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EVOLUTIONARY AND BIOGEOGRAPHIC PATTERNS IN THE ASTEROPYGINAE (TRILOBITA, DEVONIAN) DELO, 1935

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ABSTRACT

This paper presents a phylogenetic analysis of the Asteropyginae Delo, 1935. Sixty-six characters and 39 taxa were employed in a cladistic analysis that produced a single most parsimonious tree that is presented as a hypothesis of asteropyginid relationships. In addition to the phylogeny generated, 11 new genera are diagnosed: *Philipsmithiana, Coltraneia, Stummiana, Bellacartwrightia, Deloops, Tolkienia, Braunops, Armorigreenops, Kennacryphaeus, Modellops,* and *Hallandclarkeops*, and 12 new species are described: *Philipsmithiana hyfinkeli, P. burtandmimiae, Armorigreenops leoi, Pelitlina smeenki, Bellacartwrightia jennyae, B. whiteleyi, B. phyllocaudata, B. calderonae, Greenops widderensis, G. barberi, G. grabaui,* and *Kennacryphaeus harrisae.*

Traditionally, asteropyginine taxa in the Appalachian and Michigan Basins of Eastern North America had been assigned to *Greenops* Delo, 1935, or *Greenops* (*Neometacanthus*) Richter and Richter, 1948. A core of five Eastern North American species—*Greenops boothi* (Green, 1837), *G. widderensis*, new species, *G. chilmanae* Stumm, 1965, *G. grabaui*, new species, and *G. barberi*, new species—can still be assigned to *Greenops*. All other asteropyginine taxa in Eastern North America must be assigned to different genera. Species referable to *Neometacanthus* Richter and Richter, 1948, may be known from the Illinois Basin of Eastern North America, and a species referable to *Tolkienia*, new genus, may be known from the Michigan Basin of Eastern North America.

The single most parsimonious cladogram was also used to investigate biogeographic patterns. In particular, the number of times that independent lineages of asteropyginines invaded from what are now Europe and North Africa (called Armorica herein) into Eastern North America during the Devonian was ascertained. Phylogenetic analysis suggested that there must have been at least four such invasions, with clades that had primitive European or North African affinities giving rise to Eastern North American taxa, although no species are shared between Armorica and Eastern North America. One of the lineages that invaded Eastern North America subsequently reinvaded Armorica. The timing of these invasions and their relation to overall patterns of faunal evolution in the Middle Devonian of Eastern North America are also discussed. These patterns suggest that the different taxa that make up a fauna often arrive during different time intervals, not all at once.

INTRODUCTION

The Asteropyginae Delo, 1935, form an important component of Devonian trilobite diversity. The group persisted from the Lockhovian to the Frasnian (Feist, 1991) or possibly Famennian (data herein) and consisted of approximately 225 species. Species occur in strata of Eastern North America (ENA), Armorica (comprising central Europe, northern Africa, Iberia, Turkey, and Afghanistan, although some reconstructions such as that of Van der Voo [1988] view Armorica as not including northern Africa), Burma, and Venezuela, and the group attained its peak diversity in the upper Emsian (Morzadec, 1992). This paper presents a phylogenetic analysis of a large component of the generic diversity within the asteropyginid clade. Special attention is paid to the evolutionary position of the Laurentian asteropyginines, and the putative monophyly of these taxa typically assigned to the genus *Greenops* in ENA is evaluated. The relationship of Armorican taxa to Laurentian taxa in ENA, the North American part of Oliver's (1976, 1977) Eastern Americas Realm, is also discussed. Twelve new species are described, 11 new genera are diagnosed, and a parsimony analysis of the Asteropyginae is conducted using 66 characters and 39 taxa.

Before phylogenetic patterns in the Asteropyginae can be analyzed, it is necessary to place that subfamily in a higher level phylogenetic context. Following the arguments and the character evidence presented by Edgecombe (1993) and Ramsköld and Edgecombe (1993), the Asteropyginae are assigned to the superfamily Acastacea Delo, 1935, family Acastidae Delo, 1935. When considering the subfamilial relationships within the Acastacea several authors (e.g., Struve, 1959; Pillet, 1961; Gandl, 1972; Eldredge, 1979; Timm, 1981; Smeenk, 1983; Tomczykowa, 1991; Edgecombe, 1991, 1993; Ramsköld and Edgecombe, 1993) have noted that the Acastavinae Struve, 1958a, appear to be closely related, or the sister taxon, to the Asteropyginae, with both of these taxa typically placed in the Acastacea. The Acastavinae, as traditionally circumscribed, contains the genera *Acastava* Richter and Richter, 1954, *Acastella* Reed, 1925, *Acastellina* Richter and Richter, 1954, *Acastocephala* Shergold, 1966, *Pelitlina* Haas, 1968, *Centauropyge* Haas, 1968, *Mimocryphaeus* Gandl, 1972, *Chimaerastella* Gandl, 1972, and *Acastopyge* Tomczykowa *in* Tomczykowa and Witwicka, 1974. These taxa were treated as closely related because they possessed genal and pygidial marginal spines larger than those in Acastinae Delo, 1935, but not as large as those of the Asteropyginae (Ramsköld and Edgecombe, 1993). Edgecombe (1993) and Ramsköld and Edgecombe (1993) explicitly recognized that these taxa formerly assigned to the Acastavinae comprise a paraphyletic stem lineage to the Asteropyginae, although these authors did not define a monophyletic Acastavinae. Herein, a detailed analysis considering the formulation of a monophyletic Acastavinae is not pursued, but a species formerly placed within that paraphyletic grade is employed as an outgroup in the phylogenetic analysis.

There has been some disagreement on which taxa within the paraphyletic "Acastavinae" (using Wiley's [1979] quotation marks convention for paraphyletic taxa) are most closely related to true Asteropyginae and thus are the most apt choice as an outgroup for polarization of characters in an analysis of the ingroup Asteropyginae. Certain authors, such as Edgecombe (1991) and Ramsköld and Edgecombe (1993), have suggested that species of *Acastava* or *Pelitlina* are the last common ancestors of the Asteropyginae, whereas other authors have suggested that species of *Acastella* are immediately ancestral to the Asteropyginae (e.g., Timm, 1981; Smeenk, 1983; Tomczykowa, 1991). Finally, Gandl (1972) suggested that the Asteropyginae were polyphyletic, with part of the "clade" derived from his "*Acastella*" new species aff. *tiro* Richter and Richter, 1954, and the other part from other taxa in the "Acastavinae." The only one of these hypotheses of evolutionary relationship that is rigorously couched in terms of synapomorphous traits is that of Edgecombe (1991) and Ramsköld and Edgecombe (1993), and the conclusion of their analysis, that *Acastava* and *Pelitlina* are more closely related to the Asteropyginae than *Acastella* sensu stricto, is followed herein. Ramsköld and Edgecombe (1993) presented a series of characters that indicate that *Acastella* sensu stricto is sister to *Scotiella* Delo, 1935, to the exclusion of the other "Acastavinae," specifically *Acastava* and *Pelitlina*, which are themselves sister to the Asteropyginae.

When considering both *Acastava* and *Pelitlina* in relation to the Asteropyginae, it seems that species of *Pelitlina* bear at least two synapomorphous traits uniting this genus with the Asteropyginae to the exclusion of *Acastava*. The type of *Acastava*, *A. atavus* (Schmidt, 1907), has five pairs of small marginal denticles bordering the pygidium, and these denticles are also found in all of the species of *Acastella*, which in addition typically possess a long terminal pygidial spine. In both *Pelitlina goltzi* Haas, 1968, and *Pelitlina smeenki*, new species (formerly *Acastava* new species *in* Smeenk [1983]), there are five relatively broad pairs of marginal pygidial lappets bordering the pygidium. These broad marginal pygidial lappets are found in all members of the Asteropyginae, with five pairs of lappets always found except for a few exceptions in which four pairs are present, e.g., species of *Neocalmonia* Pillet, 1969. These shared characters are taken as evidence of evolutionary relationship. However, it is interesting to note the parallel development of this character in certain members of the Calmoniidae Delo, 1935, in particular, species of the "*Metacryphaeus* Group" (see Lieberman et al. [1991] and Lieberman [1993]). In addition to this synapomorphy of the pygidium, the cephalic border furrow extends onto the genal spine, partially bifurcating it, in both *Pelitlina* and the Asteropyginae (Edgecombe, 1991). Three characters are treated as synapomorphies of the Asteropyginae, with *Pelitlina* treated as a near basal member of the subfamily rather than a member of the "Acastavinae," and it is used as the outgroup in phylogenetic analysis of the Asteropyginae. A sister group relationship between the Asteropyginae and *Pelitlina* suggests that *Pelitlina* could be assigned to a new monotypic subfamily. This is a reasonable taxonomic solution; however, it is not followed at this time because designation of a new subfamily will not improve our understanding of phylogenetic patterns within the Acastacea.

At this time, "Acastavinae" is not revised, and it is placed in the family Acastidae Delo, 1935, along with Asteropyginae and Acastinae, following Pillet (1961), Holloway and Neil (1982), Cooper (1982), and Edgecombe (1991). The Acastidae can be diagnosed by the transverse S1 and S2 (Edgecombe, 1991), and L1 shorter than L2 (Destombes and Henry, 1987; Edgecombe, 1991).

For purposes of phylogenetic analysis, *Pelitlina smeenki*, new species, was used to assess the primitive conditions of characters used to deduce evolutionary relationship except for the condition of one character. This character, number 24, describes the condition of the prosopon. In *Pelitlina smeenki*, the prosopon is dominated by fine granules, and in *P. goltzi* Haas, 1968, the prosopon is dominated by fine tubercles. This character was coded as "?" for the outgroup. Aside from this character, *Pelitlina smeenki* and *P. goltzi* are nearly identical except for: the condition of S2, which extends further laterally in *P. goltzi*; the lateral margins of the cephalon, which deflect more sharply posteriorly in *P. goltzi*; and the posterior portions of the pygidial lappets, which are pointed in *P. smeenki* but bluntly rounded in *P. goltzi*.

On the basis of phylogenetic analysis, species of *Pelitlina* can be discriminated from other members of Asteropyginae on the basis of their possession of the primitive state for the following characters, which map on the tree in the derived state at the node separating the rest of the Asteropyginae from *Pelitlina*: 4, 8, 9, 20, 26, 29, 33, 36, 46, 57, 65, and 66. All of these characters show some homoplasy in the Asteropyginae, with reversions to the primitive condition for certain taxa (see tables 1 and 2 for specific cases), except for characters 26 and 46. Thus, *Pelitlina* can be distinguished from all other members of the Asteropyginae by its very short genal spines and by the condition of the pygidial axis. In *Pelitlina smeenki* it constricts posterior to the third axial ring, whereas in all other members of the Asteropyginae it constricts at various positions behind the fourth axial ring.

Where possible, type species of genera within the Asteropyginae were used in the phylogenetic analysis. When types could not be obtained, generic assignments reflect the possession of characters that diagnose the genus. Generic names follow Struve (1959), Haas (1968, 1970), Haas and Mensink (1969), Gandl (1972), and Morzadec (1983, 1992). Morphological terminology follows Eldredge and Branisa (1980) and Lieberman et al. (1991).

Several of the taxa considered herein, including species in the genera *Stummiana*, new genus, *Bellacartwrightia*, new genus, *Greenops*, *Asteropyge*, and *Kayserops*, have a peculiar set of small holes on the thoracic and pygidial pleural fields. Stumm (1953) termed these holes circular pits. He identified them as present in *Kayserops traversensis* (Stumm, 1953), and he suggested that they were caused by the weathering of coarse tubercles. These pits actually pass all the way through the exoskeleton and are present in specimens that have tubercles preserved as well as in specimens of taxa that lack coarse tubercles. Thus, Stumm's (1953) claim that weathering of tubercles explains these morphological structures is untenable. Herein, we treat these holes as structurally and perhaps functionally similar to the anatomical features Ramsköld (1991) termed fenestrae. As Ramsköld (1991) recognized, there are odontopleurids, dalmanitids, and asteropyginines that bear these fenestrae. Each of these represent lineages that must have acquired these structures independently, and thus they cannot be viewed as homologous. We speculate that these fenestrae may have performed some sensory function, possibly with setae passing through them.

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ASTEROPYGINAE IN EASTERN NORTH AMERICA

The Asteropyginae represent an important component of the trilobite fauna found in the Middle Devonian Hamilton Group strata of ENA. ENA includes the Appalachian, Illinois, and Michigan Basins (see fig. 1) as well as the Hudson Bay lowlands (not shown and not considered). The Hamilton Group strata span the latest Eifelian through Givetian and have been the subject of intense stratigraphic study (e.g., Cooper et al., 1942; Brett, 1986; Brett and Baird, 1986; Rickard, 1989). The Hamilton Group is paradigmatically developed in New York, but coeval and very similar deposits, in terms of their faunas, are known from the Illinois and Michigan Basins. Stratigraphic columns for the Middle Devonian and the Hamilton and Traverse Groups are shown in figure 2. Although this trilobite fauna is not incredibly rich in diversity, individual specimens are in places very common, and trilobite taxa have an important role in paleontological, stratigraphic, and macroevolutionary studies. After species assigned to the genus *Phacops* Emmrich, 1839, those taxa assigned to the genus *Greenops* Delo, 1935, form the most abundant and important members of this trilobite fauna. For this reason, the phylogenetic relationships of these asteropyginids is of intrinsic interest and of direct relevance to hypotheses about the origin of the Hamilton Group fauna in particular and the origin of evolutionary faunas in general.

Burton and Eldredge (1974) substantiated an ancestral-descendant relationship between *Phacops schlotheimi* (Bronn) sensu lato in the latest Eifelian and Givetian of northwestern Africa and subspecies of *Phacops rana* (Green, 1832) in the earliest part of the Hamilton Group. This notion was originally developed in Hall and Clarke (1888) and later in Eldredge (1972). In addition, both Eldredge (1972) and Burton and Eldredge (1974) recognized the close relationship between Asteropyginae in the Hamilton Group of ENA and those found in northwest Africa, Spain, and Germany (Armorica). The pattern recognized by Eldredge (1972) and Burton and Eldredge (1974) for *Phacops* conforms with broader macroevolutionary hypotheses about the origin of major faunas in the fossil record discussed in Eldredge (1985, 1989, 1995) Lieberman (1994), Brett et al. (1990), and Brett and Baird (1995). For instance, Brett et al. (1990) and Brett and Baird (1995) suggested that the Paleozoic fossil record of New York consists of approximately 13 fossil faunas spanning the Ordovician to the Devonian. Each of these fossil faunas persists for roughly 5–10 million years and consists of about 200 largely unique "species-level" taxa; very few species are shared between faunas. A fauna appears in the record rela-

Fig. 1. A paleogeographic reconstruction of Eastern North America modified from Beaumont et al. (1988) showing the extent of the major tectonic basins during the Middle Devonian mapped onto a modern geographic map of the United States. "1" represents the Appalachian Basin, "2" the Michigan Basin, and "3" the Illinois Basin.

tively rapidly and vanishes with often greater rapidity. This truncation typically appears to be associated with an extinction event of varying intensity on a global scale.

In addition to the biostratigraphic patterns predicted above by Eldredge (1985, 1989), Brett et al. (1990), and Brett and Baird (1995) Brett, Baird, and Eldredge made important predictions about the genealogical relationships among the component taxa of underlying and superposed faunas. They suggested that the appearance of new species in an overlying fauna does not seem to be the by-product of in situ evolution or evolutionary turnover of clades within a particular geographic region. Rather, they claimed that new taxa appearing in a younger fauna generally are most closely related to taxa in a different geographic region rather than to the taxa in the underlying fauna. This, of course, would indicate that taxa had invaded from a different geographic region. Thus, associated with transitions between faunas, these authors predicted that there should be a significant change in the biogeographic area relationships of component taxa in faunas.

The Asteropyginae appear to offer an excellent opportunity to test and validate these hypotheses of faunal evolution. Additional tests of these hypotheses, which are discussed later in this paper, can be found in Lieberman (1994). Only two species of asteropyginines, *Bellacartwrightia pleione* (Hall, 1861) and *B. jennyae*, new species, are known with certainty from the strata underlying the Hamilton Group and its equivalents in the Appalachian, Michigan, and Illinois Basins. In these underlying strata, referred to as the Onondaga Limestone in New York, the roughly coeval Amherstburg Formation in the Michigan Basin, and the Jeffersonville Limestone in the Illinois Basin, the bulk of the most closely related taxa all belong to the Dalmanitacea. These taxa, assigned to the genera *Odontocephalus* Conrad, 1840, *Anchiopsis* Delo, 1935, *Coronura* Hall and Clarke, 1888, and *Trypaulites* Delo, 1935, probably did not share a common ancestor with the Asteropyginae after the Ordovician. No other closer relatives of the Asteropyginae are known from ENA in the Middle Devonian. Thus, it is obvious that the Asteropyginae must have originated outside of ENA and subsequently invaded that region before or around the time of the deposition of the Onondaga Limestone and its equivalents, which are late Emsian through Eifelian in age. The actual timing of the invasions by the Asteropyginae into ENA, and their biogeographic sources, are discussed in greater detail in the sections of this paper on biogeography and faunal evolution.

There has been a significant number of phylogenetic studies performed on the Asteropyginae, chiefly by European authors, e.g., Haas (1970), Gandl (1972), Timm (1981), Morzadec (1983), and Smeenk (1983). Most of these analyses used the principles of evolutionary taxonomy, which unites taxa on the basis of information about overall morphological similarity as well as vertical and horizontal distributions in the fossil record. None of these analyses consid-

	NEW YORK SERIES AND STAGES		EUROPEAN STAGES	MAJOR LITHO-STRATIGRAPHIC UNITS IN ENA
MIDDLE DEVONIAN	ERIAN	TAGHANIC	GIVETIAN	TULLY LIMESTONE
		TIOUGHNIOGA		HAMILTON GROUP
		CAZENOVIA		
			? ? ?	
		SOUTHWOOD	EIFELIAN	ONONDAGA LIMESTONE
LOWER	ULSTERIAN	SAWKILL	? ? ? EMSIAN	BOIS BLANC LS./ SCHOHARIE GRIT

GROUP	FORMATION	MEMBER
HAMILTON	TULLY LIMESTONE	TULLY LIMESTONE / GILBOA
	MOSCOW	WINDOM SHALE
		KASHONG SHALE
		MENTETH LIMESTONE
		DEEP RUN SHALE
		TICHENOR LIMESTONE
	LUDLOWVILLE	JAYCOX SHALE
		SPAFFORD SHALE
		WANAKAH SHALE
		LEDYARD SHALE
		CENTERFIELD LIMESTONE / STONE MILL
	SKANEATELES	BUTTERNUT
		POMPEY
		DELPHI STATION
		STAFFORD LIMESTONE / MOTTVILE
	MARCELLUS	OATKA CREEK SHALE/ CHITTENANGO
		UNION SPRINGS / CHERRY VALLEY

Fig. 2. Stratigraphic columns modified from Cooper et al. (1942), Kirchgasser et al. (1985), Brett and Baird (1986), and Rickard (1989) for **(left)** Middle Devonian stages of Europe and Eastern North America, **(middle)** the Hamilton Group, and **(right)** the roughly coeval Traverse Group.

ered the North American asteropyginid species in great detail. In particular, these studies assumed that the ENA taxa represented a largely monophyletic, endemic radiation because they occurred in the same biogeographic region in sediments of the same age. The Asteropyginae of ENA were held to have diversified after the successful invasion of a single, or at most two, lineages, *Greenops* (*Greenops*) Delo, 1935, and *Greenops* (*Neometacanthus*) Richter and Richter, 1948. Although the assumption that taxa are closely related on the basis of proximity in space and time and gestalt similarity may not be a bad one, the goal of this analysis was to use a criterion independent of geographic and stratigraphic occurrence to deduce phylogenetic relationship. The criterion used was morphology.

PHYLOGENETIC ANALYSIS

A phylogenetic analysis was conducted on several members of the Asteropyginae using 39 taxa and 66 characters. The characters used in the analysis are given in table 1, and a data matrix showing the codings for all taxa considered is given in table 2. The po-

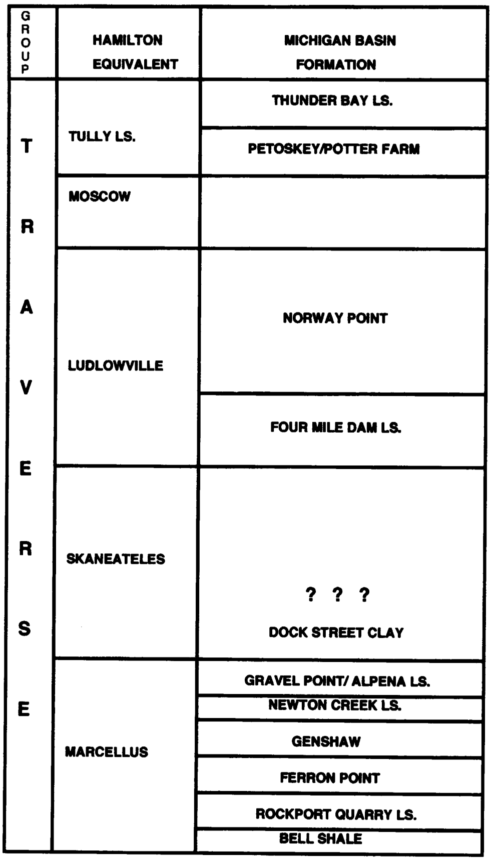

Fig. 2. (*Continued*)

sition of these characters is shown visually on a trilobite exoskeleton in figure 3. One of the multistate characters, number 9, was treated as additive (ordered), because state 2—anterior margin of frontal globe transverse—appeared to be a special case of a rounded frontal glabellar lobe modified by the ventral deflection of the anterior cephalic border, and thus it represented a clear transformation series. A single most parsimonious cladogram of 489 steps was produced by PAUP 3.0q (Swofford, 1990) using a heuristic search with stepwise addition and 200 random replications (see fig. 4). The retention index for this tree is 0.48, and when uninformative characters are excluded, the consistency index is 0.21. A bootstrap analysis was also conducted to assess the relative support for particular nodes in the cladogram. The analysis used 100 replications with a heuristic search with branch swapping using nearest neighbor interchanges that saved no more than five trees for each replication. The following nodes appeared in both the cladogram given in figure 4 and the cladogram produced by bootstrap analysis, and the number of times that these nodes were replicated in a 50% majority-rule consensus tree are: *Greenops barberi*/*Greenops chilmanae* = 0.54, *Bellacartwrightia whiteleyi*/*B. jennyae*/*B. phyllocaudata*/*B. calderonae* = 0.66, *B. whiteleyi*/*B. calderonae*/*B. phyllocaudata* = 0.45, *B. calderonae*/*B. phyllocaudata* = 0.45, *Pseudocryphaeus munieri*/*P. michelini* = 0.31, *Stummiana arkonensis*/*S. osismorum* = 0.20, *Breizhops lanceolatus*/*B. bigranulosus* = 0.21, *Kayserops inflatus*/*Kayserops traversensis* = 0.29, and *Philipsmithiana burtandmimiae*/*P. hyfinkeli* = 0.48.

This phylogeny suggested that there are two major clades within the Asteropyginae, and it can be compared with phylogenies presented by other authors such as Haas (1970), Gandl (1972), Arbizu (1979), Smeenk (1983) and Morzadec (1983) (see fig. 5).

Lesperérance and Desbiens (1995) have criticized the use of continuous variables in phylogenetic analysis, arguing that they represent arbitrarily divided discrete states. Of the characters utilized in this phylogenetic analysis, the following characters satisfy the criteria of continuous variables under Lesperérance and Desbien's (1995) definition: 6, 26, 46, 49, 57, and 60. Lesperérance (pers. comm., 1996) argued that when histograms were generated for the states of these characters, and the number of taxa possessing those states tabulated, they did in some cases approximate a normal distribution. He argued that this is strong evidence that these characters represent continuous variables and should not be included in phylogenetic analysis. The fact that a character and its states may be normally distributed across a clade is interesting, and points to possible clade-level properties of limits of variation in characters. However, these character states were invariant within species. Therefore, they potentially provide resolution of the phylogenetic relationships of these species. Similarly, the number of chambers in the heart varies across the vertebrates and has some particular distribution when the numbers of taxa are mapped by state. However, the fact that all

TABLE 1

Characters Used in Phylogenetic Parsimony Analysis, with Alternative Character States in Parentheses

"0" is the plesiomorphic state; "1"–"6" are apomorphic states. See table 2 for taxon/character matrix

1. Interior margin of genal spine: (0) evenly deflected all the way back; (1) more strongly deflected laterally posteriorly.
2. S3: (0) faintly sinusoidal, weak posterior deflection medially, weak lateral deflection anteriorly; (1) straight, anterolateral edge transverse or flexing posteriorly; (2) anterior portion convex anteriorly.
3. S2: (0) roughly transverse, weakly convex anteriorly; (1) weakly declined posteriorly at lateral edge.
4. S1 crescent shaped, medial portion developed as: (0) straight line directed anteriorly; (1) smooth curve convex posteriorly.
5. Posterior edge of visual surface: (0) anterior to transverse line tangent to anterior edge of L0; (1) posterior to transverse line tangent to anterior edge of L0.
6. Maximum number of lenses in a dorsoventral file on visual surface: (0) 8; (1) 13; (2) 4; (3) 10; (4) 7; (5) 6; (6) 9.
7. Immediately before cephalic lateral border furrow meets posterior border furrow: (0) posterior border furrow is straight; (1) posterior border furrow flexes anteriorly.
8. Facial suture lateral to eye, before flexing posteriorly flexes anteriorly to point: (0) between distal tips of S1 and S2; (1) opposite S2; (2) opposite S1.
9. Anterior margin of frontal glabellar lobe in dorsal view: (0) faintly pointed; (1) smoothly rounded; (2) transverse.
10. Distance between frontal lobe and facial suture at midline relative to laterally: (0) increases slightly; (1) constant.
11. Anterior cephalic border medially: (0) does not flex dorsally beyond plane through lateral margins of frontal lobe; (1) flexes strongly dorsally.
12. Anteriormost portion of palpebrum reaches: (0) point between medial tips of L3 and PMI; (1) opposite PMI.
13. Medially, anterior cephalic border in dorsal view: (0) pointed, lateral margins of border near midline forming a 90° angle; (1) rounded, margins forming approximately a 140° angle; (2) transverse.
14. Fixigena: (0) evenly sloping from axial furrow to palpebrum; (1) with distinct bulge medially such that portion parallels dorsal plane.
15. Ornamentation on medial part of L0: (0) absent; (1) tubercle; (2) spine.
16. Anterior cephalic border medially: (0) not deflected far anteriorly beyond margins of glabella; (1) deflected anteriorly, length (sag.) of at least L1 in front of facial suture.
17. Anterior cephalic border: (0) moderate or narrow lip; (1) developed as spatulate process, width (tr.) of process equivalent to width of L3 at its anterior edge; (2) developed as long spine, width (tr.) of spine less than width of medial portion of L1.
18. Anterior cephalic border: (0) not developed as spatulate process; (1) with lateral margins of process first diverging anteriorly then converge; (2) with lateral margins of process converging anteriorly.
19. Posteromedian impression (PMI) developed on frontal lobe of cephalic exoskeleton as: (0) linear incision; (1) rounded depression; (2) PMI absent.
20. Posterior margin of palpebrum relative to anterior margin of palpebrum deflected at an angle to transverse line that is: (0) significantly larger; (1) roughly equivalent.
21. L3: (0) flattened dorsally; (1) distinctly swollen.
22. Line from posterior to anterior edge of eye forms an angle to sagittal line that is: (0) approximately 30°; (1) approximately 45°; (2) approximately 5–10°.
23. Change in cephalic topography where librigena meets lateral border furrow: (0) insignificant; (1) significant.
24. Adult prosopon dominated by: (0) fine tubercles; (1) fine granules; (2) coarse tubercles.
25. Isolated patches of tubercles on L3: (0) absent; (1) present.
26. Genal spine developed as: (0) short triangular projection which does not extend posterior to second thoracic segment; (1) developed as long flange extending back to sixth or seventh thoracic segment; (2) developed as moderately long flange extending back to fourth thoracic segment; (3) developed as moderately long flange extending back to fifth thoracic segment; (4) developed as very long flange extending back to eighth thoracic segment.
27. Plane from medial to lateral edges of genal spine: (0) evenly inclined; (1) medially flattened ledge, laterally evenly inclined.
28. Medial edge of genal spine: (0) not significantly thickened relative to lateral edge; (1) significantly thickened relative to lateral edge.
29. Lateral margin of genal spine: (0) parallels sagittal line; (1) in medial part forms a line that departs from sagittal line by about 15–20°.
30. Lateral margin of genal spine at posterior end: (0) straight; (1) recurves posteriorly.
31. The raised ridge on the dorsal surface of the genal spine, when it flexes posteriorly at juncture of posterior border furrow and lateral border furrow: (0) is smoothly curved, convex distally; (1) forms sharp, dog legged kink.
32. Axial furrows anterior to S1 relative to furrows posterior to S1, relative to sagittal line: (0) diverge more strongly; (1) diverge at same angle.
33. Axial furrows at anterior half of L3 relative to posterior half, relative to sagittal line: (0) equally divergent; (1) less strongly divergent.

TABLE 1
(*Continued*)

34. Portion of librigena between lateral margin of eye and lateral border furrow in dorsal view: (0) visible; (1) not visible.
35. Eye rests on: (0) sloping librigenal field; (1) vertical wall of librigena.
36. Visual surfaces in dorsal view (outgroup is ?): (0) not present within sagittal lines drawn tangent to lateral margins of frontal lobe; (1) present within sagittal lines drawn tangent to lateral margins of frontal lobe.
37. Interior margin of genal spine relative to sagittal line: (0) deflected laterally 20°; (1) parallels lateral margin before deflecting laterally.
38. Broad ledge of anterior cephalic border (not considering medial projections) in dorsal view: (0) not visible anterior to anterolateral portions of frontal lobe; (1) visible anterior to anterolateral portions of frontal lobe.
39. Ornament on medial part of pygidial and thoracic axial rings: (0) absent; (1) tubercle; (2) spine.
40. Shape of terminal pygidial lappet: (0) tear-drop shaped; (1) subrectangular; (2) triangular; (3) very reduced or absent.
41. Terminal pygidial lappet, in dorsal view: (0) projects as far or further posteriorly than other pleural lappets; (1) does not project as far posteriorly as pleural lappets that project furthest posteriorly.
42. Lateral margins of pygidial lappets: (0) curved; (1) straight.
43. Medial margins of pygidial lappets: (0) curved; (1) straight.
44. Distal tips of pygidial lappets: (0) pointed; (1) at distal end of straight posterolateral margin that is inclined at 45° angle relative to sagittal line; (2) developed as blunt triangles.
45. Anterior margins of pygidial axial rings posterior to constriction of pygidial axis: (0) straight; (1) smoothly convex anteriorly.
46. Pygidial axis constricts, i.e., lateral margins of axis are roughly parallel, posterior to: (0) third axial ring; (1) fifth axial ring; (2) sixth axial ring; (3) fourth axial ring; (4) seventh axial ring.
47. Pygidial pleural field flanking posterior part of pygidial axis: (0) faintly excavated; (1) prominently excavated.
48. Anterior and posterior bands of pygidial pleural segments of: (0) equal elevation; (1) posterior band elevated above anterior band.
49. Pygidial lappet that projects furthest posteriorly in dorsal view: (0) fifth; (1) fourth; (2) third.
50. Tops of pygidial pleural segments: (0) flat; (1) rounded.
51. Pygidial pleural furrows: (0) deeper than interpleural furrows; (1) same depth as interpleural furrows.
52. Pygidial pleural furrows: (0) moderately incised, medially short (exsag.); (1) long (exsag.), almost as long as anterior pleural band; (2) developed as long (exsag.) excavated space, significantly longer than anterior pleural band.
53. In dorsal view at contact of pygidial margin and lappets: (0) lappets of constant breadth; (1) lappets expand laterally.
54. At pygidial margins: (0) surface of pygidium is not dorsally inflated; (1) surface of pygidium dorsally inflates at contact of lappets and margins; (2) surface of pygidium dorsally inflates to form fringing ring.
55. Laterally pygidial interpleural furrows: (0) arching at same angle as medially; (1) flex more strongly posteriorly; (2) flex anteriorly laterally.
56. In medial region of adjacent pygidial pleural segments: (0) posterior band of anterior segment equal in length (exsag.) to anterior band of posterior segment; (1) posterior band of anterior segment longer (exsag.) than anterior band of posterior segment.
57. Number of pygidial axial rings: (0) 9; (1) 13; (2) 11; (3) 15 or 16; (4) 18; (5) 14; (6) 12.
58. Margin of terminal pygidial lappet: (0) not rectangular; (1) subrectangular, convex posteriorly; (2) subrectangular, triangular posteriorly; (3) rectangular, transverse posteriorly.
59. Terminal pygidial lappet: (0) not triangular; (1) sharp triangle; (2) blunt triangle.
60. Terminal pygidial lappet: (0) broad anteriorly, 1.5 to 2 times width (tr.) of posterior part of pygidial axis; (1) narrow anteriorly, 1–1.1 times width (tr.) of posterior portion of pygidial axis; (2) very broad 3–4 times width (tr.) of posterior part of axis; (3) very narrow, 0.5 times width (tr.) of posterior part of axis.
61. Isolated patches of coarse or fine tubercles on L2: (0) absent; (1) present.
62. Anterior margins of first five pygidial axial rings going from axial furrows to midline: (0) evenly convex and do not arch strongly anteriorly; (1) straight, then strongly arched anteriorly medially.
63. Longest pygidial lappet (excluding terminal lappet): (0) short, length (sag.) from proximal to distal tip equal to length (sag.) of first two pygidial axial rings; (1) long, length (sag.) from proximal to distal tip equal to the length (sag.) of at least the first three pygidial axial rings.
64. Number of pairs of pygidial pleural lappets: (0) 5; (1) 4.
65. Number of transverse rows of circular fenestrae on anterior band of thoracic pleural segments (outgroup ?): (1) 1; (2) 2; (3) none.
66. Conformation of circular fenestrae on posterior band of thoracic pleural segments (outgroup ?): (1) a few fenestrae close to axis, do not extend further than half of the pleural field; (2) one transverse row of fenestrae; (3) two transverse rows of fenestrae; (4) fenestrae absent.

TABLE 2

Character States for Taxa Used in Phylogenetic Parsimony Analysis

Characters and alternative states are given in table 1. Missing data are represented by "?"

	1	1111111112	2222222223	3333333334	4444444445	5555555556	666666
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	123456
Pelitlina smeenki	0000000000	0000000000	000?000000	00000?0000	0000000000	0000000000	0000??
Treveropyge prorotundifrons	00010?0110	0000000011	0200000010	1110010000	1000010000	0000006000	0000??
Pseudocryphaeus michelini	0001000010	0001000011	0210020100	1111010001	0111010000	0100002201	0100??
P. munieri	0000031210	0000000011	0210020000	1110010001	1000010000	0100001200	0010??
Tolkienia granulispina	?00111??10	0001100001	02?00?????	?01??0?000	1000020111	0110012001	0010??
Braunops obsoletus	11000?0010	1000112001	0000020110	0110000112	0010011101	0100002011	001013
B. prostellans	01010?0000	0000010001	0000020010	1111000102	0000030100	0000012011	0010??
Hallandclarkeops cantarmoricus	0001031110	1001011101	0211111010	1110010102	1010121101	0202114011	1010?3
Neocalmonia quadricosta	0000130110	0000010000	0012111010	1110010102	1000010110	0000215010	1111??
Bellacartwrightia phyllocaudata	1001061011	0001210011	0210110100	1010010122	1010121001	0100113010	001034
B. pleione	??????????	??????????	???0??????	????????12	1110111101	0100103011	?01012
B. jennyae	1011131001	0000210001	0210140101	1100110122	1010021101	0100015011	001011
B. whiteleyi	1011101011	0001210011	0210110100	1011100122	1010021101	0100015011	101022
B. calderonae	1000001011	0001110011	0010140100	1011110112	1010041101	0100115011	101034
Coltraneia celtica	0011111221	1100000010	0210000010	0110010003	1000120001	0100003022	0010??
Bradocryphaeus afghanica	0111140111	0101000010	0212100010	1010100002	1000?11121	0100012013	1010??
Heliopyge turolensis	01110?0101	0000100011	0210111110	1010010100	1000111121	0001012001	1010??
Paracryphaeus hercyniae	02111?0000	000?00002?	0212120010	1011010101	0002130001	0000110303	1000??
Pilletina aequisulcata	0001041121	?0001?0001	0000020010	0010010001	0002010001	1000003202	0010??
Breizhops lanceolatus	0111051201	0000110000	000001000?	0011011101	0111010000	0000012201	000012
B. chaconae	0111040111	0101000001	0200011000	0010011001	0012010001	0000112201	0000??
B. bigranulosus	0111020210	0000100010	0110110000	1101101001	0011010101	0001012201	1000??
Philipsmithiana burtandmimiae	0101041100	0000010011	1000111001	0010111102	1010010001	0100003100	101034
P. hyfinkeli	0201061011	0001000000	0000111001	0010101001	1111010001	0100103100	100034
Modellops struvei	0101001111	0111000001	0000011000	0010001001	1011111001	0200005100	0100??
Neometacanthus sp. aff. *stellifer*	0101140111	000?100011	020001010?	0011011011	1000110001	0000102103	011012
Asteropyge punctata	0101141111	0010010010	0200110100	0010011103	1110110011	0001113020	011012
Rhenops babini	?001100211	0000000001	0210011000	?010011002	1002111000	0000103020	0110??
Rhenops, new species	0001141010	0100?00001	0200011101	1010111112	1111110?0	00001050?0	?010??
Greenops chilmanae	011115101?	0010100011	0000131000	0110110002	1010110000	0000102011	111011
G. grabaui	0101150011	0010000011	0000031000	0010101001	1012110000	0000102100	010011
G. widderensis	0101150011	0010000011	0200131000	0010101001	1010110000	0000102100	101011
G. barberi	0110050010	0010000011	0200030000	0010111002	1010110000	0000002011	111011
Deloops haasi	0211141211	0001100021	0000021001	0010000001	0012120000	0000105200	0100?3
Stummiana osismorum	0111141010	01111000?1	0000020001	0111001001	1012110000	0000002101	0100??
S. arkonensis	0111041110	0111100010	00001?????	?11010?011	1002110101	0000112101	111011
Armorigreenops leoi	01101?0210	0000?000?1	0000010101	0110001012	0012110000	0000102021	0100??
Kennacryphaeus harrisae	1111101011	0110200011	00000?1100	0100111012	1010010001	0000105021	0100??
Kayserops inflatus	0201100210	0000100021	1001110100	?011111012	1100111101	0001101011	001023
K. traversensis	0211141010	0?00100021	00021?010?	0111101012	10101101?1	000001?021	101012

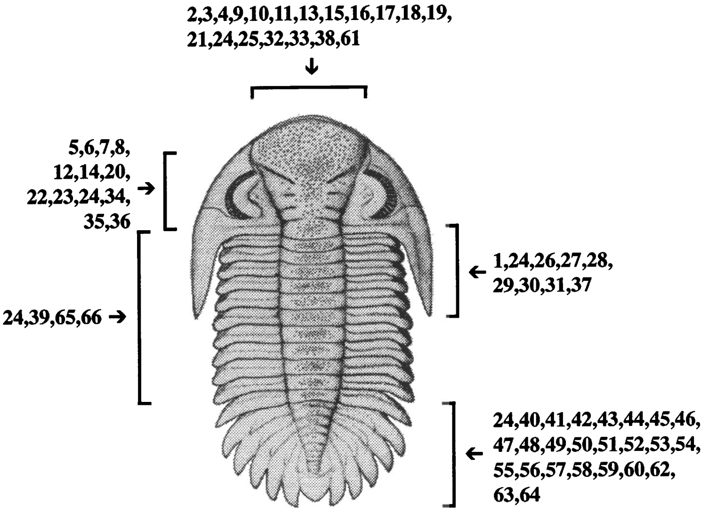

Fig. 3. An illustration of a hypothetical species of asteropyginine trilobite modified from Ludvigsen (1979) showing the approximate position of characters used in the phylogenetic analysis.

humans and chimps possess a four-chambered heart whereas all sharks do not is a valid synapomorphy providing evidence that chimps and humans share a sister group relationship to the exclusion of sharks. Thus, although Lesperérance and Desbiens (1995) made an important point—that variation within characters should be quantified—as long as character states are invariant within terminal taxa they still can and should be used to provide evidence for common descent. Vrba et al. (1994) also demonstrated how truly continuous variables can be used to determine phylogenetic relationships.

SYSTEMATIC PALEONTOLOGY

SUPERFAMILY ACASTACEA Delo, 1935

FAMILY ACASTIDAE Delo, 1935

SUBFAMILY ASTEROPYGINAE Delo, 1935

PELITLINA HAAS, 1968

Type Species: *Pelitlina goltzi.*

Assigned Taxa: *Pelitlina smeenki*, new species.

Diagnosis: Cephalic border furrow bisects genal spine; S3 faintly sinusoidal; posterior edge of visual surface anterior of transverse line tangent to L0; distance between frontal lobe and facial suture at midline relative to lateral edges increases slightly; lateral margin of genal spine at posterior end straight; five pygidial pleural lappets; pygidial margin constricts posterior of third axial ring; axial furrows at anterior half of L3 relative to posterior half equally divergent; nine pygidial axial rings; posterior pygidial terminus teardrop shaped.

Discussion: The two species in the genus are united by at most the unique possession of only two characters: the nine pygidial axial rings and the teardrop-shaped pygidial terminus. The other characters are diagnostic in combination. In addition, the first of these two characters is developed in several closely related species such as *Acastella tiro* Richter and Richter, 1954, and it is also found in the more distantly related *Paracryphaeus hercyniae* Gandl, 1972. Thus, this genus is difficult to diagnose, and is more noteworthy for the characters it lacks rather than those it uniquely possesses. The genus in many ways fits the description of a metataxon propounded by Gauthier et al. (1988), and it is certainly due to the lack of autapomorphies that

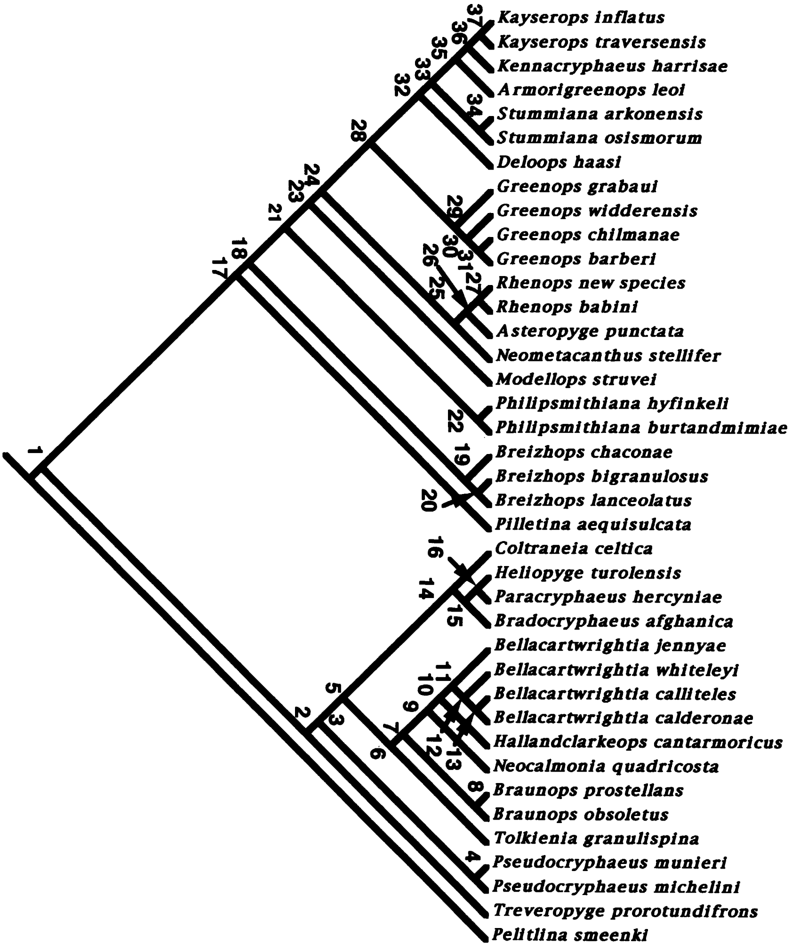

Fig. 4. The single most parsimonious tree of length 474 steps produced using a heuristic search with stepwise addition and 100 random replications by Paup 3.0q (Swofford, 1990). The retention index is 0.44, and when uninformative characters are excluded, the consistency index is 0.22. Character states at nodes optimized using ACCTRAN are as follows, with characters numbered as in table 1 and character states in parentheses: **Node 1**: 4(1), 8(1), 9(1), 11(0), 17(0), 18(0), 20(1), 21(0), 26(2), 29(1), 33(1), 36(1), 46(1), 51(0), 53(0), 54(0), 57(2), 64(0), 65(1), 66(2); **Node 2**: 19(1), 22(2), 31(1), 41(1), 66(3); **Node 3**: 23(1), 52(1), 60(1), 63(1); **Node 4**: 8(0), 29(0), 40(1), 58(2); **Node 5**: 5(1), 6(1), 48(1), 50(1), 56(1); **Node 6**: 19(0), 36(0); **Node 7**: 6(3), 16(1), 22(0), 38(1), 40(2), 59(2); **Node 8**: 2(1), 5(0), 8(0), 23(0), 41(0); **Node 9**: 25(1), 26(1), 27(1), 36(1), 57(5), 61(1); **Node 10**: 7(1), 14(1), 22(2), 43(1), 46(2); **Node 11**: 1(1), 3(1), 8(0), 10(1), 15(2), 27(0), 28(1), 29(0), 35(1), 39(2), 66(3); **Node 12**: 19(1), 34(1), 65(2); **Node 13**: 3(0), 5(0), 6(0), 55(1), 65(3), 66(4); **Node 14**: 3(1), 10(1), 12(1), 20(0), 26(0), 45(1), 60(2); **Node 15**: 2(1), 6(4), 24(2), 25(1), 49(2), 60(3), 61(1); **Node 16**: 9(0), 12(0), 20(1), 26(1), 38(1), 52(0); **Node 17**: 6(4), 7(1), 10(1), 40(1), 44(1), 50(1), 58(2); **Node 18**: 2(1), 26(1), 27(1), 29(0), 37(1), 43(1); **Node 19**: 3(1), 56(1), 60(1); **Node 20**: 6(2), 8(2), 15(1), 19(0), 27(0), 34(1); **Node 21**: 36(0), 41(1), 58(1); **Node 22**: 25(1), 30(1), 35(1), 52(1), 57(3), 61(1), 65(3), 66(4); **Node 23**: 45(1), 62(1); **Node 24**: 5(1), 19(1), 44(0), 55(1); **Node 25**: 22(2), 27(0), 28(1), 36(1), 63(1); **Node 26**: 38(1), 40(2), 42(1), 57(3), 58(0), 59(2); **Node 27**: 2(0), 8(0), 19(0), 27(1), 31(1), 44(1), 47(1), 50(0); **Node 28**: 8(0), 26(2), 44(2), 50(0), 66(1); **Node 29**: 6(5), 7(0), 13(1), 26(3), 35(1); **Node 30**: 22(2), 25(1), 44(0), 61(1), 63(1); **Node 31**: 3(1), 10(0), 36(1), 40(2), 58(0), 59(1), 60(1); **Node 32**: 3(1), 14(1), 15(1), 30(1), 44(2), 66(3); **Node 33**: 10(0), 27(0), 32(1), 39(1), 60(1); **Node 34**: 12(1), 13(1), 66(1); **Node 35**: 6(0), 14(0), 26(1), 28(1), 40(2), 58(0), 59(2); **Node 36**: 30(0), 35(1), 36(1), 44(2), 50(1), 57(1); **Node 37**: 2(2), 19(2), 24(1), 25(1), 34(1), 48(1), 62(0), 63(1).

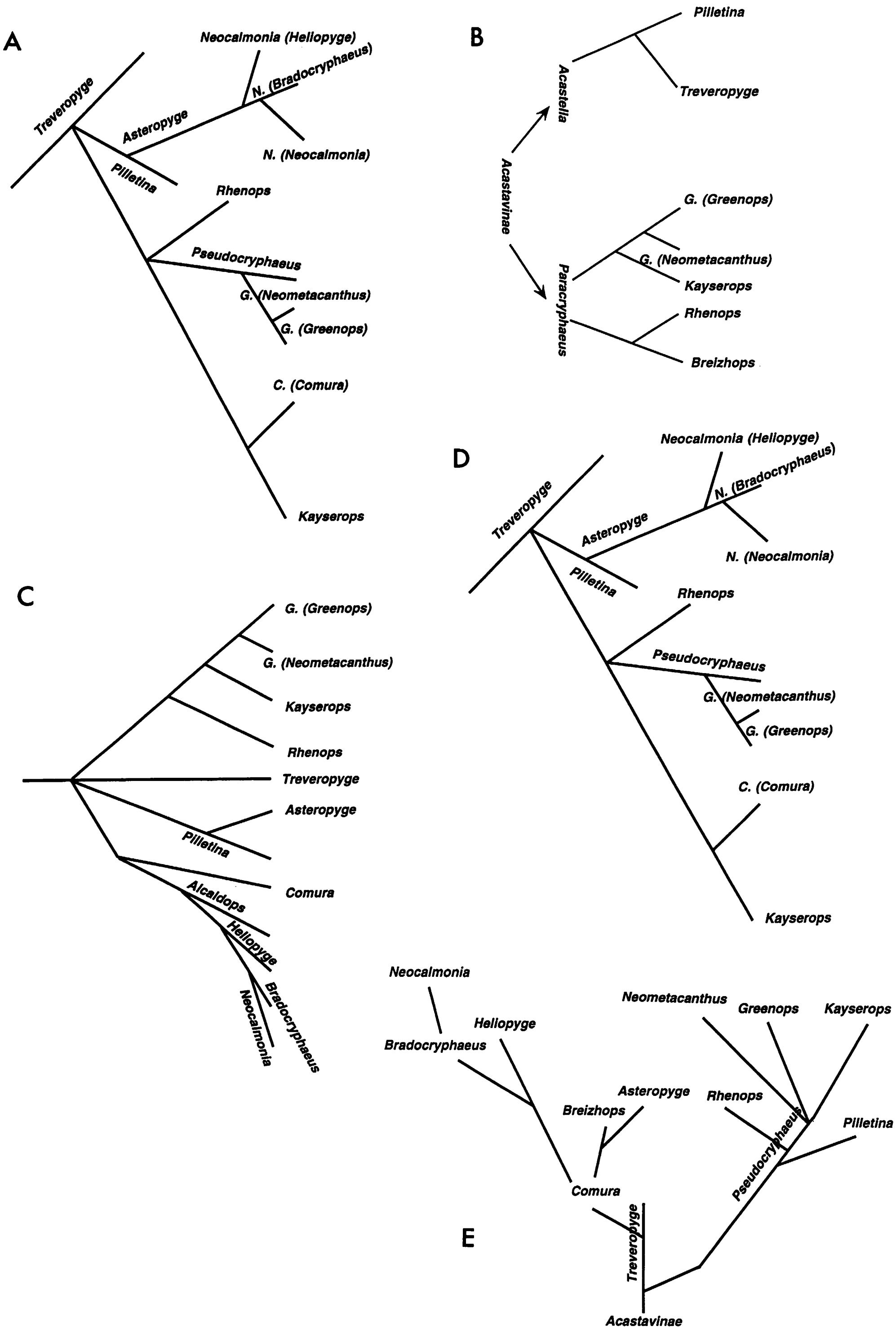

Fig. 5. Five scenarios for asteropyginid evolution hypothesized by (**A**) Haas (1970), (**B**) Gandl (1972), (**C**) Arbizu (1979), (**D**) Smeenk (1983), and (**E**) Morzadec (1983).

Pelitlina, *Acastava*, and other acastavinids have been traditionally treated as ancestral taxa by evolutionary taxonomists. The possibility exists that this genus is paraphyletic, but the two unique characters (or one) and the other characters given in combination do suggest a means of uniquely diagnosing it as a monophyletic taxon. More detailed work on other acastavinids is needed to rigorously define genera, but this work will not be pursued herein because *Pelitlina* is simply employed as an outgroup. Ingroup Asteropyginae can be separated from this and other outgroups by the following characters (state of each character given in parentheses): 4(1), 8(1), 9(1), 20(1), 26(2), 29(1), 33(1), 36(1), 46(1), 57(2), 65(1), and 66(2); however, all of these characters do show reversal within the Asteropyginae.

The two species assigned to this genus are very similar: differing principally in the condition of the prosopon, which is dominated by fine granules in *Pelitlina smeenki* but is dominated by fine tubercles in *P. goltzi* Haas, 1968; the condition of S2, which extends further laterally in *P. goltzi*; the lateral margins of the cephalon, which deflect more sharply posteriorly in *P. goltzi*; and the posterior margins of the pygidial lappets, which are pointed in *P. smeenki* and weakly rounded in *P. goltzi*. *Pelitlina goltzi* is known from the Upper Emsian of northwestern Turkey, and *P. smeenki* is known from the Lower Emsian of northern Spain.

Pelitlina smeenki, new species

Acastava n. sp. Smeenk, 1983: pl. 28, figs. 1-6.

TYPES: Holotype Rijksmuseum van Geologie en Mineralogie, Leiden, the Netherlands, RGM 339515, Smeenk (1983: pl. 28, fig. 1).

DIAGNOSIS: Same as for genus and prosopon of fine granules; posterior margins of pygidial lappets pointed.

ETYMOLOGY: Named for Z. Smeenk, who figured this species in his excellent monograph on Devonian trilobites of northern Spain.

DESCRIPTION: Cephalic length (sag.) 50% of width. Axial furrow nearly straight anterior to S1, diverging forward at about 25°, narrow, shallow; posterior to S1 diverging at 10°. Cranidial anterior border short exsagittally and medially, medially weakly upturned triangular process. Preglabellar furrow shallow and narrow. Cranidial anterior border lengthens slightly medially, developed as narrow lip. Facial suture anterior of eyes flexes laterally then medially, with smoothly convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly then posteriorly laterally. Glabellar length equal to width across frontal lobe; frontal lobe ellipsoid, about 60% of length of glabella; L1-L3 flat (sag.); frontal lobe at level of posterior glabellar region; anterior part of frontal lobe moderately declined forward, faintly pointed in dorsal view. Posteromedian cephalic impression (PMI) shallow linear incision. S3 shallow, weakly sinusoidal, equally incised medially and distally, branches diverging at about 140°. Sagittal region of L3-L2 nearly flat (tr.), lateral lobes weakly declined abaxially. L3 wedge shaped, lengthening distally, outer edge nearly straight along axial furrow. S2 roughly transverse, weakly convex anteriorly, moderately incised, shallow adjacent to axial furrow. S1 deep, crescent shaped, medial portion developed as straight line directed anteriorly, contacting axial furrow laterally. L1 short, flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 of nearly uniform length, convex anteriorly medially, deep. L0 65% of width of frontal lobe, moderately arched (tr.), longest sagittally. Large Eye Index 0.55. Anterior edge of eye contacts axial furrow opposite anterodistal corner of L3; posterior edge of eye opposite S1, anterior to transverse line tangent to L0; eye raised slightly above frontal lobe; maximum number of eight lenses in a dorsoventral file on visual surface. Fixigena evenly sloping from axial furrow to internal margin of eye. Postocular fixigenal field 30% of length of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse, weakly flexing posteriorly distally, anterior margin nearly straight, of relatively equal length (exsag.), longest posterior to palpebrum, shallowing distally. Genal spine developed as short triangular projection, cephalic lateral border furrow bisects spine; lateral and medial edges of genal spine evenly inclined; lateral margin of genal spine parallels sagittal line; lateral margin of genal spine at posterior end straight; interior margin of genal spine deflected laterally. Lateral border furrow narrow, shallow; lateral border weakly widens posteriorly. Anterior margin of cephalic doublure bluntly pointed. Prosopon of fine granules.

Thorax not known.

Pygidium broadly triangular in outline excluding marginal lappets, length about 75% of width without lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, diverging at 20° angle anterior to third pygidial axial ring; roughly parallel posterior to third pygidial axial ring. Axis 30% of pygidial width anteriorly, with nine rings; rings of nearly equal length distally and sagittally, longest sagittally; anterior and posterior edge of axial rings posterior to third axial ring from midline to distal edge first straight, then flexing posteriorly, then anteriorly, then slightly posteriorly. Ring furrows moderately incised. Lateral margins of pygidial lappets curved; medial margins curving; distal tips pointed. Axial terminus teardrop shaped, projecting further posteriorly than other lappets; postaxial region 20% of pygidial length (sag.). Pygidial pleural field flanking posterior portion of pygidial axis faintly excavated; anterior and posterior pleural segments of equal elevation; tops of segments flat; pleural furrows deeper than interpleural furrows, moderately incised, short (exsag.). Laterally pygidial interpleural furrows arch at same angle as medially. In medial region of adjacent pleural segments, posterior band of anterior segment equal in length (sag.) to anterior band of posterior segment.

DISCUSSION: This species was used as the outgroup in the phylogenetic analysis and is known from the Lower Emsian of northern Spain (Smeenk, 1983). Smeenk (1983) merely figured the specimen and did not discuss or describe it. Thus, a description is given here.

TREVEROPYGE STRUVE, 1958b

TYPE SPECIES: *Asteropyge* (*Asteropyge*) *prorotundifrons* Richter and Richter, 1943.

ASSIGNED TAXA: None (see below).

DIAGNOSIS: See Struve (1959) and *T. prorotundifrons* below.

DISCUSSION: Several species appear to share the combination of characters that the type of the genus, *Treveropyge prorotundifrons*, possesses, and they may belong to this genus. These species include *Asteropyge wallacei* Termier and Termier, 1950, *Treveropyge wallacei procerospinosa* Gandl, 1972, *Echinopyge cathamma* Haas, 1968, *Cryphaeus boopis* Richter, 1909, *Cryphaeus drevermanni* Richter, 1909, and possibly ?*Treveropyge henryi* Arbizu, 1979, and ?*Phacops rotundifrons* Emmrich, 1839. However, until material of these taxa is examined in detail, such conclusions must await further testing.

Both Haas (1970) and Morzadec (1983) concluded that *Treveropyge* was one of the basal members of the asteropyginid clade (see fig. 5a, e). This is not entirely supported by the analysis conducted herein, as *Treveropyge* is itself sister to one of the two main clades of asteropyginines. Haas (1970) viewed *Treveropyge* as part of a paraphylum sister to the rest of the asteropyginines, which in turn consisted of branches off of a basal split between the genus *Pilletina* Haas, 1970 and its descendants, which included *Neocalmonia* Pillet, 1969, *Heliopyge* Haas and Mensink, 1969, *Bradocryphaeus* Haas and Mensink, 1969, and *Asteropyge* Hawle and Corda, 1847, and the genus *Pseudocryphaeus* Pillet, 1954, and its descendants, which included *Rhenops* Richter and Richter, 1943 *Neometacanthus* Richter and Richter, 1948, *Greenops* Delo, 1935, *Comura* Richter and Richter, 1926, and *Kayserops* Delo, 1935. Morzadec (1983) viewed asteropyginid evolution as involving two branches that split early in the Devonian. He felt these two basal branches consisted of a paraphyletic *Treveropyge*, which gave rise to several other taxa including *Bradocryphaeus*, *Neocalmonia*, *Heliopyge*, and *Asteropyge*, and a paraphyletic *Pseudocryphaeus*, which gave rise to *Rhenops*, *Neometacanthus*, *Kayserops*, and *Greenops*. These conclusions about a dichotomous basal branch in the Asteropyginae are supported, but instead *Treveropyge* and *Pseudocryphaeus* are part of only one of the major branches. However, the branch containing *Treveropyge* also contains *Bradocryphaeus* and *Neocalmonia*. Smeenk (1983) concluded (see fig. 5d) that *Treveropyge* was part of a basal polytomy in the Asteropyginae along with *Pilletina* and a lineage that evolved into *Pseudocryphaeus* and *Paracryphaeus*. Although greater resolution than this classic "star phylogeny" sensu Edgecombe (1992) was possible in this analysis, the relatively close relationship between *Treveropyge* and *Pseudocryphaeus* was replicated here. Gandl (1972) (see fig. 5b) suggested that portions of *Treveropyge* were sister to certain species of *Metacanthina* Pillet, 1954. Here one of the species he assigned to *Metacanthina*, *M. munieri* (Oehlert), is treated as closely related to *Treveropyge* and is assigned to *Pseudocryphaeus*. Partially matching Gandl's (1972) conclusion, *Treveropyge* appears to be sister to *Pseudocryphaeus*, and it is discussed in greater detail below.

Treveropyge prorotundifrons
(Richter and Richter, 1943)

Asteropyge (Asteropyge) prorotundifrons Richter and Richter, 1943: 175, pl. 7, figs. 1–3.
Treveropyge prorotundifrons (Richter and Richter). Struve, 1959: O483, figs. 382, 1a, b.
Treveropyge prorotundifrons iberica Gandl, 1972: 121, pl. 10, figs. 6–10.
Treveropyge prorotundifrons prorotundifrons Richter and Richter. Gandl, 1972: 120, text figs. 16–18.
Treveropyge iberica Gandl. Smeenk, 1983: 400, pl. 6, figs. 7–9, pl. 7, figs. 1, 2.
?*Treveropyge prorotundifrons iberica* Gandl, 1972: 121, pl. 9, figs. 8–10.

TYPES: Holotype defined in Richter and Richter (1943: pl. 7, fig. 3).

DIAGNOSIS: Medial portion of S1 smooth curve directed anteriorly; lateral to eye facial suture, before flexing posteriorly, flexes anteriorly to point opposite S2; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; cephalic posterior border furrow longest (exsag.) posterior to palpebrum; demarcation between librigena lateral to eye and lateral border furrow weak; cephalic axial furrows diverge anteriorly at constant angle; genal spine developed as short triangular spine that does not extend posterior to second thoracic segment; 12 pygidial axial rings; anterior and posterior pleural segments of equal elevation when viewed laterally; terminal pygidial lappet teardrop shaped; posteriormost pair of pygidial pleural lappets project further posteriorly than terminal pygidial lappet; lateral and medial margins of pygidial lappets curved.

DISCUSSION: This species, the type of the genus, is known from the lower Emsian of northern Spain and the Eifelian of Germany, and was used to represent the phylogenetic position of *Treveropyge* in the analysis. On the basis of the absence of the derived state for several characters, it has a basal position in one of the major clades of the Asteropyginae.

The subspecies of *T. prorotundifrons* recognized by Gandl (1972), *prorotundifrons* and *iberica*, do not appear to be distinguishable on the basis of any morphological features, and are treated as synonymous here. Any differences that may exist between specimens hailing from the two different distributional areas—the former, *T. prorotundifrons prorotundifrons*, in the Eifelian of Germany, and the latter in the Lower Emsian of northeastern Spain—are so slight that, although possibly suggesting allopatric or temporal differentiation, they would not affect the coding of character states used in phylogenetic analysis.

It could not be ascertained whether the specimens shown by Gandl (1972: pl. 9, figs. 8–10) and called meraspids of *Treveropyge prorotundifrons iberica* are correctly identified. In these specimens, the pygidial terminus extends posterior to the fifth pair of pygidial lappets, whereas in *T. prorotundifrons* the lappets extend significantly further than the pygidial terminus. In addition, the pygidial terminus is teardrop shaped in typical *T. prorotundifrons*, whereas it is triangular in the specimens in Gandl's (1972) plate 9. Moreover, these specimens have significantly fewer pygidial axial rings as well as much blunter pygidial lappets. Finally, the lateral margins of the pygidial axial rings constrict posterior to the third pygidial axial ring such that the axial furrows are parallel posterior to this point in the putative meraspids, whereas in holaspid *T. prorotundifrons* the pygidial axis sharply constricts posterior to the fifth axial ring.

If these pygidia are actually meraspids (they appear to all be M9) of *T. prorotundifrons*, then we can compare morphoclines in the transformation of character states during ontogenetic development to morphoclines suggested by outgroup analysis. According to outgroup analysis, primitively the pygidial axis is held to constrict, i.e., the lateral margins of the axis are roughly parallel, posterior to the third axial ring (character 46). One of the derived states of this character is to have the constriction posterior to the fifth axial ring. In this case, ontogenetic and outgroup polarizations match. According to outgroup analysis, primitively the pygidial terminus projects further posteriorly than the other pygidial lappets (character 41). This transformation series is also supported by the possible ontogenetic transformation series provided by *T. prorotundifrons*. Of course, the number of pygidial axial rings (character 57) is lower during earlier stages of ontogeny, and it is also lowest in the outgroup taxon employed. However, the transformation of at least one character does not agree with the polarities suggested by outgroup analysis. Primitively, the shape of the terminal pygidial lappet (character 40) is held to be teardrop shaped. In *T. prorotundifrons*, it transforms from triangular to teardrop shaped in the transition from putative meraspid to holaspid.

Treveropyge prorotundifrons shares many similarities with *T. wallacei procerospinosa* Gandl, 1972, including the teardrop-shaped terminal pygidial spine, the number of pygidial axial rings, and the condition of the pygidial lappets. They differ chiefly in the length of the terminal pygidial spine, which projects further posteriorly than the pygidial lappets in *T. wallacei procerospinosa* but not in *T. prorotundifrons*.

PSEUDOCRYPHAEUS PILLET, 1954

TYPE SPECIES: *Phacops michelini* Rouault, 1851.

ASSIGNED TAXA: *Cryphaeus munieri* Oehlert, 1877.

DIAGNOSIS: Cephalic posterior border furrow longest (sag.) posterior to medial visual surface of eyes; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; PMI developed as rounded depression; posterior and anterior margins of fixigena deflected such that they intersect transverse line at roughly equivalent angle; line from posterior to anterior edge of eye intersects sagittal line forming 5° angle; demarcation between librigena lateral to eye and lateral border furrow prominent; genal spine developed as moderately long flange extending back to fourth thoracic segment; raised ridge on dorsal surface of genal spine flexes posteriorly at juncture of posterior border furrow and cephalic border furrow and forms sharp, doglegged kink; cephalic axial furrows diverge at constant angle; axial furrows opposite anterior half of L3 relative to posterior half less strongly divergent; terminal pygidial lappet triangular; pygidial axis constricts posterior to fifth ring; pygidial pleural furrows almost as long (exsag.) as anterior pleural band; lateral margins of terminal pygidial lappet anteriorly parallel, posteriorly convergent and triangular.

DISCUSSION: Three species traditionally assigned to *Pseudocryphaeus* were subjected to phylogenetic analysis. These were the type of the genus, *P. munieri* (Oehlert, 1877), and *Braunops prostellans* (Richter and Richter, 1939). *Braunops prostellans* is separated by several nodes on the cladogram from the type of the genus, and differs from *Pseudocryphaeus michelini* in the condition of the following characters: 2, 9, 14, 16, 19, 22, 23, 28, 34, 36, 38, 40, 42–44, 46, 48, 52, 56, 58, 59, 62, and 63. Therefore, this species must be assigned to a different genus, and it is discussed in greater detail below. *Pseudocryphaeus munieri* differs from *P. michelini* in the condition of several characters, including: 4, 6–8, 14, 28, 34, 42–44, 57, 60, 62, and 63.

According to the analysis conducted herein, the genus appears to have a basal phylogenetic position in one of the major clades within the Asteropyginae. *Treveropyge* is sister to this clade, and this accords well with its position in the evolutionary tree of Haas (1970) (see fig. 5a). However, Haas (1970) thought that all genera in the Asteropyginae other than *Treveropyge* were derived from either *Pseudocryphaeus* or *Pilletina*. These genera he placed as a near basal bifurcation in the evolution of the asteropyginines. In his evolutionary tree, *Pseudocryphaeus* is wildly paraphyletic, giving rise directly to at least four genera: *Rhenops*, *Greenops*, *Neometacanthus*, and *Comura*. A close relationship between *Pseudocryphaeus* and *Greenops*, *Neometacanthus*, and *Rhenops* is not supported here. As redefined here, *Pseudocryphaeus* is para- or polyphyletic, but inclusion of some taxa within the genus that had formerly been assigned to it such as *Braunops prostellans* would make *Pseudocryphaeus* paraphyletic. In addition, Haas' (1970) hypothesis that *Pseudocryphaeus* and several other asteropyginid genera should be sister to a lineage containing among other taxa *Neocalmonia*, *Heliopyge*, *Bradocryphaeus*, and *Asteropyge* is not supported. As discussed above, Morzadec (1983) (see fig. 5e) thought that *Pseudocryphaeus* was the most primitive taxon in one of the basal branches of the Asteropyginae, and he also viewed it as paraphyletic and suggested that it gave rise to same the genera Haas (1970) suggested as well as to the genus *Pilletina*. The basal position of *Pseudocryphaeus* in one of the major branches within the Asteropyginae is supported, but the overall topology of asteropyginid evolution Morzadec (1983) advocated is not. *Pilletina* is discussed further below. Arbizu (1979) suggested (see fig. 5c) that *Pseudocryphaeus* was paraphyletic and gave rise to *Kayserops*, *Rhenops*, and *Greenops*, while also being part of a basal polytomy along with *Treveropyge*, *Pilletina*, and *Comura*. Again, the relatively basal position of *Pseudocryphaeus* is supported herein; however, it does not appear to belong to a basal polytomy, only a basal bifurcation. Gandl (1972) suggested (see fig. 5b) that *Pseudocryphaeus* and *Paracryphaeus* were sister taxa, with both of these taxa related to a clade derived from a different segment of the "Acastavinae" than *Treveropyge* was. As mentioned above, Gandl's (1972) diphyletic origin of the Asteropyginae is not supported by the analysis conducted herein, as one genus within the "Acastavinae," *Pelitlina*, shares the most synapomorphous character states with the asteropyginid clade. Until another acastavine is found to share a greater or equal number of synapomorphies with the asteropyginines, and also to contain characters uniting it with *Pseudocryphaeus* and other asteropyginines to the exclusion of *Treveropyge*, Gandl's (1972) entire perspective on asteropyginine phylogeny must be called into question.

Without access to specimens and additional, detailed phylogenetic analysis, the generic status of species traditionally assigned to *Pseudocryphaeus*, e.g., *P. jonesi* (Oehlert, 1877), *P. vernensis* Morzadec, 1971, *P. oehlerti* Morzadec, 1971, *P. baconnierensis* Morzadec, 1971, and *P. spatulaeformis* Morzadec, 1971, cannot be evaluated at this time.

Pseudocryphaeus michelini
(Rouault, 1851)

Pseudocryphaeus michelini (Rouault). Struve, 1959: O482, figs. 381, 3a, b; Morzadec, 1971: 169, pl. 15, figs. 1–20, text fig. 7, see for extended synonymy; Gandl, 1972: 91.

Pseudocryphaeus cf. *michelini* (Rouault). Smeenk, 1983: pl. 2, figs. 7, 8.

TYPES: Lectotype defined in Morzadec (1971: pl. 15, fig. 20).

DIAGNOSIS: S2 weakly declined posteriorly at lateral edge; medial portion of S1 developed as smooth curve convex posteriorly; maximum of eight lenses in dorsoventral file on visual surface; medial edge of genal spine significantly thickened relative to lateral edge; librigenae between lateral margins of eyes and lateral border furrow not visible in dorsal view; terminal pygidial lappet subrectangular, triangular at distal end, projecting further posteriorly than pygidial pleural lappets; lateral and medial margins of pygidial lappets straight; nine pygidial axial rings.

DISCUSSION: This species is known from the *Athyris undata* limestones, Siegenian (?Pragian), of the Massif Armorican. The illustration in the treatise (Struve, 1959) is inaccurate in its depiction of the terminal pygidial lappet, which should be rectangular anteriorly, triangular posteriorly.

Pseudocryphaeus munieri
(Oehlert, 1877)

Cryphaeus munieri Oehlert, 1877: 582, pl. 9, fig. 3, not fig. 3a.

Pseudocryphaeus munieri (Oehlert). Haas, 1970: 119, pl. 4, figs. 8, 9; Morzadec, 1971: 171, pl. 16, figs. 1–13, text fig. 13 (see for extended synonymy).

TYPES: Lectotype defined in Morzadec (1971: pl. 16, fig. 5).

DIAGNOSIS: Maximum of 10 lenses per dorsoventral file on visual surface; immediately before cephalic lateral border furrow meets posterior border furrow, posterior border furrow flexes anteriorly; lateral to eye, facial suture before flexing posteriorly flexes anteriorly to point opposite S1; demarcation between librigena lateral to eye and lateral border furrow prominent; medial edge of genal spine not significantly thickened relative to lateral edge; medial portion of S1 developed as straight line directed anteriorly; lateral and medial margins of pygidial lappets curved; terminal pygidial lappet triangular posteriorly; last pair of pygidial lappets projects further posteriorly than pygidial terminal lappet.

DISCUSSION: This species is known from the *Athyris undata* limestones, Siegenian (?Pragian), of the Armorican Massif. Gandl (1972) figured a pygidium (pl. 7, fig. 1) that he referred to as *Metacanthina munieri* and viewed as synonymous with *Pseudocryphaeus munieri*. However, Gandl's specimen differs from *P. munieri* in the condition of several characters. In particular, the pygidial terminus extends further posteriorly than the pygidial pleural lappets in Gandl's specimen, whereas in *P. munieri* the lappets extend further posteriorly. In addition, the sides of the pygidial terminus at its anterior end are parallel in *P. munieri*, whereas they are convergent in Gandl's specimen. Finally, the lateral edges of the pleural lappets in *P. munieri* show greater curvature than they do in Gandl's figured specimen. Therefore, Gandl's specimen clearly represents a different, and possibly new, species. Because of the limited morphological information, it is difficult to ascertain whether this pygidium belongs to *Pseudocryphaeus* or to some other genus.

TOLKIENIA, NEW GENUS

TYPE SPECIES: *Comura* (*Comura*) *granulispina* Morzadec, 1983.

ASSIGNED TAXA: *Comura* (*Comura*) *cancer* Morzadec, 1983, *Comura nova* Arbizu, 1979, and *Greenops* sp. A Stumm, 1953.

DIAGNOSIS: Anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; pygidial pleural lappets bulge laterally in dorsal view at pygidial margin; pleural lappets very long; terminal pygidial lappet teardrop shaped, does not extend as far posteriorly as other pleural lappets; prosopon of fine tubercles; lateral and medial margins of pygidial pleural lappets curved; distal tips of pygidial lappets pointed; pygidial axis constricts posterior of sixth axial ring; pygidial interpleural furrows flexing at same angle laterally and medially; tops of pygidial pleural segments rounded; pleural furrows long (exsag.), almost as long as anterior pleural band; in medial region of adjacent pleural segments, posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; fourth pygidial lappet projects furthest posteriorly; anterior margins of pygidial axial rings posterior to sixth axial ring straight; terminal pygidial lappet narrow; anterior cephalic border not deflected strongly anteriorly.

ETYMOLOGY: Named for the author J. R. R. Tolkien.

DISCUSSION: This genus is known from the lower Couvinian (?Eifelian) of the Cantabrian Mountains of Spain, from the upper Emsian of the Armorican Massif, and possibly from the Givetian of the Michigan Basin of ENA. There are taxa that authors in the past have assigned to *Comura* Richter and Richter, 1926, but that are removed from that genus herein because they do not possess all of the diagnostic characters of *Comura*. Some of these forms are assigned to *Tolkienia*. For instance, contra the diagnosis of *Comura*, in *C. granulispina* Morzadec, 1983, *C. kervezensis* Morzadec, 1983, and *C. cancer* Morzadec, 1983, medially the pygidial axial rings do not flex strongly posteriorly. In addition, they do not possess a prominent medial tubercle or spine on the pygidial axial rings, which is diagnostic of *Comura*. *Comura nova* Arbizu, 1979, also differs in characters diagnostic of *Comura*. It is possible that if subjected to phylogenetic analysis, the aforementioned species might map out as very closely related to the type of *Comura*, *C. cometa*, and thus they could of course be assigned to *Comura* if an emended diagnosis were presented. However, neither the type of *Comura* nor other adequately preserved species matching the diagnosis of that genus could be obtained for the purposes of phylogenetic analysis.

Alcaldops is very similar to the type species of *Comura*. The chief difference between the two genera appears to be that although species of *Alcaldops* do have a single medial spine or tubercle present on the pygidial axial rings, these tubercles, as well as the medial portion of the pygidial axial rings, do not arch strongly posteriorly. In addition, the type species of *Alcaldops*, *A. alcaldei* Arbizu, 1979, does not possess a prominent spine on L0, unlike *Comura tuberculata* Morzadec, 1969. Until studies can be carried out on species of *Alcaldops*, particularly the type of the genus, it is treated as still valid, although it was not analyzed herein. However, the possibility exists that the genus may contain species both nested within and outside of species traditionally assigned to *Comura*, and therefore it would be either no longer valid or in need of substantial revision.

Although *Comura* could not be subjected to phylogenetic analysis herein, it is probable that it is closely related to *Tolkienia*. In particular, both genera have: very long pygidial pleural lappets that are rounded; the lateral and medial margins of the pleural lappets curved; the posterior portion of the pleural segments elevated above the anterior portion; the teardrop-shaped, narrow terminal pygidial lappet; and, in the medial region of adjacent pleural segments, the posterior region of the anterior segment is longer (sag.) than the anterior portion of the posterior segment. Arbizu (1979), Smeenk (1983), and Morzadec (1983) suggested that there was a close relationship between *Neocalmonia* Pillet, 1969, *Heliopyge* Haas and Mensink, 1969, *Bradocryphaeus* Haas and Mensink, 1969, and *Comura* Richter and Richter, 1926. This claim could not be verified herein. However, *Tolkienia* maps out on the cladogram in figure 4 within a larger clade including these genera, although it is not sister to any of them.

There exists a single pygidium from the Potter Farm Formation (Taghanic), upper Givetian, of the Michigan Basin in ENA that may be referable to *Tolkienia*. This specimen, referred to as *Greenops* sp. A by Stumm (1953), lacks nearly all of the diagnostic characteristics of the pygidium of *Greenops* and cannot be assigned to that genus henceforth. Although poorly preserved, it appears to possess some of the diagnostic characteristics of the genus *Tolkienia*, and it is tentatively placed in that genus awaiting the recovery of additional specimens. In particular, it has the very long pygidial pleural lappets with curved lateral and medial margins characteristic of *Tolkienia*. In addition, as in *Tolkienia*, the terminal pygidial lappet is very narrow; laterally the pygidial interpleural furrows arch at the same angle as medially; the pleural field flanking the terminal portion of the pygidial axis is faintly excavated; it may have a triangular terminal pygidial lappet; and the pygidial pleural lappets expand slightly where they reach the pleural field.

Tolkienia granulispina Morzadec, 1983, was used in the phylogenetic analysis because it was the most completely preserved taxon available of this new genus.

Tolkienia granulispina
(Morzadec, 1983)

Comura (*Comura*) *granulispina* Morzadec, 1983: 134, pl. 21, figs. 1–7.

TYPES: Holotype defined in Morzadec (1983: pl. 21, fig. 2).

DIAGNOSIS: Distance between frontal glabellar lobe and facial suture increases slightly from anterolateral margins to midline; S3 faintly sinusoidal; S2 roughly transverse, convex anteriorly; maximum of 13 lenses per dorsoventral file on visual surface; tubercle on L0 present; PMI developed as linear incision; posterior margin of fixigena relative to anterior margin deflected at an angle to transverse line that is roughly equivalent; medial tubercles or spines on pygidial and thoracic axial rings present; medial margins of pygidial pleural lappets curving laterally; anterior margins of pygidial axial rings posterior to sixth axial ring straight; pygidial pleural fields flanking posterior part of pygidial axis faintly excavated; 11 pygidial axial rings.

DISCUSSION: This species is known from the upper Emsian of the Armorican Massif. The PMI was treated as being developed as a linear incision in this species instead of as a rounded depression. This is because the PMI is rectangular, although not significantly so, being almost square; however, this is treated as showing greater concordance with the linear character state than with the rounded character state.

Morzadec (1983: fig. 33) held that this species was directly ancestral to *Tolkienia cancer* (Morzadec, 1983) and that this ancestral lineage gave rise to several species of *Comura* as well as to species of *Asteropyge* Hawle and Corda, 1847, such as *A. punctata* Steininger, 1831. *Tolkienia cancer* and *T. granulispina* appear to be closely related, and the relationship between *Tolkienia* and *Comura* could not be evaluated herein, although it probably is a close one. However, *Asteropyge punctata* appears to be only distantly related to *T. granulispina*, and the two taxa are separated by several nodes on the cladogram given in figure 4.

***BRAUNOPS*, NEW GENUS**

TYPE SPECIES: *Kayserops obsoletus* Gandl, 1972.

ASSIGNED TAXA: *Kayserops brevispinosus* Gandl, 1972, *Pseudocryphaeus ogivalis* Morzadec, 1976, *Asteropyge* (*Metacanthus*) *prostellans* Richter and Richter, 1939, and possibly *Pseudocryphaeus asteriferus* Haas, 1968.

DIAGNOSIS: S3 straight, anterolateral edge flexes posteriorly; posterior edge of visual surface anterior to transverse line tangent to L0; fixigena evenly sloping from axial furrow to palpebrum; facial suture lateral of eye, before flexing posteriorly flexes anteriorly to point between distal tips of S1 and S2; distance between frontal lobe and facial suture at midline relative to laterally increases slightly; medially anterior cephalic border pointed in dorsal view; posterior margin of palpebrum relative to anterior margin deflected at an equivalent angle to transverse line; L3 flattened dorsally; axial furrows diverge less strongly opposite anterior half of L3 than opposite posterior half of L3; anterior cephalic border developed as broad ledge, visible anterior to medial parts of frontal lobe; S2 roughly transverse, weakly convex anteriorly; lateral margins of pygidial lappets curved, distal extremities of lappets pointed; pleural lappets long; anterolateral margins of first five pygidial axial rings evenly convex; anterior margins of pygidial axial rings posterior to fifth ring straight; tops of pygidial pleural segments rounded; pygidial pleural furrows long (exsag.); laterally pygidial interpleural furrows arch at same angle as medially; posterior part of pygidial pleural segments elevated above anterior part.

ETYMOLOGY: Named for Chris Braun, academic compatriot.

DISCUSSION: The species in this genus are known from the lower and upper Emsian of northern Spain, from the upper Emsian of the Massif Armorican, and from the upper Siegenian (Pragian) and Emsian of northwestern Turkey. The most completely preserved species of the genus, *Braunops obsoletus* (Gandl, 1972), and *B. prostellans* (Richter and Richter, 1939), were used to code character states for this genus. Some of the species in this genus had been assigned by Gandl (1972) and Smeenk (1983) to the genus *Kayserops* Delo, 1935, but it is clear that this generic assignment cannot be upheld because these species do not match the diagnosis of the genus presented by Delo (1935), nor do they resemble the type of the genus, *Cryphaeus kochi* Kayser, 1883 in many important features. In particular, they lack the highly convex cephalon; also *Kayserops* is supposed to lack a well-developed anterior border, but they have a prominent one. In addition, the species assigned to *Braunops* do not have L2 and L3 swollen and rising above the frontal lobe, nor is L1 narrow and depressed, as is diagnostic of *Kayserops*. However, in characteristics of the pygidium, some of the species of *Braunops* do bear a resemblance to those of *Kayserops*. In particular, the long thin pleural lappets curving at their lateral margins and pointed posteriorly as well as the medial axial tubercles are characteristic of *K. kochi*, although the first two of these character states are plesiomorphic. Moreover, some species of *Braunops* do have the condition of the eyes rising high above the glabella characteristic of *K. kochi*. These similarities are treated as convergences herein.

Other species in the genus *Braunops*, such as *B. prostellans*, have in the past been assigned by authors such as Richter and Richter (1939) to *Asteropyge*. Phylogenetic topology uncovered herein indicates that *B. prostellans* is distantly related to the type of *Asteropyge*. Haas (1968) suggested that *B.*

prostellans should instead be grouped with *Pseudocryphaeus*. Although this species cannot be placed within that genus without either making it polyphyletic or having it encompassing a very large number of species, the species *B. prostellans* is included within a larger clade sister to *Pseudocryphaeus*.

A significant number of the characters supporting the genus *Braunops* are in the primitive state, and *B. prostellans*, which appears in the fossil record in the Siegenian (Pragian), has a large number of primitive character states. However, parsimony analysis conducted herein suggests that *Braunops* is not one of the basal members of the Asteropyginae, but rather sits on a side arm in one of the two main branches in the Asteropyginae.

Gandl (1972) suggested that what is recognized herein as *Braunops*, new genus, was closely related to *Greenops* (*Neometacanthus*) *stellifer*. On the basis of phylogenetic analysis this is not supported herein, and *Neometacanthus* and *Greenops* are separated on the cladogram given in figure 4 by several nodes from *Braunops*. Smeenk (1983) suggested that his *Kayserops*, here equivalent to *Braunops*, was derived from stem lineage *Paracryphaeus* Gandl, 1972. Phylogenetic analysis suggests that *Paracryphaeus* is distantly related to *Braunops*.

Braunops obsoletus (Gandl, 1972)

Kayserops n. sp. aff. *diadema* Carls and Gandl, 1968: 463.

Kayserops obsoletus Gandl, 1972: 128, pl. 12, figs. 1–7.

?*Kayserops obsoletus* Gandl. Smeenk, 1983: 403, pl. 8, figs. 7–12, text fig. 4.

TYPES: Holotype defined in Gandl (1972: pl. 12, fig. 7).

DIAGNOSIS: Same as for genus and: anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; anterior cephalic border medially flexes dorsally; tubercle on L0 developed as long spine; genal spine extends back to fourth thoracic segment; plane from medial to lateral edges of genal spine evenly inclined, medial edge thickened relative to lateral edge; lateral margin of genal spine forms line that departs from sagittal line by 15–20°; raised ridge on dorsal surface of genal spine at juncture of posterior and lateral border furrows is smoothly curved, convex distally; axial furrows diverge at same angle anterior and posterior of S1; interior margin of genal spine deflected laterally, more strongly deflected laterally posteriorly; tubercle on medial portion of pygidial and thoracic axial rings; terminal pygidial lappet triangular, projects further posteriorly than other lappets; medial margins of pygidial lappets straight; pygidial axis constricts posterior to fifth axial ring; pygidial pleural field flanking posterior portion of axis prominently excavated; in medial region of adjacent pleural segments, posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment.

DISCUSSION: This species is known with certainty from the lower Emsian of the Celtiberian Mountains of northeastern Spain. It may also be present in the Emsian of the Massif Armorican as well as in the upper lower Emsian of the southern Cantabrian Mountains of northern Spain. The specimens that Smeenk (1983) figured from the La Vid Formation (upper lower Emsian) in the southern Cantabrian Mountains of northern Spain are nearly identical to the type specimens illustrated by Gandl (1972) from the lower Emsian of the Celtiberian Mountains of northeastern Spain. However, there are some slight differences between the specimens they figure, particularly in the number of axial rings: 10 in Smeenk's (1983) specimens versus 11 in Gandl's (1972) types. It could not be ascertained whether or not these differences are within the range of variation for this species, and because of this, Smeenk's (1983) specimens are only tentatively assigned to *B. obsoletus*.

Counts of the maximum number of lenses in a dorsoventral file on the visual surface could not be obtained for Gandl's (1972) specimens, although they could be obtained from Smeenk (1983). In these specimens there are a maximum of nine lenses per file. This character, number 6, was coded with a question mark for the purposes of phylogenetic analysis, in recognition that Smeenk's (1983) specimens might not be conspecific with Gandl's (1972).

Investigation of the photographs in Gandl (1972: pl. 12) suggests that *B. obsoletus* may have structures homologous to the fenestrae found in some species of the asteropyginines in ENA and described as characters 65 and 66. These structures were scored as present, but this conclusion awaits further study of original specimens.

Braunops prostellans (Richter and Richter, 1939)

Cryphaeus pectinata Huffner, 1918: 371, pl. 30, fig. 5.

Asteropyge (*Metacanthus*) *prostellans* Richter and Richter, 1939: 17, pl. 17, figs. 14–15.

Pseudocryphaues prostellans (Richter and Richter). Haas, 1968: 151, pl. 35., figs. 13–15, text fig. 44.

DIAGNOSIS: S1 medially developed as smooth curve convex posteriorly; anterior margin of frontal glabellar lobe in dorsal view faintly pointed; anterior cephalic border medially does not flex dorsally; genal spine extends back to fourth thoracic segment; plane from medial to lateral edges of genal spine evenly inclined; lateral margin of genal spine in medial portion forms line that departs from sagittal line by 15–20°; raised ridge on dorsal surface of genal spine at juncture of posterior and lateral border furrows forms sharp, doglegged kink; cephalic axial furrows diverge at same angle anterior and posterior to S1; interior margin of genal spine deflected laterally; broad ledge of anterior cephalic border not visible anterior to anterolateral parts of frontal lobe; terminal pygidial lappet triangular; medial margins of pygidial lappets curved; pygidial axis constricts posterior to fourth axial ring; pygidial pleural field flanking posterior part of pygidial axis faintly excavated; in medial region of adjacent pygidial pleural segments, posterior region of anterior segment longer (exsag.) than anterior part of posterior segment.

DISCUSSION: This species was formerly assigned to the genus *Pseudocryphaeus*, but it differs from the type species of the genus in the condition of several characters including: 2, 9, 14, 16, 19, 22, 23, 28, 29, 36, 38, 40, 42–44, 46, 48, 52, 56, 58, 59, 62, and 63 and thus can no longer be assigned to that taxon.

NEOCALMONIA PILLET, 1969

TYPE SPECIES: *Neocalmonia quadricosta* Pillet, 1969.

ASSIGNED TAXA: Several taxa, including: *Neocalmonia* (*Neocalmonia*) *malistana* Haas and Mensink, 1969, *Neocalmonia* (*Neocalmonia*) *brinckmanni* Haas and Mensink, 1969, *Neocalmonia* (*Neocalmonia*) *imperfecta* Pillet, 1969, *Neocalmonia* (*Neocalmonia*) *batillifera* Haas and Mensink, 1969, *Neocalmonia* (*Neocalmonia*) *kakari* Haas and Mensink, 1969, *Neocalmonia* (*Neocalmonia*) *thaumata* Haas and Mensink, 1969, and *Neocalmonia cantabrica* Smeenk, 1983.

DIAGNOSIS: S3 faintly sinusoidal; lateral to eye, facial suture, before flexing posteriorly, flexes anteriorly to point opposite S2; prominent change in cephalic topography where librigena contacts lateral border furrow; isolated patches of coarse tubercles present on L2, L3, and frontal lobe; medially, genal spine flattened, laterally, evenly inclined; visual surfaces, in dorsal view, present within sagittal lines drawn tangent to distal edges of frontal glabellar lobe; S2 transverse, weakly convex anteriorly; S1 crescent shaped, medially straight; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; anterior cephalic border pointed medially in dorsal view, projecting medially and laterally far beyond frontal lobe; fixigena evenly sloping from axial furrow to palpebrum; PMI developed as linear incision; posterior margin of palpebrum relative to anterior margin deflected at angle to transverse line that is significantly larger; distal tips of pygidial lappets pointed; pygidial axis constricts posterior to fifth axial ring; pygidial pleural field flanking posterior portion of axis faintly excavated; posterior portion of pleural segment elevated above anterior portion; fourth pygidial pleural lappet projects furthest posteriorly; tops of pygidial pleural segments flat; pygidial interpleural furrows flex anteriorly laterally; posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; pygidial lappets long (exsag.); four pairs of pygidial lappets present.

DISCUSSION: The species in this genus are known from the Frasnian of Afghanistan and the lower Givetian of northern Spain. Several authors, including Haas and Mensink (1969) and Haas (1970), have suggested that *Neocalmonia* be divided into several different subgenera such as *Neocalmonia* (*Neocalmonia*), *Neocalmonia* (*Bradocryphaeus*), and *Neocalmonia* (*Heliopyge*). Herein, these subgeneric classifications are not followed. Instead, each of these subgenera is elevated to full generic status, with *Neocalmonia* now comprising what had traditionally been treated as *Neocalmonia* (*Neocalmonia*).

Smeenk (1983) figured and described a new species from the lower Givetian of the Cantabrian Mountains of northern Spain that he referred to as *Neocalmonia cantabrica*. Although the cephala of his species are homogeneous, there appear to be differences in the pygidia he recovered, with some possessing four pairs of pleural lappets and others with five pairs. In the latter, the posteriormost pair appears connected to the terminal pygidial lappet. Smeenk (1983) commented that this latter condition was also present in *Bradocryphaeus afghanica* Haas and Mensink, 1969, and he viewed his *N. cantabrica* as transitional between *Bradocryphaeus* and typical *Neocalmonia*, which possesses four pairs of pleural lappets. However, Smeenk (1983) recognized that the types of *Bradocryphaeus* and *Neocalmonia* do differ in the condition of several characters. At present, it is difficult to ascertain whether or not Smeenk's (1983) suite of specimens belongs to a single species or two species. There are clear differences between some of the pygidia he illustrates, even though these pygidia are poorly preserved. For the present, the holotype of *N. cantabrica* (Smeenk, 1983: pl. 17, fig. 3) as well as another specimen illustrated by Smeenk (1983: pl. 17, fig. 4) are treated as members of a valid species of *Neocalmonia*. However, some of the pygidia Smeenk (1983) illustrated, as well as all of the cephala he figured, appear to bear several characters diagnostic of *Bradocryphaeus* rather than *Neocalmonia*. In particular: the lateral edge of S2 is directed posteriorly; there are five pairs of pygidial pleural lappets, with the fifth pair extending from the terminal lappet; the third lappet projects furthest posteriorly; and the medial portion of S1 is developed as a smooth curve convex posteriorly. Therefore, these pygidia and cephala are treated as *Bradocryphaeus* new species. Smeenk (1983) may be correct about the transitional position of *N. cantabrica* between what he claims to be the ancestral *Bradocryphaeus* Haas and Mensink, 1969, and the derived *Neocalmonia*, but his conclusion is not supported by the phylogenetic analysis presented herein, which suggests that *Neocalmonia* is not especially closely related to *Bradocryphaeus* Haas and Mensink, 1969, or to *Heliopyge* Haas and Mensink, 1969.

Several authors have commented on the phylogenetic relationships of *Neocalmonia*. Haas and Mensink (1969) asserted that *Bradocryphaeus* was derived from *Asteropyge* Hawle and Corda, 1847, in the late Eifelian, and *Bradocryphaeus* gave rise to *Heliopyge* in the early Givetian and *Neocalmonia* in the late Givetian. This phylogenetic topology is duplicated in Haas (1970) (see fig. 5a). On the basis of the phylogenetic analysis conducted herein, *Asteropyge* appears to be distantly related to all of these genera. Part of Haas and Mensink's (1969) phylogenetic conclusions are supported in that *Bradocryphaeus* and *Heliopyge* are closely related, although not sister taxa. However, *Neocalmonia* is part of a larger clade that is in turn sister to a clade including *Bradocryphaeus* and *Heliopyge*, and thus *Neocalmonia* is not closely related to either of these genera. Arbizu (1979) suggested that *Alcaldops* gave rise to the genus *Heliopyge*, which gave rise to *Bradocryphaeus*, which in turn gave rise to *Neocalmonia* (see fig. 5c). *Alcaldops* was not analyzed herein because species of this genus were not available. However, this genus does appear to be very closely related to *Comura* and *Tolkienia*, as discussed above. On the basis of the phylogenetic analysis presented herein, *Tolkienia*, new genus, is relatively closely related to *Neocalmonia*, with these genera being separated by two nodes on the cladogram given in figure 4. Again, Arbizu's (1979) phylogeny does partially disagree with the scheme of evolutionary relationships depicted herein, in terms of the close relationship he posits between *Bradocryphaeus*, *Heliopyge*, and *Neocalmonia*. Morzadec's (1983) phylogeny is very similar to that of Arbizu (1979), differing solely in substituting *Comura* for *Alcaldops* (see fig. 5e). Smeenk (1983) asserted that *Comura* gave rise to *Bradocryphaeus*, which in turn gave rise first to *Alcaldops* and then to *Neocalmonia* (see fig. 5d). According to Smeenk (1983), *Alcaldops* also gave rise to *Heliopyge*. Smeenk (1983) felt that this entire clade had a separate origin from the rest of the Asteropyginae. Smeenk (1983) did not speculate on what might be the predecessor of this separate lineage. This phylogenetic perspective of Smeenk (1983) is not supported herein.

The two lineages sister to the clade containing *Neocalmonia* are known to first appear in the late Siegenian (Pragian) and the Emsian, respectively. This implies a gap from the late Siegenian to the lower Givetian in the fossil record, when species in the lineage leading to *Neocalmonia* should have been recovered but are unknown. This gap could be due to inadequate sampling of that time interval, but this appears unlikely. However, such species may have persisted in regions that cannot be sampled, either because they were not preserved in the fossil record or because they are in inaccessible areas. Finally, as discussed above, under the heading of *Braunops prostellans*, the actual age of first appearance was found to show some discordance with the predicted age of first appearance. In addition, several putative reversals to the primitive character state were concentrated at the node defining *Braunops*. If these primitive character states were misidentified as reversals, it is possible that the gap between the age of first appearance of *Braunops* and the first appearance of *Neocalmonia* could be an artifact of mistakes in cladogram topology. However, as such issues require additional analysis, they await further exploration by other authors.

Neocalmonia quadricosta
Pillet, 1969

Neocalmonia quadricosta Pillet, 1969: 144, figs. A, B, B1.

Neocalmonia (*Neocalmonia*) *quadricosta* Pillet. Haas and Mensink, 1969: 175, pl. 5, figs. 1–7, text fig. 6.

TYPES: Holotype defined in Pillet (1969: fig. B1).

DIAGNOSIS: Line from posterior to anterior edge of eye forms 30° angle with sagittal line; maximum of 10 lenses per dorsoventral file on visual surface; genal spine developed as long flange extending back to sixth thoracic segment; anterior margins of first five pygidial axial rings from axial furrow to midline straight, then strongly arch anteriorly; prosopon of coarse tubercles; lateral and medial margins of pygidial pleural lappets curving; pygidial pleural lappets project further posteriorly than terminal pygidial lappet; terminal pygidial lappet broad, triangular; 14 pygidial axial rings.

DISCUSSION: This species is known from the Frasnian of Afghanistan. It was chosen for phylogenetic analysis because it is the type of the genus.

HALLANDCLARKEOPS, NEW GENUS

TYPE SPECIES: *Kayserops*? *cantarmoricus* Morzadec and Arbizu, 1978.

ASSIGNED TAXA: *Asteropyge renaudae* Morzadec, 1969, *Heliopyge troaonensis* Morzadec, 1983, and *Asteropyge quelernensis* Morzadec, 1983.

ETYMOLOGY: Named by combining the names of J. Hall and J. M. Clarke, who both contributed so much to our knowledge of the Devonian of North America.

DIAGNOSIS: Fixigena with distinct bulge medially; S3 faintly sinusoidal; cephalic posterior border furrow flexes anteriorly laterally; S2 roughly transverse, weakly convex anteriorly; posterior edge of visual surfaces anterior to transverse line tangent to L0; distance between frontal lobe and facial suture increases from lateral edge to midline; anterior cephalic border medially flexes dorsally, deflected far anteriorly medially, developed as spatulate process; PMI developed as linear incision; posterior margin of palpebrum relative to anterior margin deflected at angle to transverse line that is roughly equivalent; prosopon of fine granules; isolated patches of coarse tubercles on L3 and L2 present; genal spine developed as long flange extending back to seventh thoracic segment; medially genal spine developed as flattened ledge, laterally evenly inclined; cephalic axial furrows diverge at same angle anterior and posterior to S1; terminal pygidial lappet triangular; pygidial lappets project further posteriorly than terminal lappet; medial margins of pygidial lappets straight, lateral margins curved; pygidial axis constricts posterior to sixth axial ring; anterior margins of pygidial axial rings posterior to sixth axial ring smoothly convex anteriorly; pygidial pleural field flanking posterior part of axis moderately excavated; posterior part of pleural segment elevated above anterior part; tops of pygidial pleural segments rounded; pygidial pleural furrows developed as long (exsag.) excavated spaces; at pygidial margin surface of pygidium dorsally inflates to form fringing ring; laterally pygidial interpleural furrows flex more strongly posteriorly; in medial region of adjacent pygidial pleural segments, posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; terminal pygidial lappet narrow (tr.); pygidial lappets long (exsag.).

DISCUSSION: This genus is known from the Couvinian (roughly Eifelian) and Couvinian–Givetian transition in the Cantabrian Mountains of northern Spain as well as from the Eifelian of the Massif Armorican. Authors such as Morzadec and Arbizu (1978) and Arbizu (1979) suggested that what is here treated as the type species of *Hallandclarkeops*, new genus, belonged to the genus *Kayserops* Delo, 1935. However, *H. cantarmoricus* (Morzadec) lacks several of the diagnostic characteristics of *Kayserops*, and *H. cantarmoricus* cannot be considered to be closely related to the type of *Kayserops*. Later, Morzadec (1983) changed his mind and treated *H. cantarmoricus* as well as the closely related *Asteropyge quelernensis* Morzadec, 1983, as species of *Asteropyge*. Again, *H. cantarmoricus* differs from the type species of *Asteropyge* in the condition of several characters, including those diagnostic of *Asteropyge*, and the two taxa cannot be considered closely related. Other species herein assigned to *Hallandclarkeops* had been assigned by Morzadec (1983) to *Heliopyge* Hans and Mensink, 1969.

The phylogenetic position of only one species of *Hallandclarkeops* was assessed: *H. cantarmoricus*, the type of the genus. This species is sister to *Bellacartwrightia*, a genus of ENA asteropyginines. It appears in the fossil record around the same time as *Bellacartwrightia* does. Although the other species assigned to *Hallandclarkeops* were not subjected to phylogenetic analysis, it is believed that they are all very closely related to *H. cantarmoricus* because they share a significant number of apomorphies with that species.

Hallandclarkeops cantarmoricus
(Morzadec and Arbizu, 1978)

Kayserops? *cantarmoricus* Morzadec and Arbizu, 1978: 925, pl. 1, figs. 1–9; Arbizu, 1979: 76, pl. 5, figs. 1–4.

Neocalmonia (*Heliopyge*) n. sp. Gandl *in* Carls, 1979: 38.

Asteropyge cantarmorica (Morzadec and Arbizu). Morzadec, 1983: 132, pl. 19, figs. 1–6, 8, pl. 20, figs. 1–4 (see for complete synonymy).

TYPES: Holotype figured in Morzadec (1983: pl. 20, fig. 1).

DIAGNOSIS: Line from posterior to anterior edge of visual surface forms 5° angle with sagittal line; maximum of 10 lenses per dorsoventral file on visual surface; lateral margins of spatulate process at anterior edge of cephalon first diverge anteriorly, then converge; 18 pygidial axial rings.

DISCUSSION: This species is known from the Eifelian of the Massif Armorican. Morzadec (1983) suggested that this species was sister to *Asteropyge punctata* (Steininger, 1831), the type of the genus *Asteropyge*, and both were derived from what he perceived as a paraphyletic *Comura* lineage. However, as mentioned above, this species is distantly related to *Asteropyge punctata*, differing in the condition of many characters used in phylogenetic analysis. According to the phylogenetic analysis, this species is most closely related to *Bellacartwrightia*, new genus, a genus containing several species, some of which were formerly mistakenly classified as members of *Greenops*. (However, there probably are other species of *Hallandclarkeops* that may be more closely related to *Bellacartwrightia* but that could not be considered in the phylogenetic analysis.) Illustrations in Morzadec (1983) suggest that this species may possess fenestrae on the thoracic pleural segments. It was questionably scored as having these until the actual specimens can be examined.

All articulated cephalothoraxes of this species have largely obscured thoracic regions. Thus, the exact thoracic segment that the genal spines extended back to (character 26) had to be estimated. This estimated position, the seventh segment, was used in the phylogenetic analysis.

BELLACARTWRIGHTIA, NEW GENUS

TYPE SPECIES: *Bellacartwrightia jennyae*, new species.

DIAGNOSIS: S3 faintly sinusoidal; facial suture lateral to eye, before flexing posteriorly flexes anteriorly to point between distal tips of S1 and S2; distance between frontal lobe and facial suture at midline relative to distance between frontal lobe and facial suture at lateral margins of frontal lobe equivalent; anteriormost portion of palpebrum reaches point between medial tips of L3 and PMI; medially, anterior cephalic border in dorsal view pointed; 8–10 lenses in a dorsoventral file on visual surface; anterior cephalic border developed as moderate lip, medially deflected anteriorly for length (sag.) of L1 in front of facial suture; broad ledge of anterior cephalic border visible anterior to anterolateral parts of frontal lobe; posterior margin of palpebrum relative to anterior margin deflected at angle to transverse line that is roughly equivalent; L3 flattened dorsally; significant change in cephalic topography where librigena meets lateral border furrow; isolated patches of tubercles on L3; plane from medial to lateral edges of genal spine evenly inclined; medial edge of genal spine significantly thickened relative to lateral ledge; lateral margin of genal spine parallels sagittal line; raised ridge on dorsal surface of genal spine at juncture of posterior border furrow and lateral border furrow forms sharp, doglegged kink; interior margin of genal spine evenly deflected laterally, more strongly deflected posteriorly; tubercles or spines on medial portion of thoracic and pygidial axial rings; terminal pygidial lappet triangular, does not project as far posteriorly as fifth pair of pleural lappets; 14–16 pygidial axial rings; fifth pair of lappets project furthest posteriorly; medial margins of pygidial lappets straight, distal extremities pointed; pygidial pleural field flanking posterior part of pygidial axis prominently excavated; tops of pygidial pleural segments rounded; pygidial pleural furrows long (exsag.), almost as long as anterior pleural band; anterolateral margins of first five pygidial axial rings evenly convex; pygidial lappets long (exsag.) equal to the length of the first three pygidial axial rings (sag.).

ASSIGNED TAXA: *Bellacartwrightia whiteleyi*, new species, *B. phyllocaudata*, new species, *B. calderonae*, new species, *Cryphaeus calliteles* Green, 1837, and *Dalmanites* (*Cryphaeus*) *pleione* Hall, 1861.

ETYMOLOGY: Named for Paulyn Cartwright, BSL's wife.

DISCUSSION: This genus is based on several species that have traditionally been assigned to the genus *Greenops* (e.g., Delo, 1935, 1940; Babcock and Speyer, 1987; Speyer, 1988, etc.), although sometimes (e.g., Ludvigsen, 1979; Morzadec, 1992) they had been treated as belonging to the subgenus *Neometacanthus* Richter and Richter, 1948. As discussed below under the heading of *Neometacanthus*, species of *Bellacartwrightia* differ substantially from the type of *Neometacanthus*, *N. stellifer*, in the condition of several characters, and they are significantly distanced from one another on the cladogram shown in figure 4. Thus, they cannot be treated as congeners.

In addition, the members of this genus are phylogenetically distant from species assigned to true *Greenops* Delo, 1935. Thus, past authors had been lumping very distinct phylogenetic lineages within the Asteropyginae when they assigned all ENA asteropyginines to the genus *Greenops*. These two Middle Devonian genera have not shared a common ancestor since, at latest, the Siegenian (?Pragian), based on an analysis of ghost lineages. To treat these species as members of a genus *Greenops* would necessitate placing all of the asteropyginines within the genus *Greenops*.

The presence of this genus in ENA and its phylogenetic position relative to *Greenops* have implications for the appearance of the Hamilton Group fauna in ENA. Typically, most of the asteropyginine species in ENA were viewed as a largely endemic radiation (e.g., Hall and Clarke, 1888; Delo, 1940; Stumm, 1953; Morzadec, 1983, 1992; etc.). However, the phylogenetic analysis conducted herein calls this contention into question. Rather, it suggests that the appearance of the asteropyginines in ENA was the by product of multiple biogeographic events involving invasion by Armorican lineages into ENA, and the ENA asteropyginines can be partitioned into small groups of closely related species nested within Armorican species, with these groups separated by significant phylogenetic distance. A method is discussed below for using phylogenetic analysis in conjunction with the principle of parsimony to resolve biogeographic area relationships. The method indicates that invasions occurred between the Emsian and the Givetian involving lineages entering into ENA from Armorica. The evidence suggests that the invasions represent at least four independent biogeographic events. However, whether or not they occurred contemporaneously is difficult to ascertain.

As discussed by Delo (1940), the species originally described as *Cryphaeus collitelus* Green, 1837, was based on types from strata near Huntingdon, Pennsylvania, that were subsequently lost. Authors such as Hall (1876) and Hall and Clarke (1888) recovered material from New York that they claimed was conspecific with that species, and they assigned this material to *Dalmanites* (*Cryphaeus*) *boothi* var. *calliteles* (apparently the original spelling of *collitelus* was a typographical error). Delo (1940) supported their conclusions. For several reasons, the decisions of Hall and Clarke (1888) and Delo (1940) regarding these New York specimens must be questioned.

First, these authors did not make an adequate attempt to recover material from Green's (1837) type locality to verify if the New York material differed from the Pennsylvania material. Until that is done, one cannot be sure that the material Hall and Clarke (1888) illustrated, which subsequent authors such as Grabau and Shimer (1910) and Delo (1940) also figured, actually represented that species. Instead of following Hall and Clarke's (1888) taxonomic assignment of much of their material to *D.* (*C.*) *boothi* var. *calliteles*, we are at present making excursions to recover asteropyginine material from Green's (1837) type locality. When such material is recovered it will be possible to erect a neotype for *Cryphaeus calliteles*. At this time, our analysis cannot incorporate specimens that could be assigned to *calliteles*.

Hall and Clarke (1888) are unlikely to be correct in emphasizing the exact match between specimens from New York that they treated as *calliteles* and true specimens of that species from the type locality in Pennsylvania because they assigned several different New York Hamilton Group species to *D.* (*C.*) *boothi* var. *calliteles*. At this time, the different species from New York State assigned by Hall and Clarke (1888) to *D.* (*C.*) *boothi* var. *calliteles* are assigned to two new species. A subsequent paper (Lieberman and Kloc, in prep.) will address the issue of the species *calliteles* in greater detail.

Delo's (1940) analysis of *Greenops boothi* var. *calliteles* largely followed that of Hall and Clarke (1888), and for that reason his assignments also cannot be accepted.

If there are similarities between the Pennsylvanian material and the bulk of the asteropyginid material Hall and Clarke (1888) and Delo (1940) assigned to *calliteles*, then it is likely that a redefined *calliteles* based on a neotype would be assigned to *Bellacartwrightia*, so tentatively *calliteles* is treated as a taxon referable to that genus.

Two of the species of *Bellacartwrightia* analyzed herein are not known with certainty from rocks older than the Givetian portion of the Erian; however, Hall and Clarke (1888) claimed that a specimen which on the basis of its morphology we assert belongs to either *B. phyllocaudata* or *B. jennyae* was found in the Onondaga Limestone, and would therefore be pre-Givetian. We could not verify this stratigraphic assignment, and it is treated as questionable. However, *B. pleione* (Hall, 1861) is known from the Jeffersonville Limestone (Southwoodian), equivalent to the Onondaga Limestone, from the Falls of the Ohio, Kentucky, in the Illinois Basin, and it also occurs in the Hamilton Group and possibly the Onondaga Limestone of the Appalachian Basin. Thus, the genus *Bellacartwrightia* ranges from the Southwoodian (Eifelian) to the Taghanic (Givetian), with the latest occurrences in the Appalachian Basin.

Bellacartwrightia pleione was not included in the phylogenetic analysis because of the paucity of adequately preserved material, and the absence of cephalic remains. However, based on the diagnostic pygidial characteristics of all other species of *Bellacart-*

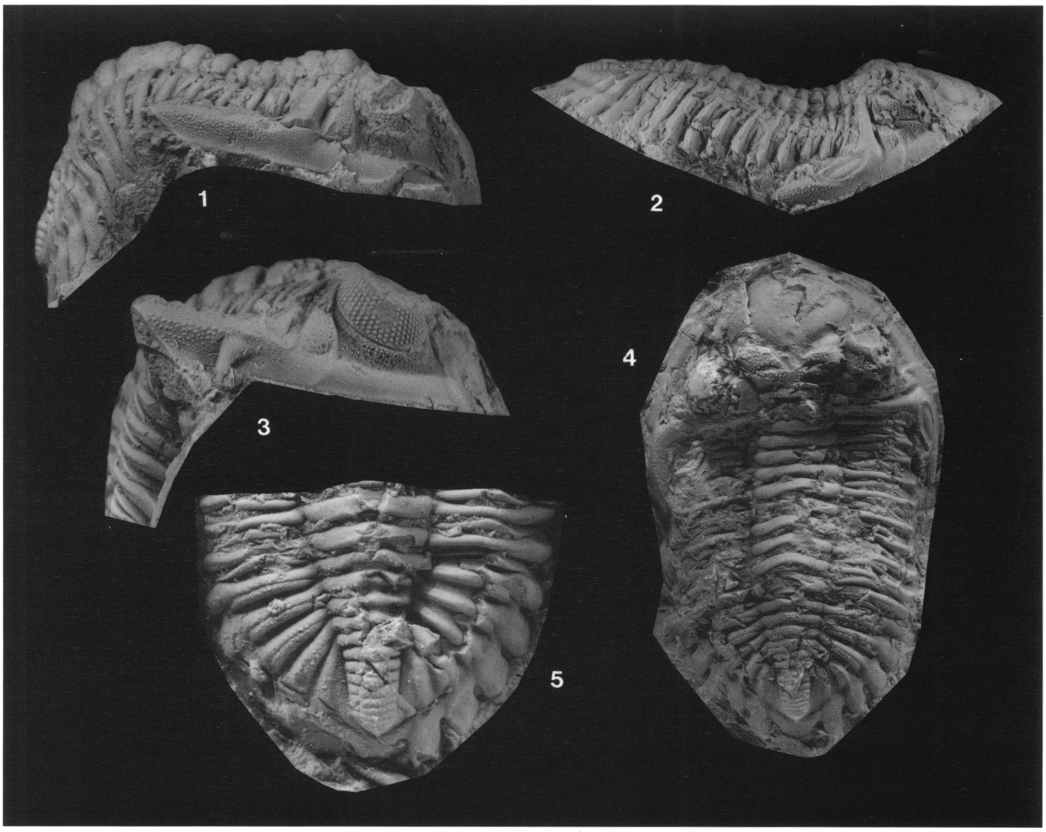

Fig. 6. *Philipsmithiana hyfinkeli*, new species, Middle Devonian, Morocco. **1**. AMNH 45261, lateral view of entire specimen, ×1.3. **2, 4**. AMNH 45262, lateral and dorsal views of entire specimen, ×1.5. **3, 5**. AMNH 45263, lateral view of cephalon and portion of thorax and dorsal view of pygidium and portion of thorax, ×2.5.

wrightia, it appears likely that *pleione* should be placed within this genus. Recovery of additional material would make it possible to incorporate this species into phylogenetic analysis and determine its phylogenetic position with greater confidence.

Bellacartwrightia jennyae, new species

Figures 14.1, 14.2, 16, 20.3–20.6, 20.8–20.11

Dalmanites (*Cryphaeus*) *boothi* var. *calliteles* (Green). Hall and Clarke, 1888: 45, pl. 16, figs. 8, 11–13, 19–21, 22, pl. 16a, figs. 9, 11, 13–15, pl. 24, fig. 15.
Neometacanthus calliteles (Green). Ludvigsen, 1979: 80, fig. 57d.
Greenops boothi (Green). Delo, 1940: pl. 10, fig. 17; Eldredge, 1971a: pl. 14, figs. 4, 5.
Greenops boothi, var. *calliteles* (Green). Delo, 1940: pl. 10, fig. 19.
?*Dalmanites* (*Cryphaeus*) *boothi*, var. *calliteles* (Green). Hall and Clarke, 1888: 45, pl. 16a, fig. 16.

TYPES: Holotype AMNH 45312, a complete specimen from the Centerfield Limestone (Tioughniogan), Ludlowville Formation, Hamilton Group, Middle Devonian, Brown's Creek, York, New York State; paratypes AMNH 45310, a complete individual from the same locality as the holotype, and AMNH 36998, a complete individual from the Centerfield Limestone, Centerfield, New York.

DIAGNOSIS: S2 weakly declined posteriorly at lateral edge; S1 developed medially as smooth curve convex posteriorly; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; anterior margin of frontal glabellar lobe in dorsal

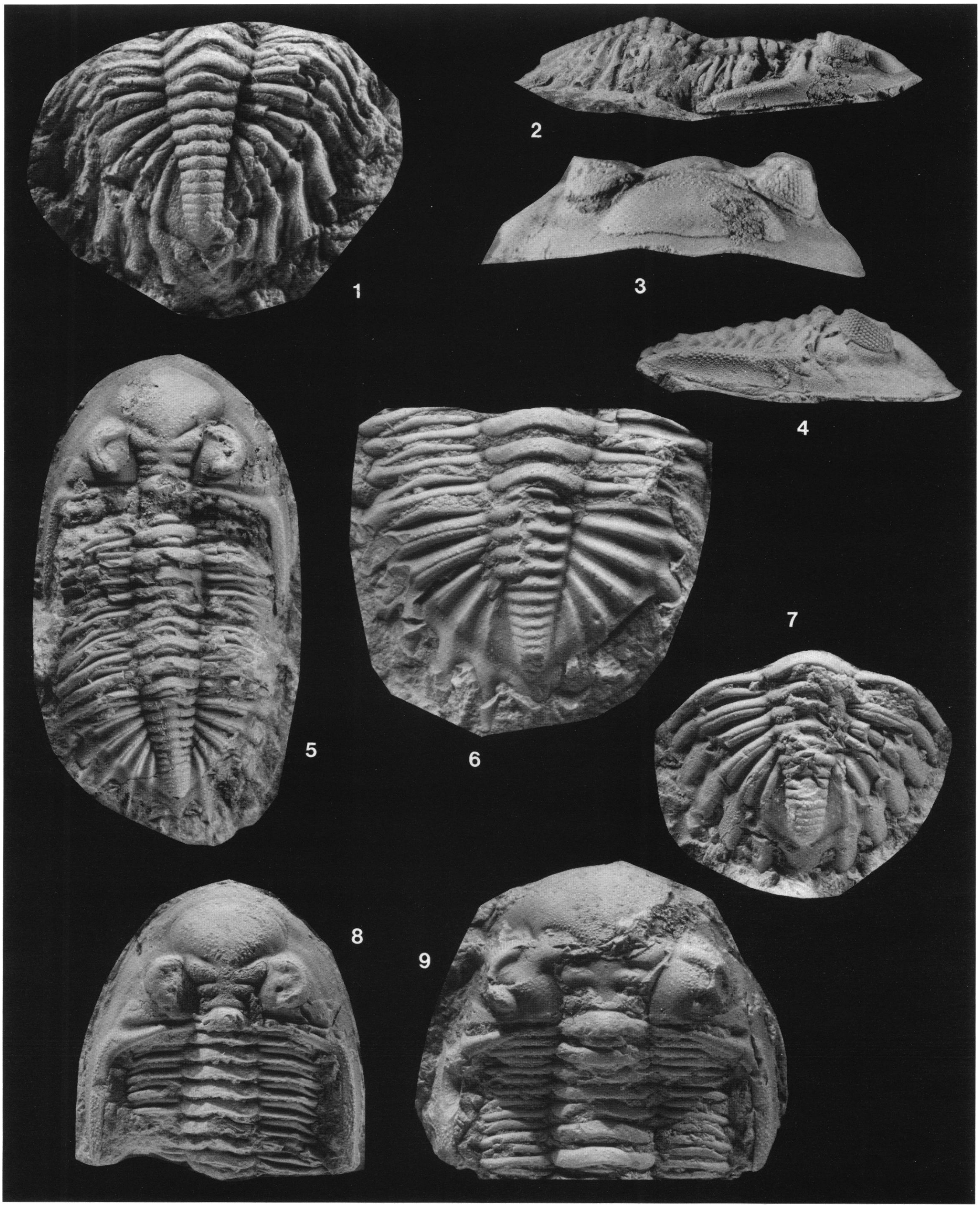

Fig. 7. *Asteropyge* and *Philipsmithiana* spp. **1**. *Asteropyge punctata* (Steininger, 1831), Middle Devonian, Eifel District, Germany, YPM 6643, dorsal view of pygidium and portion of thorax, ×2.75. **2–9**. Middle Devonian, Morocco. **2–6, 8**. *Philipsmithiana burtandmimiae*, new species. **2, 3, 5**. AMNH 45268, lateral, anterior and dorsal views of entire specimen, ×1.8, ×1.8, and ×2.3. **4, 8**. AMNH 45269, lateral and dorsal views of cephalon and portion of thorax, ×1.9. **6**. AMNH 45270, dorsal view of pygidium, ×2.0. **7, 9**. *Philipsmithiana finkeli*, new species, AMNH 45261, dorsal view of pygidium and dorsal view of cephalon and portion of thorax, ×1.5 and ×2.

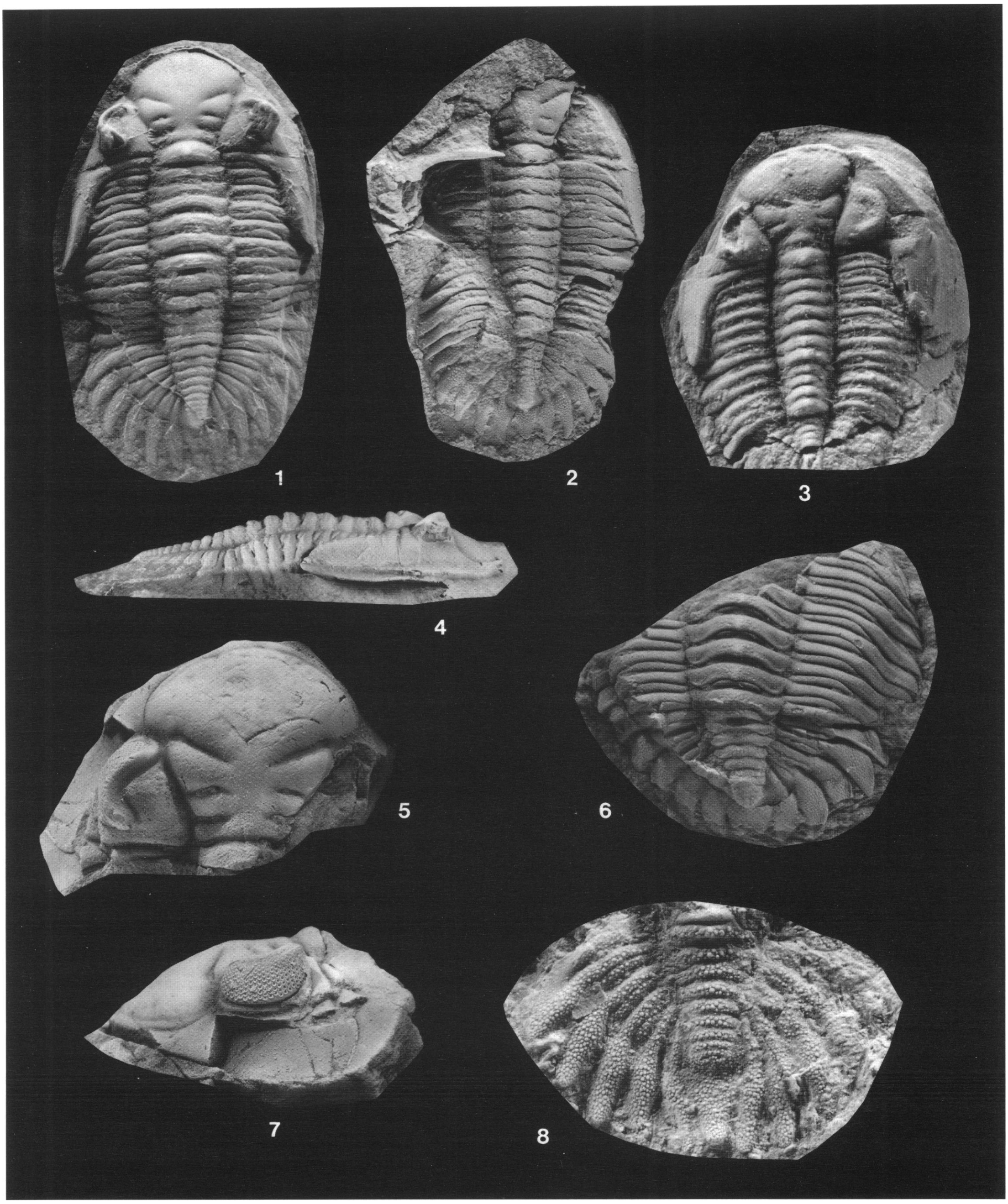

Fig. 8. *Greenops*, *Kennacryphaeus*, and *Stummiana* spp. **1, 2, 4.** *Greenops barberi*, new species, Wanakah Shale, Ludlowville Formation, Father's Camp, Lake Erie, New York. **1, 4.** AMNH 45256, dorsal and lateral views of latex cast taken from external mold of entire specimen, ×2.5. **2.** AMNH 45257, dorsal view of nearly complete specimen, ×3. **3.** *Greenops* new species from the Kashong Shale, Middle Devonian, Moscow, New York, AMNH 45255, dorsal view of cephalothorax and partial pygidium, ×3.5. **6.** *Greenops grabaui*, new species, Hamilton Group, New York, AMNH 45317, dorsal view of thoracopygidium, ×3.5. **5, 7.** *Kennacryphaeus harrisae*, new species, ?Mottville Member, Skaneateles Formation, Fitch Road, New York, AMNH 45248, dorsal and lateral views of partial cephalon, ×2.5. **8.** *Stummiana arkonensis* (Stumm, 1953), Alpena Limestone (Cazenovian), the Huron Point Cement Company, Alpena, Michigan, AMNH locality 3059, AMNH 45249, dorsal view of pygidium, ×4.

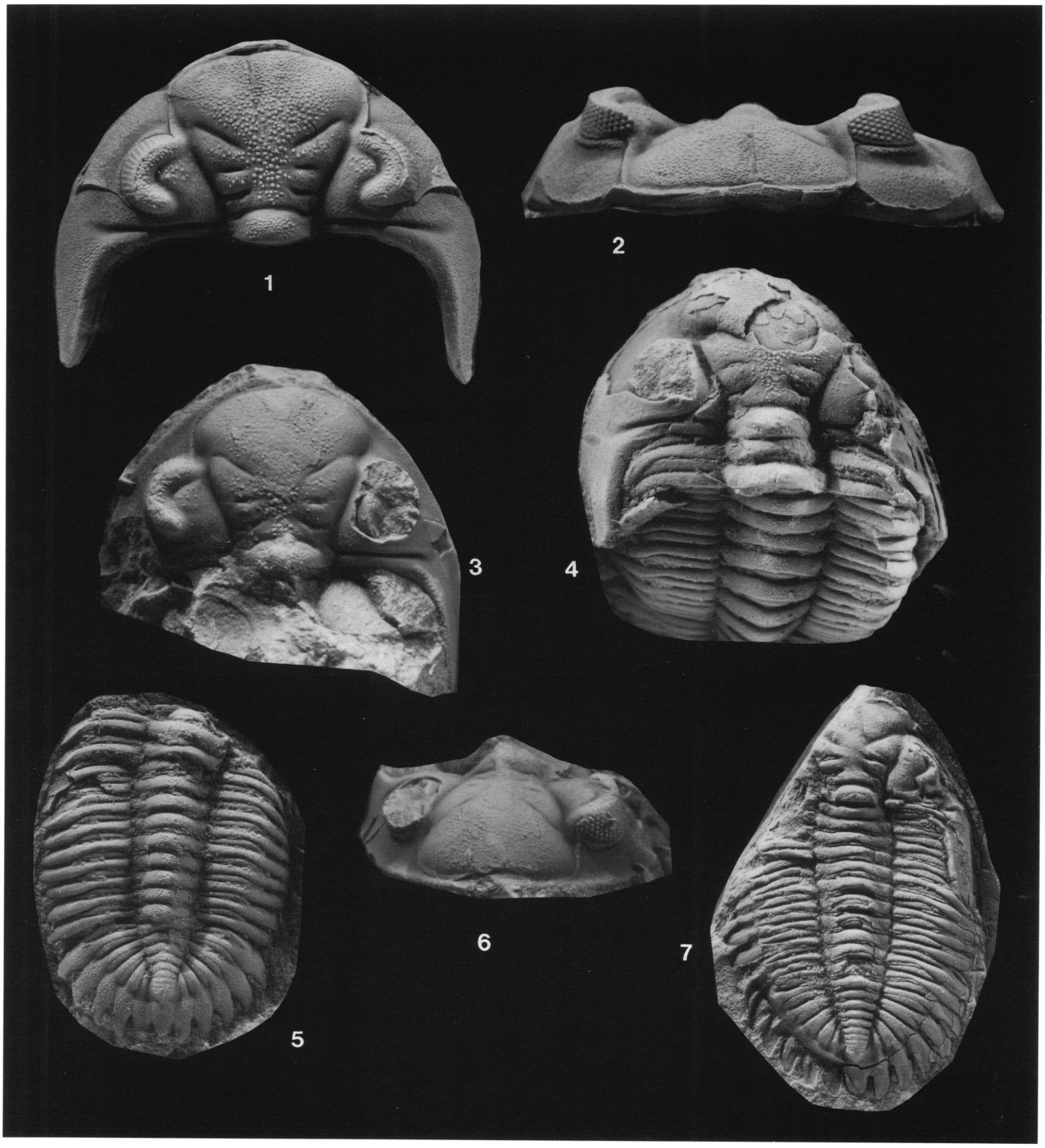

Fig. 9. *Greenops* spp. **1, 2.** *Greenops widderensis*, new species, ?Widder Formation, Traverse Group, Arkona, Ontario, Canada, ROM 1731H, dorsal and anterior views of cephalon, ×4.5. **3–7.** *Greenops grabaui*, new species. **3, 6.** Hamilton Group, shore of Lake Erie, Hamburg, New York, YPM 33778, dorsal and anterior views of cephalon, ×5.75. **4.** YPM 33788, dorsal view of cephalothorax, ×3. **5, 7.** *Greenops grabaui*, new species, Hamilton Group, New York. **5.** AMNH 45274, dorsal view of thoracopygidium, ×3.5. **7.** AMNH 45275, dorsal view of nearly complete specimen, ×2.5.

view faintly pointed; spine on L0; PMI developed as linear incision; line from posterior to anterior edge of eye forms 5–10° angle to sagittal line; maximum of 10 lenses per dorsoventral file on visual surface; cephalic axial furrows anterior to S1 diverge at same angle, at anterior half of L3 relative to posterior half equally divergent; visual surfaces in dorsal view present within sagittal line drawn tangent to frontal lobe; one transverse row of fenestrae on anterior and posterior bands of thoracic pleural segments; genal spine developed as long spine extending back to eighth thoracic segment; lateral margins of genal spine recurve posteriorly at posterior end; spine on medial portion of pygidial and thoracic axial rings; pygidial axis constricts posterior to sixth axial ring; anterior margin of pygidial axial rings posterior to constriction of pygidial axis straight; posterior parts of pygidial pleural segments elevated above anterior parts; laterally pygidial interpleural furrows arch at same angle as medially; in medial region of adjacent pleural segments posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; terminal pygidial lappet narrow; lateral margins of pygidial pleural lappets curved; 14 pygidial axial rings.

ETYMOLOGY: Named for Ms. Jenny Lieberman, BSL's sister.

MATERIAL: AMNH 28910, 36998, 45295, 45296, 45310–45312; NYSM 4289–4294, 4297, 4298, 4300, 4301, 4303, 4304; YPM 33763, 74585.

DESCRIPTION: Cephalic length (sag.) 55% of width. Axial furrow nearly straight anterior to S0, diverging forward at about 25°, narrow, shallow. Cranidial anterior border developed as moderate lip deflected moderately anterior to facial suture. Preglabellar furrow shallow and narrow. Cranidial anterior border of constant length (sag.) from lateral to medial edges of frontal lobe. Facial suture anterior to eyes flexes laterally then medially, with smoothly convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly, then posteriorly laterally. Glabellar length equal to width across frontal lobe; frontal lobe ellipsoidal, about 65% of length of glabella; frontal lobe at level of posterior glabellar region; anterior part of frontal lobe moderately declined forward, faintly pointed in dorsal view. PMI shallow linear incision. S3 shallow, weakly sinusoidal, equally incised medially and distally, branches diverging at about 140°. Sagittal region of L3–L2 nearly flat (tr.), lateral lobes weakly declined abaxially. L3 wedge shaped, bearing isolated tubercles, lengthening distally, outer edge forming smaller angle with sagittal line at anterior end than at posterior end. S2 weakly declined posteriorly at lateral edge, moderately incised, shallow adjacent to axial furrow. S1 deep, crescent shaped, medial part developed as smooth curve convex posteriorly, laterally contacting axial furrow. L1 short, flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 of nearly uniform length, convex anteriorly medially in dorsal view, deep. L0 55% of width of frontal lobe, moderately arched (tr.), longest sagittally, bearing spine on medial portion. Large Eye Index 0.55. Anterior edge of eye contacts axial furrow opposite anterodistal corner of L3; posterior edge of eye opposite S0, posterior to transverse line tangent to L0; eye raised prominently above frontal lobe; maximum of 10 lenses per dorsoventral file on visual surface. Fixigena evenly sloping from axial furrow to palpebrum. Postocular fixigenal field 15% of length of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse, weakly flexing anteriorly distally, anterior margin nearly straight. Genal spine developed as very long flange extending back to eighth thoracic segment, cephalic border furrow bisects spine; lateral and medial edges of genal spine evenly inclined; medial edge of genal spine significantly thickened and swollen relative to lateral edge, deflected more strongly laterally posteriorly; lateral margin of genal spine parallels sagittal line; lateral margin of genal spine at posterior end recurves; interior margin of genal spine deflected laterally. Raised ridge on dorsal surface of genal spine at juncture of posterior border furrow and lateral border furrow forms sharp, doglegged kink. Lateral border furrow narrow, shallow, lateral border weakly widens posteriorly. Anterior margin of cephalic doublure bluntly pointed. Prosopon of fine tubercles.

Hypostome parabolic, width (tr.) at midlength about 110% of sagittal length. Course of anterior margin (hypostomal suture) weakly convex, with moderate wings positioned far forward. Lateral margin tapering behind anterior wings at approximately 30° angle relative to sagittal line. Middle body bean shaped in outline, broadest anterior to midlength, anterior margin poorly defined; anterolateral margins defined by smooth break in slope, grading down to rather flattened anterior wing. Convexity (tr.) of middle border moderate sagittally; faintly convex (sag.) anterior and posterior lobes separated at about

Fig. 10. *Greenops* and *Bellacartwrightia* spp. **1–5**. *Greenops grabaui*, new species, Hamilton Group, New York. **1, 2**. Near 18 Mile Creek, YPM 33875, dorsal and lateral views of entire specimen, ×4.5. **3**. Near 18 Mile Creek, YPM 33783, 33784, dorsal view of two pygidia and one partial pygidium of *Phacops rana* (Green, 1832), YPM 33785, ×3.5. **4, 5**. AMNH 45254, dorsal and lateral views of pygidium, ×3.2. **6, 7**. *Bellacartwrightia phyllocaudata*, new species, Moscow Formation, Hamilton Group, Jaycox Run Creek, near Avon, Geneseo Township, Livingston County, New York. **6**. AMNH 45244, dorsal view of pygidium, ×2. **7**. AMNH 45243, dorsal view of pygidium, ×1.75.

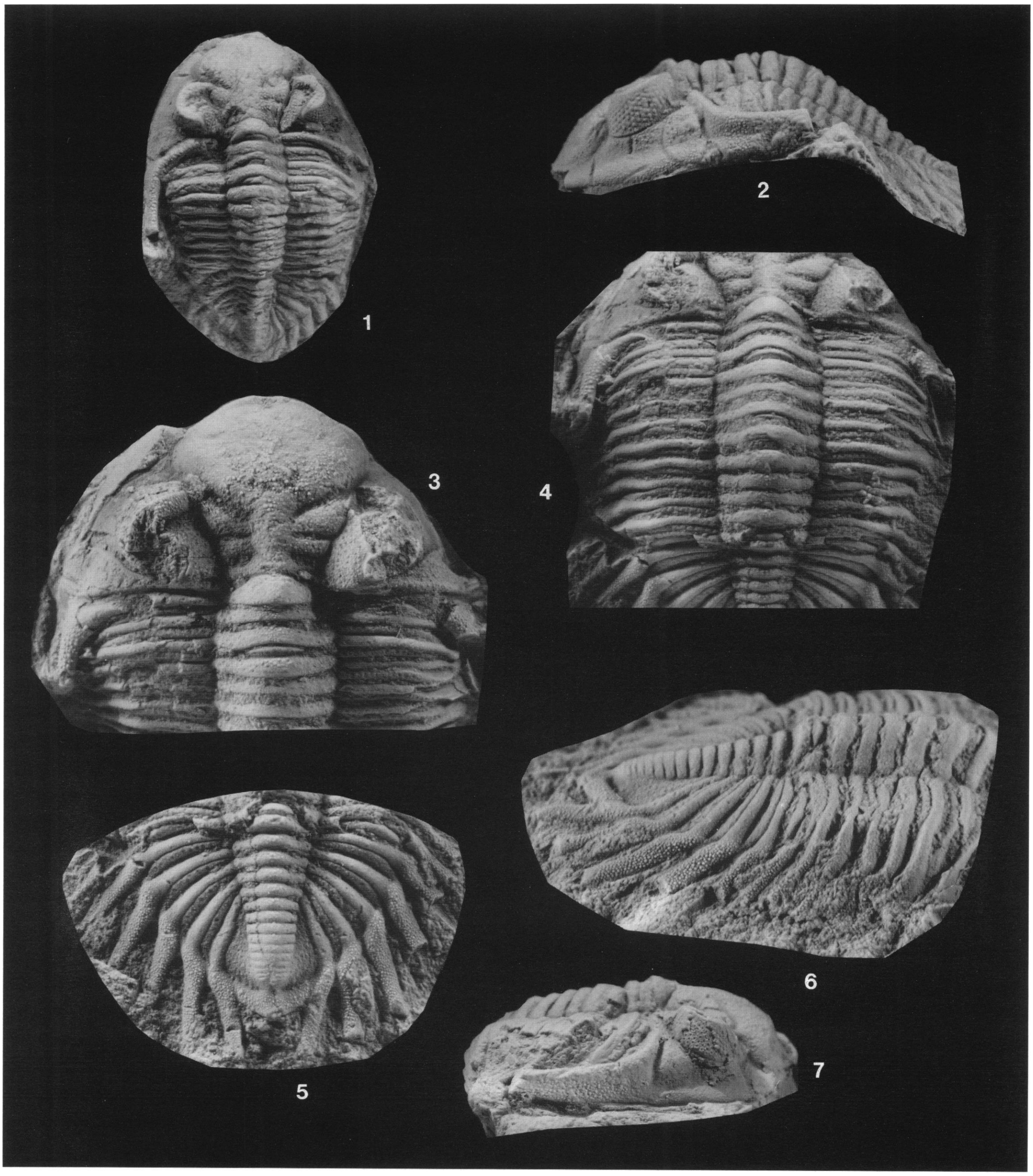

Fig. 11. *Asteropyge punctata* (Steininger, 1831). **1–6**. Calceola Beds (Eifelian), Gees Gerolstein, Eifel District, Germany, **1, 2**. AMNH 18767, dorsal and lateral views of entire specimen, ×3 and ×3.5. **3–6**. AMNH 18768, dorsal view of cephalon, dorsal view of thorax, and dorsal and lateral views of pygidium and portion of thorax, ×4, ×3.5, ×3.75, and ×3.75. **7**. Eifel District, Germany, YPM 6643, lateral views of cephalon and portion of thorax, ×2.75.

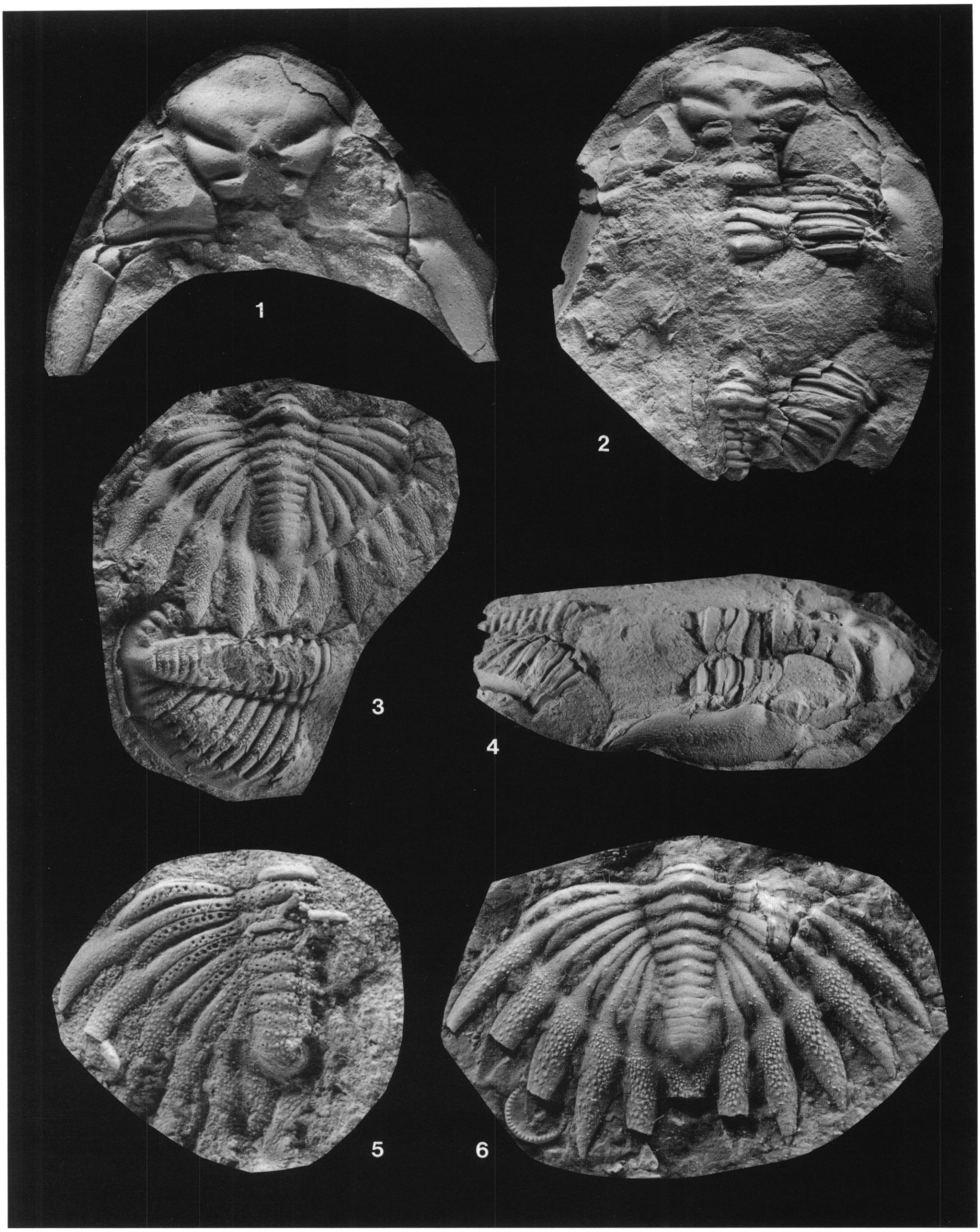

Fig. 12. *Bellacartwrightia* and *Kayserops* spp. **1–4**. *Bellacartwrightia phyllocaudata*, new species, Deep Run Member, Moscow Formation, Jaycox Run Creek, near Avon, Geneseo Township, Livingston County, New York. **1**. AMNH 45247, dorsal view of cephalon, ×2.5. **2, 4**. AMNH 45246, dorsal and lateral views of nearly complete specimen, ×1.75. **3**. AMNH 45245, dorsal view of pygidium and partial pygidium of *Monodechenella macrocephala* (Hall, 1861) (AMNH 44760), ×2.25. **5**. *Kayserops traversensis* (Stumm, 1953), Traverse Group, Four Mile Dam Limestone (Tioughniogan), Four Mile Dam, Alpena, Michigan, dorsal view of partial pygidium, AMNH 45250, ×4.25. **6**. *Bellacartwrightia whiteleyi*, new species, ?Ludlowville Formation, Canandaigua Lake, New York, AMNH 45251, dorsal view of pygidium, ×2.5.

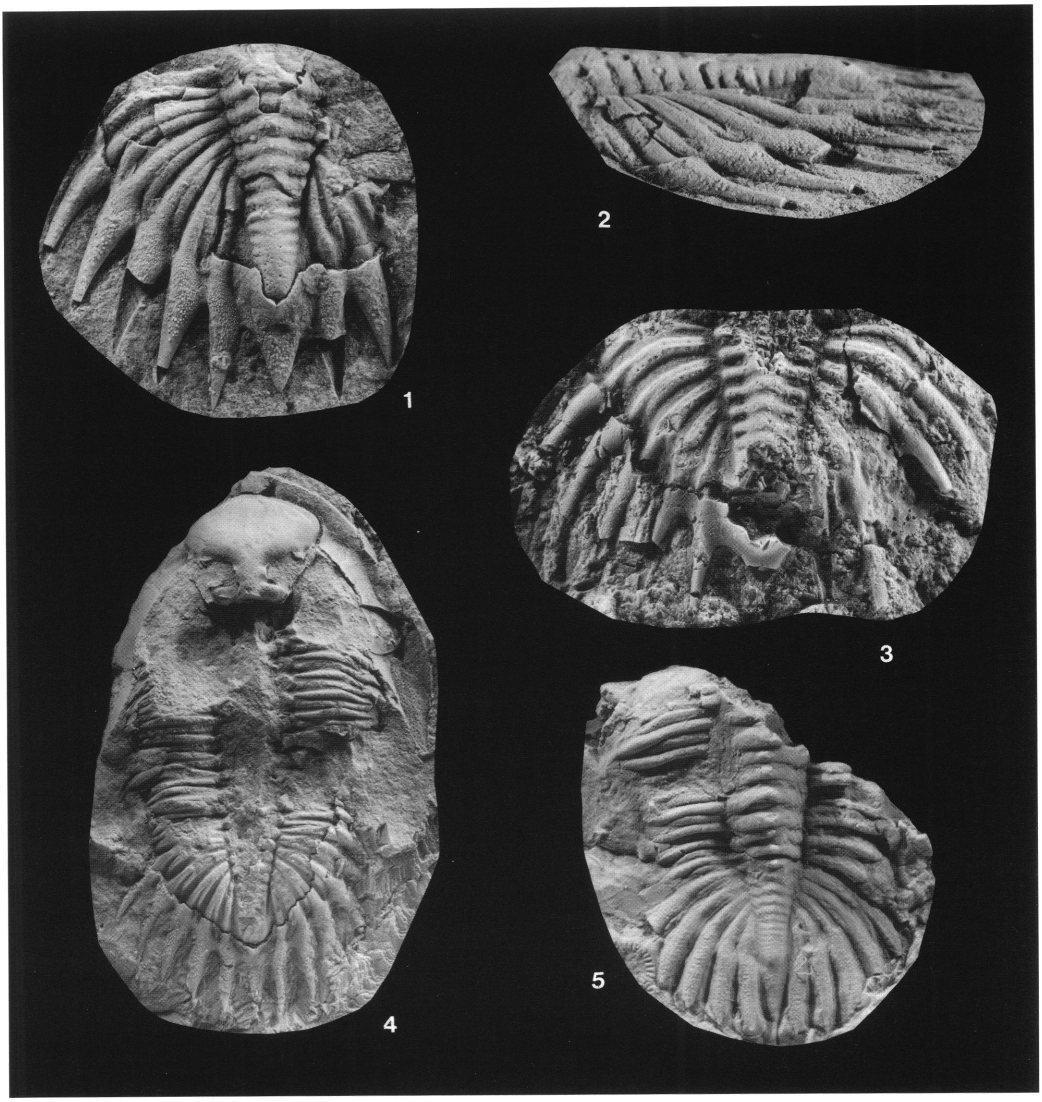

Fig. 13. *Bellacartwrightia* spp. **1–3**. *Bellacartwrightia pleione* (Hall, 1861). **1, 2**. Deep Run Member, Moscow Formation, Jaycox Run Creek, near Avon, Geneseo Township, Livingston County, New York, AMNH 45252, dorsal and lateral views of pygidium, ×2.5. **3**. Jeffersonville Limestone, falls of the Ohio River, near Louisville, Kentucky, AMNH 4248, dorsal view of holotype pygidium, ×2.5. **4**. *Bellacartwrightia calderonae*, new species, ?Windom Shale (Tioughniogan), Moscow Formation, Kashong Glen, west side of Seneca Lake, Bellona, New York, AMNH 29215, dorsal view of entire specimen, ×1.5. **5**. *Bellacartwrightia* sp. aff. *jennyae*, new species, from the Windom Shale, Moscow Formation, western New York, YPM 33789, dorsal view of thoracopygidium, ×3.

65% of length by broad, shallow middle furrow. Maculae small, low, circular swellings, positioned back about 55% of sagittal length of hypostome on middle furrow, displaced medially relative to lateral border furrow 25% of width of hypostome at midlength. Posterolateral-posterior border furrows narrow, shallow. Posterolateral border of constant length (exsag., sag.), 10% of length (sag.) of hypostome. Posterior margin rounded, apparently lacking spines.

Thorax of 11 segments. Axial ring about 25% of width of thorax, of equal length (exsag., sag.), at distal ends and medially

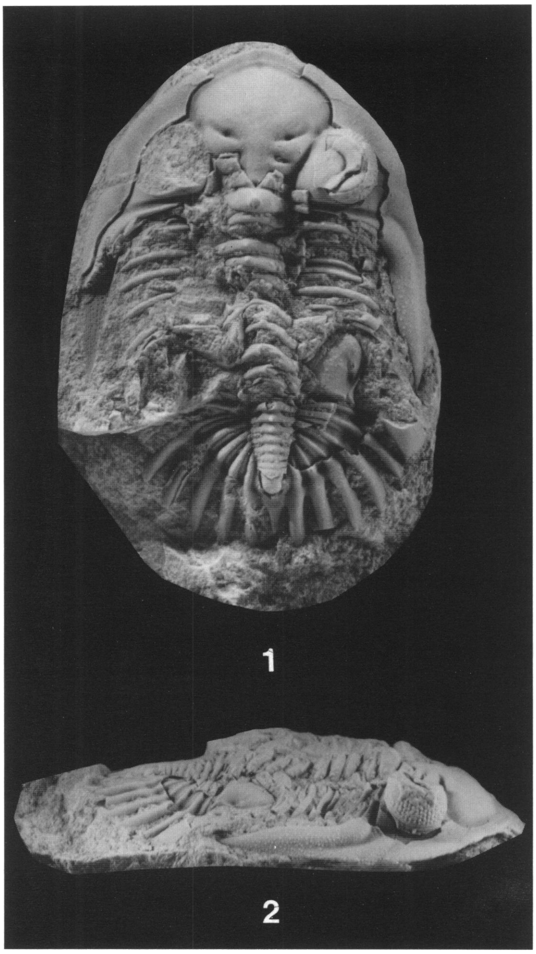

Fig. 14. *Bellacartwrightia jennyae*, new species, Centerfield Limestone, Ludlowville Formation, Centerfield, New York. **1, 2**. Dorsal and lateral views of paratype specimen, AMNH 36998, ×2.75.

flexed forward. Ring furrow of equal length (exsag., sag.), moderately incised, flexing forward medially and distally. Anterior margin of ring well defined sagittally, inclined posterodorsally, most elevated near posterior edge; scattered tubercles around medial part of axial ring, centered around medially placed, enlarged spine; single circular fenestra flanks each side of medial spine; at lateral margin of axial rings, circular fenestrae present. Articulating half ring set slightly below axial ring. Proximal part of pleura transverse, approximately horizontal; anterior segments rather evenly convex (tr.), outer part of pleurae more strongly flexed downward, straight in posterior segments. Posterior band long (exsag.), anterior margin straight, deflected at constant, small angle posteriorly; length (exsag.) shortens as length of pleural furrow increases medially, after approximate midpoint, length of pleural furrow decreases laterally, length of posterior band increases, becomes planar; posterior surface declined posterodorsally, has one transverse row of circular fenestrae near axis; anterior surface declined anterodorsally, with concave depression. Anterior pleural band short (exsag.), medially anterior margin transverse; deflecting strongly posteriorly past approximate midpoint, at roughly same level as posterior band, pinching out distally, with one transverse row of circular fenestrae.

Pygidium broadly triangular in outline excluding marginal lappets, length (sag.) about 65% of width (tr.) without lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, converging at 20 degree angle anterior to sixth pygidial axial ring, roughly parallel posterior to sixth pygidial axial ring. Axis 30% of pygidial width anteriorly, with 14 rings; rings of nearly equal length distally (exsag.) and medially (sag.), bearing medial spine; anterior and posterior edge of axial rings posterior to sixth axial ring from midline to distal edge convex, then transverse. Ring furrows moderately incised. Lateral margins of pygidial lappets curved, medial margins straight, distal tips pointed. Axial terminus triangular, does not project as far posteriorly as other lappets; postaxial region 20% of pygidial length (sag.). Pygidial pleural field flanking posterior part of pygidial axis moderately excavated; anterior band of pleural segment elevated above posterior band; tops of segments rounded; pleural furrows deeper than interpleural furrows, long (exsag.). Laterally pygidial interpleural furrows arch at same angle as medially. In medial region of adjacent pleural segments posterior region of anterior segment longer (exsag.) than anterior part of posterior segment.

DISCUSSION: This species is known from the following localities and stratigraphic horizons in the Appalachian Basin of ENA: the Centerfield Limestone (Tioughniogan), Ludlowville Formation, Buffalo Creek, Blossom,

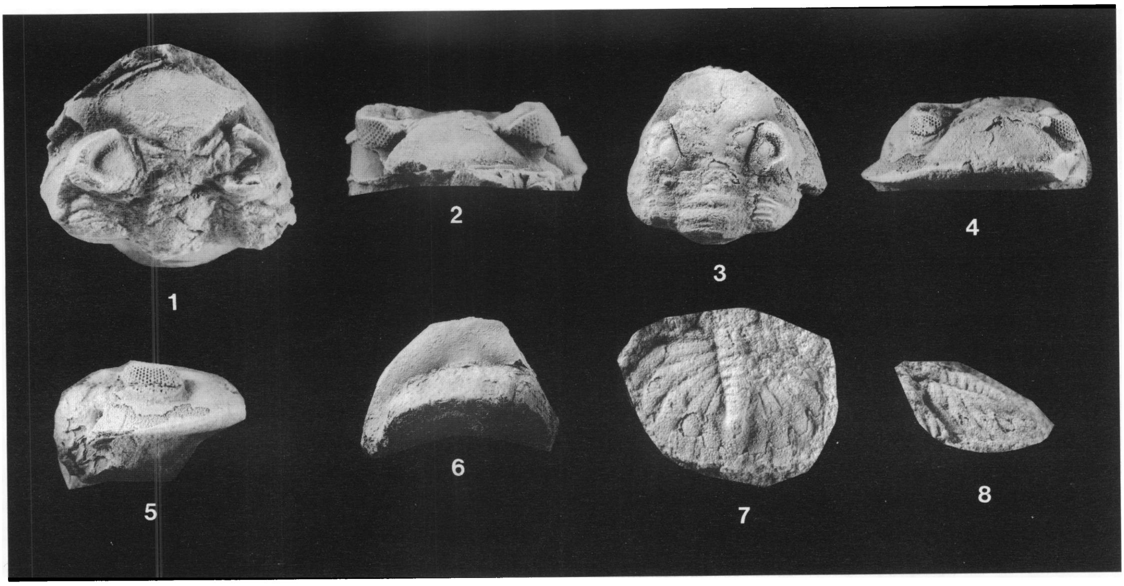

Fig. 15. *Rhenops* new species, Frasnian or Famennian of Venezuela. **1, 2**. Dorsal and anterior views of cephalon, ×1.1. **3–6**. Dorsal, anterior, lateral, and ventral views of cephalon, ×1. **7, 8**. Anterior and lateral views of pygidium, ×1.2. All housed in the Department of Geology, University of Rio de Janeiro, Brazil.

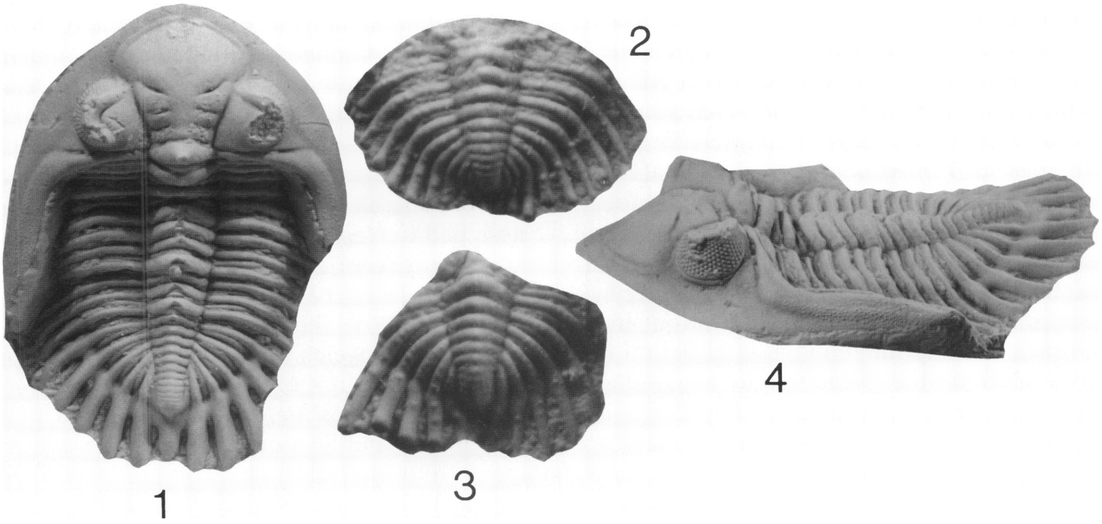

Fig. 16. *Bellacartwrightia jennyae*, new species, Centerfield Limestone, Ludlowville Formation, Centerfield, New York. **1, 4**. NYSM 4293, dorsal and lateral views of complete specimen, ×1.5. **2**. NYSM 4290, dorsal view of meraspid (M9) pygidium, ×11. **3**. NYSM 4289, dorsal view of meraspid (M6) pygidium, ×10.

New York; the Centerfield Limestone, Brown's Creek, York, New York; and ?the Onondaga Limestone (Southwoodian), Batavia, New York. Thus, it persists for a significant time in ENA, and passes through at least two stage boundaries without going extinct.

The existence of this species in ENA appears to have engendered some taxonomic confusion. It is figured in some of the earliest monographic treatments of Devonian fossils from New York, such as Hall and Clarke (1888), as well as in popular accounts of trilobite fossils, such as Ludvigsen (1979). However, in all of these, as well as in Delo (1940), it has been consistently misidentified as *calliteles* (Green), with varying generic assignments. In fact, the bulk of the specimens in the collections of the NYSM that Hall and Clarke (1888) assigned to *D.* (*C.*) *boothi* var. *calliteles* belong to *Bellacartwrightia jennyae*.

Bellacartwrightia jennyae is closely related to *B. phyllocaudata*, a species that also has consistently been misidentified as *calliteles*. However, *B. phyllocaudata* and *B. jennyae* can be distinguished by several character states. In particular, in *B. jennyae* S2 is weakly declined posteriorly at its lateral edge, whereas in *B. phyllocaudata* S2 is roughly transverse and convex anteriorly; in *B. jennyae* the posterior edge of the visual surfaces is posterior to a transverse line tangent to L0, whereas in *B. phyllocaudata* the visual surfaces are anterior to a transverse line tangent to L0; in *B. jennyae* the PMI is developed as a linear incision, whereas in *B. phyllocaudata* it is developed as a rounded depression; in *B. jennyae* the genal spine extends back to the eighth thoracic segment, whereas in *B. phyllocaudata* the genal spine extends back to the sixth thoracic segment; in *B. jennyae* the posterior part of the pleural segment is elevated above the anterior part of the pleural segment, whereas in *B. phyllocaudata* they are of equal elevation; in *B. jennyae* laterally the pygidial interpleural furrows arch at the same angle as medially whereas in *B. phyllocaudata* they flex more strongly posteriorly; in *B. jennyae* there are 14 pygidial axial rings whereas in *B. phyllocaudata* there are 15 or 16 pygidial axial rings; in *B. jennyae* the terminal pygidial lappet is relatively narrow anteriorly, whereas in *B. phyllocaudata* it is relatively broad; in *B. jennyae* there is one transverse row of circular fenestrae on the anterior and posterior parts of the thoracic pleural segments, whereas these fenestrae are absent in *B. phyllocaudata*. None of these characters in these taxa showed any intergradation, and because these two taxa represent two diagnosably distinct units, it was of course necessary to treat them as separate taxa. There appear to be at least two new species that are more closely related to *B. phyllocaudata* than *B. jennyae* is. In addition, there is at least one new species of *Bellacartwrightia* from the Windom Shale that is very similar to *B. jennyae* that is not described herein. However, it is figured as *B.* sp. aff. *jennyae* (fig. 13.5). It will be described in a forthcoming publication (Lieberman and Kloc, in prep.). *Bellacartwrightia jennyae* is relatively rare, but in certain units, such as the Centerfield Limestone, particularly where it outcrops near Blossom, New York, it is quite abundant.

Eldredge (1971a: pl. 14, fig. 4) figured a hypostome that is treated as belonging to this species. It is not associated with any specimens, but it is from a locality where *B. jennyae* is the only known asteropyginid species. It is therefore placed in that species and described. The other complete specimen Eldredge (1971a) illustrated (AMNH 36998) as *G. boothi* bears the hallmark characters of *B. jennyae* and is treated as belonging to that species. In particular, this specimen has the long pygidial lappets distally pointed, with the pleural segments prominently rounded, the spines on the medial portions of the axial rings, and the long, medially flattened genal spines.

Ludvigsen (1979) illustrated a slab from the NYSM showing two specimens that he assigned to *Neometacanthus calliteles*. These specimens were assigned by Hall and Clarke (1888) to *D.* (*C.*) *boothi* var. *calliteles*, but as discussed above they can no longer be placed within that species because a valid type for *calliteles* does not exist. A neotype for *Bellacartwrightia calliteles* will be erected in a subsequent publication. None of the specimens from the Hamilton Group of New York appear to be valid exponents of that species, and, indeed, Hall and Clarke's (1888) concept of *calliteles* included several species. The specimens Ludvigsen (1979) illustrated belong to *B. jennyae*. The species cannot be assigned to *Neometacanthus* Richter and Richter, 1948, because *Bellacartwrightia* is distantly related to *Neometacanthus*. A concept of *Neometacanthus* including *jennyae* would necessitate placing all asteropyginid species within that genus. Ludvigsen (1979) suggested that what are here named as

Greenops widderensis, new species, and *B. jennyae* were closely related; however, these taxa are distantly related on the basis of the phylogeny presented in figure 4 and must be treated as constituting totally independent lineages in ENA.

Several meraspid pygidia have been recovered from the Centerfield Limestone at Centerfield, New York and figured in Hall and Clarke (1888). They assigned these meraspids to *D.* (*C.*) *boothi* var. *calliteles*, and one of these is also figured in Delo (1940). Putting aside the problems with whether or not *calliteles* actually occurs in New York, the only species of *Bellacartwrightia* recovered from this horizon is *B. jennyae*, and therefore these meraspids are tentatively assigned to that species. Further evidence for this assignment is that the pygidial pleural lappets bear a greater resemblance to those of *B. jennyae* than to *B. phyllocaudata* or *B. pleione*. Being that the pygidia of *B. jennyae*, *B. whiteleyi*, new species, and *B. calderonae*, new species, are all quite similar, it is conceivable that these meraspids might belong to one of those taxa, but the distributional data are treated as decisive. For these reasons, these meraspids are treated as belonging to *B. jennyae*. In Hall and Clarke's (1888) illustrations, only five pairs of pleural lappets were shown on the pygidia; however, counts of the NYSM specimens figured (4289, 4290, and 4301) produced values that range between six and nine. To correct this inaccuracy, some of these meraspids are illustrated herein (fig. 16.2, 16.3).

Bellacartwrightia phyllocaudata, new species

Figures 10.6, 10.7, 12.1–12.4, 17, 18

Dalmanites (*Cryphaeus*) *boothi* (Green). Hall and Clarke, 1888: 44, pl. 16a, figs. 5–7.

Dalmanites (*Cryphaeus*) *boothi* var. *calliteles* (Green). Hall and Clarke, 1888: 45, pl. 16, figs. 16, 17, pl. 16a, fig. 17.

Cryphaeus boothi var. *calliteles* (Green). Grabau and Shimer, 1910: 330, fig. 1647c.

Greenops boothi (Green). Delo, 1935: 415, fig. 33; Shimer and Shrock, 1944: 647, pl. 274, fig. 12.

Greenops boothi var. *calliteles* (Green). Delo, 1940: 88, pl. 10, fig. 16.

Greenops (*Greenops*) *boothi* var. *calliteles* (Green). Ellison, 1965: pl. 18, fig. 9.

Greenops sp. Speyer, 1988: 134, fig. 10b.

?*Dalmanites* (*Cryphaeus*) *boothi* (Green). Hall and Clarke, 1888: 44, pl. 16, figs. 5–7.

?*Dalmanites boothi* (Green). Hall, 1876: pl. 16, fig. 7.

TYPES: Holotype AMNH 45230, a complete individual from the Deep Run Member (Tioughniogan), Moscow Formation, Hamilton Group, Middle Devonian, Jaycox Run Creek, upstream of Nations Road, south of Avon, Geneseo Township, Livingston County, New York, AMNH locality 3041; paratypes AMNH 45231, a pygidium; 45232, a cephalon; 45233, a cephalon; and 45241, a pygidium; all from the same locality as the holotype.

DIAGNOSIS: Maximum of nine lenses per dorsoventral file on visual surface of eye; fixigena with distinct bulge medially; cephalic posterior border furrow longest (exsag.) posterior to medial visual surface of eyes, deep laterally; S2 roughly transverse, anterior edge weakly convex; posterior edge of visual surfaces anterior to transverse line tangent to L0; visual surfaces in dorsal view present within sagittal line drawn tangent to frontal lobe; S1 medially developed as smooth curve convex posteriorly; line from posterior to anterior edge of eye forms an angle with sagittal line that is approximately 5–10°; anterior margin of frontal glabellar lobe in dorsal view smoothly rounded; PMI developed as rounded depression; spine present on L0; genal spine developed as long flange extending back to sixth thoracic segment; lateral margin of genal spine at posterior end straight; axial furrows anterior to S1 diverge more strongly, but anterior to L3 less strongly divergent; circular fenestrae on thoracic pleural segments absent; medial spine on pygidial and thoracic axial rings present; pygidial axis constricts posterior to sixth axial ring; 15 or 16 pygidial axial rings; in medial region of adjacent pygidial pleural segments, posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; lateral margins of pygidial lappets curved; anterior margins of pygidial axial rings posterior to constriction of pygidial axis smoothly convex anteriorly; anterior and posterior parts of pygidial pleural segments of equal elevation; laterally pygidial inter-

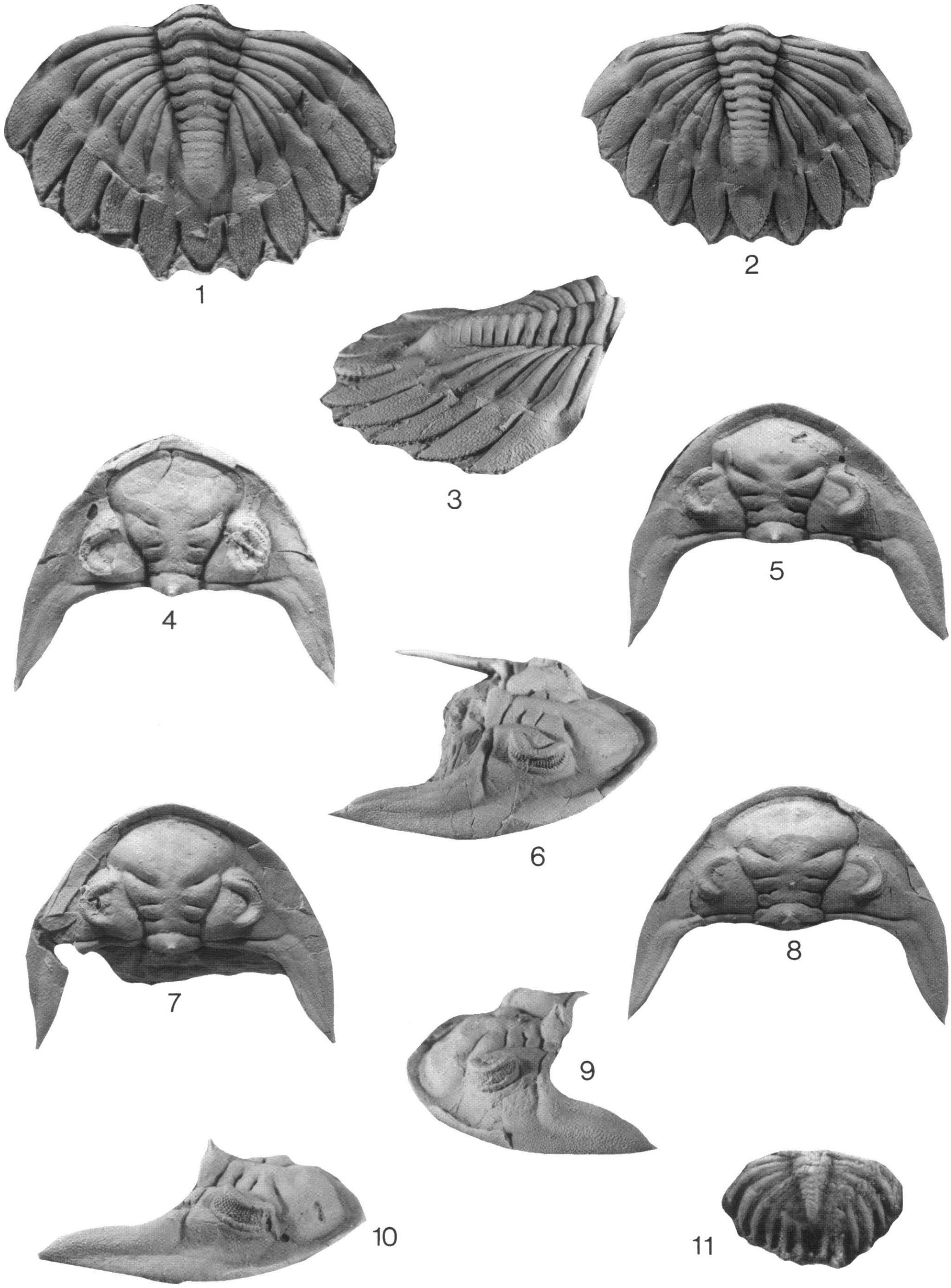

Fig. 17. *Bellacartwrightia phyllocaudata*, new species, Deep Run Member, Moscow Formation, Jaycox Run Creek, near Avon, Geneseo Township, Livingston County, New York. **1**. AMNH 45241, dorsal view of paratype pygidium, ×2.3. **2, 3**. AMNH 45231, dorsal and lateral views of paratype pygidium, ×1.5. **4**. AMNH 45233, dorsal view of paratype cephalon, ×1.9. **5, 10**. YPM 35808, dorsal and lateral views of cephalon, ×1.8. **6, 7**. AMNH 45237, lateral and dorsal views of cephalon, ×1.5. **8, 9**. AMNH 45232, dorsal and lateral views of paratype cephalon, ×1.2. **11**. AMNH 45236, dorsal view of meraspid (M6) pygidium, ×7.

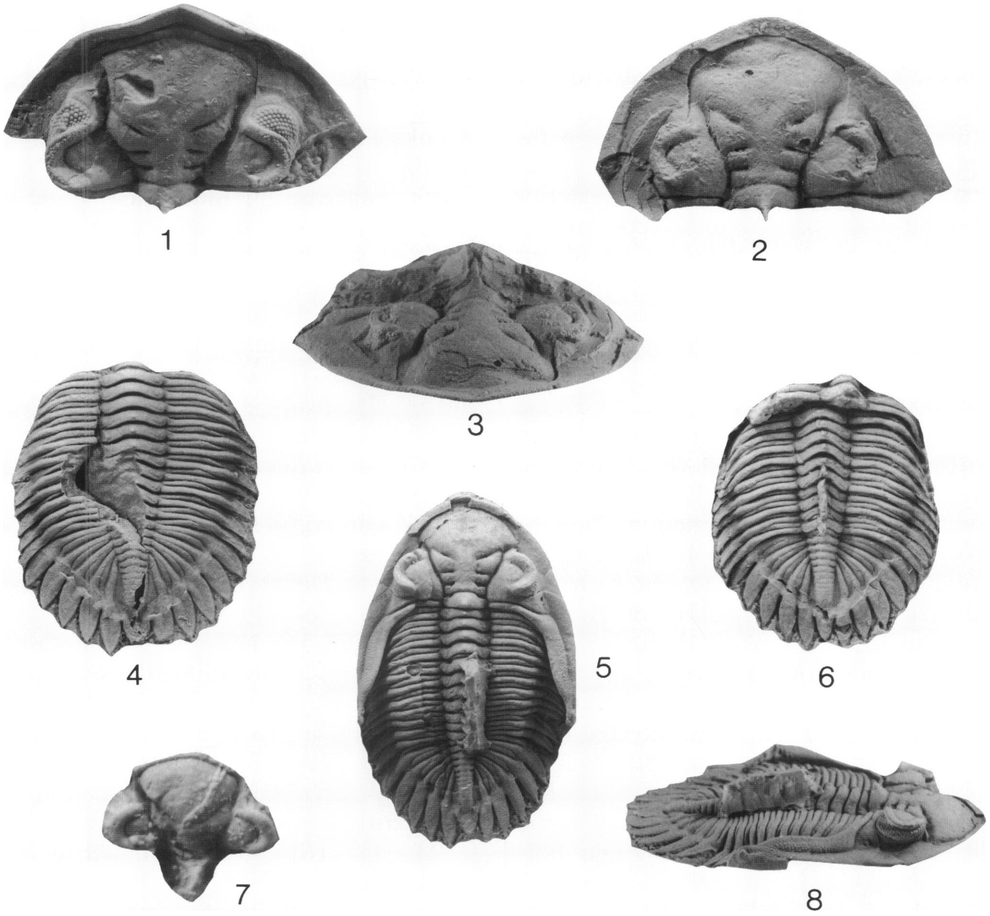

Fig. 18. *Bellacartwrightia phyllocaudata*, new species, Deep Run Member, Moscow Formation, Jaycox Run Creek, near Avon, Geneseo Township, Livingston County, New York. **1**. AMNH 45235, dorsal view of cephalon, ×3. **2, 3**. AMNH 45239, dorsal and anterior views of cephalon, ×1.7. **4**. AMNH 45238, dorsal view of cephalothorax, ×1.5. **5, 8**. AMNH 45230, dorsal and lateral views of complete holotype individual, ×1.9. **6**. AMNH 45240, dorsal view of cephalothorax, ×1.6. **7**. AMNH 45234, dorsal view of small holaspid cephalon, ×8.

pleural furrows flex more strongly posteriorly; terminal pygidial lappet broad.

ETYMOLOGY: This species is named by combining *phyllo* for leafy with *caudata* for tail, describing the leafy appearance of the pygidium of this species.

MATERIAL: AMNH 45230–45240, 45241–45247; NYSM 4285, 4287, 4295, and 4296; YPM 35808, ?33859.

DESCRIPTION: Same as for *Bellacartwrightia jennyae* except: cephalic length (sag.) 50% of width (tr.). Axial furrow diverging more strongly anterior to S1, diverging forward at about 45°, narrow, shallow. Glabellar length equal to 95% of width across frontal lobe; frontal lobe ellipsoid, about 60% of length of glabella; anterior part of frontal lobe smoothly rounded in dorsal view. PMI developed as rounded depression. L3 wedge shaped, bearing isolated tubercles, lengthening distally, outer edge forms smaller angle with sagittal line at anterior end than at posterior end. S2 roughly transverse. L0 45% of width of frontal lobe. Large Eye Index 0.45. Posterior edge of eye opposite S0, anterior to transverse line tangent to L0; maximum of nine lenses per dorsoventral file on visual surface. Postocular fixigenal field 20 percent length of eye. Genal spine developed as very long flange extending back to sixth or seventh thoracic segment; lateral margin of genal spine at posterior end straight.

Thoracic axial ring about 30% of width of thorax. Circular fenestrae absent.

Pygidial length about 60% of width without lappets. Axis with 15 or 16 rings. Anterior margins of pygidial axial rings posterior to constriction of axis smoothly convex anteriorly. Terminal pygidial lappet broad anteriorly. Postaxial region 20% of pygidial length (sag.). Anterior and posterior bands of pleural segments of equal elevation. Laterally pygidial interpleural furrows arch more strongly posteriorly.

DISCUSSION: This species is known from the following localities in the Hamilton Group in the Appalachian Basin of ENA: Windom Shale, Moscow Formation (Tioughniogan), borrow pit near Hatch's Lake, at intersection of Bradley Brook and Soule roads, 3.6 miles south of intersection of Bradley Brook Road and New York Route 26, near Eaton, New York, AMNH locality 3031, and Earlville State Lands, New York; Deep Run Member, Moscow Formation, Jaycox Run, south of Avon, New York, AMNH locality 3041; Moscow Formation, Deep Spring Quarry; Moscow Formation, Canandaigua Lake, New York; Lower Mahantango Formation, Pennsylvania Route 191, about 4 miles north of Stroudsburg, Pennsylvania, AMNH locality 3065; "Centerfield" Member (Tioughniogan), Mahantango Formation, vicinity of Pohopoco Creek, in road cut on county road 2.5 miles east of Mahoning Valley exit of the northeast extension of the Pennsylvania Turnpike, near Forest Inn, Pennsylvania, AMNH locality 3068; Donation Member, Mahantango Formation, road cut along U.S. Route 22, opposite Huntingdon, Pennsylvania, AMNH locality 3072; upper Frame Member, borrow pit along road, south flank of Mahanoy Ridge, east from Pennsylvania Route 34, south of New Bloomfield, Pennsylvania, AMNH locality 3071; and ?the Onondaga Limestone (Southwoodian), near Buffalo, New York.

The material that Hall and Clarke (1888) assigned to *Dalmanites* (*Cryphaeus*) *boothi* var. *calliteles* (Green, 1837), as mentioned above, cannot be assigned to that species because the original types were lost, and the material Hall and Clarke (1888) used was not from the type locality and cannot be demonstrably shown to be identical to Green's (1837) type material. However, over the years, several authors have followed Hall and Clarke (1888) and recognized a *boothi* var. *calliteles* in the Hamilton Group of New York, engendering much taxonomic confusion because the material they figured, the bulk of which is housed in the NYSM, actually belongs to several different species. The majority of the material they illustrated and collected actually belongs to *B. jennyae*, new species. However, some of the specimens classically treated as *calliteles*, i.e., those illustrated by Delo (1940) as *Greenops boothi* var. *calliteles*, and those illustrated by Grabau and Shimer (1910) as *Cryphaeus boothi* var. *calliteles* are assigned herein to a new species, *B. phyllocaudata*. Of three specimens Delo (1940) illustrated and assigned to *Greenops boothi* var. *calliteles* (pl. 10, figs. 13, 16, 19), one is a meraspid pygidium that, as mentioned above, probably belongs to *B. jennyae* (Delo's [1940] fig. 19), another, his fig. 13, is a new species from the Kashong Shale of the Hamilton Group that will be described in a forthcoming paper (Lieberman and Kloc, in prep.), and Delo's (1940, fig. 16) can be assigned to *B. phyllocaudata*.

Some specimens of *B. phyllocaudata* are known from Huntingdon, Pennsylvania, at AMNH locality 3072, but this is not equivalent to Green's (1837) locality. When material is recovered from Green's (1837) type locality, it will be possible to designate a neotype for *B. calliteles*. Until that time, that species name must be avoided. *Bellacartwrightia phyllocaudata* and *B. jennyae* differ in the condition of several characters, including: the pygidial pleural lappets, which are rounded in *B. jennyae* and flattened in *B. phyllocaudata*; the greater relative length (exsag.) of the genal spines in *B. jennyae*; the greater relative incision of the pygidial pleural furrows in *B. jennyae*; the relatively broader terminal pygidial lappet in *B. phyllocaudata*; the anterior and posterior portions of adjacent pygidial pleural segments are of equal elevation in *B. phyllocaudata*, whereas in *B. jennyae* the posterior part is elevated above the anterior portion; and in *B. phyllocaudata*, there are a maximum of nine lenses in a dorsoventral file on the visual surfaces, whereas in *B. jennyae* there are a maximum of 10 lenses in a dorsoventral file.

Although *Bellacartwrightia phyllocaudata* and *G. boothi* (Green, 1837) differ in the condition of a significant number of characters, there also has been considerable confusion regarding the identification and discrimination of specimens of *B. phyllocaudata* from *G. boothi*. However, the diagnostic characters for the two taxa presented herein may offer a way of consistently determining the identity of asteropyginid fossils in ENA.

Ellison (1965) suggested that his *Greenops (G.) boothi* var. *calliteles*—actually what is illustrated is a specimen of *B. phyllocaudata*—and *G. boothi* are sexual dimorphs because they generally appear together. This is not true for the Pennsylvania section according to the appendices in the back of Ellison (1965), and it is certainly not true for the New York section. In addition, their are numerous differences between the two taxa which are elaborated below under the heading of *G. boothi*. Thus, this hypothesis is highly unlikely and is not treated as valid herein.

Hall and Clarke (1888) figured some specimens that they identified as early ontogenetic stages of a species they referred to as var. *calliteles*, and a portion of this species is treated herein as *B. phyllocaudata*. However, these specimens hail from a locality in the Centerfield Limestone, from which only specimens of *B. jennyae*, new species, are known. Because of this, and because of certain morphological similarities in the pygidia, such as the rounded terminal lappets, these meraspids are referred to *B. jennyae*.

Hall and Clarke (1888) also reported the presence of *B. phyllocaudata* in the Onondaga Limestone of western New York. No material from this horizon has since been recovered, and this stratigraphic assignment for this taxon remains unsubstantiated, though not impossible, as specimens of the closely related *Bellacartwrightia pleione* (Hall) and *B. jennyae*, new species, are known from the Onondaga Limestone of the Appalachian and Illinois Basins.

Bellacartwrightia pleione (Hall, 1861)

Figure 13.1–13.3

Dalmania pleione Hall, 1861: 62; Hall, 1862: 90.

Dalmanites pleione (Hall). Hall, 1876: pl. 16, fig. 17.

Dalmanites (Cryphaeus) pleione (Hall). Hall and Clarke, 1888: 41, pl. 16a, fig. 2.

Greenops pleione (Hall). Delo, 1940: 90, pl. 10, fig. 20.

?*Dalmanites (Cryphaeus) boothi* var. *calliteles* (Green). Hall and Clarke, 1888: 45, pl. 16a, fig. 9.

?*Dalmanites (Cryphaeus) boothi* (Green). Hall and Clarke, 1888: 44, pl. 16a, fig. 4.

TYPES: As stated in Delo (1940), the holotype of the species is AMNH 4248 by monotypy, known from the Jeffersonville Limestone (Southwoodian), Falls of the Ohio River, near Louisville, Kentucky. A holotype can be designated because only a single specimen existed in the original type series of Hall (1861). This specimen is figured in Hall and Clarke (1888, pl. 16a, fig. 2) and also herein as figure 13.3.

DIAGNOSIS: Same as for genus, and: lateral margins of pygidial pleural lappets straight; pygidial axis constricts posterior to fifth axial ring; 15 pygidial axial rings; tubercle on medial portion of pygidial and thoracic axial rings; anterior margins of pygidial axial rings, posterior to constriction of pygidial axis, smoothly convex; posterior portion of pygidial pleural segments elevated above anterior portion; laterally pygidial interpleural furrows flex more strongly posteriorly; in medial region of adjacent pleural segments, posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment; terminal pygidial lappet narrow; one row of circular fenestrae on anterior band of thoracic pleural segments; on posterior band, two circular fenestrae close to axis.

MATERIAL: AMNH 4248, 45252, 45253; YPM 33779–33782.

DISCUSSION: This species is known from the following stratigraphic horizon and locality in the Illinois Basin: the Jeffersonville Limestone (Southwoodian), Falls of the Ohio River, near Louisville, Kentucky. It is known from the following horizons and localities in the Appalachian Basin of ENA: ?Onondaga

Limestone (Southwoodian), Leroy, New York; Windom Shale, Moscow Formation, borrow pit near Hatch's Lake, at intersection of Bradley Brook and Soule roads, 3.6 miles south of intersection of Bradley Brook Road and New York Route 26, near Eaton, New York, AMNH locality 3031; Deep Run Member (Tioughniogan), Moscow Formation, Jaycox Run, Avon, New York; the Portland Point Member, Moscow Formation, Lansing, New York; the Windom Member, Moscow Formation, Little Beard's Creek, 0.5 mile east of Trailer Park Road, Leicester, Livingston County, New York; Tully Limestone (Taghanic), Carpenter Road, 1 mile from "T" intersection with New York Route 80, south of Sheds, New York, AMNH Locality 3040; ?Frame Member (Tioughniogan), upper Mahantango Formation, roadcut along U.S. Route 22, opposite Huntingdon, Pennsylvania, AMNH locality 3072; ?Moscow Formation, Canandaigua Lake, New York; and at unspecified stratigraphic positions within the Hamilton Group at York and Ludlowville, New York. It is based exclusively on pygidial characteristics. However, there do exist isolated cephala associated with pygidia of *B. pleione* (YPM 33781, 33782) that are clearly asteropyginid in nature, but these are too poorly preserved to allow character analysis.

Hall and Clarke (1888) suggested that this species was very closely related to the species they treated as *D.* (*C.*) *boothi* var. *calliteles*, and that species actually appears to represent several species, none of which can be treated as Green's (1837) *Cryphaeus calliteles*. However, some of Hall and Clarke's (1888) material is treated herein as *Bellacartwrightia phyllocaudata* and *B. jennyae*, and these are held to be closely related to *B. pleione*. Hall and Clarke (1888) also commented that the adult state of *B. pleione* closely resembled the pygidia of what are treated here as juveniles of *B. jennyae*. However, *H. pleione* does not bear such a close resemblance to juveniles of *B. jennyae*, having a longer and more pronounced terminal pygidial lappet, as well as longer pleural lappets, with the fifth pleural lappet deflected the furthest posteriorly. However, again, Hall and Clarke (1888) do appear to be correct in asserting the close relationship between *B. phyllocaudata*, *B. jennyae*, and *B. pleione*. *Bellacartwrightia pleione* could not be incorporated into the phylogenetic analysis and thus it could not be determined whether it shared a sister group relationship with the other species of *Bellacartwrightia*, but shared characters do suggest that they are narrowly separated branches within a common stem lineage.

Bellacartwrightia whiteleyi, new species

Figures 12.6, 19

TYPES: Holotype AMNH 45313, a complete specimen from the Murder Creek Beds, the Wanakah Shale Member (Tioughniogan), Ludlowville Formation, Hamilton Group, Middle Devonian, Darien, New York; paratypes AMNH 45314, a complete specimen, and 45315, a cephalothorax, both from the same locality as the holotype, and 45293, a small cephalon from a loose concretion somewhere in the upper Wanakah Shale Member, along the shore of Lake Erie, south of 18 Mile Creek, Hamburg, New York, and 45294, from the Wanakah Shale Member, Murder Creek Beds, Lake Erie Shore, north of 18 Mile Creek, Hamburg, New York.

DIAGNOSIS: S2 weakly declined posteriorly at lateral edge; S1 medially developed as smooth curve convex posteriorly; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; maximum of eight lenses per dorsoventral file on visual surface; anterior margin of frontal glabellar lobe in dorsal view smoothly rounded; spine on L0; PMI developed as rounded depression; line from posterior to anterior edge of eye forms 5–10° angle with sagittal line; genal spine developed as long flange extending back to sixth or seventh thoracic segment; lateral margin of genal spine at posterior end straight; axial furrows diverge more strongly anterior to S1, diverge less strongly anterior to anterior half of L3; visual surfaces in dorsal view not present within sagittal line drawn tangent to frontal lobe; two transverse rows of circular fenestrae on anterior band of thoracic pleural segments, one transverse row on posterior band; spine on medial portions of pygidial and thoracic axial rings; lateral margins of pygidial pleural lappets

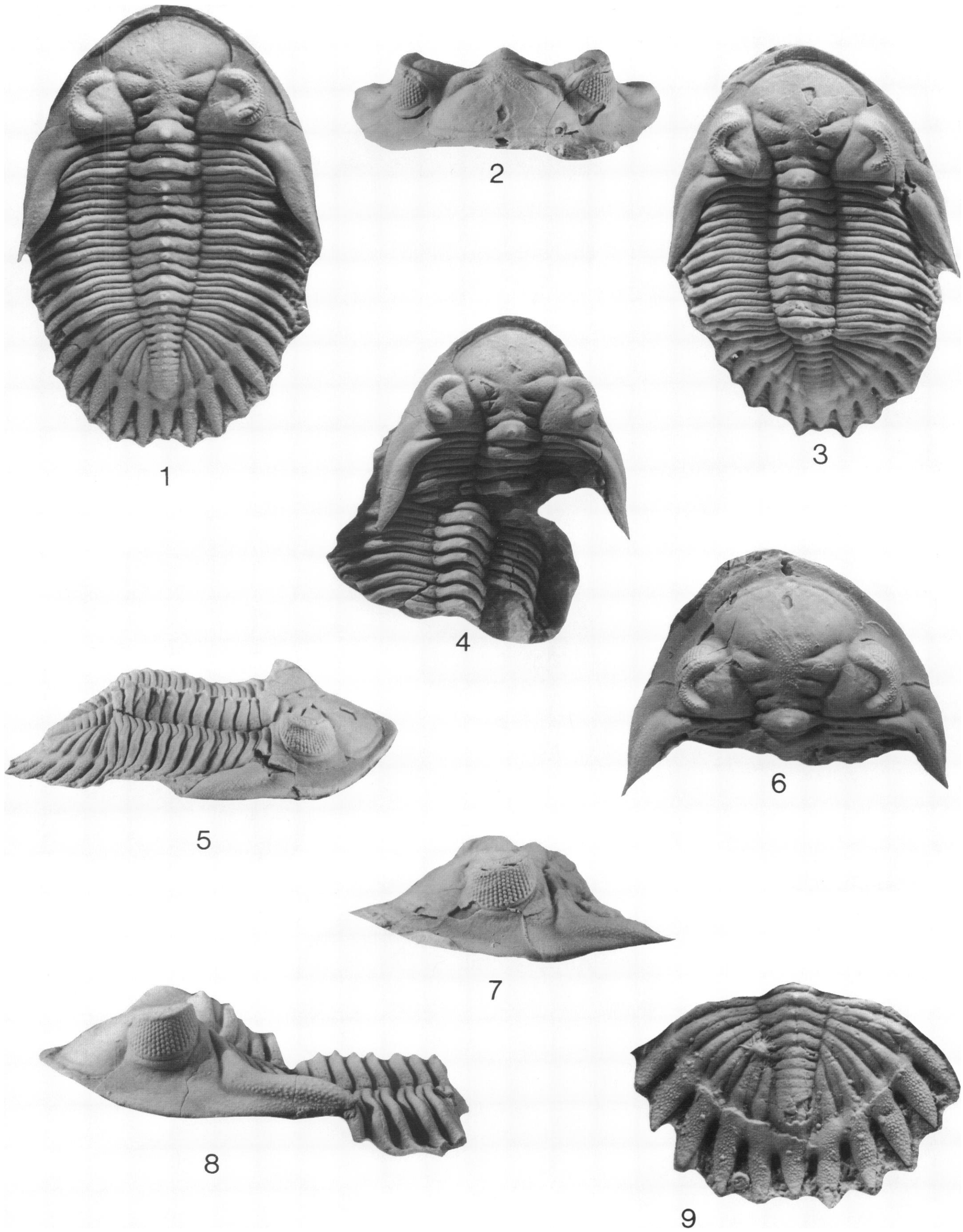

Fig. 19. *Bellacartwrightia whiteleyi*, new species, Wanakah Shale, Ludlowville Formation, New York. **1**. Murder Creek Beds, Darien, AMNH 45314, dorsal view of complete paratype individual, ×2.5. **2, 6, 7**. Upper Wanakah Shale, loose concretion along Lake Erie Shore south of 18 Mile Creek, AMNH 45293, anterior, dorsal, and lateral views of paratype cephalon, ×2.5. **3, 5**. Murder Creek Beds, Darien, AMNH 45313, dorsal and lateral views of compete holotype individual, ×2. **4, 8**. Murder Creek Beds, Darien, AMNH 45315, dorsal and lateral views of complete cephalon and partial thorax, ×2. **9**. Murder Creek Bed, Lake Erie Shore, north of 18 Mile Creek, AMNH 45294, dorsal view of paratype pygidium, ×3.

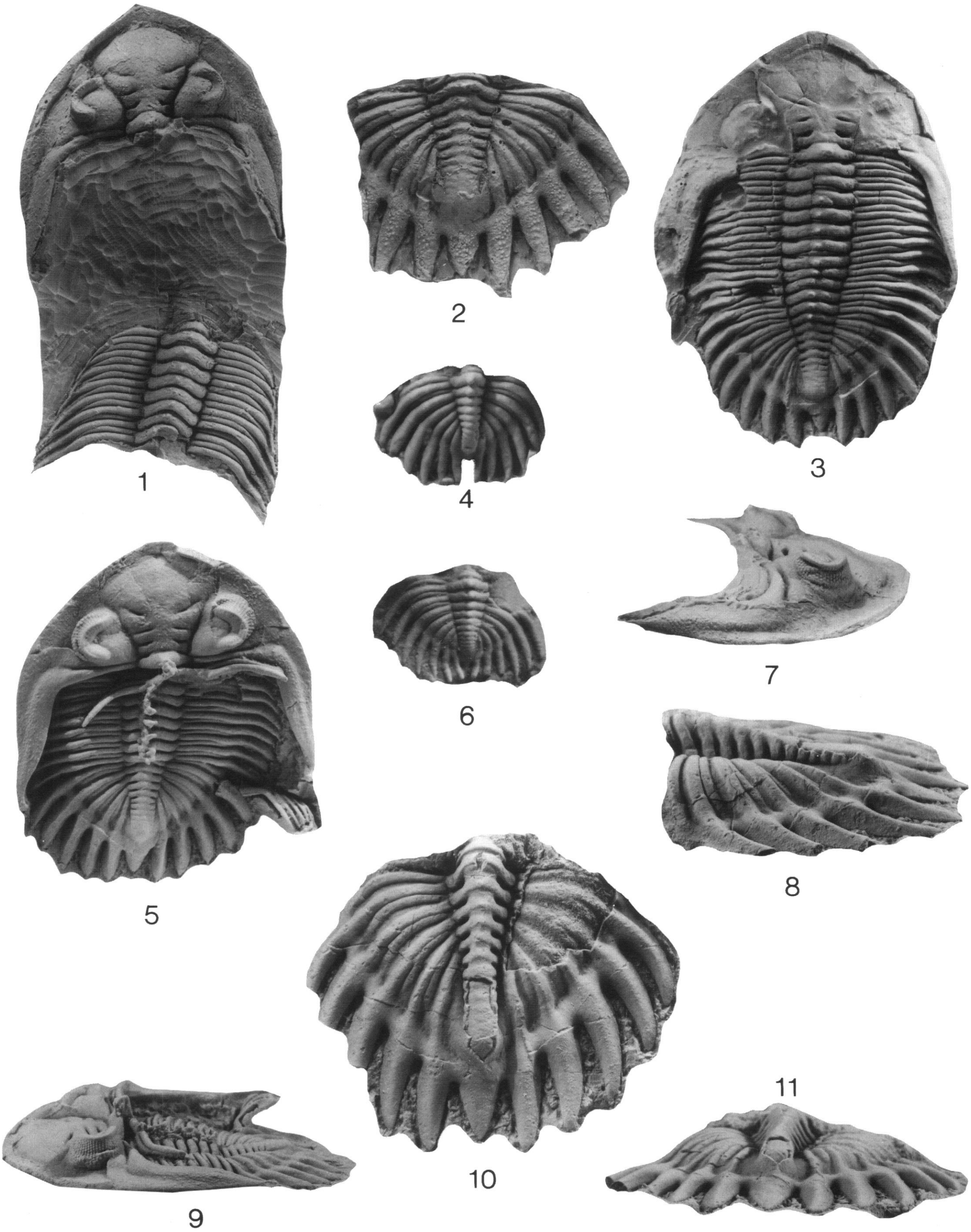

Fig. 20. *Bellacartwrightia*, spp. **1, 2, 7**. *Bellacartwrightia calderonae*, new species, Windom Shale, Moscow Formation, 2–4 feet below the Taunton Beds, Kashong Glen, west side of Seneca Lake, Bellona, New York. **1**. AMNH 45273, dorsal view of disarticulated cephalon and thorax of holotype individual, ×1.5. **2**. AMNH 45273, dorsal view of disarticulated pygidium of holotype individual, ×2. **7**. AMNH 45273, lateral view of disarticulated cephalon of holotype individual, ×1.5. **3–6, 8–11**. *Bellacartwrightia jennyae*, new species, Centerfield Limestone, Ludlowville Formation, New York. **3**. Brown's Creek, York, AMNH 45312, dorsal view of complete holotype individual, ×2.2. **4**. Salt Creek Bed, Schaffer

curved; pygidial axis constricts posterior to sixth axial ring; anterior margins of pygidial axial rings posterior to constriction of pygidial axis straight; posterior part of pygidial pleural segment elevated above anterior part; laterally pygidial interpleural furrows arch at same angle as medially; in medial region of adjacent pleural segments posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; 14 pygidial axial rings; terminal pygidial lappet narrow.

ETYMOLOGY: Named for T. Whiteley, Rochester, New York who found the type material used to define this species and who generously donated the material to the AMNH.

MATERIAL: AMNH 45293, 45294, 45313–45315.

DESCRIPTION: Same as for *B. jennyae*, except: cephalic length (sag.) 60 percent of width. Axial furrow nearly straight anterior to S1, diverging forward at about 35°, narrow, shallow; posterior to S1 diverging at 10°; diverging less strongly opposite anterior half of L3 than opposite posterior half. Frontal lobe about 60% of length of glabella. PMI developed as rounded depression. L0 45% of width of frontal lobe. Large Eye Index 0.58. Anterior edge of eye contacts axial furrow opposite anterodistal corner of L3. Maximum of eight lenses per dorsoventral file on visual surface. Fixigena with bulge medially. Genal spine developed as long flange extending back to sixth or seventh thoracic segment.

Two transverse rows of circular fenestrae on anterior band of thoracic pleural segments.

Pygidial length about 60% of width without lappets. Axis 25% of pygidial width anteriorly.

DISCUSSION: This species is known from the Murder Creek Bed, Wanakah Shale (Tioughniogan), Ludlowville Formation, Murder Creek, Darien, New York, and the same horizon from the Lake Erie Shore, New York, and below the Murder Creek Bed, Smoke Creek, Windom, New York. This species shows prominent similarity to *B. jennyae*, and these taxa are closely related, although not sister taxa. *Bellacartwrightia jennyae* precedes *B. whiteleyi* in the fossil record, and based on phylogenetic topology, it is conceivable that *B. jennyae* is ancestral to *B. whiteleyi*, although they do differ in the condition of a number of characters such that transformation between the two species might not be perceived as "easy." *Bellacartwrightia whiteleyi* could in turn be ancestral to *B. calderonae*, which follows it in the fossil record. However, this hypothesis would require that *B. phyllocaudata* follow *B. whiteleyi* in the fossil record, and this necessitates discarding the questionable occurrences of *B. phyllocaudata* in the Onondaga Limestone.

In *B. whiteleyi*, there may be some variation in the number of lenses per dorsoventral file on the visual surface, with most specimens showing a maximum of eight lenses per dorsoventral file on the visual surface, and one specimen preserving a maximum of nine lenses per dorsoventral file on the visual surface. For the purposes of the phylogenetic analysis conducted herein, this taxon was scored as having a maximum of eight lenses per dorsoventral file.

***Bellacartwrightia calderonae*, new species**

Figures 13.4, 20.1, 20.2

TYPES: Holotype AMNH 45273, a complete specimen from the Windom Shale (Tioughniogan), Moscow Formation, Hamilton Group, Middle Devonian, 2–4 feet below the Taunton Beds, Kashong Glen, west side of Seneca Lake, Bellona, New York.

DIAGNOSIS: S2 roughly transverse, weakly convex anteriorly; S1 medially developed as curve convex posteriorly; posterior edge of visual surfaces anterior to transverse line tangent to anterior edge of L0; maximum of

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Creek, Centerfield, AMNH 45295, dorsal view of meraspid pygidium, ×9. **5, 9**. Brown's Creek, York, AMNH 45310, dorsal and lateral views of complete paratype individual, ×2.2. **6**. Brown's Creek, York, AMNH 45296, dorsal view of meraspid pygidium, ×10. **8, 10, 11**. Brown's Creek, York, AMNH 45311, lateral, dorsal, and posterior views of pygidium, ×2.6.

eight lenses per dorsoventral file on visual surface; anterior margin of frontal glabellar lobe smoothly rounded; fixigena with distinct bulge medially; L0 with tubercle medially; PMI developed as rounded depression; line from posterior to anterior edge of eye forms 30° angle with sagittal line; genal spines developed as very long flanges extending back to eighth thoracic segment; lateral margin of genal spine at posterior end straight; cephalic axial furrows equally divergent anterior to S0, less strongly divergent anterior to anterior half of L3; visual surfaces in dorsal view present within sagittal line drawn tangent to frontal lobe; tubercle on medial portions of pygidial and thoracic axial rings; lateral margins of pygidial pleural lappets curving; anterior margins of pygidial axial rings posterior to seventh axial ring straight; pygidial axis constricts posterior to seventh axial ring; posterior parts of pygidial pleural segments elevated above anterior parts; laterally pygidial interpleural furrows flex more strongly posteriorly; in medial region of adjacent pleural segments posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; 14 pygidial axial rings; terminal pygidial lappet narrow; circular fenestrae on thoracic pleural segments absent.

ETYMOLOGY: Named for Mrs. Iris Calderon, Department of Invertebrates, AMNH.

MATERIAL: AMNH 29215, 45273.

DESCRIPTION: Same as for *B. jennyae*, except: cephalic length (sag.) 45% of width (tr.). Axial furrows nearly straight anterior to S1, diverging forward at about 35°, narrow, shallow; posterior to S1 diverging at 10°; diverging less strongly opposite anterior half of L3 than opposite posterior half. Frontal lobe about 50% of length of glabella, anterior margin smoothly rounded. PMI developed as rounded depression. L0 45% of width of frontal lobe. Large Eye Index 0.45. Anterior edge of eye contacts axial furrow opposite anterodistal corner of L3. S2 weakly declined posteriorly at lateral edges; S1 medially developed as straight line directed anteriorly. Maximum of eight lenses per dorsoventral file on visual surface; posterior edge of eye anterior to transverse line tangent to anterior edge of L0. Fixigena with bulge medially. Line from posterior to anterior edges of eye forms 5–10° angle with sagittal line. Lateral margin of genal spine at posterior end straight. Tubercle on L0.

Tubercle on thoracic axial rings. Circular fenestrae on thoracic pleural bands and axial rings absent.

Medial tubercle on pygidial axial rings. Axis constricts posterior to seventh axial ring. Laterally pygidial interpleural furrows flex more strongly posteriorly.

DISCUSSION: This species is known from the following locality in the Appalachian Basin of ENA: Windom Shale (Tioughniogan), Moscow Formation, 2–4 feet below Taunton Beds, Kashong Glen, west side of Seneca Lake, Bellona, NY, and from an unspecified stratigraphic horizon at Kashong Glen, on the west side of Seneca Lake. This species is very similar to *B. jennyae* and *B. whiteleyi*, but these taxa have diagnosable differences and hail from different stratigraphic horizons, and thus they should be treated as separate species. In particular, the anterior border of *B. calderonae* is much longer (sag.) than that of the other taxa. The specimen illustrated in figure 13.4 is poorly preserved but appears referable to *B. calderonae* on the basis of its long, flattened anterior cephalic border and other characters that match those found in the holotype of the species. However, the pygidial pleural lappets may be slightly longer than those found in the holotype.

COLTRANEIA, NEW GENUS

TYPE SPECIES: *Treveropyge celtica* Morzadec, 1969.

ASSIGNED TAXA: None (monotypic).

DIAGNOSIS: S3 faintly sinusoidal; cephalic posterior border furrow longest (sag.) posterior to medial visual surface of eyes; S1 deep curved pit; anterior margin of frontal glabellar lobe transverse; anterior cephalic border transverse medially, medially flexing dorsally; genal spine developed as short triangular projection; maximum of 13 lenses per dorsoventral file on visual surface; PMI developed as rounded depression; line from anterior to posterior edge of eye roughly parallels sagittal line; axial furrows diverge at constant angle; terminal pygidial lappet very reduced; lateral and medial margins of pygidial pleural lappets curved; pygidial axis constricts posterior to sixth axial ring.

ETYMOLOGY: Named for the jazz saxophonist John Coltrane.

DISCUSSION: This genus contains a single species, *Coltraneia celtica* (Morzadec, 1969), which had traditionally been assigned to the genus *Treveropyge*. However, this species differs from the type of the genus *Treveropyge* in the condition of the following characters: 3, 5, 7, 8, 9, 10, 11, 12, 20, 23, 31, 40, 45, 46, 50, 52, 57, 59, 60, and 63, and therefore cannot be assigned to that taxon. The new genus is sister to a clade including *Bradocryphaeus* Haas and Mensink, 1969, and *Heliopyge* Haas and Mensink, 1969, on the basis of the following shared characters: S2 weakly declined posteriorly at lateral edge; S1 crescent shaped, smooth curve convex posteriorly; medially anterior cephalic border pointed in dorsal view, not deflected far beyond lateral margins of cephalon; posterior margin of palpebrum deflected at an angle to transverse line that is significantly larger than at anterior margin; line from posterior to anterior edge of eye forms an angle to sagittal line that is approximately 5–10°; significant change in cephalic topography where lateral border furrow and librigenae meet; lateral margin of genal spine forms line that departs from sagittal line by about 15–20°, at posterior end straight; interior margin of genal spine evenly deflected laterally; axial furrows less strongly divergent at anterior half of L3 relative to posterior half; no ornament on medial part of pygidial and thoracic axial rings; lateral and medial margins of pygidial lappets curved, distal tips pointed; tops of pygidial pleural segments rounded; anterolateral margins of first five pygidial axial rings evenly convex and not arching strongly anteriorly; longest pygidial lappet longer (exsag.) than length (sag.) of the first three pygidial axial rings. A monotypic genus was erected rather than placing *C. celtica* in the genus *Bradocryphaeus* or *Heliopyge* because the species differed in the condition of several characters diagnostic for those genera. At this point, no additional taxa can be found that fit the diagnosis of the genus *Coltraneia*.

Coltraneia celtica (Morzadec, 1969)

Treveropyge celtica Morzadec, 1969: 37, pl. 6, fig. 4; Morzadec, 1983: 118, pl. 5, figs. 1–10.
?*Treveropyge celtica* Morzadec, 1969: 38, pl. 6, fig. 5. *Treveropyge* sp. Morzadec, 1969: 39, pl. 6, fig. 6.

TYPES: Holotype defined in Morzadec (1983: pl. 5, fig. 1).

DIAGNOSIS: Same as for genus.

DISCUSSION: This species is known from the upper Emsian of the Armorican Massif.

BRADOCRYPHAEUS
HAAS AND MENSINK, 1969

TYPE SPECIES: *Cryphaeus supradevonicus* Frech, 1888.

ASSIGNED TAXA: *Neocalmonia* (*Bradocryphaeus*) *afghanica* Haas and Mensink, 1969.

DIAGNOSIS: See Haas and Mensink (1969).

DISCUSSION: The species in this genus are known from the upper Eifelian and Givetian of western Afghanistan and the Givetian and Frasnian of Belgium. On the basis of the diagnosis of Haas and Mensink (1969), as well as the characters of the species *Neocalmonia* (*Bradocryphaeus*) *afghanica*, which they figure, it appears that a range of taxa assigned by several authors to *Bradocryphaeus* can no longer be placed in that genus. In particular, *Neocalmonia* (*Bradocryphaeus*) *psilus* Haas, 1970, does not have the third pair of pygidial pleural lappets projecting furthest posteriorly, does not have the fifth pair of pygidial pleural lappets merging with the terminal pygidial axis, does not have the narrow terminal pygidial lappet, and does not have the prominent constriction of the pygidial axis posterior to the fifth axial ring characteristic of *Bradocryphaeus*; however, it does have S3 straight, the lateral edge of S2 weakly declined posteriorly, and the PMI developed as a rounded depression, also characteristic of *Bradocryphaeus*. At present, it is excluded from *Bradocryphaeus* until more detailed study of this material is possible. Gandl's (1972) *Neocalmonia* (*Bradocryphaeus*) sp. cf. *mosana* (Richter and Richter, 1926) has the fifth pair of pygidial pleural lappets merging with the terminal pygidial lappet, the narrow terminal pygidial lappet, and the prominent constriction of the pygidial axis posterior to the fifth axial ring; however, the third pair of pygidial pleural lappets does not project furthest posteriorly. The cephalon of this species is too poorly preserved to permit detailed character comparisons. At present, it is also excluded from *Bradocryphaeus* until better material is available for study. Gandl (1972) erected a new subgenus, *Neocalmonia* (*Quadratispina*), based on the type *N.* (*Q.*) *quadratispinosa*, that bears several similarities to *Bradocryphaeus afghanica*. In the type of this subgenus, as in *B. afghanica*, the terminal pygidial lappet is very narrow, the fifth pair of pygidial pleural lappets does merge with the terminal pygidial lappet, and the third pair of pygidial pleural lappets projects furthest posteriorly; however, the pygidial axis constricts posterior to the sixth pygidial axis in the type species of *Quadratispina*. This subgenus is probably very closely related to *Bradocryphaeus*; however, because good material could not be obtained, it was not subjected to phylogenetic analysis herein. Its phylogenetic position will be considered at a later date.

Smeenk (1983) figured and assigned several species to *Bradocryphaeus*. For instance, he assigned the type of *Quadratispina*, or *Neocalmonia* (*Q.*), *Q. quadratispinosa*, to *Bradocryphaeus*. Another one of the species he assigned to *Bradocryphaeus* is treated herein as *Hallandclarkeops cantarmoricus*. This species is not closely related to *Bradocryphaeus afghanica*. Instead, *H. cantarmoricus* is part of a larger clade that is in turn sister to a clade including *Bradocryphaeus*. "*Bradocryphaeus*" *matallanensis* Smeenk, 1983 lacks the narrow terminal pygidial lappet, does not have the fifth pair of pygidial pleural lappets merging with the terminal pygidial lappet, does not have the third pair of pygidial pleural lappets projecting furthest posteriorly, and does not have the prominent constriction of the pygidial axis posterior to the fifth axial ring. For these reasons it is provisionally excluded from *Bradocryphaeus*. "*Bradocryphaeus*" *sexispiniferus* Smeenk, 1983 is also excluded from *Bradocryphaeus* for similar reasons. In addition, specimens figured by Morzadec that he assigned to *Bradocryphaeus*, such as "*B.*" *fiacrensis* (Morzadec *in* Babin et al., 1977) and "*B.*" *feisti* Morzadec, 1992, also must be excluded from *Bradocryphaeus* because they lack the characteristic morphological features of *Bradocryphaeus* stressed above.

Unfortunately, the type of the genus could not be obtained for the purposes of phylogenetic analysis. A taxon assigned to this species by the authors of the genus, in the publication where the new genus was first presented, was used instead. It is conceivable that some of the taxa that above were excluded from the genus *Bradocryphaeus* might be referable to that genus if the type of the genus was found to differ significantly from *B. afghanica*. However, this is probably unlikely.

Originally, *Bradocryphaeus* was treated as a subgenus of *Neocalmonia*. This taxonomic decision is not acceptable because these two genera are distantly related.

Several authors have commented on the phylogenetic placement of the genus *Bradocryphaeus*. In the case of several of these authors, doubtless their phylogenetic perspective on *Bradocryphaeus* is confused because the range of taxa they assign to that genus does not appear to coincide with the conception of the genus based on morphological and phylogenetic evidence presented in Haas and Mensink (1969) and herein. However, a brief overview is instructive and can be found in the discussions of *Neocalmonia* and *Heliopyge*.

Bradocryphaeus afghanica
Haas and Mensink, 1969

Neocalmonia (*Bradocryphaeus*) *afghanica* Haas and Mensink, 1969: 166, pl. 1, figs. 1, 2, pl. 2, fig. 1, text fig. 4.

TYPES: Holotype figured in Haas and Mensink (1969: pl. 1, fig. 2).

DIAGNOSIS: S3 straight; lateral edge of S2 weakly declined posteriorly; maximum of seven lenses per dorsoventral file on visual surface; distance between frontal lobe and facial suture constant from lateral edges to midline; anterior cephalic border medially not deflected anteriorly beyond lateral margins of cephalon; PMI developed as rounded depression; axial furrows diverge more strongly anterior to S1 than posterior to S1; cephalic posterior border furrow straight distally; lateral to eye facial suture, before flexing posteriorly, flexes anteriorly to point opposite S2; anterior cephalic border in dorsal view pointed medially; fixigena with distinct bulge medially; posterior margin of palpebrum relative to anterior margin deflected at angles with transverse line that are roughly equivalent; demarcation between librigena and lateral border furrow prominent; prosopon of coarse tubercles; genal spine developed as short triangular projection; lateral margin of genal spine evenly inclined, departs from sagittal line by about 15-20°; terminal pygidial lappet triangular, very narrow; lateral and medial margins of pygidial lappets curved; distal tips of pygidial lappets pointed; posterior pleural field flanking posterior portion of pygidial axis moderately excavated; posterior part of pleural segments elevated above anterior parts; tops of pygidial pleural segments rounded; pygidial pleural furrows long (exsag.); laterally pygidial interpleural furrows arching at same angle as medially; in medial region of adjacent pleural segments, posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; anterolateral margins of first five pygidial axial rings do not arch strongly anteriorly; pygidial lappets long; third pygidial lappet projects furthest posteriorly.

DISCUSSION: This species is known from the upper Eifelian and Givetian of Afghanistan. It was used to epitomize the genus *Bradocryphaeus* in the phylogenetic analysis because it offered the best material of the genus that could be obtained, it matched the original diagnosis of *Bradocryphaeus*, and it was published in the work in which the taxon *Bradocryphaeus* was erected.

HELIOPYGE HAAS AND MENSINK, 1969

TYPE SPECIES: *Asteropyge* (*Comura*) *helios* Richter and Richter, 1926.

ASSIGNED TAXA: *Neocalmonia* (*Heliopyge*) *caelata* Haas and Mensink, 1969, *Asteropyge* (*Asteropyge*) *hispanica* Richter and Richter, 1926, *Heliopyge troaonensis* Morzadec, 1983, *Heliopyge*, new species aff. *helios* (Richter and Richter, 1926), *Neocalmonia* (*Heliopyge*) *turolensis* Gandl, 1972, and *Heliopyge porsguenensis* Morzadec, 1983.

DIAGNOSIS: S3 straight; S2 weakly declined posteriorly at lateral edge; S1 crescent shaped, medial part developed as smooth curve, convex posteriorly; posterior edge of visual surfaces anterior to transverse line tangent to L0; lateral to eye, facial suture before flexing posteriorly flexes anteriorly to point opposite S2; distance between frontal lobe and facial suture constant from lateral edge to midline; tubercle on L0 present; anterior cephalic border not deflected far anteriorly medially; PMI developed as rounded depression; posterior margin of palpebrum relative to anterior margin deflected at angles with transverse line that are roughly equivalent; line from posterior to anterior edge of eye intersects sagittal line at roughly 0-5° angle; prosopon of fine tubercles; isolated patches of coarse tubercles present on eye ridge, L3, L2, and frontal lobe; genal spine developed as long flange extending back to sixth thoracic segment; medially genal spine developed as flattened ledge, laterally evenly inclined; medial edge of genal spine significantly thickened relative to lateral edge; axial furrows diverge more strongly anterior to S1 than posterior to S1; broad ledge of anterior cephalic border visible anterior to anterolateral positions of frontal lobe; terminal pygidial lappet teardrop shaped, narrow; lateral and medial margins of pygidial lappets curved, lappets long; anterior margins of pygidial axial rings posterior to fifth ring smoothly convex anteriorly; pygidial pleural field flanking posterior portion of axis moderately excavated; tops of pygidial pleural segments rounded; at pygidial margins, surface of pygidium dorsally inflates at contact of lappets and margins; laterally, pygidial interpleural furrows arch at same angle as medially; anterolateral margins of first five pygidial axial rings proceeding from axial furrows to midline do not arch strongly anteriorly; five pairs of pygidial pleural lappets; third pair of pygidial pleural lappets projects furthest posteriorly.

DISCUSSION: Species of this genus are known from the Givetian of Afghanistan, the Frasnian of the Cantabrian Mountains of northern Spain, the Givetian of northeastern Spain, the Frasnian of Belgium, the lower Frasnian of the Massif Armorican, and the Eifelian of the Massif Armorican. An emended diagnosis is given to that provided by

Haas and Mensink (1969) because the diagnosis they gave is inadequate to differentiate the members of this genus from other genera. Originally, Haas and Mensink (1969) considered *Heliopyge* to be a subgenus of *Neocalmonia*. Herein, these taxa are treated as two distinct genera because subgeneric classifications were not pursued and because *Heliopyge* and *Neocalmonia* are distantly related. Instead, *Heliopyge* is sister to *Paracryphaeus*, and the clade they form is in turn sister to *Bradocryphaeus*. *Heliopyge* may be closely related to *Quadratispina* Gandl, 1972; however, the type species of this genus (a subgenus of *Neocalmonia* according to Gandl [1972]) was not analyzed herein. The genus name is treated as still valid, and the relationships of this genus will be considered at a later time. An autapomorphy of *Quadratispina* is the condition of the third pair of pygidial pleural lappets. The lateral and medial margins of this pair of lappets are straight, and the body of the lappets essentially parallels a sagittal line instead of being deflected laterally or medially.

In the past, a wide range of species had been assigned to *Heliopyge* that can no longer be assigned to it on the basis of their differences from the emended diagnosis presented herein. For example, consider the species ?*Heliopyge iberica* Haas, 1970, ?*Heliopyge asturica* Haas, 1970, ?*Heliopyge coallajuensis* Arbizu, 1979, ?*Heliopyge nodosa* Morzadec, 1983, and ?*Heliopyge zornensis* Morzadec, 1983. In none of these taxa does the third pygidial pleural lappet project further posteriorly than the other lappets. It is conceivable that some of these species, if subjected to phylogenetic analysis, would map out as sister to *H. turolensis* or other valid species of *Heliopyge* or form part of a stem-lineage of *Heliopyge*. However, such analysis was not pursued at this time, as it would require the study and incorporation of a ponderous number of taxa, none of which could be obtained. *Heliopyge troaonensis* Morzadec, 1983, is the oldest species of *Heliopyge*. It is known only from pygidia, but it appears to be a valid species of *Heliopyge*. However, Morzadec's (1983, text fig. 23) illustration of the species may be inaccurate, showing the fourth pygidial pleural lappet projecting further posteriorly than the third pleural lappet. This does not appear to be the case on the specimens Morzadec (1983) figured in his plates. If Morzadec's (1983) illustration is correct, then *H. troaonensis* is probably not a valid species of *Heliopyge*. Several authors have commented on the phylogenetic affinities of the genus *Heliopyge*. As mentioned in the section of this paper dealing with the genus *Neocalmonia*, Morzadec (1983) thought that *Heliopyge* was sister to *Bradocryphaeus*, with that lineage being derived from part of the lineage comprising *Comura*. Of course, this would make *Comura* paraphyletic. The paraphyly of *Comura* was not assessed herein. However, Morzadec (1983) appears to be correct in asserting the close relationship between *Bradocryphaeus* and *Heliopyge*, although they are not sister taxa unless *Paracryphaeus* Gandl, 1972, is lumped with *Heliopyge*.

Haas and Mensink (1969) and Haas (1970) suggested that *Heliopyge* was derived from a paraphyletic *Bradocryphaeus*, which was in turn derived from a paraphyletic *Asteropyge*. The validity of paraphyletic genera is not supported herein, and, in addition, *Asteropyge* appears to be distantly related to *Heliopyge* and *Bradocryphaeus*. *Heliopyge* and *Bradocryphaeus* are closely related, but *Heliopyge* is sister to *Paracryphaeus*.

Arbizu (1979) suggested that *Heliopyge* was derived from *Alcaldops*, and it in turn gave rise to *Bradocryphaeus*. *Alcaldops* was not analyzed in depth herein, but it is treated as closely related to *Tolkienia*. It is not closely related to *Bradocryphaeus* or *Heliopyge*. Similarly, Smeenk (1983) suggested that *Heliopyge* was derived from *Alcaldops*, although he claimed that it was somewhat more distantly related to *Bradocryphaeus*. Thus, the details of the phylogeny he advocated do not appear to be entirely correct.

Heliopyge turolensis was chosen for the purposes of the character analysis conducted herein because it offered the most morphologically complete material available.

Heliopyge turolensis (Gandl, 1972)

Comura (*Comura*) n. sp. Carls and Gandl, 1978: 463.

Neocalmonia (*Heliopyge*) *turolensis* Gandl, 1972: 142, pl. 14, figs. 4–10.

TYPES: Holotype defined in Gandl (1972: pl. 14, fig. 7).

DIAGNOSIS: Anterior cephalic border pointed in dorsal view; anterior margin of frontal glabellar lobe faintly pointed in dorsal view; 11 pygidial axial rings; medial tubercles on pygidial and thoracic axial rings absent.

DISCUSSION: This species is known from the Givetian of northeastern Spain.

PARACRYPHAEUS GANDL, 1972

TYPE SPECIES: *Cryphaeus jonesi* Oehlert, 1877.

ASSIGNED TAXA: *Paracryphaeus hercyniae* Gandl, 1972, *P.* sp. aff. *hercyniae*, *P. praejonesi* Gandl, 1972, *P. alcoleae* Gandl, 1972, *P. caboi* Smeenk, 1983, *P.* cf. *jonesi* Smeenk, 1983, and *Pseudocryphaeus izensis* Morzadec, 1971.

DIAGNOSIS: See Gandl (1972).

DISCUSSION: Only a single species of this genus was considered in the phylogenetic analysis. Gandl (1972) did illustrate specimens of the type of the genus, *P. jonesi*, and these do show some similarities with the types of *P. hercyniae* he illustrated. In particular, both have: the long terminal pygidial lappet; the pygidial interpleural furrows that do not flex strongly posteriorly laterally; the pygidial axis constricting posterior to the third axial ring; the anterior margins of the pygidial axial rings posterior to the third axial ring straight; and the anterior margins of the first three pygidial axial rings smoothly convex anteriorly. However, they do differ in: the condition of the pygidial pleural furrows, which are longer (exsag.) in *P. jonesi* than in *P. hercyniae*; the condition of the terminal pygidial lappet, which is long and triangular in *P. jonesi* but long and rectangular in *P. hercyniae*; the position of the fifth pair of pygidial pleural lappets, which are separated from the terminal pygidial lappet in *P. jonesi* but connected to the terminal lappet in *P. hercyniae*; the condition of the dorsal surfaces of the pygidial pleural segments, which are flat in *P. jonesi* but rounded in *P. hercyniae*; the condition of the posterior portion of the pleural segment, which is elevated above the anterior portion of the pleural segment in *P. jonesi*, but of equal elevation in *P. hercyniae*; and the condition of the posterolateral margins of the pygidial pleural lappets, which are straight in *P. jonesi* but developed as blunt triangles in *P. hercyniae*. The cephala of these two taxa also differ. In particular, L1 is very reduced in *P. jonesi* but not in *P. hercyniae*; S2 is transverse in *P. jonesi*, but its lateral margin is directed posteriorly in *P. hercyniae*; and the anterior margin of the frontal glabellar lobe is faintly pointed in *P. hercyniae*, whereas it is smoothly rounded in *P. jonesi*. Based on the similarities presented above, it is conceivable that *P. hercyniae* and *P. jonesi* are closely related, and thus *P. hercyniae* is tentatively retained within *Paracryphaeus*. However, a phylogenetic analysis incorporating more complete material of *P. jonesi* might also suggest that these taxa are not sister taxa and thus that *P. hercyniae* does not belong in the genus *Paracryphaeus*. For now, these two species are treated as belonging to the same genus.

The phylogenetic position of *Paracryphaeus* is somewhat counter to that suggested by past authors. In particular, herein *Paracryphaeus hercyniae* is sister to *Heliopyge turolensis* Gandl, 1972, whereas Gandl (1972) suggested that *Paracryphaeus* was the root stock from which *Greenops* Delo, 1935, *Neometacanthus* Richter and Richter, 1948, *Rhenops* Richter and Richter, 1943, and *Kayserops* Delo, 1935, evolved (see fig. 5b). Smeenk (1983) argued for a relatively similar phylogenetic position for *Paracryphaeus* (see fig. 5d). It should be stressed that until material from the type of the genus can be obtained and incorporated into the phylogenetic analysis, the exact position of *Paracryphaeus* must remain ambiguous; however, the phylogenetic analysis of *P. hercyniae* suggests that it is distantly related to these genera. It is important to point out that there are several interesting convergences between species of *Breizhops* Morzadec, 1983, and species of *Paracryphaeus*. For instance, *B. bigranulosus* Morzadec, 1983, and *P. hercyniae* both have: the longest pygidial lappet very short, with the length (sag.) equal to the length of the first two pygidial axial rings; the anterolateral margins of the first five pygidial axial rings evenly convex; isolated patches of tubercles on L2 and L3; in the medial region of adjacent pygidial pleural segments, the posterior region of the anterior segment is longer (exsag.) than the anterior part of the posterior segment; the tops of the pygidial pleural segments rounded; the lateral margins of the pygidial lappets curved; the terminal pygidial lappet projecting furthest posteriorly, and subrectangular; no ornament on the thoracic and pygidial axial rings; the interior margin of the genal spine evenly deflected laterally; the raised ridge on the dorsal surface of the genal spine forming a doglegged kink; the lateral margin of the genal spine at its posterior end parallels a sagittal line; the medial edge of the genal spine not significantly thickened; significant change in cephalic topography where the librigena meets the lateral border furrow; L3 flattened dorsally; anterior cephalic border medially not deflected far anteriorly beyond the lateral margins of the cephalon; the anterior cephalic border pointed in dorsal view; the distance between the frontal lobe and the facial suture at the midline relative to laterally increased slightly; S1 crescent shaped, medially developed as a smooth curve convex posteriorly; and S2 weakly declined posteriorly at its lateral edge. However, most of these shared character states are actually the primitive condition of characters, and thus they do not necessarily have relevance for phylogenetic analysis. An approach using parsimony implies that a smaller number of convergences is required to group *P. hercyniae* with *Heliopyge turolensis* than with *Breizhops bigranulosus*.

Important synapomorphies uniting *H. turolensis* and *P. hercyniae* include: the anteriormost part of the palpebrum reaching a point between the medial tips of L3 and the PMI; isolated patches of tubercles present on L2 and L3; a broad ledge of the anterior cephalic border visible anterior to the anterolateral portions of the frontal lobe; and the pygidial pleural furrows moderately incised, short (exsag.). Thus, at this time we suggest that the interesting similarities shared between *Breizhops bigranulosus* and *P. hercyniae* are convergences, whereas the characters uniting *H. turolensis* and *P. hercyniae* denote actual propinquity of descent.

Timm (1981) figured a series of taxa from the Lower Devonian that he assigned to *Paracryphaeus*. He treated these taxa as evolving out of a paraphyletic *Acastella*. However, this taxonomic assignment appears to be questionable, with Timm's (1981) figured specimens lacking characters that are found in *Paracryphaeus* but also that define the Asteropyginae. For instance, on those specimens where it is preserved, the genal spine is reduced to a very small nub, and the cephalic border furrow does not extend onto the genal spine and does not bifurcate it. Even in taxa with highly reduced genal spines, such as *Pelitlina smeenki*, new species, which is the putative sister taxon of the Asteropyginae, the cephalic border furrow extends onto the genal spine, bifurcating it. This synapomorphy characterizes both this species and all of the Asteropyginae (Edgecombe, 1991). In addition, *Pelitlina* and all the Asteropyginae have broad pygidial pleural lappets bordering the pygidium. In Timm's (1981) *Paracryphaeus lata* and *P. effae*, there are no pygidial pleural lappets, only small marginal denticles, as in all species of *Acastava* and *Acastella*. Thus, on the basis of these characters, these taxa cannot be treated as belonging to the Asteropyginae or *Paracryphaeus*, while *P. hercyniae* certainly possesses these characters and belongs to the ingroup Asteropyginae. *Paracryphaeus jonesi*, the type of *Paracryphaeus*, possesses the pygidial characteristics of the Asteropyginae, but the condition of the genal spines could not be determined. If *P. jonesi* and *P. hercyniae* are closely related, as predicted by this analysis, then it is most likely that *P. jonesi* has the cephalic border furrow bisecting the genal spine, as it does in all the other members of the asteropyginines. Thus, it is unlikely that the two aforementioned taxa that Timm (1981) illustrated belong to *Paracryphaeus*. More likely, they should be assigned to *Acastella*. Timm's (1981) *P. gerrinensis* does not have the cephalic posterior border furrow bifurcating the genal spine, but the condition of the pygidium bears mentioning. It does have five pairs of extremely narrow pygidial pleural lappets that do reach considerable length, sharing the condition found in *Pelitlina* and the Asteropyginae. However, it differs from *P. hercyniae* in the condition of several characters, including: the interpleural furrows weakly arched instead of being arched more strongly posteriorly laterally as they are in *P. hercyniae*; S3 sinusoidal instead of being convex anteriorly as in *P. hercyniae*; and the pygidial axis constricting posterior to the fifth axial ring instead of posterior to the third as in *P. hercyniae*. Thus, this species, like the other species figured in Timm's (1981) paper, probably should not be placed in *Paracryphaeus*. Overall, Timm's (1981) specimens are very poorly preserved, but it seems likely that they cannot be assigned to *Paracryphaeus*. At this time it is more likely that they belong to *Acastella* or some other taxon within a paraphyletic Acastavinae, but better material will need to be examined to ascertain the phylogenetic placement of these species with certainty.

Paracryphaeus hercyniae Gandl, 1972

Paracryphaeus hercyniae Gandl, 1972: 87, pl. 11, figs. 6–10.

TYPES: Holotype defined in Gandl (1972: pl. 11, fig. 7).

DIAGNOSIS: S3 convex anteriorly; cephalic posterior border furrow shallow distally and longest (sag.) posterior to palpebrum; posterior edge of visual surface posterior to transverse line tangent to L0; distance between frontal lobe and facial suture from lateral margins to midline increases slightly; PMI absent; line from posterior to anterior edge of eye parallels sagittal line; prominent demarcation between librigenae and lateral border furrow; prosopon dominated by coarse tubercles; isolated patches of coarse tubercles present on L2, L3, frontal glabellar lobe, and eye ridge; genal spine developed as moderately long flange extending back to fourth thoracic segment; lateral margin of genal spine forms line that departs from sagittal line by about 15–20°; interior margin of genal spine deflected laterally; posterolateral margins of pygidial pleural lappets developed as blunt triangles; anterior margin of pygidial axial rings posterior to pygidial axial constriction smoothly convex anteriorly; pygidial axis constricts posterior to fourth axial ring; tops of pygidial pleural lappets rounded; pygidial interpleural furrows flex strongly posteriorly laterally; nine pygidial axial rings; margin of terminal pygidial lappet rectangular, transverse posteriorly; terminal pygidial lappet very narrow, half width of posterior portion of axis; pygidial pleural lappets project from terminal lappet.

DISCUSSION: This species is known from the upper Emsian of northern Spain. Morzadec (1983) claimed that the species *Paracryphaeus hercyniae* Gandl, 1972, was actually closely related to *B. lanceolatus*, and he suggested that it be assigned to the genus *Breizhops*. His predictions were tested herein but appear to be incorrect. The phylogenetic analysis suggests that *Paracryphaeus hercyniae* is distantly related to other species of *Breizhops* such as *B. lanceolatus* Morzadec, 1983, *B. bigranulosus* Morzadec, 1983, and *B. chaconae* (Arbizu, 1979). Important differences between *Paracryphaeus* and *Breizhops* include: in *P. hercyniae* S3 is convex anteriorly, whereas in all species of *Breizhops* it is straight, with the anterolateral edge transverse; in *P. hercyniae* the posterior edge of the visual surfaces is posterior to a transverse line tangent to the anterior edge of L0, whereas in all species of *Breizhops* the posterior edge of the visual surfaces are anterior to a transverse line tangent to the anterior edge of L0; in *P. hercyniae* the adult prosopon is dominated by coarse tubercles, whereas in species of *Breizhops* the prosopon is dominated by fine tubercles; in *P. hercyniae* the genal spine is developed as a moderately long flange extending back to the fourth thoracic segment, whereas in species of *Breizhops* it is a long flange that extends back to the sixth thoracic segment; in *P. hercyniae* the lateral margin of the genal spine in its medial portion forms a line that departs from a sagittal line by about 15–20°, whereas in *Breizhops* the lateral margin of the genal spine parallels a sagittal line; in *P. hercyniae* the interior margin of the genal spine is deflected laterally at a 20° angle to a sagittal line, whereas in *Breizhops* the interior margin of the genal spine parallels the lateral margin of the genal spine before deflecting laterally; in *P. hercyniae* the medial margins of the pygidial lappets are curved, whereas in *Breizhops* the medial margins of the pygidial lappets are straight; in *P. hercyniae* the pygidial axis constricts posterior to the fourth axial ring, whereas in *Breizhops* the pygidial axis constricts posterior to the fifth axial ring; in *P. hercyniae* the anterior margins of the pygidial axial rings posterior to the constriction of the pygidial axis are smoothly convex anteriorly, whereas in *Breizhops* the anterior margins of the pygidial axial rings posterior to the constriction of the pygidial axis are straight; in *P. hercyniae* there are nine pygidial axial rings, whereas in *Breizhops* there are 11 pygidial axial rings; in *P. hercyniae* the margin of the terminal pygidial lappet is rectangular and transverse posteriorly, whereas in *Breizhops* the terminal pygidial lappet is rectangular and triangular posteriorly; in *P. hercyniae* the terminal pygidial lappet is very narrow, 0.5 times the width (tr.) of the posterior portion of the axis, whereas in *Breizhops* the terminal pygidial lappet is narrow, about 1–1.1 times the width (tr.) of the posterior portion of the pygidial axis. Thus, on the basis of these differences, it is hard to support Morzadec's (1983) conclusion that *P. hercyniae* Gandl, 1972, should be assigned to *Breizhops*.

Smeenk (1983) assigned a series of cephala and pygidia from different localities, horizons, and formations to *G.* (*G.*) *chaconae*, and he asserted that these were conspecific with Arbizu's (1979) *G. chaconae*. However, the pygidia appear to belong to a completely different species. This species, *Paracryphaeus* sp. aff. *hercyniae*, is nearly identical to *P. hercyniae* Gandl, 1972, and they share the constriction of the pygidial axis posterior to the fourth pygidial axial ring, the very long pleural lappets, and the long pygidial terminal lappet that has rectangular margins. Although the pygidia Smeenk (1983) figured are poorly preserved, it appears that they may have one more pygidial axial ring than do those of *P. hercyniae*, and thus until better material can be found they are tentatively assigned to *P.* sp. aff. *hercyniae*. These pygidia also differ from those of *P. hercyniae* in the condition of the posterior margin of the terminal pygidial lappet. The margin is triangular in *P.* sp. aff. *hercyniae* but was coded as transverse in *P. hercyniae*, as that is its condition in some of the paratype material that Gandl (1972) figured, e.g., plate 10, figure 10. However, there does seem to be some variation in this character, with one of the other paratype pygidia having a terminal pygidial lappet that appears to be pointed.

The pygidia of *P.* sp. aff. *hercyniae* are also very similar to those of *B. bigranulosus*, differing principally in being relatively narrower, in having a longer terminal pygidial lappet, in having the pygidial axis constricting posterior to the fourth axial ring instead of posterior to the fifth axial ring, and in having the posterior part of the pleural segments not elevated above the anterior part. However, these similarities must be taken as convergences, because the phylogenetic analysis suggests that *Paracryphaeus* and *Breizhops* are distantly related.

Smeenk (1983) illustrated some interesting trilobites that he assigned to *Greenops*; however, none of the cephala and pygidia are associated, making it impossible to ascertain whether or not they come from the same species. At least some of the cephala Smeenk (1983) illustrated do appear to be conspecific with *B. chaconae*, but some of the specimens Smeenk (1983) illustrated show intriguing similarities to *P.* sp. aff. *hercyniae*. These are from casts of external molds. In these specimens, the frontal glabellar lobe appears pointed instead of rounded, as it is in *B. chaconae*. However, in other specimens, the frontal glabellar lobe appears rounded. The frontal glabellar lobe is pointed in *P. hercyniae*. Other interesting features include the condition of the posterior edge of the visual surfaces, which is posterior to a transverse line tangent to L0 in *P. hercyniae*, whereas is anterior to such a line in *P.* sp. aff. *hercyniae* (and in *B. chaconae*), and the condition of S3, which is convex anteriorly in *P. hercyniae* and straight in *B. chaconae* and in the cephala Smeenk (1983) figured. It is conceivable that the pygidia and cephala Smeenk (1983) illustrated belong to a single species of trilobite, indicating that the cephalic characters largely match *B. chaconae* but the pygidial characters are closer to *P. hercyniae*. However, because of the poor state of the material, until complete articulated specimens are available, the pygidia are treated as closely related to *P. hercyniae* and the cephala are treated as questionably conspecific with *B. chaconae*.

PILLETINA HAAS, 1970

TYPE SPECIES: *Metacanthina oehlerti praecursor* Pillet, 1958.

ASSIGNED TAXA: *Metacanthina aequisulcata aequisulcata* Gandl, 1972, *Metacanthina aequisulcata matutina* Gandl, 1972, and *Asteropyge* (*Metacanthina*) *oehlerti oehlerti* Pillet, 1954.

DIAGNOSIS: See Haas (1970).

DISCUSSION: Examination of figures in Pillet (1958) (the author who described and illustrated the species designated the type of *Pilletina*) of *P. praecursor* (pl. 1, figs. 2, 2a, 2b; pl. 2, fig. 2) indicates that *Metacanthina aequisulcata* Gandl, 1972, shares several features of the pygidium in common with *P. praecursor*, and therefore it is tentatively placed in the genus *Pilletina*, contra Gandl's (1972) assignment to *Metacanthina*, but following Haas's (1970) and Smeenk's (1983) assignment. In particular, *P. praecursor* and *P. aequisulcata* share the following characters: the lateral and medial margins of the pygidial pleural lappets are curved; the terminal pygidial lappet projects further posteriorly than the other pleural lappets; the pygidial axis constricts posterior to the fifth axial ring; the anterior margins of the pygidial axial rings are straight; posterior to the fifth axial ring, the tops of the pygidial pleural segments are rounded; and the pygidial interpleural furrows arch at the same angle medially and laterally. However, differences between these taxa include the length and depth of the pleural furrows. They are deeper than the interpleural furrows in *P. praecursor*, but of equal depth in *P. aequisulcata*, and they are almost as long (exsag.) as the anterior pleural band in *P. praecursor* but short in *P. aequisulcata*. In addition, the posterior portions of the pleural segments are more strongly deflected posteriorly in *P. praecursor* than in *P. aequisulcata*.

Pillet's (1954) *Asteropyge* (*Metacanthina*) *oehlerti oehlerti*, treated herein as *Pilletina oehlerti oehlerti* (Pillet, 1954), more closely resembles *P. aequisulcata* than the type of the genus does. In addition to the characters enumerated above, both taxa also share the form of the pygidial terminal lappet, which has parallel margins anteriorly and is triangular posteriorly, and the posterior pleural segments in both taxa are not directed as strongly posteriorly as they are in *P. praecursor*. Therefore, if *P. oehlerti* and *P. aequisulcata* are correctly assigned to the genus *Pilletina*, they are probably more closely related to each other than either is to *P. praecursor*.

The only species of *Pilletina* available for character analysis was *P. aequisulcata*, and the phylogenetic position of the species actually analyzed rather than the genus is what is to be emphasized. Gandl (1972) suggested that *Pilletina aequisulcata* was the sister taxon of *Pseudocryphaeus munieri* (which he referred to as *Metacanthina munieri*). This does not appear to be true, and they can be distinguished by the condition of several characters, including: 6, 7, 8, 9, 10, 15, 19, 22, 23, 28, 29, 31, 32, 41, 44, 50, 51, 52, 57, 58, and 60. Haas (1970) argued for a basal phylogenetic position for *Pilletina* (see fig. 5a), which he held to be part of a stem lineage that led to several other genera, and this lineage was held to be sister to a lineage that had *Pseudocryphaeus* as the basal taxon. This is not supported herein, as *Pilletina* appears to be sister to a large clade including *Breizhops*, *Greenops*, *Rhenops*, and *Kayserops*. It is not closely related at all to *Pseudocryphaeus*. Morzadec (1983) suggested that *Pilletina* was a distinct lineage derived from a paraphyletic *Pseudocryphaeus* (see fig. 5e). Again, this is not supported.

Pilletina aequisulcata
(Gandl, 1972)

Metacanthina aequisulcata aequisulcata Gandl, 1972: 109, pl. 8, figs. 6–8, 10, not fig. 9, not pl. 9, fig. 1.

TYPES: Holotype defined in Gandl (1972: pl. 8, fig. 10).

DIAGNOSIS: Anterior margin of frontal glabella lobe transverse medially; lateral margin of genal spine in medial portion forms line that departs from sagittal line by 15–20°; maximum of seven lenses per dorsoventral file on visual surface; S3 faintly sinusoidal; cephalic posterior border furrow longest (exsag.) posterior to medial visual surface of eyes; distance between frontal lobe and facial suture constant from lateral margin of frontal lobe to midline; anterior cephalic border in dorsal view pointed medially; line from anterior to posterior edge of eye intersects sagittal line at 30° angle; demarcation between librigena lateral to eye and lateral border furrow weak; cephalic axial furrows anterior to S1 diverge more strongly; distal tips of pygidial lappets blunt triangles; lateral and medial margins of pygidial pleural lappets curving; pygidial pleural furrows moderately incised, short (sag.); terminal pygidial lappet very broad; pygidial pleural furrows and interpleural furrows equally incised.

DISCUSSION: This species is known from the Siegenian (Pragian?) of northeastern Spain. Gandl (1972) described the species *Metacanthina aequisulcata*, which he divided into two subspecies, *aequisulcata* and *matutina*. These two taxa can be discriminated by several characters, including the form of the pygidial terminal lappet, the number of pygidial axial rings, and the shape of the medial margins of the pygidial pleural lappets. The subspecies *aequisulcata* is considered to be worthy of specific status and is treated herein as *Pilletina aequisulcata*. Some of the specimens illustrated by Gandl (1972: pl. 8, fig. 9, pl. 9, fig. 1) and assigned to *M. aequisulcata aequisulcata* do not belong to *P. aequisulcata*. They differ in the number of pygidial axial rings, 14 vs. 15, and in the shape of the terminal pygidial lappet, which is triangular, and not subrectangular with parallel sides anteriorly. Therefore, these specimens should be assigned to a new species.

This species when first described was assigned to the genus *Metacanthina* by Gandl (1972). However, on the basis of morphological characters of the types of *Pilletina* and *Metacanthina* discussed above, it appears that it should be henceforth assigned to *Pilletina*.

BREIZHOPS MORZADEC, 1983

TYPE SPECIES: *Breizhops lanceolatus* Morzadec, 1983.

ASSIGNED TAXA: *Breizhops bigranulosus* Morzadec, 1983, and *Greenops* (*Greenops*) *chaconae* Arbizu, 1979.

DIAGNOSIS: S3 straight, anterolateral edge transverse; S2 weakly declined posteriorly at lateral edge; medial portion of S1 smooth curve directed anteriorly; anterior cephalic border medially does not flex dorsally beyond plane through lateral margins of frontal lobe; anterior cephalic border in dorsal view pointed medially; lateral margins of border near midline form a 110° angle; anterior cephalic border developed as narrow lip; L3 dorsally flattened; genal spine developed as long flange extending back to sixth thoracic segment; medial edge of genal spine not significantly thickened relative to lateral edge; lateral margin of genal spine parallels sagittal line, interior margin parallels lateral margin before deflecting laterally; terminal pygidial lappet narrow, subrectangular, convex posteriorly; terminal pygidial lappet projects further posteriorly than other lappets; pygidial pleural field flanking posterior part of pygidial axis faintly excavated; fifth pygidial pleural lappet projects further posteriorly than other pleural lappets; all pleural lappets shorter (exsag.) than length (sag.) of first two pygidial axial rings; pleural furrows moderately incised, short (exsag.); at medial region of adjacent pygidial pleural segments, posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; anterolateral margins of first five pygidial axial rings from axial furrows to midline smoothly convex anteriorly.

DISCUSSION: All species in this genus are known from the upper Emsian of Armorica (the Massif Armorican and northern Spain). The genus is sister to a large clade including *Philipsmithiana*, new genus, *Rhenops* Richter and Richter, 1943, *Greenops* Delo, 1935, *Kayserops* Delo, 1935, *Stummiana*, new genus, and *Deloops*, new genus, although Morzadec (1983) suggested that *Breizhops* was closely related to *Asteropyge* Hawle and Corda, 1847. Morzadec (1983: text fig. 33) showed *Breizhops* arising out of a lineage of *Comura* Richter and Richter, 1926, in the upper Emsian, which also gave rise to *Asteropyge* later in the upper Emsian. The close relationship between *Asteropyge* and *Breizhops* is not supported by the phylogenetic analysis conducted herein. In fact, when comparing the types of the two genera, *A. punctata* (Steininger, 1831) and *B. lanceolatus*, they are found to differ in the condition of several characters listed in table 1 including: 3, 5, 6, 8, 9, 13, 15, 19, 22, 28, 34, 40, 41, 44, 45, 49, 50, 54, 55, 57, 58, 59, 60, 62, and 63. The close relationship between *Comura* and *Breizhops* is also not supported herein. Although species of *Comura* could not be obtained for the purposes of the phylogenetic analysis, a species of the closely related genus, *Tolkienia*, new genus (discussed above), was coded for character analysis, and was found to be distantly related to *Breizhops*.

Breizhops lanceolatus Morzadec, 1983

Breizhops lanceolatus Morzadec, 1983: 129, pl. 16, figs. 1–5.

TYPES: Holotype defined in Morzadec (1983: pl. 16, fig. 1).

DIAGNOSIS: Cephalic posterior border furrow deep laterally, longest (sag.) posterior to medial visual surfaces of eyes; posterior edge of visual surface anterior to transverse line tangent to L0; maximum of six lenses per dorsoventral file on visual surfaces; facial suture lateral to eye before flexing posteriorly flexes anteriorly to point opposite S1; anterior margin of frontal glabellar lobe faintly pointed in dorsal view; posterior margin of palpebrum relative to anterior margin of fixigena deflected at a significantly larger angle to transverse line; portion of librigena between lateral margin of eye and lateral border furrow not visible in dorsal view; broad ledge of anterior cephalic border visible anterior to anterolateral portions of frontal lobe; distal tips of pygidial lappets at distal end of posterolateral margin inclined at approximately 45° angle relative to sagittal line; pygidial axis constricts posterior to fifth axial ring; laterally, pygidial interpleural furrows arching at same angle as medially; 11 pygidial axial rings.

DISCUSSION: This species is known from the upper Emsian of the Massif Armorican. Morzadec (1983) suggested that it was very closely related to *Paracryphaeus hercyniae* Gandl, 1972, but this conclusion is not supported by the phylogenetic analysis conducted herein, and these taxa appear to be distantly related. The part of Morzadec's (1983: text fig. 33) evolutionary tree that suggested that *B. lanceolatus* is a direct ancestor of *B. bigranulosus* is correct in the exact details only if *B. lanceolatus* is paraphyletic, but the two species are sister taxa.

Breizhops chaconae (Arbizu, 1979)

Greenops (*Greenops*) *chaconae* Arbizu, 1979: 73, pl. 2, figs. 3–7.

?*Greenops* (*Greenops*) *chaconae* Arbizu. Smeenk, 1983: 405, pl. 10, figs. 1–3, 7, 8, pl. 25, fig. 5.

TYPES: Holotype defined in Arbizu (1979: pl. 2, fig. 3).

DIAGNOSIS: S3 straight, anterolateral edge flexes posteriorly; posterior edge of visual surface anterior to transverse line tangent to L0; lateral to eye, facial suture before flexing posteriorly flexes anteriorly to point opposite S2; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; distance between frontal lobe and facial suture from lateral edge to midline constant; anteriormost portion of palpebrum opposite PMI; PMI developed as linear incision; demarcation between librigena lateral to eye and lateral border furrow weak, prosopon dominated by fine tubercles; genal spine developed as long flange extending back to sixth thoracic segment; medial edge of genal spine developed as flattened ledge, lateral edge evenly inclined; lateral margin of genal spine parallels sagittal line; medial margins of pygidial lappets straight; pygidial axis constricts posterior to fifth axial ring; anterior margins of pygidial axial rings posterior to fifth axial ring straight; 11 pygidial axial rings; terminal pygidial lappet narrow, with sides parallel anteriorly, triangular posteriorly.

DISCUSSION: This species is known from the upper Emsian of northern Spain. As mentioned above, Smeenk (1983) figured and assigned some pygidia to *G. chaconae* that differ from those typical of that species (here *B. chaconae*) and instead appear to be very similar to pygidia of *P. hercyniae* and are thus referred to here as *P.* sp. aff. *hercyniae*. These taxa share the constriction of the pygidial axis posterior to the fourth axial ring as well as the length and shape of the terminal pygidial lappet and the other pleural lappets. They do differ in the number of pygidial axial rings they possess as well as possibly in the shape of the posterior margin of the terminal pygidial lappet. This margin is pointed in *P.* sp. aff. *hercyniae*, whereas it is transverse in at least some of the specimens of *P. hercyniae*. However, at least one pygidium of *P. hercyniae* illustrated by Gandl (1972: pl. 10, fig. 9) may have the posterior margin of the pygidium pointed, so there may be some variation in this character for

P. hercyniae. It could not be ascertained whether the posterior margin of this pygidium was completely preserved or partially broken. The posterior margin of the terminal pygidial lappet was treated as transverse in the phylogenetic analysis conducted herein.

Breizhops bigranulosus Morzadec, 1983

Pseudocryphaeus sp. Morzadec, 1969: 43, pl. 8, fig. 9.

Breizhops bigranulosus Morzadec, 1983: 130, pl. 17, figs. 1–11.

TYPES: Holotype defined in Morzadec (1983: pl. 17, fig. 2).

DIAGNOSIS: S3 straight, anterolateral edge flexes posteriorly; posterior edge of visual surfaces anterior to transverse line tangent to L0; maximum of four lenses in a dorsoventral file on the visual surface; lateral to eye, facial suture before flexing posteriorly flexes anteriorly to point opposite S1; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; tubercle on L0 present; anterior cephalic border not deflected far anteriorly beyond lateral margins of cephalon; line from posterior to anterior edge of eye forms roughly 45° angle with sagittal line; demarcation between librigenae and lateral border furrow prominent; prosopon dominated by fine tubercles; isolated patches of coarse tubercles present on L2, L3, frontal glabellar lobe, and eye ridge; genal spine developed as long flange extending back to sixth thoracic segment; lateral margin of genal spine forms a line that departs from sagittal line by about 15-20°; cephalic axial furrows anterior to S1 diverge at same angle as posterior to S1; axial furrows at anterior and posterior halves of L3 equally divergent; portion of librigena between lateral margin of eye and lateral border furrow not visible; interior margin of genal spine parallels lateral margin before deflecting laterally; terminal pygidial lappet with sides parallel anteriorly, triangular posteriorly; distal tips of pygidial lappets at distal end of straight posterolateral margin inclined at approximately 45° angle relative to sagittal line; pygidial axis constricts posterior to fifth axial ring; posterior portion of pleural segment elevated above anterior portion of pleural segment; tops of pleural segments rounded; pygidial interpleural furrows arch at same angle laterally as medially; 11 pygidial axial rings; terminal pygidial lappet narrow.

DISCUSSION: This species is known from the upper Emsian of the Massif Armorican. As discussed above, Morzadec (1983) considered this species to be a direct descendant of *B. lanceolatus*. Phylogenetic analysis indicates that these species are closely related. However, Morzadec (1983) also recognized the close affinity between *P. hercyniae* Gandl, 1972, and *B. bigranulosus*, but this conclusion is not supported by the phylogenetic analysis conducted herein. (See the section on *Paracryphaeus hercyniae* for more elaboration.)

PHILIPSMITHIANA, NEW GENUS

TYPE SPECIES: *Philipsmithiana hyfinkeli*, new species.

ASSIGNED TAXA: *Philipsmithiana burtandmimiae*, new species.

DIAGNOSIS: Anterior cephalic border pointed in dorsal view, developed as narrow lip; line from posterior to anterior edge of eye intersects sagittal line at 30° angle; axial furrows at anterior half of L3 relative to posterior half less strongly divergent; posterior edge of visual surface anterior to transverse line tangent to anterior edge of L0; eye rests on vertical wall of librigena; immediately before cephalic lateral border furrow meets posterior border furrow, posterior border furrow flexes anteriorly; ornamentation on L0 absent; plane between medial and lateral edges of genal spine medially flattened ledge, laterally evenly inclined; medial edge of genal spine not significantly thickened, lateral edge parallels sagittal line; interior margin parallels lateral margin before deflecting laterally; isolated patches of tubercles on L2; medial edge of genal spine not significantly thickened relative to lateral edge; lateral margin of genal spine at posterior end straight; circular fenestrae absent; pleural furrows almost as long (sag.) as anterior pleural band; 15 or 16 pygidial axial rings; prosopon of fine tubercles; pygidial pleural field flanking posterior portion of pygidial axis faintly excavated; terminal pygidial lappet broad, margin rectangular, convex posteriorly, does not project as far posteriorly as longest pleural lappets.

ETYMOLOGY: Named for BSL's grandfather, Philip Smith, who passed away during the course of this study.

DISCUSSION: This new genus is erected to accommodate two new species that bear a close phylogenetic relationship to certain Armorican and Eastern North American taxa traditionally assigned to *Greenops*; however, they lack certain derived features found in these taxa while also possessing certain derived characters absent in these taxa, and for this reason they are assigned to a separate genus that is sister to a clade including *Greenops*, *Rhenops*, and *Neometacanthus*. Phylogenetically informative differences between members of *Philipsmithiana* and *Greenops* include the maximum number of lenses in a dorsoventral file on the visual surface, six in *Greenops*, seven or nine in *Philipsmithiana*; the condition of the anterior cephalic border, rounded in *Greenops*, pointed in *Philipsmithiana*; the genal spine, developed as a moderately long flange extending back to the fifth thoracic segment in *Greenops*, extending back to the sixth or seventh thoracic segment in *Philipsmithiana*; and the tops of the pygidial pleural segments, flat in *Greenops*, rounded in *Philipsmithiana*.

The species *P. burtandmimiae* and *P. hyfinkeli* appear to be sister taxa on the basis of the shared possession of identical states for the following characters: 13, 25, 30, 35, 45, 65, and 66.

Philipsmithiana hyfinkeli, new species

Figures 6.1–6.5, 7.7, 7.9, 21.2, 21.5–21.9, 22.1, 22.2, 22.5, 22.6, 22.8, 22.9, 22.11

TYPES: Holotype AMNH 45259, a complete specimen from the Middle Devonian of Morocco, near Mt. Issomour, exact locality and stratigraphic position unknown; paratypes AMNH 45260, 45264, and 45265, nearly complete specimens from the same locality as the holotype.

DIAGNOSIS: S3 convex anteriorly; maximum of nine lenses per dorsoventral file on visual surfaces; lateral to eye, before facial suture flexes posteriorly, suture flexes anteriorly to point between distal tips of S1 and S2; distance between frontal lobe and facial suture constant from midline to lateral edges of frontal lobe; fixigena with distinct bulge medially such that it parallels dorsal plane; anterior cephalic border medially not deflected far anteriorly; PMI developed as linear incision; L3 lies in flat plane; isolated patches of coarse tubercles on L3; visual surfaces in dorsal view present within sagittal line drawn tangent to lateral edge of frontal lobe; terminal pygidial lappet subrectangular.

ETYMOLOGY: The species was named for Hy Finkel, BSL's uncle.

MATERIAL: AMNH 45259–45265.

DESCRIPTION: Cephalic length (sag.) 50% of width. Axial furrow nearly straight anterior to S1, diverging forward at about 30°, narrow, shallow; posterior to S1 diverging at 10°. Cranidial anterior border short exsagittally and medially, lying in constant dorsoventral plane; pointed medially in dorsal view. Preglabellar furrow moderately incised and narrow. Cranidial anterior border lengthens slightly medially, developed as narrow lip. Facial suture anterior to eyes flexes laterally, then medially, with smoothly convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly then posteriorly laterally. Glabellar length equal to width across frontal lobe; frontal lobe ellipsoid, about 60% of length of glabella; L1-L3 flat (sag.); frontal lobe at level of posterior glabellar region; anterior part of frontal lobe moderately declined forward, smoothly rounded in dorsal view. PMI shallow linear incision. S3 moderately incised, convex anteriorly, branches diverging at about 130°. Sagittal region of L3-L2 nearly flat in dorsal view, lateral lobes weakly declined abaxially. L3 wedge-shaped, lengthening distally, outer edge posteriorly flexes laterally, anterior end flexing less strongly laterally, with isolated patches of coarse tubercles. S2 roughly transverse, weakly convex anteriorly, moderately incised, shallow adjacent to axial furrow. S1 deep, crescent shaped, medial portion developed as smooth curve directed anteriorly, contacting axial furrow. L1 short, flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 of nearly uniform length, convex anteriorly medially, deep. L0 55% of width of frontal lobe, moderately arched (tr.), longest

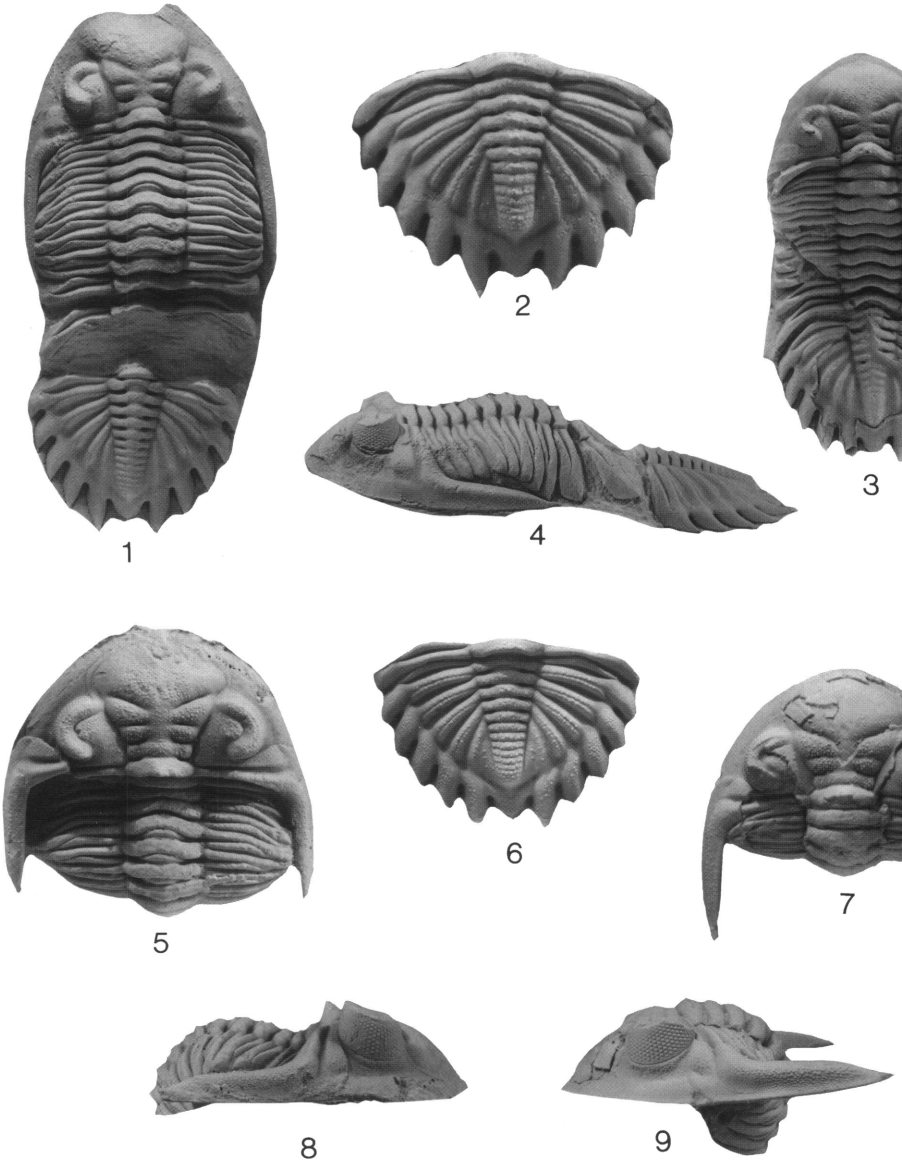

Fig. 21. *Philipsmithiana* spp., Middle Devonian, Mt. Issomour, Morocco. **1, 3, 4**. *P. burtandmimiae*, new species. **1, 4**. AMNH 45266, dorsal and lateral views of nearly complete holotype individual, ×1.2. **3**. AMNH 45267, dorsal views of nearly complete paratype individual, ×2.1. **2, 5–9**. *P. hyfinkeli*, new species. **2**. AMNH 45264, dorsal view of pygidium of complete paratype individual, ×2. **5, 8**. AMNH 45264, dorsal and lateral views of cephalon and portion of thorax of complete paratype individual, ×2. **6**. AMNH 45265, dorsal view of pygidium of complete paratype individual, ×2. **7, 9**. AMNH 45265, dorsal and lateral views of cephalon and portion of thorax of complete paratype individual, ×2.

sagittally. Large Eye Index 0.45. Anterior edge of eye adjacent to axial furrow opposite anterodistal corner of L3; posterior edge of eye opposite S1, anterior to transverse line tangent to L0; eye raised slightly above frontal lobe; maximum of nine lenses in a dorsoventral file on visual surface; isolated patches of coarse tubercles on eye ridge. Fixigena with distinct bulge roughly paralleling dorsoventral plane. Postocular fixigenal field

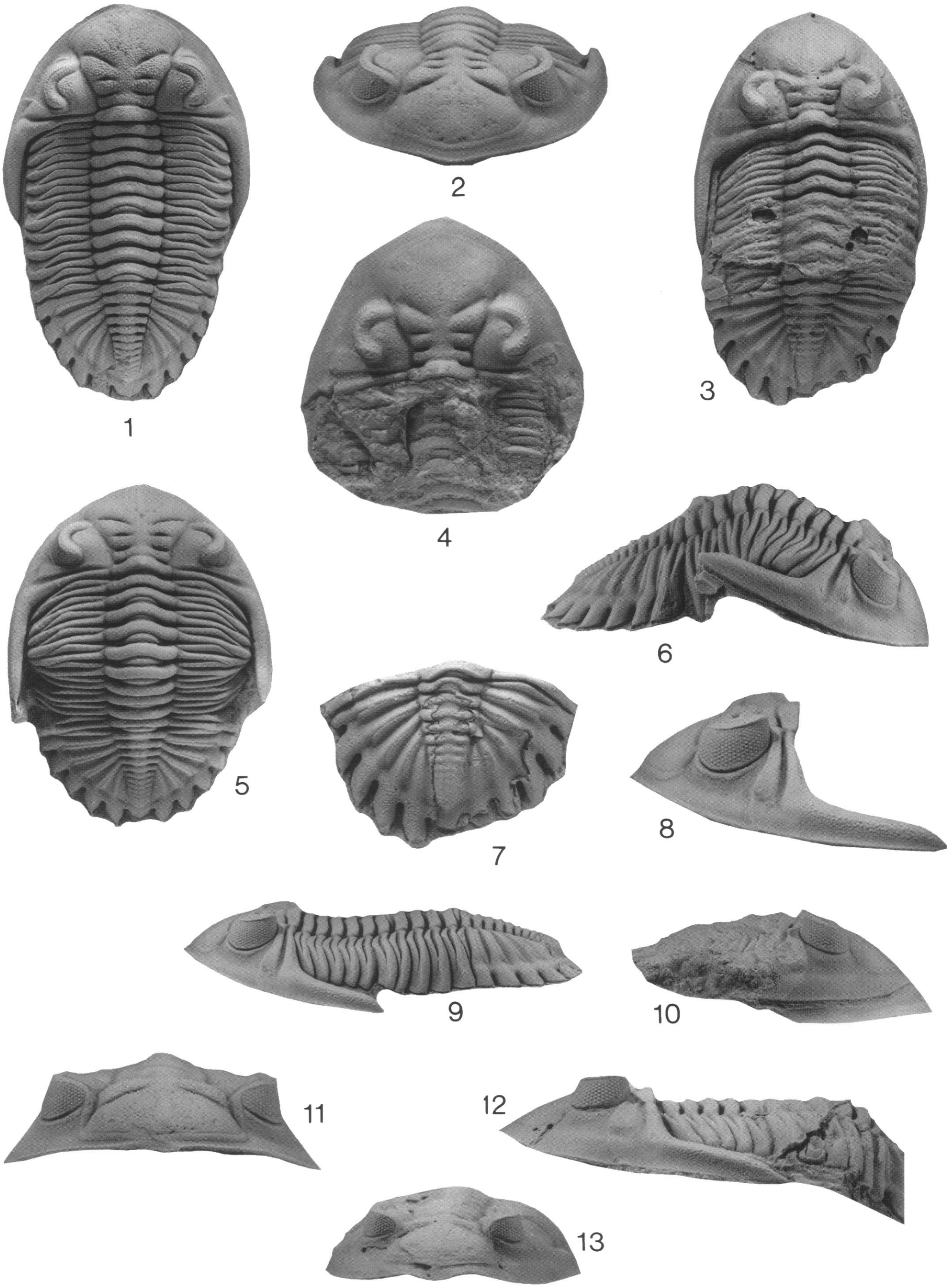

Fig. 22. *Philipsmithiana* spp., Middle Devonian, Mt. Issomour, Morocco. **1, 2, 5, 6, 8, 9, 11**. *P. hyfinkeli*, new species. **1, 9, 11**. AMNH 45260, dorsal, lateral, and anterior views of complete paratype individual, ×1.3. **8**. AMNH 45260, lateral view of cephalon of paratype individual, ×2.1. **2, 5, 6**. AMNH 45259, anterior, dorsal, and lateral views of complete holotype individual, ×1.7. **3, 4, 7, 10, 12, 13**. *P. burtandmimiae*, new species. **3, 12, 13**. AMNH 45271, dorsal, lateral, and anterior views of complete individual, ×1.6. **7**. AMNH 45271, dorsal view of pygidium, ×2. **4, 10**. AMNH 45272, dorsal and lateral views of cephalon, ×1.6.

30% of length of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse, weakly flexing anteriorly distally, anterior margin nearly straight, of relatively constant length, longest posterior to medial visual surfaces of eyes, deep distally. Genal spine long flange extending back to sixth thoracic segment; cephalic lateral border furrow bisects spine; medial edge of genal spine flattened, lateral edge evenly inclined; lateral margin of genal spine parallels sagittal line, at posterior end recurves; interior margin of genal spine parallels lateral margin before deflecting laterally. Lateral border furrow narrow, shallow; lateral border weakly widens posteriorly. Anterior margin of cephalic doublure bluntly pointed. Prosopon of fine tubercles.

Thorax of 11 segments. Axial ring about 25% of width of thorax; rings of equal length (exsag.) at distal ends, and medially flexed forward. Ring furrow of equal length, moderately incised, flexing forward medially and distally. Anterior margin of ring well defined sagittally, inclined posterodorsally, most elevated near posterior edge; scattered tubercles around medial portion of axial ring; articulating half ring set slightly below axial ring. Proximal part of pleura transverse, approximately horizontal; anterior segments rather evenly convex (tr.); outer part of pleurae more strongly flexed downward, straight in posterior segments. Posterior band long (exsag.); anterior margin straight, deflected at constant, small angle posteriorly, length (exsag.) shortens as length of pleural furrow increases medially; after approximate midpoint, length (exsag.) of pleural furrow decreases laterally, length of posterior band increases, becomes planar; posterior surface declined posterodorsally; anterior surface declined anterodorsally, with concave depression. Anterior pleural band short (exsag.), medially transverse, deflecting strongly posteriorly past approximate midpoint, at roughly same level as posterior band, pinching out distally.

Pygidium broadly triangular in outline excluding marginal lappets; length about 75% of width excluding lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, converging at 20° anterior to fifth pygidial axial ring, roughly parallel posterior to fifth pygidial axial ring. Axis 25% of pygidial width anteriorly, with 15 rings; rings of nearly equal length distally and sagittally, longest distally; anterior and posterior edges of axial rings anterior to fifth axial ring from midline to distal edge weakly arch anteriorly. Ring furrows moderately incised. Lateral margins of pygidial lappets straight, medial margins straight, distal tips at distal end of posterolateral margin inclined at approximately 45° angle relative to sagittal line. Axial terminus subrectangular, convex posteriorly, projecting not as far posteriorly as fifth pair of pleural lappets, broad, 1.5 times width of posterior portion of pygidial axis; postaxial region 20% of pygidial length (sag.). Pygidial pleural field flanking posterior portion of pygidial axis faintly excavated; anterior and posterior pleural segments of equal elevation; tops of segments rounded; pleural furrows deeper than interpleural furrows, moderately incised, long (exsag.). Laterally pygidial interpleural furrows arching more strongly than medially. In medial region of adjacent pleural segments, posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment.

DISCUSSION: This species is known from a series of specimens from an unspecified limestone in the Middle Devonian of Morocco. It bears a strong resemblance to *Greenops boothi* from Eastern North America, but as discussed above, character analysis suggests that the taxa belong to two separate subclades that are relatively closely related but that are not sister taxa. The discovery of the new Moroccan taxa indicates that possibly a diverse new asteropyginid fauna may be recovered from these localities.

Philipsmithiana burtandmimiae, new species

Figures 7.2–7.6, 7.8, 21.1, 21.3, 21.4, 22.3, 22.4, 22.7, 22.10, 22.12, 22.13

TYPES: Holotype AMNH 45266, a complete specimen from the Middle Devonian of Morocco, near Mt. Issomour, exact locality and stratigraphic horizon unknown; paratype AMNH 45267, a nearly complete specimen from the same locality as the holotype.

DIAGNOSIS: S3 straight; anterolateral edges flexes posteriorly; maximum of seven lenses per dorsoventral file on visual surface; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; distance between frontal lobe and facial suture increases slightly from lateral edges to midline; visual surfaces present within sagittal line drawn tangent to frontal lobe; fixigena evenly sloping from axial furrow to internal margin of eye; anterior cephalic border medially deflected anteriorly beyond lateral margins of cephalon; isolated patches of coarse tubercles on L3 absent; PMI developed as rounded depression; anterior and posterior margins of palpebrum deflected at equal but opposite angles relative to transverse line; L3 distinctly swollen; terminal pygidial lappet triangular; lateral margins of pygidial lappets curved, distal tips pointed; pygidial lappets long, length (exsag.) from proximal to distal tip approximately equals length of first three (sag.) pygidial axial rings; pygidial interpleural furrows arch at same angle laterally as medially.

ETYMOLOGY: Named for Burt and Mimi Lieberman, BSL's parents.

MATERIAL: AMNH 45266–45272.

DESCRIPTION: Same as for *P. hyfinkeli* except: Cephalic length (sag.) 55% of width. Distance between frontal glabellar lobe and facial suture increases slightly from lateral edges of frontal lobe to midline; anterior cephalic border medially deflected anteriorly beyond facial suture by length (sag.) of L1; S3 straight, anterolateral edge flexes posteriorly; PMI developed as rounded depression; maximum of seven lenses per dorsoventral file on visual surfaces; fixigena evenly sloping from axial furrow to internal margin of eye; posterior and anterior margins of palpebrum deflected at equal but opposite angles relative to transverse line.

Thoracic axial ring about 30% of width of thorax.

Length of pygidium about 70% of width excluding lappets; axis 30% of pygidial width anteriorly; lateral margins of pygidial lappets curved, distal tips of lappets at distal end of straight posterolateral margin inclined at 45° angle relative to sagittal line; terminal pygidial lappet triangular; pygidial interpleural furrows arch at same angle laterally and medially; pygidial lappets long (exsag.), length (sag.) of first three axial rings; postaxial region 25% of pygidial length (sag.).

DISCUSSION: This species is also known from an unspecified limestone of Middle Devonian age in Morocco.

MODELLOPS, NEW GENUS

TYPE SPECIES: *Greenops struvei* Morzadec, 1969.

ASSIGNED TAXA: None (monotypic).

DIAGNOSIS: S3 straight, anterolateral edge flexes posteriorly; S2 roughly transverse, weakly convex anteriorly; posterior and anterior margins of palpebrum deflected at angles to transverse line that are roughly equivalent; posterior edge of visual surface anterior to transverse line tangent to anterior edge of L0; maximum of eight lenses per dorsoventral file on eye surfaces; immediately before cephalic lateral border furrow meets posterior border furrow, posterior border furrow flexes anteriorly; axial furrows diverge more strongly anterior to S1, less strongly anterior to anterior half of L3; facial suture lateral to eye, before flexing posteriorly, flexes anteriorly to point opposite S2; eye rests on sloping librigenal field; anterior cephalic border rounded in dorsal view, developed as narrow lip; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; posterior and anterior margins of fixigena deflected at equal but opposite angles relative to transverse line; ornamentation on L0 absent; lateral margin of genal spine parallels sagittal line, at posterior end straight; interior margin of genal spine deflected laterally at approximately 20° angle to sagittal line; terminal pygidial lappet subrectangular, convex posteriorly, broad, does not project as far posteriorly as lappets that project furthest posteriorly; lateral margins of pygidial lappets curved, medial margins straight; anterior margins of pygidial axial rings posterior to fifth ring smoothly convex anteriorly; tops of pygidial pleural segments rounded; pygidial pleural field flanking posterior portion of pygidial axis moderately excavated; in medial region of adjacent pleural segments, posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment; pleural furrows developed as long (exsag.) excavated space; laterally pygidial interpleural furrows arching at same angle as medially; 14 pygidial axial rings.

ETYMOLOGY: Named for Andrew Modell, Department of Invertebrates, who took the photographs used in this publication.

DISCUSSION: This monotypic genus is erected to accommodate a species sister to a clade including *Asteropyge*, *Neometacanthus*, *Greenops*, and *Kayserops*, along with several other genera. The lone species assigned to this genus differs from *Philipsmithiana* in the condition of several characters important to the phylogenetic analysis conducted herein, and thus the species could not be included within that genus without making it paraphyletic.

Modellops struvei (Morzadec, 1969)

Greenops ? *struvei* Morzadec, 1969: 40, pl. 7, figs. 1–5, pl. 8, figs. 1–8.

Greenops struvei Morzadec. Morzadec, 1983: 122, pl. 8, figs. 1–11.

TYPES: Holotype defined in Morzadec (1983: pl. 8, fig. 1).

DIAGNOSIS: Same as for genus.

DISCUSSION: This species is known from the upper Emsian of the Massif Armorican. Morzadec (1969) originally assigned this species to the genus *Greenops* with some question because of differences he perceived between it and the type of the genus, *G. boothi*. In particular, he saw differences in the length of the genal spines and in the number of pygidial axial rings. However, Morzadec (1983) suggested that other species assigned to *Greenops*, such as *G. chaconae* Arbizu, 1979 (discussed above and here assigned to *Breizhops* Morzadec, 1983), had genal spines similar to those found in *Modellops struvei*. He suggested that because of this and the condition of the anterior margins of the pygidial axial rings, which laterally are straight and medially are strongly arched anteriorly, the species should be assigned to *Greenops*. Morzadec (1983) also suggested that it must be one of the oldest species of the genus *Greenops*, and he treated it as a direct ancestor of *G. osismorum* Morzadec, 1983 (here *Stummiana osismorum*). As discussed above, there are several differences between species assigned herein to *Philipsmithiana* and *Greenops boothi*, and the same is true for the taxon assigned to *Modellops*. However, *M. struvei* does converge on *G. boothi* in certain aspects of its morphology. In particular, the lateral margin of the genal spine at its posterior end is straight, and the anterolateral margins of the first five pygidial axial rings laterally are straight and medially arch strongly anteriorly, but the bulk of the character evidence suggests the separation of *M. struvei* from *Greenops*. Therefore, Morzadec's (1983) contention that *M. struvei* is an ancestor of any species of *Greenops* is not upheld herein. In addition, *M. struvei* cannot be a direct ancestor of *Stummiana osismorum* as these taxa are separated by several nodes comprising different genera in the phylogeny given in figure 4.

NEOMETACANTHUS RICHTER AND RICHTER, 1948

TYPE SPECIES: *Phacops stellifer* Burmeister, 1843.

ASSIGNED TAXA: *Neometacanthus* sp. aff. *stellifer* (Burmeister, 1843), and possibly *Greenops* (*Neometacanthus*) new species Hickerson, 1992, *Dalmanites* (*Cryphaeus*) *barrisi* Hall and Clarke, 1888, and *Asteropyge fitzpatricki* Walter, 1923.

DIAGNOSIS: S3 straight; anterolateral edge flexes posteriorly; cephalic posterior border furrow longest (sag.) posterior to palpebrum, shallow and transverse laterally; S2 nearly transverse, weakly convex anteriorly; maximum of seven lenses per dorsoventral file on visual surface; anterior cephalic border pointed medially; tubercle on L0; line from posterior to anterior edge of eye roughly parallel to sagittal line; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; prosopon of fine tubercles; genal spine developed as long flange extending back at least to sixth thoracic segment; medial edge of genal spine significantly thickened relative to lateral edge; plane between medial and lateral edges of genal spine evenly inclined; cephalic axial furrows diverge more strongly anterior to S1; interior margin of genal spine parallels lateral margin before deflecting laterally; terminal pygidial lappet subrectangular anteriorly; convex posteriorly, not projecting as far posteriorly as fifth pygidial pleural lappet; lateral and medial margins of pygidial lappets curved; tops of pygidial pleural segments rounded; pleural furrows moderately incised, short (exsag.); laterally pygidial interpleural furrows flex more strongly posteriorly; posterior region of anterior pleural segment equal in length (exsag.) to anterior part of posterior segment.

DISCUSSION: This generic name is applied to two species with surety, but may also contain three additional species. The genus *Neometacanthus*, based on the phylogeny presented herein, can no longer be treated as a monotypic subgenus of a larger genus *Greenops* (or vice versa) as certain authors had suggested in the past, e.g., Haas (1970), Gandl (1972), Smeenk (1983), and Morzadec (1983). Several authors have suggested that *Neometacanthus* was closely related to *Greenops*, and this conclusion is partially supported by the analysis conducted herein. However, the genera are not sister taxa. Instead, *Neometacanthus* appears to be sister to a larger clade including *Rhenops* Richter and Richter, 1943, and *Asteropyge* Hawle and Corda, 1847, on the basis of the following character states: 5(1), 22(2), 36(1), 55(1), 57(1), and 63(1). This clade is in turn sister to a clade containing *Greenops* Delo, 1935, *Kayserops* Delo, 1935, and some other new genera.

Kielan (1954) described a new species that she referred to as *Asteropyge* (*Neometacanthus*) *czarnockii*. Although the specimens she figured are poorly preserved (Kielan, 1954: pl. 7, figs. 6–11), they do share several characters of the pygidium with the type of the genus *Asteropyge*, *A. punctata* (Steininger, 1831), and it is therefore provisionally placed in that genus. In particular, they share the following characters: the fourth pair of pygidial pleural lappets projects further posteriorly than the fifth pair of pygidial pleural lappets; laterally the pygidial interpleural furrows arch more strongly posteriorly; the tops of the pygidial pleural segments are rounded; the pygidial terminal lappet is greatly reduced, the lateral and medial margins of the pygidial pleural lappets are straight; the distal tips of the pygidial pleural lappets are pointed; the pygidial axis constricts posterior to the fifth axial ring; the anterior margins of the pygidial axial rings posterior to the fifth axial ring are smoothly convex anteriorly; and the pleural furrows are moderately incised and short (exsag.). However, it is important to state that some of these characters are also found in *N. stellifer*, and the two genera *Asteropyge* and *Neometacanthus* appear to be closely related. Because *Asteropyge czarnockii* shares more characters with *Asteropyge punctata* than with *Neometacanthus stellifer*, it is tentatively assigned to *Asteropyge*. *Neometacanthus* could still be viewed as a subgenus of *Asteropyge*, but that would also necessitate lumping the genus *Rhenops* within *Asteropyge*. As there appear to be good diagnostic characters for *Rhenops*, discussed below, this is not done, and *Neometacanthus* is treated as a separate genus. *Asteropyge czarnockii* differs from *N. stellifer* in the condition of several characters. In particular, the pygidial pleural lappets are relatively much longer in Kielan's (1954) species than they are in *N. stellifer*: the fourth pair of pygidial pleural lappets project further posteriorly than the fifth pair in *A. czarnockii*, whereas in *N. stellifer* the fifth pair of pygidial pleural lappets projects further posteriorly.

Smeenk (1983: pl. 27, fig. 2) figured a pygidium that he assigned to *Greenops* (*Neometacanthus*) sp.; however, it is too poorly preserved to assign with surety to any genus.

Authors such as Morzadec (1992) and Hickerson (1992) have remarked on the presence of the genus *Neometacanthus* in ENA. On the basis of the phylogenetic analysis performed herein, the sole species in North America traditionally assigned to *Neometacanthus*, what has traditionally been referred to as *Greenops* (*Neometacanthus*) *calliteles* (Green, 1837), is distantly related both to the type of *Neometacanthus* and to the type of the genus *Greenops*. Instead, that species is assigned to a new genus, *Bellacartwrightia*, discussed in greater detail above under the appropriate heading. However, for various reasons discussed above, the specific name *calliteles* can no longer be assigned to this taxon, and it is instead referred to as *Bellacartwrightia phyllocaudata*, new species. That species differs from *N.* sp. aff. *stellifer* in the condition of several characters, including the following listed in table 1: 1, 2, 5, 6, 7, 8, 15, 16, 23, 25, 31, 34, 38, 39, 40, 43, 46, 47, 48, 52, 56, 57, 58, 59, 62, 65, and 66.

In addition, Ludvigsen (1979: fig. 57d) figured a slab showing two trilobites that he assigned to *Neometacanthus calliteles* (Green). These taxa are not conspecific with what is treated herein as *Bellacartwrightia phyllocaudata*. Instead, they belong to a new species, *Bellacartwrightia jennyae*, which can be distinguished both from the other species of *Greenops* that occur in ENA, which are discussed below, and from *B. phyllocaudata* on the basis of the structure of the pygidial pleural lappets, the number of pygidial axial rings, the presence of tubercles on L0 and on the thoracic and pygidial axial rings, and the condition of the genal spines, which in *Bellacartwrightia jennyae* have a large flattened shelf dorsally and project very far posteriorly (back to the eighth thoracic segment).

There are, however, a series of taxa from the Middle–Upper Devonian (following the stratigraphic perspective of Hickerson [1992]) of Iowa that may belong to the genus *Neometacanthus*. *Greenops* (*Neometacanthus*) new species Hickerson, 1992, could not be obtained because it was under study by Hickerson. The illustrations of this species given in Hickerson (1992) are too poor to assess its relationship with *N. stellifer*. Thus, it was impossible to ascertain whether or not this new species should be assigned to the genus *Neometacanthus*. It is questionably placed in that genus (but no longer treated as a subgenus of *Greenops*) until the actual type material can be examined. Hickerson (1992) also suggested that *Neometacanthus barrisi* (Hall and Clarke, 1888) belonged in the genus *Neometacanthus*. The holotype of this species is lost and no other type material is known (Delo, 1940). Again, the illustrations in Hall and Clarke (1888) and Delo (1940) are too crude to merit comment on the possible generic affinities of this asteropyginid taxon. It does appear to lack the diagnostic characters of *Greenops* and is not retained in that genus. However, the pygidium does have the long pleural lappets that curve laterally and medially and the well-developed terminal pygidial lappet characteristic of *Neometacanthus*, and it is also tentatively placed in that genus. Finally, *Asteropyge fitzpatricki* Walter, 1923, is another poorly preserved taxon from Iowa that was under study by Hickerson and could not be obtained in this analysis. The figures in Walter (1923) are too poor to ascertain with surety the generic affinities of this species, but like *N. barrisi* it has the long pygidial lappets curving laterally and medially as well as the well-developed terminal pygidial lappet. This taxon is also questionably placed in the genus *Neometacanthus*.

Gandl (1972) suggested that the taxa *G. traversensis* Stumm, 1953, and *G. aequituberculatus* Stumm, 1953, and a pygidium that he referred to as *G.* (*Neometacanthus*?) sp. M should be assigned to the subgenus *Neometacanthus*. *Greenops aequituberculatus* is not treated as valid herein, and instead appears to comprise a series of taxa. *Greenops traversensis* Stumm, 1953, and *G. alpenensis* Stumm, 1953, are synonymized herein and are assigned to the genus *Kayserops*. They are discussed in greater detail below, under the heading for that genus. The species *Kayserops traversensis* differs from *Neometacanthus* sp. aff. *stellifer* in the condition of several characters, including: 2, 3, 7, 8, 10, 19, 22, 24, 25, 32, 36, 40, 43, 48, 55, 56, 58, 59, 60, 61, and 62, and they are closely related. Gandl's (1972) *G.* (*N.*?) sp. M is known only from a pygidium, and thus is too incompletely preserved to ascertain its exact phylogenetic position. However, when compared with *N. stellifer*, it is found to differ in the condition of several characters, including: the terminal pygidial lappet, which is pointed in Gandl's species and subrectangular in *N. stellifer*; the pygidial lappets, which project further posteriorly than the terminal pygidial lappet in *N. stellifer* whereas the terminal lappet projects further posteriorly in Gandl's species; and the pygidial pleural field flanking the pygidial axis, which is faintly excavated in *N. stellifer*, whereas it is prominently excavated in Gandl's species. They do share similar margins of the pygidial pleural lappets, and the condition of the interpleural furrows. At this time it is probably safe to say that Gandl's sp. M is not closely related to *Neometacanthus*.

Neometacanthus sp. aff. *stellifer* (Burmeister, 1843)

Phacops stellifer Burmeister, 1843: 115, pl. 4, fig. 8.
Neometacanthus (*Neometacanthus*) *stellifer* (Burmeister). Pillet, 1961: 104, pl. 3, figs. 1–6.
Greenops (*Neometacanthus*) *stellifer* (Burmeister). Struve, 1959: O480, fig. 380, 1.

DIAGNOSIS: Eleven pygidial axial rings.

MATERIAL: YPM 6642.

DISCUSSION: This species is known from the Couvinian (mostly Eifelian) of Gees Gerolstein, the Eifel District, Germany; the Eifelian of the Armorican Massif in Spain and Portugal; possibly the Middle Devonian of Romania; and the Givetian of Morocco. Pillet (1961) commented on how poorly known this species is considering that it is a "classic" taxon in the history of Devonian trilobitology and on how the poor figures given by past authors do not permit discussion of the affinities of their specimens. His assessment is correct, making it difficult to verify the synonymies given by 19th century authors for lost or unavailable specimens assigned to *N. stellifer*. Pillet (1961) illustrated taxa from several different stratigraphic horizons and geographic localities that he assigned to *N. stellifer*. First it is necessary to verify that Pillet's (1961) suite of specimens do represent a single species, as he illustrated pygidia from the type locality of this species, from the Eifelian of Germany, as well as from the Givetian of Morocco. The pygidia he illustrated from the different localities do seem to be very similar, sharing the long (exsag.) and narrow (tr.) pygidial pleural lappets curving laterally and medially, the narrow terminal pygidial lappet that is convex posteriorly, the nodes on the pygidial axial rings, and the wide dished space between adjacent pleural lappets. However, the pygidia from Morocco that he figured do not have such a broad distance along the pygidial margin between the lappets as is found in pygidia from the type locality, and, in addition, the pygidial interpleural furrows flex more strongly posteriorly laterally in the Moroccan pygidia. Thus, it appears that there may be some slight differences between the German and Moroccan pygidia that Pillet (1961) assigned to the taxon *N. stellifer*; however, for the purposes of this analysis, these pygidia are treated as tentatively conspecific, because the slight differences manifested between pygidia hailing from different localities would have no effect on this taxon's phylogenetic position as they do not include characters employed in phylogenetic analysis. In addition, as a wide range of specimens could not be seen, it was impossible to ascertain whether these differences represent variation within a species or differences between two distinct species. As the types of *N. stellifer* could not be obtained, it could not be determined with absolute certainty whether or not the specimens Pillet (1961) illustrated are conspecific with *N. stellifer*; therefore, they cannot be assigned to that species. However, they do appear to be very similar to illustrated specimens of *N. stellifer*, and they are therefore assigned to *N.* sp. aff. *stellifer* (Burmeister) until the types of that species can be obtained.

ASTEROPYGE HAWLE AND CORDA, 1847

TYPE SPECIES: *Olenus punctatus* Steininger, 1831.

DIAGNOSIS: See Struve (1959).

ASSIGNED TAXA: *Asteropyge* (*Neometacanthus*) *czarnockii* Kielan, 1954.

DISCUSSION: Species in this genus are known from the Givetian of Poland, from the Eifelian of the Eifel District in Germany, and possibly from the Middle Devonian of Dasburg. There exist species that in the past had been assigned to *Asteropyge* that are not assigned to *Asteropyge* herein because they differ from the type species in the condition of a few characters diagnostic of the genus. These species were poorly preserved or were not available for study. Although they are not assigned to this genus at this time, the possibility exists that if incorporated into a phylogenetic analysis, they might appear in a monophyletic clade including the type of the genus *Asteropyge* and excluding all of the other genera analyzed herein.

As discussed above under the heading of *Neometacanthus*, Kielan (1954) figured and described the species *Asteropyge* (*Neometacanthus*) *czarnockii* from the Givetian of Poland. Although poorly preserved, this species does appear to possess the characteristics diagnostic of the genus *Asteropyge*. In particular, it has the long (exsag.) pygidial pleural lappets curving laterally and medially, and it has a very reduced or absent terminal pygidial lappet, though the field that would have been occupied by this lappet is narrower transversely than it is in *A. punctata* (Steininger, 1831). In addition, L3 is swollen and the fourth pygidial pleural lappet projects further posteriorly than the other pleural lappets. The genus *Asteropyge* is very closely related to *Neometacanthus*, but *Neometacanthus* can no longer be considered a subgenus of *Asteropyge* unless *Asteropyge* were expanded to include not only *Neometacanthus* but also *Rhenops*. This is not done herein, and thus these two genera will be treated as two independent and distinct entities.

Walter (1923) figured and discussed two taxa from the Middle–Upper Devonian (following the stratigraphy of Hickerson [1992]) that he assigned to *Asteropyge barrisi* (Hall and Clarke, 1888) and *A. fitzpatricki* Walter, 1923. Unfortunately the types of species were under study by Hickerson and could not be obtained for this analysis, and the figures of Walter's (1923) specimens do not permit a detailed analysis because of their poor reproduction. Both taxa do have the long (exsag.) pygidial pleural lappets curving laterally and medially that are characteristic of *Asteropyge*. However, in these taxa the terminal pygidial lappet is well developed and narrow, unlike its condition in the type of *Asteropyge*. It is conceivable that these taxa are derived from a lineage of *Asteropyge* that convergently reacquired a narrow terminal pygidial lappet, or these taxa could belong to stem lineage *Asteropyge* and thus have retained the terminal pygidial lappet, which was later lost in more derived members of *Asteropyge* such as *A. punctata*. Until this material can be obtained and studied, assignment of a generic name to these specimens remains difficult, and at present they are questionably placed in the genus *Neometacanthus*, as discussed above under that generic subheading.

Morzadec and Arbizu (1978) described a new species *Kayserops cantarmoricus* that Morzadec (1983) later assigned to the genus *Asteropyge*. This assignment is not supported by the phylogenetic analysis conducted herein as this species differs from *A. punctata* in the condition of several characters, including: 2, 3, 5, 6, 10, 11, 13, 14, 17, 18, 19, 23, 24, 27, 28, 29, 31, 32, 37, 40, 42, 46, 47, 48, 49, 52, 54, 57, 59, 60, 61, 62, and 66. It is henceforth assigned to the genus *Hallandclarkeops*, new genus, which is discussed in greater detail above. *Hallandclarkeops* is distantly related to *Asteropyge*.

In several cases, taxa that share numerous similarities with *A. punctata* have been assigned to the genus *Heliopyge*. However, there exist many differences between true *Heliopyge*, such as the type *H. helios* (Richter and Richter, 1926) and *H. turolensis* Gandl, 1972, and the type of *Asteropyge*. The type of *Asteropyge* does not appear to be closely related to *Heliopyge* in the cladogram shown in figure 4, and they differ in the condition of a significant number of character states (see tables 1, 2).

Several authors have commented on the phylogenetic relationships of the genus *Asteropyge*. In particular, Morzadec (1983) suggested that it was closely related to *Breizhops* and *Comura* (see fig. 5E). The close relationship between *Asteropyge* and *Breizhops* is not supported herein, as they are separated by several nodes on the cladogram given in figure 4. In regard to *Comura*, the type of *Asteropyge* is separated from a representative species of a genus closely related to *Comura*, such as *Tolkienia granulispina* (Morzadec, 1983), by several nodes on the cladogram in figure 4, and differs from it in the condition of many characters. Both Haas (1970) and Smeenk (1983) suggested that *Asteropyge* was closely related to *Pilletina* (see fig. 5A, D). Again, these taxa are separated by several nodes on the cladogram given in figure 4, and any similarities between these taxa must be treated as either homoplasy or symplesiomorphy. Haas (1970) also suggested that *Asteropyge* gave rise to the genus *Neocalmonia* (see fig. 5a). The type species of the genera are separated by several nodes on the single most parsimonious cladogram of the Asteropyginae and differ in the condition of several characters, including: 2, 4, 6, 7, 10, 13, 19, 22, 23, 24, 25, 27, 28, 29, 31, 32, 37, 40, 42, 43, 45, 48, 50, 54, 55, 57, 59, 61, and 64. However, they do share some similarities in their pygidial morphology. In particular, the terminal pygidial lappet is very reduced in both taxa. In addition, in *A. punctata* the fourth pygidial lappet projects further posteriorly than the other lappets. In *N. quadricosta* Pillet, 1969, the third pleural lappet projects furthest posteriorly. However, *N. quadricosta* only has four pleural lappets as opposed to five in *A. punctata*. Depending on how the pygidial pleural segments were lost developmentally and phylogenetically (following the phylogeny in fig. 4 that indicates *Neocalmonia* is a derived asteropyginid), the pleural lappets that project furthest posteriorly in the two taxa could be serial homologues, implying the same character state for these two taxa. *Neocalmonia quadricosta* was scored as having the fourth pygidial lappet projecting furthest posteriorly, assuming that its third lappet is serially homologous to the fourth lappet of all the other asteropyginines with five pleural lappets.

Asteropyge punctata (Steininger, 1831)

Figures 7.1, 11

Olenus punctatus Steininger, 1831: 356, pl. 21, fig. 7.

Asteropyge punctata (Steininger). Struve, 1959: 0478, figs. 378, 379, 9a, b.

DIAGNOSIS: Broad ledge of anterior cephalic border visible anterior to anterolateral portions of frontal lobe; S3 straight; maximum of seven lenses per dorsoventral file on visual surface; distance between frontal lobe and facial suture from anterolateral edges to midline constant; immediately before cephalic posterior border furrow contacts lateral border furrow, posterior border furrow flexes anteriorly; anterior cephalic border rounded medially; tubercle on L0 absent; anterior cephalic border deflects anteriorly medially; demarcation between librigena lateral to eye and lateral border furrow weak; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; anterior margin of frontal lobe smoothly rounded in dorsal view; posterior margin of fixigena relative to anterior margin deflected at an angle to transverse line that is significantly larger; plane between medial and lateral edges of genal spine evenly inclined; lateral margin of genal spine parallels sagittal line; interior margin of genal spine parallels lateral margin before deflecting laterally; lateral and medial margins of pygidial lappets straight; pygidial pleural field flanking posterior portion of pygidial axis faint; anterior and posterior portions of pygidial pleural segments of equal elevation; fourth pygidial pleural lappet projects further posteriorly than other lappets; in medial region of adjacent pleural segments posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; 15 pygidial axial rings; terminal pygidial lappet broad anteriorly; terminal pygidial lappet very reduced, developed as blunt triangle; anterolateral margins of first five pygidial axial rings when proceeding from axial furrows to midline are evenly convex and weakly arched anteriorly.

MATERIAL: AMNH 18767, 18768, 18770; YPM 6643.

DISCUSSION: This species is known from the Calceola beds, Gees, Gerolstein, the Eifel District, Germany, and Steininger (1831) also reported it from the graywacke of Dasburg. This species is another case of a "classic" asteropyginid taxon that is poorly known. We hope the additional illustrations of this material are helpful.

RHENOPS RICHTER AND RICHTER, 1943

TYPE SPECIES: *Cryphaeus anserinus* Richter (1916).

DIAGNOSIS: See Struve (1959).

ASSIGNED TAXA: *Cryphaeus lethaeae* Kayser, 1889, *Rhenops redonesianus* Morzadec, 1981, *Rhenops babini* Morzadec, 1983, *Rhenops circumapodemus* Smeenk, 1983, *Asteropyge* (*Rhenops*) *index* Richter and Richter, 1943, and *Rhenops* new species.

DISCUSSION: Species in this genus are known from the upper Emsian of northern Spain, the Armorican Massif, and Germany; the Eifelian of Morocco; and the Frasnian or Famennian of Venezuela. *Rhenops* is the only asteropyginid genus known to occur in Gondwana. The species from Venezuela, *Rhenops* new species, is known from rocks that may be either Frasnian or Famennian in age, though this assignment could be questionable (Carvalho, personal commun.). If recovered from the Famennian, then it would be the youngest asteropyginid known, as all species of this subfamily were thought to have died out at the end of the Frasnian, directly following the Kellwasser anoxic event (Feist, 1991; Morzadec, 1992).

The type species of the genus was not available for analysis because the Senckenberg Museum, where the types are housed, would not allow loan of the original specimens. Instead, a species that appears to be closely related to it on the basis of illustrated material, *R. babini*, was used to code character information. The chief differences between that taxon and *R. anserina* are the condition of the terminal pygidial lappet, which projects further than the pleural lappets in *R. anserina* but not in *R. babini*, and the anterior cephalic border, which appears pointed in *R. babini* but it is rounded in *R. anserina*. The other species listed above were assigned to *Rhenops* because they possess the characters diagnostic of the genus. However, the possibility exists that if these taxa were subjected to phylogenetic analysis they might not map out as sister to *R. babini*.

Morzadec (1983) suggested that this genus was derived from the *Pseudocryphaeus* lineage and is sister to a clade containing *Kayserops* Delo, 1935, *Neometacanthus* Richter and Richter, 1948, and *Greenops* Delo, 1935 (see fig. 5e). Some of these evolutionary conclusions are supported by the analysis conducted herein, as *Rhenops* does appear to be closely related to *Neometacanthus* and it, along with *Asteropyge*, forms a clade sister to *Neometacanthus*. However, *Rhenops* is distantly related to both *Pseudocryphaeus* and *Kayserops*. Haas's (1970) phylogeny of the asteropyginines depicted essentially the same relationships as Morzadec's (1983) did, except he treated *Kayserops* as distantly related to *Pseudocryphaeus* and *Rhenops* (see fig. 5a). His phylogenetic perspective is thus also not supported, except with respect to the close affinity between *Neometacanthus* and *Rhenops*. Smeenk (1983) suggested that *Rhenops* was derived from the *Paracryphaeus* lineage (see fig. 5d). Again, this conclusion is not supported by the phylogenetic topology for the asteropyginines promulgated herein.

Rhenops babini Morzadec, 1983

Rhenops babini Morzadec, 1983: 121, pl. 7, figs. 1–7.

TYPES: Holotype defined in Morzadec (1983: pl. 7, fig. 1).

DIAGNOSIS: S3 faintly sinusoidal; lateral to eye, facial suture before flexing posteriorly flexes anterior to point opposite S1; maximum of eight lenses per dorsoventral file on visual surface; PMI developed on external mold as linear incision; line from posterior to anterior edge of eye forms an angle to sagittal line that is approximately 0–5°; posterior edge of visual surface posterior to transverse line tangent to L0; demarcation between librigena and lateral border furrow prominent; genal spine developed as long flange extending back to sixth thoracic segment; medially, genal spine developed as flattened ledge, laterally evenly inclined; terminal pygidial lappet triangular; distal tips of pygidial lappets developed as blunt triangles; pygidial pleural fields flanking posterior portion of pygidial axis prominently excavated; when proceeding from axial furrows to midline, anterolateral margins of first five pygidial axial rings first straight, then arch strongly anteriorly.

DISCUSSION: This species is known from the upper Emsian of the Armorican Massif. It does appear to be somewhat closely related to *Greenops*, as Eldredge (1993) suggested, as it belongs to a larger clade including *Asteropyge* and *Neometacanthus* that is sister to a clade including *Greenops* and other North American asteropyginines such as species of *Kayserops* Delo, 1935, and *Stummiana*, new genus. Prominent similarities between species of *Rhenops* and *Greenops* include aspects of their pygidial morphology. In particular, *Rhenops babini* and many species of *Greenops* both have the distal tips of the pygidial lappets developed as blunt triangles, and both also have the anterior margins of the first five pygidial axial rings first straight and then flexing strongly anteriorly when proceeding from the axial furrows to the midline.

Rhenops, new species

Figure 15

DIAGNOSIS: Distance between frontal lobe and facial suture increases slightly from lateral edge of glabella to midline; librigena strongly arched; S3 faintly sinusoidal; S2 transverse, convex anteriorly; maximum of seven lenses per dorsoventral file on visual surface; anterior cephalic border pointed medially; PMI developed as linear incision; genal spine developed as long flange extending back to sixth or seventh thoracic segment; medial edge of genal spine significantly thickened relative to lateral edge; lateral margin of genal spine at posterior end recurves posteriorly; interior margin of genal spine parallels lateral margin before deflecting laterally; broad ledge of anterior cephalic border visible anterior to anterolateral portions of frontal lobe; medial tubercles on pygidial and thoracic axial rings present; terminal pygidial lappet triangular; pygidial pleural field flanking posterior portion of pygidial axis moderately excavated; lateral and medial margins of pygidial pleural lappets straight; distal tips of pygidial lappets at distal end of straight posterolateral margin inclined at 45° angle relative to sagittal line; pygidial lappets long; 14 pygidial axial rings.

MATERIAL: One internal mold of cephalon and first three thoracic axial rings missing left genal spine, three external molds of cephala, and one external mold of a pygidium, all housed in the Department of Geology, University of Rio de Janeiro, Brazil.

DISCUSSION: This species is known from strata in Venezuela that have been provisionally assigned to the Frasnian or Famennian (Carvalho, personal commun.). It is the only species of Asteropyginae known from Gondwanaland, and if the strata do turn out to be of Famennian age it is the only species of Asteropyginae to survive into the Famennian. Access to the specimens illustrated herein was provided by M. de. G. Carvalho (Department of Geology, University of Rio de Janeiro), and we thank her. This is the only species of Asteropyginae known from Gondwanaland. Oliver (1977) and Eldredge and Ormiston (1979) recognized the close relationship that northern Gondwanaland had both to ENA and to northern Africa/Armorica, and Oliver (1977) treated ENA and northern Gondwana as a single biogeographic unit, the Appohimchi Subprovince. However, their analyses were largely confined to biogeographic patterns in the Middle Devonian, and Eldredge and Ormiston (1979) did not discuss Upper Devonian trilobites. This species is part of a clade containing taxa from Armorica, suggesting that the patterns Oliver (1977) and Eldredge and Ormiston (1979) recognized for the Middle Devonian may also hold for the Upper Devonian. At least one other trilobite species from northern Gondwana (Colombia), *Monodechenella boteroi* (Caster and Richter *in* Richter and Richter, 1950), is sister to a clade of ENA species (see Lieberman, 1994).

This species is only informally diagnosed and illustrated herein. It will be fully described in a forthcoming publication by M. de G. Carvalho.

GREENOPS DELO, 1935

TYPE SPECIES: *Cryphaeus boothi* Green, 1837.

ASSIGNED TAXA: *Greenops chilmanae* Stumm, 1965, *G. widderensis*, new species, *G. barberi*, new species, *G. grabaui*, new species, *Greenops* new species from the Kashong Shale, and *Greenops* sp. B.

DIAGNOSIS: L3 dorsally flattened; eye socle rests on vertical wall of librigena; maximum of six lenses in dorsoventral file on visual surfaces; facial suture lateral to eye, before flexing posteriorly, flexes anteriorly to point between distal tips of S1 and S2; genal spine developed as moderately long flange extending back to fifth thoracic segment; demarcation between librigena lateral to eye and lateral border furrow weak; lateral margin of genal spine parallels sagittal line; medial edge of genal spine not significantly thickened; faint or prominent raised ridge on dorsal surface of genal spine at its posterior flexure at juncture of posterior border furrow and cephalic border furrow is smoothly curved, convex distally; cephalic axial furrows equally divergent opposite margins of L3; relatively sparse circular fenestrae on posterior band of thoracic pleural segment close to thoracic axis; lateral margins of pygidial lappets curved; anterior margins of pygidial axial rings posterior to constriction of axis smoothly convex anteriorly; 11 pygidial axial rings; pygidial pleural field flanking posterior portion of pygidial axis faintly excavated; fifth pair of pygidial pleural lappets project furthest posteriorly; tops of pygidial pleural segments flat; pleural furrows moderately incised.

DISCUSSION: Central to the entire *Greenops* problem is the issue of what the actual type of the genus is. Delo (1935) erected and diagnosed the genus *Greenops*, and he designated *Cryphaeus boothi* Green as the type. However, because the original types of Green's (1837) species are lost, this taxonomic action did not serve to clear the waters. Delo (1935) figured two specimens as representative of his *Greenops boothi*. Unfortunately, he figured two different species. One is a new species that will be figured in an upcoming paper (Lieberman and Kloc, in prep.). It cannot be considered a valid type or neotype for the species because it hails from a very different stratigraphic horizon and geographic locale than Green's (1837) species, and because it differs significantly from Green's (1837) original material. The other (Delo [1935: fig. 32] equals Hall and Clarke [1888: pl. 16a, fig. 7]) is actually *Bellacartwrightia phyllocaudata*, new species, which some earlier authors treated as *G. calliteles*. Delo's (1935) actions compounded the problems initiated by Hall and Clarke (1888), who figured a range of species from New York state that they assigned to *Dalmanites* (*Cryphaeus*) *boothi*. The only solution that can stabilize the taxonomic problems associated with this genus is to designate a neotype for *Greenops boothi* from the type locality of Green (1837) in Pennsylvania. This is done in this paper. In addition, the phylogenetic relationships of several species within the genus *Greenops* were evaluated using the new type concept.

A range of specimens traditionally assigned to *G. boothi* from New York state are discussed herein. These include some of the specimens Hall and Clarke (1888) assigned to *Dalmanites* (*Cryphaeus*) *boothi*. Most of these are described herein and assigned to *G. barberi*, new species, and *G. grabaui*, new species. However, there are several other new species from the Hamilton Group of New York state probably referable to *Greenops* that were recognized in this study. These new taxa shall be described in an upcoming paper along with asteropyginines from the Tully Limestone (Lieberman and Kloc, in prep.). One, from the Kashong Shale, is figured herein (fig. 8.3). The purpose of the analysis presented herein was to come up with a suitable type for the genus *Greenops* and to evaluate the relative phylogenetic position of that genus within the family Asteropyginae.

In addition to designating the new genus *Greenops*, Delo (1935) placed *Greenops* in the subfamily he created, the Asteropyginae, which he in turn placed in the Dalmanitidae. However, as discussed above, the Asteropyginae can no longer be placed in the Dalmanitidae and instead should be assigned to the Acastidae (Edgecombe, 1991, 1993; Ramsköld and Edgecombe, 1993).

The genus *Greenops* surely represents one of the most important genera of asteropyginines, from both a phylogenetic and a biogeographic perspective. Several authors have commented on the phylogenetic position of *Greenops*, e.g., Haas (1970), Gandl (1972), Arbizu (1979), Smeenk (1983), and Morzadec (1983, 1992). In addition, species that past paleontologists have assigned to *Greenops* in the literature have been recovered from sediments in both ENA and Armorica. As discussed below, *Greenops* is henceforth restricted to a clade of ENA asteropyginines. Ludvigsen (1979) commented that the ancestry of *Greenops* lies with Early Devonian trilobites of Europe and North Africa, and this assertion appears to be correct, as discussed above and below. As discussed above, paleontologists have since the time of Delo (1935) assigned the Middle Devonian Laurentian assemblage of asteropyginines to *Greenops* and *Greenops* (*Neometacanthus*). However, on the basis of the phylogeny presented in figure 4, the validity of assigning all of these species to that genus is questioned. Some were recognized to instead belong to a genus distantly related to *Greenops*, referred to as *Bellacartwrightia*, new genus.

Many asteropyginine taxa from ENA have been figured in Hall and Clarke (1888), Delo (1940), Stumm (1953, 1965), Eldredge (1971a), Ludvigsen (1979), and Speyer (1988). Of these species, only *Greenops boothi* (Green, 1837), *G. chilmanae* Stumm, 1965, *G. widderensis*, new species, *G. grabaui*, new species, and *G. barberi*, new species, can henceforth be considered to belong in the genus *Greenops*. All other ENA species, e.g., *G. alpenensis* Stumm, 1953, *G. traversensis* Stumm, 1953, *G. aequituberculatus* Stumm, 1953, *G. arkonensis* Stumm, 1953, *G. pleione* (Hall, 1861), *G. boothi* var. *calliteles* (Green, 1837), *G.* sp. A Stumm, 1953, and *G.* (*Neometacanthus*) new species Hickerson, 1992, are either synonyms of other taxa or represent species whose evolutionary histories are quite distinct from the genus *Greenops*, when based on a phylogenetic perspective incorporating the type species of the genus. In addition, some of the specimens figured by the authors and assigned to *G. boothi* are actually incorrectly identified and represent new and/or very phylogenetically distinct taxa. Other asteropyginine species from ENA that Delo (1940) assigned to *Greenops*, such as *G. barrisi* (Hall and Clarke, 1888), *G. comis* (Hall and Clarke, 1888), and *G. kindlei* Delo, 1940, could not be obtained or were too poorly preserved to be incorporated in the phylogenetic analysis. However, when possible, the evolutionary relationships of these species are discussed below under the subheadings of their probable congeners. None of these species can be retained within the genera *Greenops* or *Neometacanthus*, except possibly *N. barrisi* (Hall and Clarke) (discussed under the heading of *Neometacanthus*).

Thus, an upshot of this analysis is that what were traditionally treated as species of the genus *Greenops* in ENA actually belong to a range of phylogenetically disjunct lineages. This, in combination with the biogeographic distributions of genera in the Asteropyginae, indicates that there must have been several independent invasions of the Asteropyginae from Armorica into ENA. For instance, the species *G. grabaui*, *G. chilmanae*, *G. barberi*, and *G. widderensis* are sister to a clade including taxa from ENA and Armorica.

Stumm (1953, etc.) presented systematic analyses based on idealized views of repeated patterns of allopatric differentiation in several different clades of trilobite taxa, in which different but closely related species of each clade of Middle Devonian trilobites are found in the different tectonic basins within ENA. These views largely do appear to be upheld in the case of the genus *Greenops*. Indeed, for one of the few instances where Stumm (1953) claimed that a species occurred in both the Appalachian and Michigan Basins, in this case, *Greenops boothi*, it appears that he was incorrect, and that species is restricted to the Appalachian Basin. The specimens from the Michigan Basin of southwestern Ontario that he assigned to *G. boothi* instead belong to *G. widderensis*. *Greenops chilmanae* and *G. arkonensis*, both originally described by Stumm (1953, 1965), were treated as restricted to the Traverse Group of the Michigan Basin. Herein, *G. arkonensis* is assigned to the new genus *Stummiana* and is not part of a clade of ENA *Greenops*; it is instead sister to a species from the Armorican Massif, while *G. chilmanae* is still treated as a Michigan Basin endemic.

In further support of Stumm's (1953) emphasis on allopatric differentiation in Middle Devonian trilobites of ENA, the two new taxa assigned herein to *Greenops*, *G. barberi* and *G. widderensis*, are known exclusively from the Appalachian and Michigan Basins, respectively. When the biogeographic states of taxa assigned to *Greenops* are mapped onto the phylogeny given in figure 4, a taxon from the Appalachian Basin is sister to a species endemic to the Michigan Basin. In turn, these are sister to a taxon from the Michigan Basin, implying a close relationship between the faunas of the Appalachian and Michigan Basins, also supported by Lieberman (1994) and Lieberman and Eldredge (1996).

Lieberman (1994) and Lieberman and Eldredge (1996) also concluded that the Illinois Basin was an area outside the Appalachian and Michigan Basin sister area grouping. In concordance with this, asteropyginines known from Hamilton Group equivalents (late Eifelian–Givetian), and possibly from the Frasnian of the Illinois Basin, do not appear to belong to the genus *Greenops*, and more likely belong to the genus *Neometacanthus*, which is phylogenetically distantly related to *Greenops*. (See discussion under that generic name and under *Asteropyge*.) Thus, on the whole the asteropyginines of the Michigan and Appalachian Basins are much more closely related to one another than either is to those in the Illinois Basin. Only a single species in the Asteropyginae considered herein, *Bellacartwrightia pleione* (Hall, 1861), occurs in both the Middle Devonian of the Illinois and Appalachian Basins. This in turn can be construed as suggesting either that different clades of Armorican taxa invaded different basins of ENA, or that there was some ecological preference that confined these clades to a single basin.

All of the species of *Greenops* are known from the Givetian portion of the Hamilton and Traverse Groups. New species probably assignable to *Greenops* to be described in Lieberman and Kloc (in prep.) hail from several horizons in the Givetian of the Appalachian Basin, including the Hamilton Group and the overlying Tully Limestone from the Taghanic stage. The genus *Greenops* is sister to a clade including one species from the late Emsian, and the clade they comprise is in turn sister to a clade including another species from the late Emsian. Therefore, the lineage leading to *Greenops* had probably differentiated by the late Emsian and invaded ENA some time between the late Emsian and the Givetian. Thus, there could be some gap in the history of this clade that is missing from the fossil record.

In addition to the ENA taxa discussed, certain Armorican taxa traditionally assigned to *Greenops* also must be excluded from that genus. In particular, *Modellops struvei* (Morzadec, 1969), discussed above, and *Breizhops chaconae* (Arbizu, 1979), also discussed above, must be excluded from *Greenops* because of their possession of certain characters and absence of others. Gandl's (1972: 140, pl. 8, fig. 5) *Greenops* (*Neometacanthus*?) sp. M. aff. *aequituberculatus* was discussed above under the heading of *Neometacanthus* and was found to differ from the type of that genus in the condition of several characters. Gandl's species can be distinguished from *Greenops* in the condition of the following characters, suggestive that it probably should not be assigned to that genus either: the pygidial pleural field flanking the posterior part of the axis is well excavated, and the anterior margins of the first five pygidial axial rings proceeding from the axial furrows to the midline are not first straight and then strongly arched anteriorly but rather are evenly convex anteriorly. However, the distal tips of the pleural lappets are blunt triangles, and this character is found in one species of *Greenops*, *G. grabaui*; however, it is also found in *Pilletina aequisulcata* (Gandl, 1972). As Gandl's species does not possess some of the diagnostic characters of *Greenops*, it is excluded from that genus. Until more complete material of Gandl's (1972) species can be obtained, its phylogenetic position must remain ambiguous.

Smeenk (1983: pl. 11, figs. 1–6) illustrated and described a new species from the lower Frasnian of northern Spain that he referred to as *G.* (*G.*) *ultimus*. He claimed that it is the youngest species of *Greenops* known, and he recognized that it differed from other species of *Greenops* in the condition of several characters. He suggested that these deviations from the typical *Greenops* morphotype may represent adaptations by the genus in a doomed attempt to survive. He figured pygidia and cephala and treated one of the pygidia as the holotype. None of the pygidia and cephala are articulated to a common thorax, making it difficult to ascertain whether they do indeed belong to the same species. Although the material is poorly preserved and could not be obtained for phylogenetic analysis, some comment is worthwhile on the affinities of this material, for if it does indeed belong to *Greenops*, this would extend the stratigraphic range of that genus up into the lower Frasnian, whereas it had usually been thought to go extinct at the end of the Givetian. The pygidia do have the following traits, which are common to some species of *Greenops*: flattened pygidial pleural lobes; the same condition of the anterior margins of the five anteriormost pygidial axial rings; posterior flexion of the pygidial interpleural furrows laterally; curving lateral margins of the pygidial pleural lappets; anterior and posterior pleural segments of equal elevation; and pleural furrows moderately incised and short (exsag.). However, Smeenk's illustrated specimens do differ from *Greenops* in the condition of the anterior margins of the pygidial axial rings posterior to the constriction of the fifth axial ring; in addition, in Smeenk's (1983) *G. ultimus*, the terminal pygidial lappet is teardrop shaped, and this condition is not known in any other species of *Greenops*. Smeenk's (1983) cephalon differs from *Greenops* in the condition of the following salient characters: the lateral margin of the genal spine recurves medially posteriorly, and the distance between the frontal glabellar lobe and the facial suture is constant from the lateral edge of the frontal lobe to the midline; however, it resembles *Greenops* in some of the other characters considered in this study. This cursory analysis suggests that Smeenk's (1983) taxonomic assignment of his new species to *Greenops* may not be correct; however, this species must be coded into the data matrix and run on a parsimony algorithm to ascertain its phylogenetic and taxonomic position with confidence. Because of the poor state of the material and because it was not available for analysis, this cannot be done at this time but it will be pursued at a later date. Thus, contra Smeenk (1983), the stratigraphic range of the genus *Greenops* is at this point not extended into the lower Frasnian. Another taxon formerly assigned to *Greenops* that must be excluded is *G. osismorum* Morzadec, 1983, here *Stummiana osismorum.* Although this species does resemble *Greenops* in the condition of the facial suture lateral to the eye and in having the tops of the pygidial pleural segments flat, it differs in the condition of the following characters: in *S. osismorum* the posterior border furrow flexes laterally immediately before it meets the cephalic lateral border furrow, whereas in *Greenops* it is straight laterally; there are a maximum of seven lenses in a dorsoventral file on the visual surface in *S. osismorum*, whereas there are no more than six in *Greenops*; the genal spine extends back to the fourth thoracic segment in *S. osismorum,* in *Greenops* it extends back to the fifth segment; the genal spine is evenly inclined from its medial to lateral edges in *S. osismorum,* whereas in *Greenops* the medial edge is thickened; in *S. osismorum* the eye socle rests on a sloping librigenal field, whereas in *Greenops* it sits on a vertical wall; and in *S. osismorum* the lateral margin of the genal spine at its posterior end recurves posteriorly, but in *Greenops* it is straight. On the basis of these and other characters, *Stummiana osismorum* from the Armorican Massif is instead treated as sister to *S. arkonensis* (Stumm, 1953).

Stummiana arkonensis from ENA, also formerly assigned to *Greenops*, must be excluded from a monophyletic *Greenops*. It differs from *Greenops* in most of the characters listed above for the comparison with *S. osismorum,* although for some of these characters the states had to be coded as unknown for *S. arkonensis*. It does differ from *S. osismorum* in having the condition of the eye socle as in *Greenops*. In both, the eye socle rests on a vertical wall of the librigena. *Stummiana arkonensis* is another example of an asteropyginid from ENA traditionally assigned to *Greenops* that must be excluded on the basis of phylogenetic evidence.

Additionally, taxa such as *Greenops* (*Greenops*) sp. cf. *boothi* in Gandl (1972), here *Armorigreenops leoi,* new species, and *A.* sp. cf. *leoi* must be excluded from *Greenops*. Although this species bears strong superficial similarity to *G. boothi,* it differs in the condition of several characters utilized in the phylogenetic analysis presented herein. In particular, in *A. leoi* and its closely related congener, the facial suture lateral to the eye flexes anteriorly to a point opposite S1, rather than to a point between S1 and S2 as in *Greenops*; the genal spine extends back to the sixth or seventh thoracic segment rather than back to the fifth thoracic segment as in *Greenops*; the lateral margin of the genal spine at its posterior end recurves posteriorly rather than being straight as in *Greenops*; and the eye socle rests on a sloping librigenal field rather than on a vertical wall as in *Greenops*.

What was formerly *Greenops chaconae* Arbizu, 1979, also treated as a species of *Greenops* by Smeenk (1983), must be excluded from *Greenops* and is instead assigned to *Breizhops* Morzadec, 1983. The taxon differs from all species of *Greenops* in the condition of the following characters, all defining nodes of the phylogeny in figure 4: 6, 8, 26, 35, 41, 45, and 50.

Finally, one of the taxa traditionally assigned to *Greenops boothi* var. *calliteles* (here *Bellacartwrightia phyllocaudata*) plays an important part in the confusion surrounding the definition and recognition of the genus *Greenops*. A problem similar to that of *Greenops boothi*, involving lost types for this species, has engendered taxonomic confusion leading to such ramifications as a host of different species being assigned to "*calliteles*."

To resolve the problems fully with this species would require designation of a neotype, as was done here for *G. boothi.* This will be done in Lieberman and Kloc (in prep.), and it involves preparation of material from the type locality of this species in Pennsylvania. However, much of the confusion can be erased by recognizing that species closely related and/or traditionally assigned to *calliteles* are very distantly related to true *Greenops*, comprising a genus that lies in the other one of the major clades within the Asteropyginae. They differ in the condition of many of the character states given in table 1, and they were only grouped together by earlier paleontologists because of their geographic and temporal proximity. These species and this taxonomic problem are discussed extensively under the heading of *Bellacartwrightia*, new genus. The upshot of the phylogeny presented herein is that these taxa could not have shared a common ancestor more recently than the Siegenian (?Pragian).

Several authors have discussed the evolutionary relationships of the genus *Greenops* with other taxa in the Asteropyginae. Haas (1970), Gandl (1972), Arbizu (1979), Smeenk (1983), and Morzadec (1983) treated the genus as sister to *Neometacanthus* and/or treated *Neometacanthus* as a subgenus of *Greenops* (see fig. 5a–e). The phylogenetic analysis conducted herein does not suggest a close relationship between *Neometacanthus* and *Greenops*. Because of the topology of phylogenetic relationships presented in figure 4, *Neometacanthus* cannot be treated as a valid subgenus of *Greenops* without erecting additional subgenera and treating *Greenops* as a relatively broad genus. This approach is not pursued herein.

Gandl (1972) and Arbizu (1979) also suggested that *Greenops* was closely related to *Kayserops*. The type of the genus, *Kayserops kochi* (Kayser, 1883), could not be obtained for the purposes of phylogenetic analysis. However, *Kayserops inflatus* Morzadec, 1983, was analyzed and coded for characters herein, and it seems to satisfy the diagnostic characters of *Kayserops* given by Delo (1935). This species is discussed in greater detail below. However, it is clear that *Greenops* is sister to a larger clade containing *Kayserops*, but the two genera are not themselves sister taxa. In particular, important differences between the two genera include: in *Kayserops* S3 is convex anteriorly, whereas in *Greenops* it is straight and transverse anterolaterally; in *Kayserops* the PMI is absent, whereas it is a rounded depression in *Greenops*; in *Kayserops* the medial edge of the genal spine is significantly thickened, whereas in *Greenops* it is not; in *Kayserops* there is a prominent tubercle developed on the medial portion of the pygidial and thoracic axial rings, whereas in *Greenops* there is none; in *Kayserops* the posterior part of the pygidial pleural segment is elevated above the anterior part, whereas in *Greenops* they are of equal elevation; and in *Kayserops* the tops of the pygidial pleural segment are rounded, whereas in *Greenops* they are flat.

Greenops boothi (Green, 1837)

Figure 23

Cryphaeus boothi Green, 1837: 343.
?*Greenops boothi* (Green). Ellison, 1965: 160, pl. 18, fig. 8

TYPES: Neotype YPM 35807, a complete specimen from an exposure of 30 ft of the lower Frame Shale Member, Mahantango Formation, in a road cut 450 ft long on the west side of Route 26 (Standing Stone Road) and about 600 ft northeast of the intersection of Church Street and Second Street. The neotype was collected from a zone of large concretions and was preserved in a large concretion 4 in. thick and 20 in. long. The outcrop is below Riverview Cemetery and across from the armory in the Huntingdon 7.5-minute quadrangle, on the east side of Huntingdon, Huntingdon County, Pennsylvania.

Future taxonomic work in the Asteropyginae depends on the designation of a stable neotype for the type of the genus *Greenops*, *G. boothi* (Green, 1837). However, in order to do this, several problems need to be successfully addressed. First, we must focus on how the species has been treated historically. The type of the species described and figured by Green (1837: 343, text figure) from Huntingdon, Pennsylvania has been lost for many years (Delo, 1940).

Hall and Clarke (1888) redescribed and illustrated *Dalmanites* (*Cryphaeus*) *boothi* and

D. (*C.*) *boothi* var. *calliteles* using material from New York. They did not illustrate or study Green's (1837) specimen. Hall and Clarke (1888) suggested that the specimens they assigned to *Dalmanites* (*Cryphaeus*) *boothi*, all from New York, were identical to Green's (1837) *Cryphaeus boothi*, though from a different locality. Delo (1940) supported their contention.

However, the conclusions of each of these authors appear to be incorrect. When we examined the material that Hall and Clarke (1888) used to redescribe *D.* (*C.*) *boothi*, largely housed at the NYSM, although there is also material at the AMNH, it appears that Hall and Clarke (1888) assigned several different species to *D.* (*C.*) *boothi*. The specimens they used to redescribe *D.* (*C.*) *boothi* were illustrated on plates 16 and 16a of Hall and Clarke (1888). These are referable to the following species: *Greenops* new species from the Kashong Shale of the Hamilton Group (Hall and Clarke, 1888: pl. 16, figs. 1, 2); *G. grabaui*, new species (Hall and Clarke, 1888: pl. 16, fig. 4); *Bellacartwrightia* new species from the Windom Shale of the Hamilton Group (Hall and Clarke, 1888: pl. 16a, figs. 4, 6); and *Bellacartwrightia phyllocaudata*, new species (Hall and Clarke, 1888: pl. 16a, figs. 5, 7). None are conspecific with a species of *Greenops* recovered from what is inferred to be Green's (1837) type locality in Pennsylvania (rationale for determination of type locality given below).

For their redescription of *D.* (*C.*) *boothi* var. *calliteles*, Hall and Clarke (1888) used specimens referable to the following species: *Greenops* new species from the Kashong Shale (Hall and Clarke, 1888: pl. 16, figs. 9, 14, 15); *Bellacartwrightia jennyae*, new species (Hall and Clarke, 1888: pl. 16, figs. 7, 8, 10–13, 19–22); and *Bellacartwrightia phyllocaudata*, new species (Hall and Clarke, 1888: pl. 16, figs. 16, 17). We have not yet recovered a specimen that can undoubtedly be referred to *Bellacartwrightia calliteles* (proposed generic assignment for that species) from Green's (1837) type locality in Pennsylvania, but it is unlikely that any of the species in New York are conspecific with it. (See sections on *Bellacartwrightia*, *B. jennyae*, and *B. phyllocaudata* for further discussion.)

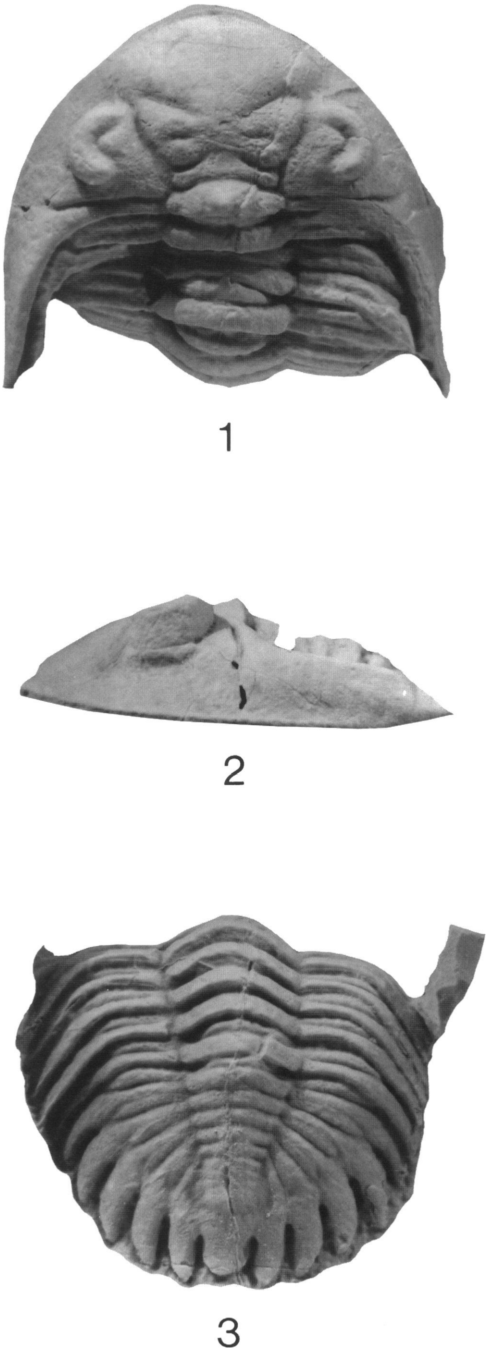

Fig. 23. *Greenops boothi* (Green, 1837), lower Frame Member, Mahantango Formation, Huntingdon, Pennsylvania. **1, 2**. YPM 35807, dorsal and lateral views of cephalon and part of thorax of complete neotype individual, ×2.5. **3**. YPM 35807, dorsal view of pygidium and partial thorax of complete neotype individual, ×2.5.

Thus, there are two problems evident in Hall and Clarke's (1888) analysis that have engendered significant taxonomic confusion. First, each species and/or variety was actually described using several separate species, and second, there is substantial overlap in the taxa used to define the different species/varieties. This has obviously created significant problems in terms of coming up with a series of characteristics diagnostic for *G. boothi*, and, since that species is the type of the genus, this has created confusion surrounding the genus *Greenops*.

Delo (1935) proposed the name *Greenops*, and he designated *Cryphaeus boothi* Green, 1837 as the type species of the genus. Delo (1935: 415, figs. 32, 33) illustrated a pygidium and small cephalon that he assigned to his new genus *Greenops* and designated the type of the genus. From examination of material in the NYSM, the pygidium is that illustrated in Hall and Clarke (1888) as plate 16a, figure 7, which is NYSM 4287, and it is actually a specimen of *Bellacartwrightia phyllocaudata* distinguished from *G. boothi* and *G. grabaui* by its possession of a greater number of pygidial axial rings, its possession of spines on the axial rings, and its pointed terminal pygidial lappet. The small cephalon Delo (1935) illustrated as figure 33 is equivalent to Hall and Clarke's (1888) plate 16, figure 3, which is NYSM 4282. This species actually belongs to a new species of *Greenops* from the Kashong that will be discussed in a forthcoming work. Thus, the material on which Delo (1935) based the type species of his genus *Greenops* does not appear to represent true *G. boothi*, throwing considerable confusion around the species and the genus *Greenops*, and necessitating that they be properly designated here.

Delo (1940) redescribed *G. boothi*, and he also treated "*calliteles*" as a variety of that species. The illustrations in Delo (1940) are taken from Hall and Clarke (1888), and he used *Greenops* new species from the Kashong Shale (Delo, 1940: pl. 10, figs. 13, 15). Delo (1940) basically reinforced the decisions made in Delo (1935). In this publication he presented a redescription of *G. boothi* based on new material because the original types had been lost or destroyed by fire. Delo (1940) figured the material he used to redescribe *G. boothi*. His plate 10, figure 14, is identical to the pygidium illustrated as figure 32 in Delo (1935), which is a specimen of *B. phyllocaudata*. Delo's (1940) plate 10, figure 15 is a dorsal view of a complete cephalothorax. His illustration is equivalent to Hall and Clarke's (1888) plate 16, figures 1 and 2, which are NYSM 4281. This specimen has characters differing from true *G. boothi*. In particular, it has axial nodes on the thoracic axial rings and L0, there are a maximum of seven lenses in a dorsoventral file on the visual surface, S3 is sinusoidal, and the terminal pygidial lappet is pointed posteriorly. These characters are the same as those found in a new species of *Greenops* from the Kashong, and thus the material Delo (1940) used to redescribe *Greenops boothi* represents two species, neither of which can be treated as true *G. boothi*. Delo's (1940) figure 17, which he also treated as *G. boothi*, appears to represent the pygidium of another new species from the Windom Shale of the Moscow Formation, and this species is most likely referable to the genus *Bellacartwrightia*, new genus. It shall also be described in a forthcoming paper (Lieberman and Kloc, in prep.).

Later, Stumm (1953) used what is treated here as *G. widderensis*, new species, from the Hamilton Group of southwestern Ontario to describe *G. boothi*. As elaborated in the discussion sections for this species and *G. widderensis*, these two taxa cannot be treated as conspecific. Additional misidentifications of *G. boothi* since the publication of Stumm (1953) are elaborated in the discussion section for this species below.

From this analysis it is apparent that there is significant confusion in the literature over the identity of *Greenops boothi*, the type of the genus *Greenops*. It is essential to establish nomenclatorial stability for the genus and the species, which are considered "important" taxa within the subfamily Asteropyginae. In the case of *Greenops boothi*, no holotype, lectotype, or syntype exists. To establish such stability it is necessary that we designate a neotype for *G. boothi*. This work is clearly "revisory" in nature, as it is a critical study of the Asteropyginae, particularly those in ENA. In addition, there has been significant confusion in the identification and recognition of different species of Asteropyginae in the Middle Devonian of ENA, partially engendered by the absence of types for most of the species studied in this family and by the fact that the Eastern North American exponents of this subfamily have not been thoroughly revised in over 50 years nor have they been illustrated as photographs in taxonomic studies. Thus, this case meets all of the requirements for the erection of a neotype. Following Article 75 of the Code of Zoological Nomenclature, the taxonomic strategy employed in this case is the designation of a neotype for the purposes of nomenclatorial stability. A series of diagnostic characters requisite for the identification of this species is presented below in the diagnosis of *Greenops boothi*.

The Code of Zoological Nomenclature states that if the types are lost, attempts should be made to designate the neotype from the type locality. Green's (1837) original type locality was in the vicinity of Huntingdon, Pennsylvania. Any attempt to select a neotype from Hall and Clarke's (1888) material in geographically distant New York State would be unacceptable without assiduously searching for material in the Huntingdon region, even though so many workers have referred to the New York material in subsequent analyses of *G. boothi*.

To try to reconstruct the exact position of Green's (1837) locality, we referred to Ellison's (1965) excellent analysis of the Devonian stratigraphy of Pennsylvania. Asteropyginines have only been recovered in Pennsylvania from the Mahantango Formation (Middle Devonian, Tioughniogan), which is partially coeval with the Hamilton Group of New York. Ellison (1965) described the Mahantango Formation as consisting of five members with a total thickness of 959 ft. To determine the stratigraphic position of the type locality of *G. boothi*, we must first turn to Green (1837). Green (1837: p. 341) stated that "this magnificent trilobite was found near the town of Huntingdon" and that "all were found in the same locality." Although Green's (1837) site description is vague and of little help regarding where to begin searching, he did report something about the rock type *G. boothi* was recovered from. He referred to the rock as a ferruginous clay slate filled with other petrifications, and stated that this stratum rests on a coarse-grained sandstone filled with organic remains. It is highly likely that this description corresponds to the fossiliferous Frame Shale Member of the Mahantango Formation, which overlies the fossiliferous Donation Siltstone Member.

Ellison (1965: p. 162) suggested that in the Huntingdon, Pennsylvania, area *G. boothi* and *Bellacartwrightia calliteles* have only been found in the upper part of the Frame Shale Member. Ellison (1965) added that the two taxa occur side by side and that Green (1837) must have collected them in that area. These conclusions appear to be partly erroneous. First, Green did not collect specimens of *G. boothi* or *Bellacartwrightia calliteles*. The specimens of these taxa were given to Green by collectors. In fact, Green (1837) named the species *G. boothi* in honor of the collector, Professor James C. Booth. He received a pygidium of *B. calliteles* from Dr. R. M. S. Jackson. Green (1837) gave no indication that he ever visited the collecting site. In addition, nowhere did Green (1837) state that the taxa were collected together, contra Ellison (1965). In fact, Green (1837) gave no detailed locality information for *B. calliteles*, and stated that it occurred in a soft ferruginous slate that had sparkling particles of iron pyrite sparsely disseminated throughout. This rock description is different from the one he gave for *G. boothi*. Thus, there is no indication from Green's (1837) descriptions to support Ellison's (1965) assertion that the trilobites were collected side by side.

In the summer of 1995, GJK visited Huntingdon, Pennsylvania, to collect Asteropyginae in the Mahantango Formation. It soon became apparent, as in New York, that there are many different species of asteropyginines occurring at different levels. At least three species of *Greenops* and two species of *Bellacartwrightia* were collected in that formation. This certainly makes it difficult to select an appropriate neotype for *G. boothi*. However, using Green's (1837) statements, Ellison's (1965) fieldwork, and the results from GJK's collections in Huntingdon, we conclude that the most likely type horizon for *G. boothi* is the Frame Member of the Mahantango Formation. This is based on the following: (1) the lithology of the Frame Member fits Green's (1837) description of the rock type in which *G. boothi* was collected; (2) Green (1837) stated that *G. boothi* occurs in the ferruginous clay slate that reposes on a coarse-grained sandstone, and this description corresponds to the Frame Member, which sits on the Donation Member; (3) Green (1837) stated that the rock is filled with petrifications, and the Frame Member is quite fossiliferous; and (4) the site where specimens were collected appears to have been quite fossiliferous, attracting several collectors who found *G. boothi*, according to Green (1837). This suggests that the site most likely occurs at an interval in the fossil record where *G. boothi* is common. Ellison (1965: 54) stated that *G. boothi* occurs at five different horizons in the Frame Member, and it is far more abundant in this member than in any of the other members of the Mahantango Formation.

However, even within the Frame Member of the Mahantango Formation, two different species referable to *Greenops* were collected. One species occurs in Ellison's (1965: 247) section 16 in the 7–12 ft interval below the top of the Frame. The other species occurs at a lower level and was collected from concretions in a road cut along Route 26. This creates a new problem. Green's (1837) description of *Greenops boothi* is not sufficiently detailed to determine which species should be chosen as the neotype of *G. boothi*. However, one of the two species of *Greenops* that occurs in the Frame Member occurs in the more shaly intervals of that member and is always thoroughly distorted by tectonic processes. If we are to erect a neotype for *G. boothi* for the purposes of providing nomenclatorial stability, it is essential that we be able to provide a series of characters that are diagnostic of that species and that allow it to be distinguished from other taxa easily. In the case of the deformed specimens this was not possible. However, the other species of *Greenops* in the Frame Member is known from a single specimen preserved in a limestone concretion. When it was prepared, it was found to be of exceptional quality, showing in excellent detail the features needed for a suitable description and a list of diagnostic characters. Thus, this specimen, YPM 35807, is designated the neotype for *Greenops boothi* because: (1) it fits Green's (1837) description; (2) it is from the type locality in Huntingdon, Pennsylvania; (3) although the specimen is from a limestone concretion, the concretion occurs in rocks fitting the lithology described by Green (1837); and (4) the exceptional quality of the specimen will avoid confusion over diagnostic characters.

DIAGNOSIS: S2 roughly transverse, weakly converse anteriorly; S1 crescent shaped, medial portion developed as smooth curve convex posteriorly; posterior edge of visual surfaces posterior to transverse line tangent to anterior edge of L0; distance between frontal lobe and facial suture at midline relative to laterally increases slightly; medially anterior cephalic border in dorsal view pointed; line from posterior to anterior edge of eye forms an angle to sagittal line that is approximately 30°; plane from medial to lateral edges of genal spine evenly inclined; axial furrows anterior to S1 relative to furrows posterior to S1 relative to sagittal line diverge more strongly; visual surface in dorsal view not present within sagittal line drawn tangent to lateral margins of frontal lobe; interior margin of genal spine relative to sagittal line deflected laterally 20°; terminal pygidial lappet broad anteriorly, subrectangular, convex posteriorly; distal tips of pygidial lappets developed as blunt triangles; laterally pygidial interpleural furrows flex more strongly posteriorly; anterior margins of first five pygidial axial rings going from axial furrows to midline straight, then strongly arched anteriorly medially; pygidial lappets long; two transverse rows of circular fenestrae on anterior band of thoracic pleural segments.

MATERIAL: YPM 35807.

DESCRIPTION: Cephalic length (sag.) 45% of width. Axial furrow diverges more strongly anterior to S1 than posterior to S1, diverges less strongly anterior to anterior half of L3, diverging forward at about 25°, narrow, moderately incised. Cranidial anterior border developed as moderate lip deflected moderately anterior to facial suture. Preglabellar furrow shallow and narrow. Length (sag.) of cranidial anterior border increases slightly from lateral to medial edges of frontal lobe. Facial suture anterior to eyes flexes laterally then medially, with smoothly convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly then posteriorly laterally. Glabellar length equal to 100% of width across frontal lobe; frontal lobe ellipsoid, about 55% of length of glabella; L1-L3 flat (sag.); frontal lobe at level of posterior glabellar region; anterior part of frontal lobe moderately declined forward, smoothly rounded in dorsal view. PMI rounded depression. S3 shallow, straight, anterolateral edge transverse, equally incised medially and distally, branches diverging at about 140°. Sagittal region of L3-L2 nearly flat (tr.), lateral lobes weakly declined abaxially. L3 wedge shaped, lengthening distally, outer edge forms smaller angle with sagittal line at anterior end than at posterior end. S2 weakly convex anteriorly, roughly transverse, moderately incised, shallow adjacent to axial furrow. S1 deep, crescent shaped, medial portion developed as smooth curve convex anteriorly, laterally contacting axial furrow. L1 short, flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 of nearly uniform length, convex anteriorly medially, deep. L0 55% of width of frontal lobe, moderately arched (tr.), longest sagittally, bearing single tubercle medially. Large Eye Index 0.50. Anterior edge of eye contacts axial furrow opposite anterodistal corner of L3; posterior edge of eye opposite S0, posterior to transverse line tangent to L0; eye raised above frontal lobe; maximum of six lenses per dorsoventral file on visual surface. Fixigena evenly sloping from axial furrow to palpebrum. Postocular fixigenal field 30% of length of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse, anterior margin nearly straight. Genal spine developed as moderately long flange extending back to fifth thoracic segment, cephalic border furrow bisects spine; genal spine evenly inclined from medial to lateral edge; medial edge of genal spine not significantly thickened relative to lateral edge; lateral margin of genal spine parallels sagittal line, straight at posterior end; interior margin of genal spine deflecting laterally. Raised ridge on dorsal surface of genal spine at juncture of posterior border furrow and lateral border furrow forms smooth curve convex distally. Lateral border furrow narrow, shallow; lateral border weakly widens posteriorly. Anterior margin of cephalic doublure pointed. Prosopon of fine tubercles.

Thorax of 11 segments. Axial ring about 25% of width of thorax, of equal length (exsag., sag.), at distal ends and medially flexed forward. Ring furrow of equal length, moderately incised, flexing forward medially and distally. Anterior margin of ring well defined sagittally, inclined posterodorsally, most elevated near posterior edge; at lateral margin of axial rings, circular fenestrae present. Articulating half ring set slightly below axial ring. Proximal part of pleura transverse, approximately horizontal; anterior segments rather evenly convex (tr.), outer part of pleurae more strongly flexed downward, straight in posterior segments. Posterior band long (exsag.), anterior margin straight, deflected at constant small angle posteriorly; length shortens as length of pleural furrow increases medially; after approximate midpoint, length of pleural furrow decreases laterally; length of posterior band increases, becomes planar; posterior surface declined posterodorsally, with few circular fenestrae near axis; anterior surface declined anterodorsally, with concave depression. Anterior pleural band short (exsag.), medially transverse; deflecting strongly posteriorly past approximate midpoint, at roughly same level as posterior band, pinching out distally, with two transverse rows of circular fenestrae.

Pygidium broadly triangular in outline excluding marginal lappets, length about 50% of width without lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, converging at 25° angle anterior to fifth pygidial axial ring, roughly parallel posterior to fifth pygidial axial ring. Axis 30% of pygidial width anteriorly, with 11 rings; rings of nearly equal length distally and sagittally, longest sagittally; anterior edge of axial rings posterior to fifth axial ring from midline to distal edge convex anteriorly. Ring furrows moderately incised. Lateral margins of pygidial lappets curved, medial margins straight, distal tips developed as blunt triangles. Axial terminus subrectangular, convex posteriorly, broad, does not project as far posteriorly as other lappets; postaxial region

25% of pygidial length (sag.). Pygidial pleural field flanking posterior portion of pygidial axis faintly excavated; anterior and posterior bands of pleural segment equally elevated; tops of segments flat; pleural furrows deeper than interpleural furrows, short (exsag.). Laterally pygidial interpleural furrows flex more strongly posteriorly. In medial region of adjacent pleural segments posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment.

DISCUSSION: This species is only known from the type locality. Hall and Clarke (1888) assigned a series of species to their *Dalmanites* (*Cryphaeus*) *boothi*. However, the bulk of the taxa they illustrated are different from true *G. boothi* in having: axial nodes on the thoracic and pygidial axial rings and L0; a maximum of seven dorsoventral files; terminal pygidial lappet subrectangular yet pointed posteriorly; and S3 sinusoidal. It is interesting to note that these characteristics are not actually as they are depicted in Hall and Clarke's (1888), plates which more closely resemble true *G. boothi* and *G. grabaui*, new species. The specimens they illustrated represent a new species of asteropyginid from the Kashong Shale of the Hamilton Group, which shall be described in a forthcoming work (Lieberman and Kloc, in prep.). Only one of the species in the NYSM's numbered type collections for *Dalmanites* (*Cryphaeus*) *boothi* represents *G. grabaui*. None represent *G. boothi* as defined using a neotype from Green's (1837) type locality.

Delo's (1935, 1940) papers as they bear on the problem of *G. boothi* are discussed above in the section on the designation of a neotype, which is necessary for nomenclatorial stability. Shimer and Shrock's (1944: 647, pl. 274, figs. 11, 12) illustrations of material they assigned to *G. boothi*, being based on Delo (1940), are thus also not correctly designated as *G. boothi*.

Many of the taxa that Eldredge (1971a), Ludvigsen (1979), and Babcock and Speyer (1987) figured as *G. boothi* or assigned to the genus *Greenops* can no longer be considered to belong to either of these taxa. In particular, Eldredge's (1971a: pl. 14, fig. 4) material belongs to *Bellacartwrightia jennyae*, new species, on the basis of the structure of the pygidial pleural lappets, the number of pygidial axial rings, the presence of tubercles on L0 and on the thoracic and pygidial axial rings, and the genal spines that have a large flattened shelf dorsally and project very far posteriorly (back to the eighth thoracic segment).

Ludvigsen (1979: fig. 55a, b) illustrated two specimens from Hamilton Group aged strata in the Michigan Basin from southwestern Ontario that he assigned to *G. boothi*. Ludvigsen's (1979) illustrated taxa appear to be conspecific with the taxon from southwestern Ontario that Stumm (1953: pl. 7, figs. 1–3) assigned to *G. boothi*. These taxa differ from *G. boothi* in the condition of a few of their character states, and on the basis of these consistent character differences they must be assigned to *G. widderensis*, new species. *Greenops widderensis* can be differentiated from *G. boothi* by the following characters: in *G. widderensis* the distance between the frontal lobe and the facial suture at the midline, relative to the distance at its lateral margin, is constant, and in *G. boothi* the distance increases slightly; in *G. widderensis* there is no prominent ornamentation on the medial portion of L0, and in *G. boothi* there is a single tubercle; in *G. widderensis* a line from the posterior to the anterior edge of the eye forms an angle to a sagittal line that is approximately 10°, and in *G. boothi* the angle is approximately 30°; in *G. widderensis* medially the genal spine is developed as a flattened ledge and laterally it is evenly inclined, and in *G. boothi* the genal spine is evenly inclined from its medial to lateral edges; in *G. widderensis* the interior margin of the genal spine parallels the lateral margin before deflecting laterally, and in *G. boothi* the interior margin of the genal spine is deflected evenly laterally; in *G. widderensis* the distal tips of the pygidial lappets are pointed, and in *G. boothi* they are developed as blunt triangles; and in *G. widderensis* there is one transverse row of circular fenestrae on the anterior band of the thoracic pleural segments, and in *G. boothi* there are two transverse rows of circular fenestrae.

Greenops boothi and *G. widderensis* are probably closely related, but the exact phylogenetic position of *G. boothi* relative to the other species of *Greenops* was not determined. This shall be done in a forthcoming publication (Lieberman and Kloc, in prep.).

Ludvigsen (1979: fig. 54b) illustrated a reconstruction of *G. boothi*. His reconstruction actually combines characters of both *G. grabaui* and *G. widderensis*, with the pygidium resembling those more typical of *G. grabaui* (having a broad terminal lappet convex posteriorly) and the head conforming more closely to that typical of *G. widderensis*.

Hall and Clarke (1888) and other authors traditionally treated one of the divergent asteropyginine morphotypes in the Hamilton Group of ENA as a variety of *G. boothi*. They referred to this species as *Dalmanites* (*Cryphaeus*) *boothi* var. *calliteles*. However, this species is in fact distantly related to *G. boothi* and is instead assigned to a new genus. These taxa differ in the condition of several characters, including: 1, 2, 4, 5, 6, 7, 14, 15, 16, 23, 25, 26, 28, 31, 35, 38, 39, 46, 47, 50, 52, 55, 56, 57, 60, 61, 62, 65, and 66, and they can no longer be considered as separate varieties of a single species. They belong to divergent evolutionary lineages that last shared a common ancestor sometime in the Early Devonian (?Pragian), significantly predating the Middle Devonian (largely Givetian) Hamilton Group. Hall and Clarke (1888) originally separated the two taxa based on characters of the pygidia that they claimed were correlated with differences in other features. They recognized that these differences were evident in early ontogenetic stages, and they claimed that they were "genetic," meaning real rather than ecophenotypic differences. Although the differences do appear to be real, that is, the taxa are diagnosably distinct, the propinquity of descent suggested by Hall and Clarke (1888) is probably an artifact of their systematic method, which united the taxa because they were recovered from similar-aged sediments in similar localities.

Hall and Clarke (1888) erroneously assigned a range of taxa to both *Dalmanites* (*Cryphaeus*) *boothi* and *D.* (*C.*) *boothi* var. *calliteles*; however, they recognized the range of variation inherent in their samples of asteropyginine taxa, which they largely allocated to two distinct taxa. They claimed that the bulk of variation from what they perceived as the type of *Cryphaeus boothi* was in characters of the pygidial fimbria. In addition, they stated that no variation has taken place in this feature without correlative variation in certain other respects. They suggested that in many individuals, particularly the specimens they recovered from the limestones of the Hamilton Group and the underlying Onondaga Limestone, the lobes of the pygidial pleural segments are narrow, lanceolate, and elevated, rather than flat, broad, and contiguous, as they typically are in *G. boothi*. They recognized that the pygidia with the narrow, rounded, and elevated pygidial pleural segments are identical to those described by Green (1837) as *Cryphaeus calliteles*, whereas the types with the flat, broad, and contiguous pygidial pleural segments are conspecific with the form described by Green (1837) as *C. boothi*. Both species were first described using specimens from the same Hamilton Group locality in Huntingdon, Pennsylvania. However, these types were later lost, and Hall and Clarke's (1888) taxa were based on specimens from Hamilton Group aged sediments in New York, not Pennsylvania. There are also probably two more new species in the set of types they figured that will be discussed in a forthcoming work (Lieberman and Kloc, in prep.). Not counting the two new species to be described in a forthcoming paper, this range of variation that they figured and discussed can actually be assigned to three distinct taxa instead of the two they called *Dalmanites* (*Cryphaeus*) *boothi* and *D.* (*C.*) *boothi* var. *calliteles*. The three taxa are *G. grabaui*, *Bellacartwrightia phyllocaudata*, and *Bellacartwrightia jennyae*.

Struve (1959) illustrated a cephalon and pygidium that he assigned to *Greenops* (*Greenops*) *boothi*. The cephalon bears a strong resemblance to *G. boothi*. However, it is based on a specimen from Ontario, Canada. *Greenops widderensis*, new species, a close relative of *G. boothi*, is the only species of *Greenops* described from Ontario, though *Stummiana arkonensis* (Stumm, 1953) also occurs in the Middle Devonian of Ontario. The cephalon as drawn bears the diagnostic characteristics of *Greenops* rather than *Stummiana*, and it is presumed that the cephalon illustrated belongs to *G. widderensis* rather than *G. boothi*. The pygidium, figure 381, 1b, hails from Naples, New York, and has 11 axial rings, with a broad rectangular pygidial terminal lappet that is convex posteriorly, the distal tips of the lappets developed as blunt triangles, and the pleural lappets relatively short. All these morphological features are characteristic of *G. grabaui*, and because the specimen is from New York it is treated as that taxon rather than *G. boothi*, which appears to be restricted to Pennsylvania. The assertion that the locality this pygidium hails from is Naples, New York, appears dubious. Only Upper Devonian strata are known from this locality, and no species of asteropyginines are known from the Upper Devonian of ENA. Thus, this pygidium and the locality data are problematic.

Speyer (1988) figured two specimens from the Kashong Shale of the Hamilton Group that he referred to as *Greenops boothi* and *Greenops* sp. These taxa differ from *G. boothi* in the condition of several characters, and they represent a new species that will be described in a forthcoming paper (Lieberman and Kloc, in prep.). Speyer (1988) also illustrated specimens from New York (figs. 1c, d, 9c) that, because of their state of preservation, must be ambiguously assigned to either *G. grabaui*, new species, or *G. barberi*, new species, rather than *G. boothi*. Speyer's (1988) figures 7a, 8c, d, which he assigned to *G. boothi*, must instead be assigned to *G. barberi* because of the condition of the pygidial pleural lappets, the pygidial axis, and the genal spines.

Babcock and Speyer (1987) illustrated specimens (figs. 4.1–4.5) from the Ledyard Shale of New York that they assigned to *G. boothi*. Because of the state of preservation of these taxa, it could not be ascertained whether these specimens should be assigned to *G. grabaui* or *G. barberi*. They are unlikely to represent true *G. boothi*.

Ellison (1965: pl. 18, fig. 8) illustrated a specimen he assigned to *Greenops* from the upper shale member of the Mahantango Formation at Girty's Notch, Pennsylvania. This specimen is only preserved as an internal mold, and it is impossible to determine for sure which species of *Greenops* it belongs to. It is questionably assigned to *G. boothi*.

Burns (1991) illustrated specimens from the Mahantango Formation (Erian/Givetian) of West Virginia and Virginia that he referred to as *G. boothi*. However, because of the nature of his illustrations it could not be determined whether the taxa he discussed belong to *G. boothi*, some other species of *Greenops*, *Bellacartwrightia phyllocaudata*, or some other species of *Bellacartwrightia*. As only *B. phyllocaudata*, *B. calliteles*, and *G. boothi* are known from localities further south in the Appalachian Basin, probably one of these is depicted.

Other authors have suggested that *Greenops boothi*, or a form nearly identical to it, is also known from Armorica. Keyser (1878) suggested that the species that had been referred to as *Cryphaeus boothi* and *C. calliteles* were in fact synonymous with other European asteropyginid taxa such as *Cryphaeus stellifer*. *Cryphaeus stellifer* is discussed above as *Neometacanthus stellifer*, and it does differ in the condition of several characters from *G. boothi*. The two cannot be considered synonyms, and they are not close evolutionarily. Moreover, Hall and Clarke (1888) gave several other cogent arguments why Keyser (1878) could not be correct, and now his contention of synonymy between the Armorican and ENA asteropyginine taxa he discussed appears untenable. In more recent times, other authors have advanced different arguments along similar lines. In particular, Gandl (1972) referred to a series of specimens as *Greenops* sp. cf. *boothi*, and these were also discussed by Smeenk (1983). These specimens belong to *Armorigreenops leoi*, new species, which is closely related to the ENA *Greenops* clade, but it is not sister to *G. boothi*. It differs from that taxon in the condition of several characters that are discussed below. The specimen Arbizu (1979) referred to as *G.* sp. cf. *boothi* belongs to a different species, *Deloops* sp. aff. *haasi*, and is also discussed below.

Haas (1970: 4, fig. 10) figured a pygidium housed at Universität Munster that he referred to as *G. (G.) boothi*. This specimen has similarities with species of *Greenops*. In particular, the pygidial interpleural furrows flex more strongly posteriorly laterally, the lateral margins of the pygidial pleural lappets are curved, the fifth pair of pygidial pleural lappets projects further posteriorly than the terminal pygidial lappet, and the tops of the pygidial pleural segments are flattened. It also bears some of the characters found in some, though not all, of the species in the genus *Greenops*. In Haas's (1970) pygidium, the anterior parts of the first five pygidial axial rings are not straight and then strongly arching anteriorly when proceeding from the axial furrows to the midline. Rather, they are gently convex anteriorly. In addition, it differs from all species of *Greenops* in the condition of the anterior part of the pygidial axial rings posterior to the fifth axial ring, which are straight instead of gently convex. This pygidium can be further distinguished from *G. boothi* by the possession of 12 axial rings and by the condition of the distal tips of the pygidial pleural lappets, which are at the distal end of a straight posterolateral margin inclined at a 45° angle relative to a sagittal line in Haas's (1970) pygidium but developed as blunt triangles in *G. boothi*, though this character does not diagnose all species of *Greenops* (no species of *Greenops* have the pygidial lappets as they are in Haas's pygidium). Without a cephalon present, it is difficult to ascertain the precise phylogenetic position of this specimen. However, the pygidium does possess some of the diagnostic characters found in some species of *Philipsmithiana*, new genus. In particular, Haas's (1970) pygidium has the distal tips of the pygidial pleural lappets at the distal end of a straight posterolateral margin of the pygidial pleural lappets, as well as the short (exsag.) pygidial lappets, and the condition of the anterior margins of the pygidial axial rings that characterizes all species of *Philipsmithiana*. Without further material it is not possible to determine if this species should be assigned to *Philipsmithiana* or *Greenops*. However, Haas's (1970) plate 4, figure 11, from the Wanakah Shale of the Ludlowville Formation does appear referable to a close relative of *G. boothi*, *G. grabaui*, new species.

Morzadec (1983) presented an evolutionary tree (his fig. 33) that depicts the phylogenetic relationships of some of the species of *Greenops*. Morzadec (1983) suggested that *Greenops boothi* is sister to a clade containing what are here *Deloops haasi* and *Stummiana osismorum*. He was correct in asserting the close relationship of these taxa, although the precise topology of his phylogenetic scheme is not supported herein. Presumably, he assumed monophyly of the ENA *Greenops*, though he did not discuss this point. A questionable aspect of his evolutionary tree is his placement of *G. struvei* as a direct ancestor of *G. osismorum* (here *Stummiana osismorum*). As discussed above, Morzadec's (1983) *G. struvei* is assigned herein to a new genus, *Modellops*. This genus appears to be distantly related to *Greenops*, and any similarities the genera share are the result of primitive retentions in *Greenops*, or convergences.

Greenops chilmanae Stumm, 1965

Greenops chilmanae Stumm, 1965: 165, pl. 1, fig. 9; Stumm, 1967: 114, pl. 2, figs. 4, 5; Kesling et al., 1974: pl. 12, fig. 29; Kesling and Chilman, 1975: 154, pl. 31, figs. 5–7.

Greenops aequituberculatus Stumm, 1953: 131, pl. 8, fig. 9.

TYPES: Holotype defined in Stumm (1965: pl. 1, fig. 9).

DIAGNOSIS: Anterior cephalic border rounded; fixigenae evenly sloping from axial furrows to internal margins of eye; line from posterior to anterior edge of eye forms an angle to sagittal line that is approximately 0–5°; before cephalic lateral border furrow meets posterior border furrow, posterior border furrow flexes anteriorly; tubercle present on L0; cephalic axial furrows diverge at same angle anterior and posterior to S1; one transverse row of circular fenestrae on anterior band of thoracic pleural segments; terminal pygidial lappet triangular, does not project as far posteriorly as pygidial pleural lappets flanking it; lateral margins of pygidial lappets curved, medial margins straight; distal tips of lappets pointed; longest pygidial lappet longer than sagittal length of first three pygidial axial rings.

DISCUSSION: This species is known from the following latest Eifelian and/or Givetian localities in the Traverse Group of the Michigan Basin in ENA: Gravel Point Formation (Cazenovian), *Longispina emmetensis* zone, Lake Michigan at Gravel Point, 1.5–2 miles west of Charlevoix, Michigan; Silica Shale (Cazenovian), north quarry of the Medusa Portland Cement Company at Silica, 1.5

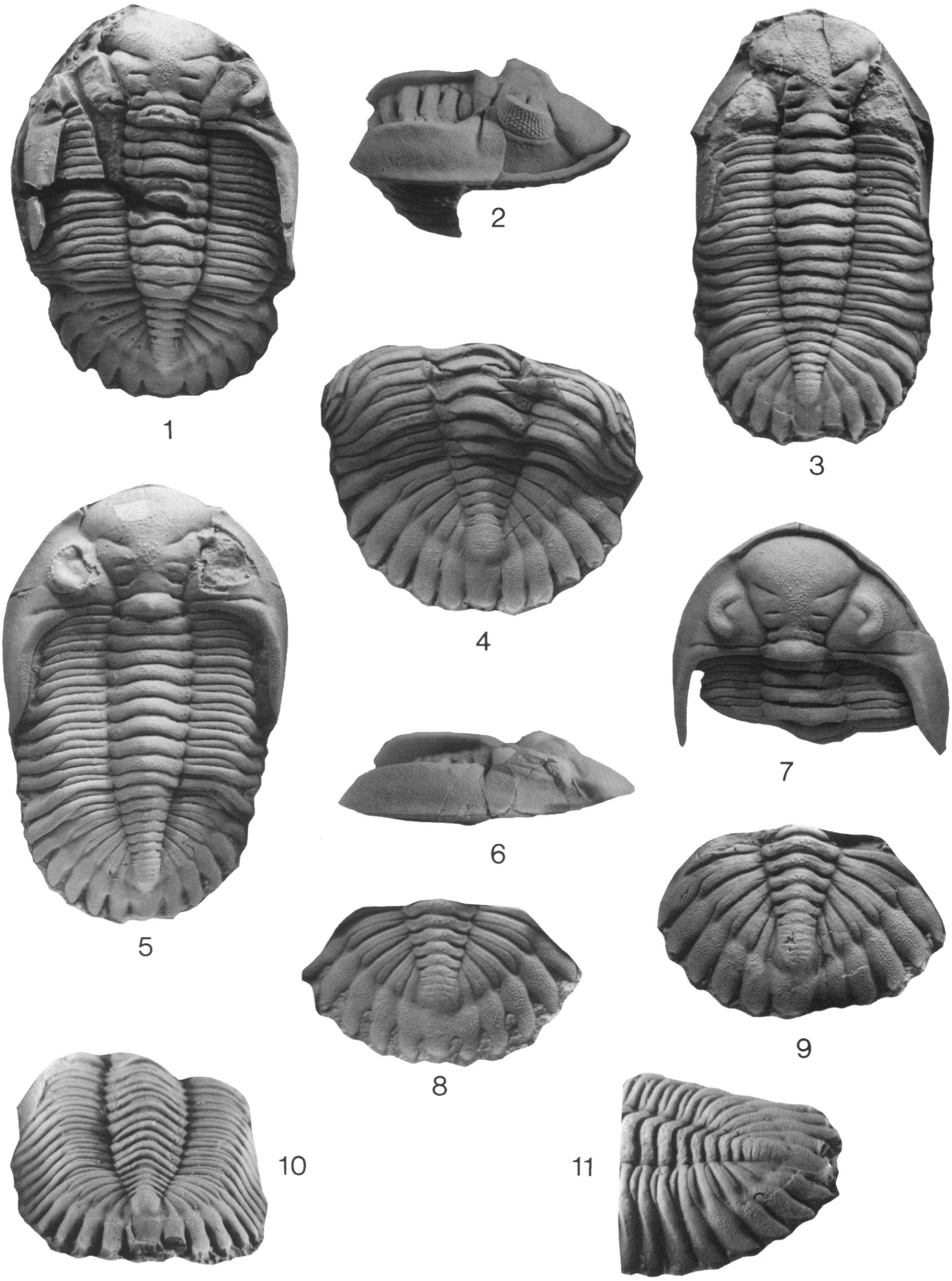

Fig. 24. *Greenops grabaui*, new species, Ludlowville Formation, New York. **1**. Murder Creek Beds, Wanakah Shale, Darien, AMNH 45307, dorsal view of complete specimen, ×2.4. **2, 7**. AMNH 45290, lateral and dorsal views of cephalon and portion of thorax of complete individual, ×4. **8**. AMNH 45290, dorsal view of pygidium of complete individual, ×4. **3, 10**. Murder Creek Beds, Wanakah Shale, Darien, AMNH 45309, dorsal and posterior views of complete individual, ×3. **11**. Murder Creek Beds, Wanakah Shale, Darien, AMNH 45309, lateral view of pygidium of complete individual, ×3. **4**. AMNH 45291,

miles southwest of Sylvania, Lucas County, Ohio, AMNH locality 3063. No specimens are known from post-Cazenovian strata.

As discussed above, *G. aequituberculatus* encompassed a series of species and can no longer be considered valid. One of the specimens Stumm (1953) designated as a paratype of *G. aequituberculatus* is actually a pygidium of *G. chilmanae*. Stumm (1965) suggested that *G. chilmanae* was most closely related to *G. boothi* (Green). These taxa are certainly very closely related, but at this time the precise phylogenetic position of *Greenops boothi* was not examined, so this proposition could not be tested. Instead, *G. chilmanae* is sister to *G. barberi*, new species, and *G. widderensis*, new species, is sister to the clade they comprise. However, considering that Stumm (1965) was unaware at the time he wrote the paper of the two new species of *Greenops* described herein, and he had not used a concept of *G. boothi* based on material from Green's (1937) type locality, his conclusion is not too far off base. The sister group relationship between *G. chilmanae* and *G. barberi* is supported by their shared possession of the following characters: S2 weakly declined posteriorly at lateral edge; visual surfaces in dorsal view present within sagittal lines drawn tangent to the margins of the frontal lobe; and terminal pygidial lappet triangular and narrow.

***Greenops grabaui*, new species**

Figures 8.6, 9.3–9.7, 10.1–10.5, 24, 25.1–25.5, 25.7, 25.8

Dalmanites (*Cryphaeus*) *boothi* (Green). Hall and Clarke, 1888: 42, pl. 16, fig. 4, pl. 16a, fig. 3.

Greenops boothi (Green). Babcock and Speyer, 1987: figs. 4.1–4.5; Speyer, 1988: figs. 1c, d, 8c, d, 9c.

?*Greenops boothi* (Green). Eldredge, 1971a: pl. 14, fig. 6.

?*Greenops* (*Greenops*) *boothi* (Green). Struve, 1959: O480, fig. 381, 1b; Haas, 1970: 113, pl. 4, fig. 11.

?*Dalmanites* (*Cryphaeus*) *boothi* (Green). Hall and Clarke, 1888: pl. 16a, fig. 3.

TYPES: Holotype BMS E25857, a complete specimen from the Murder Creek bed of the Wanakah Shale (Tioughniogan), Ludlowville Formation, Hamilton Group, along the shore of Lake Erie, north of 18 Mile Creek, Hamburg, New York. Paratypes AMNH 45228 and 45229, complete specimens from the lower Ledyard Shale (Tioughniogan), Ludlowville Formation, Hamilton Group, Jaycox Run Creek, upstream from Nations Road, Geneseo Township, Livingston County, New York, AMNH locality 3041; and AMNH 45308, a complete specimen from the Murder Creek Beds, Wanakah Shale (Tioughniogan), Ludlowville Formation, Hamilton Group, Darien, New York.

DIAGNOSIS: Anterior cephalic border rounded; distance between frontal lobe and facial suture at midline relative to distance between frontal lobe and facial suture at lateral margins of frontal lobe equivalent; anteriormost part of palpebrum between medial tip of L3 and PMI; fixigena evenly sloping from axial furrow to internal margin of eye; cephalic axial furrows anterior to S1 diverge more strongly than furrows posterior to S1; S2 weakly convex anteriorly; line from posterior to anterior edge of eye forms 30° angle to sagittal line; posterior edge of visual surface posterior to transverse line tangent to L0; lateral to eye, facial suture before flexing posteriorly flexes anterior to point opposite distal tip of S2; posterior margin of fixigena relative to anterior margin of fixigena deflected at an angle to transverse line that is roughly equivalent; tubercle on L0 absent; interior margin of genal spine parallels lateral margin before deflecting laterally; medial tubercles on pygidial and thoracic axial rings absent; single pair of circular fenestrae on thoracic axial rings flanking medial part of axis; one transverse row of circular fenestrae on anterior band of thoracic pleural seg-

←

dorsal view of pygidium and portion of thorax of complete individual, ×3. **6**. AMNH 45291, lateral view of cephalon of complete individual, ×3. **5**. Murder Creek Beds, Wanakah Shale, Darien, AMNH 45308, dorsal view of complete paratype individual, ×4. **9**. AMNH 45292, dorsal view of pygidium, ×3.

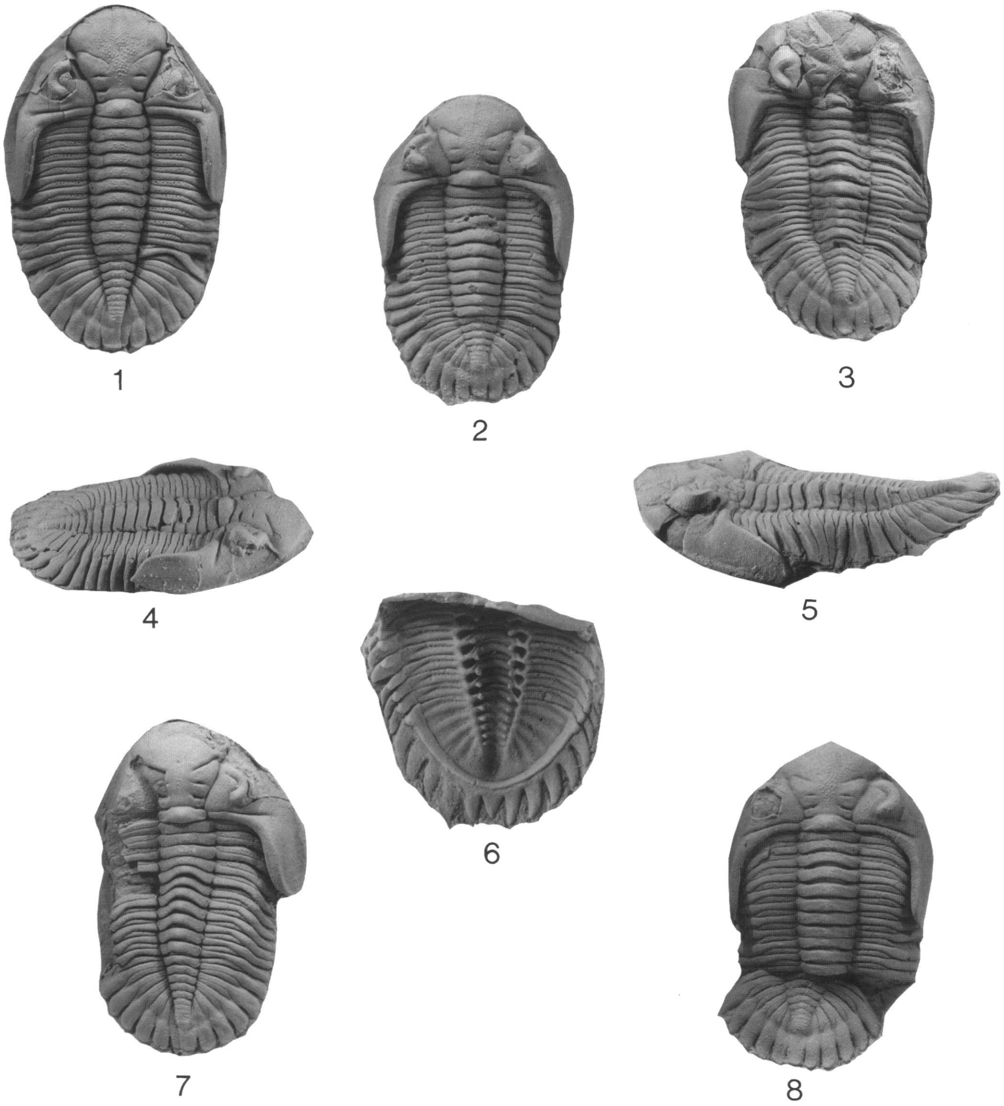

Fig. 25. *Greenops* spp. **1–5, 7, 8**. *Greenops grabaui*, new species, New York. **1**. Ledyard Shale, Ludlowville Formation, Jaycox Run Creek, upstream of Nations Road, Geneseo Township, Livingston County, AMNH 45228, dorsal view of complete paratype individual, ×1.8. **2, 4**. Murder Creek Bed, Wanakah Shale, Ludlowville Formation, along Lake Erie shore, north of 18 Mile Creek, Hamburg, BMS E25857, dorsal and lateral views of complete holotype individual, ×2. **3, 5**. ?Ludlowville Formation, Canandaigua Lake, NYSM 4281, dorsal and lateral views of complete individual, ×1.7. **7**. Ledyard Shale, Ludlowville Formation, Jaycox Run Creek, upstream of Nations Road, Geneseo Township, Livingston County, AMNH 45229, dorsal view of complete paratype individual, ×2. **8**. Murder Creek Bed, Wanakah Shale, Ludlowville Formation, along Lake Erie shore, north of 18 Mile Creek, Hamburg, BMS E25856, dorsal view of complete individual, ×2. **6**. *Greenops barberi*, new species, Smoke Creek Bed, Windom Shale, Moscow Formation, Penn Dixie Quarry at intersection between Big Tree and Bayview Roads, BMS E25855, ventral view of pygidium and portion of thorax, ×2.

ments; terminal pygidial lappet subrectangular, broad, 1.5 times width (tr.) of posteriormost part of pygidial axis; medial margins of pygidial lappets straight; distal tips of pygidial lappets developed as blunt triangles; pygidial pleural lappets relatively short (exsag.); anterior and posterior pleural bands of pygidial segments of equal elevation; tops of pygidial pleural segments flat; in medial region of adjacent pleural segments posterior band of anterior segment equal in length (exsag.) to anterior band of posterior segment.

ETYMOLOGY: Named for A. Grabau, who made many important contributions to stratigraphic methodology in general, and the stratigraphy of the trilobite beds of the Wanakah Shale in particular, which is the type locality of the species.

MATERIAL: AMNH 45228, 45229, 45254, 45274, 45275, 45290–45292, 45307–45309, 45317; BMS E25856, E25857; NYSM 4283; YPM 6603, 6665, 33764, 33783–33785, 33787, 33855–33858, 35740, ?33778, ?33786–?33788, ?35742.

DESCRIPTION: Cephalic length (sag.) 45% width. Axial furrow diverges more strongly anterior to S1 than posterior to S1, diverges less strongly anterior to anterior half of L3, diverging forward at about 25°, narrow, moderately incised. Cranidial anterior border developed as moderate lip deflected moderately anterior to facial suture. Preglabellar furrow shallow and narrow. Length (exsag., sag.) of cranidial anterior border constant from lateral to medial edges of frontal lobe. Facial suture anterior to eyes flexes laterally then medially, with smoothly convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly then posteriorly laterally. Glabellar length (sag.) equal to 100% of width (tr.) across frontal lobe; frontal lobe ellipsoid, about 55% of length of glabella; L1-L3 flat (sag.); frontal lobe at same elevation as posterior glabellar region; anterior part of frontal lobe moderately declined forward, smoothly rounded in dorsal view. PMI a rounded depression. S3 shallow, straight, anterolateral edge transverse, equally incised medially and distally, branches diverging at about 140°. Sagittal region of L3-L2 nearly flat (tr.), lateral lobes weakly declined abaxially. L3 wedge shaped, lengthening (exsag.) distally, outer edge forms smaller angle with sagittal line at anterior end than at posterior end. S2 weakly convex anteriorly, moderately incised, shallow adjacent to axial furrow. S1 deep, crescent shaped, medial part developed as smooth curve convex anteriorly, laterally contacting axial furrow. L1 short, flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 convex anteriorly medially, deep. L0 55% of width (tr.) of frontal lobe, moderately arched (tr.), longest sagittally. Large Eye Index 0.50. Anterior edge of eye contacts axial furrow opposite anterodistal corner of L3; posterior edge of eye opposite distal tip of S0, posterior to transverse line tangent to L0; eye raised above frontal lobe; maximum of six lenses per dorsoventral file on visual surface. Fixigena evenly sloping from axial furrow to palpebrum. Postocular fixigenal field 30% of length (exsag.) of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse. Genal spine developed as moderately long flange extending back to fifth thoracic segment, cephalic border furrow bisects spine; medial part of genal spine flattened, lateral part evenly inclined; medial part of genal spine not significantly thickened relative to lateral part; lateral margin of genal spine parallels sagittal line, straight at posterior end; interior margin of genal spine parallels lateral margin before deflecting laterally. Raised ridge on dorsal surface of genal spine at juncture of posterior border furrow and lateral border furrow forms smooth curve convex distally. Lateral border furrow narrow, shallow, lateral border weakly widens (tr.) posteriorly. Anterior margin of cephalic doublure rounded. Prosopon of fine tubercles.

Thorax of 11 segments. Axial ring about 25% of width of thorax, of equal length (exsag., sag.), at distal ends and medially flexing forward. Ring furrow of equal length (exsag., sag.), moderately incised, flexing forward medially and distally. Anterior margin of ring well defined, inclined posterodorsally, most elevated near posterior edge; at lateral margin of axial rings, circular fenestrae present. Articulating half ring set slightly below axial ring. Proximal part of pleura transverse, approximately horizontal;

anterior segments rather evenly convex (tr.), outer part of pleurae more strongly flexed downward, straighter in posterior segments. Posterior band long (exsag.), anterior margin straight, deflected at constant small angle relative to transverse line posteriorly; length (exsag.) shortens as length of pleural furrow increases medially; posterior surface declined posterodorsally, with few circular fenestrae near axis. Anterior pleural band short (exsag.), medially transverse; deflecting strongly posteriorly past approximate midpoint, at roughly same level as posterior band, pinching out distally, with one transverse row of circular fenestrae.

Pygidium broadly triangular in outline excluding marginal lappets, length about 50% of width without lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, converging at 25° angle anterior to fifth pygidial axial ring, roughly parallel posterior to fifth pygidial axial ring. Axis 30% of pygidial width anteriorly, with 11 rings; rings of nearly equal length distally and medially, but longest medially; anterior edge of axial rings posterior to fifth axial ring from midline to distal edge convex anteriorly. Ring furrows moderately incised. Lateral margins of pygidial lappets curved, medial margins straight, distal tips developed as blunt triangles. Axial terminus subrectangular, convex posteriorly, broad, does not project as far posteriorly as other lappets; postaxial region 25% of pygidial length (sag.). Pygidial pleural field flanking posterior part of pygidial axis faintly excavated; anterior and posterior bands of pleural segment equally elevated; tops of segments flat; pleural furrows deeper than interpleural furrows, short (exsag.). Laterally pygidial interpleural furrows flex more strongly posteriorly. In medial region of adjacent pleural segments posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment.

DISCUSSION: This species is known from the following Givetian stratigraphic horizons and localities in the Hamilton Group of the Appalachian Basin in ENA: lower Ludlowville Formation including the Stone Mill Limestone (Tioughniogan), Robert's Road Quarry, north of New York Route 26 on Robert's Road, West Eaton, New York, AMNH locality 3032; Centerfield Limestone, Ludlowville Formation, Brown's Creek, York, New York; Ledyard Shale, Ludlowville Formation, cut along tracks of Delaware and Western Railroad, 3 miles west of East Bethany, New York, AMNH locality 3045; lower Ledyard Shale, 11 Mile Creek, Darien, New York; Wanakah Shale, Ludlowville Formation, Cazenovia Creek, near Transit Road, Erie County, New York, AMNH locality 3048; Ledyard Shale, Spring Creek, Alden, New York; Wanakah Shale, Ludlowville Formation, Bethany, New York; trilobite beds, Wanakah Shale, Smoke Creek, Windom, New York; Wanakah Shale, Murder Creek Beds, Darien, New York; Ludlowville Formation, Seymour Pond, New York; ?Frame Member (Tioughniogan), upper Mahantango Formation, road cut along U.S. Route 22 opposite Huntingdon, Pennsylvania; ?upper Mahantango Formation (Tioughniogan), Cumberland, Maryland, James Hall AMNH locality 10; and ?Mahantango Formation (Tioughniogan), Koshong Creek, Maryland.

This species is very common in the Ludlowville Formation. In the Taghanic Tully Limestone, poorly preserved specimens are known that appear to be referable to *Greenops*. They are probably closely related to *G. grabaui*, but until better material is recovered, this species will not be described.

Struve (1959: fig. 381, 1b) illustrated a pygidium from the Hamilton Group of Naples, New York, that he assigned to *Greenops* (*Greenops*) *boothi*. The pygidium has 11 axial rings with a broad rectangular pygidial terminal lappet that is convex posteriorly, and the distal tips of the lappets are developed as blunt triangles. It is difficult to tell from a drawing, but these morphological features are characteristic of *G. grabaui*, and the pygidium, being from New York, is questionably treated as belonging to that species rather than *G. boothi*, which is not known to occur in New York. However, Naples, New York, is an exclusively Upper Devonian locality, and no species belonging to the Asteropyginae are known from the Upper Devonian of ENA. Thus, the veracity of this locality must be treated as dubious.

Several modern authors (e.g., Eldredge, 1971a; Ludvigsen, 1979; Babcock and Speyer, 1987) have assigned a range of asteropyginine specimens in the Appalachian Basin of ENA to *G. boothi*. First, on the basis of character analysis performed herein it appears that *G. boothi* is not the sole representative of the Asteropyginae in the Appalachian Basin. In addition, *Greenops boothi* appears to be absent from the portion of the Appalachian Basin preserved in modern-day New York. There are, however, at least two other species of *Greenops* known from the Appalachian Basin of New York: *G. barberi*, new species, and *G. grabaui*, new species. *Greenops grabaui* can be discriminated from *G. boothi* by the condition of the following: in *G. grabaui* the distance between the frontal lobe and the facial suture at the midline, relative to laterally, is constant, whereas in *G. boothi* this distance increases slightly; in *G. grabaui* medially the anterior cephalic border in dorsal view is rounded, whereas in *G. boothi* it is pointed; in *G. grabaui* there is no prominent ornamentation on the medial portion of L0, whereas in *G. boothi* there is a single tubercle; in *G. grabaui* the medial edge of the genal spine is flattened, and laterally it is evenly inclined, whereas in *G. boothi* the genal spine is evenly inclined from its medial to lateral edges; in *G. grabaui* the interior margin of the genal spine parallels the lateral margin before deflecting laterally, whereas in *G. boothi* the interior margin of the genal spine is deflected laterally; in *G. grabaui* the pygidial lappets are relatively short (exsag.), whereas in *G. boothi* they are relatively long; and in *G. grabaui* there is one transverse row of circular fenestrae on the anterior band of the thoracic pleural segments, whereas in *G. boothi* there are two rows.

Speyer (1988) illustrated specimens from New York (figs. 1c, d, 8c, d, 9c) that are assigned herein to *G. grabaui*, new species, rather than *G. boothi*.

Babcock and Speyer (1987) illustrated specimens (figs. 4.1–4.5) from the Ledyard Shale of New York that they assigned to *G. boothi*. Because of the state of preservation of these taxa, it could not be ascertained whether these specimens should be assigned to *G. grabaui* or to *G. barberi*. They are unlikely to represent true *G. boothi*.

Greenops grabaui, although clearly diagnosable herein, does show some intraspecific variation in at least one feature. That is the terminal pygidial lappet, which can show some variation in breadth from sample to sample.

Smeenk (1983: pl. 10, figs. 9, 10) figured two preservationally deformed pygidia that he referred to as *Greenops* (*Greenops*) sp. Although poorly preserved, these specimens do possess some of the characters found in various species of the genus *Greenops*. These characters include: the form of the anterior margin of the first five pygidial axial rings, which from axial furrow to midpoint are first straight and then arch strongly anteriorly; the shape of the pygidial interpleural furrows, which laterally flex more strongly posteriorly; the lateral margins of the pygidial pleural lappets are curved; the pygidial axis constricts posterior to the fifth axial ring; the anterior margins of the pygidial axial rings posterior to the constriction of the fifth ring are smoothly convex anteriorly; the pygidial pleural field flanking the posterior portion of the pygidial axis is faintly excavated; and the pleural furrows are moderately incised and short (exsag.). Awaiting the recovery of cephalothoraxes, which of course contain phylogenetically relevant characters, these pygidia are assigned to the genus *Greenops*. In addition to these characters bespeaking the affinity of these pygidia with the genus *Greenops*, these pygidia share common character states with *G. grabaui*, and they may be closely related to that species. These characters include the following: the terminal pygidial lappet is broad, 1.5 times the width (tr.) of the posterior part of the pygidial axis; it is rectangular and convex posteriorly; the medial margins of the pygidial lappets curve laterally; the distal tips of the pygidial lappets are developed as blunt triangles; the anterior and posterior bands of pleural segments are of equal elevation; the tops of the pygidial pleural segments are flat; when comparing adjacent pleural segments the posterior region of the anterior segment is equal in length (exsag.) to the anterior part of the posterior segment; and the longest pygidial lappet is short (exsag.), equal to the length (sag.) of the first two pygidial axial rings. The pygidia Smeenk figured do differ from those of *G. grabaui* in the possession of 12 pygidial axial rings (versus 11 in *G.*

grabaui). These specimens are tentatively referred to as *G.* sp. B, and are treated as very closely related to *G. grabaui*. However, until better as well as more completely preserved specimens are recovered, this phylogenetic hypothesis cannot be tested.

This potentially close relationship between *G. grabaui* and *G.* sp. B raises the possibility of an additional instance of a sister group relationship between asteropyginines in ENA and Armorica. As discussed above and below, there are at least four instances of invasion from Armorica into ENA by the asteropyginines, with several lineages of Armorican taxa sister to one or more clades of ENA taxa. However, if *G.* sp. B is sister to *G. grabaui*, then it would imply that there may have been some invasion from ENA back into Armorica. It would also imply that the five species of *Greenops* in ENA (including *Greenops boothi*) would not be monophyletic to the exclusion of Armorican *Greenops*. *Greenops* sp. B was not incorporated into the phylogenetic analysis conducted herein because of the dearth of material and because of its poor state of preservation. Tentatively, the five species of *Greenops* in ENA are treated as monophyletic until additional material of *G.* sp. B becomes available, allowing additional testing of this hypothesis.

Greenops barberi, new species

Figures 8.1, 8.2, 8.4, 25.6, 26.1–26.7

Greenops boothi (Green). Speyer, 1987: fig. 7g.

TYPES: Holotype PRI 41947, a complete specimen from the Smoke Creek Bed, Windom Shale (Tioughniogan), Moscow Formation, Hamilton Group, Buffalo Creek, Erie County, New York; paratypes PRI 41948, a pygidium from the same locality as the holotype, PRI 41949, a cephalothorax from the same locality as the holotype, PRI 41951, a nearly complete specimen from the same locality as the holotype, and AMNH 45277 and 45278, two pygidia from the same locality as the holotype.

DIAGNOSIS: Anterior cephalic border rounded; S2 weakly declined posteriorly at lateral edge; medial part of S1 developed as straight line directed anteriorly; posterior edge of visual surface anterior to transverse line tangent to anterior edge of L0; immediately before cephalic lateral border furrow meets posterior border furrow, posterior border furrow straight; distance between frontal lobe and facial suture at midline greater than distance between frontal lobe and facial suture at lateral margins of frontal lobe; ornamentation absent on L0; line from posterior to anterior edge of eye forms 5–10° angle to sagittal line; isolated patches of tubercles on L3 absent; plane from medial to lateral edges of genal spine evenly inclined; axial furrows anterior to S1 relative to furrows posterior to S1 diverge more strongly relative to sagittal line; visual surfaces in dorsal view present within sagittal lines drawn tangent to frontal lobe; interior margin of genal spine parallels lateral margin before deflecting laterally; one transverse row of circular fenestrae on anterior band of thoracic pleural segments; terminal pygidial lappet developed as narrow (tr.) sharply pointed triangle; distal tips of pygidial lappets pointed; pygidial lappets long (exsag.); laterally pygidial interpleural furrows arch at same angle as medially; anterolateral margins of first five pygidial axial rings going from axial furrows to midline straight, then strongly arched anteriorly medially.

ETYMOLOGY: Named for Fred Barber, who contributed the specimens used to define this species.

MATERIAL: AMNH 45256, 45257, 45277–45279; BMS E25855; PRI 41947–41951; YPM ?33778, ?33786, ?33788, ?33855, ?33856.

DESCRIPTION: Cephalic length (sag.) 50% of width. Axial furrow diverges more strongly anterior to S1 than posterior to S1, diverges less strongly anterior to anterior half of L3, diverging forward at about 25°, narrow, moderately incised. Cranidial anterior border developed as moderate lip deflected moderately anterior to facial suture. Preglabellar furrow shallow and narrow. Length (exsag., sag.) of cranidial anterior border increases slightly from lateral to medial edges of frontal lobe. Facial suture anterior to eyes flexes laterally then medially, with smoothly convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly then posteriorly laterally. Glabellar length (sag.) equal to 100% of width (tr.) across frontal

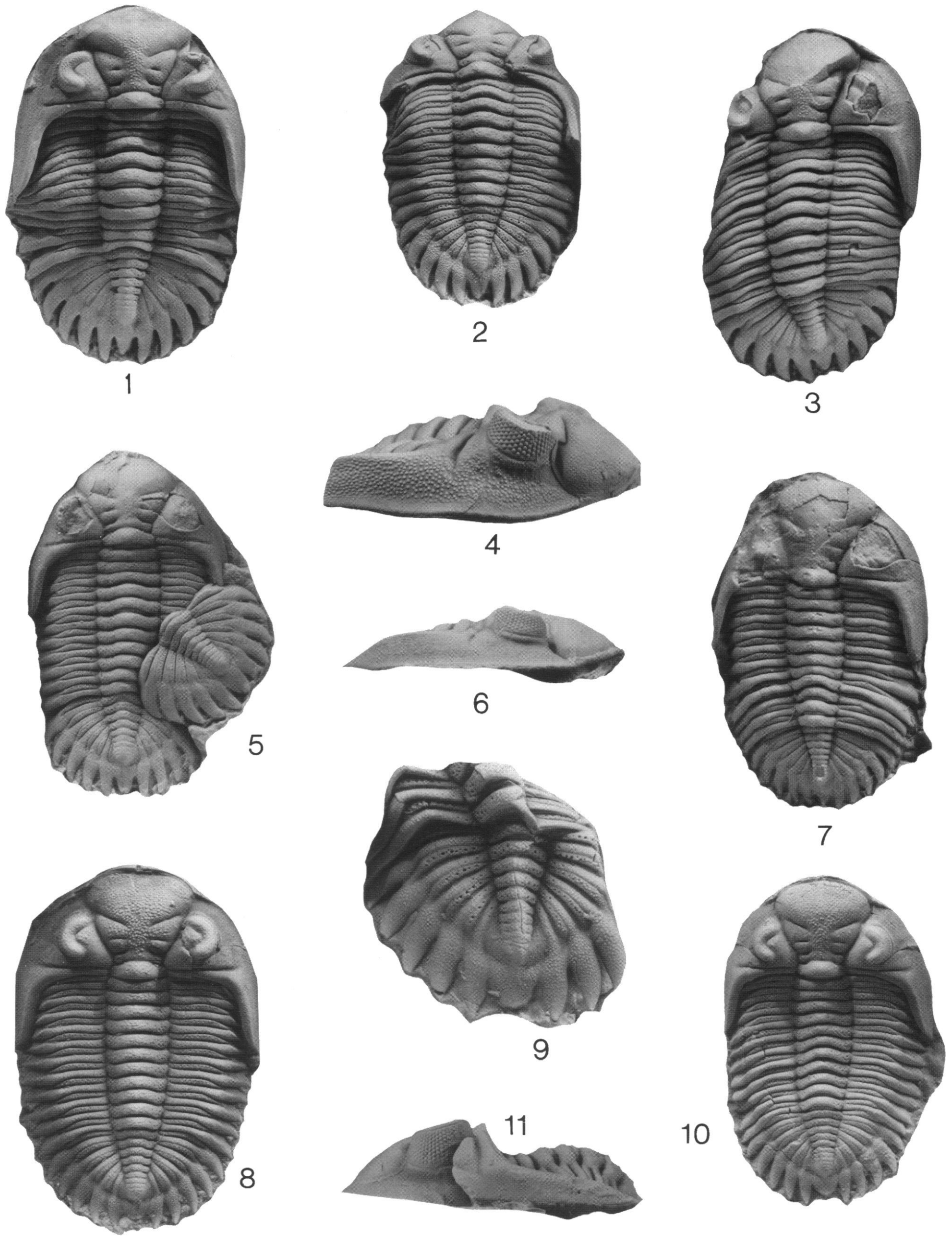

Fig. 26. *Greenops* spp. **1–7**. *Greenops barberi*, new species, Smoke Creek Bed, Windom Shale, Moscow Formation, Buffalo Creek, New York. **1**. AMNH 45277, dorsal view of complete paratype individual, ×2.3. **2, 4**. AMNH 45278, dorsal and lateral views of complete paratype individual, ×2 and ×3. **3**. PRI 41951, dorsal view of nearly complete paratype individual, ×2.3. **5**. PRI 41947, dorsal view of complete holotype individual and PRI 41948, dorsal view of paratype pygidium, ×2. **6**. PRI 41949, lateral view of paratype cephalon and partial thorax, ×2.5. **7**. AMNH 45279, dorsal view of complete individual, ×4. **8–11**. *Greenops widderensis*, new species, Widder Formation (Tioughniogan), Traverse Group, Hungry Hollow, Arkona, Ontario. **8**. AMNH 45276, dorsal view of complete paratype individual, ×2.1. **9**. AMNH 45316, dorsal view of pygidium and partial thorax of partially complete individual, ×2. **11**. AMNH 45316, lateral view of cephalon of partially complete individual, ×2.5. **10**. AMNH 45258, dorsal view of complete holotype individual, ×2.1.

lobe; frontal lobe ellipsoid, about 55% length (sag.) of glabella; L1-L3 flat (sag.); frontal lobe at same elevation as that of posterior glabellar region; anterior part of frontal lobe moderately declined forward, smoothly rounded in dorsal view. PMI a rounded depression. S3 shallow, straight, anterolateral edge transverse, equally incised medially and distally, branches diverging at about 140°. Sagittal region of L3-L2 nearly flat (tr.), lateral lobes weakly declined abaxially. L3 wedge shaped, lengthening distally, outer edge forms smaller angle with sagittal edge at anterior end than at posterior end. S2 weakly declined posteriorly at lateral edge, moderately incised, shallow adjacent to axial furrow. S1 deep, crescent shaped, medial part developed as straight line directed anteriorly, laterally contacting axial furrow. L1 short, flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 of nearly uniform length, convex anteriorly medially, deep. L0 50% of width of frontal lobe, moderately arched (tr.), longest sagittally. Large Eye Index 0.50. Anterior edge of eye contacts axial furrow opposite anterodistal corner of L3; posterior edge of eye opposite L1 distal edge of, anterior to transverse line tangent to L0; eye raised above frontal lobe; maximum of six lenses per dorsoventral file on visual surface. Fixigena evenly sloping from axial furrow to palpebrum. Postocular fixigenal field 25% of length (exsag.) of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse, anterior margin nearly straight. Genal spine developed as moderately long flange extending back to fifth thoracic segment, cephalic border furrow bisects spine; lateral and medial edges of genal spine evenly inclined; medial edge of genal spine not significantly thickened relative to lateral edge; lateral margin of genal spine parallels sagittal line, straight at posterior end; interior margin of genal spine evenly deflected laterally. Raised ridge on dorsal surface of genal spine at juncture of posterior border furrow and lateral border furrow forms smooth curve convex distally. Lateral border furrow narrow, shallow, lateral border weakly widens posteriorly. Anterior margin of cephalic doublure rounded. Prosopon of fine tubercles.

Thorax of 11 segments. Axial ring about 25% of width (tr.) of thorax, of equal length (exsag., sag.), at distal ends and medially flexed forward. Anterior margin of ring well defined sagittally, inclined posterodorsally, most elevated near posterior edge; at lateral margin of axial rings, circular fenestrae present. Articulating half ring set slightly below axial ring. Proximal part of pleura transverse, approximately horizontal; anterior segments rather evenly convex (tr.), outer part of pleurae more strongly flexed downward, more straight in posterior segments. Posterior band long (exsag.), anterior margin straight, deflected at constant, small angle posteriorly relative to transverse line; length of posterior band increases laterally, becomes planar; posterior surface declined posterodorsally, with few circular fenestrae near axis; anterior surface declined anterodorsally, with concave depression. Anterior pleural band short (exsag.), medially transverse; deflecting strongly posteriorly past approximate midpoint, at roughly same level as posterior band, pinching out distally, with one transverse row of circular fenestrae.

Pygidium broadly triangular in outline excluding marginal lappets, length about 60% of width without lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, converging at 25° angle anterior to fifth pygidial axial ring, roughly parallel posterior to fifth pygidial axial ring. Axis 30% of pygidial width (tr.) anteriorly, with 11 rings; rings of nearly equal length (exsag., sag.) distally and medially, longest medially; anterior edge of axial rings posterior to fifth axial ring from midline to distal edge convex anteriorly. Ring furrows moderately incised. Lateral margins of pygidial lappets curved, medial margins straight, distal tips pointed. Axial terminus triangular, does not project as far posteriorly as other lappets; postaxial region 15% of pygidial length (sag.). Pygidial pleural field flanking posterior part of pygidial axis faintly excavated; anterior and posterior bands of pleural segment equally elevated; tops of segments flat; pleural furrows deeper than interpleural furrows, short (exsag.). Laterally pygidial interpleural furrows arch at same angle as medially. In medial region of adjacent pleural segments, posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment.

DISCUSSION: This species is known from the following localities in the Givetian of the Appalachian Basin: Wanakah Shale, Ludlowville Formation (Tioughniogan), loose concretion, Spring Brook concretionary bed, Cazenovia Creek, Spring Brook, New York; Windom Shale, Moscow Formation (Tioughniogan), Smoke Creek Bed, Buffalo Creek, Erie Co., New York; upper Windom Shale, Big Tree road, near Hamburg, New York; Windom Shale, Moscow Formation, Hatch's Lake, New York.

There appears to be some variation in this taxon. In particular, some specimens have S2 roughly transverse and weakly convex anteriorly, whereas others have S2 weakly declined posteriorly at its lateral edge; some specimens have, in dorsal view, the visual surfaces present within sagittal lines drawn tangent to the lateral edges of the frontal, whereas in others the visual surfaces are not present within such lines; in some specimens the medial margins of the pygidial lappets are curved, whereas in others they are straight; and, finally, in some the anterolateral margins of the first five pygidial axial rings going from the axial furrows to the midline are evenly convex and do not arch strongly anteriorly, whereas in others these margins were first straight and then strongly arched anteriorly medially. The species was scored in phylogenetic analysis as having the derived state for all these characters. At this time, this variation does not appear to have any stratigraphic consistency.

Greenops widderensis, new species

Figures 9.1, 9.2, 26.8–26.11

Greenops boothi (Green). Stumm, 1953: 130, pl. 7, figs. 1–3; Ludvigsen, 1979: 80, figs. 54b, 55a, b.

Greenops (*Greenops*) *boothi* (Green). Struve, 1959: O480, fig. 381, 1a.

?*Greenops* (*Greenops*?) *collitelus* (Green). Struve, 1959: O480, fig. 379, 5.

TYPES: Holotype AMNH 45258, a complete specimen from the Widder Formation (Tioughniogan), Hamilton Group, Hungry Hollow, Arkona, Ontario; paratype AMNH 45276, from the same locality as the holotype.

DIAGNOSIS: Anterior cephalic border rounded; S2 roughly transverse, weakly convex anteriorly; medial part of S1 developed as smooth curve convex posteriorly; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; immediately before cephalic lateral border furrow meets posterior border furrow, posterior border furrow straight; distance between frontal lobe and facial suture at midline relative to laterally is constant; ornamentation on L0 absent; line from posterior to anterior edge of eye forms an angle to sagittal line that is approximately 5–10°; isolated patches of tubercles present on L3; medially genal spine flattened ledge, laterally evenly inclined; axial furrows anterior to S1 relative to posterior diverge more strongly; visual surfaces in dorsal view not present within sagittal line drawn tangent to frontal lobe; interior margin of genal spine parallels lateral margin before deflecting laterally; one transverse row of circular fenestrae on anterior band of thoracic pleural segments; terminal pygidial lappet broad, subrectangular, convex posteriorly; distal tips of pygidial lappets pointed; pygidial lappets long (exsag.); laterally pygidial interpleural furrows flex more strongly posteriorly; anterior margins of first five pygidial axial rings going from axial furrows to midline evenly convex and do not arch strongly anteriorly.

ETYMOLOGY: The name of this species is derived from the locality where the specimens were collected, the Widder Formation of the Hamilton Group, Hungry Hollow, Arkona, Ontario.

MATERIAL: AMNH 45258, 45276, 45316; ROM 1731H; YPM 7039, 35738, 35739.

DESCRIPTION: Cephalic length (sag.) 50% of width (tr.). Axial furrow diverges more strongly anterior to S1 than posterior to S1, diverges less strongly anterior to anterior half of L3, diverging forward at about 25°, narrow, moderately incised. Cranidial anterior border developed as moderate lip deflected moderately anterior to facial suture. Preglabellar furrow shallow and narrow. Length (exsag., sag.) of cranidial anterior border constant from lateral to medial edges of frontal lobe. Facial suture anterior to eyes flexes laterally then medially, with smoothly convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly then posteriorly laterally. Glabellar length (sag.) equal to 100% of width (tr.) across frontal lobe; frontal lobe ellipsoid, about 55% length (sag.) of glabella; L1-L3 flat (sag.); frontal lobe at same elevation as posterior glabellar region; anterior part of frontal lobe moderately declined forward, smoothly rounded in dorsal view. PMI a rounded depression. S3 shallow, straight, anterolateral edge transverse, equally incised medially and distally, branches diverging at about 140°. Sagittal region of L3-L2 nearly flat (tr.), lateral lobes weakly declined abaxially. L3 wedge shaped, lengthening distally, outer edge forms smaller angle with sagittal edge at anterior end than at posterior end. S2 weakly declined posteriorly at lateral edge, moderately incised, shallow adjacent to axial furrow. S1 deep, crescent shaped, medial part developed as smooth curve convex anteriorly, laterally contacting axial furrow. L1 short (exsag.), flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 convex anteriorly medially, deep. L0 50% width (tr.) of frontal lobe, moderately arched (tr.), longest sagittally. Large Eye Index 0.50. Anterior edge of eye contacts axial furrow opposite anterodistal corner of L3; posterior edge of eye opposite distal tip of S0, posterior to transverse line tangent to L0; eye raised above frontal lobe; maximum of six lenses per dorsoventral file on visual surface. Fixigena evenly sloping from axial furrow to palpebrum. Postocular fixigenal field 25% of length (exsag.) of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse, anterior margin nearly straight. Genal spine developed as moderately long flange extending back to fifth thoracic segment, cephalic border furrow bisects spine; medial edge of genal spine flattened, lateral edge evenly inclined; medial edge of genal spine not significantly thickened relative to lateral edge; lateral margin of genal spine parallels sagittal line, straight at posterior end; interior margin of genal spine parallels lateral margin before deflecting laterally, evenly deflected laterally. Raised ridge on dorsal surface of genal spine at juncture of posterior border furrow and lateral border furrow forms smooth curve convex distally. Lateral border furrow narrow, shallow, lateral border weakly widens posteriorly. Anterior margin of cephalic doublure rounded. Prosopon of fine tubercles.

Thorax of 11 segments. Axial ring about 25% of width (tr.) of thorax, of equal length (exsag., sag.), at distal ends and medially flexed forward. Anterior margin of ring well defined sagittally, inclined posterodorsally, most elevated near posterior edge; at lateral margin of axial rings, circular fenestrae present. Articulating half ring set slightly below axial ring. Proximal part of pleura transverse, approximately horizontal; anterior segments rather evenly convex (tr.), outer part of pleurae more strongly flexed downward, straight in posterior segments. Posterior band long (exsag.), anterior margin straight, deflected at constant, small angle posteriorly relative to transverse line; length (exag.) of posterior band increases laterally, band becomes planar laterally; posterior surface declined posterodorsally, with few circular fenestrae near axis; anterior surface declined anterodorsally, with concave depression. Anterior pleural band short (exsag.), medially transverse; deflecting strongly posteriorly past approximate midpoint, at roughly same level as posterior band, pinching out distally, with one transverse row of circular fenestrae.

Pygidium broadly triangular in outline excluding marginal lappets, length about 50% of width without lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, converging at 25° angle anterior to fifth pygidial axial ring, roughly parallel posterior to fifth pygidial axial ring. Axis 30% of pygidial width anteriorly, with 11 rings; rings of nearly equal length (exsag., sag.) distally and medially, longest medially; anterior edge of axial rings posterior to fifth axial ring from midline to distal edge convex anteriorly. Ring furrows moderately incised. Lateral margins of pygidial lappets curved, medial margins straight, distal tips pointed. Axial terminus subrectangular, convex posteriorly, broad, does not project as far posteriorly as other lappets; postaxial region 15% of pygidial length (sag.). Pygidial pleural field flanking posterior part of pygidial axis faintly excavated; anterior and posterior bands of pleural segment equally elevated; tops of segments flat; pleural furrows deeper than interpleural furrows, short (exsag.). Laterally pygidial interpleural furrows flex more strongly posteriorly. In medial region of adjacent pleural segments posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment.

DISCUSSION: This species is known from the Widder Formation (Tioughniogan) of the Hamilton Group, Hungry Hollow, Arkona, Ontario, Canada. Struve (1959) showed an illustration of a cephalon from the Middle Devonian of Ontario, Canada, that he assigned to *G.* (*G.*) *boothi*. The specimen appears similar to *G. boothi*, but it is also very similar to *G. widderensis*. Because *G. widderensis* is the only species of *Greenops* described from Ontario, and because the specimen illustrated does not appear to be referable to *Stummiana arkonensis* (Stumm, 1953), also from the Hamilton Group of Ontario, Struve's (1959) specimen is assigned to *G. widderensis*. Struve (1959) also figured a hypostome from Ontario that he assigned to *Greenops* (*Greenops*?) *calliteles* (Green). It is conceivable that this hypostome belongs to *Greenops widderensis*, one of only two species of asteropyginines described from Ontario. The hypostome could also belong to *Stummiana arkonensis* (Stumm, 1953), and thus this hypostome is questionably assigned to either of these taxa. Recovery of articulated specimens with hypostomes for each of these species would make it possible to resolve this issue.

As discussed above under the heading of *G. boothi*, Stumm (1953) illustrated three specimens from the Widder Formation and possibly the Hungry Hollow Formation of the Michigan Basin in southwestern Ontario. These specimens do bear some resemblance to *G. boothi*, *G. grabaui*, and *G. barberi*. However, they belong to a new species that is restricted to the Michigan Basin, whereas *G. boothi*, *G. grabaui*, and *G. barberi* are restricted to the Appalachian Basin. *Greenops widderensis* can be discriminated from *G. grabaui* by the following characters: in *G. widderensis* a line from the posterior to the anterior edge of the eye forms an angle to a sagittal line that is approximately 10°, whereas in *G. grabaui* the angle is approximately 30°; in *G. widderensis* the distal tips of the pygidial lappets are pointed, whereas in *G. grabaui* they are developed as blunt triangles; in *G. widderensis* the anterolateral margins of the first five pygidial axial rings are evenly convex, whereas in *G. grabaui*, when proceeding from the axial furrow to the midline, the anterior margin is straight, then arches anteriorly; and in *G. widderensis* the longest pygidial pleural lappet is the length (exsag.) of the length (sag.) of the first three pygidial axial rings, whereas in *G. grabaui* it is the length (sag.) of the first two pygidial axial rings. Characters for distinguishing *G. barberi* from *G. widderensis* include the condition of the terminal lappet, which in *G. widderensis* is subrectangular, broad anteriorly, and convex posteriorly, whereas in *G. barberi* it is a sharply pointed triangle, narrow anteriorly; and the condition of the genal spine, which in *G. widderensis* is flattened medially, is evenly inclined in *G. barberi*. Other characters for distinguishing *G. widderensis* from *G. barberi* are given under the heading of *G. barberi*.

Ludvigsen (1979) figured a cephalon and a complete individual from the Hamilton Group, Thedford, Ontario, Canada, that he assigned to *G. boothi*. As discussed above under the heading of *G. boothi*, these taxa must instead be treated as *G. widderensis*. In particular, they differ from *G. boothi* in the characters enumerated above in the section on *G. boothi*. For the same reasons, Ludvigsen's (1979: fig. 54b) reconstruction of *G. boothi* must instead be treated as a reconstruction of *G. widderensis*.

DELOOPS, NEW GENUS

TYPE SPECIES: *Greenops haasi* Morzadec, 1983.

ASSIGNED TAXA: *Greenops* (*Greenops*) cf. *boothi* Arbizu, 1979: pl. 13, figs. 1, 2.

DIAGNOSIS: S3 convex anteriorly; S2 weakly declined posteriorly at lateral edge; S1 crescent shaped, medial part developed as smooth curve convex posteriorly; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; maximum of seven lenses in dorsoventral file on visual surface; facial suture lateral to eye, before flexing posteriorly, flexes anteriorly to point opposite S1; anterior margin of frontal glabellar lobe smoothly rounded; anterior cephalic border pointed, developed as narrow lip; PMI absent; posterior and anterior margins of palpebrum deflected at angle to transverse line that is roughly equivalent; line from posterior to anterior edge of eye forms an angle to sagittal line that is approximately 30°; distance between facial suture and frontal lobe constant from lateral edges of lobe to midline; tubercle on L0; cephalic axial furrows diverge more strongly anterior to S1 than posterior to S1; fixigenae with distinct bulge medially; genal spine extending back to fourth thoracic segment; medially genal spine developed as flattened ledge, laterally as an evenly inclined plane; medial edge of genal spine not significantly thickened, lateral margin parallels sagittal line, recurves at posterior end, interior margin of genal spine deflected laterally; tops of pygidial pleural segments flat; lateral margins of pygidial lappets curved, medial margins straight, distal tips blunt triangles; anterior margins of pygidial axial rings posterior to sixth axial ring smoothly convex anteriorly; 14 pygidial axial rings; pygidial axis constricts posterior to sixth axial ring; anterior and posterior parts of pygidial pleural segments of equal elevation; tops of pygidial pleural segments flat; pleural furrows moderately incised, short (exsag.); laterally pygidial interpleural furrows flex more strongly posteriorly; in medial region of adjacent pleural segments posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment; terminal pygidial lappet subrectangular, broad (tr.), projects further posteriorly than pleural lappets.

ETYMOLOGY: Named by combining *Delo* for the paleontologist who did some of the important early work revising and describing asteropyginines of North America and Europe with *Ops* for eyes. This name follows the etymological style of Delo (1935), who established several new genera and named these new taxa by combining the names of important paleontologists with the suffix *-ops*.

DISCUSSION: This genus contains two species, each of which had originally been treated as closely related to species of the genus *Greenops*. However, placing these taxa in the genus *Greenops* would have required the expansion of that genus into a particularly large and cumbersome taxonomic unit, and this decision was not pursued. This genus represents one of a series of Armorican forms that bear a strong resemblance and have some phylogenetic affinity with the core species of the genus *Greenops* from North America, but none of the species of *Deloops* have a sister group relationship with *Greenops* to the exclusion of all other genera. Thus, these two species can no longer be treated as belonging to the genus *Greenops*, but their close affinity to taxa in that genus, and to those taxa in the genus *Stummiana*, which also contains a North American species, is important to point out.

Arbizu (1979) figured a cephalothorax and a pygidium from the Givetian of Spain that he assigned to *Greenops* (*Greenops*) cf. *boothi*. This species is nearly identical to *Deloops haasi* (Morzadec, 1983). The only significant difference between the two taxa is that the terminal pygidial lappet is relatively broader in *D. haasi*. Therefore, Arbizu's (1979) specimens are treated as a new species closely related to *D. haasi*, termed *D.* sp. aff. *haasi*.

Deloops haasi (Morzadec, 1983)

Greenops haasi Morzadec, 1983: 125, pl. 10, figs. 1–7, pl. 11, figs. 1–11. (See for complete synonymy.)

TYPES: Holotype defined in Morzadec (1983: pl. 11, fig. 6).

DIAGNOSIS: Same as for genus.

DISCUSSION: This species is known from the Massif Armorican, upper Givetian. It shares some similarities with some species traditionally assigned to *Greenops* by Morzadec (1983), in particular his *G. osismorum*, here *Stummiana osismorum* (Morzadec, 1983). However, the shared similarities appear to be primitive retentions or convergences. Similarities between *S. osismorum* and *D. haasi* include the condition of S3 and the overall shape of the genal spines. However, these taxa differ in a variety of features, including: the condition of the terminal pygidial lappet, which is relatively narrower (tr.) in *S. osismorum*; the cephalic axial furrows, which diverge more strongly anterior to S1 in *D. haasi*, but not in *S. osismorum*; the medial edge of the genal spine, which is flattened in *D. haasi* but not in *S. osismorum*;

the distance between the frontal lobe and the facial suture, which increases at the midline relative to laterally in *S. osismorum*, whereas this distance is constant in *D. haasi*; and by the possession of a greater number of pygidial axial rings (14) in *D. haasi*.

Originally, Morzadec (1983) treated *D. haasi* and *S. osismorum* as sister taxa. Here, the phylogenetic analysis suggests that they are closely related, but *D. haasi* is sister to a clade including *S. osismorum* and *Kayserops*.

STUMMIANA, NEW GENUS

TYPE SPECIES: *Greenops arkonensis* Stumm, 1953.

ASSIGNED TAXA: *Greenops osismorum* Morzadec, 1983.

DIAGNOSIS: S3 straight, anterolateral edge deflected posteriorly; S2 weakly declined posteriorly at lateral edge; maximum of seven lenses in a dorsoventral file on visual surface; anterior margin of frontal glabellar lobe smoothly rounded; distance between frontal lobe and facial suture at midline increases slightly relative to laterally; anteriormost portion of palpebrum opposite PMI; anterior cephalic border rounded in dorsal view; fixigena with distinct bulge medially; tubercle on L0; L3 flattened dorsally; line from posterior to anterior edge of eye forms a 30° angle to sagittal line; axial furrows more strongly divergent anterior to anterior half of L3; interior margin of genal spine evenly deflected laterally posteriorly; terminal pygidial lappet narrow (tr.), subrectangular, does not project as far posteriorly as fifth pair of pleural lappets; fifth pair of pleural lappets project furthest posteriorly; lateral margins of pygidial lappets curved, distal tips developed as blunt triangles; pygidial axis constricts posterior to fifth axial ring; anterior margins of pygidial axial rings posterior to constriction of pygidial axis smoothly convex anteriorly, anterior to constriction margins straight laterally, strongly arched medially anteriorly; pygidial pleural furrows moderately incised, short (exsag.); 11 axial rings.

ETYMOLOGY: This genus is named for the paleontologist Erwin Stumm, who contributed so much to our knowledge of the Middle Devonian faunas of the Michigan Basin.

DISCUSSION: This genus contains two species, one from the Middle Devonian of the Michigan Basin of ENA and one from the Middle Devonian of Armorica. It is one of only two cases in the phylogeny of the Asteropyginae presented herein where a species from Armorica is sister to a species from ENA. In all other cases, a species from Armorica or ENA is sister to a larger clade from ENA or Armorica.

Both taxa in this genus had originally been assigned to the genus *Greenops*. However, the results presented here suggest that these two taxa must be excluded from that genus. Characters suggesting exclusion of species assigned to *Stummiana* from the *Greenops* clade include: the condition of the anteriormost portion of the palpebrum, which is opposite the PMI in *Stummiana* but opposite a point between the medial part of L3 and the PMI in *Greenops*; the fixigena, which has a distinct bulge medially in *Stummiana* but is evenly sloping from the axial furrow to the palpebrum in *Greenops*.

The two species in *Stummiana* share a large number of synapomorphies, but they can be discriminated on the basis of the relative position of the eyes, differences in the development of tubercles, and differences in the form of the pygidial pleural segments and lappets.

Stummiana osismorum Morzadec, 1983

Greenops osismorum Morzadec, 1983: 124, pl. 9, figs. 1–12.

?*Greenops osismorum* Morzadec, 1983: 124, pl. 9, fig. 13.

TYPES: Holotype defined in Morzadec (1983: pl. 9, fig. 3).

DIAGNOSIS: Lateral to eye facial suture before flexing posteriorly flexes anteriorly to point between distal margins of S1 and S2; anterior cephalic border in dorsal view rounded; S1 crescent shaped, medial portion smooth curve directed anteriorly; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; posterior and anterior margins of palpebrum deflected at an equivalent angle to transverse line; medial margins of pygidial pleural lappets straight; terminal pygidial lappet subrectangular, convex posteriorly; anterior and posterior portions of pygidial pleural segments of equal elevation.

DISCUSSION: This species is known from the Givetian of Armorica. Morzadec (1983) suggested that this species was closely related to *G. boothi*, but the phylogenetic analysis conducted herein does not entirely support his conclusions. *Stummiana osismorum* in fact appears to be part of a larger clade (including several genera) that is sister to the four ENA taxa assigned to *Greenops*. Morzadec (1983) also suggested that this species was closely related to Arbizu's (1979: pl. 3, figs. 1, 2) *Greenops* sp. cf. *boothi*. However, as discussed above, these specimens appear to be more closely related to *D. haasi* on the basis of pygidial characteristics, and they are tentatively referred to as *D.* sp. aff. *haasi* until more detailed material can be obtained. Morzadec's (1983: pl. 9, fig. 13) is a pygidium that he questionably assigned to *G. osismorum*, because it appears to have slightly longer pleural lappets than the holotype. It does not appear to differ in the condition of any other characteristics, and until more detailed material is obtained, it is retained within *S. osismorum*.

Morzadec (1983) treated his *G. osismorum* as a direct lineal descendant of what he termed *Greenops struvei*. This direct ancestor-descendant relationship between the two taxa cannot be upheld herein. As discussed above, *G. struvei* must henceforth be assigned to a new genus, *Modellops*, and it is not particularly closely related to any of the species assigned to the genera *Greenops* or *Stummiana*. It shares a close, though not a sister group, relationship with *Philipsmithiana*, new genus. Differences between *Philipsmithiana* and *Greenops* are discussed under the heading of the former.

Stummiana arkonensis Stumm, 1953

Figure 8.8

Greenops arkonensis Stumm, 1953: 134, pl. 8, figs. 10–14.

Greenops aequituberculatus Stumm, 1953: 131, pl. 7, fig. 5, 6, *non* 4, pl. 8, figs. 6–8, *non* 5, 9.

?*Greenops aequituberculatus* (Stumm). Stumm, 1967: 115, pl. 2, fig. 6.

?*Greenops* (*Greenops*?) *collitelus* (Green). Struve, 1959: O480, fig. 379.5.

TYPES: Holotype defined in Stumm (1953: pl. 8, fig. 13).

DIAGNOSIS: Genal spine extends back to fifth thoracic segment; lateral margin of genal spine at posterior end straight; posterior edge of visual surface anterior to transverse line tangent to L0; fixigena with distinct bulge medially; tubercle on L0 present; cephalic axial furrows diverge at constant angle anterior and posterior to S1; axial furrows at anterior half of L3 relative to posterior much less strongly divergent; isolated patches of tubercles present on L2 and L3; facial suture lateral to eye before flexing posteriorly flexes anteriorly to point opposite S2; S3 straight, at anterior end recurves posteriorly; posterior margin of palpebrum relative to anterior margin of palpebrum deflected at an angle to transverse line that is significantly larger; medial tubercle present on pygidial and thoracic axial rings; one row of circular fenestrae on anterior part of thoracic pleural segments; medial margins of pygidial pleural lappets curving; distal tips of pygidial lappets blunt triangles; posterior parts of pleural segments elevated above anterior parts; pygidial interpleural furrows arch more strongly posteriorly distally; medial margins of pygidial lappets curving laterally; pygidial pleural lappets long; 11 pygidial axial rings.

MATERIAL: AMNH 45249.

DISCUSSION: This species is known from the following Givetian localities in the Traverse Group, Michigan Basin, ENA: Gravel Point Formation (Cazenovian), *Longispina emmetensis* zone, Gravel Point west of Charlevoix, Michigan, on shore of Lake Michigan; the Alpena Limestone (Cazenovian), the Huron Point Cement Company, Alpena, Michigan, AMNH locality 3059; Dock Street Clay (Cazenovian), abandoned quarry of the Thunder Bay Limestone Company, eastern edge of Alpena, Michigan, AMNH locality 3062; the Arkona Shale (Cazenovian), Hungry Hollow on the Aux Sable River, north of Arkona, Ontario, AMNH locality 3053; the Widder Formation, Rock Glen, Arkona, Ontario, AMNH locality 3055; and the Norway Point Formation (Tioughniogan), bank of Thunder Bay River on Potter Farm, about 1 mile below Four Mile Dam, Michigan. Thus, this species is known from the Cazenovian and Tioughniogan of the Michigan Basin, based on the stratigraphic correlations presented in figure 2.

Stumm (1953) considered this species to be endemic to the Michigan Basin, and this conclusion appears to be correct. However, his assignment of this species to the genus *Greenops* can no longer be supported. *Stummiana arkonensis* can be distinguished from *Greenops boothi* by several characters, including the following: in *G. boothi* there are a maximum of six lenses pre dorsoventral file on the visual surface, whereas in *S. arkonensis* there are a maximum of seven lenses; in *G. boothi* the facial suture lateral to the eye before flexing posteriorly flexes anteriorly to point between the distal tips of S1 and S2, whereas in *S. arkonensis* it flexes to a point opposite the distal tip of S2; in *G. boothi* medially the anterior cephalic border in dorsal view is pointed, whereas in *S. arkonensis* it is rounded; in *G. boothi* the posterior margin of the palpebrum relative to the anterior margin is deflected at an angle to a transverse line that is roughly equivalent, whereas in *S. arkonensis* the angle the posterior margin forms with a transverse line is relatively larger; in *G. boothi* the axial furrows anterior to S1, relative to those posterior to S1, diverge more strongly, whereas in *S. arkonensis* they diverge at the same angle; in *G. boothi* the medial margins of the pygidial lappets are straight, whereas in *S. arkonensis* they are curved; in *G. boothi* the anterior and posterior parts of the pygidial pleural segments are of equal elevation, whereas in *S. arkonensis* the posterior part of the pygidial pleural segment is elevated above the anterior part; in *G. boothi* the tops of the pygidial pleural segments are flat, whereas in *S. arkonensis* they are rounded; in *G. boothi* in the medial region of adjacent pleural segments, the posterior region of the anterior segment is equal in length (exsag.) to the anterior part of the posterior segment, whereas in *S. arkonensis* the posterior region of the anterior segment is longer (exsag.) than the anterior part of the posterior segment; in *G. boothi* the terminal pygidial lappet is relatively broad, whreas in *S. arkonensis* it is relatively narrow; and in *G. boothi* there are two transverse rows of circular fenestrae on the anterior band of thoracic pleural segments, whereas in *S. arkonensis* there is only one row.

Stumm (1953) suggested that *S. arkonensis* was closely related to *G. aequituberculatus* Stumm, 1953. On some level, this is correct; however, Stumm's (1953) conception of *G. aequituberculatus* appears to have encompassed at least three distinct species: *S. arkonensis*, *G. chilmanae*, and *Kayserops traversensis*. Most of the paratypes of *G. aequituberculatus* including USNM 117872 should be referred to *S. arkonensis* by the following logic. The cephala Stumm (1953) assigned to *Greenops traversensis* and *G. alpenensis* are identical, and the species they comprise is assigned to the genus *Kayserops* and is discussed more fully below. The cephalon Stumm (1953: pl. 7, fig. 4) designated as a paratype of *G. aequituberculatus* shows no differences from the cephala designated the holotypes of *G. alpenensis* and *G. traversensis*. This suggests that this cephalon formerly designated *G. aequituberculatus* has been misassigned. However, the thoracopygidium and pygidia Stumm (1953) assigned to *G. aequituberculatus* appear to belong to *S. arkonensis* rather than to *K. traversensis*. The pattern of fenestrae on the thoracic pleural segments is serially repeated on the pleural segments of the pygidium, and the holotype of "*Greenops*" *traversensis*, here assigned to *Kayserops*, has a single row of circular fenestrae on the posterior band of the thoracic pleural segments, and this is also seen on the paratype of *Kayserops traversensis*. By contrast, examining the specimens used to establish *G. aequituberculatus* indicates that there are a few circular fenestrae on the posterior band of the thoracic pleural segments near the thoracic axis, not a row of fenestrae. This is the character state found in *S. arkonensis*. This character state is also found in some of the pygidia that Stumm (1953: pl. 8, figs. 6, 7) assigned to *G. aequituberculatus*, and these pygidia clearly differ from the pygidia of *Kayserops traversensis* and *G. chilmanae* Stumm, 1965, in the condition of many other characters. In addition, although the patterns of the fenestrae are not visible on the thoracopygidium or the pygidium in Stumm's (1953) plate 7, figures 5 and 6, the lappets, the condition of the interpleural furrows, and the number, form, and condition of the pygidial axial rings, i.e., all those characters of the pygidium used in the phylogenetic analysis, appear to be identical to those shown in Stumm's (1953) plate 8, figures 6 and 7, and the specimens are treated as conspecific. These character states are identical to what is found in *S. arkonensis*, both in Stumm's (1953) type material and in material housed at the AMNH. Therefore, these specimens formerly assigned to *G. aequituberculatus* are placed in *S. arkonensis*, and the species name *G. aequituberculatus* is no longer considered valid.

Stumm (1967: pl. 2, fig. 6) figured a pygidium in ventral view that he assigned to *Greenops aequituberculatus* but that is questionably referred to herein as *S. arkonensis*. Although not well preserved, it bears a terminal pygidial lappet very similar in shape to those known for *S. arkonensis*. In addition, the form of the pygidial lappets is very similar to what is known for *S. arkonensis*.

Struve (1959) figured a hypostome from Ontario that he assigned to *Greenops* (*Greenops*?) *calliteles* (Green). It is conceivable that this hypostome belongs to *Greenops widderensis*, one of only two species of asteropyginines described from Ontario. However, the hypostome could also belong to *Stummiana arkonensis* (Stumm, 1953), and thus this hypostome is questionably assigned to either of these taxa. Recovery of articulated specimens with hypostomes for each of these species would make it possible to resolve this issue.

The condition of S3 is treated as straight in *S. arkonensis* rather than convex anteriorly. Nearly the entire portion of S3 is straight, as it is in *G. chilmanae* and *G. boothi*. In these two taxa, at its anterior end, S3 is transverse, whereas in *S. arkonensis*, it recurves posteriorly. This is considered to be an autapomorphy of *S. arkonensis* rather than homologous with the structure of S3 in such taxa as *D. haasi* (Morzadec, 1983), which appear to have a large portion of S3 convex.

ARMORIGREENOPS, NEW GENUS

TYPE SPECIES: *Armorigreenops leoi*, new species.

ASSIGNED TAXA: *Armorigreenops* sp. aff. *leoi*.

DIAGNOSIS: S3 straight, anterolateral edge transverse; S2 weakly declined posteriorly at lateral edge; S1 crescent shaped, medial portion developed as straight line directed anteriorly; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; distance between frontal lobe and facial suture at midline relative to lateral margins increases slightly; frontal glabellar lobe smoothly rounded in dorsal view; anterior cephalic border in dorsal view pointed, developed as narrow lip; facial suture lateral to eye, before flexing posteriorly, flexes anteriorly to point opposite S1; line from posterior to anterior edge of eye forms a 30° angle to sagittal line; axial furrows anterior to S1 diverge at same angle as furrows posterior to S1, less strongly divergent anterior to anterior half of L3; fixigena evenly sloping from axial furrow to palpebrum; posterior and anterior margins of palpebrum deflected at an angle to transverse line that is roughly equivalent; lateral margin of genal spine parallels sagittal line, at posterior end recurves posteriorly; genal spine long flange extending back to sixth thoracic segment, medial edge significantly thickened relative to lateral edge, plane from medial to lateral ledge evenly inclined, interior margin parallels lateral margin before deflecting posteriorly; tubercle present on medial part of pygidial and thoracic axial rings; tops of pygidial pleural segments flat; lateral margins of pygidial lappets curved, medial margins straight, distal tips developed as blunt triangles; anterior and posterior parts of pygidial pleural segments of equal elevation; laterally pygidial interpleural furrows flex more strongly posteriorly; in medial region of adjacent pleural segments posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment; terminal pygidial lappet developed as blunt triangle.

ETYMOLOGY: Name derived by combining *Armorica*, the region the genus is known from, with *Greenops* to denote its resemblance to those taxa herein assigned to *Greenops* that hail from ENA.

DISCUSSION: This genus contains a single described species that shows some similarity to taxa treated here as belonging to *Greenops*, and this species was originally treated as a form closely related to *G. boothi* by Gandl (1972). However, this taxon differs from *Greenops boothi* in the condition of the following characters: 5, 8, 13, 22, 26, 28, 30, 32, 35, 36, 39, 41, 44, 59, 61, and 63.

On the basis of the phylogenetic analysis conducted herein, *Armorigreenops leoi* is more closely related to taxa such as *Kayserops* Delo, 1935. Thus, this species must be excluded from *Greenops*, or *Greenops* would be paraphyletic. It would also be possible to place *A. leoi* in a greatly expanded *Greenops* that contained a variety of new and old genera including *Kayserops*. This latter taxonomic decision is not followed in order to retain the structure in the Asteropyginae, and instead the species is placed in a new genus.

Armorigreenops leoi, new species

Greenops (*Greenops*) sp. Gandl. Carls and Gandl, 1968: 462.

Greenops (*Greenops*) sp., cf. *boothi* (Green). Gandl, 1972: 137, pl. 14, figs. 1–3.

TYPES: Holotype Gandl's (1972: pl. 14, fig. 1), Senckenberg Museum, Frankfurt (SMF) 21681.

DIAGNOSIS: Same as for the genus.

ETYMOLOGY: Named for my other grandfather, Leo Lieberman, who recently passed away.

DESCRIPTION: Cephalic length (sag.) 60% of width. Axial furrow nearly straight anterior to S0, diverging forward at about 30°, narrow, shallow. Cranidial anterior border short exsagittally and medially, lying in constant dorsoventral plane, pointed medially in dorsal view. Preglabellar furrow moderately incised and narrow. Cranidial anterior border lengthens slightly medially, developed as narrow lip. Facial suture anterior to eyes flexes laterally then medially, with smoothly convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly then posteriorly laterally. Glabellar length (sag.) equal to width (tr.) across frontal lobe; frontal lobe ellipsoid, about 60% of length of glabella; L1-L3 flat (sag.); frontal lobe at same level as posterior glabellar region; anterior part of frontal lobe moderately declined forward, smoothly rounded in dorsal view. PMI not visible. S3 moderately incised, straight, anterolateral edge flexes posteriorly, branches diverging at about 140°. Sagittal region of L3-L2 nearly flat (tr.), lateral lobes weakly declined abaxially. L3 wedge shaped, lengthening distally, outer edge posteriorly flexes laterally, anterior end flexing less strongly laterally. S2 weakly convex anteriorly, moderately incised, shallow adjacent to axial furrow, weakly declined posteriorly at lateral edge. S1 deep, crescent shaped, medial part developed as straight line directed anteriorly, contacting axial furrow. L1 short (exsag.), flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 convex anteriorly medially, deep. L0 55% of width (tr.) of frontal lobe, moderately arched (tr.), longest medially. Large Eye Index 0.40. Anterior edge of eye adjacent to axial furrow opposite antero-distal corner of L3; posterior edge of eye opposite L1, posterior to transverse line tangent to L0; eye raised slightly above frontal lobe. Fixigena evenly sloping from axial furrow to internal margin of eye. Postocular fixigenal field 15% of length (exsag.) of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse, anterior margin nearly straight. Genal spine long flange extending back to sixth thoracic segment, cephalic lateral border furrow bisects spine; medial and lateral edges of genal spine evenly inclined; medial edge thickened; lateral margin of genal spine parallels sagittal line; lateral margin of genal spine at posterior end recurves; interior margin of genal spine parallels lateral margin before deflecting laterally. Lateral border furrow narrow, shallow, lateral border weakly widens posteriorly. Anterior margin of cephalic doublure bluntly pointed. Prosopon of fine tubercles.

Thorax of 11 segments. Axial ring about 30% width (tr.) of thorax, of equal length (exsag., sag.), at distal ends and medially flexed forward. Ring furrow of equal length, moderately incised, flexing forward medially and distally. Anterior margin of ring well defined sagittally, inclined posterodorsally, most elevated near posterior edge; raised prominent tubercle on medial portion of axial ring. Articulating half ring set slightly below axial ring. Proximal part of pleura transverse, approximately horizontal; anterior segments rather evenly convex (tr.), outer part of pleurae more strongly flexed downward, straight in posterior segments. Posterior band long (exsag.), anterior margin straight, deflected at constant small angle posteriorly relative to transverse line, laterally, length of posterior band increases, becomes planar; posterior surface declined posterodorsally; anterior surface declined anterodorsally, with concave depression. Anterior pleural band short (exsag.), medially transverse, deflecting strongly posteriorly past approximate midpoint, at roughly same level as posterior band, pinching out distally.

Pygidium broadly triangular in outline excluding marginal lappets, length (sag.) about 55% of width (tr.) excluding lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, converging at 20° anterior to fifth pygidial axial ring, roughly parallel posterior to fifth pygidial axial ring. Axis 25% of pygidial width (tr.) anteriorly, with 11 rings; rings of nearly equal length (exsag., sag.) distally and medially, longest medially; anterior and posterior edge of axial rings anterior to fifth axial ring from midline to distal edge straight, then strongly arch anteriorly. Ring furrows moderately incised. Lateral margins of pygidial lappets curved, medial margins straight, distal tips developed as blunt triangles. Axial terminus triangular, pointed posteriorly, projecting further posteriorly than fifth pair of pleural lappets, narrow, 1.1 times width of posterior portion of pygidial axis; postaxial region 30% of pygidial length (sag.). Pygidial pleural field flanking posterior portion of pygidial axis faintly excavated; anterior and posterior pleural segments of equal elevation; tops of segments flat; pleural furrows deeper than interpleural furrows, moderately incised, short (exsag.). Laterally pygidial interpleural furrows arching more strongly than medially. In medial region of adjacent pleural segments, posterior region of anterior segment equal in length (exsag.) to anterior part of posterior segment.

DISCUSSION: This species is known from the Givetian of northeastern Spain. It bears a strong resemblance to *Greenops boothi*, and Gandl (1972) originally suggested that it might indeed belong to that species. However, the taxa differ in the condition of several characters, discussed above, and it must be assigned to a new genus.

Haas (1970) figured a pygidium from Middle Asturia in northern Spain, at Vaca de Luanco in the lower Candas Kalke, that he assigned to *Greenops boothi*. This species is very similar to *A. leoi*, differing chiefly in the number of pygidial axial rings, 12 in Haas's species versus 11 in *A. leoi*. In addition, in Haas's species the anterior margin of the first five pygidial axial rings follows the same general course found in *A. leoi* and in all other species of the genus *Greenops*; however, the anterior flexion of the axial ring medially is not so strong as in *A. leoi* or in the other species of *Greenops*. Haas's (1970) figured pygidium is tentatively treated as a new species, *Armorigreenops* sp. aff. *leoi*.

Arbizu (1979) also figured a specimen that he referred to as *Greenops* (*G.*) cf. *boothi*. However, this specimen is not conspecific with *A. leoi*, counter to Morzadec's (1983) conclusions. In particular, they differ in the condition of the distal tips of the pygidial pleural lappets; in the shape of the terminal pygidial lappet; in the condition of S3, which are convex anteriorly in Arbizu's specimen; and in the structure of the genal spine, which is flattened medially and smoothly arched laterally in Arbizu's figured specimen. The species appears to be closely related to *G. haasi* Morzadec, 1983, here *Deloops haasi*, and is discussed above under the heading of that genus.

Gandl (1972) treated *A. leoi* (his *G.* (*G.*) sp. cf. *boothi*) as closely related to the form he called *G.* (*Neometacanthus*?) sp. M. aff. *aequituberculatus*. This species was discussed above under the heading of the genus *Neometacanthus*, and it appears that Gandl's pygidium cannot be assigned to that genus. The pygidium also differs from *Armorigreenops* in the condition of several characters. In particular, the anterior margin of the five anteriormost pygidial axial rings, when proceeding from the axial furrows to the midline, is smoothly convex anteriorly instead of being straight and then flexing strongly anteriorly; the anterior margins of the pygidial axial rings posterior to the fifth pygidial axial rings are straight instead of convex anteriorly; the pygidial interpleural furrows do not flex more strongly posteriorly laterally; and the tops of the pygidial pleural segments are rounded instead of flat. The evolutionary affinities of Gandl's (1972) isolated pygidium are difficult to ascertain; however, it seems clear that it is not closely related to *Armorigreenops leoi*, new species. Gandl (1972) also asserted that *Neometacanthus stellifer* was a close relative of *A. leoi*. As discussed above, *Neometacanthus* is sister to a clade containing *Rhenops* and *Asteropyge*, and thus *N. stellifer* is not a particularly close relative of *A. leoi*.

KENNACRYPHAEUS, NEW GENUS

TYPE SPECIES: *Kennacryphaeus harrisae*, new species.

DIAGNOSIS: S3 straight medially, anterolateral edge transverse; S1 developed medially as smooth curve convex posteriorly; posterior edge of visual surface posterior to transverse line tangent to anterior edge of L0; maximum of eight lenses per dorsoventral file on visual surface; facial suture lateral to eye, before flexing posteriorly, flexes anteriorly to point between distal tips of S1 and S2; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; distance between facial suture and frontal lobe at midline relative to distance between facial suture and frontal lobe at lateral margins of frontal lobe equivalent; medially anterior cephalic border in dorsal view rounded; spine on L0; anterior cephalic border medially not deflected anteriorly beyond lateral margins of cephalon; PMI developed as rounded depression; posterior margin of palpebrum relative to anterior margin deflected at an angle to transverse line that is roughly equivalent; line from posterior to anterior edge of eyes forms an angle to sagittal line that is approximately 30°; change in cephalic topography where librigena meets lateral border furrow insignificant; genal spine medially developed as flattened edge, laterally evenly inclined; medial edge of genal spine significantly thickened relative to lateral edge; raised ridge on dorsal surface of genal spine, at juncture of posterior border furrow and lateral border furrow, is smoothly curved, convex distally; axial furrows anterior to S1 relative to posterior to S1 diverge at same angle; visual surfaces present within sagittal line drawn tangent to lateral margins of frontal lobe; interior margin of genal spine parallels lateral margin before deflecting laterally; interior margin of genal spine more strongly deflected laterally posteriorly; tubercles present on medial portion of pygidial and thoracic axial rings; terminal pygidial lappet developed as blunt triangle, does not project as far posteriorly as fifth pair of pleural lappets; lateral margins of pygidial lappets curved, medial margins straight; distal tips of lappets pointed; anterior margins of first five pygidial axial rings straight; pygidial axis constricts posterior to fifth axial ring; pygidial pleural field flanking posterior portion of pygidial axis faintly excavated; anterior and posterior parts of pygidial pleural segments of equal elevation; tops of pygidial pleural segments rounded; pleural furrows moderately incised, short (exsag.); laterally pygidial interpleural furrows flex more strongly posteriorly; in medial region of adjacent pleural segments posterior region of anterior segment equal in length (exsag.) to anterior portion of posterior segment; 14 pygidial axial rings; anterolateral margins of first five pygidial axial rings going from axial furrows to midline straight, then strongly arched anteriorly; longest pygidial lappet short (exsag.), length from proximal to distal tip equal to length (sag.) of first two pygidial axial rings.

ASSIGNED TAXA: None (monotypic).

ETYMOLOGY: Named for Malcolm McKenna, Department of Vertebrate Paleontology, AMNH, whose advice and assistance over the years are greatly appreciated.

DISCUSSION: This genus was created to accommodate *K. harrisae*, new species. The genus *Kennacryphaeus* is sister to the genus *Kayserops* Delo, 1935. *Kennacryphaeus harrisae* could have been lumped with *Kayserops*, but this would have required substantial modification of the diagnosis of *Kayserops*. Instead, a new monotypic genus is erected.

Kennacryphaeus harrisae, new species

Figures 8.5, 8.7, 27

Greenops (*Greenops*) *boothi* (Green). Eldredge, 1971a: 54, text fig. 1.

TYPES: Holotype AMNH 45298, a cephalon from the Mottville Member (Cazeonovian), Skaneateles Formation, Pratt's Falls, 2.4 miles northwest of Pompey Center, New York. Paratypes AMNH 45302, a pygidium from the Mottville Member, road cut on U.S.

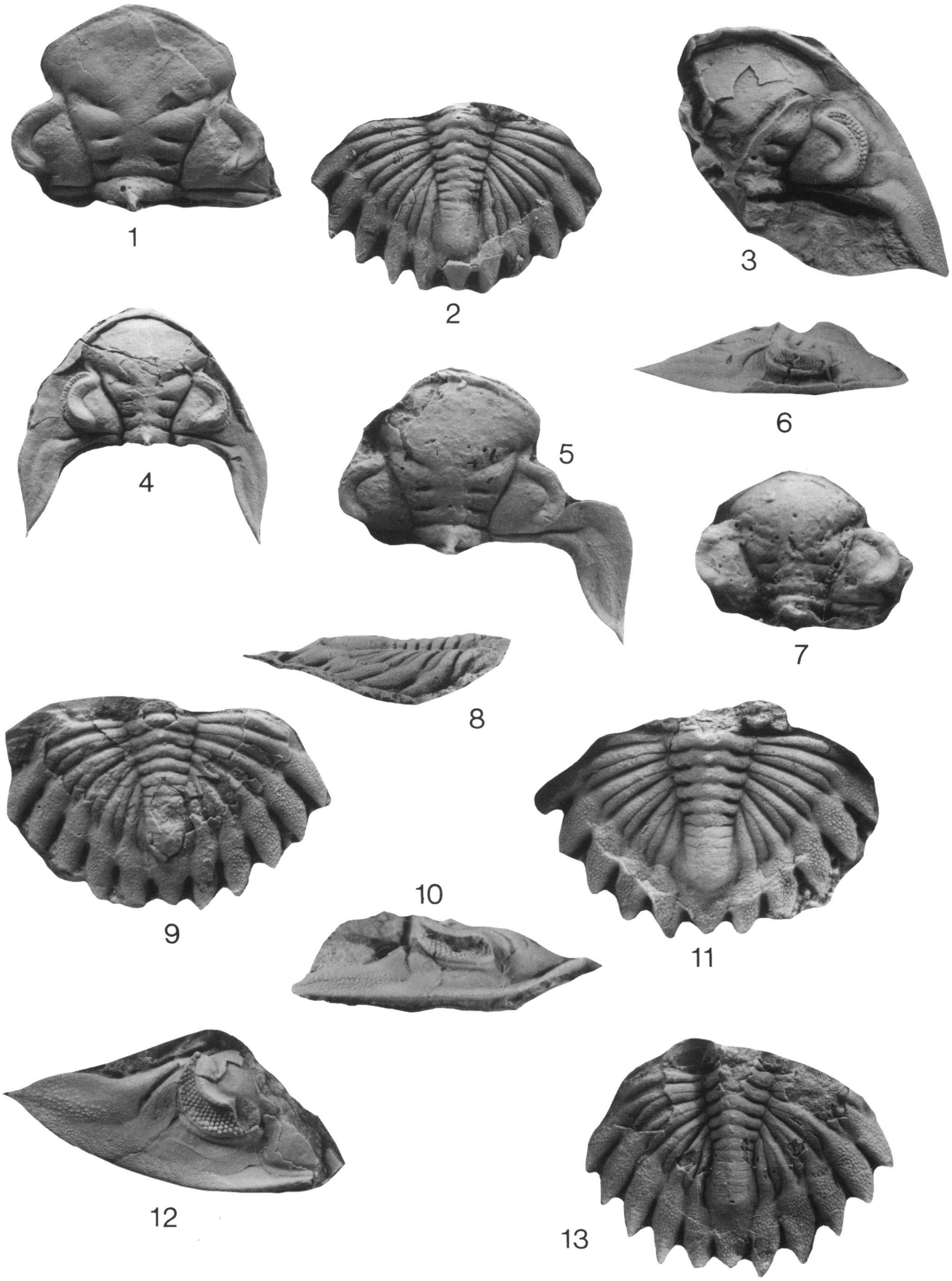

Fig. 27. *Kennacryphaeus harrisae*, new species, Mottville Member, Skaneateles Formation, New York. **1**. Pratt's Falls, 2.4 miles northwest of Pompey Center, AMNH 45304, dorsal view of cranidium, ×2.1. **2**. U.S. Route 20, road cut just west of Pompey Center, AMNH 45302, dorsal view of paratype pygidium, ×2.3 **3, 10**. Pratt's Falls, 2.4 miles northwest of Pompey Center, AMNH 45300, dorsal and lateral views of partial cephalon, ×2.5. **4, 6**. Pratt's Falls, 2.4 miles northwest of Pompey Center, AMNH 45298, dorsal and lateral views of holotype cephalon, ×2. **5**. Pratt's Falls, 2.4 miles northwest of Pompey Center, AMNH 45301, dorsal view of partial cephalon, ×2.2. **7**. Pratt's Falls, 2.4 miles northwest of

Route 20, just west of Pompey Center, New York; AMNH 45297, a pygidium from the same locality as the holotype; and AMNH 45299, a pygidium from the same locality as the holotype.

DIAGNOSIS: Same as for genus.

ETYMOLOGY: Named for Ms. Meg Harris, who contributed some of the specimens used to diagnose this species.

MATERIAL: AMNH 29006, 45248, 45297–45306.

DESCRIPTION: Cephalic length (sag.) 55% of width (tr.). Axial furrow nearly straight anterior to S1, diverging forward at about 30°, narrow, shallow. Cranidial anterior border short exsagittally and medially, lying in constant dorsoventral plane, rounded medially in dorsal view. Preglabellar furrow moderately incised and narrow. Cranidial anterior border lengthens slightly medially, developed as narrow lip. Facial suture anterior to eyes flexes laterally then medially with smooth convex margin laterally. Posterior branch of facial suture flexes weakly anteriorly, then posteriorly laterally. Glabellar length equal to width across frontal lobe; frontal lobe ellipsoidal, about 50% of length of glabella; L1-L3 flat; frontal lobe with same elevation as posterior glabellar region; anterior part of frontal lobe moderately declined forward, smoothly rounded in dorsal view. PMI developed as rounded depression. S3 moderately incised, straight, anterolateral edge flexes posteriorly, branches diverging at about 140°. Sagittal region of L2 and L3 nearly flat (tr.), lateral lobes weakly declined abaxially. L3 wedge shaped, lengthening distally, outer edge posteriorly flexes laterally, anterior end flexing less strongly laterally. S2 weakly declined posteriorly at lateral edge, moderately incised, shallow adjacent to axial furrow. S1 deep, crescent shaped, medial portion developed as smooth curve convex posteriorly, contacting axial furrow. L1 short, flexed forward strongly medially and weakly abaxially, depressed only slightly below L2 laterally. S0 of nearly uniform length, convex anteriorly at medial portion in dorsal view, moderately incised. L0 45% of width (tr.) of frontal lobe, moderately arched (tr.), longest sagittally medially, bearing spine. Large Eye Index 0.45. Anterior edge of eye adjacent to axial furrow opposite anterodistal corner of L3; posterior edge of eye opposite L1, posterior to transverse line tangent to anterior edge of L0; eye raised above frontal lobe. Fixigena evenly sloping from axial furrow to palpebrum. Postocular fixigenal field 15% of length (sag.) of eye. Librigenal field moderately declined to lateral border furrow. Posterior border furrow nearly transverse medially, laterally flexing anteriorly, anterior margin nearly straight, shallow distally. Cephalic lateral border furrow bisects genal spine; medially genal spine flattened ledge, laterally evenly inclined; medial edge thickened; lateral margin of genal spine at posterior end straight; interior margin of genal spine parallels lateral margin before deflecting laterally. Lateral border furrow narrow, shallow. Anterior margin of cephalic doublure rounded. Prosopon of fine tubercles.

Thorax not known.

Pygidium broadly triangular in outline excluding marginal lappet. Length (sag.) about 60% of width (tr.) excluding lappets, with five pairs of pleural lappets. Axial furrows shallow, narrow, converging at 20° anterior to fifth pygidial axial ring, roughly parallel posterior to fifth pygidial axial ring. Anterior margins of pygidial axial rings posterior to constriction of pygidial axis straight, anterior to constriction laterally straight, medially arched anteriorly. Axis 35% of pygidial width (tr.) anteriorly, with 14 rings. Terminal pygidial lappet blunt triangle, narrow, does not project as far posteriorly as other lappets; postaxial region 20% of pygidial length

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Pompey Center, AMNH 45305, dorsal view of small cranidium, ×5. **8, 9**. Pratt's Falls, 2.4 miles northwest of Pompey Center, AMNH 45297, lateral and dorsal view of paratype pygidium, ×2.5. **11**. U.S. Route 20, road cut just west of Pompey Center, AMNH 45306, dorsal view of pygidium, ×2.6. **12**. Pratt's Falls, 2.4 miles northwest of Pompey Center, AMNH 45303, lateral view of partial cephalon, ×2.6. **13**. Pratt's Falls, 2.4 miles northwest of Pompey, AMNH 45299, dorsal view of paratype pygidium, ×2.5.

(sag.). Lateral margins of pygidial lappets curved, medial margins straight, distal tips pointed. Tops of pygidial pleural segments rounded. Pleural furrows moderately incised, short (exsag.), laterally flex more strongly posteriorly.

DISCUSSION: This species comes from the following localities in the Cazenovian (Givetian) of the Appalachian Basin, ENA: Mottville Member (Cazenovian), Skaneateles Formation, road cut, Route 20, west of Pompey Center, New York; Mottville Member, Pratt's Falls, New York; ?Mottville Member, Fitch Road, New York; Stafford Limestone, Skaneateles Formation, road cut, Route 488, north of the bridge that crosses Flint Creek, Phelps, New York.

Eldredge (1971a) originally treated this species as identical to *Greenops boothi*. However, the two taxa can be distinguished in the condition of several characters, including the following: in *G. boothi* the interior margin of the genal spine is evenly deflected laterally all the way back, whereas in *K. harrisae* the interior margin parallels the lateral margin before deflecting laterally; in *G. boothi* there is a maximum of six lenses per dorsoventral file on the visual surface, whereas in *K. harrisae* there is a maximum of eight lenses; in *G. boothi* the distance between the frontal lobe and the facial suture at the midline relative to laterally increases slightly, whereas in *K. harrisae* it is constant; in *G. boothi* there is a single tubercle on L0, whereas in *K. harrisae* there is a spine; in *G. boothi* a plane from the medial to the lateral edges of the genal spine is evenly inclined, whereas in *K. harrisae* medially the genal spine is developed as a flattened ledge; in *G. boothi* the medial edge of the genal spine is not significantly thickened relative to the lateral edge, whereas in *K. harrisae* the medial edge is significantly thickened relative to the lateral edge; in *G. boothi* the axial furrows anterior to S1 deflect more strongly laterally relative to the furrows posterior to S1, whereas in *K. harrisae* they are equally divergent anterior and posterior to S1; in *G. boothi* the anterior margins of the pygidial axial rings posterior to the constriction of the pygidial axis are smoothly convex anteriorly, whereas in *K. harrisae* they are straight; in *G. boothi* the tops of the pygidial pleural segments are flat, whereas in *K. harrisae* they are rounded; in *G. boothi* there are 11 pygidial axial rings, whereas in *K. harrisae* there are 14 pygidial axial rings; in *G. boothi* the terminal pygidial lappet is subrectangular anteriorly and convex posteriorly, whereas in *K. harrisae* it is a bluntly pointed triangle; and in *G. boothi* the longest pygidial lappet is relatively long (exsag.), whereas in *K. harrisae* it is relatively short, equal to the length (sag.) of the first two pygidial axial rings.

Kennacryphaeus harrisae is the only species of asteropyginine described from the Skaneateles Formation (Cazenovian) of the Hamilton Group of the Appalachian Basin, and it appears to be restricted to the lower part of this formation.

Kennacryphaeus harrisae does show similarity with *Bellacartwrightia phyllocaudata*. In particular, they both have: the medial portion of the genal spine significantly thickened relative to the lateral edge; the interior margin of the genal spine more strongly deflected laterally posteriorly; the medial portion of S1 developed as a smooth curve convex posteriorly; the frontal lobe smoothly rounded in dorsal view; the distance between the frontal lobe and facial suture at the midline relative to laterally constant; a spine on the medial portion of L0; the shape of the terminal pygidial lappet triangular, and not projecting as far as the other lappets; the medial margins of the pygidial lappet straight; the tops of the pygidial pleural segments rounded; and laterally the pygidial interpleural furrows flexing more strongly posteriorly. However, these two taxa differ in the condition of several characters. In particular, in *K. harrisae* S3 is straight with the anterolateral edge transverse, whereas in *B. phyllocaudata* S3 is sinusoidal; in *K. harrisae* S2 is weakly declined posteriorly at its lateral edge, whereas in *B. phyllocaudata* S2 is roughly transverse; in *K. harrisae* the posterior edge of the visual surfaces is posterior to a transverse line tangent to the anterior edge of L0, whereas in *B. phyllocaudata* it is anterior to such a line; in *K. harrisae* there are a maximum of eight lenses per dorsoventral file on the visual surfaces, whereas in *B. phyllocaudata* there are a maximum of nine lenses; in *K. harrisae* the anterior cephalic border is rounded in dorsal view, whereas in *B. phyllocaudata* it is pointed; in *K. harrisae* the anterior cephalic border medially is not deflected far laterally beyond the lateral margins of the glabella, whereas in *B. phyllocaudata* it is deflected far anteriorly; in *K. harrisae* a line from the posterior to the anterior edge of the eye forms an angle to a sagittal line that is approximately 30°, whereas in *B. phyllocaudata* the angle is approximately 5°; in *K. harrisae* medially the genal spine is a flattened ledge, whereas in *B. phyllocaudata* a plane from the medial to the lateral edges of the genal spine is evenly inclined; in *K. harrisae* the interior margin of the genal spine parallels the lateral margin before deflecting laterally, whereas in *B. phyllocaudata* it just deflects laterally; in *K. harrisae* the axial furrows anterior to S1 relative to posterior to S1 diverge at the same angle, whereas in *B. phyllocaudata* they diverge more strongly; in *K. harrisae* the axial furrows at the anterior half of L3 relative to the posterior half of L3 are equally divergent, whereas in *B. phyllocaudata* the axial furrows are less strongly divergent at the anterior half of L3; in *K. harrisae* there are tubercles on the medial portions of the pygidial and thoracic axial rings, whereas in *B. phyllocaudata* there are spines; in *K. harrisae* the anterior margins of the pygidial axial rings posterior to the constriction of the pygidial axis are straight, whereas in *B. phyllocaudata* they are smoothly convex anteriorly; in *K. harrisae* the pygidial axis constricts posterior to the fifth axial ring, whereas in *B. phyllocaudata* it constricts posterior to the sixth ring; in *K. harrisae* the pygidial pleural field flanking the posterior portion of the pygidial axis is faintly excavated, whereas in *B. phyllocaudata* it is prominently excavated; in *K. harrisae* the pygidial pleural furrows are moderately incised and medially short (exsag.), whereas in *B. phyllocaudata* they are relatively long (exsag.); in *K. harrisae* in the medial region of adjacent pleural segments, the posterior region of the anterior segment is equal in length (exsag.) to the anterior part of the posterior segment, whereas in *B. phyllocaudata* the posterior region is longer (exsag.); in *K. harrisae* there are 14 pygidial axial rings, in *B. phyllocaudata* there are 15 or 16; in *K. harrisae* the terminal pygidial lappet is a blunt triangle, whereas in *B. phyllocaudata* it is a sharp triangle; in *K. harrisae* the terminal pygidial lappet is relatively narrow, whereas in *B. phyllocaudata* it is relatively broad; and in *K. harrisae* the longest pygidial lappet is short, with its length (exsag.) equal to the length (sag.) of the first two pygidial axial rings, whereas in *B. phyllocaudata* it is long (exsag.), with the length equal to the length (sag.) of the first three pygidial axial rings.

Thus, although there are a fair number of character states that *K. harrisae* and *B. phyllocaudata* share, there are also many in which they differ. Phylogenetic analysis indicates that it is more parsimonious to view the characters they differ in as being shared with other taxa than it is to view the characters they share as synapomorphies, and according to the cladogram in figure 4 they are distantly related. Thus, their shared features must be viewed as either plesiomorphy or homoplasy. However, it is important to point out that these taxa may converge on each other in certain aspects of their morphology.

KAYSEROPS DELO, 1935

TYPE SPECIES: *Cryphaeus kochi* Kayser, 1883.

ASSIGNED TAXA: *Kayserops inflatus* Morzadec, 1983, *Kayserops*, new species, aff. *inflatus* Morzadec, 1983, *Greenops traversensis* Stumm, 1953, and ?*Cryphaeus kerfornei* Pichard, 1930.

DIAGNOSIS: S3 convex anteriorly; L2 and L3 prominently inflated; isolated patches of tubercles present on L3; eyes substantially elevated above glabella; line from posterior to anterior edge of eye forms 30° angle with sagittal line; anterior cephalic border does not deflect far beyond lateral margins of frontal glabellar lobe; S1 crescent shaped, medially developed as smooth curve convex posteriorly; anterior margin of frontal glabellar lobe smoothly rounded in dorsal view; distance between frontal lobe and facial suture increases slightly from lateral margins to midline; anterior cephalic border pointed medially; PMI absent; fixigena evenly sloping from axial furrow to palpebrum; posterior margin of palpebrum relative to anterior margin deflected at angle to transverse line that is roughly equivalent; demarcation between librigena and lateral border furrow weak; tubercle on L0; medial edge of genal spine significantly thickened relative to lateral edge; plane from medial to lateral edges of genal spine evenly inclined; lateral margin of genal spine parallels sagittal line; axial furrows less strongly divergent at anterior half of L3 than at posterior half; interior margin of genal spine parallels lateral margin before deflecting laterally; medial tubercles on pygidial and thoracic axial rings present; posterior part of pygidial pleural segment elevated above anterior part; tops of pygidial pleural segments rounded; terminal pygidial lappet narrow, triangular; pygidial lappets flanking terminal lappet project further posteriorly than terminal lappet; distal tips of lappets pointed; anterior margins of pygidial axial rings posterior to fifth ring smoothly convex anteriorly; pygidial axis constricts posterior to fifth axial ring; pygidial pleural furrows moderately incised, short (exsag.); anterolateral margins of first five pygidial axial rings do not arch strongly anteriorly; pygidial lappets long (exsag.); five pairs of pygidial pleural lappets present.

DISCUSSION: The species in this genus are known from the upper Emsian of Germany and the Armorican Massif, and from the Givetian of the Michigan Basin of ENA. When first erected by Delo (1935), this genus was thought to consist of a single species. However, it now appears that additional taxa can be assigned to *Kayserops*. These are figured in Morzadec (1983) and Stumm (1953). There exist several additional taxa that Gandl (1972), Arbizu (1979), and Smeenk (1983) assigned to *Kayserops* but that can no longer be retained within that genus. These taxa are separated by several nodes on the cladogram in figure 4 from those taxa treated as *Kayserops* herein on the basis of phylogenetic and morphological evidence, and they are discussed above under the headings of the genera *Bradocryphaeus* Haas and Mensink, 1969, *Hallandclarkeops*, new genus, and *Braunops*, new genus.

A slightly emended diagnosis is presented to that of Delo (1935) and Struve (1959), as phylogenetic analysis indicated that a few species could be assigned to *Kayserops*. These taxa could have been assigned to separate genera, but instead they were treated as belonging to a single genus. Some of the species that have been assigned to *Kayserops* herein were not subjected to phylogenetic analysis. One of these species, *K. kerfornei* (Pichard), appears to be very similar morphologically to *K. inflatus*. However, they do differ by the former's possession of a very long spine on the medial portion of the anterior cephalic border. *Kayserops kerfornei* also may lack the tubercle on L0, a diagnostic feature of the genus (the occipital ring of this taxon was too poorly preserved to ascertain this for sure). This species also lacks another character treated as diagnostic for *Kayserops*, the presence of a tubercle on the medial region of the thoracic and pygidial axial rings. Thus, the taxon appears to differ in characters diagnostic for the genus as presented here. However, it is conceivable that phylogenetic analysis would show this species as sister to the rest of *Kayserops*, and therefore it would be reasonable to place the species within an emended *Kayserops*. This could only be done if this taxon were incorporated into the phylogenetic analysis. This was not done herein, and thus it is only possible to questionably place this species within *Kayserops* and point out the characters in which it may depart from the rest of the genus.

Unfortunately, the type of the genus, *K. kochi*, also was not available for study. However, on the basis of figures and diagnoses, it appears to be very similar to *K. inflatus*, and it seems reasonable to use the phylogenetic position of the latter to anchor the phylogenetic topology of the genus *Kayserops*. It would be unlikely, but not impossible, that analysis of this species instead of, or in addition to, *K. inflatus* might change the topological position of the genus *Kayserops*. Such analysis was not possible at this time but will be pursued at a later date.

On the basis of the phylogenetic analysis conducted herein, *Kayserops* appears to be part of a large clade that includes exponents originally assigned to *Greenops*, as well as some new taxa, and this clade is in turn sister to *Greenops*. Several authors have commented on the phylogenetic relationships of this genus. Some of their conclusions differ from those promulgated herein, as their conceptions of the genus *Kayserops* do not coincide with that developed here using cladistic evidence. Haas (1970) claimed that *Kayserops* was a subgenus of *Comura* and was either derived from a paraphyletic *Comura* (*Comura*) or part of a basal polytomy along with all the subgenera in *Comura* (see fig. 5A). *Comura* was not treated as paraphyletic herein, nor for that matter were any of the other genera of the Asteropyginae. In addition, species of *Comura* were not subjected to phylogenetic analysis herein, making the issue of paraphyly of *Comura* impossible to test. The cladogram in figure 4 shows that *Kayserops* is distantly related to *Tolkienia*, a close relative of *Comura*, and Haas's (1970) phylogenetic topology does not appear to be upheld in the case of *Kayserops*. Gandl (1972) suggested that *Kayserops* was closely related to the genera *Neometacanthus* and *Paracryphaeus* (see fig. 5B). This contention is not supported by the analysis conducted herein, though it must be stated that Gandl's (1972) concept of *Kayserops* corresponds to the genus *Braunops* herein. However, some of the members of the large clade that includes *Kayserops*, such as *Stummiana osismorum* (Morzadec) and *S. arkonensis* (Stumm), as well as *Deloops haasi* (Morzadec), had traditionally been assigned to the genus *Greenops*, which had been treated, incorrectly, as closely related to *Neometacanthus* by some authors. Arbizu (1979) suggested that *Kayserops* was derived from a paraphyletic *Pseudocryphaeus* and was relatively closely related to *Greenops* and *Neometacanthus* (see fig. 5C), and Morzadec (1983) essentially advocated the same phylogenetic placement of *Kayserops* (see fig. 5E). The relatively close relationship between *Kayserops* and *Greenops* predicted by these authors appears to be supported. Smeenk (1983) suggested that *Kayserops* was derived from a paraphyletic *Paracryphaeus* (see fig. 5D). This does not appear to be supported. However, Smeenk's (1983) conception of *Kayserops* corresponds to what is treated herein as *Braunops*.

This genus is known from the upper Emsian of Armorica and the Givetian of ENA.

Kayserops inflatus Morzadec, 1983

Kayserops inflatus Morzadec, 1983: 127, pl. 14, figs. 1–8, pl. 15, figs. 1–4, 6.

TYPES: Holotype defined in Morzadec (1983: pl. 15, fig. 1).

DIAGNOSIS: S3 convex anteriorly; PMI not visible; line from posterior to anterior edge of eye forms 30° angle to sagittal line; prosopon of fine granules; isolated coarse tubercles present on L3 and palpebrum; librigena not visible in dorsal view between lateral margin of eye and lateral border furrow; broad ledge of anterior cephalic border not visible anterior to anterolateral portions of frontal lobe; maximum of eight lenses per dorsoventral file on visual surface; lateral to eye, facial suture before flexing posteriorly flexes anteriorly to point opposite S1; tubercle on L0 present; L3 distinctly swollen; genal spine evenly inclined from medial to lateral edge; lateral margin of genal spine at posterior end straight; medial margins of pygidial pleural lappets curving laterally; distal tips of pygidial lappets pointed; tops of pygidial pleural segments rounded; posterior part of pygidial pleural segments elevated above anterior part; terminal pygidial lappet triangular and narrow; at pygidial margins surface of pygidium dorsally inflates at contact of lappets and margins; 13 pygidial axial rings.

DISCUSSION: This species is known from the upper Emsian of the Armorican Massif. One of the pygidia that Morzadec (1983: pl. 15, fig. 5) figured appears to differ from the other pygidia of *K. inflatus* in a few features. These taxa possess two fewer pygidial axial rings, have broader pygidial lappets, and have the pygidial interpleural furrows deflected less strongly posteriorly laterally. As all the other pygidia Morzadec (1983) figured are identical, and these are the more abundant, these were used to code *K. inflatus* for character analysis. The pygidium in Morzadec (1983: pl. 15, fig. 5) appears similar to pygidia typical of *K. inflatus* in several other respects, and it is treated as *Kayserops* new species aff. *inflatus* Morzadec. *Kayserops inflatus* is also probably closely related to *K. kerfornei* (Pichard, 1930). Morzadec (1983) suggested that *K. inflatus* is also closely related to Gandl's (1972) "*Kayserops*" new species N. This species appears to lack several of the characters diagnostic of *Kayserops* and cannot be considered to be closely related to that genus. It may belong to *Philip-*

smithiana, new genus. The relationships of Gandl's (1972) species were not considered further at this time.

The illustrations in Morzadec (1983), particularly plate 14, figure 4a, suggest that circular fenestrae on the thoracic pleural segments are present in this taxon, and thus this species was coded as having these structures. However, until the actual specimens can be obtained, this cannot be determined with certainty.

Kayserops traversensis (Stumm, 1953)

Figure 12.5

Greenops traversensis Stumm, 1953: 132, pl. 8, figs. 1–4.
Greenops alpenensis Stumm, 1953: 133, pl. 7, fig. 7.
Greenops aequituberculatus Stumm, 1953: 131, pl. 7, fig. 4, pl. 8, fig. 5.

TYPES: Holotype an external mold of cephalothorax, USNM 117871, from the Traverse Group, Gravel Point Formation, upper blue shale, abandoned "Bell" quarry and ledges on shore about 2 miles east of Bay Shore, Emmet County, Michigan, designated by Stumm (1953: pl. 8, figs. 1, 3, 4). Paratype an external mold of pygidium, UMMP 28668, upper Gravel Point Formation, Emmet County, Michigan.

DIAGNOSIS: S3 convex anteriorly; S2 weakly declined posteriorly at lateral edge; tubercle present on L0; PMI absent; line from posterior to anterior edge of eye forms an angle to sagittal line that is approximately 30°; prosopon of coarse tubercles; genal spine evenly inclined laterally; cephalic axial furrows diverge at same angle anterior and posterior to S1; maximum of seven lenses per dorsoventral file on visual surface; broad ledge of anterior cephalic border absent anterior to anterolateral edges of glabella; one transverse row of circular fenestrae on anterior and posterior bands of thoracic pleural segments; circular fenestrae present at lateral margins of thoracic axial rings, and scattered about medial part of thoracic axial rings; lateral margins of pygidial lappets curved; distal tips of lappets pointed; pygidial pleural field flanking posterior part of axis moderately excavated; posterior part of pygidial pleural segment elevated above anterior part; tops of pygidial pleural segments rounded; in medial region of adjacent pleural segments posterior region of anterior segment longer (exsag.) than anterior part of posterior segment; terminal pygidial lappet blunt triangle, narrow anteriorly; 14 pygidial axial rings.

MATERIAL: AMNH 45250.

DISCUSSION: This species is known from the following stratigraphic horizons and localities in ENA from the Middle Devonian Traverse Group of the Michigan Basin: the Gravel Point Formation (uppermost Cazenovian), upper blue shale, zone 6, abandoned "Bell" quarry and ledges on shore about 2 miles east of Bay Shore, Emmet County, Michigan; the Dock Street Clay (lowermost Tioughniogan), abandoned quarry of the Thunder Bay Limestone Company, eastern edge of Alpena, Alpena County, Michigan; the Norway Point Formation (Tioughniogan), shale bank on south side of Thunder Bay River on Potter Farm about 1 mile below Four Mile Dam, Alpena County, Michigan; and the Thunder Bay Limestone (Taghanic), bluffs on northeastern shore of Partridge Point, 4 miles south of Alpena, Alpena County, Michigan. Thus, in terms of New Yorkian stages, it ranges from the latest Cazenovian into the Taghanic.

Stumm (1953) appears to have parsed a single species into three separate species: his *Greenops aequituberculatus*, *G. traversensis*, and *G. alpenensis*. The holotypes of *G. aequituberculatus*, *G. alpenensis*, and *G. traversensis*, all cephala, are identical and they are treated as conspecific. However, the single glabella and two pygidia that Stumm (1953) illustrated as paratypes of *G. aequituberculatus* are referable to *G. arkonensis* Stumm, 1953, and are discussed in greater detail above under the heading of that species. Stumm (1953) illustrated only two specimens of *G. alpenensis*, a cephalon and pygidium. The pygidium (Stumm, 1953: pl. 7, fig. 8), a paratype, differs significantly from all other asteropyginines except for ?*Greenops comis* (Hall and Clarke, 1888), which is known from a single pygidium found in the Onondaga Limestone of Ontario, and it is treated as closely related if not conspecific with that species. Both species share the small, triangular, postaxial process, as well as the relatively short (exsag.) pygidial pleural lappets, the narrow, convex overall form of the pygidium, and the pygidial axis with approximately 11 axial rings. However, at this time no generic appellation can be given to this species because of the many autapomorphies it bears, as well as the absence of a thorax and cephalon. It is clear that it should not be assigned to *Greenops* because it lacks most of the diagnostic pygidial characters of that genus. It is possible that Stumm's (1953: pl. 7, fig. 8) pygidium belongs to the same species as the cephalon of *G. alpenensis*, but this does not appear likely on the basis of the following logic. Although Stumm (1953) claimed that his *G. alpenensis* and *G. traversensis* differed in the condition of the shape of the tubercles present on the head shield, the tubercles appear identical, and any dissimilarities probably can be accounted for by differences in preservation, as these different cephala are known from rocks with different lithologies. Moreover, they match each other in all features of preserved cephalic morphology. In addition, the holotype of what was referred to as *G. traversensis* also preserves a thorax that bears a prominent medial tubercle on each of the axial rings. In all asteropyginine taxa with medial tubercles on the thoracic axial rings, these are repeated in a serially homologous fashion on the pygidial axial rings. In Stumm's (1953: pl. 8, fig. 3) paratype pygidium of *G. traversensis*, such medial tubercles are present, whereas they are not developed on the paratype pygidium of *G. alpenensis* that closely resembles ?*Greenops comis*. Thus, it seems likely that the specimens that Stumm (1953) illustrated and designated holotypes and paratypes of *G. traversensis* all belong to the same species.

As mentioned above, the holotype cephalon of *G. alpenensis* is identical with the holotype cephalon of *G. traversensis*. Because the types of *G. traversensis* represent a homogeneous series whereas those of *G. alpenensis* do not, the latter species is considered no longer valid, and the pygidium is assigned to ?*G.* sp. aff. *comis*, while the cephalon is treated as identical with *traversensis*, which is treated herein as a species of the genus *Kayserops*. The species *Greenops aequituberculatus* Stumm, 1953, was discussed in detail above under the heading of *Greenops arkonensis* Stumm, 1953, and it is no longer considered a valid species. Most of the specimens of *G. aequituberculatus* appear referable to *G. arkonensis*; however, one, the glabella, which was a paratype, UMMP 25438, is identical with the glabella of the holotype specimen of *Kayserops traversensis*, and the two should be treated as conspecific.

MORPHOLOGICAL THEMES IN THE EVOLUTION OF THE ASTEROPYGINAE

On the basis of evidence presented by Edgecombe (1993), the Acastidae Delo, 1935, which includes the Acastinae Delo, 1935, the "Acastavinae" Struve, 1958a, and the Asteropyginae Delo, 1935, is sister to the Calmoniidae Delo, 1935. Several authors have discussed the diversification of the calmoniids as an important example of an adaptive radiation (e.g., Eldredge and Cracraft, 1980; Fortey and Owens, 1990), although the adaptive character of at least part of the calmoniid radiation has been called into question by some (e.g., Lieberman, 1993). Still, it is clear that a substantial taxic proliferation occurred in the diversification of the calmoniids. In one of the clades nested within the Calmoniidae, the "*Metacryphaeus* group," most of the morphological differences between taxa are associated with variation in characters of the glabella, such as its furrows and overall shape. As argued cogently by Eldredge (1971a), these morphological features seem to govern food gathering and processing. Thus, any changes in these features through phylogenetic time may indicate changes in mode of feeding. Therefore, the taxic proliferation that occurred in the "*Metacryphaeus* group" appears to involve a proliferation of feeding or digestive modes.

Although not typically characterized as an adaptive radiation, the asteropyginines are clearly a diverse group of Devonian trilobites, and in their evolution there is a clear predilection toward differentiation in certain characters or character complexes. In particular, in the asteropyginines the greatest variation is found in characters of the pygidium, such as the shape of the lappets and the axial terminus, in the shape and size of the genal spine, and in the array of fenestrae and furrows on the thoracopygidium. These consistently important character complexes, in terms of their utility for providing resolution in phylogenetic analysis, may indicate the possibility that changes in modes of sediment stabilization and burrowing frequently occurred in the Asteropyginae. Whether or not these character differences involve adaptive diversification is another question that would require functional analysis as well as statistical tests, phylogenetic tests, and assumptions about character optimization, and the answers to such questions are not considered herein. However, the consistent manifestation of differences in these particular character complexes in the Asteropyginae is worthy of mention.

BIOGEOGRAPHIC PATTERNS AND THE APPEARANCE OF THE ASTEROPYGINAE IN EASTERN NORTH AMERICA

As mentioned in the introduction, one of the reasons for studying the phylogeny of the Asteropyginae was to assess how many times the subfamily had invaded ENA. We also wished to pinpoint where these invasions came from, and to deduce whether any invasion of lineages occurred from ENA into other biogeographic regions. Biogeographic patterns in the Asteropyginae can be deduced in a preliminary way by using parsimony algorithms to optimize biogeographic states to ancestral nodes on the phylogeny of the Asteropyginae. With this information, we can witness transformations between biogeographic areas and deduce the number of times that ENA was invaded from a primitively Armorican lineage. Armorica is treated as comprising Spain, the Massif Armorican, Germany, and northern Africa, as well as Afghanistan and Turkey. Eastern North America and northern Gondwanaland (Venezuela) were also treated as separate biogeographic areas. Taking the phylogeny of the Asteropyginae given in figure 4, the biogeographic state of each terminal taxon is mapped onto the tree, with a "0" for Armorica, a "1" for ENA, and a "2" for northern Gondwanaland. Fitch optimization (Fitch, 1971) was used to ascertain the biogeographic states of ancestral nodes on the phylogeny in figure 4. The optimizations, as well as the states of the terminal taxa, are shown in figure 28. These results indicate that there may have been four invasions by the Asteropyginae from Armorica into ENA. In some ways this is not surprising, because the asteropyginines in ENA do not comprise a single monophyletic clade, but it points out how there were major shifts in biogeographic areas occupied by the subfamily, as well as an asymmetrical transformation vector leading from Armorica to ENA.

It is instructive to consider which lineages mark the biogeographically invasive lineages and, in addition, using phylogenetic information in conjunction with information about the first appearance of species in the fossil record, it is possible to put some temporal bounds on when these different invasions occurred. This method follows the ghost-lineage method utilized by Edgecombe (1992). One of the invasions marks the establishment of the genus *Bellacartwrightia* in ENA; using the ghost-lineage method, this invasion must have occurred by the Eifelian. Species in this genus first appear in the Eifelian Onondaga Limestone, so there is good congruence between the predicted and actual stratigraphic patterns. Another of these invasions marks the establishment of the genus *Greenops* in ENA (in this analysis, unlike others, we conclude that *Greenops* is restricted to ENA). According to the ghost-lineage method, based on phylogenetic patterns, this invasion occurred some time between the upper Emsian and the Givetian. Members of this genus actually first appear in the Givetian portion of the Hamilton Group. Thus, there is a gap in the record between the predicted and the actual time of invasion. An-

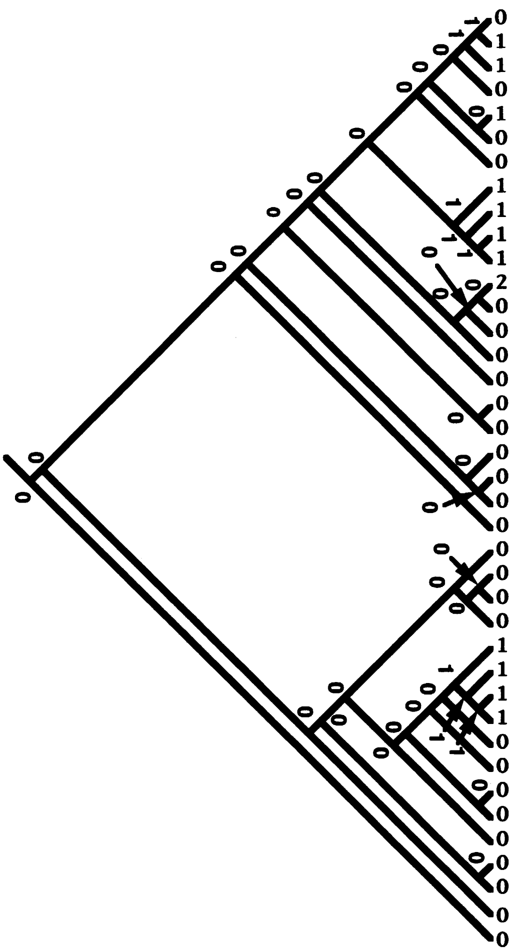

Fig. 28. The mapping of biogeographic states of taxa onto the single most parsimonious tree shown in figure 4. Nodes were optimized using Fitch's (1971) algorithm. "0" indicates presence in Armorica, "1" in Eastern North America, and "2" in northern Gondwanaland.

other of the invasions marks the appearance of *Kennacryphaeus harrisae* and *Kayserops traversensis* in ENA, and the ghost-lineage method indicates that this invasion must have occurred by the Upper Emsian. However, the genus *Kennacryphaeus* does not appear in the fossil record until the latest Eifelian or earliest Givetian. Thus, again there appears to be a significant gap in the history of this genus between the time it invaded from Armorica, based on stratigraphic evidence, and the time it actually appeared. The final invasion marks the appearance of *Stummiana arkonensis* in ENA, and it occurred during the Givetian, based on phylogenetic topology. This species first appears in the Givetian Traverse Group, and thus it shows close congruence between predicted and actual first occurrence.

The results from this analysis indicate that the timing of invasive events is spread out over the interval from the upper Emsian to the Givetian. Thus, the invasions cannot be consigned to one unique biogeographic event, such as the initiation of the Acadian Orogeny. Instead, the invasions span an interval including both the initial development of the Acadian Orogeny (in the upper Emsian) and the reintensification of that orogeny (in the late Eifelian) (timing of orogenic events from Ettensohn [1985]). This time interval also corresponds to an interval when there were multiple episodes of relative sea-level rise, probably related to the orogenic events (Johnson et al., 1985; Hallam, 1992). This pattern of multiple episodes of invasion within a clade spanning the upper Emsian to the Givetian corresponds to the pattern recognized to have occurred in the proetid trilobites by Lieberman (1994). In the proetids there were several invasions from different regions into ENA, and these invasions occurred at different times throughout the Lower and Middle Devonian and could not be consigned to a single eustatic or tectonic event. For further discussion of the driving forces behind these biogeographic changes, see Lieberman and Eldredge (1996).

In addition, it is likely that other invasions of asteropyginines may have occurred from Armorica into Laurentia. For instance, some species from the Givetian of the Illinois Basin may be referable to the genus *Neometacanthus*. Unfortunately, they were under study by another author and could not be incorporated into the phylogenetic analysis conducted herein. If they are actually species of *Neometacanthus*, it would imply at least one more instance of invasion from Armorica into ENA. Finally, Stumm's (1953) *Greenops* sp. A may constitute another invasion from Armorica into ENA. This species is probably referable to *Tolkienia*, new genus, and all other species in that genus are restricted to Armorica. Thus, there are at least four, and perhaps as many as six, invasions by independent asteropyginine lineages into ENA.

The results of this analysis also indicate that at least once an ENA lineage reinvaded Armorica. The latter conclusion matches that of Oliver (1977), who suggested that rugose coral lineages common to ENA had invaded Armorica during the Middle Devonian. The invasions by asteropyginines from ENA into Armorica must have occurred by the Upper Emsian, based on phylogenetic topology. Thus, there appears to be some asymmetry in the pattern of invasion between Armorica and ENA. Perhaps this is not surprising, as Armorican asteropyginine diversity is much greater than that of ENA, and the subfamily is primitively present within Armorica and primitively absent from ENA.

These conclusions about the timing of the invasion of Armorican lineages into ENA and the timing of reinvasion of ENA lineages back into Armorica are a bit troubling, for they suggest that a portion of the fossil record of the asteropyginines is obscured, as most members of the subfamily do not appear in ENA until the latest Eifelian or Givetian. It is possible that lineages persisted in other biogeographic regions for long periods of time without being preserved in the fossil record.

It is clear from phylogenetic analysis that many invasions of Armorican asteropyginine lineages into ENA occurred, but the exact timing of these invasions cannot always be exactly ascertained, although they were almost certainly between the upper Emsian and the Givetian. In addition, almost all of the other trilobites in the order Phacopida that occur in the Hamilton Group are forms that invaded from Armorica. This pattern of invasion by Hamilton Group trilobites from Armorica into ENA suggests that some of the taxa that populate faunas usually come from different biogeographic areas. In addition, the timing of these invasions was piecemeal, with different elements arriving at different times and certain lineages reinvading ancestral biogeographic regions. This suggests that faunas are often put together from immigrant lineages but, more importantly, it indicates faunas tend to be put together piecemeal contra the conclusions of Brett and Baird (1995).

For some other trilobite lineages that occur in the Hamilton Group, phylogenetic analyses have also been conducted, and these results further reiterate how transition times for invasions from Armorica into ENA show broad scatter. In particular, *Phacops* Delo, 1935, analyzed by Eldredge (1972) and Burton and Eldredge (1974), invaded ENA from Armorica around the Eifelian–Givetian transition, and the genus *Basidechenella* Kayser, 1880, analyzed by Lieberman (1994), may have invaded from Armorica into ENA in the Emsian. Thus, it is obvious that those trilobite taxa that appear in the Hamilton Group represent a series of invasions, some of which significantly predate the appearance of the first Hamilton Group sediments.

In summary, recruitment of the trilobite fauna of the Hamilton Group was piecemeal, with different taxa arriving from different regions at different times, counter the predictions of Brett and Baird (1995). This points out that faunal origination, at least in the case of the Hamilton Group, cannot be consigned to a single evolutionary event (Lieberman, 1994; Lieberman and Eldredge, 1996).

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