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 dublure; 8) differentiation of the opisthosaoma; 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, uniramus 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, Megalograptoidea, and Brachyopterelloidea, and five new families, Brachyopterellidae, Adelophthalmidae, Lanarkopteridae, Eriopteridae, and Hardieopteridae, are proposed.

INTRODUCTION

 Anatomy of eurypterids is generally well known (see Stormer, 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), semi-oval (Hall, 1859, p. 404), trapezoidal (Clarke and Ruedemann, 1912, p. 162), and sub-quadrate (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 dublure; 8) differentiation of the opisthosaoma; 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 Stormer (1974) and Waterston (1979).

MORPHOLOGICAL STANDARDS

Shape of the prosoma.—The term prosoma is preferable to the synonym cephalothorax (Stormer, 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 sub-quadrate 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 Stormer (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.

Truly 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 Stormer 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 (Stormer, 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 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>
<thead>
<tr>
<th>Present revision</th>
<th>Previously included</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quadrade</td>
<td>Quadrade, square</td>
</tr>
<tr>
<td>Subquadrade</td>
<td>Subquadrade, subtrapezoidal</td>
</tr>
<tr>
<td>Trapezoidal</td>
<td>Trapezoidal, subquadrade, subtrapezoidal, roundish, semioval</td>
</tr>
<tr>
<td>Horseshoe-shaped</td>
<td>Horseshoe-shaped, subrectangular</td>
</tr>
<tr>
<td>Campanulate</td>
<td>Campanulate, bell-shaped, semitriangular</td>
</tr>
<tr>
<td>Semicircular</td>
<td>Semicircular, hemicircular, semioval, subcircular</td>
</tr>
<tr>
<td>Triangular</td>
<td>Triangular, semitriangular, subtriangular</td>
</tr>
<tr>
<td>Parabolic</td>
<td>Parabolic, semielliptical, hemielliptical, suboval, semioval, subelliptical, elliptical</td>
</tr>
<tr>
<td>Pentagonal</td>
<td>Pentagonal</td>
</tr>
<tr>
<td>Turbine</td>
<td>Turbine, subquadrade, quadrade, subtrapezoidal</td>
</tr>
<tr>
<td>Spatulate</td>
<td>Spatulate</td>
</tr>
<tr>
<td>Wide rectangular</td>
<td>Wide rectangular, subquadrade</td>
</tr>
<tr>
<td>Long rectangular</td>
<td>Long rectangular, quadrade</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Shape</th>
<th>Length : width ratio</th>
<th>Lateral angle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quadrade</td>
<td>0.95-1.05</td>
<td>90</td>
</tr>
<tr>
<td>Subquadrade</td>
<td>0.65-0.85</td>
<td>85-95</td>
</tr>
<tr>
<td>Trapezoid</td>
<td>0.65-0.80</td>
<td>95-105</td>
</tr>
<tr>
<td>Horseshoe-shaped</td>
<td>0.70-0.90</td>
<td>60-85</td>
</tr>
<tr>
<td>Semicircular</td>
<td>0.50-0.65</td>
<td>110-120</td>
</tr>
<tr>
<td>Parabolic</td>
<td>0.90-1.40</td>
<td>100-115</td>
</tr>
<tr>
<td>Triangular</td>
<td>0.75-0.90</td>
<td>105-120</td>
</tr>
<tr>
<td>Pentagonal</td>
<td>0.95-1.05</td>
<td>55-65</td>
</tr>
<tr>
<td>Turbine</td>
<td>0.90-1.10</td>
<td>75-85</td>
</tr>
<tr>
<td>Spatulate</td>
<td>1.05-1.20</td>
<td>60-75</td>
</tr>
<tr>
<td>Wide rectangular</td>
<td>0.50-0.65</td>
<td>85-95</td>
</tr>
<tr>
<td>Long rectangular</td>
<td>1.25-1.50</td>
<td>85-95</td>
</tr>
<tr>
<td>Campanulate A</td>
<td>0.80-0.90</td>
<td>95-105</td>
</tr>
<tr>
<td>Campanulate B</td>
<td>0.60-0.80</td>
<td>120-140</td>
</tr>
</tbody>
</table>

Figure 2—Schematic diagrams of the 14 standard shapes of prosomas. 1, parabolic; 2, trapezoid; 3, quadrade; 4, subquadrade; 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.
“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 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.

<table>
<thead>
<tr>
<th>Shape</th>
<th>Length: width ratio</th>
<th>Lateral angle</th>
<th>Angle of cordation</th>
<th>Position of greatest width</th>
<th>Character of anterior</th>
<th>Character of posterior</th>
<th>Character of sides</th>
<th>Character of shoulder</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Circular</td>
<td>1.25–1.35</td>
<td>45°</td>
<td>150°</td>
<td>Central</td>
<td>Shallowly cordate</td>
<td>Broadly rounded</td>
<td>Broadly convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>2. Oval</td>
<td>1.35–1.40</td>
<td>70°</td>
<td>110°–160°</td>
<td>Central</td>
<td>Shallowly cordate</td>
<td>Rounded</td>
<td>Convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>3. Oblate</td>
<td>1.55–1.50</td>
<td>70°</td>
<td>110°–150°</td>
<td>Anterior third</td>
<td>Cordate</td>
<td>Rounded</td>
<td>Convex</td>
<td>Round</td>
</tr>
<tr>
<td>4. Rhombiovate</td>
<td>1.35–1.70</td>
<td>75°</td>
<td>65°</td>
<td>Central</td>
<td>Cordate</td>
<td>Rounded</td>
<td>Convex</td>
<td>Semicircular</td>
</tr>
<tr>
<td>5. Rhomboid</td>
<td>1.80–2.10</td>
<td>65°</td>
<td>80°</td>
<td>Central</td>
<td>Narrowly but deeply</td>
<td>Rounded</td>
<td>Convex</td>
<td>Angular</td>
</tr>
<tr>
<td>6. Elliptical</td>
<td>1.90–2.10</td>
<td>65°</td>
<td>125°</td>
<td>Central</td>
<td>Shallowly cordate</td>
<td>Truncated</td>
<td>Convex</td>
<td>Semi-elliptical</td>
</tr>
<tr>
<td>7. Petaloid A</td>
<td>1.80</td>
<td>75°</td>
<td>160°</td>
<td>Anterior third</td>
<td>Shallowly cordate</td>
<td>Truncated</td>
<td>Convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>8. Petaloid B</td>
<td>1.90–2.10</td>
<td>80°</td>
<td>None</td>
<td>Anterior third</td>
<td>Rounded</td>
<td>Truncated</td>
<td>Straight, converging posteriorly</td>
<td>Rounded</td>
</tr>
<tr>
<td>9. Petaloid C</td>
<td>2.40</td>
<td>80°</td>
<td>135°</td>
<td>Anterior third</td>
<td>Shallowly cordate</td>
<td>Rounded point</td>
<td>Convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>10. Petaloid D</td>
<td>2.9–3.0</td>
<td>80°</td>
<td>135°</td>
<td>Anterior third</td>
<td>Shallowly cordate</td>
<td>Rounded</td>
<td>Slightly convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>11. Vase-shaped</td>
<td>1.7</td>
<td>70°–75°</td>
<td>80°</td>
<td>Anterior third</td>
<td>Cordate</td>
<td>Rounded</td>
<td>Convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>12. Elongate vase-shaped</td>
<td>1.9–2.1</td>
<td>100°</td>
<td>110°</td>
<td>Anterior third</td>
<td>Shallowly cordate</td>
<td>Rounded</td>
<td>Convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>13. Elongate cardoid</td>
<td>2.35–2.40</td>
<td>75°</td>
<td>60°</td>
<td>Anterior third</td>
<td>Deeply cordate</td>
<td>Truncated</td>
<td>Nearly straight, converging posteriorly</td>
<td>Rounded</td>
</tr>
<tr>
<td>14. Elongate petaloid</td>
<td>2.7</td>
<td>60°</td>
<td>55°</td>
<td>Central</td>
<td>Deeply cordate</td>
<td>Rounded</td>
<td>Slightly convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>15. Doliform</td>
<td>1.0–1.1</td>
<td>110°–115°</td>
<td>140°</td>
<td>Central</td>
<td>Broadly cordate</td>
<td>Broadly concave</td>
<td>Broadly convex</td>
<td>Angular</td>
</tr>
<tr>
<td>16. Opbryiform</td>
<td>1.55–1.65</td>
<td>90°</td>
<td>None</td>
<td>Anterior third</td>
<td>Broadly concave</td>
<td>Narrowly rounded</td>
<td>Convex</td>
<td>Sigmoid</td>
</tr>
<tr>
<td>17. Obturbinate</td>
<td>1.00–1.10</td>
<td>105°–120°</td>
<td>None</td>
<td>Posterior</td>
<td>Broadly concave</td>
<td>Broadly rounded</td>
<td>Convex, converging anteriorly</td>
<td>Angular</td>
</tr>
<tr>
<td>18. Obtriangular</td>
<td>1.00–1.33</td>
<td>60°</td>
<td>None</td>
<td>Anterior</td>
<td>Truncated</td>
<td>Truncated</td>
<td>Straight, converging posteriorly</td>
<td>None</td>
</tr>
<tr>
<td>19. Lyrate</td>
<td>2.00–2.15</td>
<td>85°</td>
<td>130°</td>
<td>Anterior</td>
<td>Cordate</td>
<td>Variable</td>
<td>Nearly straight, converging posteriorly</td>
<td>Variable</td>
</tr>
<tr>
<td>20. Rectangular</td>
<td>2.2</td>
<td>80°–85°</td>
<td>40°</td>
<td>Anterior third</td>
<td>Deeply cordate</td>
<td>Truncated</td>
<td>Slightly convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>21. Subquadrate</td>
<td>1.55</td>
<td>90°</td>
<td>None</td>
<td>Posterior</td>
<td>Broadly concave</td>
<td>Broadly concave</td>
<td>Convex</td>
<td>Semi-elliptical</td>
</tr>
<tr>
<td>22. Pear-shaped</td>
<td>1.10–1.20</td>
<td>70°</td>
<td>95°</td>
<td>Posterior</td>
<td>Deeply cordate</td>
<td>Concave</td>
<td>Convex, converging anteriorly</td>
<td>Angular</td>
</tr>
<tr>
<td>23. Circucardioi</td>
<td>0.95</td>
<td>50°</td>
<td>115°</td>
<td>Anterior third</td>
<td>Broadly cordate</td>
<td>Rounded</td>
<td>Convex, converging posteriorly</td>
<td>Rounded</td>
</tr>
<tr>
<td>24. Shield-shaped</td>
<td>0.9–1.50</td>
<td>90°</td>
<td>None</td>
<td>Anterior</td>
<td>Broadly concave</td>
<td>Broadly rounded</td>
<td>Sigmoid</td>
<td>Rounded</td>
</tr>
<tr>
<td>25. Cardoid</td>
<td>1.25–1.30</td>
<td>60°</td>
<td>None</td>
<td>Anterior third</td>
<td>Broadly concave</td>
<td>Rounded</td>
<td>Convex, converging posteriorly</td>
<td>Rounded</td>
</tr>
<tr>
<td>27. Pararectangular</td>
<td>0.75–0.85</td>
<td>70°</td>
<td>85°</td>
<td>Anterior third</td>
<td>Deeply cordate</td>
<td>Truncated</td>
<td>Convex</td>
<td>Rounded</td>
</tr>
<tr>
<td>28. Paralliptical</td>
<td>1.9–2.1</td>
<td>75°</td>
<td>135°</td>
<td>Central</td>
<td>Cardate</td>
<td>Truncated</td>
<td>Convex</td>
<td>Angular</td>
</tr>
</tbody>
</table>

1 Some genera and species with “teeth.”
2 Truncated in some species, rounded in others.
3 Angular in some species, rounded in others.
Greatest value at the levels of suborder, superfamily, and family considered in establishing these standards. Furthermore, the Eurypterida (Caster and Kjellesvig-Waering, 1964, p. 306).

Ptérygotid type, with large rami with teeth. The chelicerae are

ferous legs; 2) nonspiniferous legs; and 3) swimming legs. The

taxonomic value of development of the legs is most important

categorization of his work.

In establishing these standards, the prime consideration is

morphism. The degree and direction of development of the

legs are deemed to be of greater value in the study of the phy-

logeny 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


Chelicera. — Two types of chelicera are recognized: 1) the eu-

rypterid type, with relatively small, toothless rami; and 2) the

pterygotid type, with large rami with teeth. The chelicerae are

the only morphological character used to define suborders of


Legs. — Three general types of legs are recognized: 1) spin-

iferous legs; 2) nonspiniferous legs; and 3) swimming legs. The

overall arrangement of these general types of legs is the taxo-

nomic basis for defining superfamilies. The arrangement of the

individual types of legs is the taxonomic basis for defining fam-

ilies. Each individual type of leg is illustrated, briefly described,

and differentiated from similar types.


four types of spiniferous legs: a Hughmilleria type, a Mixopterus
type, a Slimonia type, and a Hibbertopterus type. His arrange-

ment is modified to include as distinct types of spiniferous legs, a Hughmilleria type, Carcinosoma type, Eriopterus type, Ade-
lolithalmus type, Ctenopterus type, Hardieopterus type, Lam-

montopterus type, Megalograptus type, and Mixopterus types A, B, and C. Following the alternative interpretation of Störmer

(1974, p. 362), the Slimonia type is recognized as a type of

nonspiniferous leg. The Hibbertopterus type, with the develop-

ment 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 (Fig-

ure 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 Eriep-
terus type (Figure 8.4) has a single, short to moderately long

spine on only the last two or three podomeres. The Lamontop-
terus type (Figure 8.5) has a single pair of short spines at the
distal end of each podomere, thereby resembling the Hughmil-

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 Adelolithalthmus type

(Figure 8.7) has a single, long spine on the penultimate podo-

mere, and serrate distal margins on each podomere. If not for

the presence of the spine, the Adelolithalthmus type of spiniferous leg could easily be mistaken for the Slimonia type of nonspi-

niferous 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 podo-

mere, with the distal pair of spines on the third podomere being

extremely long. The Mixopterus type B (Figure 8.9) has nu-

merous 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 podo-

meres 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 in-

creasing in size distally. Furthermore, the number of spines on

all but the last podomere remains the same.

Nonspiniferous legs. — Störmer (1974, p. 364) recognized only

two types of nonspiniferous legs, the Stylopronus type and the

Moselopterus type. Nine types are proposed here (Figure 9):

Slimonia type, Kokomopterus type, Pagea type, Drepanopterus
type, Dolichopterus type, Eurypetes type, Hardieopterus type,

Parastyluronus type, and Brachyopterella type.

The Slimonia type (Figure 9.1) has distally serrated or fringe-

like margins on each podomere. The Kokomopterus type (Fig-

ure 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 Drepa-

nopterus 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 Störmer’s Moselopterus type. The

two characterizations differ, however, in that Störmer indicated

its primitiveness to the swimming leg, while here no such de-
development 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 Hardieopterus 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 Brachyopterella 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.—Stormer (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 type, Slimonia type, Dolichopterus type, Erieopterus 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 Erieopterus type (Figure 10.6) is synonymous with Stormer’s (1934a, 1974) Onychopterella type, and is characterized by the 9th podomere present as a prominent terminal claw. Although the term Onychopterella type has priority over the term Erieopterus 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
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 appendages 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 Hugmillieriidae), while some genera in different families show similar genital appendages (e.g., Hugmilleria 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, epi- mera, 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., Mycteros). 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., styliform 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 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, Eriopterus type; 7, Eurypterus type; 8, Adelophthalmus type. (Redrawn from various sources.)

**Figure 11**—Schematic diagram for eurypterid doublures. 1, Eurypterus type; 2, Eriopterus type; 3, Hughmilleria type; 4, Pterygotus type; 5, Stylonurus type; 6, Megalograptus type.
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) Stormer’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 supports many, if not all, of the hypotheses concerning the relationships of several genera (e.g., Hughmilleria and Carcinosoma, in Størmer, 1974, p. 362; Eriotheus 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, Cyrtococcus Størmer and Waterston, 1968, and Dunnopterus 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, uniramus 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
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 prosoma; 8) ornamentation of the opisthosoma; 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.

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 Stormer 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 superfamilies Drepanopteroidea Kjellesvig-Waering, 1966 (nom. trans. Størmer, 1974, p. 372), is taxonomically synonymous with the superfAMILY Stylonuroidea Diener, 1924, and is abandoned. The superfamilies Megalograptoidea Caster and Kjellesvig-Waering, 1964, and Kokomopteroidea Kjellesvig-Waering, 1966, are here raised from the rank of family. The superfamilies Brachyopterelloidea is new.

Twenty-two families are recognized, five of which are new:
Adelophthalmidae, Lanarkopteridae, Eriopteridae, 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 Stormer and Waterston, 1968; and Dunnopterus Waterston, 1968. The type of the genus Clarkeipterus Kjellesvig-Waering, 1966, has already been discussed (Toller-ton, 1987b). Following the suggestion of Stormer (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.
must be abandoned, and the family Slimoniidae placed in the superfamily Pterygotoidae.

**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.


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

**Superfamily HUGHMILLERIOIDEA** Kjesleveig-Waering, 1951 (nom. trans. Stormer 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.* — Doubtles of *Hughmilleria* type. Opisthosoma shows a second order differentiation (lateral epimera on only the sixth segment).

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


**Family CARCINOSOMATIDAE** Stormer, 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.


*Remarks.* — Doubtles 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 (Stormer, 1974, p. 362), require its transfer from the superfamily Mixopteroidea to this superfamily. The genus *Holmipetus* 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 Kjesleveig-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.


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

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


*Remarks.* — Doubtles 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 Kjesleveig-Waering, 1955

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

**Family MIXOPTERIDAE**

Caster and Kjesleveig-Waering, 1955


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

*Stratigraphic range.* — Upper Silurian.


**Family LANARKOPTERIDAE** n. fam.

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


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

*Stratigraphic range.* — Upper Silurian.


### Table 8—Partial summary of eurypterid genera.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Shape of prosoma</th>
<th>Shape of metastoma</th>
<th>Shape of telson</th>
<th>Stratigraphic range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthopterus</td>
<td>Subquadrate</td>
<td>Obovate</td>
<td>Paddle-shaped</td>
<td>U. Sil.–L. Dev.</td>
</tr>
<tr>
<td>Adelophtalmus</td>
<td>Parabolic</td>
<td>Oval</td>
<td>Stylistiform</td>
<td>U. Dev.–L. Perm.</td>
</tr>
<tr>
<td>Baltoeurypterus</td>
<td>Trapezoid</td>
<td>–</td>
<td>Stylistiform</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Bassipterus</td>
<td>Parabolic</td>
<td>Vase-shaped</td>
<td>Stylistiform</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Brachyoptypterus</td>
<td>Spatulate</td>
<td>–</td>
<td>Stylistiform</td>
<td>U. Ord.</td>
</tr>
<tr>
<td>Carcinosoma</td>
<td>Triangular</td>
<td>Shield-shaped</td>
<td>Stylist of post-telson</td>
<td>U. Ord.–U. Sil.</td>
</tr>
<tr>
<td>Ctenopterus</td>
<td>Triangular</td>
<td>–</td>
<td>Stylistiform</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Dolichopterus</td>
<td>Subquadrate</td>
<td>Lyrate</td>
<td>Stylistiform</td>
<td>L. Ord.–L. Dev.</td>
</tr>
<tr>
<td>Doropterus</td>
<td>–</td>
<td>–</td>
<td>Long styliform</td>
<td>L. Dev.</td>
</tr>
<tr>
<td>Drepanopterus</td>
<td>Horseshoe-shaped</td>
<td>Oval</td>
<td>Stylistiform</td>
<td>L. Sil.–U. Dev.</td>
</tr>
<tr>
<td>Erettopterus</td>
<td>Semicircular</td>
<td>Obovate</td>
<td>Bilobed</td>
<td>U. Ord.–L. Dev.</td>
</tr>
<tr>
<td>Eurypterus</td>
<td>Trapezoid</td>
<td>Elliptical</td>
<td>Stylistiform</td>
<td>L. Dev.–U. Dev.</td>
</tr>
<tr>
<td>Glossopterus</td>
<td>Trapezoid</td>
<td>–</td>
<td>V</td>
<td>U. Dev.</td>
</tr>
<tr>
<td>Hallipterus</td>
<td>Triangular</td>
<td>–</td>
<td>–</td>
<td>L. Ord.–U. Sil.</td>
</tr>
<tr>
<td>Hastedima</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>M. Dev.–L. Perm.</td>
</tr>
<tr>
<td>Holmipterus</td>
<td>Parabolic</td>
<td>Petaloid A</td>
<td>Lancelolate</td>
<td>U. Ord.–U. Sil.</td>
</tr>
<tr>
<td>Jaekelopterus</td>
<td>Trapezoid</td>
<td>–</td>
<td>Paddle-shaped</td>
<td>L. Dev.</td>
</tr>
<tr>
<td>Klaeropterus</td>
<td>Subquadrate</td>
<td>–</td>
<td>–</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Kokomopterus</td>
<td>Subquadrate</td>
<td>–</td>
<td>–</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Lamontopterus</td>
<td>Turbinate</td>
<td>–</td>
<td>–</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Lanarkopterus</td>
<td>Trapezoid with rostrum</td>
<td>Cardioi</td>
<td>Curved styliform</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Laurieopterus</td>
<td>Spatulate</td>
<td>Subquadrate</td>
<td>–</td>
<td>L. Sil.</td>
</tr>
<tr>
<td>Mazonipterus</td>
<td>Triangular</td>
<td>–</td>
<td>–</td>
<td>Penn.</td>
</tr>
<tr>
<td>Megalopterus</td>
<td>Quadratet with rostrum</td>
<td>Doliform</td>
<td>Lancelolate with cercal blades</td>
<td>U. Ord.</td>
</tr>
<tr>
<td>Melbournepterus</td>
<td>Campanulate A</td>
<td>–</td>
<td>–</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Mixopterus</td>
<td>Quadratet with rostrum</td>
<td>Obpyriform</td>
<td>Curved styliform</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Moscheopterus</td>
<td>Horseshoe-shaped</td>
<td>Oval</td>
<td>Short curved styliform</td>
<td>L. Dev.–U. Dev.</td>
</tr>
<tr>
<td>Mystrops</td>
<td>Triangular</td>
<td>–</td>
<td>–</td>
<td>Carb.</td>
</tr>
<tr>
<td>Nanhythmillipterus</td>
<td>Parabolic</td>
<td>Elongate vaso-shaped</td>
<td>Lancelolate</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Onychopterella</td>
<td>Subquadrate</td>
<td>–</td>
<td>Clavate</td>
<td>U. Sil.–U. Sil.</td>
</tr>
<tr>
<td>Pagea</td>
<td>Turbinate</td>
<td>Petaloid B</td>
<td>Stylistiform</td>
<td>L. Dev.</td>
</tr>
<tr>
<td>Paracarcinosoma</td>
<td>Triangular</td>
<td>Obtriangular</td>
<td>Curved styliform</td>
<td>U. Sil.–L. Dev.</td>
</tr>
<tr>
<td>Paralymphillipterus</td>
<td>Semicircular</td>
<td>Paralliptical</td>
<td>Lancelolate</td>
<td>U. Sil.–L. Dev.</td>
</tr>
<tr>
<td>Pittsfordipterus</td>
<td>Trapezoid</td>
<td>–</td>
<td>Clavate</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Pterygopterus</td>
<td>Trapezoid</td>
<td>Circular</td>
<td>Paddle-shaped</td>
<td>L. Ord.–M. Dev.</td>
</tr>
<tr>
<td>Rhinocarcinosoma</td>
<td>Campanulate B</td>
<td>–</td>
<td>–</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Ruwedenmannipterus</td>
<td>Turbinete</td>
<td>–</td>
<td>–</td>
<td>U. Ord.</td>
</tr>
<tr>
<td>Salteropterus</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>U. Sil.</td>
</tr>
<tr>
<td>Silmonia</td>
<td>Long rectangular</td>
<td>Elongate cardioid</td>
<td>Triangular</td>
<td>L. Sil.–L. Dev.</td>
</tr>
<tr>
<td>Strobilipterus</td>
<td>Semicircular</td>
<td>–</td>
<td>Foliate</td>
<td>L. Dev.</td>
</tr>
<tr>
<td>Syntomopterus</td>
<td>Semicircular</td>
<td>–</td>
<td>–</td>
<td>L. Dev.</td>
</tr>
<tr>
<td>Tarsoptera</td>
<td>Subquadrate</td>
<td>–</td>
<td>Clavate</td>
<td>L. Dev.</td>
</tr>
<tr>
<td>Truncatiramus</td>
<td>Trapezoid</td>
<td>Obovate</td>
<td>Bilobed</td>
<td>U. Sil.–L. Dev.</td>
</tr>
<tr>
<td>Typoptera</td>
<td>Horseshoe-shaped</td>
<td>–</td>
<td>Stylistiform</td>
<td>U. Sil.–L. Dev.</td>
</tr>
<tr>
<td>Unionopterus</td>
<td>Subquadrate</td>
<td>–</td>
<td>–</td>
<td>Miss.</td>
</tr>
<tr>
<td>Vernopterus</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Penn.</td>
</tr>
<tr>
<td>Waerengopterus</td>
<td>Subquadrate</td>
<td>Petaloid C</td>
<td>Xiphous</td>
<td>L. Ord.–U. Sil.</td>
</tr>
<tr>
<td>Willmerathia</td>
<td>Wide rectangular</td>
<td>–</td>
<td>–</td>
<td>L. Dev.</td>
</tr>
<tr>
<td>Woodwardopterus</td>
<td>Trapezoid</td>
<td>–</td>
<td>–</td>
<td>Miss.</td>
</tr>
</tbody>
</table>

### Superfamily Megalograptoideae

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

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

### Family Megalograptoideae

Caster and Kjellesvig-Waering, 1955

**Diagnosis.**—Leg II spiniferous, Megalograptus type; leg III spiniferous, Mixopterus type A; leg IV spiniferous, Megalograptus type; leg V non-spiniferous, 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.**—Megalopterus Miller, 1874, p. 343; Echinognathus Walcott, 1882, p. 213.
Superfamily EUPHYTRODEA Burmeister, 1843

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

Family EURHYTROIDEA Burmeister, 1843


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.


Family DOLICHOPTERIDAE Kjellesvig-Waering and Störmer 1952

Diagnosis. — Legs II-IV spiniferous, *Hughmilleria* type; leg V non-spiniferous, *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.


Family ERIEOPTERIDAE n. fam.

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

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


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


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-IV spiniferous, *Ctenopterus* type; legs V-VI non-spiniferous, *Pagea* type.

Secondary characters. — Opisthosoma undifferentiated.


Superfamily BRACHYOPTERELLIDAE n. fam.

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


Diagnosis. — Legs II-V spiniferous, *Hardieopterus* type; leg VI non-spiniferous, *Hardieopterus* type.

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


Superfamily DREPTOPTERELLIDAE n. superfam.

Diagnosis. — Legs II-III spiniferous, all one type; legs IV-VI non-spiniferous, all one type.

Family DREPTOPTERIDAE Kjellesvig-Waering, 1966

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

Secondary characters. — Opisthosoma undifferentiated. Pro-soma horseshoe-shaped, with marginal rim.


Family PARASTYLOPEURIDAE Waterston, 1979


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.

Superfamily RHENOPTEROIDEA Størmer, 1951

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

Family RHENOPTERIDAE Størmer, 1951


Superfamily MYCTEROPOIDEA Cope, 1886

Diagnosis. — Opisthosa 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


Family WOODWARDOPTERIDAE Kjellesvig-Waering, 1959

Diagnosis. — Opisthosa shows a third order differentiation where first two segments are greatly lengthened. Stratigraphic range. — Woodwardopterus Kjellesvig-Waering, 1959, p. 255; Vernop terus Waterston, 1968, p. 12.

Suborder PTERGYOTINA

Caster and Kjellesvig-Waering, 1964

Diagnosis. — Chelicera large, rami with teeth.

Superfamily PTERGYOTOIDEA

Clarke and Ruedemann, 1912

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

Family PTERGYOTIDAE Clarke and Ruedemann, 1912


Superfamily RHENOPTEROIDEA Størmer, 1951

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

Family RHENOPTERIDAE Størmer, 1951


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; Pittsfordopterus Kjellesvig-Waering and Leutze, 1966, p. 1111; Tarsopt erella Størmer, 1951, p. 421; Tylopterus Waterston, 1969, p. 26.

ACKNOWLEDGMENTS

I thank the administration of Utica College of Syracuse University for allowing me use of the research facilities of the Geology Department while I was an undergraduate Teaching Assistant. I thank the New York State Museum for the loan of type specimens for study. I am especially thankful to S. Morris and his staff at the British Museum of Natural History for access to the eurypterid collections and for their generous assistance. I extend my gratitude to the reference staff at the Utica College Library, especially to Ms. Burchard for her persistence in obtaining critical material on interlibrary loan. Most of all, I thank my wife, Mary, for her patience, encouragement, and understanding in this and all my studies.

REFERENCES


ACCEPTED 3 MARCH 1989

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 column), 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 columns.

INTRODUCTION

Traditional 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 columns, 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;