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## MORPHOLOGY, TAXONOMY, AND CLASSIFICATION OF THE ORDER EURYPTERIDA BURMEISTER, 1843

V. P. TOLLERTON, JR.

Geology Department, Utica College of Syracuse University, Utica, New York 13502

**ABSTRACT**—Standards have been empirically developed to describe various morphological characters of eurypterids. The standards pertain to the following characters: 1) shape of the prosoma; 2) shape of the metastoma; 3) shape of the eyes; 4) position of the eyes; 5) types of prosomal appendages; 6) types of swimming leg paddles; 7) structure of the doublure; 8) differentiation of the opisthosoma; 9) structure of the genital appendages; 10) shape of the telson; and 11) types of ornamentation.

For the first time, a uniform, standardized taxonomy is proposed for classification and identification of most genera. The taxonomy is based on the observation that most higher taxonomic levels for arthropods are based on the structure and arrangement of the appendages. Details of the taxonomy rely on the morphological standards proposed here.

The order Eurypterida Burmeister, 1843, is here defined by the presence of only six pairs of prosomal appendages, the first pair being the chelicera, the next five pairs being the gnathobasic, uniramous legs. Suborders are characterized by the gross morphology of the chelicera. Superfamilies and families are characterized by the use of a single character complex, specifically the structure and arrangement of the second through sixth pairs of prosomal appendages. Genera are recognized by more specific standards.

A new classification of the order Eurypterida is proposed. Three new superfamilies, Kokomopteroidea, Megalogrptoidea, and Brachyopteroidea, and five new families, Brachyopteroellidae, Adelophthalmidae, Lanarkopteroidea, Eriopteridae, and Hardieopteroidea, are proposed.

### INTRODUCTION

**A**NATOMY of eurypterids is generally well known (see Størmer, 1955); however, many inconsistencies are evident when comparing two or more published descriptions of the same species. For example, the shape of the prosoma of *Eurypterus remipes* Dekay, 1825 (Figure 1) has been described as roundish (Dekay, 1825, p. 375; Hall, 1859, p. 404), semioval (Hall, 1859, p. 404), trapezoidal (Clarke and Ruedemann, 1912, p. 162), and subquadrate (Hall and Clarke, 1888, p. 50; Kjellesvig-Waering, 1958b, p. 1110). But according to Kjellesvig-Waering (1979a), the shape of the prosoma of a genus and species is constant. Similar examples of inconsistency are recognized for other morphological characters; therefore, a number of morphological standards are developed herein.

The proposed standards pertain to the following characters: 1) shape of the prosoma; 2) shape of the metastoma; 3) shape of the eyes; 4) position of the eyes; 5) types of prosomal appendages; 6) types of swimming leg paddles; 7) structure of the doublure; 8) differentiation of the opisthosoma; 9) structure of the genital appendages; 10) shape of the telson; and 11) types of ornamentation. These particular characters have been chosen because they have been used by other authors to establish various taxonomic levels in classifications. Not all of the proposed standards are of significant or of equal taxonomic value.

A search for taxonomic principles for eurypterids was fruitless and led to the empirical development of a uniform taxonomy based on the observation that most arthropod higher taxonomic levels are dependent on knowledge of appendages (Manton, 1969, 1977; Hammen, 1977). The taxonomy proposed here relies heavily on both the historical taxonomic concepts for eurypterids

and on the morphological standards. The subsequent classification is modified from Størmer (1974) and Waterston (1979).

### MORPHOLOGICAL STANDARDS

*Shape of the prosoma.*—The term prosoma is preferable to the synonym cephalothorax (Størmer, 1955, p. 5, 7, 8; 1959, p. 5, fig. 1c, d, p. 9) in that it is unambiguous in denoting the anteriormost tagma of the eurypterid organism.

The shape of the prosoma is characterized by two sets of measurements: 1) the length : width ratio, and 2) the lateral angle (Figure 1). Fourteen standard shapes are recognized (Figure 2, Table 1). The relationships between shapes are shown in Figure 3. A partial revision of prosoma shape terms is given in Table 2.

The shape of the prosoma is not easily determined by visual inspection because of the continuum of shapes (Figure 3), and measurements must be made to determine the shape. It was noted that the shape of the prosoma changes during ontogeny (see also Andrews et al., 1974; Brower and Veinus, 1978), for example, from subquadrate in juveniles to trapezoid in adults of *Eurypterus remipes*. Also, the shape of the prosoma is highly susceptible to postmortem alterations (compaction, desiccation, predation, and distortion). Failure to observe either the ontogenetic shape changes or the susceptibility to alterations has probably resulted in the establishment of too many genera and species (Tollerton, 1987b).

Following the suggestions of Størmer (1974) and Waterston (1979), the shape of the prosoma is considered to be of taxonomic importance only at the level of genus.

*Shape of the metastoma.*—The metastoma consists of a ven-

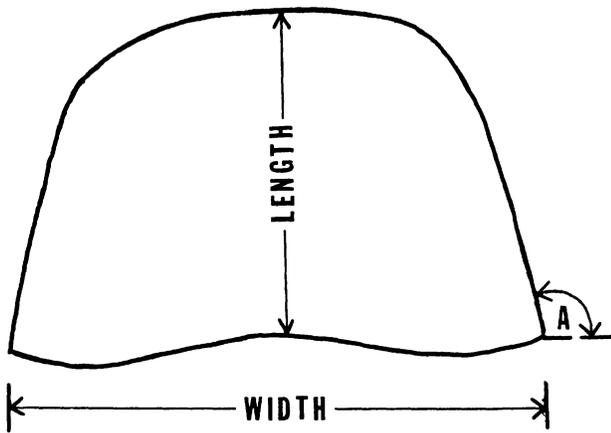


FIGURE 1—Schematic diagram for recognition of standard shapes of prosomas. A = lateral angle.

trally located single plate which is usually cordate at the anterior end. The shape of the metastoma is described using eight parameters (Figure 4). Some of the parameters may be of little or no value, while others not yet studied may be of great value in the characterization of the metastoma. A minimum of 28 distinctly different shapes of metastomas are recognized to date (Figure 5, Table 3). Many more shapes may be possible, because the metastoma is totally unknown for a great number of genera and species.

The posterior cleft plates of the genera *Campylocephalus* Eichwald, 1860, and *Hibbertopterus* Kjellesvig-Waering, 1959, as illustrated in Waterston (1957, p. 272–273, text-figs. 2, 3), and suggested by Waterston et al. (1985, p. 343) in *Cyrtoctenus* Størmer and Waterston, 1968, are not considered here as true metastomas.

The taxonomic importance of the metastoma of eurypterids has long been recognized. Its taxonomic value has been, however, historically assigned at either the level of genus (Clarke and Ruedemann, 1912, p. 58) or family (Størmer, 1951, p. 410; Kjellesvig-Waering, 1966, p. 172).

A qualitative comparative morphological study on eurypterid metastomas (as characterized here) has revealed the following. First, the shape of the metastoma is relatively constant for any one genus. Second, the metastoma is less susceptible to postmortem alterations than the prosoma because nearly all metastomas examined do not show signs of postmortem alterations (see Tollerton, 1987b). Third, there are no clear relations between the shape of the metastoma and 1) the shape

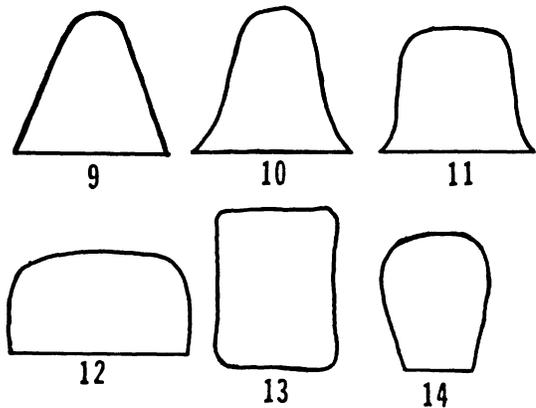
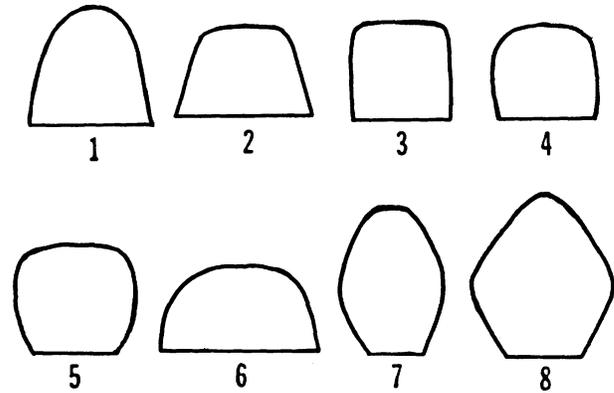


FIGURE 2—Schematic diagrams of the 14 standard shapes of prosomas. 1, parabolic; 2, trapezoid; 3, quadrate; 4, subquadrate; 5, horseshoe-shaped; 6, semicircular; 7, spatulate; 8, pentagonal; 9, triangular; 10, campanulate B; 11, campanulate A; 12, wide rectangular; 13, long rectangular; 14, turbinate.

of the prosoma, 2) the structure and arrangement of the prosomal appendages, and 3) either family or superfamily classifications. Based on these observations, and in light of the fact that the metastoma is known in only half of all eurypterid genera, the shape of the metastoma is here considered of greatest taxonomic value at the genus level.

*Shape of the eyes.*—The term “eyes” is preferred to the terms

TABLE 1—Characterization of the 14 standard shapes of prosomas.

Shape	Length : width ratio	Lateral angle
Quadrate	0.95–1.05	90
Subquadrate	0.65–0.85	85–95
Trapezoid	0.65–0.80	95–105
Horseshoe-shaped	0.70–0.90	60–85
Semicircular	0.50–0.65	110–120
Parabolic	0.90–1.40	100–115
Triangular	0.75–0.90	105–120
Pentagonal	0.95–1.05	55–65
Turbinate	0.90–1.10	75–85
Spatulate	1.05–1.20	60–75
Wide rectangular	0.50–0.65	85–95
Long rectangular	1.25–1.50	85–95
Campanulate A	0.80–0.90	95–105
Campanulate B	0.60–0.80	120–140

TABLE 2—Partial revision of prosoma shape terms.

Present revision	Previously included
Quadrate	Quadrate, square
Subquadrate	Subquadrate, subtrapezoidal
Trapezoidal	Trapezoidal, subquadrate, subtrapezoidal, roundish, semioval
Horseshoe-shaped	Horseshoe-shaped, subrectangular
Campanulate	Campanulate, bell-shaped, semitriangular
Semicircular	Semicircular, hemicircular, semioval, subcircular
Triangular	Triangular, semitriangular, subtriangular
Parabolic	Parabolic, semielliptical, hemielliptical, suboval, semioval, subelliptical, elliptical
Pentagonal	Pentagonal
Turbinate	Turbinate, subquadrate, quadrate, subtrapezoidal
Spatulate	Spatulate
Wide rectangular	Wide rectangular, subquadrate
Long rectangular	Long rectangular, quadrate

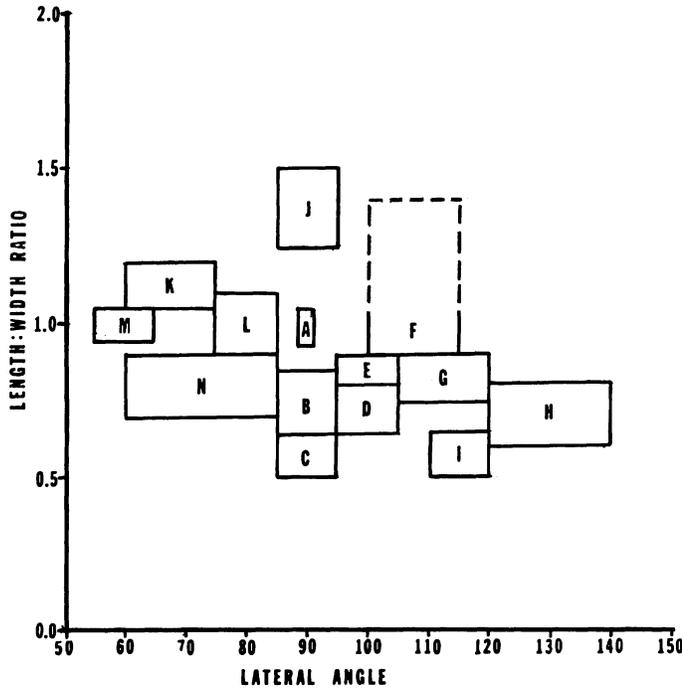


FIGURE 3—Graph for the recognition of the standard shapes of prosomas. A, quadrate; B, subquadrate; C, wide rectangular; D, trapezoid; E, campanulate A; F, parabolic; G, triangular; H, campanulate B; I, semicircular; J, long rectangular; K, spatulate; L, turbinate; M, pentagonal; N, horseshoe-shaped.

“compound eyes” and “lateral eyes,” which may denote, respectively, faceted eyes or eyes located on the sides of the prosoma. The shape of the eyes is easily determined by visual inspection and comparison with the proposed standards (Figure 6). The shape of the eyes, as yet, has not been studied in sufficient detail to warrant its use above the level of genus with certainty.

The major nontaxonomic importance of this morphological character is the determination of postmortem alterations of the prosoma. In particular, postmortem alterations are indicated

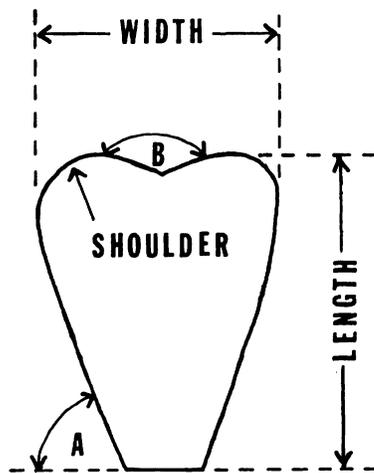


FIGURE 4—Schematic diagram for the characterization of standard shapes of metastomas. A = lateral angle, B = angle of cordation. The other parameters are: 1) length : width ratio; 2) position of greatest width; and 3) character of the anterior, posterior, sides, and shoulder.

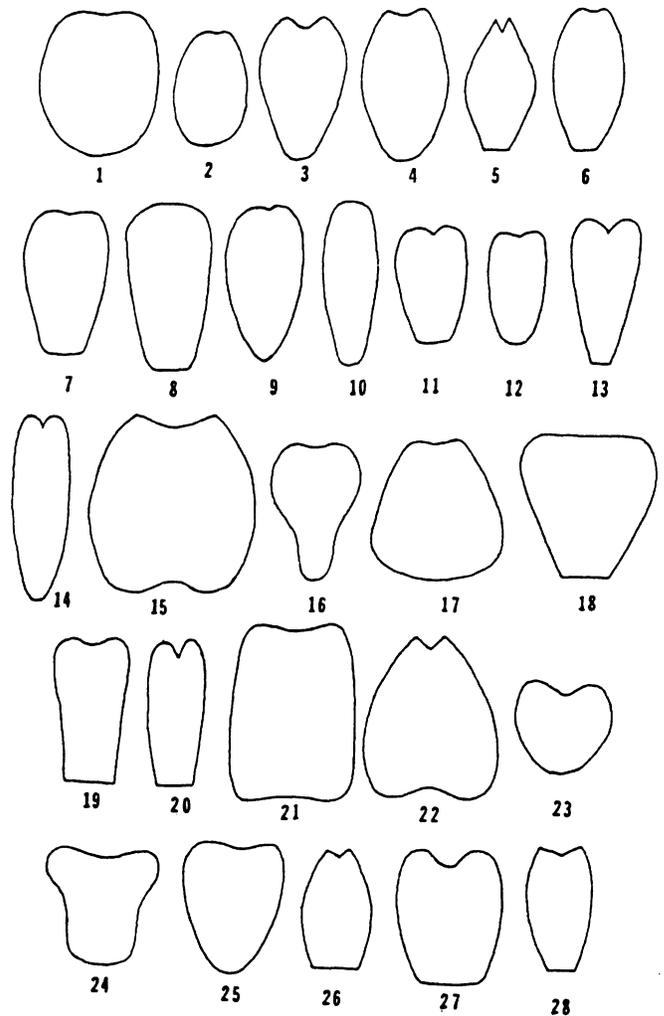


FIGURE 5—Schematic diagram of the 28 known shapes of metastomas. 1, circular; 2, oval; 3, obovate; 4, rhombioovate; 5, rhomboid; 6, elliptical; 7, petaloid A; 8, petaloid B; 9, petaloid C; 10, petaloid D; 11, vase-shaped; 12, elongate vase-shaped; 13, elongate cardioid; 14, elongate petaloid; 15, doliform; 16, obpyriform; 17, obturbinate; 18, obtriangular; 19, lyrate; 20, rectangular; 21, subquadrate; 22, pear-shaped; 23, circucardioid; 24, shield-shaped; 25, cardioid; 26, pararhomboid; 27, pararectangular; 28, paraelliptical. (Redrawn from various sources.)

when the comparative shape of the eyes on any one specimen is highly asymmetrical and/or when the eyes are excessively wrinkled. The shape of the eyes may also be of paleoecological importance (Waterston, 1979, p. 295, 316).

*Position of the eyes.*—As described in the literature, this morphological character is even more inconsistently applied than either the shape of the prosoma or metastoma. This may be due in part to either a lack of an adequate system for denoting the position of the eyes or an apparent change in the position of the eyes during ontogeny.

Description of the position of the eyes is based on a designated quadrant system (Figure 7). If the eyes are small enough or the prosoma large enough, the anterior or posterior position within a quadrant can also be noted.

This morphological character is of doubtful taxonomic utility above the genus level. The prime nontaxonomic importance of eye position is its potential to trace phylogenies (Kjellesvig-

TABLE 3.—Complete characterization of the 28 known shapes of metastomas.

Shape	Length: width ratio	Lateral angle	Angle of cordation	Position of greatest width	Character of anterior	Character of posterior	Character of sides	Character of shoulder
1. Circular	1.25-1.35	45°	150°	Central	Shallowly cordate	Broadly rounded	Broadly convex	Rounded
2. Oval	1.35-1.40	70°	110°-160°	Central	Shallowly cordate <sup>1</sup>	Rounded	Convex	Rounded
3. Obovate	1.60-1.70	65°-75°	60°-95°	Anterior third	Cordate	Variable <sup>2</sup>	Convex	Variable <sup>3</sup>
4. Rhombovate	1.35-1.70	75°	65°	Central	Cordate	Rounded	Semi-angular	Semi-angular
5. Rhomboid	1.80-2.10	65°	80°	Central	Narrowly but deeply cordate <sup>1</sup>	Truncated	Angular	Angular
6. Elliptical	1.90-2.10	65°	125°	Central	Shallowly cordate	Truncated	Convex	Semi-angular
7. Petaloid A	1.80	75°	160°	Anterior third	Shallowly cordate	Truncated	Convex, converging pos- teriorly	Rounded
8. Petaloid B	1.90-2.10	80°	None	Anterior third	Rounded	Truncated	Straight, converging posteriorly	Rounded
9. Petaloid C	2.40	80°	135°	Anterior third	Shallowly cordate	Rounded point	Convex	Rounded
10. Petaloid D	2.9-3.0	80°	None	Central	Rounded	Rounded	Slightly convex	Rounded
11. Vase-shaped	1.7	70°-75°	80°	Anterior third	Cordate	Truncated	Convex	Rounded
12. Elongate vase-shaped	1.9-2.1	100°	110°	Central	Shallowly cordate	Rounded	Slightly convex	Rounded
13. Elongate cardioid	2.35-2.40	75°	60°	Anterior third	Deeply cordate	Truncated	Nearly straight, con- verging posteriorly	Rounded
14. Elongate petaloid	2.7	60°	55°	Central	Deeply cordate	Rounded	Slightly convex	Rounded
15. Dolliform	1.0-1.1	110°-115°	140°	Central	Broadly cordate	Broadly concave	Broadly convex	Angular
16. Obyriform	1.55-1.65	90°	None	Anterior third	Broadly concave	Narrowly rounded	Sigmoid	Rounded
17. Obturbinate	1.00-1.10	105°-120°	None	Posterior	Broadly concave	Broadly rounded	Straight, converging an- teriorly	Angular
18. Obturiangular	1.00-1.33	60°	None	Anterior	Truncated	Truncated	Straight, converging posteriorly	None
19. Lyrate	2.00-2.15	85°	130°	Anterior	Cordate <sup>1</sup>	Variable <sup>2</sup>	Nearly straight, con- verging posteriorly	Variable <sup>3</sup>
20. Rectangular	2.2	80°-85°	40°	Anterior third	Deeply cordate	Truncated	Slightly convex	Rounded
21. Subquadrate	1.55	90°	None	Posterior	Broadly concave	Broadly concave	Nearly straight	Semi-angular
22. Pear-shaped	1.10-1.20	70°	95°	Posterior	Deeply cordate	Concave	Convex, converging an- teriorly	Angular
23. Circuacardioid	0.95	50°	115°	Anterior third	Broadly cordate	Rounded	Convex, converging pos- teriorly	Rounded
24. Shield-shaped	0.9-1.50	90°	None	Anterior	Broadly concave	Broadly rounded	Sigmoid	Rounded
25. Cardioid	1.25-1.30	60°	None	Anterior third	Broadly concave <sup>1</sup>	Rounded	Convex, converging pos- teriorly	Rounded
26. Pararhomboid	1.60-1.70	60°-65°	110°-115°	Central	Cordate	Truncated	Convex	Angular
27. Pararectangular	0.75-0.85	70°	85°	Anterior third	Deeply cordate	Truncated	Convex	Rounded
28. Paraelliptical	1.9-2.1	75°	135°	Central	Cordate	Truncated	Convex	Angular

<sup>1</sup> Some genera and species with "teeth."<sup>2</sup> Truncated in some species, rounded in others.<sup>3</sup> Angular in some species, rounded in others.

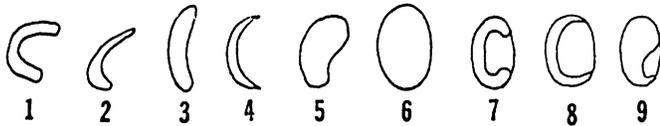


FIGURE 6—Schematic diagram for the nine standard shapes of eyes. 1, crescentic; 2, arcuate; 3, allantoid; 4, lunate; 5, remiform; 6, oval; 7, ovocrescentic; 8, ovolute; 9, ovoreniform.

Waering, 1961b, 1964) and document ontogenies, and its paleoecological significance. The symmetry of the eyes is significant in the recognition of postmortem alterations (Tollerton, 1987b).

**Prosomal appendages.**—Two categories of prosomal appendages are recognized: 1) the first (I) prosomal appendage, or chelicera; and 2) the second through sixth (II–VI) prosomal appendages, or legs. Roman numerals are used as a shorthand notation for the position of the prosomal appendages. Systematic characterizations of eurypterid legs are by Størmer (1934a, 1944, 1973, 1974). The standards proposed here are a modification of his work.

In establishing these standards, the prime consideration is morphology. The degree and direction of development of the legs are deemed to be of greater value in the study of the phylogeny and evolution of eurypterids, and therefore have not been considered in establishing these standards. Furthermore, the taxonomic value of development of the legs is most important at the levels of superclass, class, and order, while anatomy is of greatest value at the levels of suborder, superfamily, and family (Manton, 1969, 1977; Hammen, 1977).

**Chelicera.**—Two types of chelicera are recognized: 1) the eurypterid type, with relatively small, toothless rami; and 2) the pterygotid type, with large rami with teeth. The chelicera are the only morphological character used to define suborders of the Eurypterida (Caster and Kjellesvig-Waering, 1964, p. 306).

**Legs.**—Three general types of legs are recognized: 1) spiniferous legs; 2) nonspiniferous legs; and 3) swimming legs. The overall arrangement of these general types of legs is the taxonomic basis for defining superfamilies. The arrangement of the individual types of legs is the taxonomic basis for defining families. Each individual type of leg is illustrated, briefly described, and differentiated from similar types.

**Spiniferous legs.**—Størmer (1974, p. 363–364) characterized four types of spiniferous legs: a *Hughmilleria* type, a *Mixopterus* type, a *Slimonia* type, and a *Hibbertopterus* type. His arrangement is modified to include as distinct types of spiniferous legs, *Hughmilleria* type, *Carcinosoma* type, *Erieopterus* type, *Adelophthalmus* type, *Ctenopterus* type, *Hardieopterus* type, *Lamontopterus* type, *Megalograptus* type, and *Mixopterus* types A, B, and C. Following the alternative interpretation of Størmer (1974, p. 362), the *Slimonia* type is recognized as a type of nonspiniferous leg. The *Hibbertopterus* type, with the development of lade instead of coxa, is considered not to belong to true eurypterids.

The *Hughmilleria* type (Figure 8.1) has a single pair of short spines on each podomere, whereas the *Megalograptus* type (Figure 8.2) has numerous pairs of short spines on each podomere. At times, depending upon the state of preservation, the spines of the *Megalograptus* type may appear as a spiny “plate” instead of as separate pairs of spines. The *Carcinosoma* type (Figure 8.3) has a single, long spine on each podomere, while the *Erieopterus* type (Figure 8.4) has a single, short to moderately long spine on only the last two or three podomeres. The *Lamontopterus* type (Figure 8.5) has a single pair of short spines at the distal end of each podomere, thereby resembling the *Hughmil-*

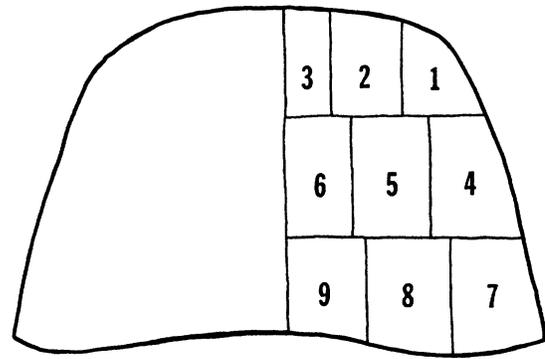


FIGURE 7—Schematic diagram for the nine standard positions of eyes. 1, antelateral; 2, antemesial; 3, antecentral; 4, centrilateral; 5, centrimesimal; 6, central; 7, posterolateral; 8, posteromesial; 9, postero-central.

*leria* type. However, the length of the podomeres are distinctly different, those of *Lamontopterus* type being much longer than those of the *Hughmilleria* type. If not for the presence of the spines, the *Lamontopterus* type of spiniferous leg could easily be mistaken for the *Kokomopterus* type of nonspiniferous leg (Figure 9.2). The *Hardieopterus* type (Figure 8.6) has numerous single spines on only the last two or three podomeres, giving it the appearance of a medieval mace. The *Adelophthalmus* type (Figure 8.7) has a single, long spine on the penultimate podomere, and serrate distal margins on each podomere. If not for the presence of the spine, the *Adelophthalmus* type of spiniferous leg could easily be mistaken for the *Slimonia* type of nonspiniferous leg (Figure 9.1). The *Mixopterus* type A spiniferous leg (Figure 8.8) has numerous pairs of spines on each podomere, the spines generally increasing in length distally on each podomere, with the distal pair of spines on the third podomere being extremely long. The *Mixopterus* type B (Figure 8.9) has numerous pairs of spines on each podomere, the spines regularly increasing in size distally except for the most distal pair which are about twice as long as the preceding pair. Furthermore, the number of spines on alternating podomeres is the same, thus differing from the *Mixopterus* types A and C. The *Mixopterus* type C (Figure 8.10) has fewer pairs of spines on fewer podomeres than the other *Mixopterus* types, and the spines on each podomere alternate in size, with the longer spines increasing in size distally. The *Ctenopterus* type (Figure 8.11) has numerous pairs of spines on the last four podomeres, the spines being relatively shorter than the *Mixopterus* types and regularly increasing in size distally. Furthermore, the number of spines on all but the last podomere remains the same.

**Nonspiniferous legs.**—Størmer (1974, p. 364) recognized only two types of nonspiniferous legs, the *Stylonurus* type and the *Moselopterus* type. Nine types are proposed here (Figure 9): *Slimonia* type, *Kokomopterus* type, *Pagea* type, *Drepanopterus* type, *Dolichopterus* type, *Eurypterus* type, *Hardieopterus* type, *Parastylonurus* type, and *Brachyoptereilla* type.

The *Slimonia* type (Figure 9.1) has distally serrated or fringe-like margins on each podomere. The *Kokomopterus* type (Figure 9.2) has relatively short podomeres, with a length to width ratio of less than three, while the similar looking *Pagea* type (Figure 9.3) has a length to width ratio greater than three. The *Drepanopterus* type (Figure 9.4) has a single flat, lobate projection, appearing in form and position much like a basitarus. It is morphologically the same as Størmer's *Moselopterus* type. The two characterizations differ, however, in that Størmer indicated its primitiveness to the swimming leg, while here no such de-

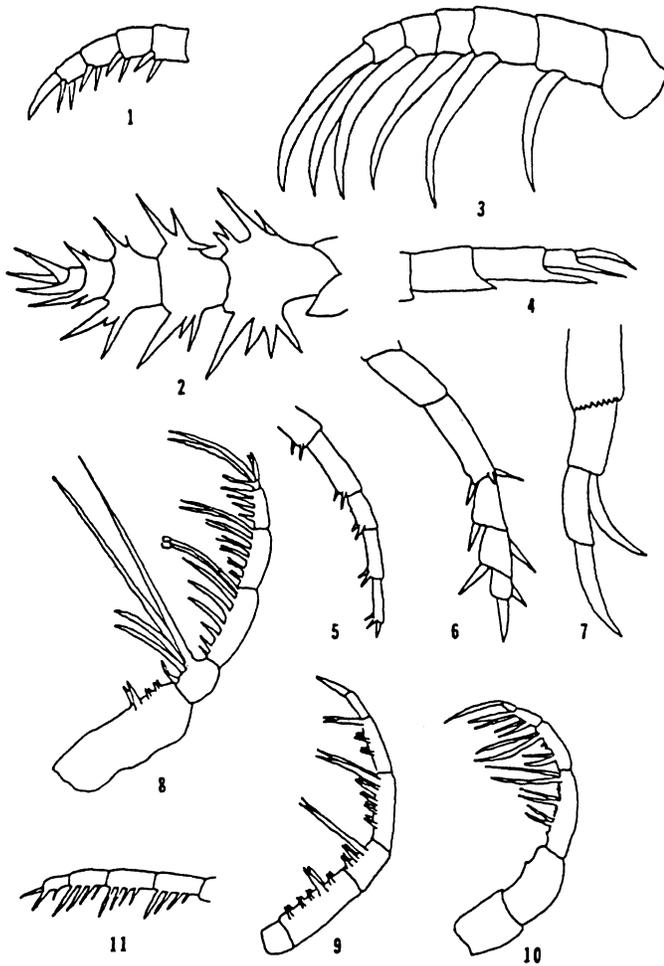


FIGURE 8—Schematic diagram for the 11 standard types of spiniferous legs. 1, *Hughmilleria* type; 2, *Megalograptus* type; 3, *Carcinosoma* type; 4, *Eriopteris* type; 5, *Lamontopterus* type; 6, *Hardiopterus* type; 7, *Adelophthalmus* type; 8, *Mixopterus* type A; 9, *Mixopterus* type B; 10, *Mixopterus* type C; 11, *Ctenopterus* type. (Redrawn from various sources.)

velopment is intended, implied, or required for the recognition of this type of leg. To avoid these conceptual problems, the term *Drepanopterus* type is preferred to *Moselopterus* type. The *Dolichopterus* type (Figure 9.5) has a lobate penultimate podomere, which, depending upon the state of preservation, may or may not seem to be a spine-like projection. The *Eurypterus* type (Figure 9.6) has two spines at the distal end of the penultimate podomere and a single terminal spine, giving the appearance of three terminal spines. The *Hardiopterus* type (Figure 9.7) differs from all other nonspiniferous legs in the irregularity of podomere lengths and in the stoutness of the keeled terminal spine. The *Parastylonurus* type (Figure 9.8) has distally fringed or serrate margins on the last four podomeres, as well as long lateral lobes on the last four podomeres. In the *Brachyopterebella* type (Figure 9.9) the last two podomeres are long and narrow while the proximal podomeres are wider and may show a pronounced lobation as well as an armor-like surface.

*Swimming legs.*—Størmer (1974, p. 364–365) recognized only three types of swimming legs, the *Eurypterus* type, the *Onychopterus* type, and the *Dolichopterus* type. Eight types are recognized here: *Hughmilleria* type, *Carcinosoma* type, *Mixopterus*

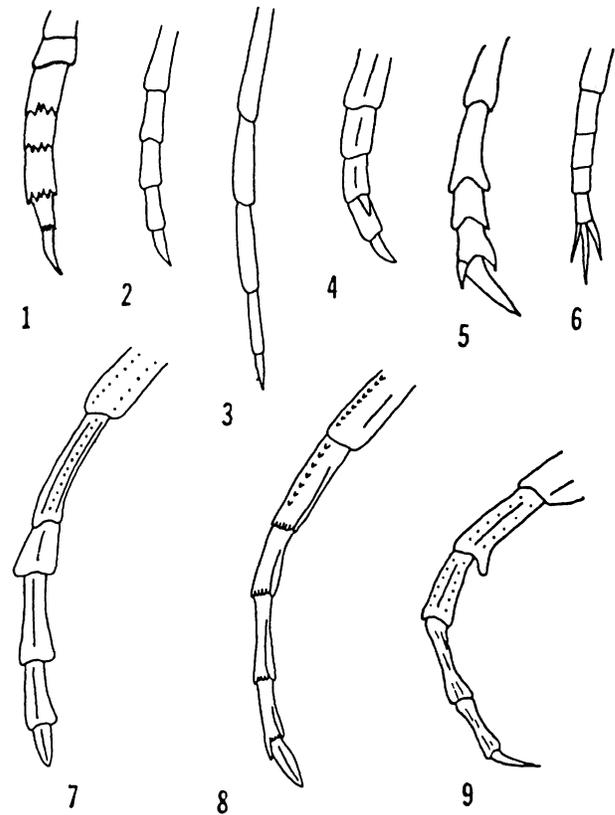


FIGURE 9—Schematic diagram for the nine standard types of nonspiniferous legs. 1, *Slimonia* type; 2, *Kokomopterus* type; 3, *Pagea* type; 4, *Drepanopterus* type; 5, *Dolichopterus* type; 6, *Eurypterus* type; 7, *Hardiopterus* type; 8, *Parastylonurus* type; 9, *Brachyopterebella* type. (Redrawn from various sources.)

type, *Slimonia* type, *Dolichopterus* type, *Eriopteris* type, *Eurypterus* type, and *Adelophthalmus* type (Figure 10).

The *Hughmilleria* type of swimming leg (Figure 10.1) is characterized by narrow 7th and 8th podomeres that are both approximately twice as long as wide; the 9th podomere is very small. The *Carcinosoma* type (Figure 10.2) has narrow 7th and 8th podomeres, with the 8th podomere being slightly narrower than the 7th and being approximately twice as long as wide; the 9th podomere is very prominent. The *Mixopterus* type (Figure 10.3) has a very wide 7th podomere, while the *Slimonia* type (Figure 10.4) has a very long 7th podomere. The *Dolichopterus* type (Figure 10.5) has an expanded 9th podomere which forms the terminal part of the paddle. The *Eriopteris* type (Figure 10.6) is synonymous with Størmer's (1934a, 1974) *Onychopterebella* type, and is characterized by the 9th podomere present as a prominent terminal claw. Although the term *Onychopterebella* type has priority over the term *Eriopteris* type, the change is here considered necessary to conform in principle with Article 64 and Recommendation 64A of the International Code of Zoological Nomenclature on the establishment of families (1985, p. 119). The *Eurypterus* type (Figure 10.7) has 7th and 8th podomeres that in general are wider than the preceding podomeres and are about equal in length; the shield guard is very prominent. The *Adelophthalmus* type (Figure 10.8) has the 7th podomere like that in the *Hughmilleria* type and the 8th podomere like that in the *Eurypterus* type except that the 8th podomere is partially coarsely serrated.

*Swimming leg paddles.*—The terminology and methods of

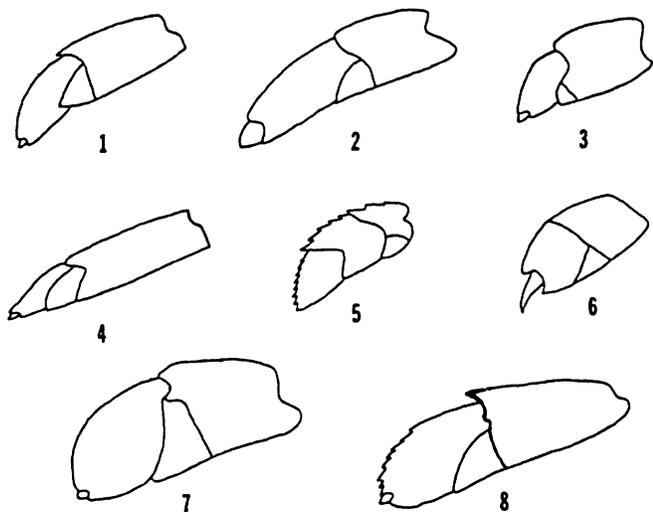


FIGURE 10—Schematic diagram for the eight standard types of swimming legs. 1, *Hughmilleria* type; 2, *Carcinosoma* type; 3, *Mixopterus* type; 4, *Slimonia* type; 5, *Dolichopterus* type; 6, *Eriopecterus* type; 7, *Eurypterus* type; 8, *Adelophthalmus* type. (Redrawn from various sources.)

Størmer (1973, p. 125, 129, text-fig. 1) are here proposed as standards for swimming leg paddles. The taxonomic value of the type of swimming leg paddles is in the identification of genera. Caution is advised, however, regarding postmortem alterations which can be misleading.

**Doublure.**—The terminology given by Størmer (1934a, p. 18, fig. 2) is proposed as the morphological standard for the doublure. The known types are illustrated in Figure 11 and are easily distinguished by visual inspection. The taxonomic value of the doublure is uncertain due in part to the occurrence of similar doublures in different families and superfamilies (e.g., *Eurypterus* and *Rhenopterus*) and the total lack of knowledge of the doublure in a great number of genera. Until further research proves otherwise, it seems prudent to follow the suggestion of Waterston (1979, p. 294) and restrict use of this character to levels no higher than genus, although it may prove useful as a secondary character at the family level.

**Differentiation of the opisthosoma.**—This term denotes recognition of two or more divisions of the eurypterid body. The two types of opisthosomal divisions (preabdomen and postabdomen, and mesosoma and metasoma) as given in Størmer (1955, p. 8, 24) are proposed as the standard. Several categories of differentiation are known (Figure 12). Differentiation is accomplished by several means (Table 4). The opisthosoma of individual specimens may be difficult to differentiate due to postmortem alterations. Differentiation of the opisthosoma is here regarded as a major secondary morphological character of greatest utility at the family level; however, most eurypterids display more than one category of differentiation.

**Genital appendages.**—Two types of genital appendages are known (Figure 13), referred to as type A and type B, the differences being attributed to sexual dimorphism (see Størmer and Kjellesvig-Waering, 1969, for a review). The question of which structural type represents which sex has yet to be resolved.

The terminology illustrated in Figure 14 is proposed as standards for the uniform description of genital appendages of eurypterids.

Although presumably of importance in eurypterid taxonomy (Waterston, 1964, 1979; Størmer, 1973, 1974), the genital ap-

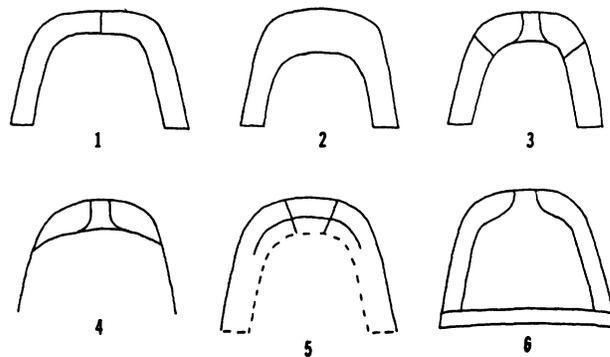


FIGURE 11—Schematic diagram for eurypterid doublures. 1, *Eurypterus* type; 2, *Eriopecterus* type; 3, *Hughmilleria* type; 4, *Pterygotus* type; 5, *Stylonurus* type; 6, *Megalagraptus* type.

pendages of a great many genera are either very poorly known or are totally unknown. Some genera within any one family show morphologically different genital appendages, both types A and B (e.g., the family Hughmilleriidae), while some genera in different families show similar genital appendages (e.g., *Hughmilleria* and *Carcinosoma*, *Buffalopterus* and *Eurypterus*). It therefore seems best to restrict the taxonomic use of genital appendages to the level of genus. With further study, the general structure of this morphological character (especially the type A genital appendage) may be found to be of taxonomic value at the family level (as it currently is for the pterygotids).

In general, the overall structure of both types of genital appendages displays marked degrees of variation, in part due to ontogeny (Holm, 1898; Waterston, 1960; Wills, 1964). Additional factors that also appear to affect the degree of variation are molting, postmortem alterations, and state of preservation.

**Telsons.**—The shape of the telson is easily determined by visual inspection. The 14 standard shapes are illustrated in Figure 15. Although the shape of the telson remains relatively constant for any particular genus, the major differences in telsons are in the marginal ornamentation. For this reason, it seems best to restrict the taxonomic use of telsons to the levels of genus and species.

**Ornamentation.**—Ornamentation currently constitutes several different types of markings, among which are: 1) the "skin" markings such as scales, mucrones, pustules, and other surface sculpture; 2) marginal features, including serrations, spines, epimera, and lobes; and 3) trilobation.

Surface markings and/or sculpture are generally of no taxonomic value at any level, as one species usually will display two or more types of sculpture on any one morphological character, generally grading from one type to another (Seldon, 1981, p. 11, fig. 1). Exceptions are known, however, whereby a particular genus is identifiable simply by the surface ornamentation (e.g., *Mycterops*). Marginal features (Figure 16) are of use in the identification of species and genera, especially when a particular morphological character is very common (e.g., styliiform telsons). Trilobation is useful in the determination of the differentiation of the opisthosoma.

#### TAXONOMY

It is generally accepted that morphological characters demonstrated to be homologous are of prime importance in classification. Although the homologous nature of the eurypterid prosomal appendages is presumed to have been demonstrated by Størmer (1974, p. 361–367), no taxonomic scheme for eurypterids has been based on that premise. A review of existing

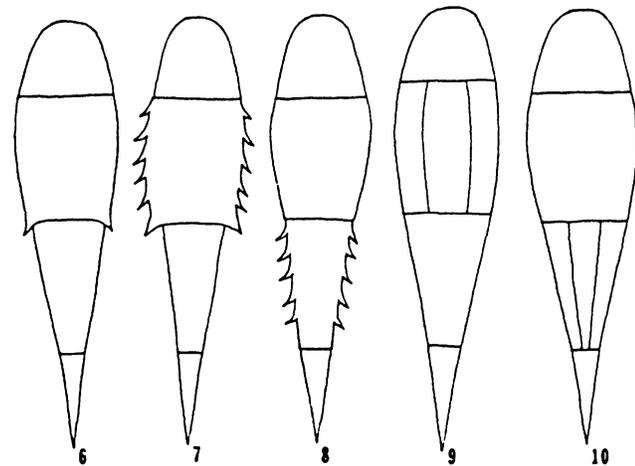
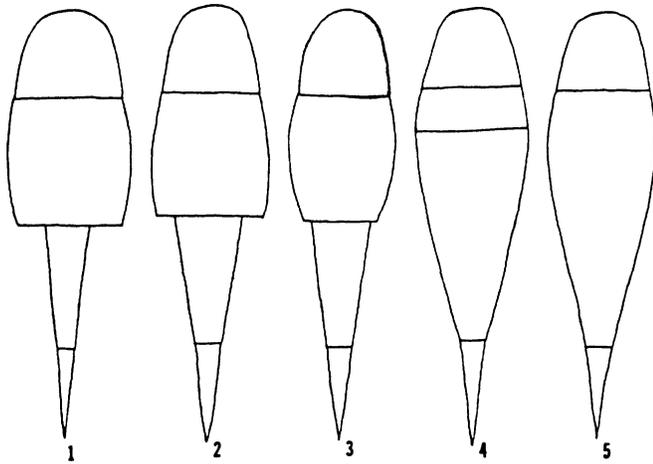


FIGURE 12—Schematic diagram for recognition of broad categories of the differentiation of the opisthosoma. 1, abrupt first order; 2, moderate first order; 3, slight first order; 4, third order; 5, undifferentiated; 6, midsection second order; 7, anterior second order; 8, posterior second order; 9, anterior fourth order; 10, posterior fourth order.

taxonomies for eurypterids (partially summarized in Table 5) found them all to be deficient in uniformity of coverage and inconsistent in application of criteria. The taxonomy proposed here is based on the earlier contention of Størmer (1951, p. 410) that a classification of eurypterids can be founded on the prosomal appendages. This new taxonomy is substantiated by: 1) Størmer's (1974) demonstration of the homologous nature of these characters; 2) historical taxonomic research (Table 5); 3) the taxonomic procedures for most arthropods in general (Manton, 1969, 1977, p. 487–494), and for chelicerates in particular (Hammen, 1977); and 4) Plotnick's (1983, p. 216) conclusion from cladistic analysis that "monophyletic groups of eurypterids can be defined on the basis of limb morphology. . ."

The taxonomy was made as practicable as possible by purposely avoiding a priori judgements on the degree and direction of development of the prosomal appendages or on any other morphological character (except to note and use the gross morphological similarities and differences) and on the hierarchy of the characters used. The proposed taxonomic application of eurypterid prosomal appendages is inclusive of families.

This procedure is extremely useful in several ways. First, it

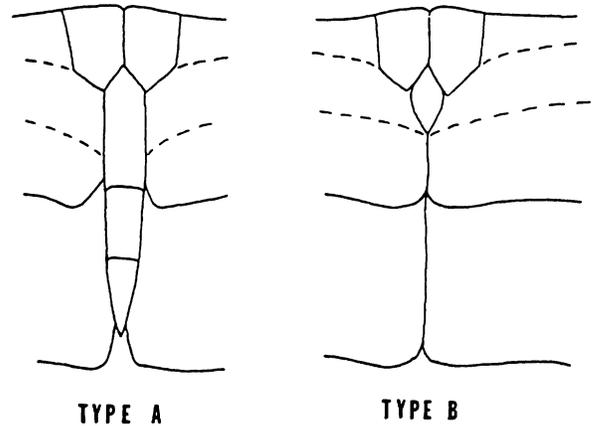


FIGURE 13—Schematic diagram of the two types of eurypterid genital appendages.

supports many, if not all, of the hypotheses concerning the relationships of several genera (e.g., *Hughmilleria* and *Carcinosoma*, in Størmer, 1974, p. 362; *Erieopterus* and *Onychopterella*, in Størmer, 1974, p. 382) without negating the established relationships of other genera.

Second, use of a standardized morphology within the taxonomy enables: 1) recognition of new taxa at the superfamily and family levels; 2) recognition of taxonomically synonymous taxa at the same levels (Tollerton, 1987a); and 3) postulation of the existence of at least five and possibly a sixth totally unknown taxa at the superfamily level (Table 6).

Third, several genera (specifically, *Hibbertopterus* Kjellesvig-Waering, 1959, *Campylocephalus* Eichwald, 1860, *Cyrtoctenus* Størmer and Waterston, 1968, and *Dunnsopterus* Waterston, 1968, included in the Eurypterida by Waterston, et al., 1985) are objectively determined not to be representatives of the order.

A more rigorous numerical analysis of this taxonomy, to include eurypterid phylogeny, is in progress and will be presented when completed. Currently, the results are inconclusive as to the primitive or derived nature of eurypterid morphological characters and any judgements here would be premature.

**Order.**—The order Eurypterida Burmeister, 1843, is here defined by the presence of only six pairs of prosomal appendages, the first pair being the chelicera, the next five pairs being the gnathobasic, uniramous legs.

**Suborders.**—Historically, suborders are defined on the basis of the structure of the first pair of prosomal appendages (chelicera) (Caster and Kjellesvig-Waering, 1964). Suborders are here defined on this basis.

**Superfamilies.**—All currently accepted superfamilies were originally defined as families, using different morphological characters. Superfamilies are here defined on the basis of a generalized scheme of the morphology and arrangement of the II–VI prosomal appendages (Table 7).

**Families.**—Families have been defined on differences of many

TABLE 4—Orders of differentiation of the opisthosoma.

First order	Recognized by changes in shape from one division to the next
Second order	Recognized by changes in lateral ornamentation
Third order	Recognized by changes in size of the body segments
Fourth order	Recognized by changes in dorsal and/or ventral surface ornamentation

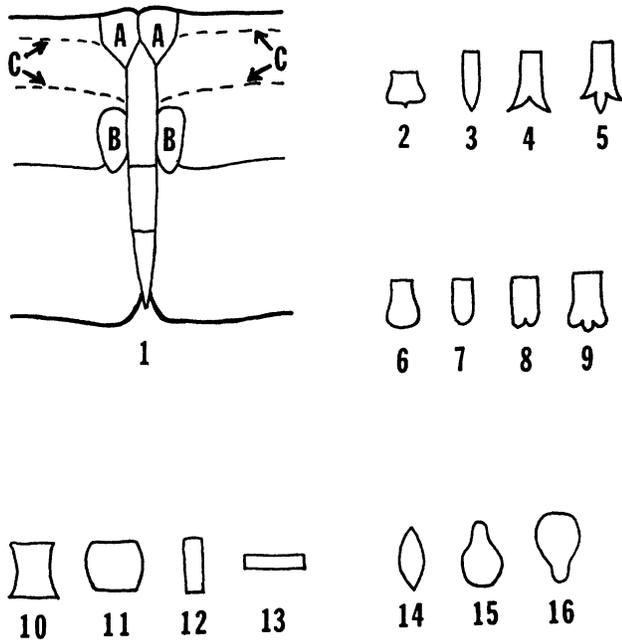


FIGURE 14—Schematic diagram of standard characters of eurypterid genital appendages. 1, terms applicable to the opercula of both types (A and B): A = deltoïd plates; B = spatulae; C = transverse sutures. 2-9, terms applicable to the terminations of both types (A and B): 2, nippleate; 3, unicate; 4, bifurcate; 5, tricate; 6, spatulate; 7, unilobed; 8, bilobed; 9, trilobed. 10-13, terms applicable to the segments of both types (A and B); 10, biconvex; 11, doliform; 12, tubular; 13, wafer. 14-16, overall shapes of type B genital appendages: 14, lozenge-shaped; 15, pyriform; 16, obpyriform. (Redrawn from various sources.)

different morphological characters (see Table 5). They are here defined on the basis of an expanded scheme of the morphology and arrangement of the II-VI prosomal appendages, in which the individual types of legs are placed in the generalized scheme (Table 7). Important secondary characters are: 1) differentiation of the opisthosoma; 2) structure of the doublure; and 3) structure of the genital appendages.

*Genera.*—These have been defined on any extreme difference or variation from previously defined genera. Genera are here defined on the basis of the following: 1) shape of the prosoma; 2) shape of the metastoma; 3) structure of the paddle of the swimming leg (when present); 4) structure of the genital appendages; 5) shape of the telson; 6) position of the eyes; 7) ornamentation of the opisthosoma; 8) ornamentation of the prosoma; 9) tooth structure of the rami of the chelicera; and 10) morphology of the legs. No hierarchy is intended or implied in the above list. Whenever known, the ventral anatomy is more diagnostic than the dorsal, especially in the differentiation of genera, but both are necessary.

*Species.*—Species are defined on the basis of differences within the range of variation of any morphological character for the genus.

#### SYSTEMATIC PALEONTOLOGY

In the following classification, the diagnoses of the suborders, superfamilies, and families have been restricted to the prosomal appendages, and any exceptions are noted. Secondary characters are noted, and additional characters or comments that may aid in clarification of a particular taxa are included as "remarks." Stratigraphic ranges are given for the families.

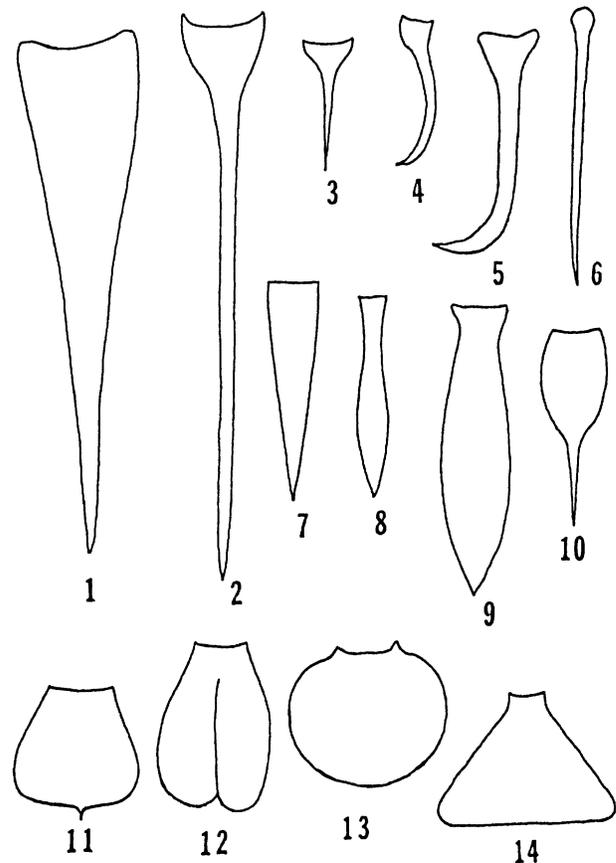


FIGURE 15—Schematic diagram of the 14 standard shapes of telsons. 1, lanceolate; 2, styliform; 3, short styliform; 4, short curved styliform; 5, curved styliform; 6, needle; 7, wedge-shaped; 8, clavate; 9, xiphous; 10, foliate; 11, paddle-shaped; 12, bilobed; 13, circular; 14, triangular. (Redrawn from various sources.)

Two suborders are recognized, based on the morphology of the first pair of prosomal appendages (chelicera): Eurypterina Burmeister, 1843, and Pterygotina Caster and Kjellesvig-Waering, 1964. The suborder Hibbertopterina Størmer, 1974, is not recognized as a suborder of true eurypterids. The presence of a posteriorly cleft "metastoma," lade instead of coxa at the base of the prosomal appendages, and biungulate prosomal appendages II and III are deemed sufficient for its removal from the order. It is here lowered to the rank of family and transferred to the order Cyrtoctenida Størmer and Waterston, 1968. The suborder Woodwardopterina Kjellesvig-Waering, 1959 (nom. trans. Kjellesvig-Waering, 1979b, p. 295), is not recognized as a valid suborder of eurypterids because it was defined on the basis of the greatly expanded anterior body segments and not on any morphological differences in the chelicera (which remain unknown for its representatives).

Eleven superfamilies are recognized. On the basis of the morphology and arrangement of the prosomal appendages, the superfamily Drepanopteroidea Kjellesvig-Waering, 1966 (nom. trans. Størmer, 1974, p. 372), is taxonomically synonymous with the superfamily Stylonuroidea Diener, 1924, and is abandoned. The superfamilies Megalopteroidea Caster and Kjellesvig-Waering, 1964, and Kokomopteroidea Kjellesvig-Waering, 1966, are here raised from the rank of family. The superfamily Brachyopteroidea is new.

Twenty-two families are recognized, five of which are new:

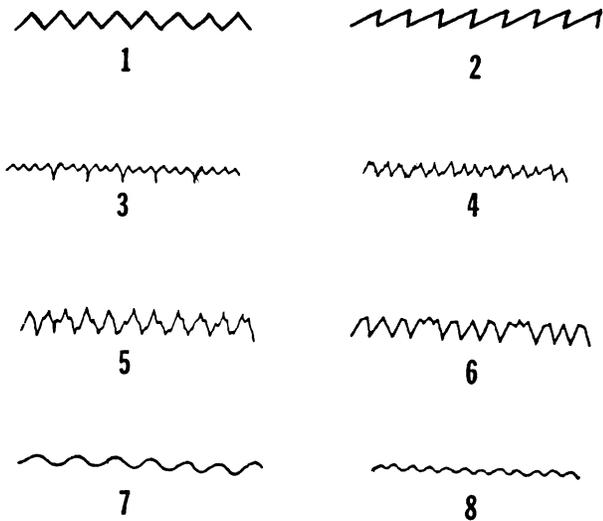


FIGURE 16—Schematic diagram of marginal ornamentations. 1, dentate; 2, serrate; 3, fimbriate; 4, lacerate; 5, incised; 6, lacinate; 7, crenate; 8, crenulate. (From Snell and Dick, 1971, Pl. 8, figs. 1–8.)

Adelophthalmidae, Lanarkopteridae, Erieopteridae, Hardieopteridae, and Brachyopterellidae. Use of the genital appendages as the taxonomic basis for families of the pterygotids is provisionally accepted, because the II–VI prosomal appendages are poorly known. The best available evidence concerning these legs suggests the possibility of three families; however, the evidence is very poor, and does not yet warrant the establishment of a new family. Further research may yet substantiate the observations of Kjellesvig-Waering (1958a; Caster and Kjellesvig-Waering, 1964) concerning the positional significance of the spines on legs II–V in the Carcinosomatidae. As yet, not enough material is known to warrant the establishment of a new family.

Sixty-two genera are recognized. The following hibbertopteroid genera are not recognized as true eurypterids: *Campylocephalus* Eichwald, 1860; *Hibbertopterus* Kjellesvig-Waering, 1959; *Cyrtoctenus* Størmer and Waterston, 1968; and *Dunn-*

TABLE 6—Unknown but predicted superfamilies.

Group	Legs	Character
A	II–V VI	Spiniferous, mixed types Nonspiniferous
B	II–IV V–VI	Spiniferous, mixed types Nonspiniferous, all one type
C	II–IV V–VI	Spiniferous, mixed types Nonspiniferous, mixed types
D	II–IV V–VI	Spiniferous, all one type Nonspiniferous, mixed types
E	II–V VI	Nonspiniferous, mixed types Swimming leg
F	II–VI	Nonspiniferous, mixed types

It may be that either groups E or F may be found to constitute the present superfamily Mycteropoidea.

*sopterus* Waterston, 1968. The type of the genus *Clarkeipterus* Kjellesvig-Waering, 1966, has already been discussed (Tollerton, 1987b). Following the suggestion of Størmer (1972, p. 17), the genus *Borchgrevinkium* Novojilov, 1959, is reassigned to the order Xiphosurida Latreille, 1802. No new genera are proposed.

A revision of the diagnoses of eurypterid genera utilizing the morphological standards has not yet been completed. However, a brief partial summary is presented as Table 8, and includes stratigraphic ranges.

#### Order EURYPTERIDA Burmeister, 1843

##### Suborder EURYPTERINA Burmeister, 1843

(nom. trans. Caster and Kjellesvig-Waering 1964)

*Diagnosis.*—Chelicera comprised of small, simple rami, without teeth.

##### Superfamily SLIMONIOIDEA Novojilov, 1962

*Diagnosis.*—Legs II–V nonspiniferous, all one type; leg VI swimming leg.

*Remarks.*—Chelicera unknown. If the rami are found to be without teeth, then this superfamily remains valid. On the other hand, if the rami are found with teeth, then this superfamily

TABLE 5—Historical summary of taxonomic research.

Character	Kjellesvig-Waering, 1948	Kjellesvig-Waering, 1961	Kjellesvig-Waering, 1971	Størmer, 1973	Størmer, 1974	This paper
Shape of prosoma	Genera and species	Major, but level not specified	Genera	Not mentioned	Not mentioned	Genera
Shape of eyes	Not mentioned	Not mentioned	Not mentioned	Major, but level not specified	Not mentioned	Recognition of distortion
Position of eyes	Not mentioned	Not mentioned	Genera	Major, but level not specified	Not mentioned	Genera; also can document ontogenies
Shape of metastoma	Not mentioned	Major, but level not specified	Families	Not mentioned	Major, but level not specified	Genera
Doublure	Not mentioned	Not mentioned	Families	Major, but level not specified	Major, but level not specified	Possibly of secondary family use
Genital appendages	Not mentioned	Not mentioned	Not mentioned	Major, but level not specified	Major, but level not specified	Genera
Swimming leg	Not mentioned	Major, but level not specified	Families	Not mentioned	Family and genus	Superfamilies and families
Swimming leg paddle	Not mentioned	Not mentioned	Not mentioned	Not mentioned	Genus	Genera
Walking legs	Genera	Major, but level not specified	Families	Not mentioned	Family and genus	Superfamilies and genera
Chelicera	Not mentioned	Major, but level not specified	Not mentioned	Suborder	Not mentioned	Suborders
Telson	Not mentioned	Major, but level not specified	Not mentioned	Not mentioned	Not mentioned	Genera

TABLE 7—Generalized taxonomic scheme for superfamilies and families.

Chelicera	Legs	Character
Without teeth	II–V VI	Nonspiniferous, all one type Swimming leg
Without teeth	II–V VI	Spiniferous, all one type Swimming leg
Without teeth	II–V VI	Spiniferous, mixed types Swimming leg
Without teeth	II–IV V VI	Spiniferous, mixed types Nonspiniferous Swimming leg
Without teeth	II–IV V VI	Spiniferous, all one type Nonspiniferous Swimming leg
Without teeth	II–IV V–VI	Spiniferous, all one type Nonspiniferous, all one type
Without teeth	II–V VI	Spiniferous, all one type Nonspiniferous
Without teeth	II–III IV–VI	Spiniferous, all one type Nonspiniferous, all one type
Without teeth	II–VI	Nonspiniferous, all one type
With teeth	II–V VI	Nonspiniferous, all one type Swimming leg

must be abandoned, and the family Slimoniidae placed in the superfamily Pterygopteroidea.

#### Family SLIMONIIDAE Novojilov, 1962

*Diagnosis.*—Legs II–V nonspiniferous, *Slimonia* type; leg VI swimming leg, *Slimonia* type.

*Secondary characters.*—Opisthosoma undifferentiated.

*Stratigraphic range.*—Lower Silurian to Lower Devonian.

*Included genera.*—*Slimonia* Page, 1856, p. 135; *Salteropterus* Kjellesvig-Waering 1951, p. 14.

*Remarks.*—Doublures unknown. *Slimonia* known except for the chelicera. Only the telson and metastoma are known in *Salteropterus*.

#### Superfamily HUGHMILLERIOIDEA Kjellesvig-Waering, 1951 (nom. trans. Størmer 1974)

*Diagnosis.*—Legs II–V spiniferous, all one type; leg VI swimming leg.

#### Family HUGHMILLERIIDAE Kjellesvig-Waering, 1951

*Diagnosis.*—Legs II–V spiniferous, *Hughmilleria* type; leg VI swimming leg, *Hughmilleria* type.

*Secondary characters.*—Doublure of *Hughmilleria* type. Opisthosoma shows a second order differentiation (lateral epimera on only the sixth segment).

*Stratigraphic range.*—Lower Ordovician to Upper Devonian.

*Included genera.*—*Hughmilleria* Sarle, 1903, p. 1087; *Nanahughmilleria* Kjellesvig-Waering, 1961b, p. 796; *Grossopterus* Størmer, 1934b, p. 286–288; *Waeringopterus* Leutze, 1961, p. 51–52.

#### Family CARCINOSOMATIDAE Størmer, 1934a

*Diagnosis.*—Legs II–V spiniferous, *Carcinosoma* type; leg VI swimming leg, *Carcinosoma* type.

*Secondary characters.*—Opisthosoma shows a first order differentiation into an abdomen and postabdomen.

*Stratigraphic range.*—Lower Ordovician to Lower Devonian.

*Included genera.*—*Carcinosoma* Claypole, 1890, p. 400; *Rhinocarcinosoma* Novojilov, 1962, p. 413; *Eocarcinosoma* Caster and Kjellesvig-Waering, 1964, p. 314; *Paracarcinosoma* Caster

and Kjellesvig-Waering, 1964, p. 312; ?*Holmipterus* Kjellesvig-Waering, 1979a, p. 122.

*Remarks.*—Doublures unknown. The differences in the morphology and arrangement of the spiniferous legs of this family, as well as the inferred relationship of these legs with the Hughmilleriidae (Størmer, 1974, p. 362), require its transfer from the superfamily Mixopteroidea to this superfamily. The genus *Holmipterus* is included in this family on the basis of a fragment of a walking leg and an incomplete paddle of a swimming leg. The description and reconstruction of the telson is believed to be in error, especially those remarks by Kjellesvig-Waering (1979a) pertaining to the cercal blades. It seems more likely that the original description is based on material belonging to two genera.

#### Family ADELOPHTHALMIDAE n. fam.

*Etymology.*—The name of the family is derived from the type genus.

*Type genus.*—*Adelophthalmus* Jordan and Meyer, 1854, p. 8.

*Diagnosis.*—Legs II–V spiniferous, *Adelophthalmus* type; leg VI swimming leg, *Adelophthalmus* type.

*Secondary characters.*—Opisthosoma shows both a first and second order differentiation into a mesosoma and metasoma.

*Stratigraphic range.*—Upper Silurian to Lower Permian.

*Included genera.*—*Adelophthalmus* Jordan and Meyer, 1854, p. 8; *Parahughmilleria* Kjellesvig-Waering, 1961b, p. 805–806; *Bassipterus* Kjellesvig-Waering and Leutze, 1966, p. 1111; *Unionopterus* Chernyshev, 1948, p. 127.

*Remarks.*—Doublures unknown. The legs of some species of *Adelophthalmus* may be nonspiniferous. If so, then those species with truly nonspiniferous legs will constitute a new genus of a new family in the superfamily Slimonioidea. The material available at present of all species of *Adelophthalmus* is insufficient to warrant the establishment of a new genus.

#### Superfamily MIXOPTEROIDEA Caster and Kjellesvig-Waering, 1955

*Diagnosis.*—Legs II–V spiniferous, mixed types; leg VI swimming leg.

#### Family MIXOPTERIDAE Caster and Kjellesvig-Waering, 1955

*Diagnosis.*—Legs II–III spiniferous, *Mixopterus* type C; legs IV–V spiniferous, *Hughmilleria* type; leg VI swimming leg, *Mixopterus* type.

*Secondary characters.*—Opisthosoma shows both a first and fourth order (trilobation of the abdomen) differentiation.

*Stratigraphic range.*—Upper Silurian.

*Included genus.*—*Mixopterus* Ruedemann, 1921, p. 209.

*Remarks.*—Doublure unknown. Prosoma quadrate with rostrum.

#### Family LANARKOPTERIDAE n. fam.

*Etymology.*—The name of the family is derived from the type genus.

*Type genus.*—*Lanarkopterus* Ritchie, 1968, p. 335.

*Diagnosis.*—Leg II spiniferous, *Hughmilleria* type; leg III spiniferous, *Mixopterus* type B; legs IV–V spiniferous, *Hughmilleria* type; leg VI swimming leg, *Mixopterus* type.

*Secondary characters.*—Opisthosoma shows both a first and fourth order (trilobation of the abdomen) differentiation.

*Stratigraphic range.*—Upper Silurian.

*Included genera.*—*Lanarkopterus* Ritchie, 1968, p. 335.

*Remarks.*—Doublure unknown. Prosoma trapezoid with rostrum.

TABLE 8—Partial summary of eurypterid genera.

Genus	Shape of prosoma	Shape of metastoma	Shape of telson	Stratigraphic range
<i>Acutiramus</i>	Subquadrate	Obovate	Paddle-shaped	U. Sil.—L. Dev.
<i>Adelophthalmus</i>	Parabolic	Oval	Styliform	U. Dev.—L. Perm.
<i>Alkenopterus</i>	Horseshoe-shaped	—	Very short styliform	L. Dev.
<i>Baltoeurypterus</i>	Trapezoid	Oval	Styliform	U. Sil.
<i>Bassipterus</i>	Parabolic	Vase-shaped	Styliform	U. Sil.
<i>Brachyopterella</i>	Pentagonal	—	Styliform?	U. Ord., U. Sil.
<i>Brachyopterus</i>	Spatulate	—	Styliform	U. Ord.
<i>Buffalopterus</i>	Semicircular	—	Circular	U. Ord., U. Sil.
<i>Carcinosoma</i>	Triangular	Shield-shaped	Styliform with post-telson	U. Ord.—U. Sil.
<i>Ctenopterus</i>	Triangular	—	—	U. Sil.
<i>Dolichopterus</i>	Subquadrate	Lyrate	Styliform	L. Ord.—L. Dev.
<i>Dorfopterus</i>	—	—	Long styliform	L. Dev.
<i>Drepanopterus</i>	Horseshoe-shaped	Oval	Styliform	L. Sil.—U. Dev.
<i>Echinognathus</i>	Trapezoid?	Circumcardioid	—	U. Ord.
<i>Eocarcinosoma</i>	Triangular	—	—	L. Ord.—U. Ord.
<i>Erettopterus</i>	Subquadrate	Obovate	Bilobed	U. Ord.—L. Dev.
<i>Erieopterus</i>	Semicircular	Pararhomboid	Styliform	L. Ord.—L. Dev.
<i>Eurypterus</i>	Trapezoid	Elliptical	Styliform	U. Ord.—L. Dev.
<i>Grossopterus</i>	Turbinate	—	—	L. Dev.—U. Dev.
<i>Hallipterus</i>	Triangular	—	—	U. Dev.
<i>Hardieopterus</i>	Horseshoe-shaped	Pararectangular	Clavate	L. Sil.—U. Sil.
<i>Hastimima</i>	—	—	Xiphous	M. Dev.—L. Perm.
<i>Holmipterus</i>	—	—	Styliform with cercal blades	U. Sil.
<i>Hughmilleria</i>	Parabolic	Petaloid A	Lanceolate	U. Ord.—U. Sil.
<i>Jaekelopterus</i>	Trapezoid	—	Paddle-shaped	L. Dev.
<i>Kiaeropterus</i>	Subquadrate	—	—	U. Sil.
<i>Kokomopterus</i>	Subquadrate	Pear-shaped	Clavate	U. Sil.
<i>Lamontopterus</i>	Turbinate	—	Styliform	L. Sil.
<i>Lanarkopterus</i>	Trapezoid with rostrum	Cardioid	Curved styliform	U. Sil.
<i>Lauriepterus</i>	Spatulate	Subquadrate	—	L. Sil.
<i>Mazonipterus</i>	Triangular	—	—	Penn.
<i>Megalograptus</i>	Quadrate with rostrum	Doliform	Lanceolate with cercal blades	U. Ord.
<i>Melbournopterus</i>	Campanulate A	—	—	U. Sil.
<i>Mixopterus</i>	Quadrate with rostrum	Obpyriform	Curved styliform	U. Sil.
<i>Moselopterus</i>	Horseshoe-shaped	Oval	Short curved styliform	L. Dev.—U. Dev.
<i>Mycterops</i>	Triangular	—	—	Carb.
<i>Nanahughmilleria</i>	Parabolic	Elongate vase-shaped	Lanceolate	U. Sil.
<i>Onychopterella</i>	Subquadrate	—	Clavate	L. Sil.—U. Sil.
<i>Pagea</i>	Turbinate	Petaloid B	Styliform	L. Dev.
<i>Paracarcinosoma</i>	Triangular	Obtriangular	Curved styliform	U. Sil.—L. Dev.
<i>Parahughmilleria</i>	Semicircular	Paraelliptical	Lanceolate	U. Sil.—L. Dev.
<i>Parastylonurus</i>	Horseshoe-shaped	Elongate petaloid	Wedge-shaped	U. Ord.—U. Dev.
<i>Pittsfordipterus</i>	Trapezoid	—	—	U. Sil.
<i>Pterygotus</i>	Trapezoid	Circular	Paddle-shaped	L. Ord.—M. Dev.
<i>Rhenopterus</i>	Parabolic	Obturbinate	—	L. Dev.—U. Dev.
<i>Rhinocarcinosoma</i>	Campanulate B	—	—	U. Sil.
<i>Ruedemannipterus</i>	Turbinate	—	—	U. Ord.
<i>Salteropterus</i>	—	Petaloid D	Triangular	U. Sil.
<i>Slimonia</i>	Long rectangular	Elongate cardioid	Foliate	L. Sil.—L. Dev.
<i>Strobilopterus</i>	Semicircular	—	—	L. Dev.
<i>Stylonurella</i>	Subquadrate	—	—	U. Ord.—U. Dev.
<i>Stylonuroides</i>	Parabolic	—	—	U. Ord.—U. Sil.
<i>Stylonurus</i>	Horseshoe-shaped	—	Long styliform	L. Dev.—U. Dev.
<i>Syntomopterus</i>	Semicircular	—	—	L. Dev.
<i>Tarsopterella</i>	Subquadrate	—	Clavate	L. Dev.
<i>Truncatiramus</i>	Trapezoid	Obovate	Bilobed	U. Sil.—L. Dev.
<i>Tylopterella</i>	Horseshoe-shaped	—	Styliform	U. Sil.
<i>Unionopterus</i>	Subquadrate	—	—	Miss.
<i>Vernopterus</i>	—	—	—	Penn.
<i>Waeringopterus</i>	Subquadrate	Petaloid C	Xiphous	L. Ord.—U. Sil.
<i>Willwerathia</i>	Wide rectangular	—	—	L. Dev.
<i>Woodwardopterus</i>	Trapezoid	—	—	Miss.

## Superfamily MEGALOGRAPTOIDEA

Caster and Kjellesvig-Waering, 1955 (nom. trans.)

*Diagnosis.*—Legs II–IV spiniferous, mixed types; leg V non-spiniferous; leg VI swimming leg.

## Family MEGALOGRAPTIDAE

Caster and Kjellesvig-Waering, 1955

*Diagnosis.*—Leg II spiniferous, *Megalograptus* type; leg III

spiniferous, *Mixopterus* type A; leg IV spiniferous, *Megalograptus* type; leg V nonspiniferous, *Eurypterus* type; leg VI swimming leg, *Mixopterus* type.

*Secondary characters.*—Opisthosoma shows both a first and fourth order (trilobation of mesosoma) differentiation into a mesosoma and metasoma. Doublure of *Megalograptus* type.

*Stratigraphic range.*—Upper Ordovician.

*Included genera.*—*Megalograptus* Miller, 1874, p. 343; *Echinognathus* Walcott, 1882, p. 213.

## Superfamily EURYPTEROIDEA Burmeister, 1843

*Diagnosis.*—Legs II–IV spiniferous, all one type; leg V non-spiniferous; leg VI swimming leg.

## Family EURYPTERIDAE Burmeister, 1843

*Diagnosis.*—Legs II–IV spiniferous, *Hughmilleria* type; leg V nonspiniferous, *Eurypterus* type; leg VI swimming leg, *Eurypterus* type.

*Secondary characters.*—Opisthosoma shows a second order differentiation into a mesosoma and metasoma by the presence of lateral epimera on the metasomal segments. Doublure of *Eurypterus* type.

*Stratigraphic range.*—Upper Ordovician to Lower Devonian.

*Included genera.*—*Eurypterus* De Kay, 1825, p. 375; *Baltoeurypterus* Størmer, 1973, p. 129.

## Family DOLICHOPTERIDAE

Kjellesvig-Waering and Størmer 1952

*Diagnosis.*—Legs II–IV spiniferous, *Hughmilleria* type; leg V nonspiniferous, *Dolichopterus* type; leg VI swimming leg, *Dolichopterus* type.

*Secondary characters.*—Opisthosoma shows a second order differentiation into a mesosoma and metasoma by the presence of lateral epimera on the metasomal segments.

*Stratigraphic range.*—Lower Ordovician to Lower Devonian.

*Included genera.*—*Dolichopterus* Hall, 1859, p. 414; *Strobilopterus* Ruedemann, 1935a, p. 129–130; *Ruedemannipterus* Kjellesvig-Waering, 1966, p. 174; *Syntomopterus* Kjellesvig-Waering, 1961a, p. 91.

## Family ERIOPTERIDAE n. fam.

*Etymology.*—The name of the family is derived from the type genus.

*Type genus.*—*Erieopterus* Kjellesvig-Waering 1958b, p. 1110.

*Diagnosis.*—Legs II–IV spiniferous, *Erieopterus* type; leg V nonspiniferous, *Eurypterus* type; leg VI swimming leg, *Erieopterus* type.

*Secondary characters.*—Opisthosoma shows a first order differentiation into a mesosoma and metasoma. Doublure of *Erieopterus* type.

*Stratigraphic range.*—Lower Ordovician to Lower Devonian.

*Included genera.*—*Erieopterus* Kjellesvig-Waering, 1958b, p. 1110; *Onychopterella* Størmer, 1951, p. 421; *Buffalopterus* Kjellesvig-Waering and Heubusch, 1962, p. 212.

## Superfamily STYLONUROIDEA Diener, 1924

(=DREPANOPTEROIDEA Kjellesvig-Waering, 1966)

*Diagnosis.*—Legs II–IV spiniferous, all one type; legs V–VI nonspiniferous, all one type.

## Family STYLONURIDAE Diener, 1924

(=PAGEIDAE Kjellesvig-Waering, 1966, in Waterston, 1979)

*Diagnosis.*—Legs II–IV spiniferous, *Hughmilleria* type; legs V–VI nonspiniferous, *Pagea* type.

*Secondary characters.*—Opisthosoma undifferentiated.

*Stratigraphic range.*—Upper Ordovician to Upper Devonian.

*Included genera.*—*Stylonurus* Page, 1856, p. 135–136; *Stylonurella* Kjellesvig-Waering, 1966, p. 179; *Kiaeropterus* Waterston, 1979, p. 291.

## Family DREPANOPTERIDAE Kjellesvig-Waering, 1966

*Diagnosis.*—Legs II–IV spiniferous, *Hughmilleria* type; legs V–VI nonspiniferous, *Drepanopterus* type.

*Secondary characters.*—Opisthosoma undifferentiated. Prosoma horseshoe-shaped, with marginal rim.

*Stratigraphic range.*—Lower Silurian to Upper Devonian.

*Included genera.*—*Drepanopterus* Laurie, 1892, p. 159; *Alkenopterus* Størmer, 1974, p. 386; *Moselopterus* Størmer, 1974, p. 389.

## Family PARASTYLONURIDAE Waterston, 1979

*Diagnosis.*—Legs II–IV spiniferous, *Hughmilleria* type; legs V–VI nonspiniferous, *Parastylonurus* type.

*Secondary characters.*—Opisthosoma shows a second order differentiation into a mesosoma and metasoma by the presence of lateral epimera on the metasomal segments. Doublure of *Eurypterus* type.

*Stratigraphic range.*—Upper Ordovician to Upper Devonian.

*Included genera.*—*Parastylonurus* Kjellesvig-Waering, 1966, p. 180; *?Stylonuroides* Kjellesvig-Waering, 1966, p. 178; *?Brachyopterus* Størmer, 1951, p. 416.

## Family LAURIEIPTERIDAE Kjellesvig-Waering, 1966

*Diagnosis.*—Legs II–IV spiniferous, *Ctenopterus* type; legs V–VI nonspiniferous, *Pagea* type.

*Secondary characters.*—Opisthosoma undifferentiated.

*Stratigraphic range.*—Upper Silurian to Carboniferous.

*Included genera.*—*Laurieipterus* Kjellesvig-Waering, 1966, p. 190; *Ctenopterus* Clarke and Ruedemann, 1912, p. 286–287; *Hallipterus* Kjellesvig-Waering, 1963a, p. 491; *Pagea* Waterston, 1962, p. 137–138; *?Mazonipterus* Kjellesvig-Waering, 1963b, p. 100.

Superfamily KOKOMOPTEROIDEA Kjellesvig-Waering, 1966  
(nom. trans.)

*Diagnosis.*—Legs II–V spiniferous, all one type; leg VI non-spiniferous.

## Family KOKOMOPTERIDAE Kjellesvig-Waering, 1966

*Diagnosis.*—Legs II–V spiniferous, *Lamontopterus* type; leg VI nonspiniferous, *Kokomopterus* type.

*Secondary characters.*—Opisthosoma undifferentiated.

*Stratigraphic range.*—Lower Silurian to Upper Silurian.

*Included genera.*—*Kokomopterus* Kjellesvig-Waering, 1966, p. 186; *Lamontopterus* Waterston, 1979, p. 278.

## Family HARDIEOPTERIDAE n. fam.

*Etymology.*—The name of the family is derived from the type genus.

*Type genus.*—*Hardieopterus* Waterston, 1979, p. 271.

*Diagnosis.*—Legs II–V spiniferous, *Hardieopterus* type; leg VI nonspiniferous, *Hardieopterus* type.

*Secondary characters.*—Opisthosoma shows both a second and fourth order differentiation into a mesosoma and metasoma. Doublure of *Eurypterus* type.

*Stratigraphic range.*—Lower Silurian to Upper Silurian.

*Included genera.*—*Hardieopterus* Waterston 1979, p. 271.

## Superfamily BRACHYOPTERELLOIDEA n. superfam.

*Diagnosis.*—Legs II–III spiniferous, all one type; legs IV–VI nonspiniferous, all one type.

## Family BRACHYOPTERELLIDAE n. fam.

*Etymology.*—The name of the family is derived from the type genus.

*Type genus.*—*Brachyopterella* Kjellesvig-Waering, 1966, p. 181.

*Diagnosis.*—Legs II–III spiniferous, *Hughmilleria* type; legs IV–VI nonspiniferous, *Brachyopterella* type.

*Secondary characters.*—Opisthosoma undifferentiated.

*Stratigraphic range.*—Upper Ordovician to Upper Silurian.  
*Included genus.*—*Brachyopterella* Kjellesvig-Waering, 1966, p. 181.

Superfamily RHENOPTEROIDEA Størmer, 1951

*Diagnosis.*—Legs II–VI nonspiniferous, all one type.

Family RHENOPTERIDAE Størmer, 1951

*Diagnosis.*—Legs II–VI nonspiniferous, *Kokomopterus* type.  
*Secondary characters.*—Doublure of *Eurypterus* type.  
*Stratigraphic range.*—Lower Devonian to Upper Devonian.  
*Included genus.*—*Rhenopterus* Størmer, 1936, p. 62.

Superfamily MYCTEROPOIDEA Cope, 1886

*Diagnosis.*—Opisthosoma shows a third order differentiation, with first one or two segments greatly enlarged.

*Remarks.*—This superfamily is based on secondary characters, when they are known, because the legs essentially are unknown. Previous characterizations of the prosomal appendages seem to be based on supposition and on the presumed similarity with genera that may not necessarily be related. The only proper course would be to abandon this superfamily and place the included genera in classification uncertain. However, to do so would introduce an unnecessary instability into eurypterid classification and render worthless the value of the secondary characters.

Family MYCTEROPIDAE Cope, 1886

*Diagnosis.*—Opisthosoma with greatly lengthened first (and only known) segment. Ornamentation coarsely reticulate.

*Stratigraphic range.*—Carboniferous.

*Included genus.*—*Mycterops* Cope, 1886, p. 1029.

Family WOODWARDOPTERIDAE Kjellesvig-Waering, 1959

*Diagnosis.*—Opisthosoma shows a third order differentiation where first two segments are greatly lengthened.

*Stratigraphic range.*—Carboniferous.

*Included genera.*—*Woodwardopterus* Kjellesvig-Waering, 1959, p. 255; *Vernopterus* Waterston, 1968, p. 12.

Suborder PTERYGOTINA

Caster and Kjellesvig-Waering, 1964

*Diagnosis.*—Chelicera large, rami with teeth.

Superfamily PTERYGOTOIDEA

Clarke and Ruedemann, 1912

*Diagnosis.*—Legs II–V nonspiniferous, all one type; leg VI swimming leg.

Family PTERYGOTIDAE Clarke and Ruedemann, 1912

*Diagnosis.*—Type A genital appendage long, comprised of a single segment; type B small, lozenge-shaped, comprised of a single segment.

*Secondary characters.*—Opisthosoma undifferentiated.

*Stratigraphic range.*—Lower Ordovician to Middle Devonian.

*Included genera.*—*Pterygotus* Agassiz, 1844, p. 19; *Acutiramis* Ruedemann, 1935b, p. 70; *Erettopterus* Salter, 1859, p. 230; *Truncatiramis* Kjellesvig-Waering, 1961b, p. 813.

Family JAEKELOPTERIDAE Størmer, 1974

*Diagnosis.*—Type A genital appendage long, comprised of three segments; type B small, pyriform, comprised of three segments.

*Secondary characters.*—Opisthosoma undifferentiated.

*Stratigraphic range.*—Lower Devonian.

*Included genera.*—*Jaekelopterus* Waterston, 1964, p. 30.

INCERTAE SEDIS

Some genera are not assigned to families at this time because the prosomal appendages and all or most of the opisthosoma are unknown or very poorly known. Most specimens of these genera have been reported as fragments, or consist of morphological parts that are not indicative of either family or superfamily assignment. The genera are: *Melbournopterus* Caster and Kjellesvig-Waering, 1953, p. 153; *Dorfopterus* Kjellesvig-Waering, 1955, p. 696; *Hastimima* White, 1908, p. 589; *Pittsfordipterus* Kjellesvig-Waering and Leutze, 1966, p. 1111; *Tarsoptrella* Størmer, 1951, p. 421; *Tyloptrella* Størmer, 1951, p. 421; and *Willwerathia* Størmer, 1969, p. 26.

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## GROWTH OF THE XENOMORPHIC CRINOID COLUMN (*TAXOCRINUS*, LATE MISSISSIPPIAN)

JULIE I. WULFF AND WILLIAM I. AUSICH

Department of Geology and Mineralogy, 125 South Oval Mall,  
The Ohio State University, Columbus 43210

**ABSTRACT**—Two alternative hypotheses for proximal column growth are tested in *Taxocrinus* cf. *T. whitfieldi*, a late Mississippian flexible crinoid. The first hypothesis states that new columnals are added at the base of the proximal column (immediately above the generating columnal), whereas the second hypothesis has columnals of the proximal column inserted beneath the aboral cup. In both hypotheses, middle column columnals are inserted beneath the generating columnal and are independent from the proximal column.

External features used to determine points of columnal insertion include wedge-shaped columnals and sharp changes in columnar morphology. Sagittal sections reveal the presence of small columnals, some of which can be interpreted as the last columnals inserted prior to death. Data collected on *Taxocrinus* cf. *T. whitfieldi* confirm the first hypothesis. This hypothesis may be applicable to other crinoids with xenomorphic columnals.

### INTRODUCTION

**T**RADITIONAL INTERPRETATIONS for the growth of crinoid columns hold that all new columnals are inserted at the top (proximal) end of the column immediately beneath the aboral cup. As new columnals are added, earlier formed columnals are progressively displaced farther away from the calyx, so that a complete column preserves the different ontogenetic stages of crinoid columnal growth in progression (Ubaghs, 1978). This interpretation was developed to explain growth in crinoids with homeomorphic columnals, which are columns composed of a single type of columnal. This traditional interpretation, with modification, can also explain growth in most heteromorphic columns. In heteromorphic columns morphologically different columnals are present along the column, typically with larger (wider and higher) nodals separated by one or more smaller internodals (Jeffords and Miller, 1968; Ubaghs, 1978). Growth of a heteromorphic column with nodals and internodals proceeds with all new nodals added directly beneath the aboral cup. Internodals are added later during column ontogeny and are inserted farther down the column (Jeffords and Miller, 1968; Ubaghs, 1978). It is not known whether the internodal columnals

are first secreted at some position distal to the aboral cup or if they were initially secreted in the same position as nodals but their further growth delayed.

A third column type is xenomorphic, in which the complete crinoid column is divisible into three distinct regions defined by columnals with different morphologies (Figure 1). From the proximal to distal column these regions will be referred to as the proximal column, middle column, and distal column (see discussion by Philip, 1980). In flexible crinoids the proximal column is typically less than 2 cm in length and is composed of very thin columnals with approximately equal height that narrow in diameter distally. The most proximal columnal of the proximal column (the proximale, Bather, 1900) may be fused to the base of the calyx. Columnals of the middle column are higher. The columnals in the proximal part of this column segment commonly become progressively wider and higher for a short distance. In the distal column, columnals are modified, in part, for the holdfast. The traditional growth interpretation has typically been applied to the xenomorphic column, with the exception that new columnals are all added beneath the proximale if present (Wachsmuth and Springer, 1897, p. 39–40;