulus* and other merostomes, and is critical to the interpretation of similar features in other taxa conventionally considered synziphosurans.

Although the arguments adduced in this section will necessitate some comparisons with other merostomes, full comparisons of *Legrandella* with other merostome genera are presented in conjunction with an analysis of relationships, following the redescrptions or discussions of the other taxa treated herein.

Mode of Preservation. The holotype is unequivocally preserved in a siltstone concretion, so typical of the mode of preservation of the Devonian fauna of Bolivia. The precise mode of occurrence of the other specimens is unknown. The holotype appears completely uncrushed and

undistorted; the paratypes have been somewhat dorsoventrally flattened. The anterior five opisthosomal segments (as interpreted herein) in the holotype are directly articulated with the prosoma; segments 6-8 form an articulated series slightly disassociated, but still "in line," with the preceding segments. The postabdomen and telson are in an articulated series, but had been disassociated and twisted with respect to the preabdomen, so that the telson was found lying close to the left lateral side of preabdominal segments 7 and 8.

Loosely speaking, all three specimens appear to be casts of the interior side of the dorsal exoskeleton. However, the matter is not quite so simple. There is a thin, rust-colored powdery layer over much of the holotype, taken to represent vestiges of the original "chitinous" integument. In addition, a thin semitranslucent dark brown layer, probably altered "chitin," is present over much of the left side of the prosoma of the holotype. Few pieces of the external impressions were available for study, but in general, these fragments are closely associated with the internal cast and preserve mirror-image features. Examination of unprepared areas of one of the paratypes (AMNH 29275) shows an extremely narrow space between the overlying matrix and the specimen itself. From these scant observations, plus the presence of some "wrinkling" of the prosomal surface of the holotype, I conclude that the integument was quite thin and probably "chitinous" (no traces of carbonate or phosphate minerals were observed); but there is still no definitive indication that the structures observed are entirely internal features, a combination of internal and external features, or whether indeed both the internal and external features may have been exactly the same. Specifically, it is impossible to determine whether the pockety depressions or pits so characteristic of the dorsal surface of these specimens are reflections of tubercles developed on the visceral surface, with the external surface either smooth or tuberculate; or whether the external surface was also pitted; or, finally, whether tubercles were emplaced in the pits and now eroded away. The postabdomen and telson of the holotype, which were embedded in matrix prior to this study, show the pits on the "internal cast" and concomitant pus-

tules on the impression left on the overlying matrix. Sectioning of this latter material through the pustules failed to yield definite proof that *Legrandella* was externally tuberculate. Rare, isolated patches of firm, light brown material (possibly preserved "chitin") over the prosoma of the holotype show that, in all probability, pitting was not so extensively developed on the external surface as it was on the internal cast. More specimens will have to be recovered before the external surficial ornament of *Legrandella* can be known with assurance.

The "composite mold" nature of preservation is further shown by the development of ?bryozoan and ?sessile annelid traces, especially on the surface of the holotype. The colonial ?bryozoans, clearly epizootic structures on preabdominal segment 4, can be seen on the exfoliated external mold projecting from a flat base and extending some short distance into the matrix. No trace is left on the specimen itself. However, laterally, these structures can be recognized extending down into the segment, clearly indicating a superposition of external and internal features. The "worm borings," especially on the prosoma of the holotype, show no traces of a lining secreted by the boring organism, and must be presumed to have been borings into the integument of the merostome. Some of these cause a positive inflection of the surface of the specimen, with the pitted ornament retained, whereas most are sinuous and generally smooth grooves lower than the external surface of the specimen. Again, interpretation is difficult, and a feature of the integument, namely the borings, is preserved in a variety of ways indicating a compound mold mode of preservation.

Several other peculiarities should be mentioned with regard to preservation. First of all, the entire matrix surrounding the holotype is riddled with generally short, narrow sinuous tubes, usually lined with a rust-brown powder similar to that seen on the surface of the holotype specimen. Latex casts of some of these tubes have revealed no apparent structure. It is possible that they represent setal "spines" which may well have covered *Legrandella lombardii* in life. There are several alternative explanations (postburial borings in either soft or indurated substrate; or simply parts of another organism, e.g., chonetid

spines) and the point will not be labored further.

Also, the matrix directly beneath the ornamented exterior of the holotype seems to consist of a coarser grade of light gray silt, quite different from the dark, finer grained material that forms the surrounding concretion. These few remarks are sufficient to show that the holotype specimen of *Legrandella lombardii* had an interesting, if checkered, history after death or molting and immediately prior to its final enclosure in the hard matrix of the surrounding concretion.

Morphology of the Visual Surface. The description of the visual surface given above, which obviously incorporated a degree of interpretation, nevertheless was intended as much as possible to reveal what could actually be seen. Superficially, the eyes are so entirely unlike those of *Limulus* and eurypterids that more detailed interpretation and comparison of the structures of the visual surfaces are warranted.

The left eye of the holotype appears to be preserved with much, if not all, of the integument intact. A thin rind of "chitin" with a smooth exterior (no facets observed) forms the outermost layer. The lensar structures described above appear in general to be solid. These structures are also composed of preserved integument, i.e., they are not simple casts of the internal structure of the eye. Vertical walls separating these lensar structures are simple visceral extensions of the corneal membrane. The morphology of the visual surface is illustrated in figure 4.

This arrangement, and in particular the relatively large size of the lensar structures, at first seems entirely unique for the Merostomata. Particularly in view of the fact that synziphosurans are usually said to be blind (cf. Størmer, 1955) it is at least a possibility that the visual surface of *Legrandella lombardii* is a unique neomorphic specialization. However, comparable structures, also disproportionately large, are now known in *Bunaia woodwardi* Clarke, *Bunodes lunula* Eichwald, and in species of *Pseudoniscus* Nieszkowski (see below). But the question remains, to what extent do these structures differ from those of other merostomes?

The internal structure of the eyes of eurypterids have been discussed by Clarke and Ruedemann (1912); at the very least, the size of the facets, hence presumably also of the internal lens-

ar structures, of "*Eurypterus fisheri*" Eichwald are exceedingly small, and in fact quite comparable with those of *Limulus polyphemus* L. The internal morphology of the sclerotized portion of the eye in *Limulus*, however, shows that it is very similar indeed to *Legrandella*. The cones emanating from the visceral wall of the cornea are large solid structures which, when removed, reveal a smaller, solid globular body adhering to the internal corneal wall (fig. 4b). The only difference in the arrangement of the sclerotized portion of the visual apparatus thus seems to be the size of the individual lensar structures. In *Legrandella* the individual cones are much larger and fewer, and more conspicuously spaced, so that a thin corneal wall is developed between them. In both *Limulus* and *Legrandella* these subcorneal structures are formed of concentric layers of sclerotized exoskeletal material. The size and arrangement of these structures is unique (and apparently a specialization of at least some Synziphosurina), but the structures are by no means novel to the Merostomata. The further question, concerning vision in the Synziphosurina as a whole, is discussed following descriptions of some of the other taxa in this group.

Number of Segments of the Opisthosoma. The structure described above as the first opisthosomal segment looks like, and undoubtedly functioned as, an articulating ring. And at first glance, so it appears. Also, in view of the fact that reexamination of other synziphosuran (and related) taxa has shown that the preabdomen typically is composed of seven free segments (whereas the postabdomen has three, totaling 10), it is perhaps implausible to claim that the most anterior feature of the opisthosoma of the holotype specimen of *Legrandella* is in fact an eighth preabdominal segment. But so it must be. Admittedly the specimen is equivocal. There is a groove between the pleura of this segment and the next succeeding, which appears to be a plane of articulation; but it may be fused. Also, axially, the two segments are quite far apart, but the critical area between them has been destroyed. There is, however, a trace of an articulating half-ring structure on the next succeeding segment (i.e., the segment interpreted herein as opisthosomal segment 2), and on the whole the specimen does seem to support the

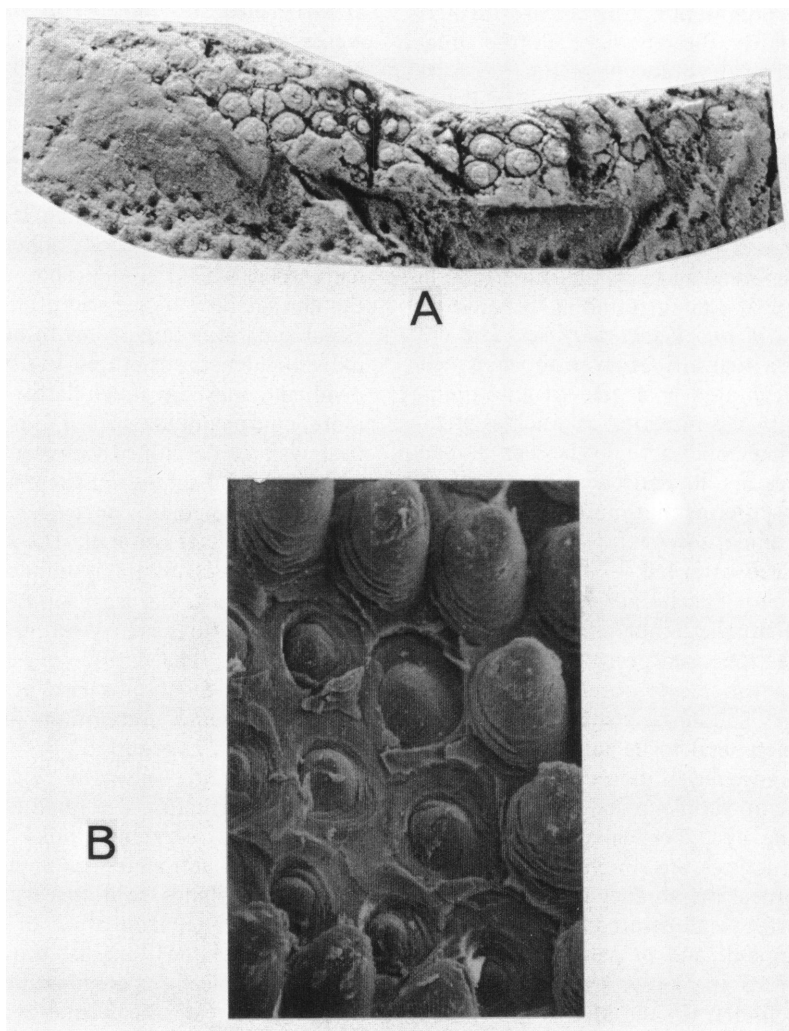


FIG. 4. A. Anterior region of left visual surface of *Legrandella lombardii*, new species. Holotype, AMNH 29273. Approximately $\times 10$. B. Scanning electron microscope photograph of the interior of a molted eye of *Limulus polyphemus*. The corneal cones in the center had been excised prior to photography. Approximately $\times 100$.

interpretation rendered in the above description. However, in one of the paratypes (AMNH 29274) this first segment is missing. What is here-in interpreted as segment 2 is present and closely associated, if not actually articulated, with the prosoma. No preparation was possible, as only a plaster cast of this specimen was available for the present study.

Why then interpret the first, small, predomi-

nantly axial structure of the preabdomen of the holotype as forming the first opisthosomal segment? There are two lines of evidence supporting this view. The first is that in *Bunodes lunula*, *Limuloides limuloides*, and the three species of *Pseudoniscus*, there is a small, depressed, predominantly axial segment unequivocally free from both the prosoma and the next opisthosomal segments (see below for descriptions and

discussions of these features and figs. 6, 7, 9). Each of these first two segments has a clearly distinct articulating half-ring. In *Bunodes*, the first segment is frequently not seen in articulated specimens, simply because it is buried beneath the posterior region of the prosoma. Whether this fact implies that functionally this structure was acting as an articulating ring or not is moot; but these first anterior opisthosomal segments seem comparable in all respects to that in the holotype of *Legrandella* and for this reason I homologize them.

Furthermore, the classical interpretation (which appears to stem from Benham, 1885) of the segmentation in the region of the prosomal-opisthosomal articulation in *Limulus*, is that the anterior region of the eighth body segment (primitively the first opisthosomal segment) was fused with the prosoma, the posterior region remaining with the (fused) opisthosoma. The argument involved is less embryological than functional-morphological in nature: apodemes arise on the primitive intersegmental lines and their distribution in *Limulus* (one pair on the prosoma, then a series on the opisthosoma, set back from the anterior margin by what seems like more than the expected length of a single segment) leads to the conclusion that the first opisthosomal segment was split, the anterior moiety fusing with the prosoma. I shall not attempt to refute this interpretation directly. However, as the primitive condition in merostomes was obviously one wherein the opisthosoma was comprised of a number of "free" segments (i.e., capable of dorsoventral flexion), it seems strange that such a novel arrangement was needed to accomplish a movable articulation between the prosoma and the fused opisthosoma when such an articulation was already present. The argument paraphrased above assumes that primitively, there was no such movable articulation between the prosoma and the fused opisthosoma. This is a patent absurdity.

There is no development of a pair of prosomal apodemes in *Legrandella* nor in any other synziphosuran known to me. Therefore, fusion of the anterior moiety of the first opisthosomal segment with the prosoma is not indicated. We are left simply with a reduced first opisthosomal segment which apparently functioned as an articu-

lating ring. Fusion of all preabdominal segments in a generalized synziphosuran with such an anterior preabdominal segment would explain entirely the morphology of the prosoma of *Limulus* in this regard. The pair of prosomal apodemes in *Limulus* could as easily be explained by the necessity of a strong insertion area for the arthrotergal muscle enlarged for the support and flexion of the (now fused) opisthosoma.

No known synziphosurans can even remotely be considered as directly ancestral to any known Limulina (see discussion below). However, the presence of a reduced, essentially axial, first opisthosomal segment in this group seems excellently preadapted to form the "articulating half-ring" of the opisthosoma of *Limulus*. The expansion of the pleura of this segment in *Limulus* can also be regarded as a specialization (see Eldredge, 1970, for a functional analysis of this structure), although there is no reason to assume that the common ancestor of the Xiphosurida (i.e., Synziphosurina and Limulina) actually had the pleura of the first opisthosomal segment reduced as much as it was in *Legrandella*, *Bunodes*, and *Pseudoniscus*.

In conclusion, whereas the anatomy of the two relevant specimens of *Legrandella* is ambiguous, comparison with *Pseudoniscus*, *Limuloides*, and particularly *Bunodes*, and the arguments classically adduced for *Limulus*, support the interpretation that the first apparent segment of the opisthosoma of the holotype of *Legrandella* is in fact a greatly reduced true first opisthosomal segment. Although the complete argument that the eighth body segment in *Limulus* is split between the prosoma and opisthosoma is somewhat questionable, there is no doubt that the first segment of the opisthosoma of *Limulus* is formed of a greatly reduced eighth segment; regardless of which version is accepted, the presence of a reduced anterior segment, acting axially as an articulating ring, in *Limulus* strongly substantiates the present interpretation of *Legrandella*.

Prosomal-Opisthosomal Articulation. Related to the question discussed immediately above is the problem of homology of structures involved in the articulation of the prosoma and opisthosoma when *Limulus* and *Legrandella* are compared. The cardiac region, comprising the cardiac lobe, cardiac furrows, and cardiac ridges in *Le-*

grandella is ill defined at the posterior margin of the prosoma. On the other hand, the cardiac furrow is distinctly impressed in the posterior region of the prosoma in *Limulus*. The axial region of the opisthosoma in *Legrandella* corresponds to the entire posterior width of the interophthalmic area of the prosoma, whereas in *Limulus* the articulating half-ring and entire opisthosomal axial region posterior to it correspond strictly to the cardiac lobe of the prosoma. However, in *Limulus* there is a line of articulation from the cardiac furrows running distally to the ophthalmic ridge. Thus, the single, rather trilobite-like point of articulation (in the axial furrow) between the prosoma and opisthosoma seen in *Legrandella* and other synziphosurans is comparable with and probably homologous with the broad line of articulation in *Limulus*. Phylogenetically, the axial region of the opisthosoma seems to have become constricted (trans.) in *Limulus* from the primitive condition. Under this interpretation, the homologies between the various interophthalmic structures, including the radiating furrows and ridges, advocated between *Limulus* and *Legrandella* in the preceding description, are secure. It may be noted that the line of articulation in the (derived) limuline condition, rather than the single point of articulation in the synziphosurans, is a plausible, even necessary, concomitant of fusion of the opisthosoma into a single massive tergal tagma in the limulines.

The relationship of *Legrandella* with other synziphosurans is considered in the concluding portion of this paper.

WEINBERGINA OPITZI
RICHTER AND RICHTER, 1929

Weinbergina opitzi is known from three specimens. The holotype was described with characteristic clarity and thoroughness by Richter and Richter (1929); the remaining specimens were described by Lehmann (1939, 1956) and reviewed by Kutscher (1965). Only a cast of the holotype (Senck. Mus. VIII 7a) was available to me for the present study, and consequently no formal revision of this important species will be attempted herein.

However, because in many aspects of its morphology, *Weinbergina opitzi* more closely re-

sembles *Legrandella lombardii* than any other known taxon, some of its features bear discussion, and in a few instances reinterpretation. In addition to their overall close resemblance, both taxa are Lower Devonian (Siegenian for *Weinbergina*; Siegenian or Lower Emsian for *Legrandella*) in age and are the only known synziphosurans associated unequivocally with a marine fauna.

The three specimens of *W. opitzi* are all compressed and pyritized. All three preserve prosomal appendages and other sternal structures, and Lehmann (1956) has figured opisthosomal sternites in both of the specimens recovered subsequent to Richter and Richter's (1929) description of the holotype. This added information more than compensates for our total lack of knowledge concerning the actual shape of the dorsal features of the exoskeleton of *W. opitzi*.

As shown in table 1, the three specimens of *W. opitzi* are of nearly equal size, and just slightly smaller than the three specimens of *L. lombardii*. The prosoma is flattened in all three specimens, and in the holotype, severely deformed on the right side. As preserved, the prosoma of the holotype is indeed semicircular and few features are immediately discerned except the surficial granulation. However, keeping *Legrandella* in mind, it is apparent that Richter and Richter (1929) underestimated the amount of deformation undergone by the holotype, and proper identification of the true axis of both the prosoma and the opisthosoma reveals more of the morphology of the dorsal exoskeleton than has been discussed previously.

Richter and Richter interpreted the two rows of knobs on the opisthosoma as features of the axial furrows, correlated, especially on the left side, with projections from the posterior margin of the prosoma. Their interpretation is correct for the left side, but examination of a cast of the holotype clearly shows that the "knobs" on the right side are actually axial nodes, i.e., prominences on the posterior margin of each opisthosomal segment at the midline. Lehmann (1956) noted axial nodes on another specimen of *W. opitzi*. As in *Legrandella*, these axial nodes are absent on the fifth and sixth opisthosomal segments. (It will be argued below that, as in *Legrandella*, the first opisthosomal segment is re-

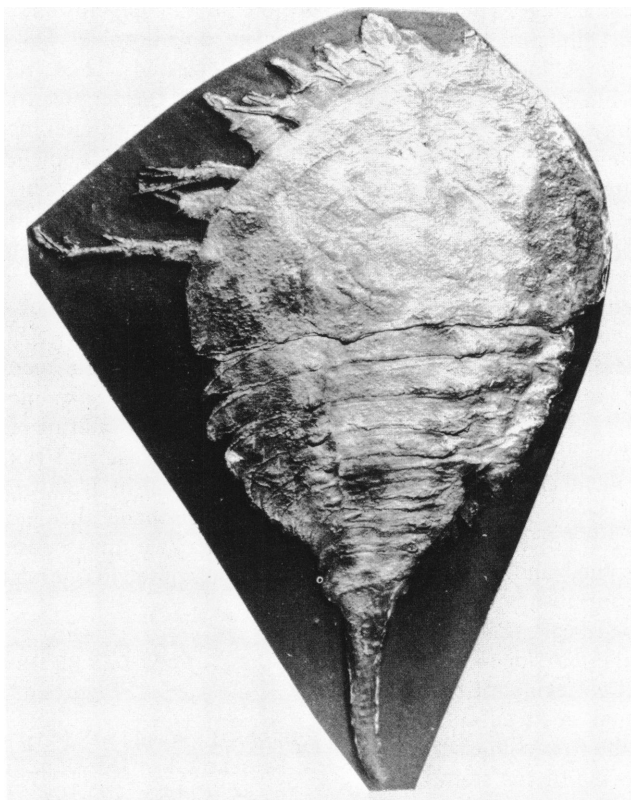


FIG. 5. *Weinbergina opitzi* Richter and Richter. Dorsal view of plaster cast of holotype, Senck. Mus. VIII 7a. X1.

duced and in all three specimens of *Weinbergina* hidden beneath the prosoma. Hence the preabdominal segments lacking axial nodes are *interpreted* as actually segments 6 and 7.) In any case, the true axial furrow on the right side lies close to the right-hand margin of the specimen. Thus, the compressed axial nodes of the opisthosoma of *Weinbergina* imply a rather more highly vaulted profile than previously reconstructed.

Furthermore, by analogy with the reinterpretation of opisthosomal features, the main projection from the posterior margin of the prosoma on the right side is the compressed remains of the posterior prosomal axial prominence, and the true "posterior reflection" (i.e., that feature in *Legrandella* which arises near the posterior margin of the ophthalmic ridge) is seen to lie near the right prosomal margin of the holotype of *W.*

opitzi. Thus, *Legrandella* and *Weinbergina* share essentially identical basic plans of structural organization. Further similarity is expressed in the equivalent development of the prosomal double in both genera.

What of the cardiac and ophthalmic features in *Weinbergina*? I believe that the holotype can be interpreted in the following manner. A cardiac lobe, tapering anteriorly can be discerned although it is evidently highly compressed and somewhat distorted. The interophthalmic area on the left side has become secondarily stretched out and exaggerated, but a definite cardiac ridge and the faint traces of at least five pairs of radiating furrows and ridges are preserved in the holotype. A crescentic, if somewhat discontinuous, ridge arises just anterior and distal to the left posterior prosomal reflection, and can only be

interpreted as the ophthalmic ridge. The "second Frankfurt specimen" (see Lehmann, 1956, pl. 1) does not reveal these features, but the so-called "Bonner specimen" (Lehmann, 1956, pl. 2) shows, particularly in X-ray, the radiating structures of the interophthalmic area correctly interpreted by Lehmann as sites of muscle insertion.

It is noteworthy, too, that, with commendable caution, Lehmann (1956, p. 70, fig. 3) tentatively discussed and figured two subparallel curvilinear rows of "pyrite tubercles" from the left dorsal side of the Bonner specimen, which he interpreted as lenses. These tubercles are probably the equivalent of the lensar structures of *Legrandella*.

I shall not discuss the morphology or significance of the prosomal appendages at this point. The opisthosoma shows seven definite preabdominal segments and three postabdominal segments. The pleura are spined and unfurrowed, except perhaps the anteriormost (= second segment of *Legrandella*) which bears some slight indication of a furrow on the left side of the holotype. Thus, there is no direct evidence from the dorsal side of an additional, reduced opisthosomal segment anterior to the first visible segment. However, Lehmann's drawing of the sternites of the second Frankfurt specimen, which is supported by his photographs, shows the anterior sternites as fused, with a furrow between two broad plates, and another, discontinuous furrow separating a short (sag.) additional segment anterior to the main body of this sternal plate. This small sternal structure evidently represents an eleventh opisthosomal structure, and is of a length and width expected from the dorsal morphology of *Legrandella*. It should be noted that, in the Bonner specimen, these sternites do not appear to be fused (unless we are not actually looking at the true ventral surface!) and no indication of a reduced anterior opisthosomal segment can be seen. Thus, as is typical in the study of even well-preserved synziphosurans, the issue of the actual number of opisthosomal segments in *Weinbergina* remains equivocal.

A final remark concerning the sternites of the opisthosoma is in order. Of all synziphosurans, only in *Weinbergina* are the sternites preserved in the preabdomen. Whether or not a true fused "opercular" series was present in the anterior

region of the opisthosoma, it is clear that there were no opisthosomal walking legs as are found in the aglaspids. The presence of sternites, merged with the tergites to form the cylindrical segments of the postabdomen, is characteristic of all Synziphosurina (as emended and restricted below); these are present in *Weinbergina*, and as would be expected seem more fully sclerotized than do the sternites of the preabdomen.

What differences, then, are there between *Legrandella* and *Weinbergina*? Aside from the differences in ornament, perhaps only the lack of a clearly defined anterior median projection of the prosoma in *Weinbergina* may be added. But the true degree of the vaulting remains moot, and the presence of cardiac and ophthalmic features remains equivocal in *Weinbergina*, although seemingly more probable than heretofore thought. On the evidence, we must consider these two genera distinct yet quite closely related.

BUNODES EICHWALD, 1854

Figures 6, 7

Bunodes Eichwald, 1854, p. 107; 1860, p. 1444.

Nieszkowski, 1859, p. 378. Schmidt, 1883, p. 34. Clarke, 1913, p. 777. Størmer, 1955, p. P16.

Exapinurus Nieszkowski, 1959, p. 380.

[?] *Hemiaspis* [in part]: Woodward, 1872, p. 179.

Emended Diagnosis (based mainly on type species, *B. lunula* Eichwald, 1854). Intermediate-sized Synziphosurina with highly vaulted prosoma, semicircular to subquadrate in plan view. Cardiac and interophthalmic regions well differentiated. No posterior, lateral, or anterior marginal furrows present. Cardiac lobe defined by broad cardiac furrows, arising just anterior to but not reaching posterior prosomal margin. Cardiac furrows nearly transverse posteriorly, becoming reflected anteromesially. Cardiac lobe divided into distinct anterior and posterior sections; posterior section tapering anteriorly approximately 37 percent of length of prosoma, bounded anteriorly by broad median (transverse) furrow connecting two cardiac furrows. Cardiac ridges broad, highly vaulted, and higher than posterior section of cardiac lobe. Anterior section of cardiac lobe narrow, bounded laterally by straight furrows, and

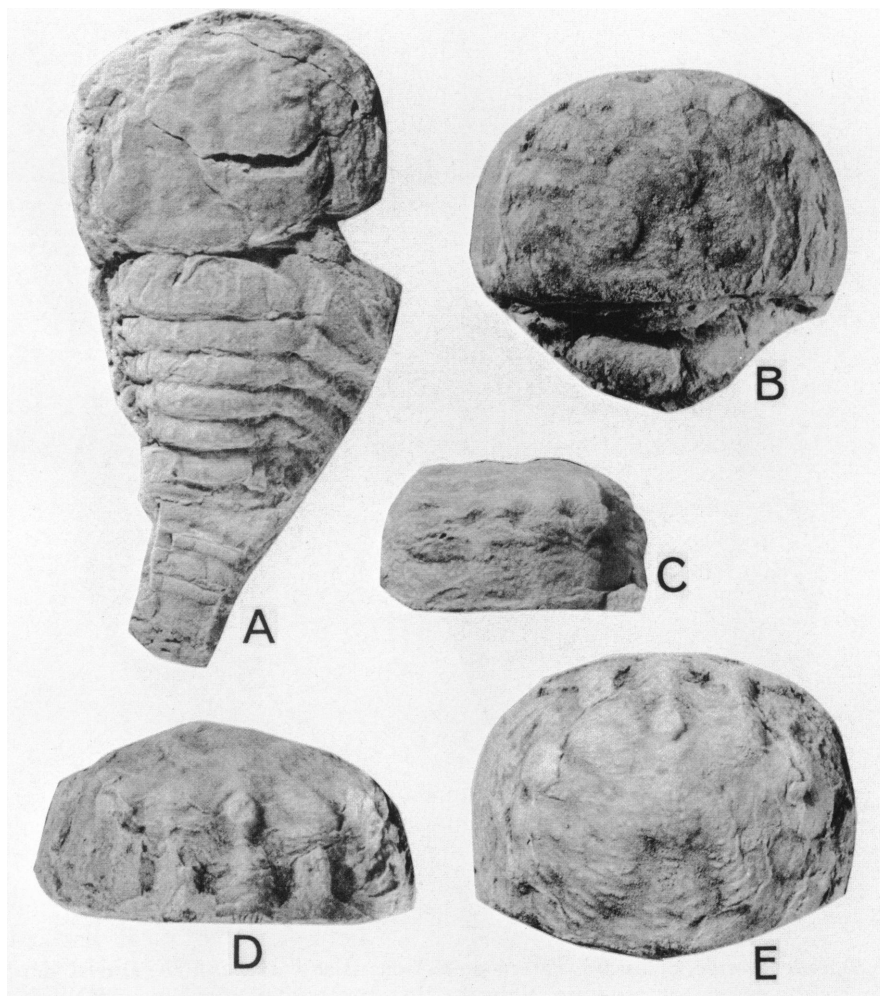


FIG. 6. *Bunodes lunula* Eichwald. Patten collection, Island of Oesel. A. Dorsal view of prosoma and opisthosoma, AMNH 28734. $\times 2$. B, C. Dorsal and right lateral views of prosoma and anterior opisthosomal segments (in dorsal view only), AMNH 29277. $\times 3$. D, E. Frontal and oblique anterodorsal views of prosoma, AMNH 29278. $\times 3$.

elevated above posterior section of cardiac lobe and cardiac ridges, in lateral view.

Interophthalmic region nearly horizontal, sloping gently downward toward anterior and lateral prosomal margins. Interophthalmic area with series of five radiating ridges arising from each cardiac ridge, separated by shallow furrows. Radiating furrows sometimes discontinuous, with some concomitant anastomosing of radiating ridges. Ridges produced into swollen "pouches"

distally, not completely conjoined into true ophthalmic ridge; radial furrows continued between swollen pouches terminating near lateral prosomal margin. Furrow and ridge system of interophthalmic area thus continuous over cheek regions. Swollen pouches describing arc similar to ophthalmic ridge of *Legrandella*; second pouch (counting from anterior) produced farther distally than the others, bearing lensar structures. Median pouch or swelling, possibly sensory in

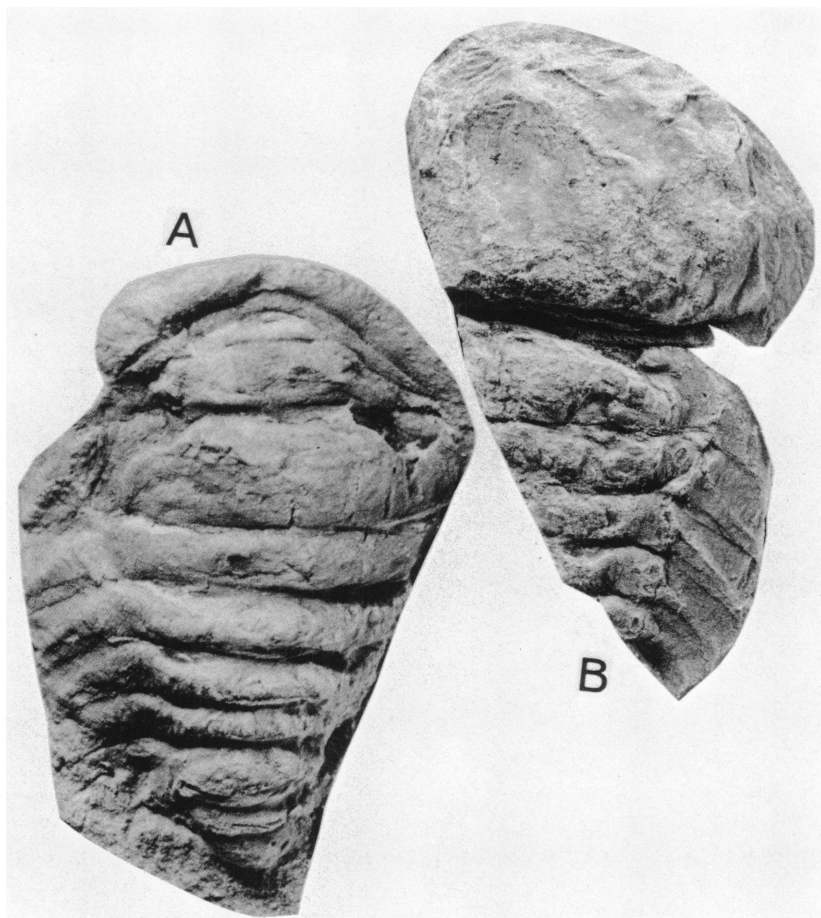


FIG. 7. *Bunodes lunula* Eichwald. Patten collection, Island of Oesel. A. Dorsal view of opisthosoma and posterior margin of prosoma. Note the first opisthosomal segment. AMNH 29279. $\times 4$. B. Dorsal view of prosoma and right anterior region of opisthosoma, AMNH 29276. $\times 3$.

function, occurring on anterior region of anterior section of cardiac lobe, situated at point of sharp change in prosomal slope. Median pouch roughly opposite first pair of radial pouches. Anterior section of cardiac lobe continuous as distinct ridge to prosomal margin. Lensar structures not observed on other pouches comprising "ophthalmic ridge area."

Cheek region (i.e., lateral and anterior region distal to radial pouches) nearly vertical, in sharp contrast to nearly flat cardiac, and gently sloping interophthalmic areas of prosoma. Doublure closely appressed to vertical cheek region, en-

tirely vertical, running up as far as "ophthalmic ridge area." No anterior median projection or genal spines present.

In posterior view, posterior margin of prosoma vertical, invaginated (trans.) into deep furrow running entire width comprising interophthalmic and cardiac areas. Short, ringlike projection beneath furrow, below which first segment of opisthosoma articulated.

Opisthosoma with 10 free segments consisting of preabdomen of seven segments and postabdomen with three segments. Axial furrows converging posteriorly, and broad throughout length of

preabdomen, confluent with flat field of articulating half-ring of opisthosomal segment 2. First opisthosomal segment greatly reduced (frequently hidden under prosoma), depressed well below axial surface of prosoma and second opisthosomal segment. Pleura of first segment flat, bluntly terminated, hardly extending beyond axial furrow. First segment with narrow articulating half-ring clearly set off by deep transverse furrow. Second opisthosomal segment hypertrophic, longer (sag.) than the others, and inflated to height of posterior margin of dorsal surface of prosoma. Axial region of second opisthosomal segment with distinct sagittal furrow in anterior part; anterior margin of axial ring crescentic, running posterolaterally from midline. Articulating half-ring short, expanding into flat field at distal region of axial ring; axial ring constricted distally, forming node. Axial furrow bounded distally on all segments by steep wall produced into node on proximal end of pleuron; pleura triangular in profile (ex-sag.), with broad, shallow furrow anterior to median ridge. Pleura terminating in bluntly rounded form anterodistally, and sharply angular posteriorly. Preabdomen widest at approximately fourth opisthosomal segment.

Each succeeding segment with small articulating half-ring; axial ring straight (trans.) medially, becoming reflexed anteriorly distally near axial furrow at apparent site of articulation with succeeding segment. Seventh opisthosomal segment constricted (trans.) to narrow axial region and larger (sag.) than immediately preceding segments; pleura apparently without median ridge and bluntly rounded distally.

Postabdomen of three cylindrical segments, corresponding in width to axial region of preabdomen, and lacking distinct pleura, although short pleural spines possibly present; articulating surfaces present and postabdominal segments generally heavily sclerotized ventrally. Telson styliform.

Ornament consisting of tubercles of mixed size classes occurring all over prosoma except for radial pouches and deeper furrows, and covering opisthosoma everywhere except on articulating surfaces and deeper furrows. Telson ornament inadequately known, apparently also tuberculate.

Remarks. The preceding emended diagnosis of *Bunodes* is based on a large suite of topotypi-

cal specimens of the type species, *B. lunula*, from the "Eurypterus" beds (Upper Silurian) of the Island of Oesel. Further study of British species probably referable to *Bunodes* (e.g., *Hemiaspis salweyi* Woodward, 1872, and *H. horridus* Woodward, 1872) may necessitate some revision of the diagnosis to encompass morphological peculiarities of these species, but on the whole the diagnosis given seems appropriate for these species as well. No attempt will be made to redescribe *B. lunula* formally; judging from the material at hand, however, it seems reasonable to conclude that only one species, *B. lunula*, is present in the Oesel fauna, a conclusion shared by Jan Bergström (personal commun.). Consequently "*Exapinurus*" *schrenki* Nieszkowski and *B. rugosus* Eichwald are best considered as synonyms of *B. lunula*.

Material Examined. Ninety-six prosomas, 41 opisthosomal portions, and one telson, were available for examination. These totals include nine reasonably complete specimens. All are in the collections of the American Museum of Natural History, Department of Invertebrate Paleontology. They represent a part of a large collection which also contains cephalaspid ostracoderms, eurypterids, and the xiphosurid *Pseudoniscus aculeatus* Eichwald, as well as other invertebrates, collected by William Patten in 1901. This excellent collection is the direct result of scientific theory, for if Patten had not so assiduously pursued confirmation of his belief that arthropods and vertebrates are closely related, the material would never have been assembled.

Preservation. As nearly all the specimens are deformed in some way, no detailed series of measurements were taken. Most of the material is preserved in a soft dolomitic matrix; the specimens are preserved as molds covered by a very thin layer of dark brown material, taken to be a residue of the original exoskeletal material. Frequently, fragments of "*Eurypterus fischeri*" Eichwald are associated with *Bunodes* specimens on the same bedding plane, and the difference in preservation is striking. "*Eurypterus fischeri*" is most commonly preserved as thin, light brown patches of integumental material. Specimens of *Pseudoniscus aculeatus* are generally preserved as internal molds with thin, light brown coatings of

organic residue occasionally adhering to different regions of the body. Thus, each one of the three prominent merostomes of the Oesel fauna presents its own unique appearance because of the different chemical properties of their original integument.

Discussion. The genus *Bunodes* has been rather badly misinterpreted and misunderstood through the years; this is surprising because *Bunodes lunula* is the only abundant and moderately well-preserved synziphosuran species. The relationships of *Bunodes* to other Synziphosurina is considered below. However, some points of its morphology warrant closer attention and comparison with other forms here.

The prosoma is highly vaulted. The cardiac region, including the cardiac lobe, cardiac furrows, and the system of radiating furrows and ridges on the interophthalmic area, are very similar to *Legrandella*, *Bunaia*, and other taxa discussed here. The major peculiarity of the prosoma is that the radiating ridges of the interophthalmic area do not coalesce to form a complete ophthalmic ridge as in other related taxa (except *Limuloides*) but rather define the position of such a ridge by being produced into swollen pouches arrayed in crescentic form along the outer edge of the dorsal surface of the prosoma. The ridges and intervening furrows are continuous beyond this point and are strongly developed on the very steep lateral regions of the prosoma.

The cardiac lobe is also peculiar. The posterior section bounded by typical furrows and cardiac ridges is rather ordinary synziphosuran morphology. However, that structure here considered the anterior section of the cardiac lobe, is essentially a median ridge comparable with the radiating ridges of the interophthalmic area, and like the latter, continuous down the steep (anterior) slope of the prosoma. It is noteworthy that in "*Hemiaspis*" (= *Bunodes*) *salweyi*, this anterior section of the cardiac lobe does not appear to be continuous with the median ridge on the steep anterior slope of the prosoma. The anteromedian ridge does appear to be continuous with the cardiac lobe in *Limuloides limuloides*, however. Thus, an incomplete ophthalmic ridge, presence of a distinct ?sensory node on the anterior section of the cardiac lobe, presence of radiating ridges and furrows distal to the ophthalmic ridge area,

and presence of distinct eyes only on the second (from anterior) pouch are specializations found only in *Bunodes*, and to a degree at least in *Limuloides*. The lensar structures on the second ophthalmic lobe or pouch are rather small and globular and are rarely clearly discernible. As discussed under *Pseudoniscus aculeatus* below, the presence of carbonate crystals in the matrix compounds the problem of accurate recognition of true lensar structures in the merostomes collected from the Oesel beds. However, a number of specimens of *Bunodes lunula* in the Patten collection display these globular structures on the second pouch only, and it seems quite likely that these structures were in fact a part of the visual apparatus.

In addition, the depressed nature of the posterior section of the cardiac lobe, and the very flat conformation of the overall dorsal prosomal surface of *Bunodes* is unique within the Synziphosurina with the possible exception, again, of *Limuloides*. The presence of a distinct transverse furrow along the posterior wall of the prosoma is also known only in *Bunodes*.

The conformation of the opisthosoma in *Bunodes*, however, is more classically synziphosuran in aspect. The presence of a greatly reduced anterior first opisthosomal segment is unambiguous and previously ignored; the significance of this structure is discussed in conjunction with *Legrandella* above and its systematic importance is considered below. Clarke (1902, p. 87) noted that specimens figured by Schmidt (1883, pl. 7) showed 10 segments. It is ironic that I cannot agree with Clarke on the interpretation of Schmidt's figures, although 10 is the true number of segments in *Bunodes*. Schmidt's plates (both 1 and 7) do show the first reduced segment, but not in a complete specimen, and the significance of that segment has remained obscured in subsequent work. Clarke (1913, p. 777) later reiterated his view that 10 segments are present in *Bunodes*, but considered the preabdomen to consist of six, and the postabdomen to consist of four, segments.

There is no clear evidence that opisthosomal segment 7 is in fact double; such a fusion has been suggested for *Limuloides limuloides* (e.g., Størmer, 1955; in reference to the sixth, herein considered the seventh, opisthosomal segment),

and the large size of this segment in *Bunodes lunula* is perhaps suggestive of fusion. The pleuron of this segment is simple, lacking distinct grooves or ridges. But in any case, there are unambiguously 10, not nine, free segments in *Bunodes lunula*.

LIMULOIDES SALTER IN WOODWARD, 1865

I shall not attempt a rediagnosis of *Limuloides* herein; only a single specimen has been described from North America which has been referred to this genus, i.e., *Hemiaspis*? (= *Limuloides*) *eriensis* Clarke, 1924, from the Bertie Waterlime of New York State (Clarke, 1924, p. 119). As Clarke pointed out, the specimen is very poorly preserved and only doubtfully referable to this genus.

It is important merely to reiterate herein that, at least in *Limuloides limuloides* Woodward, the type species, there is a distinct cardiac lobe (with an anterior section very similar to that of *Bunodes*), an interophthalmic area apparently with typical radiating ridges and furrows, and ophthalmic ridges. The radiating ridges continue distally beyond the ophthalmic ridges, a condition otherwise known only in *Bunodes*.

The opisthosoma consists of distinct preabdominal and postabdominal regions. Although the opisthosoma of *Limuloides* is always said to have nine segments, with the "sixth" possibly a fused, double segment (e.g., Størmer, 1934, p. 9; 1955, p. P16), one specimen in the British Museum (examined personally and from a photograph kindly furnished by Dr. Jan Bergström) clearly shows the presence of a reduced first anterior opisthosomal segment. The second segment is hypertrophic and its overall morphology appears closely similar to that described above for *Bunodes*. The postabdomen consists of three apparently cylindrical segments with short pleural spines. Thus the opisthosoma consists of 10 free segments, of which the seventh is possibly double (as in *Bunodes*). *Limuloides* and *Bunodes* are very closely related, and it is noteworthy that both retain suggestions of the full primitive complement of 11 opisthosomal segments.

BUNAIA CLARKE, 1919

Bunaia Clarke, 1919, pp. 531-532; 1920, p. 129.

Ruedemann, 1925, p. 79. Størmer, 1955, p. P16 [in part], non figure 11, no. 10. [non] *Bunaia*: Størmer, 1934, p. 19-20.

Emended Diagnosis. Small merostomes with well-defined cardiac lobe tapering anteriorly, with at least five pairs of radiating furrows and ?six pairs of radiating ridges on the interophthalmic area. Ophthalmic ridges present, long and crescentic in outline, bearing lensar structures. Prosoma semicircular, with large genal spines (or cornua) and no pronounced anterior median projection. Faint suggestion of circumprosomal marginal furrow present. Ornament apparently smooth. Degree of prosomal vaulting unknown. Opisthosoma with at least eight segments; pleura unknown. Telson long, striate, and styliform. No sternal structures known.

Remarks. Insofar as the morphology of the type and only species herein referred to the genus is known, *Bunaia* differs from *Legrandella* in the presence of genal cornua, its apparent lack of an anterior median projection, a circumprosomal marginal furrow, smooth ornamentation, and smaller size. As discussed below, the four specimens of *B. woodwardi*, the type species, may well prove to be young individuals of *Pseudoniscus clarkei* Ruedemann.

Referred Species. In addition to *B. woodwardi* Clarke, Størmer (1934) referred a single prosoma, termed *B. heintzi* Størmer, to this genus. That specimen agrees with *B. woodwardi* in possessing a marginal furrow and genal spines, but differs in its subquadrate shape, heavily developed granulation, and larger size. Most importantly, "*B.*" *heintzi* appears to lack ophthalmic ridges, and the cardiac lobe, as noted by Størmer is narrower and of a different shape in "*B.*" *heintzi*. The radiating furrows on the interophthalmic area are apparently primitive for the Xiphosurida, if not for a larger group of Merostomata, and themselves are not indicative of close relationship among species. For these reasons, "*B.*" *heintzi* should probably be referred to a separate (new) genus, the description of which should await the discovery of further material. Indeed, there is at present insufficient morphological information to allow definite

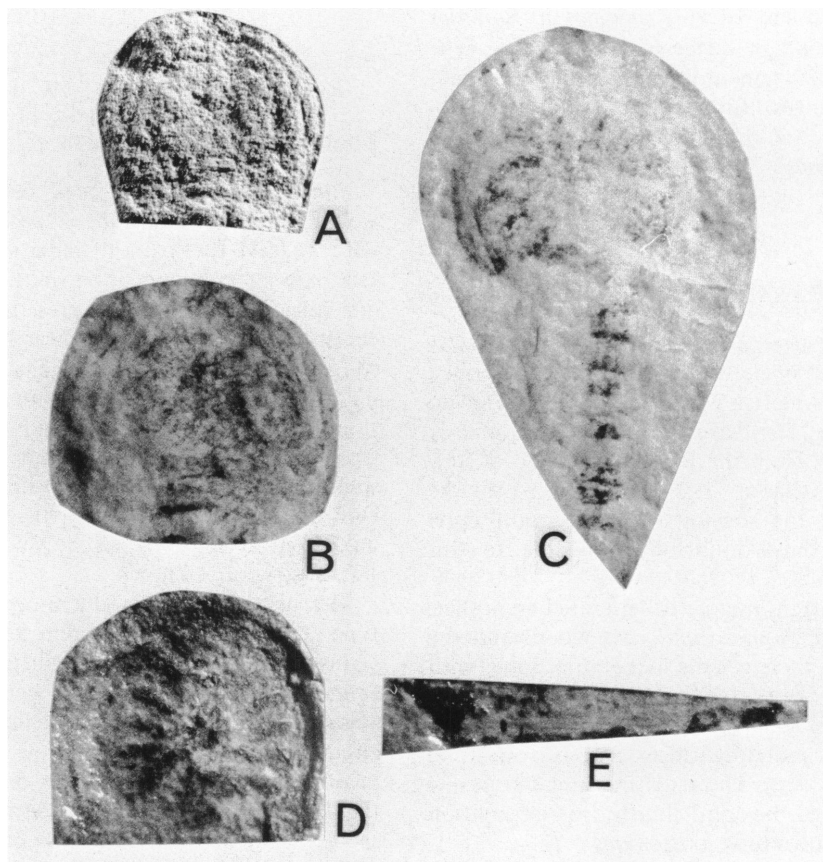


FIG. 8. *Bunaia woodwardi* Clarke. A, B. Dorsal views of prosoma and anterior region of opisthosoma of lectotype, NYSM 9909. A. Specimen photographed coated with ammonium chloride. $\times 4$. B. Specimen photographed wet. $\times 5$. C. Dorsal view of prosoma and axial region of opisthosoma, NYSM 9911. $\times 5$ (photographed wet). D. Dorsal view of prosoma, NYSM 9910. $\times 5$ (photographed wet). E. Telson, NYSM 9912. $\times 5$ (photographed wet).

placement within the order Xiphosurida of this species.

BUNAIA WOODWARDI CLARKE, 1919

Figure 8

Bunaia woodwardi Clarke, 1919, p. 531-532, pl. 14, figs. 1-4; 1920, p. 129, pl. 1, figs. 1-4. Ruedemann, 1925, p. 79, pl. 24, figs. 1-3.

Revised Description. The prosoma of this species is semicircular. The posterolateral margins of the prosoma are produced into stout genal cornua. A faint circumprosomal marginal furrow is

present and confluent across the posterior margin, defining an "occipital ring." Axially, the posterior margin of the prosoma is curved slightly anteriorly.

The cardiac region consists of a cardiac lobe, broadest posteriorly, which tapers regularly anteriorly, then broadens slightly to form an anterior region; it is not distinctly bounded by furrows anteriorly and its length is approximately 70 percent of the total length of the prosoma. Two small circular patches of white (? "chitinous") material are situated near the midline just anterior to, and slightly to the side of, the anterior margin of the cardiac lobe in the

lectotype specimen. These structures are similar in shape, position, and appearance to those described on the holotype of *Legrandella lombardii*. They may represent the median sensory organs of the prosoma; no lensar structures were observed on these patches.

The cardiac furrow is not deeply emplaced in any of the three available specimens. Its position is largely indicated by a dark, organic stain. Distal to the cardiac furrows there is a broad field that is largely featureless in all but one of the specimens. This specimen (NYSM 9910), an external mold, shows five radiating ridges with some exoskeletal material adhering to the matrix on the left side. The right side shows the same features preserved as dark stained ridges of matrix material. These ridges correspond to the linear depressions of *Legrandella*, *Bunodes*, etc., and similarly extend from the cardiac region across the interophthalmic area to the ophthalmic ridge.

The ophthalmic ridges arise near the posterior marginal furrow and curve anteriorly subparallel with the lateral prosomal margin. It is impossible to be certain of the true distance between the prosomal margin and the ophthalmic ridge due to compaction of the specimens, but the relations of these features seen on the lectotype (NYSM 9909; fig. 8) are probably most reliable. Lensar structures, comparable in relative size with those of *Legrandella* and other related taxa, are present at places along the right ophthalmic ridge of the lectotype, and of paratype NYSM 9910, and on both ophthalmic ridges of paratype NYSM 9911. These structures are preserved simply as sub-spherical tubercles and display none of the structural features observed in *Legrandella*. The prosoma, judging from isolated fragments of exoskeleton adhering to the molds, is apparently smooth.

The opisthosoma is known from two fragmentary free segments articulated to the prosoma of the lectotype, and a series of eight free segments closely associated as an external mold with paratype NYSM 9911. Only axial areas are preserved, and there is no information on the nature of the axial furrows (if present), the pleura, articulatory surfaces, or possible subdivision of the opisthosoma into a preabdomen and a postabdomen. A telson, lying close to the lecto-

type prosoma, and which is incomplete at the proximal end, is slightly more than 11 mm. in length, perhaps not overly large for attribution to this species. Faint longitudinal striae cover the telson, and its original cross-sectional profile has been lost by crushing.

Types. I designate NYSM 9909 as lectotype, and NYSM 9910-9912 as three paratypes. These specimens are also catalogued as NYSM 13150/1-4.

Material Examined. Only four specimens of *B. woodwardi* have been reported. All are associated on a single slab of Bertie Waterlime (Cayugan) collected in East Buffalo, New York. All four specimens were described and illustrated by Clarke (1919) and are included in the syntypic series.

Discussion. With the exception of general shape, and presence of a cardiac lobe, the radiating ridges and grooves of the interophthalmic area, and the prosomal marginal furrow, this description and interpretation of *B. woodwardi* differs markedly from Clarke's (1919) original work.

The specimens are poorly preserved, and only faintly discernible. The lectotype is an internal mold with little exoskeletal material present. Paratypes NYSM 9910 and 9911 are external molds with traces of the exoskeleton present as patches of a soft white material and dark "organic" stains. Little relief is present, and while the prosoma may have been as highly vaulted as in *Bunodes* and *Legrandella*, the point is moot. Flower's (1968, p. 40) remarks on the generally poor preservation of most "synziphosurans" are quite true, and *Bunaia woodwardi* is a good example of this sad state of affairs.

Yet this species is tantalizing. As described and reconstructed herein, the prosoma is effectively a miniature version of *Legrandella lombardii* with a marginal furrow and large prosomal cornua, resembling some cephalaspid agnatha in general aspect. Clarke (1919) thought the ridges and other structures, especially as preserved on NYSM 9910, to represent true prosomal appendages. This is not so; these features are the by now familiar radiating ridges and furrows of the interophthalmic area. The structures Clarke took to be chelicerae actually appear to be simply patches of the dorsal exoskeleton, perhaps the same as those two patches described above from

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF THREE PROSOMAS AND
ONE TELSON OF *BUNAIA WOODWARDI* CLARKE

	NYSM 9909	NYSM 9910	NYSM 9911	NYSM 9912
Prosomal length	4.5	4.5	4.5	—
Maximum prosomal width	7.15	7.15	6.36	—
Maximum width between ophthalmic ridges	4.68	5.26	4.61	—
Length of cardiac lobe	2.66	?2.53	?3.12	—
Telson length	—	—	—	11.24

the lectotype as possible median sensory organs.

Clarke (1919, p. 532) also took the series of eight (shown as six in his figure) opisthosomal segments in NYSM 9911 to represent a series of very narrow segments. However, it is clear that the segments have been broken off distally on both sides, and there is no evidence that the opisthosoma was actually that narrow. Indeed, faint transverse grooves behind the prosoma of the lectotype indicate that the true width of the anterior region of the opisthosoma approximated the posterior width of the prosoma, as it does in all related taxa.

As in *Legrandella*, and some other taxa discussed in the present paper, the fact that in the small sample available the prosomal measurements are all nearly equal (see table 2) implies that we are perhaps dealing with terminal adult size. In the *B. woodwardi* sample, all closely associated on a single slab, there is the possibility that the three prosomas represent molts of three individuals of the same size class. But in general, the probability that all specimens are the same size, if the sample is random, would be small unless the terminal, or approximately terminal, growth size was reached. In *Limulus*, growth is continuous throughout life, but molts become increasingly infrequent and size is increased but little in the final stages (Waterman, 1954).

Despite the argument that terminal size may have been reached there still remains the possibility that the four known specimens of *B. woodwardi* may ultimately prove to be young specimens of *Pseudoniscus clarkei*. One of the two available specimens of that species (see discussion below) shows a general cardiac and ophthalmic morphology similar to *B. woodwardi*; they, to-

gether with *Neolimulus* Woodward, are the only genera conventionally considered synziphosurans to possess pronounced genal cornua. *Pseudoniscus* does not generally show a well-developed cardiac lobe and radiating ridge and furrow system on the interophthalmic area; nevertheless these structures are also faint on *B. woodwardi* and could conceivably have become even less apparent during the course of ontogeny. (The specimens of *B. woodwardi* are only about one-half the size of those of *P. clarkei*.) Differences in shape between the two taxa may well be artifacts of preservation. Both species come from the Bertie Waterlime of New York State. However, the evidence is inconclusive, and I will choose the conservative path and retain the traditional, separate nomenclature. In any case, the exact affinities of *B. woodwardi* will remain obscure until better material, especially of the opisthosoma, comes to light.

PSEUDONISCUS NIESZKOWSKI, 1859

Figures 9-11

Pseudoniscus Nieszkowski, 1859, p. 381. Eichwald, 1860, p. 1445. Schmidt, 1883, p. 40. Clarke, 1902, p. 83; 1913, p. 777. Ruedemann, 1916, p. 105. Størmer, 1955, p. P17.

Type Species. *Pseudoniscus aculeatus* Nieszkowski.

Emended Diagnosis. Small xiphosurids with obscure cardiac and ophthalmic morphology. Prosoma narrow, with pronounced genal cornua and anterior median projection. Cardiac lobe obscure; when visible, rather narrow posteriorly, tapering anteriorly, then expanding, possibly merging with ophthalmic ridges anteromedially. Inter-

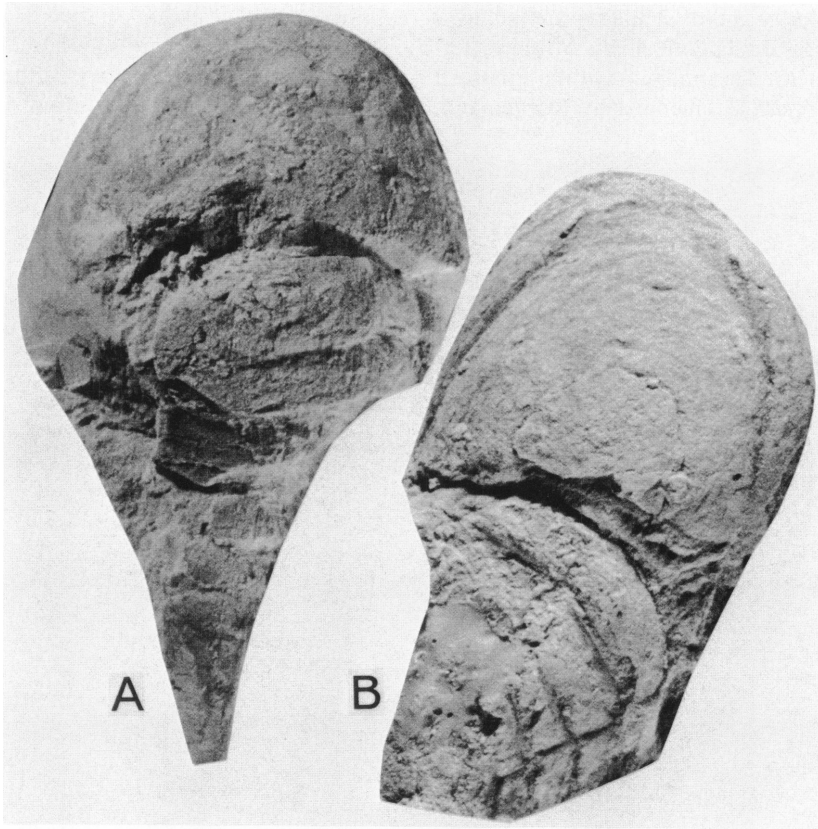


FIG. 9. *Pseudoniscus aculeatus* Nieszkowski. Patten collection, Island of Oesel. A. Dorsal view of prosoma and flexed opisthosoma, AMNH 29280. B. Dorsal view of prosoma and right anterior region of opisthosoma, AMNH 29281. Both $\times 4$.

ophthalmic radiating ridges and furrows obscure, similar to *Legrandella* and *Bunaia*. Ophthalmic ridges present generally as dark organic stain, bearing lensar structures anterolaterally, and possibly along its entire extent. Prosoma generally lightly tuberculate.

Opisthosoma approximately same length as prosoma, with 10 segments, and with no clear subdivision into preabdominal and postabdominal moieties. First opisthosomal segment reduced in both length and width, with short pleura. Second segment the largest, but not hypertrophic. Pleura simple, spined posterodistally, and flat, sometimes with median ridge. Pleura becoming progressively shorter and more posteriorly directed in the posterior region of the opisthosoma. Axial furrows pronounced and simple,

converging posteriorly. Articulating half-rings simple, short (sag.); sixth and seventh opisthosomal segments possibly fused in some species. Telson styliiform.

Referred Species. In addition to the type species, *P. aculeatus* Nieszkowski from the Upper Silurian "Eurypterus" beds of the island of Oesel, *P. roosevelti* Clarke, 1902, from the Silurian Pittsford Shale of New York State, and *P. clarkei* Ruedemann, 1916, from the Silurian Bertie Waterlime of New York are also referred to this genus. Also, two specimens from the Silurian of Great Britain are referable to *Pseudoniscus*.

Discussion. There is no real necessity to present a rediagnosis of each of the three described species referred to *Pseudoniscus*. The major

points of similarity and dissimilarity are included in the following discussion. Many of the differences between the specimens from the Pittsford shale (*P. roosevelti* as emended by Ruedemann,

1916) and *P. clarkei*, as specifically noted by Ruedemann (1916), are accurate observations of the actual material, but may be the result simply of differences in preservation. Furthermore,

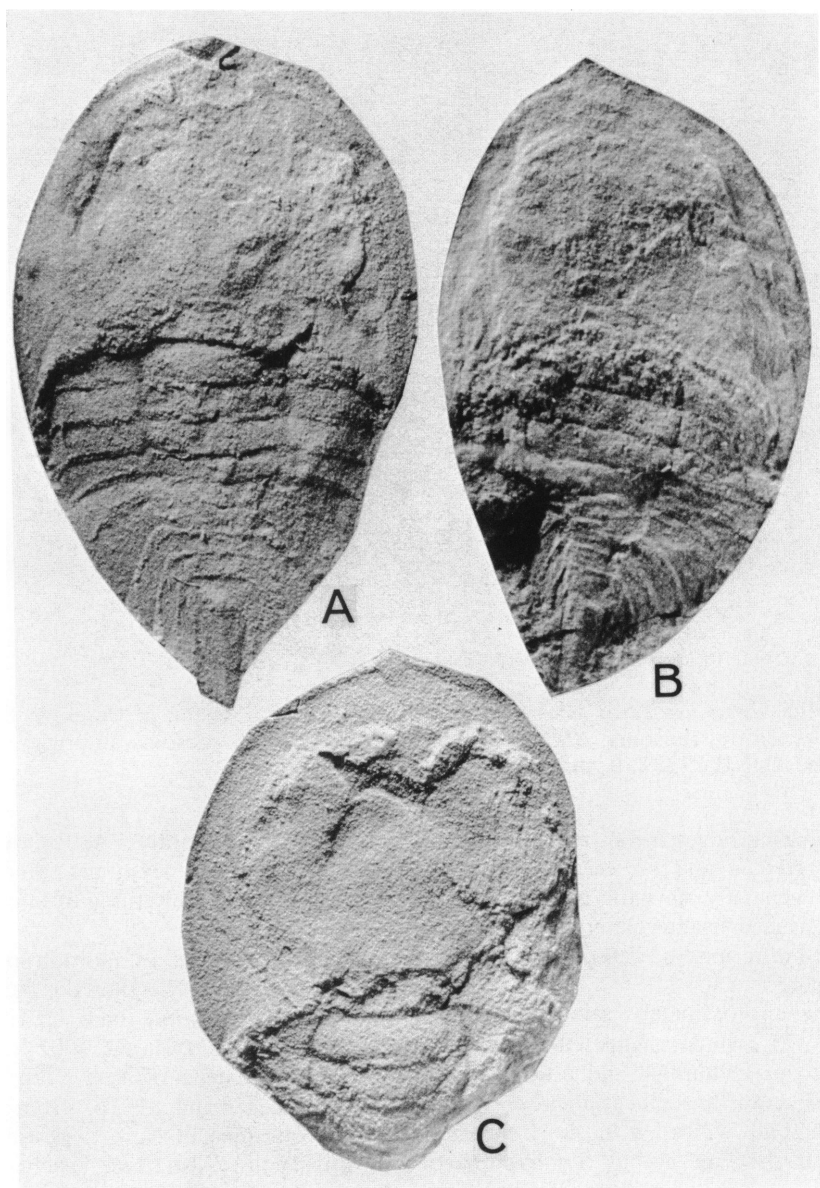


FIG. 10. *Pseudoniscus roosevelti* Clarke. A. Dorsal view of prosoma, opisthosoma, and telson of a nearly complete individual, NYSM 4762 (=NYSM 14020/1). B. Dorsal view of a nearly complete specimen, NYSM 4763 (=NYSM 14020/2). C. Dorsal view of prosoma and anterior opisthosomal segments of an enrolled individual, NYSM 10165 (=NYSM 14020/6). All views $\times 4$.

there is no reliable yardstick, and the data are far too scant to be confident in any case that we really are dealing with two distinct biological species within the New York material.

Although much of the available material of all three species is rather flattened, some specimens of *P. aculeatus* from Oesel indicate a moderately highly vaulted profile of the exoskeleton. All

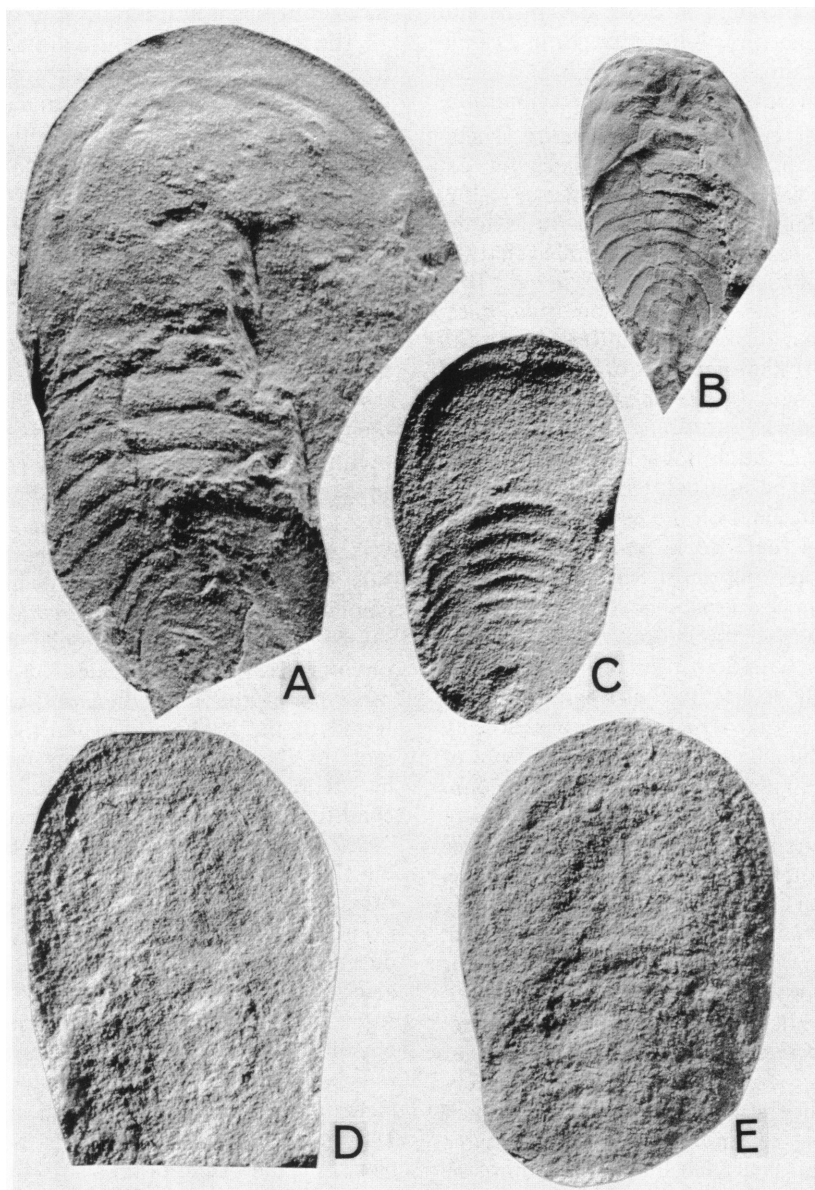


FIG. 11. *Pseudoniscus*. A. *P. roosevelti* Clarke, dorsal view, NYSM 10164 (14020/5). X4. B. *Pseudoniscus* sp., RSM 1957.1.625. X2. C-E. *P. clarkei* Ruedemann. C. Dorsal view of external mold of prosoma and opisthosoma, NYSM 10163 (=NYSM 14016/1). X3. D, E. Dorsal views of part (E) and counterpart (D) of NYSM 4765 (=NYSM 14020/4). X4.

three species are united in having a long, relatively spatulate-shaped prosoma, an appearance accentuated by the large genal cornua, and the presence of an anterior median projection. This last structure appears to be a simple anterior extension of the prosoma in most specimens, but there is a distinct possibility that, as in *Legrandella*, this structure projected at perhaps a rather steep angle ventrally, in the uncrushed condition.

The original figure of *P. aculeatus* (Nieszkowski, 1859, pl. 2, fig. 15) indicates the existence of a facial suture and eye. Clarke (1902; 1913, p. 777) failed to find such structures in the material from New York and concluded that the genus was blind. Ruedemann (1916, pp. 105-106) reviewed the literature on this question and reached the conclusion (based on additional material) that facial sutures are present and that small eyes are situated along the sutures in an anterolateral position. The presence of facial sutures on the dorsal side of the prosoma would of course be unusual, to say the least, for the Merostomata, and on the basis of all material available to me (detailed below), I can find no evidence in corroboration of Ruedemann's view. What is present is a long crescentic band in the appropriate position for an ophthalmic ridge and expressed as a wrinkle, or simply a dark color band, and rarely as a feature of significant topographic relief. Lensar structures are occasionally preserved, seemingly throughout the length of the ophthalmic ridges, but most often encountered in the anterolateral portions. It is essential, however, to emphasize that, whereas these structures resemble in overall form and arrangement the lensar structures of *Legrandella* they are nevertheless small and poorly preserved; furthermore, similar structures occur in other areas of the prosoma of some *P. aculeatus* specimens. It is in fact possible that the "lensar structures" in *P. aculeatus* are actually formed of (?dolomite) microcrystals, or perhaps more likely are microornamental features consisting of small tubercles arising from pits. In this connection, it should be mentioned that the ornament of *P. aculeatus* also includes coarse tubercles, whereas the New York material is generally more finely tuberculate. Specimens of *P. roosevelti*, e.g., NYSM 14020/6, do seem to show small excrescences (Ruedemann's "eyes") anterolaterally on

each side, on which conspicuous tubercles are organized into clusters in a much more regular fashion than are the general ornamental tubercles over the remainder of the prosoma. In any case, the presence of eyes in *Pseudoniscus* remains moot, but seems at least to me to be quite likely.

The apparent absence of cardiac and ophthalmic morphology in most specimens of *Pseudoniscus* poses a challenge: how, in fact, are we to believe these species are properly regarded as Xiphosurida on the basis of their prosomal morphology, and indeed is the absence of such structures to be considered primitive or derived? Fortunately, the two specimens of *P. clarkei* (particularly NYSM 14020/4) which are preserved in hard compact Bertie Waterlime show definite traces of cardiac, interophthalmic, and ophthalmic morphology. The cardiac lobe is relatively narrow posteriorly, tapering anteriorly to a point, then apparently expanding and merging with the ophthalmic ridges at the midline. The cardiac furrows are rather broad sinuses; the radiating furrows of the interophthalmic area are weakly developed, and particularly noticeable on the right side of NYSM 14020/4. Thus interpreted, *P. clarkei* resembles *Bunaia*, *Legrandella*, and other "synziphosuran" taxa; although details remain obscure it is safe to conclude that on the basis of prosomal morphology, *Pseudoniscus* is validly referred to the Xiphosurida, and the obscurity of most of the typical xiphosuran morphology can be attributed to secondary reduction, i.e., its condition is to be considered derived.

Pseudoniscus is also a problem in terms of its opisthosomal morphology. It agrees with most other "synziphosurans" in having well-developed axial furrows converging posteriorly, a greatly reduced first (anterior) opisthosomal segment, and a series of free, rather than fused, opisthosomal segments. Although there is some indication that opisthosomal segments 6 and 7 are fused in *P. roosevelti*, the evidence is exiguous; these segments do not appear to be fused in *P. aculeatus*. The main problem, of course, is the presence of pleura on the posterior segments, in marked contrast to the condition, insofar as it is known, in all other taxa conventionally regarded as Synziphosurina. It is, however, almost certain that posterior segments with pleura is the primitive condition for the Merostomata, and its retention

in *Pseudoniscus* does not automatically disbar this genus from the Synziphosurina. This problem is discussed more extensively below.

Two undescribed specimens of *Pseudoniscus* from the Silurian of Great Britain were also available for this study. One of these (RSM 1957-1.625) from the Logan Water at Lesmahagow, Lanarkshire (see fig. 11B) is of exceptional interest in that it retains a cardiac lobe and traces of the radiating ridge and furrow system of the interophthalmic areas. In other respects, the specimen is closely comparable with the other species of *Pseudoniscus*; there is no indication that any of the opisthosomal segments are fused.

The second British specimen is now housed in the collections of the British Museum (Natural History), BMNH 48428. It is nearly complete but preserves no detail sufficient to distinguish it from other described species and is recorded here for the sake of completeness. The specimen was collected from the Lower Ludlow beds at Church Hill, in the Ludlow region, England.

Material Examined. *Pseudoniscus aculeatus*: Seven prosomas, nine opisthosomas or portions thereof, including four reasonably complete specimens. Patten Collection, the American Museum of Natural History, Department of Invertebrate Paleontology; Upper Silurian ("Eurypter" beds), island of Oesel.

Pseudoniscus roosevelti: Six prosomas; four opisthosomas, including three reasonably complete specimens. NYSM 14020/1, 14020/2, 14020/5, 14020/6. All specimens from the "Pittsford shale," Pittsford, New York (Lower Cayugan).

Pseudoniscus clarkei. Two nearly complete specimens, including one counterpart. Both specimens from the Bertie Waterlime; NYSM 14020/4 from Jerusalem Hill, Herkimer County, New York, and NYSM 14016/1 from Litchfield, New York.

Neither Clarke (1902) nor Ruedemann (1916) designated holotypes for their species. As neither *P. roosevelti* Clarke nor *P. clarkei* Ruedemann has been formally revised herein no lectotypes are designated. Consequently, the specimens examined for each species should be considered syntypic suites. Ruedemann (1916, p. 107) removed one specimen (NYSM 14020/4) from the suite of specimens used by Clarke (1902) to for-

mulate his (Clarke's) original conception of *P. roosevelti*. Ruedemann (1916) referred this specimen to *P. clarkei*, and it should be considered a syntype with NYSM 14016/1 until a lectotype for *P. clarkei* is chosen. Furthermore, as mentioned above, *P. clarkei* may well prove to be a junior synonym of *P. roosevelti*, and that Ruedemann separated these species mainly on the basis of stratigraphic occurrence. Finally, as discussed above, it should be recollected that *Bunaia woodwardi* may be conspecific with *P. clarkei* (both are from the Bertie Waterlime). If so, *Bunaia* would be synonymous with *Pseudoniscus*, and the species *B. woodwardi* would be a junior synonym of *P. clarkei*.

NEOLIMULUS FALCATUS WOODWARD, 1868

Neolimulus falcatus, described by Woodward (1868, pp. 1-3) from the Upper Silurian of England, is poorly known and as conceded by Størmer (1952) generally relegated to the Synziphosurina at least partially because of its age. The ophthalmic ridges apparently meet anteriorly at the midline, and Woodward's figure (1868, pl. 1, fig. 1a) indicates the presence of radiating ridges and furrows on the interophthalmic area, as well as a cardiac lobe divided into distinct anterior and posterior sections, as in *Bunodes* and *Limuloides*. However, the genal angles are produced into broad cornua and, with the presence of ophthalmic ridges, the prosoma of *Neolimulus* is thus more reminiscent of *Bunaia* and perhaps *Pseudoniscus*. The cardiac lobe, as is typical of these Middle Paleozoic forms in general, is narrower than the axial region of the anterior opisthosomal segments.

The opisthosoma is incompletely known (only eight segments have thus far been demonstrated), but there is enough evidence to suggest that they were all free, and there was no differentiation into preabdominal and postabdominal moieties. The pleura are large and flat. Although primitive in aspect, thus not necessarily indicative of close affinity, the condition of the opisthosoma in *Neolimulus* is closest to *Pseudoniscus* among all genera conventionally assigned to the Synziphosurina.

INCERTAE SEDIS

Unfortunately I have been unable to examine any of the type material of the following taxa, but examination of the literature prompts the following observations. *Bembicosoma* Laurie, 1899, referred by Størmer (1955, p. P16) to the Bunodidae, is too poorly known to treat with confidence and should be considered *incertae sedis*. Lamont (1955, p. 212) considered it a stylonurid eurypterid. *Cyamocephalus* Currie, 1927, is likewise too poorly known to allow confident assignment to any well established higher taxon within the Merostomata. *Bunodella* Matthew, 1899, does not appear to me even to be a merostome. The genera *Eolimulus* Bergström, *Archeolimulus* Chlupáč, and *Lemoneites* Flower, are considered briefly below.

RELATIONSHIPS AMONG PALEOZOIC MEROSTOMATA

Clearly, the taxa described and discussed above are all related in some manner. It is equally obvious that they are related to other merostomes both known and unknown. The problem, then, is to seek out the most reasonable (actually, the least objectionable) system of relationships among those taxa described in detail herein, and to elucidate their relationships with other merostomes. By "relationship" I mean solely phylogenetic affinity, expressed in terms of recency of common ancestry. This approach therefore looks for pairs, or sister-groups, among taxa; the general criterion for the recognition of such groups are characters held in common that are specializations not shared with other taxa, for only such shared derived characters can be used to delimit monophyletic taxa (Schaeffer, Hecht, and Eldredge, 1972).

Problems arise with such an approach. These problems, however, stem not so much from the inadequacies of the method as from the inherent difficulty of accurate identification of derived versus primitive character states, and the problem of comparing characters in generally poorly preserved material. The second problem cannot be surmounted; there are three general lines of argument that may be used toward a solution of the first. Because primitive character states may be retained in a variety of forms not particularly

closely related, for any stated problem, examination of character distribution in related taxa outside the group in question, may help to identify primitive character conditions. If the question is, for example, is the shape of the pterygotid telson primitive or derived among the eurypterids, we may conclude it is derived, as all major merostome groups, including other eurypterids, have at least some taxa within their membership which possess a styliiform telson. In fact, we may be justified in concluding that a styliiform telson is primitive for the Merostomata in general.

A second source of inference is morphogenesis. In this regard, the remarks above concerning the composition of the first (anterior) reduced opisthosomal segment in certain taxa were buttressed in part by reference to the embryology of *Limulus polyphemus*.

A third criterion, relative stratigraphic position, recently rejected by some authors (e.g., Schaeffer, Hecht, and Eldredge, 1972), is frequently used by paleontologists. In the morphocline formed of free opisthosomal segments (primitive) to fused opisthosomal segments (derived) within the Limulina (as defined below) it is clear that there is rough agreement between primitive-derived character states and geological occurrence. But there is much stratigraphic overlap among taxa exhibiting critical phases of this morphocline, and the stratigraphic criterion is not reliable for the formulation of specific hypotheses of relationship.

Some 41 characters were investigated in the formulation of relationships presented below. Those which proved valuable are summarized in table 3. For clarity and documentation, I shall initiate the arguments for relationships using those taxa specifically treated in detail herein.

Insofar as *Legrandella lombardii* is concerned, the possibility alluded to above that this taxon may actually prove to be at least congeneric with *Weinbergina opitzi*, leads to the simple conclusion that they are sister taxa. But in view of their different modes of preservation, derived characters shared only by these two species are difficult to enumerate. Both have axial nodes on all but the sixth and seventh opisthosomal segments. If the assertion that there are ophthalmic ridges in *Weinbergina* proves correct, this is an adequate criterion. General shape, and certainly size, are

TABLE 3
A COMPARISON OF CHARACTER STATES FOR *LEGRANDELLA*,
WEINBERGINA, *BUNODES*, *LIMULOIDES*, *BUNAIA*, *PSEUDONISCUS*, AND *NEOLIMULUS*

	LEGR	WEIN	BUNO	LIMU	BUNA	PSEUD	NEOL
GC	0	0	0	0	+	+	+
AMP	+	0	0	0	0	+	0
CL	+	?	+	+	+	+	+
CF	+	?	+	+	+	+	+
CR	+	?	+	+	?	?	?
R/F S-I	+	?	+	+	+	+	+
R/F S-G	0	0	+	+	0	0	0
OR	+	?	0	0	+	+	+
OP	0	0	+	+	0	0	0
OR-M	0	0	0	0	?	+	+
MARGF	0	0	0	0	+	0	0
DOUBV	+	+	+	?	?	+	?
ORN	PITS	TUBS	TUBS	TUBS	?	TUBS	?
O/A-F=CF	0	0	0	0	?	0	0
NOS	11	10-11	10	?10	?	10	?
PR-PO AB	+	+	+	+	?	0	0
NPOAB	3	3	3	3	?	0	0
FOPS-R	+	?	+	+	?	+	?
SOPS-H	0	0	+	+	?	0	?
REL SIZE	L	L	M	M	S	M-S	S

Abbreviations: BUNA, *Bunaia*; BUNO, *Bunodes*; LEGR, *Legrandella*; LIMU, *Limuloides*; NEOL, *Neolimulus*; PSEUD, *Pseudoniscus*; WEIN, *Weinbergina*. AMP, anterior median projection of prosoma; CF, cardiac furrow; CL, cardiac lobe; CR, cardiac ridge; DOUBV, prosomal doublure vertical; FOPS-R, first opisthosomal segment reduced; GC, genal cornua; MARGF, marginal furrows on prosoma; NOS, number of opisthosomal segments; NPOAB, number of postabdominal segments; O/A-F=CF, axial furrow of opisthosoma equal in width to cardiac furrow at tagma boundary; OP, ophthalmic pouch; OR, ophthalmic ridge; OR-M, ophthalmic ridges converge anteriorly, meeting at midline; ORN, nature of ornament; PR-PO AB, opisthosoma differentiated into a preabdomen and a postabdomen; REL SIZE, relative size among included genera only; R/F S-G, radiating ridge and furrow system extends to genal area; R/F S-I, radiating ridge and furrow system on interophthalmic area; SOPS-H, second opisthosomal segment hypertrophic; TUBS, tubercles.

Symbols: +, character state present; 0, character state absent; ?, character state unknown or ambiguous; S, M, and L, small, medium, and large, respectively.

also shared and probably derived (albeit ambiguous) features arguing for a close relationship among these taxa.

Bunodes and *Limuloides* also clearly form a sister group. Here, the shared-derived characters are far more easily enumerated: continuation of the radiating ridge and furrow system distal to the ophthalmic region; bulbous eyes on the second radiating "pouch"; possession of 10 opisthosomal segments (reduced from a primitive 11), of which the seventh appears to be double; and the presence of a hypertrophic second opisthosomal segment. The bipartite nature of the cardiac lobe, and especially its overall configuration, is also

probably a shared-derived feature, although it is to be noted that other taxa, e.g., *Neolimulus falcatus*, are similar to *Bunodes* and *Limuloides* in this regard.

These four taxa, moreover, can be united into a single, monophyletic taxon in view of their shared possession of a distinct postabdomen comprised of three cylindrical segments lacking pleura, in which the sternal elements are well sclerotized. Such a conformation is known elsewhere only in the genus *Lemoneites* Flower (Flower, 1968); it will be shown below, however, that *Lemoneites* is not otherwise to be considered closely related to these taxa. These four

taxa, then, comprise a closely knit group, and are to be considered the Synziphosurina *sensu stricto*, in turn comprising the two families Weinberginidae and Bunodidae. Although superficially rather dissimilar, the large crescentic ophthalmic ridges of the Weinberginidae (or at any rate of *Legrandella*) could easily have been derived through the coalescence of the distinct pouches formed on the radiating ridges of the interophthalmic areas of *Bunodes* and *Limuloides*. These families are simply not so dissimilar as they first appear. As thus restricted, the Synziphosurina is a reasonably compact, and certainly monophyletic assemblage of four genera. Their relationships are epitomized in figure 12.

The Synziphosurina as understood herein are clearly allied with all Upper Paleozoic and younger Xiphosurida (i.e., the suborder Limulina). The characters I consider to be derived that are shared by these two suborders, and which set them off from the orders Eurypteridida, Aglaspidida, and Chasmataspidida, are: prosoma and opisthosoma of nearly equal size (length); prosoma highly vaulted; presence of distinct cardiac furrows (secondarily reduced in some *Pseudoniscus*); a well-defined system of cardiac ridges and radiating ridges and furrows on the interophthalmic area (admittedly also seen on the ?aglaspid *Chraspedops* Raasch and obscure in some advanced Limulina); ophthalmic ridges (in primitive form in the Bunodidae but advanced nonetheless

over the simple eyes of all other Merostomata); well-defined axial furrows on the opisthosoma (admittedly a few eurypterids and aglaspids also display this feature, but seemingly in parallel); opisthosoma with 11 or fewer segments; tendency for opisthosoma to be differentiated into a preabdominal section (with eight or fewer, but no less than six, segments), and a postabdominal section (with no more than three segments; postabdomen ill-defined or lost in some taxa); reduction of the first opisthosomal segment; presence of distinct articulating half-rings on the anterior axial portion of all free segments.

These characters, all of which are derived with respect to the primitive merostome condition, strongly indicate, when taken together, that the Synziphosurina are closely related to all other Middle Paleozoic and younger xiphosurans. I shall hereafter refer to this combined group as the order Xiphosurida. Before examining the nature of these relationships in detail, however, three taxa deserve particular attention, as they appear to share some of these character states.

The Ordovician genus *Lemoneites* Flower (Flower, 1968, p. 37 ff.) has a highly vaulted exoskeleton with a small prosoma of aglaspid aspect, followed by a longer opisthosoma consisting of 11 free segments, and a telson. There is no cardiac or ophthalmic (ridge) morphology present, and the opisthosoma lacks axial furrows. However, the presence of a slightly reduced first opisthosomal segment, of a postabdomen of three distinct cylindrical segments, and articulating half-rings on all opisthosomal segments tends to unite *Lemoneites* with the Synziphosurina-Limulina group as defined above. The cylindrical segments of the postabdomen, however, which are most closely comparable with those of the Synziphosurina, must be parallelisms under the present scheme, because the Xiphosurida as defined above also share well-defined derived characters of cardiac and ophthalmic morphology. *Lemoneites* must therefore be considered *incertae sedis* within the subclass Xiphosura.

Perhaps less ambiguous are the genera *Eolimulus* Bergström, 1968, (a Lower Cambrian taxon) and *Archeolimulus* Chlupáč, from the Bohemian Ordovician. Unfortunately, the opisthosomas are unknown for both of these genera, clouding their precise allocation within the Xiphosurida. *Eo-*

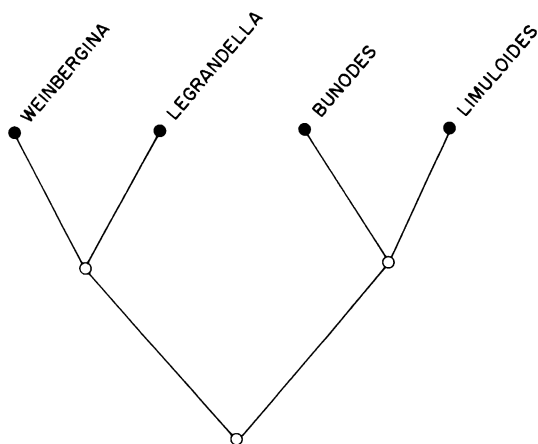


FIG. 12. Relationships among the four genera comprising the suborder Synziphosurina.

limulus possesses cardiac furrows and ridges, and a suggestion of an ophthalmic ridge, features generally characteristic of the Xiphosurida. Likewise, the highly vaulted prosoma of *Archeolimulus* possesses a cardiac lobe, and the suggestion of an ophthalmic ridge, and also appears referable to the Xiphosurida. However, prosomal morphology alone is inadequate for the determination of affinities (certain aglaspids occasionally show cardiac lobes, radiating ridges, and furrows on the interophthalmic area, etc.) and for the moment I prefer to classify *Eolimulus* and *Archeolimulus* as *incertae sedis* but probably within the order Xiphosurida. Other rare taxa, variously treated as aglaspids or xiphosurids, are discussed by Chlupáč (1965) and Bergström (1968) and are not belabored here.

The relationships among *Pseudoniscus*, *Bunaia*, and *Neolimulus*, three taxa discussed at length above, remain to be considered. These are best approached first by a consideration of those shared-derived characters that unite the suborder Limulina (which also includes all Upper Paleozoic and younger merostomes) and distinguish it from the suborder Synziphosurina. These characters are: presence of large genal cornua; ophthalmic ridges which, in the anterior section, are recurved and merge at the midline just anterior to the cardiac lobe (reduced in advanced members, but present in young individuals of *Limulus polyphemus*); and a tendency toward fusion of two or more posterior preabdominal segments (if differentiated).

Among the Limulina, two major groups can further be differentiated: those with, and those without, an opisthosoma with all segments fused. The former group is comprised of the Euproopidae and Limulidae, which are united by further characters that need not be elaborated here. The sister group of these two families (superfamily Limulacea) appears to be those remaining Limulina in which the axial furrows of the opisthosoma are aligned directly with the cardiac furrows, not with the ophthalmic ridges as in the Synziphosurina and other, more primitive Limulina. The significance of this character, as discussed under *Legrandella* above, is that only in taxa with the axial furrows of the opisthosoma directly in line with the prosomal cardiac furrows, is there a well-developed transverse line

of articulation developed between these two tagmata. This character is therefore of fundamental significance. Those taxa allied with the Limulacea in this regard are *Neobelinuopsis rossicus* (Tschernyschew) and certain species of the genus *Belinurus* Koenig (apparently including the type species *B. bellulus* Koenig).

I therefore consider *Belinurus sensu stricto* and *Neobelinuopsis* as closely related (sister) taxa, which together form the sister taxon of the superfamily Limulacea. This latter taxon is herein termed for convenience the infraorder Limulina. Its sister taxon within the suborder Limulina as defined above consists of the remainder of the taxa yet to be considered: All species of "*Belinurus*" with the opithosomal axis broader than the cardiac lobe, *Bunaia*, *Pseudoniscus*, and *Neolimulus*. No formal arguments will be adduced herein to defend a particular theory of relationships among these four taxa, for although they may be diagnosed as a coherent group, all the characters known to me which are shared by all four genera are primitive for the Limulina as a whole, and thus valueless for ascertaining their interrelationships. The suggested relationships indicated in figure 13 and in the classification are therefore to be considered highly tentative.

Finally, the relationships of the order Xiphosurida are worthy of a brief discussion. Essentially, the best hypothesis appears to be that the Eurypteridida and Chasmataspida are sister taxa (shared-derived feature: similarities in prosomal limb morphology, although "paddles" may certainly have evolved independently). Admittedly most of the similarities between these taxa probably involved characters primitive for the Merostomata in general, and there are rather formidable differences between the Eurypteridida and the Chasmataspida.

The Aglaspida seem to be the sister group of the Xiphosurida in the development of a radiating ridge and furrow system distal to the cardiac region (seen only in some aglaspids) and a tendency (slight but definite in some Aglaspida excluding *Beckwithia*) to form a postabdomen of three segments. These relationships are diagrammed in figure 14.

Finally, the following characters of the dorsal exoskeleton are considered common to the entire class Merostomata—shared derived characters

when compared with other Arthropoda, but primitive within the Merostomata: 1) presence of a cardiac "lobe" (a cardiac lobe need not be defined by sharply emplaced cardiac furrows, but instead may be distinguished by slight differences in topography, "ornament," or simply color of the "glabellar area." "*Eurypterus fischeri*" Eichwald and *Chasmatspis laurencii* Caster and Brooks are examples within their nominate

orders; several Aglaspida and all Xiphosurida have cardiac lobes to complete the survey). 2) Ocelli, or at any rate, paired median sensory organs, seemingly distributed among at least some taxa within all four orders. 3) The presence of eyes (probably primitive for Arthropoda if not some larger taxon). 4) Opisthosoma with 12 segments. 5) Presence of a styliform telson.

At least one character state, thought to be

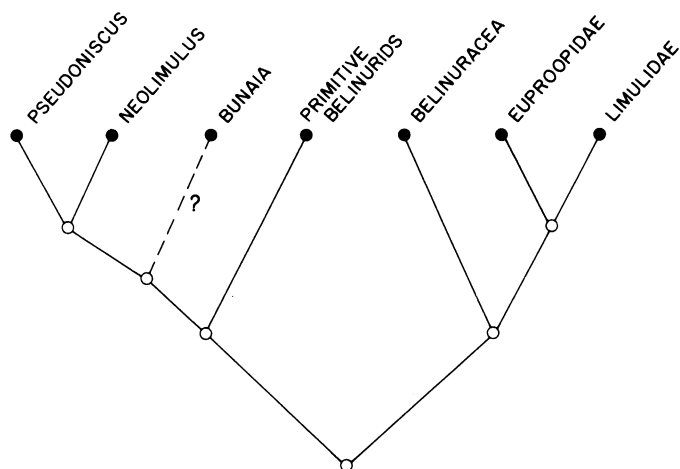


FIG. 13. Relationships among the taxa of the suborder Limulina.

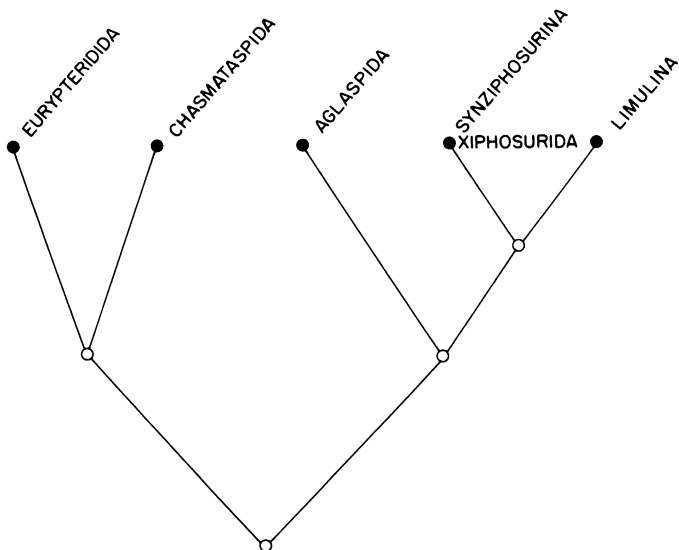


FIG. 14. Relationships among the orders of the class Merostomata.

derived, was given above to support the delimitation of each sister group. However, diagnoses of higher taxa need not be so restrictive, as groups may be defined and recognized by a peculiar, intrinsic combination of a variety of primitive and derived character states. The following diagnosis of the Synziphosurina presents such a combination of character states.

SUBORDER SYNZIPHOSURINA PACKARD, 1886

Emended Diagnosis. Small to intermediate sized Xiphosurida with highly vaulted prosoma bearing well-developed cardiac lobe, cardiac furrows, and system of radiating furrows and ridges over interophthalmic area. Ophthalmic ridges large, crescentic, not meeting anteromedially, or incompletely formed, being defined as disconnected swellings or pouches of the radiating ridge system of the interophthalmic area. Opisthosoma with 10 or 11 segments, with well-defined axial furrows aligned with ophthalmic ridges and convergent posteriorly. Opisthosoma strongly differentiated into preabdomen of seven or eight segments with pleura, and postabdomen consisting of three cylindrical segments with well-developed sternites and short pleural spines. First opisthosomal segment greatly reduced, in axial height and in sagittal length, and in reduced width of pleura. Second opisthosomal segment frequently hypertrophic. All segments of opisthosoma with well-developed articulating half-rings on axial lobe. Telson styliform.

Referred genera. *Weinbergina*, *Legrandella* (family Weinberginidae); *Bunodes*, *Limuloides* (family Bunodidae).

I shall defer a formal diagnosis of the Limulina, the sister suborder to the Synziphosurina, pending a thorough revision of all included taxa. However, the taxa *Pseudoniscus*, *Bunaia*, and *Neolimulus* have been classified together with some "*Belinurus*" species, as the infraorder Pseudoniscina in the classification, page 38, and warrants formal diagnosis.

INFRAORDER PSEUDONISCINA, NEW INFRAORDER

Diagnosis. Generally small Limulina with well-developed genal cornua, ophthalmic ridges recurved anteriorly and meeting immediately anterior to cardiac lobe. Cardiac and ophthalmic

morphology generally well defined, may be obsolescent. Opisthosoma with deeply emplaced axial furrows aligned with ophthalmic ridges and tapering posteriorly. Postabdomen weakly defined, absent, or unknown; when present, with well-developed pleura and poorly developed sternites. First opisthosomal segment greatly reduced; second segment not hypertrophic. Opisthosoma with 10, or, usually, fewer segments. When present, preabdomen of seven or fewer segments. Tendency to fusion of posterior two or more segments of opisthosoma; when preabdomen present, tendency to fusion of last two segments anterior to postabdomen. All free opisthosomal segments with well-defined articulating half-rings. Telson styliform.

Referred Genera. *Pseudoniscus*, ?*Bunaia*, *Neolimulus* (Pseudoniscidae); species of "*Belinurus*" in which axis of opisthosoma is broader than posterior width of cardiac lobe.

CLASSIFICATION OF THE MEROSTOMATA

A suggested phylogenetic classification of the Merostomata is given on page 38. There the relationships, as well as I have been able to grasp them, are precisely expressed. The classification is different in some respects from those of Størmer (1955) and Bergström (1968), the two most recent attempts to systematize this group. The hierarchical levels may not prove satisfactory to those workers specifically interested in some of the contained taxa, especially those herein considered as the superfamily Limulacea. Størmer (1955), for example, considered those taxa herein referred to the Limulacea as three separate superfamilies: Belinuracea, Euproopacea, and Limulacea, the last containing three families. The present classification admittedly "cramps" this last group and an adjustment in hierarchical level of this group will probably be indicated once these taxa are satisfactorily revised and relationships among the included genera are more adequately understood.

XIPHOSURIDA AND MEROSTOMATA: EVOLUTIONARY PATTERNS

A number of students have commented on the main features of xiphosuran evolution, such as progressive phyletic size increase and "gradual"

A CLASSIFICATION OF THE MEROSTOMATA WITH EMPHASIS ON TAXA SPECIFICALLY TREATED HEREIN

- Class Merostomata Dana, 1852
 - Subclass Eurypterida Burmeister, 1843
 - Order Eurypteridida Burmeister, 1843
 - Order Chasmataspida Caster and Brooks, 1956
 - Subclass Xiphosura Latreille, 1802
 - Incertae sedis* *Lemoneites* Flower, 1968
 - Order Aglaspida Walcott, 1911
 - Order Xiphosurida Latreille, 1802
 - Incertae sedis* *Eolimulus* Bergström, 1968
 - Incertae sedis* *Archeolimulus* Chlupáč, 1963
 - Suborder Synziphosurina Packard, 1886
 - Family Weinberginidae Richter and Richter, 1929
 - Weinbergina* Richter and Richter, 1929
 - Legrandella*, new genus
 - Family Bunodidae Packard, 1886
 - Bunodes* Eichwald 1854
 - Limuloides* Salter in Woodward, 1865
 - Suborder Limulina Richter and Richter, 1929
 - Infraorder Pseudoniscina, new infraorder
 - Superfamily Pseudoniscacea Packard, 1886
 - Family Pseudoniscidae Packard, 1886
 - Pseudoniscus* Nieszkowski, 1859
 - Neolimulus* Woodward, 1868
 - ?*Bunaia* Clarke, 1919
 - Family (Unnamed, primitive belinurids)
 - Infraorder Limulicina Richter and Richter, 1929
 - Superfamily Belinuracea Zittel and Eastman, 1913
 - Superfamily Limulacea Zittel, 1885
 - Family Euproopidae Eller, 1938
 - Family Limulidae Zittel, 1885

(or, more accurately, progressive) increase in number of fused opisthosomal segments (starting with the posterior segments and working anteriorly apparently). These general trends were undoubtedly adaptive, and we badly need an evaluation of them, as well as others, in terms of functional morphology.

Some genera (e.g., *Eolimulus* and *Beckwithia* of the Cambrian; *Chasmataspis*, *Lemoneites*, and perhaps *Archeolimulus* of the Ordovician; *Diploaspis* Størmer, *Heteroaspis* Størmer, *Borchgrevinkium* Novojilov of the Devonian), most of which have been described only in recent years from at least moderately well-preserved material, have served to confound, rather than simply modify or clarify, our previous concepts of merostome diversity and phylogeny. In fact, in its modest way, the Merostomata as a group is beginning to resemble the early Paleozoic Echinodermata, com-

posed as they both are of a number of diverse structural types, each itself of low diversity, and separated by rather formidable morphological gaps. Schaeffer (1965) has explored the role of "experimentation" in the origin of higher taxa; there seems to have been much such experimentation, but little consequent radiation (increased diversity; read "success") within the Merostomata throughout the truly long and continuing history of the class. (The Eurypterida constitute a possible exception to this generalization.) It is ironic that the greatest "success" of any of these morphological (and concomitant ethological) "experiments" was the single, or perhaps double (i.e., scorpions and spiders independently), invasion of the terrestrial realm, although even in this instance the Insecta were invariably far more diverse than the Arachnida.

The extraordinarily conservative nature of

Limulus (one of our more familiar "living fossils") has excited the curiosity of evolutionary biologists, and prompted several hypotheses to explain its impressive overall morphological stasis: lack of available genetic variability; lack of intense selection pressures; presence of powerful stabilizing selection forces; high genetic homeostasis. These hypotheses are not all mutually exclusive; Selander et al. (1970) have shown that *Limulus* is about as polymorphic at a sample of its genetic loci as are most other marine organisms. I (Eldredge, 1970) have argued that in terms of its basic external morphology, *Limulus* is highly adapted for burrowing, and undoubtedly to other behavioral syndromes simultaneously, and thus more than likely existing under a regime of rather intense stabilizing selection. Whatever the explanation(s), a relevant observation is that most variation, i.e., diversity of structural type, within the Merostomata occurs at the higher taxonomic levels. Species tend to exhibit little real (phenotypic) variability, and genera and families tend to have low membership. This latter phenomenon is not strictly an artifact of taxonomic methodology; but it is impossible to estimate the amount of sampling bias, because most merostomes apparently lived in marginal marine environments, on the whole rather poorly represented in the geologic record. But it is at least possible that the diversity among living xiphosurans (possibly oversplit into three genera and five species) represents a situation not at all atypical throughout the history of the Xiphosurida.

Stanley (1973) has recently commented on the common phenomenon of advanced types appearing to have been derived from the more generalized taxa within the antecedent group. Viewed cladistically, this generalization is readily explained: the structurally generalized taxa conform (not quite of necessity, but certainly as a rule) more closely to the hypothetical morphotype for the whole group, and thus closer to the morphotype of its common ancestor with the advanced group.

But this observation does not exhaust the interest in the generalization. Arguments emphasizing adaptive and developmental constraints are available, and I shall not explore these further at the present time. But examples of this phenome-

non have emerged in the present study. For instance, the number of opisthosomal segments was reduced from the primitive condition (11), not by eliminating the undoubtedly highly functional postabdominal segments as developed, e.g., in the Synziphosurina, but rather apparently by simple elimination and fusion of rather undifferentiated posterior segments (with pleura), such as those seen in the Pseudoniscina. The Pseudoniscina were advanced over the Synziphosurina in some characters of the prosoma, but in the character complex under discussion herein the Pseudoniscina were far more plesiomorphic than the Synziphosurina.

These concluding remarks on some of the features of merostome and specifically xiphosuran evolution have been included mainly in the hope that the pressing need for careful analysis of the functional morphology of these taxa will be seen to be prerequisite to the solution of these and other interesting problems. Coupled with a detailed and accurate understanding of the phylogenetic relationships among merostome taxa, a goal to which the study hopefully contributes, an analysis of the functional morphology of the exoskeleton of the various merostomes could well contribute greatly to general paleontological evolutionary theory.

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