EVOLUTION OF THE TRILOBITE SUBFAMILY PROETINAE SALTER, 1864, AND THE ORIGIN, DIVERSIFICATION, EVOLUTIONARY AFFINITY, AND EXTINCTION OF THE MIDDLE DEVONIAN PROETID FAUNA OF EASTERN NORTH AMERICA

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ABSTRACT

This study considers the biogeographic origins, evolutionary affinities, and patterns of diversification and extinction in a portion of the Lower and Middle Devonian proetid trilobite fauna of Eastern North America. Four generic clades comprising about 45 species are known from the strata of the upper Emsian (Sawkillian) Bois Blanc Limestone and Schoharie Grit, the Eifelian (Southwoodian) Onondaga Limestone, and the Givetian (Cazenovian, Tioughniogan, Taghanic) Hamilton Group. These taxa have traditionally been assigned to the subfamilies Proetinae Salter, 1864, and/or Dechenellinae Pribyl, 1946. These are *Crassiproetus* Stumm, 1953a, *Basidechenella* Richter, 1912, *Dechenella* Kayser, 1880, and *Monodechenella* Stumm, 1953a, which were originally considered to be closely related. A higher-level phylogenetic analysis of the Proetinae is conducted to see if these taxa were indeed closely related and thus represent a single endemic radiation of species in Eastern North America or rather a series of independent lineages in that region. In the course of discerning characters that defined the Proetinae, it was discovered that *Monodechenella* lacks several of the characters that define the Proetinae, and the members of this genus therefore must be excluded from this subfamily. They instead appear to belong to a larger group informally referred to as the "*Thebanaspis* clade," which appears to be closely related to the Proetinae. A phylogenetic analysis is performed on proetine ingroup taxa using 21 taxa and 53 characters, and several of the major generic clades in the Proetinae are considered.

The phylogenetic analysis of the Proetinae is used to ascertain the ancestral biogeographic states for the three genera in the Proetinae that form an important component of the Lower and Middle Devonian trilobite fauna of Eastern North America. This information is used to determine if these taxa are ancestrally present in Eastern North America or rather represent a series of invasions from other biogeographic regions. Other taxa occurring in Eastern North America at this time appear to represent elements that invaded from Armorica. This invasion of taxa has been related to the collision between plates that produced the Acadian Orogeny during the Middle Devonian. Patterns in these proetid taxa are compared with those known for other groups to ascertain what control the Acadian Orogeny as a biogeographic event may have had on the appearance of these taxa in Eastern North America.

Phylogenetic analysis is then performed on all available species in each of these generic clades that occur in Eastern North America. Species that belong to these clades but which hail from other biogeographic regions are also considered. These phylogenies were used to assess macroevolutionary patterns such as diversification and extinction within each of these clades in Eastern North America. In addition to being an important paleogeographic event, the Acadian Orogeny also caused major paleoenvironmental changes. The impact of these changes on the proetid fauna of Eastern North America is assessed. It appears that a phenomenon analogous to Vrba's (1985, 1992) Turnover Pulse Hypothesis may have mediated elevated speciation rates in the proetid taxa over the period considered. However, eventually the profound changes in environment appear to have led to the extinction of much of the proetid trilobite fauna of Eastern North America.

Information on patterns of occurrence in different geographic regions is combined with information from the phylogenetic analyses of the individual generic clades to consider large-scale biogeographic patterns in the late Lower and Middle Devonian. A method for considering biogeographic patterns using cladistic information is developed. This method is based on Brooks Parsimony Analysis, but it allows multiple events of range expansion and subsequent vicariant splitting to occur within each generic clade. This biogeographic method was used to evaluate the relationships between the Arctic, Armorican, and Eastern North American paleobiogeographic regions. The relationships between the different major sedimentary basins in Eastern North America, the Appalachian, Illinois, and Michigan basins, are also considered.

Finally, the origin of major evolutionary faunas in the fossil record is discussed. Included is a brief discussion of a depauperate proetid fauna of the Emsian and Eifelian whose members do not belong to the four generic clades considered in detail.

In this work four new genera are recognized: *Plesiowensus*, *Arcticormistonia*, *Aayemenaytcheia*, and *Milesdavis*. In addition, 12 new species are described: *Arcticormistonia edgecombei*, *Crassiproetus halliturgidus*, *C. neoturgidus*, *C. stummi*, *C. schohariensis*, *Basidechenella cartwrightae*, *B. timwhitei*, *Dechenella perscheii*, *D. carvalhoae*, *Pedinodechenella modelli*, *Milesdavis eldredgei*, and *Monodechenella legrandsmithi*. Diagnoses and discussions for all of the taxa considered are presented.

INTRODUCTION

Proetides (sensu Fortey and Owens, 1975) represent the most persistent and long-ranging of the trilobite orders. They were first found in the earliest Ordovician (Tremadoc), but probably originated in the Middle Cambrian (based on an analysis of ghost lineages by Edgecombe [1992]), and they survived until the upper Permian. In the intervening periods they underwent several periods of diversification and extinction. One of the most taxonomically and morphologically diverse families in this order is the Proetidae Salter, 1864. This analysis considers the phylogenetic relationships within one of the subfamilies in this family, the Proetinae Salter, 1864. Several generic and tribal classifications exist for this subfamily, but none has been couched rigorously in terms of groups whose monophyly has been assessed by detailed character analysis. The analysis herein presents a phylogeny of most of the major Silurian and Devonian generic groups within this clade, particularly those bearing on the relationships of the proetids that are known from the Lower and Middle Devonian of Eastern North America. Fifty-three characters are employed in an analysis of 21 taxa. The monophyly of the Proetinae is supported by several distinct morphological traits. In addition, the recognition of some subfamilies within the Proetidae (e.g., Schizoproetinae Yolkin, 1968, Dechenellinae Pribyl, 1946, and Crassiproetinae Osmolska, 1970a) would make the Proetinae paraphyletic because these subfamilies represent only a partial list of the descendant forms assigned to the Proetinae. The recognition of some of these subfamilies would be permissible in a monophyletic classification, but only if several additional stem-group taxa are elevated to subfamilial status. This is not advocated at this time. In this section three new genera are recognized (*Plesiowensus*, *Arcticormistonia*, and *Aayemenaytcheia*) and two new species are described (*Arcticormistonia edgecombei* and *Dechenella perscheii*).

The phylogenetic relationships among the different genera within the Proetinae are stressed. Because of the existence of so many different classificatory schemes, proposing a new one herein would only serve to further cloud the waters. The main goal is to assess the evolution of the different "species groups" of Siluro-Devonian Proetinae, rather than to construct a classification. However, one set of genera within the Proetinae that is particularly plagued by polyphyletic or paraphyletic taxonomic appellations is addressed, and a monophyletic classification is advocated for it. The included genera—*Dechenella*, *Crassiproetus*, *Schizoproetus* and *Basidechenella*—are scrutinized herein, and recommendations for a revised generic classification of these taxa are presented. It is suggested that some of these generic names as they have been previously conceived are paraphyletic and/or polyphyletic, and the lumping of different genealogical groups arises because of a marked predilection toward homeomorphy in the family. Because of the large degree of convergence, only a phylogenetic analysis that includes many characters can hope to confidently discern natural, genealogical taxonomic groupings. For this reason, such an analysis is performed herein.

Along with the higher-level phylogeny of the Proetinae is a study designed to ascertain the origins of the Middle Devonian proetid fauna of Eastern North America. (The Otarionidae Richter and Richter, 1926, and the Aulacopleuridae Angelin, 1854, were not considered in this analysis.) There appear to be at least 45 species of Proetidae known from the Lower and Middle Devonian Ulsterian and Erian Series in Eastern North America. This region has been treated as part of the Eastern Americas Realm faunal province (Oliver, 1976, 1977), which spans the Appalachian Basin, Michigan Basin, Illinois Basin, and the Hudson Bay Lowlands, as well as northern South America.

Two major unconformity-bounded lithostratigraphic packages are developed at this time in New York State and in other regions of Eastern North America (abbreviated as ENA) (Cooper et al., 1942; etc.). The first such package is the Schoharie Grit/Onondaga Limestone and its correlates, which persist through the Southwoodian and perhaps into the lowermost portion of the Cazenovian stage; these New York stage names may be correlative with the uppermost Emsian through late Eifelian European stages (Kirchgasser et al., 1985). Therefore, the Onondaga Limestone may conceivably represent both uppermost Lower Devonian and Middle Devonian depositional intervals. However, following the suggestion of Kirchgasser et al. (1985) and Oliver (1989) the base of the Onondaga Limestone is taken to mark the Lower–Middle Devonian boundary, that is, the Emsian–Eifelian transition.

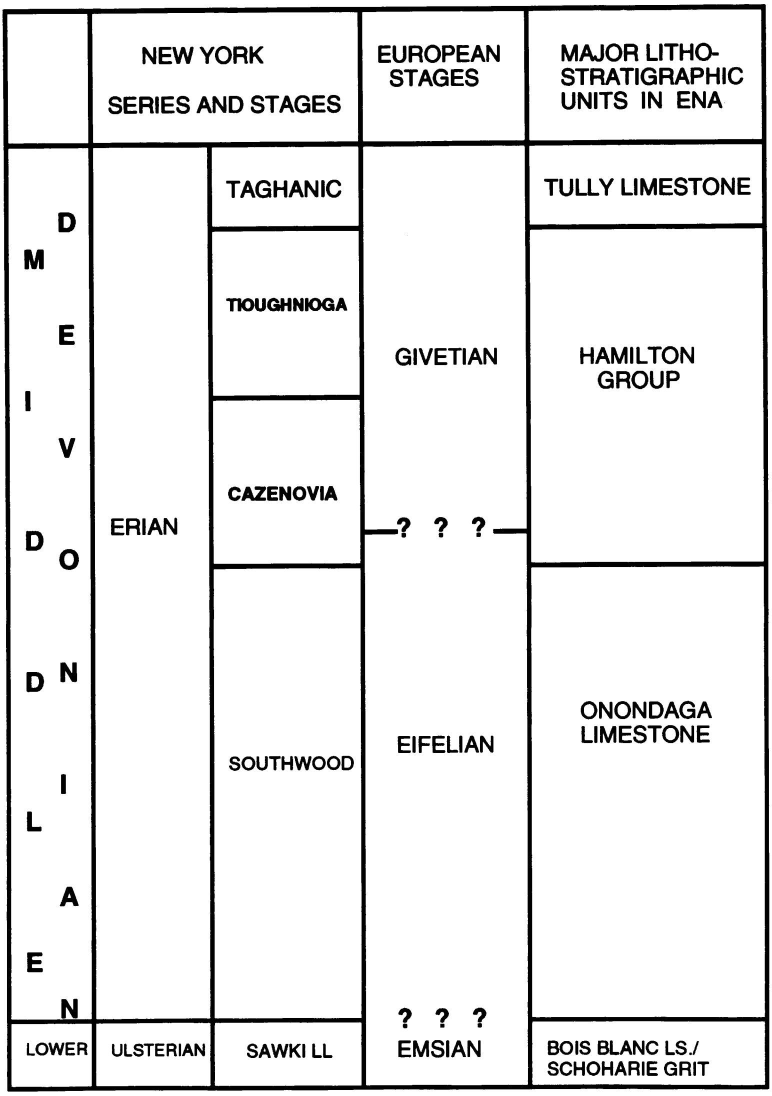
The second major lithostratigraphic package, the Hamilton Group and its correlates, documents Cazenovian, Tioughniogan, and Taghanic deposition, and is roughly equivalent to latest Eifelian through late Givetian (Kirchgasser et al., 1985; Oliver, 1976, 1989; Rickard, 1989, etc.). All units above the Cherry Valley Limestone in the Hamilton Group are treated as Givetian following Griffing and ver Straeten (1991). A stratigraphic column for the late Lower and Middle Devonian in ENA is presented with both European and New York Stage names (fig. 1), as are more detailed stratigraphic columns for the formations and members within the rocks of the Hamilton Group in the northern Appalachian Basin in New York State (fig. 2) and the rocks of the Traverse Group in the Michigan Basin (fig. 3).

Four "genus-level" proetine clades recognized in the Ulsterian and Erian Stages of the ENA Realm are subjected to separate phylogenetic analyses that consider almost all of the known ENA species in each of these clades. Three of the clades belong to the Proetinae Salter, 1864. Analyses are conducted on the genus *Crassiproetus* using 14 taxa and 33 characters, on the genus *Basidechenella* using 16 taxa and 25 characters, and on the genus *Dechenella* using 21 taxa and 49 characters. In addition, a phylogenetic analysis is presented for another "genus-level" proetid clade that appears to lie outside the Proetinae, the genus *Monodechenella*. This analysis employs 10 taxa and 20 characters. The evolution of all of these taxa through the Ulsterian and Erian Stages (Lower–Middle Devonian) is traced. Eleven new species belonging to these four clades are described, and the biogeographic origin of each clade is discussed. In addition, the evolutionary relationships within each of these four clades are applied to answer questions about biogeographic and environmental subdivision within Eastern North America. Particular attention is paid to the role that biogeographic and environmental factors play in controlling diversification, distribution, and extinction.

Beyond discussing the origin of the proetine trilobites of the Middle Devonian Ulsterian–Erian of North America, proetine trilobites that do not belong to the aforementioned four "genus-level" clades are also recognized as present in, and restricted to, the upper Ulsterian Series. In particular, the late Early Devonian Sawkill Stage has trilobites that belong to the Proetinae. These taxa are known from the Bois Blanc and Grand Grève Limestones and the Schoharie Grit, and thus are age equivalent to taxa in the European Emsian Stage (Kirchgasser et al., 1985; Oliver, 1976, 1989; Rickard, 1989). Most of the overlying Erian (Eifelian–Givetian) taxa are not derived from these Ulsterian (Emsian) proetines; however, in the past some authors had suggested that they were related. Although detailed phylogenetic analyses are not presented for these taxa due to the paucity of available material, a commentary on biogeographic origins and evolutionary relationships for taxa is given.

An abrupt transition between the Sawkillian Stage (uppermost Ulsterian) and the Erian Series is consistent with a particular pattern of diversification hypothesized to occur both at the level of species (Eldredge and Gould, 1972) and clades (Palmer, 1965; Fagerstrom, 1977; Eldredge, 1985). Authors have therefore hypothesized that in situ evolution seems to be the exception rather than the rule, and that the establishment of species and evolutionary faunas in the fossil record appears to be the by-product of extinction with subsequent invasion from elsewhere, which was facilitated either by changes in global eustasy or by tectonic effects driving not a vicariant biogeographic process, but an agglomerative one.

However, during the Sawkillian, Southwoodian, Cazenovian, and Tioughniogan a proetine trilobite fauna persists that undergoes in situ evolution and diversification



	NEW YORK SERIES AND STAGES		EUROPEAN STAGES	MAJOR LITHOSTRATIGRAPHIC 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

Fig. 1. A stratigraphic column for the uppermost Lower and Middle Devonian showing the New York series and stage names, their possible stratigraphic relationships with European stages, and the major lithostratigraphic sequences developed in Eastern North America at this time. Modified from Kirchgasser et al. (1985) and Rickard (1989).

within Eastern North America. It has been often recognized that there is an important disjunction between Onondagan (Southwoodian) and Hamilton (Cazenovian–Tioughniogan) faunas (e.g., Eldredge, 1972, 1973, 1985; Burton and Eldredge, 1974; Rollins et al., 1971; Bailey, 1983; Boucot, 1975) in terms of their taxonomic compositions and biogeographic affinities. When several different phyla are considered, most of the Sawkillian and Southwoodian taxa appear to be lineal descendants of earlier Eastern North American taxa, and most of those in the subsequent Cazenovian and Tioughniogan appear to have European and North African (Avalonian-Armorican) affinities (Boucot, 1975; Eldredge, 1985; Oliver, 1976, 1977). However, in the proetines, a faunal turnover showing this paleobiogeographic pattern with concomitant changes in the area relation-

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

Fig. 2. A stratigraphic column for the Middle Devonian Hamilton Group in the Appalachian Basin in New York State showing all the formations and the most prominent members. When two members are listed in the same box it implies that they are developed in different geographic regions. Modified from Cooper et al. (1942), Kirchgasser et al. (1985), Brett and Baird (1986), Griffing and ver Straeten (1991), and Rickard (1989).

ships of taxa is not prominent. If it occurs at all it appears to predate this Eifelian–Givetian transitional event, and more likely occurred around the Emsian–Eifelian transition interval.

Thus, at least for some of the proetine trilobites, this switch between endemic Eastern North American faunas and those with outside affinities occurred earlier than that in other groups, e.g., the phacopid trilobites

GROUP	HAMILTON EQUIVALENT	MICHIGAN BASIN FORMATION
TRAVERSE	TULLY LS.	THUNDER BAY LS.
		PETOSKEY/POTTER FARM
	MOSCOW	
	LUDLOWVILLE	NORWAY POINT
		FOUR MILE DAM LS.
	SKANEATELES	? ? ? DOCK STREET CLAY
	MARCELLUS	GRAVEL POINT/ ALPENA LS.
		NEWTON CREEK LS.
		GENSHAW
		FERRON POINT
		ROCKPORT QUARRY LS.
		BELL SHALE

Fig. 3. A stratigraphic column for the Middle Devonian Traverse Group, roughly coeval with the Hamilton Group and developed in the Michigan Basin, principally in Michigan, Ohio, and southwest Ontario. Formations from the Traverse Group and coeval deposits in the Hamilton Group are shown side by side. Limestone is abbreviated by ls. Modified from Cooper et al. (1942) and Rickard (1989).

(Burton and Eldredge, 1974; Eldredge, 1985), the bivalves (Bailey, 1983), and the rugose corals (Oliver, 1976, 1977). Because of this, we can document the continuity and in situ evolution of the Proetinae within Eastern North America across the transitional Eifelian–Givetian interval. This interval is marked by prominent changes in the environment mediated by orogenic events caused by collisions between different plates. The goal of this analysis is to relate the phylogenetic patterns deduced to certain macroevolutionary patterns. Particular attention is paid to the role that environmental and biogeographic factors play in influencing the origin, diversification, and extinction of major evolutionary fossil faunas. It is the profound environmental changes that occur at the Eifelian–Givetian transition that make the four "genus-level" clades of proetid trilobite taxa in the ENA Realm important in terms of analyses of macroevolutionary patterns and processes. In addition, the phylogenetic position of these taxa has implications for the higher-level phylogenetic patterns in the Proetinae and the Proetidae.

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The repositories of collections used in this study are abbreviated as follows:

AMNH	American Museum of Natural History
BMNH	British Museum of Natural History
BMS	Buffalo Museum of Science
CU	Columbia University
GSb, GSM	British Geological Survey
GSC	Geological Survey of Canada
NYSM	New York State Museum
OCGM	Oberlin College Geological Museum
OSU	Orton Museum, Ohio State University Department of Geological Sciences
PMO	Paleontologisk Museum of Oslo, Norway
ROM	Royal Ontario Museum
SAM	South African Museum
SDSNH	San Diego Natural History Museum
SM	Sedgwick Museum, Cambridge University
UMMP	University of Michigan Museum of Paleontology
USNM	Smithsonian Institution, National Museum of Natural History
YPM	Yale Peabody Museum of Natural History

HIGHER-LEVEL PHYLOGENY OF THE PROETINAE

In considering the phylogeny of Proetinae Salter, 1864, it is first necessary to document certain synapomorphies that distinguish it as a natural genealogical unit and allow assessment of ingroup membership so that the ingroup taxa can be compared to an outgroup. The following are synapomorphies of the Proetinae. They can be seen on the trilobite *Basidechenella rowi* (Green, 1838) shown in figure 4.1 and 4.3. Synapomorphies that may be ambiguous are annotated by the words "see below": (1) cephalic doublure with panderian opening at base of genal spine (Owens, 1973); (2) thoracic articulating half-ring with preannulus (Richter and Richter, 1956; Owens, 1973) and pygidial articulating half-ring with preannulus; (3) pygidial pleural ribs scalloped in exsagittal section (Owens, 1973) (see below); (4) S2 a flexed arc, convex *anteriorly* and directed posteriorly; (5) articulating half ring on anterior edge of pygidium longer sagittally (sag.) than length of first pygidial axial ring; (6) anterior and posterior pleural bands of pygidium of equal length exsagittally (exag.) when viewed dorsally; (7) L0 short (sag.), equal to or less than exsagittal length between distal tips of S2 and S3; (8) eye sits on a flattened pedestal developed on librigenae that is broadest posteriorly and laterally, to be distinguished from the eye socle (see below); (9) anterior lineations that circumscribe cephalic anterior brim not visible on lateral margins of cephalon in dorsal view; (10) anterior lineations developed on cephalic anterior brim not visible on interior margin of genal spine in dorsal view; (11) facial sutures between eyes and posterior border furrow first parallel a sagittal line and then expand laterally posteriorly (may also appear in Cornuproetinae Richter and Richter, 1956, and see more comments below); (12) in dorsal view, pygidial pleurae not expressed behind axis; (13) when viewing anterior portion of pygidium in dorsal aspect at its medial portion at contact of anteriormost portion of pygidial pleural field and articulating facet, pygidium arches anteriorly medially, forming a triangular structure; (14) when viewing anterior edge of thoracic pleural segment in dorsal aspect, when proceeding laterally in a course from the axis, it arches first anteriorly and then posteriorly (medially, anterior edge of thoracic pleural segments straight); thus, anterior edge of thoracic pleura has triangular swelling in medial portion when viewed dorsally [could be a serially homologous repetition of 13], which is referred to as a Fulcrum-Fortsatz following Lutke [1980]); (15) anterior edge of cephalon (anterior border/cephalic brim) flattened when viewed in lateral aspect (see below); (16) S3 directed posteriorly (see below).

Because the Cyrtosymbolinae Hupe, 1953, the Warburgellinae Owens, 1973, the Tropidocoryphinae Pribyl, 1946, and the Cornuproetinae Richter and Richter, 1956, lack these characters (though see below for the Cornuproetinae), they must be excluded from the Proetinae. Of these subfamilies, the Cyrtosymbolinae is most likely not a monophyletic taxon. It appears to be polyphyletic (Fortey and Owens, 1975; Owens, 1973; Engel and Morris, 1989) and in need of substantial revision. However, all "Cyrtosymboline taxa" surveyed (e.g., Richter and Richter, 1950; Chlupac, 1966; Osmolska, 1970b; Snajdr, 1980; Engel and Morris, 1989; etc.) clearly lack most of the characters of the Proetinae, and therefore are not ingroup Proetinae. Several interesting phylogenetic questions are certainly posed by this group; however, they are not of direct relevance to the phylogeny of the Proetinae and are not treated further here. In addition, until a substantial revision of this group is undertaken, it will remain difficult to ascertain its phylogenetic position within the order Proetida.

BRIEF DISCUSSION OF HIGHER-LEVEL PHYLOGENY OF THE PROETIDAE

There has been considerable debate about the phylogenetic relationships of the Warburgellinae, the Tropidocoryphinae, and the Brachymetopinae Prantl and Pribyl, 1951. Originally, Owens (1973) suggested that the Warburgellinae were derived from members of the Tropidocoryphinae (making this subfamily paraphyletic), and thus both belonged to the Proetidae. However, later Owens and Thomas (1975) and Thomas (1978) discussed several characters that suggested that the Warburgellinae were Brachymetopidae rather than Proetidae, and formed a clade with the Brachymetopinae. Campbell (1977) questioned this grouping and suggested that the Warburgellinae, or at least the genus *Warburgella* Reed, 1931, belonged in the Proetidae, with the Brachymetopinae related to the Otarionidae.

These conflicting perspectives may be clarified when considered in light of the suggested synapomorphies of the Proetinae and their presence in certain problematic taxa, in particular, the subgenus "*Dechenella*" (*Monodechenella*) Stumm, 1953a. The single species Stumm (1953a) assigned to this subgenus, *M. macrocephala* (Hall, 1861) (four addi-

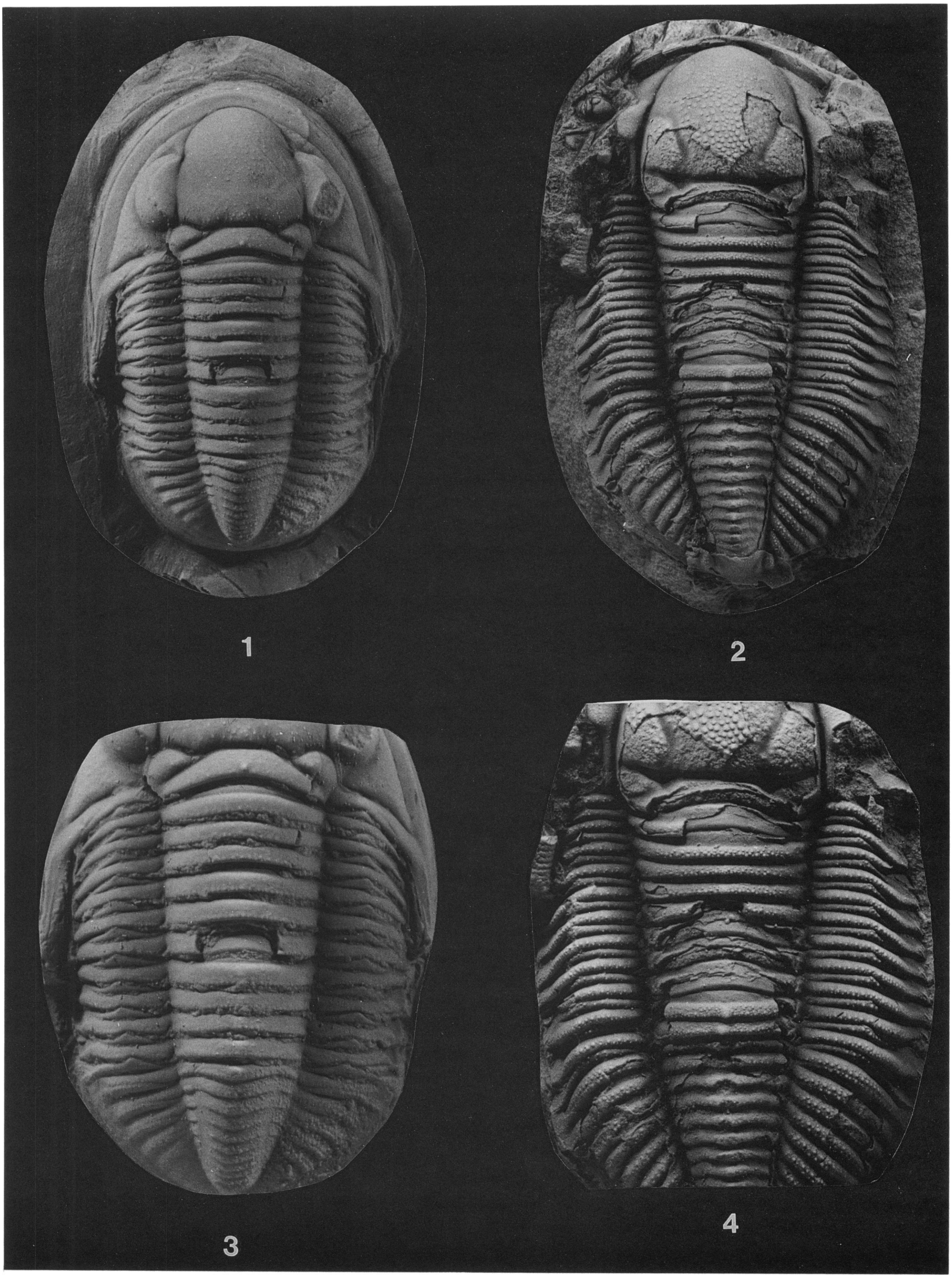

Fig. 4. *Basidechenella* and *Monodechenella* spp. **1, 3.** *Basidechenella rowi* (Green, 1838). Ludlowville Formation, Centerfield Limestone, East Bethany, New York, BMS E5433, dorsal views of entire spec-

tional species are added to this taxon herein, and the subgeneric name is elevated to generic status [see section on origin of the Middle Devonian Proetid fauna of Eastern North America for more extensive discussion]) appears to be related to the genera *Thebanaspis* Lutke, 1990, *Hedstroemia* Pribyl and Vanek, 1978, *Milesdavis*, new genus, and *Mannopyge* Ludvigsen, 1987 (the latter is not treated as a valid genus concept herein) on the basis of the following traits: the anterior pygidial pleural bands sagittal length increases distally; when pairs of adjacent pleurae are considered, the anterior pleural bands dorsally elevate distally relative to the posterior band (as a special case of imbricate [Owens, 1973] pygidial structure); the posterior portion of the thoracic pleural band arches strongly posteriorly distally; and the posterior portion of the eye is rotated laterally relative to a sagittal line through its anterior portion. *Latiproetus latilimbatus* (Grabau, 1925) *in* Lu (1962: 171–172, pl. 1, figs. 7, 8) might have possessed the traits that characterize the "*Thebanaspis* clade," although the material was too poorly preserved to state this definitively. Owens (1973) suggested that *Latiproetus* was related to *Decoroproetus*. However, Sun's (1990) revision of *Latiproetus*, which included figures of the type of the genus, proved that this genus is not referable to the "*Thebanaspis* clade." In particular, in the type of the genus the eyes are not rotated laterally, the posterior portion of the thoracic pleural band is not arching strongly posteriorly distally, and the anterior pleural bands do not elevate distally. Sun (1990) supported Owens' (1973) contention that *Latiproetus* is closely related to *Decoroproetus*, and he placed that genus in the Proetidellinae Hupe, 1953.

This "*Thebanaspis* clade" lacks several of the characters of the Proetinae given above, and therefore it must be excluded from that subfamily. In particular (see fig. 4.2, 4.4), (1) the anterior edges of the thoracic pleural segments lack a triangular projection, or Fulcrum-Fortsatz, medially, and (2) they lack a triangular projection on the pygidium between the anteriormost portion of the pleural field and the facet. In addition, (3) the pygidial pleurae are developed behind the pygidial axis, (4) the occipital ring medially has a sagittal length greater than the distance between the distal tips of S1 and S2, (5) the articulating half-ring on the anterior edge of the pygidium is shorter than the length of the first pygidial axial ring, (6) the thoracic articulating half-rings and (7) the pygidial articulating half-ring lack a preannulus, (8) the pygidial pleural ribs are not scalloped in sagittal section, (9) the anterior and posterior bands of the pygidial pleurae are not of equal length (exsag.), (10) the anterior lineations that circumscribe the cephalic anterior brim are visible on the lateral margins of the cephalon in dorsal view, (11) the anterior lineations developed on the cephalic anterior brim are visible on the interior margin of the genal spine in dorsal view, (12) S2 is sinusoidal, with the distal end convex posteriorly and the proximal end convex anteriorly, and (13) L0 medially arches strongly posteriorly when viewed in dorsal aspect. Most of these characters appear to be primitive for both the Proetidae and the Brachymetopidae, with their subsequent alteration in the Proetinae. However, character 13 appears to be unique to the "*Thebanaspis* clade" and the Tropidocoryphinae, the Cornuproetinae and the Eremiproetinae.

The phylogenetic relevance of the genera *Thebanaspis*, *Hedstroemia*, *Milesdavis*, and *Monodechenella* lies in the combination of characters they bear. These appear to be a mix of traits found in the Tropidocoryphinae, the Cornuproetinae, the Eremiproetinae Alberti, 1967, and the Proetinae. The first characteristic of relevance in these taxa is the elevation of the anterior portion of the pleural segments relative to the adjacent posterior portion, and this appears to be homologous with the high elevation of anterior portions of the pygidial pleural bands associated with

←

imen, ×2.5 and ×3. **2, 4.** *Monodechenella macrocephala* (Hall, 1861). Moscow Formation, Kashong Shale, Bowen Brook, near Attica, 2 mi. northwest of Alexander, New York, BMS E4253, dorsal views of entire specimen, ×1.8 and ×2.2.

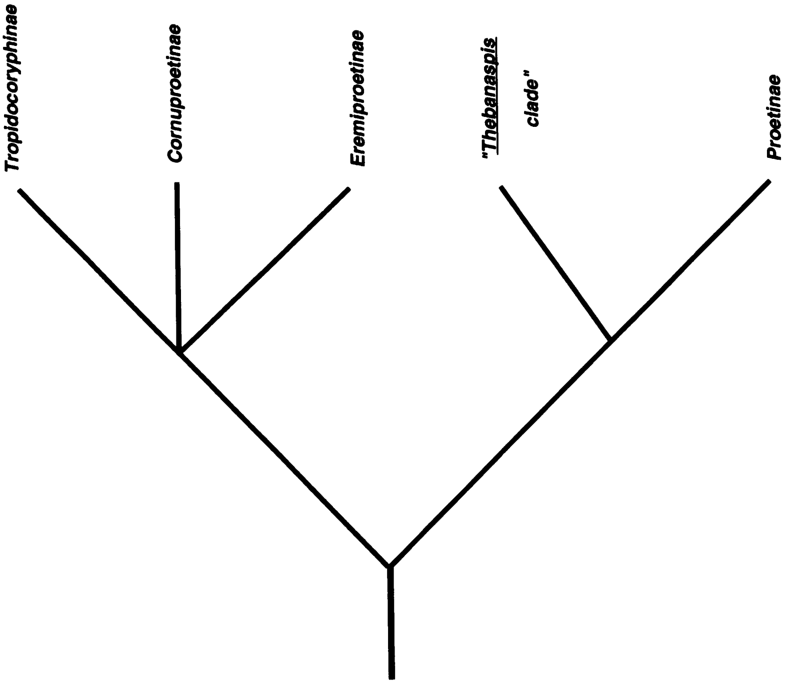

Fig. 5. A cladogram showing phylogenetic arrangements among some of the subfamilies within the Proetidae proposed on the basis of character evidence given in the text. The newly proposed but informal higher taxonomic grouping, the "*Thebanaspis* clade," is treated as the sister taxon of the Proetinae Salter, 1864.

imbricate structure. This trait is not well developed in *Monodechenella macrocephala* (Hall, 1861), *Monodechenella legrandsmithi*, new species, *Monodechenella curvimarginatus* (Hall and Clarke, 1888), and *Monodechenella halli* (Stumm, 1953b) because of the effaced pygidial interpleural furrows in these taxa; however, when the pygidia of *M. macrocephala* and *M. halli* are carefully examined (pygidia for the other species of *Monodechenella* do not provide such detailed preservation, but they also both appear to be very closely related to *Monodechenella macrocephala*), two parallel bands of tubercles surround a faint dark line on the pygidial pleural segment that demarcates the zone of the anterior and posterior pygidial pleural bands and also the position of the interpleural furrow. Using this structure to homologize parts, we recognize that the anterior pleural segments distally lengthen antero-posteriorly and very weakly elevate dorsally. If we accept the apparent presence of similar but transformed structures in different organisms of the putative members of the "*Thebanasipis* clade," and this of course is the original meaning of homology, then these forms do have the characteristic imbricate pygidial pleural rib structure elucidated by Owens (1973). In such brachymentopine taxa as *Radnoria* (Owens and Thomas, 1975) and *Mystrocephala* Whittington, 1960, it is the posterior pygidial pleural band that rises above the anterior pygidial pleural band. Elevation of the pygidial pleural bands is thus exactly the opposite of its expression in the "*Thebanaspis* clade," and therefore these pygidial pleural structures probably do not share homologous modification.

Although Lutke (1990) stated that these similar pygidial pleural structures shared by the Tropidocoryphinae and the "*Thebanaspis* clade" are not comparable, he provided no justification for this conclusion, which seems to be based on his implicit assumption that this clade belongs to the Proetinae. Herein these similar pygidial structures are accepted as homologous until further evidence is presented that contradicts this, following Hennig's (1966) auxiliary principle. Thus, this "*Thebanaspis* clade" shares at least two derived characters with the tropidocoryphine, cornuproetine, and eremiproetine clade. However, as discussed below, Lutke's (1990) suggestion that the *Thebanaspis* clade is closely related to the Proetinae seems to have some support.

The condition of the pygidial pleural ribs and the posteriorly directed flexure of L0, along with other features elucidated below, also suggests that *Monodechenella halli* (Stumm, 1953b) does not belong to the Warburgellinae (contra Ludvigsen's [1987] suggestion) and rather may be related to the clade composed of the Tropidocoryphinae, the Cornuproetinae, and the Eremiproetinae. Thus, any similarities shared between such forms as *Monodechenella* and the Proetinae cannot be used as evidence of close affinity of the Warburgellinae and the Proetinae, which is a relationship that Yolkin and Sheltonogowa (1974) have advocated.

There are also additional important characters found in *Thebanaspis*, *Hedstroemia*, and *Monodechenella* that suggest a relationship with the Proetinae (no cephala of *Milesdavis* are preserved). These are: (1) S3 arches posteriorly, (2) eyes sit on a flattened pedestal on librigena (though in this case this broad pedestal does not widen laterally and posteriorly), and (3) the anterior margin of the cephalon, anterior of the glabella, is flat when viewed laterally. These characters could be homoplasious acquisitions of the "*Thebanaspis* clade." However, it may be more parsimonious to view them as evidence of relationship with the Proetinae. It is not advocated that they be viewed as part of the ingroup Proetinae. However, they may share a sister-taxon relationship with this clade. In addition, the two traits shared by the Tropidocoryphinae, the Cornuproetinae, the Eremiproetinae, and the "*Thebanapis* clade" may suggest a relationship between the two clades, with the latter serving as a phylogenetic link between the Tropidocoryphinae and the Proetinae. Although clearly more detailed character study is needed, the phylogenetic relationship ([Tropidocoryphinae, Cornuproetinae, Eremiproetinae]["*Thebanaspis* clade", Proetinae]) shown in figure 5 is proposed.

IMPLICATIONS FOR POST-DEVONIAN PROETID CLASSIFICATION

The consideration of synapomorphous features of the Proetinae may have some implications for the placement of Carboniferous trilobite genera and species into a subfamilial classification, and thus merits brief discussion here. These comments on Carboniferous trilobites are not intended as a panacea that will allow quick resolution of some of the problems in higher-level post-Devonian trilobite systematics. However, it is suggested that if the characters presented above are valid, both for defining the Proetinae and for demonstrating the monophyly of a closely related "*Thebanaspis* clade," then they may have relevance for elucidating some of the relationships of the trilobites that survived the Givetian and Frasnian–Famennian extinction events.

For example, the unique thoracic and pygidial structure, with triangular projections developed medially both on the anterior portion of the pygidial pleural field and the anterior portion of the thoracic pleural segments of the Proetinae (Salter, 1864), as well as the other characters presented above, allows recognition of those Carboniferous trilobites that should be referred to, or excluded from, this subfamily. For instance, study of the specimens figured in the important works of Osmolska (1970a) and Hessler (1963) suggests that the genera *Bollandia* Reed, 1943, *Cummingella* Reed, 1942, and *Reediella* Osmolska, 1970a, are probably truly members of a monophyletic Proetinae as conceived herein.

Phillipsia Portlock, 1843, *Piltonia* Goldring, 1955, *Eocyphinium* Reed, 1942, *Particeps* Reed, 1943, and *Breviphillipsia* Hessler, 1963, all possess the primitive anterior pygidial and thoracic pleural structure, and they also have a tuberculose prosopon, a pedestal on the librigenae developed as a crescent, the development of pygidial pleurae behind the axis, a portion of the cephalon anterior of the glabella that is flat in lateral aspect, and the posterior portion of the thoracic ribs flexing strongly posteriorly distally. These features suggest that these genera share affinity with the "*Thebanaspis* clade," and they must be excluded from a monophyletic Proetinae.

In addition, the phylogenetic analysis conducted herein suggests that the Proetinae certainly survive into the Carboniferous, contra Feist's (1991) suggestion. The genus *Pudoproetus* Hessler, 1963, is known from the Lower Carboniferous of North America and the Urals. *Basidechenella timwhitei*, new species, is also known from the Lower Carboniferous of North America. In addition, "*Proetus*" *longicaudus* Hall, 1861, appears to be closely related to *Ormistoniella malaca* Cooper, 1982, from the Middle Devonian of Gondwanaland, and is undoubtedly a species of the Proetinae. The diversity of the Proetinae in the Carboniferous is certainly much greater than has been appreciated and needs to be documented by further studies.

MORPHOLOGICAL EVOLUTION IN THE PROETIDS

It has often been noted that proetid taxa display a high degree of homoplasy and convergence across broad, supposedly real genealogical entities (e.g., Fortey and Owens, 1975, 1990). The causes for this could be ascribed to at least two mechanisms. The first might rely on certain features in proetid trilobite developmental systems. In particular, there might exist constraints, along with a level of plasticity and lability present in proetids, but absent in other orders, that allowed the repeated acquisition of similar features in proetids, while thwarting such repeated developments in other orders. Testing this proposition would require a detailed study of the relative amounts of morphospace occupied by species and clades of proetids and other trilobites, similar to the studies performed by Foote (1991) and Hughes (1991).

Another possibility is that their propensity for convergence was accentuated by their long temporal persistence in the fossil record. If morphology evolves as a simple random walk through a finite morphospace, the proetids, by outliving the other trilobite orders, would have the opportunity to occupy a greater total percentage of trilobite morphospace, when their entire stratigraphic range was considered; also, by chance, they could strike upon similar morphologies. Repeated convergence, when viewed in light of a corroborated phylogeny, might offer some insights into the evolution of morphology.

PHYLOGENY OF THE PROETINAE

A phylogeny of the Proetinae was constructed using parsimony analysis. When possible, the type species of a genus was analyzed. It would be impossible to document the evolution of every species of Proetinae known from the Siluro-Devonian. In addition, because so many different generic and subgeneric names exist for the same species, it would be impossible to satisfy every student of proetid trilobite systematics. Instead, the goal was to attain a broad representation of the morphological and generic diversity of the Proetinae. Particular attention was paid to the origins of *Dechenella* and those taxa formerly assigned to the Dechenellinae, and the relationships of the proetid taxa that occur in the Middle Devonian of ENA. A revised generic classification based on this phylogeny is suggested, in the hope that it will encourage further testing of the hypotheses of relationship propounded herein.

Twenty-one taxa were considered and 53

characters were employed in phylogenetic analysis. Two most parsimonious trees were produced of 151 steps, consistency index .38, and retention index .56 using the **ie*** option on Hennig86 (Farris, 1988). The same results were produced when an heuristic search using PAUP 3.0q (Swofford, 1990) was conducted. This heuristic search used 10 random replications with stepwise addition to obtain the same two most parsimonious trees. The two trees differed only in the placement of a single taxon, *Longiproetus tenuimargo* (Richter, 1909), and a strict consensus tree of the two trees is shown (fig. 6). The outgroup used was *Falcatoproetus falcatus* (Owens, 1973). This taxon is certainly a primitive or basal member of the Proetinae, perhaps an early phylogenetic branch off the main line of the Proetinae (Lutke, 1990). An ingroup proetine was chosen because controversy exists about what may be the most basal member of the Proetinae. If the genus *Cyphoproetus* is the sister taxon of the rest of the Proetinae, as Owens (1973) suggested, then it would also be a valid outgroup. However, certain problems would be introduced by employing this taxon in a phylogenetic analysis. First of all, the genus had a long history, Late Ordovician (Ashgill) to Late Silurian (Wenlock) (Owens, 1973), and during this time it underwent substantial evolution, including alteration in certain characters whose polarity would be vital for the determination of proetine phylogeny. Therefore, it would be difficult to assess the character states that were primitive for this genus without a phylogeny of *Cyphoproetus*. Secondly, because of the unusual morphology of *Cyphoproetus* it would be difficult to recognize homologous characters that would provide resolution for the rest of the Proetinae. For these reasons a basal proetine taxon was chosen as the outgroup. Other taxa treated as members of the ingroup in this analysis (e.g., *Proetus latifrons* [McCoy, 1846]) could be used as the outgroup simply by rerooting the cladogram at that node.

A bootstrap analysis was conducted to assess the amount of confidence we can have in this phylogeny. It would appear that one of the fundamental assumptions of the bootstrap analysis, that all units to be sampled are to be independent, is not met. However, bootstrap analysis is also based on the assumption that the objects being sampled have the statistical property that they converge to a value as the number of samples increases to infinity, and this is also an assumption of most systematic studies that assume that the phylogeny converges to a true answer as the number of characters sampled increases. Thus, if characters are consistent estimators of phylogeny then one can use bootstrap analysis. If characters are not consistent estimators of phylogeny then bootstrap analysis cannot be applied. However, if this were the case then there would be no point in doing character analysis for systematics. This implies that bootstrap values can at least give some qualitative indication of the relative support of nodes in a phylogeny.

One hundred bootstrap replications were performed on the character data matrix, and for each replication five trees were held. These trees were generated by simple addition with tree bi-section reconnection. Values for the percentage of times that those branches that appear in the phylogeny in figure 6 appeared in the 50% majority rule consensus cladogram produced by the bootstrap analysis are (*concinnus/latifrons*) = 65%, (*cuvieri*(*concinnus/latifrons*) = 59%, (*folliceps/ryckholti*) = 33%, (*rowi/globosus/alpenensis/perscheii/norrisi/onyx/richteri /paragranulata*) = 46%, and (*alpenensis/perscheii*) = 37%. None of these values are significant at the .95 level.

The characters employed in this phylogenetic analysis are given in table 1, and the character states for each of the taxa considered are given in table 2. Generic names follow Owens (1973), Alberti (1969), Ormiston (1967, 1975a), Thomas (1978), Hessler (1963), and Lutke (1990). Each taxon considered is briefly discussed, and new material is illustrated in some cases. The taxonomic units considered herein are actual species, not agglomerations of characters common to a genus, chiefly because most genera appear to be para- or polyphyletic. In those instances where there appear to be characters that vary within a particular genus these are stated. The species concept used here follows that of Eldredge and Cracraft (1980) and Cracraft (1989). Species are held to be the smallest diagnos-

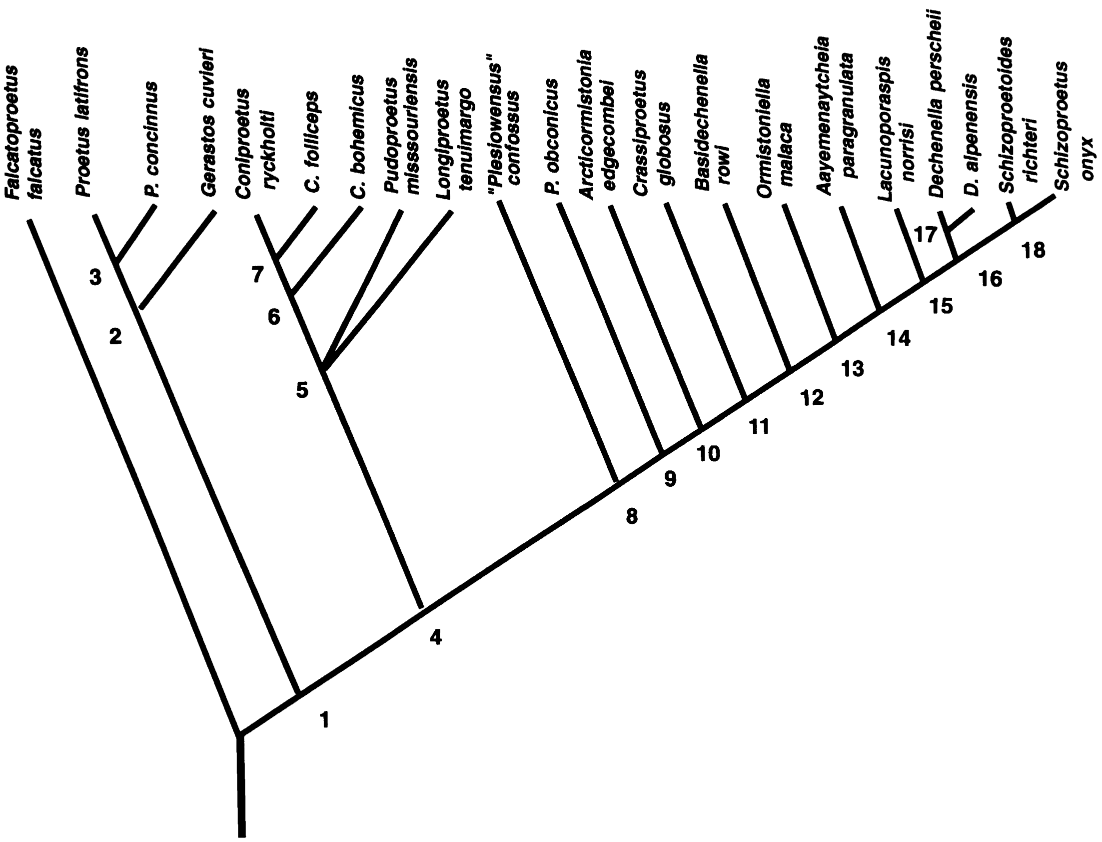

Fig. 6. A strict consensus cladogram of the two most parsimonious trees showing the proposed phylogenetic relationships of genera in the subfamily Proetinae (generated using analysis of the data matrix given in table 2). The two most parsimonious trees were of length 151 steps, consistency index .38, and retention index .56 and were produced using the **ie*** option (exhaustive search) of Hennig86 (Farris, 1988) and a heuristic search on PAUP 3.0q (Swofford, 1990) using stepwise random addition with 10 replications. The length of the consensus tree is 152 steps. All multistate characters were treated as unordered, nonadditive. Characters were optimized using ACCTRAN and are shown for each node with unambiguous apomorphies depicted by parentheses, ( ), and ambiguous apomorphies, either due to missing data or multiple equally parsimonious resolutions, depicted by brackets, [ ]. Node 1: 5(1), 6(1), 12(1), 13(1), 25(1); Node 2: 7(1), 18(1), 31[0,1], 32[0,1]; Node 3: 2(1), 3(1), 31(1); Node 4: 9(1); Node 5: 0[0,1], 35[0,1], 40(1), 52(1); Node 6: 0(1), 31(1), 35(1), 51(1); Node 7: 2(1), 18(1); Node 8: 11(1), 14(1), 19(1), 24(1), 36(1), 37(1); Node 9: 8(1), 10(1), 13(0); Node 10: 0(1), 1(1), 51(1); Node 11: 6[1,2,3], 16(1), 24(0), 25(0), 32[0,1]; Node 12: 6[1,3], 8(0), 14(0), 15(1), 20(1), 32(1); Node 13: 1(2), 9[0,1], 17(1), 22(1), 26[0,1], 28[0,1], 43(1); Node 14: 6(1), 24(1), 26(1), 47(1), 48(1); Node 15: 9(1), 12(0), 21(1), 28(0); Node 16: 32(0); Node 17: 27(1), 29(1), 47(0); Node 18: 17(0), 46(1), 50(1).

ably distinct clusters of organisms (accounting for sexual dimorphism) that are putatively interbreeding.

It appears that major phylogenetic lines in the subfamily had been established by Wenlockian times, and taxa from this stage serve as some of the key phylogenetic links between the Silurian and Devonian forms. This is illustrated to point out the relative concordance, at least on a coarse scale, between phylogeny and stratigraphy, which has already been demonstrated at a detailed level by the fine scale analysis of Norell and Novacek (1992). Discussions of cladogram topology are given under the headings of the various genera listed below.

TABLE 1

Characters Used in Phylogenetic Analysis of the Subfamily Proetinae

"0" is the plesiomorphic state. Character matrix is given in table 2

0. Dorsal pygidial border: (0) absent, (1) present.

1. Number of pygidial axial rings: (0) 10, (1) 11–12, (2) 15–17, (3) 14.

2. Posterior portion of glabella, in transverse profile: (0) arched, (1) flat.

3. Intraoccipital lobes: (0) do not bulge exsagittally significantly beyond the margin of the glabella, such that they do not reach the visual surface, (1) bulge significantly exsagittally beyond the margin of the glabella, such that they reach the visual surface of the eyes.

4. Apodemes on lateral fields of the pygidial axis: (0) present, (1) absent.

5. Genal spine furrow: (0) follows course of the lateral edge of the anterior border furrow, (1) deflects about 10° exsagittally from course followed by the lateral edge of the anterior border furrow.

6. Genal spines extend back to: (0) eighth thoracic segment, (1) third or fourth thoracic segment, (2) reduced to very small nub or absent, (3) extends back to 5th thoracic segment.

7. Anterior portion of glabella: (0) rounded, (1) squared off.

8. Pygidial axial rings behind the third segment: (0) flex posteriorly, (1) flex anteriorly medially, flex posteriorly laterally, (2) straight.

9. Pygidial axis: (0) flattened posteriorly, (1) of even height.

10. Anterior brim of cephalon: (0) rounded ledge, (1) flattened ledge.

11. Pygidial axis, in dorsal view: (0) straight (tr.) posterior terminus, (1) rounded or pointed terminus.

12. S1: (0) rounded arc, (1) flexed transversely posteriorly and anteriorly.

13. Facial suture anterior of eye: (0) deflects sharply laterally, at about a 45° angle from a sagittal line drawn from the inner edge of the eye, past exsagittal margin of inner edge of eye, (1) does not deflect sharply, about 20° or less from a sagittal line drawn from the inner edge of the eye.

14. Genal spine furrow: (0) intersects the outer edge of the genal spine, (1) intersects the inner edge of the genal spine or the midpoint.

15. Margin of glabella near the eyes: (0) straight, (1) bulging at the midline of the eye.

16. Intraoccipital lobes posteriorly: (0) not separated from L0, (1) separated from L0 and topographically elevated.

17. Posterior border furrow: (0) straight, (1) directed posterolaterally.

18. Space between the posterior portion of S1 and S0: (0) small, much less than the antero-postero length of L0, (1) large, greater than antero-postero length of L0.

19. Anterolateral portion of S0, anterior of the intraoccipital lobes: (0) straight, (1) flexes strongly anterolaterally.

20. Interpleural furrows: (0) present, as deep as pleural furrows, (1) very faint.

21. Preglabellar field between the glabella and the anterior border furrow: (0) absent, (1) present.

22. Pygidial border: (0) parallels pleurae, (1) flattened shelf.

23. Pygidial axial rings medially: (0) separated by distinct inter-ring furrows, (1) fused.

24. Posterior edge of lateral occipital lobes: (0) straight, parallelling posterior border furrow, (1) flexes anterolaterally.

25. Anterior border: (0) developed as a long (sag.) ledge 1.5 times as long as the length of LO medially, (1) very thin, ledge developed only furthest anteriorly, with length equal to length of L0 medially.

26. Pygidial border: (Outgroup = ?) (0) narrow, posteriorly narrower or equal to width anterolaterally, (1) wide, posteriorly wider than anterolaterally.

27. S0 and L0: (0) straight medially, with a slight posterior kink of S0 mesially, (1) curve prominently anteriorly.

28. Pygidial pleurae: (0) gently rounded, slightly curving ventrally laterally, (1) steeply arched laterally, medially forming a parallel flattened shelf.

29. Pygidial axis, in lateral section: (0) steeply curved, (1) flat.

30. Anterior edge of the pygidial axis transversely: (0) equal to width of the pleural field, (1) narrow, about 50 to 65 percent of the width of the pleural field.

31. Furrow on genal spine: (0) straight, (1) has a dog-leg, deflects sharply laterally near the lateral border furrow, then deflects back to a line parallel with a line extended from the anterior border furrow.

32. Anterior branches of facial suture: (0) diverging from glabellar margin, (1) parallel each other.

33. Eyes: (0) large, anterior end (where the anterior end is taken as equivalent to the elevated palpebral ridge) opposite S2, (1) small, anterior end between S1 and S2, (2) large, anterior end opposite S3 (posterior edge is at the anterior end of S0).

34. Genal spine: (0) cylindrical projection, (1) triangular lappet curving inward posteriorly.

TABLE 1—(*Continued*)

35. Posterior edge of librigena posterior of eyes: (0) straight or evenly arched, (1) flexing anteriorly, then posteriorly.

36. S3: (0) transverse, inclined at a 10° angle measured from a line through the anterior end of S3 and parallel to the posterior border, (1) flexing posteriorly, inclined at a 45° angle relative to transverse line through anterior edge of S3.

37. S2: (0) transverse, inclined at a 10° angle measured from a line through the anterior end of S2 and parallel to the posterior border, (1) flexing posteriorly.

38. Genal spine: (0) present, (1) absent.

39. Tubercle on L0: (0) present, (1) absent.

40. Posterior portion of glabella in relation to L0: (0) equal in height, (1) elevated far above L0.

41. Number of thoracic segments: (0) 10, (1) 9.

42. Anterior and lateral border furrow of cephalon: (0) present, (1) absent.

43. Anterior margin of posterior pygidial pleurae: (0) convex, (1) siniform, concave anteriorly.

44. Transition between pygidial pleural bands and pleural furrows: (0) gradual, pleurae at anterior and posterior margins smoothly swale downward, (1) abrupt, pleurae flattened, elevated blocks.

45. Anterior border of occipital lobe: (0) pinches in next to a mesial bulge, (1) parallel to the posterior edge of L0.

46. Prosopon: (0) smooth or with very small granules, (1) covered with large tubercles greater than or equal to 0.2 mm in diameter.

47. Eye sits on a pedestal of the free cheek that is: (0) broad flat space, (1) broad flat space bounded distally by a ridge.

48. Incision of S1 and S2: (0) faint, (1) deep.

49. Preglabellar ridge: (0) absent, (1) present.

50. Facial sutures at the anterior edge of the eye meet as: (0) rounded curve, (1) two straight lines that intersect to form a right angle.

51. Longitudinal lineations on the anterior border rim of the cephalon: (0) generally straight but wavy and separated, (1) closely packed and linear.

52. Glabella anteriorly, in lateral view: (0) inclined at a 40° angle relative to a perpendicular drawn to an imaginary dorsal plane, (1) steeply arched, developed as a vertical wall.

SYSTEMATIC PALEONTOLOGY OF TAXA USED IN PHYLOGENETIC ANALYSIS OF THE PROETINAE

FAMILY PROETIDAE SALTER, 1864

SUBFAMILY PROETINAE SALTER, 1864

GENUS *PROETUS* STEININGER, 1831

TYPE SPECIES: *Calymene concinna* Dalman, 1827.

DIAGNOSIS: Intraoccipital lobes bulging significantly beyond margin of glabella; furrow on genal spine dog-legged; longitudinal lineations on anterior border rim of cephalon generally straight but wavy and separated; posterior portion of glabella flat in anterior view flat; anterior portion of glabella appears squared off in dorsal view; anterior border ledge short, less than length of L0 medially; dorsal pygidial border absent.

DISCUSSION: There has been considerable discussion of the genus *Proetus* in the literature. In particular, Erben (1951), Richter and Richter (1952, 1956), Campbell (1967), Ormiston (1967), Whittington and Campbell (1967), Owens (1973), Thomas (1978), Snajdr (1980), and Lutke (1980, 1990) all comment extensively on the diagnostic characters of, and differentiated groups within, this genus. In order to avoid redundancy, only a short comment will be given here; for more information on the original authors' perspectives one is referred to their works.

For a long time the genus *Proetus* has been a taxonomic grab bag of Ordovician to Carboniferous trilobite species that appeared to share a similar morphology. Phylogenetic revision suggests that the broad conception of this genus could be tightened considerably. However, it has long been recognized that phylogenetic structure existed within the broadly conceived *Proetus*, and several authors had divided the genus into either subgenera or species groups. Pribyl (1946) and Erben (1951) suggested the following morphological species groups within the genus *Proetus*: *concinnus*, *cuvieri*, *bohemicus*, and *orbitatus*. These species groups were later assigned to the genera or subgenera *Proetus*, *Gerastos* Goldfuss, 1843, *Coniproetus* Alber-

TABLE 2

Character State Distribution for species Used in Phylogenetic Analysis of the Subfamily Proetinae

Characters and states are listed in table 1. Missing data are indicated by "?"

		1	11111	11112	22222	22223	33333	33334	44444	44445	55
	012345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12
Falcatoproetus falcatus	000000	00000	00000	00000	0?000	?0000	00000	00000	00000	00000	00
Proetus latifrons	001111	11200	0?100	10?00	0?001	?0000	10?00	??000	00000	00000	00
Proetus concinnus	001101	11000	01100	00100	0?001	?0000	11000	00000	00000	00000	01
Gerastos cuvieri	000001	21000	011?0	00100	0?001	?0010	?10?0	00100	00001	00000	10
Coniproetus folliceps	111001	20011	011?1	00111	00001	00010	?01?1	00101	00000	00000	11
Coniproetus ryckholti	101001	10011	01100	00110	10010	00000	10001	00000	00000	00000	10
Coniproetus bohemicus	100001	10010	01100	10010	00001	00000	10001	00001	00000	01000	11
Pudoproetus missouriensis	100001	30010	01101	00000	00001	00000	01000	00001	00000	00100	01
Longiproetus tenuimargo	000001	10010	01100	00000	00001	?0000	00001	00001	?0000	10000	01
"Plesiowensus" confossus	000000	10010	11110	00010	0?011	?0000	00010	11000	?0000	00000	00
Plesiowensus obconicus	000001	10111	11010	00010	0?010	?0000	10000	11000	00000	00000	00
Arcticormistonia edgecombei	110001	10111	110?0	00010	10011	00001	00001	01000	00000	00000	10
Crassiproetus globosus	131000	20110	01110	10?10	00001	01000	0?000	11000	00000	00000	11
Basidechenella rowi	110101	30011	11001	10011	00000	00000	01000	11000	00000	00000	10
Ormistoniella malaca	120001	30201	110?1	01001	01000	?0100	01000	10000	10101	00000	10
Aayemenaytcheia paragranulata	12000?	10001	11001	11011	01011	10100	01200	01000	?0110	11100	10
Lacunoporaspis norrisi	120001	10011	10001	01011	11010	10001	01000	11000	?0000	01100	10
Dechenella alpenensis	120011	10011	10001	01011	01110	11011	00200	01010	00110	00100	10
Dechenella perscheii	120001	10011	10001	11011	11000	11010	00000	11000	?0100	00100	10
Schizoproetoides richteri	12001	10011	11000	10011	11010	10100	00101	10000	?0110	11111	10
Schizoproetus onyx	130011	10011	00001	10010	10011	10000	00000	11000	?0100	11101	?0

ti, 1966, and *Orbitoproetus* Pillet, 1969, respectively. Many of these classificatory schemes partially considered morphological evidence that suggested that each of these groups was a unique evolutionary entity. However, several schemes were also based on the supposition that certain characters provided evidence of generic or subgeneric status. Such arguments do employ a nascent parsimony, and reflect the recognition that certain characters are more consistent than others. However, for the phylogeny produced herein, parsimony was applied algorithmically to assess character consistency and relationships. After a phylogeny has been constructed, it is conceivable that other sorts of evidence could be used to determine the particular rank to which a series of sister taxa should be elevated. However, a cladogram depicting the relationships of these taxa is needed before this type of analysis can proceed.

Subgeneric categories of *Proetus* are not advocated on the basis of the phylogeny produced herein unless they comprise clades including the monophyletic sister taxa *P. concinnus* and *P. latifrons* to the exclusion of the "*Proetus cuvieri* species group." Otherwise they would make the genus *Proetus* paraphyletic. Monophyletic groups could be recognized within this clade and could be classified as subgenera; however, such an analysis is not pursued herein. It is recommended that the generic name *Proetus* be applied only to these two sister taxa and all other taxa that would be monophyletic excluding the "*Proetus cuvieri* species group." This essentially follows the recommendations given by Pillet (1969). However, although the *P. concinnus/P. latifrons* clade and the "*P. cuvieri* species group" are assigned to different genera, they do appear to be closely related, as has been suggested by Richter and Richter (1956) and Whittington and Campbell (1967). In addition, Campbell (1967) also recognized the close affinity shared between *P. concinnus* and *P. latifrons* and he suggested that *P. foculus* Campbell, 1967, was also closely related to these species. *Proetus vaningeni* Foerste, 1923, figured by Holloway (1980) may also be related to the *P. concinnus/P. latifrons* clade.

Proetus concinnus (Dalman, 1827)

Calymene concinna Dalman, 1827: 234, pl. 1, fig. 5a–c.
Proetus concinnus (Dalman). Campbell, 1967: 15; Whittington and Campbell, 1967: 456, pl. 3, figs. 4, 5, 9, 11, 12; Owens, 1973: 12, pl. 2, figs. 1–5, 7–13, pl. 3, fig. 1 (with synonymy).
Proetus (*Proetus*) *concinnus* (Dalman). Thomas, 1978: 36, pl. 9, figs. 1–9 (with synonymy).

DIAGNOSIS: Posterior portion of glabella flat in anterior view; anterior brim of cephalon rounded ledge; anterior branch of facial sutures diverging from glabellar margin; posterior edge of lateral occipital lobes straight, paralleling posterior border furrow.

MATERIAL: SM 28269.

DISCUSSION: This species is known from the Wenlock of Sweden, the British Isles, Estonia, and Germany (Owens, 1973; Thomas, 1978). It has received extensive illustration in Owens (1973) and Thomas (1978), and is therefore not figured herein. In addition, Owens (1973) presented a detailed diagnosis, which is not emended herein.

The analysis herein suggests that *Proetus* forms a monophyletic group comprising *P. latifrons* (McCoy, 1846), *P. concinnus*, and the "*P. cuivieri* species group." It is suggested that the generic name *Proetus* be restricted to this clade which includes the type species.

Proetus latifrons (McCoy, 1846)
Figure 7.1–7.5

Forbesia latifrons McCoy, 1846: 49, pl. 4, fig. 11.
Proetus latifrons (McCoy). Campbell, 1967: 15.
Proetus (s.l.) *latifrons* (McCoy). Owens, 1973: 21, pl. 1, figs. 11, 12, pl. 2, figs. 1, 2, 4 (with synonymy); Thomas, 1978: 40, pl. 9, figs. 12, 13.

DIAGNOSIS: Anterior brim of cephalon rounded ledge; intraoccipital lobes posteriorly separated from L0 and topographically elevated; glabella anteriorly, in lateral view, inclined at 40° angle relative to a perpendicular drawn to dorsal plane; posterior portion of glabella in anterior view flat; pygidial axial rings behind third segment straight.

MATERIAL: YPM 33801–33806.

DISCUSSION: This species is known from the upper Llandovery Beds at Egool, Ballaghaderreen, County Roscommon, Ireland, and the Coalbrookdale Formation, Dudley, the British Isles, Wenlockian (Owens, 1973; Thomas, 1978). This species has been discussed and diagnosed by Owens (1973) and Thomas (1978). The appellation *Proetus* s.l. *latifrons* adopted by Owens and Thomas is replaced simply by *P. latifrons* herein.

FALCATOPROETUS LUTKE, 1990

TYPE SPECIES: *Proetus* (s.l.) *falcatus* Owens, 1973.

DIAGNOSIS: See Lutke (1990).

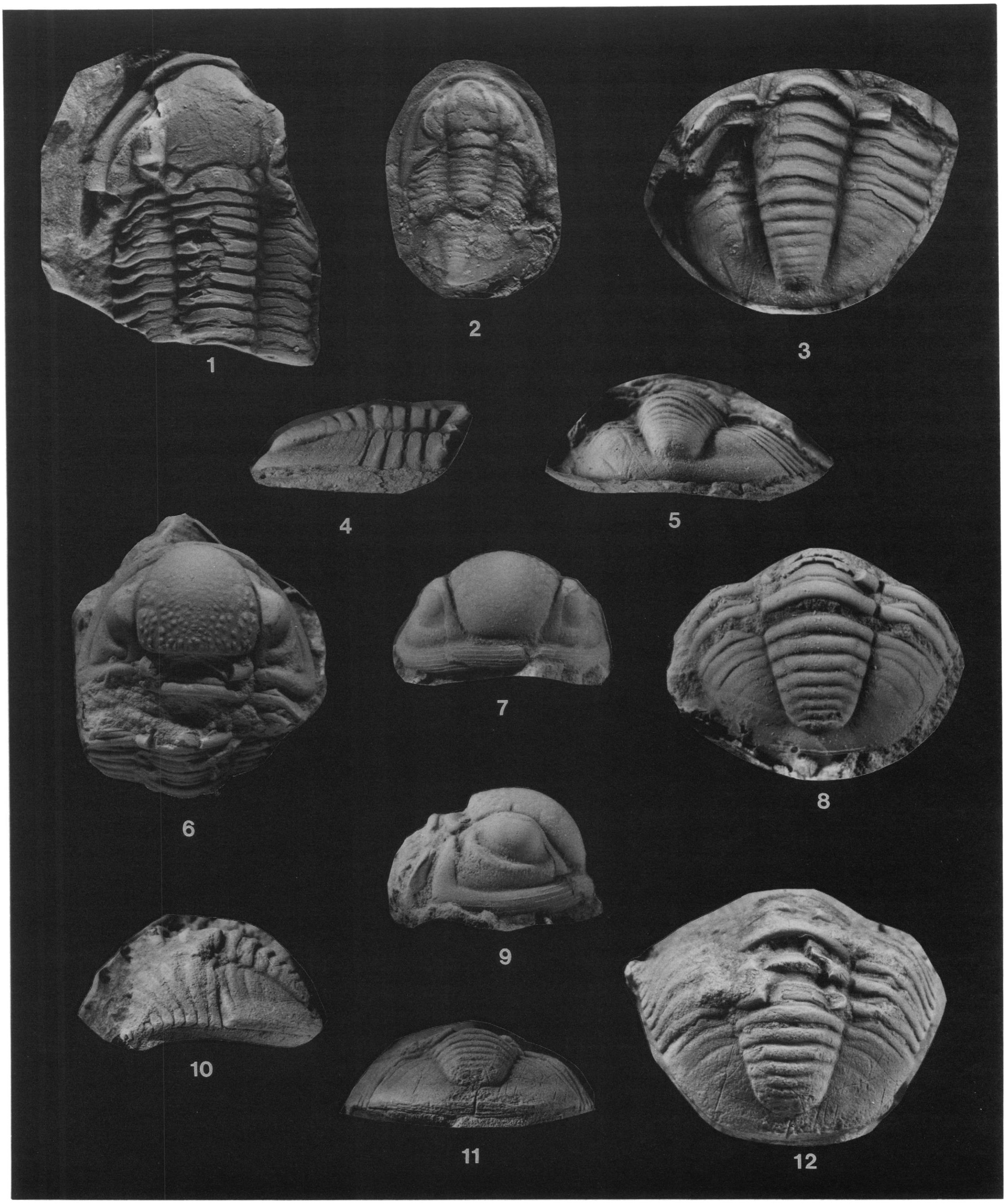

Fig. 7. *Proetus* and *Gerastos* spp. **1-5.** *Protetus latifrons* (McCoy, 1846). Coalbrookdale Formation, Wenlockian, Silurian, England. **1-2** YPM 33805, dorsal views of cephalothoraxes, ×3.75. **3-5** YPM 33804, dorsal, lateral, and posterior views of pygidium and partial thorax, ×2. **6-12.** *Gerastos cuvieri* (Steininger, 1831). Calceola Beds, Eifelian, Middle Devonian, Eifel District, Gees Gerostein, Germany. **6-9** AMNH 18772, dorsal and anterior views of cephalon, dorsal view of pygidium, and lateral view of cephalon, ×3.75 except 8, ×4.5. **10-12** YPM 2549, lateral, posterior, and dorsal views of pygidium and partial thorax, ×3 except for 12, ×4.

Discussion: Lutke (1990) suggested that this genus is the oldest member of the tribe Unguliproetini and is closely connected to the ancestry of the bulk of the Proetinae. It consists of a single species.

Falcatoproetus falcatus (Owens, 1973)

Proetus (s.l.) *falcatus* Owens, 1973: 23–24, pl. 2, figs. 8, 13.
Falcatoproetus falcatus (Owens). Lutke, 1990: 37, pl. 8, figs. 53–54.

Diagnosis: See Owens (1973) and Lutke (1990).

Discussion: This material is known from the Wenlock and possibly Lower Ludow at Dudley, United Kingdom. The species was used as the outgroup taxon in this analysis. Owens (1973) commented on some of the distinctive features of the cephalon and pygidium of *F. falcatus*, and suggested that it was not closely related to the clade comprising *Proetus concinnus* and *P. latifrons*. Lutke (1990) recognized *F. falcatus* as the most basal member of the tribe Unguliproetini, a group he considered to be sister to most of the rest of the Proetinae. It is obvious that *F. falcatus* is one of the most basal members of the Proetinae, and may represent an early offshoot from the branch that went on to comprise the rest of the Proetinae. For these reasons, *F. falcatus* was chosen as the outgroup in this analysis.

GERASTOS GOLDFUSS, 1843

Type Species: *Proetus cuvieri* Steininger, 1831.

Diagnosis: See Owens (1973) and Lutke (1990).

Discussion: The monophyletic group comprising the "*Proetus cuvieri* species group" and sister to the genus *Proetus* is referred to *Gerastos*, essentially following Snajdr (1980), Lutke (1980, 1990), Ellermann (1992), and others. Other authors (e.g., Lutke [1990]) have referred two subgenera to this genus, *G.* (*Gerastos*) and *G.* (*Devonoproetus*). These subgenera are not treated herein.

The genera *Proetus* and *Gerastos* are united as sister taxa on the basis of the following unique characters: anterior portion of glabella squared off and space between posterior portion of S1 and S0 large (not definitive for *P. latifrons*).

Gerastos cuvieri (Steininger, 1831)

Figure 7.6–7.12

Proetus Cuvieri Steininger, 1831: 355, pl. 21, fig. 6.
Proetus (*Proetus*) *cuvieri* Steininger. Richter and Richter, 1956: 353, pl. 1, figs. 2, 3, pl. 2, figs. 6, 7, pl. 3, figs. 13–16, pl. 4, figs. 18–22, pl. 5, figs. 31–33, pl. 6, figs. 35–37 (with synonymy); Alberti, 1969: 74; Alberti, 1970: 34–36.
Proetus cuvieri Steininger. Campbell, 1967: 15; Whittington and Campbell, 1967: 457, pl. 3, figs. 1–3.
Proetus (*Gerastos*) *cuvieri* (Steininger). Owens, 1973: 9–10: text-fig. 3a, b.
Gerastos (*Gerastos*) *cuvieri* (Steininger). Pillet, 1972: 120–121; Snajdr, 1980: 44; Lutke, 1980: 88; Lutke, 1990: 8, 24–25; Ellermann, 1992: 6.

Diagnosis: S1 flexes transversely posteriorly and anteriorly; space between posterior portion of S1 and S0 large, equal to sagittal length of L0; anterior border of occipital lobe parallel to posterior edge of L0; longitudinal lineations on anterior border of cephalon generally straight but wavy and separated; anterior border narrow ledge in dorsal view; dorsal pygidial border absent; pygidial axis in sagittal section steeply curved.

Material: AMNH 18772/1,2 and 44754; YPM 33844.

Discussion: This species is known from the Middle Devonian (Eifelian) of the Eifel District of Germany. It appears that *Gerastos cuvieri* is only one of several species that belong to what is termed here the "*G. cuvieri* species group." Some other representative forms clearly belong to this group on the basis of the following features in combination: absent dorsal pygidial border, genal spines reduced to very small nub or absent, anterior portion of glabella rounded, small space between posterior portion of S1 and S0, pygidial axis in sagittal section steeply curved, pygidial axis wide anteriorly, and pygidial axis in dorsal view with a flat posterior terminus. These species are *G. protuberans* (Hall, 1859), *G. akrechanus* (Alberti, 1969), *G. prox* (Richter and Richter, 1956), *G. granulosus* (Goldfuss, 1843), *G. tuberculatus* (Barrande, 1846), *G. africanus* (Alberti, 1967), and all of the other forms that Alberti (1969) assigned to

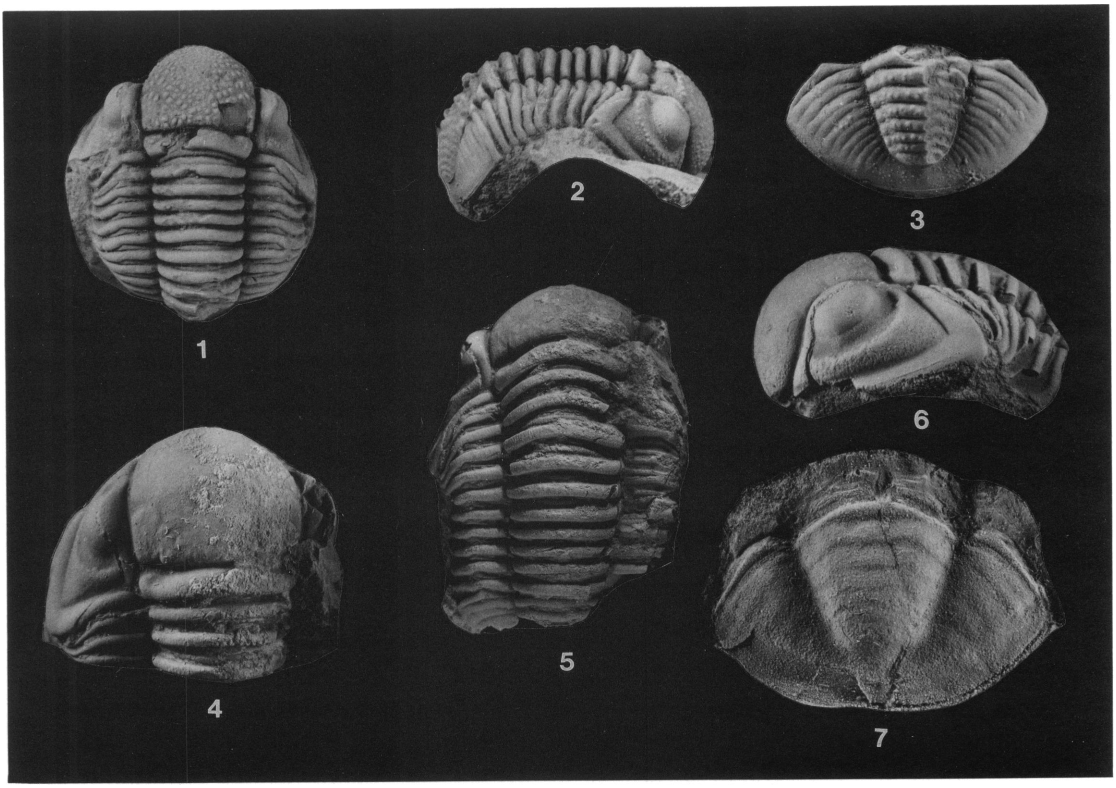

Fig. 8. *Gerastos* spp. **1-3.** *Gerastos* sp. aff. *prox* (Richter and Richter, 1956). Emsian or Eifelian, Morocco, AMNH 44753, dorsal and lateral views of entire specimen and pygidium, ×3 except for 3, ×3.5. **4-6.** *Gerastos laevigatus* (Barrande, 1846). Eifelian, Pelm, Eifel District, Germany, YPM 6639. **4**, Dorsal view of cephalothorax, ×3.5; **5**, dorsal view of thorax, ×3; **6**, lateral view of cephalothorax, ×3.7. **7.** *Gerastos protuberans* (Hall, 1859). Bois Blanc Formation, Sawkillian (upper Emsian), shore of Garden Island, Lake Michigan, UMMP 29510, dorsal view of pygidium, ×3.5.

Proetus (*Proetus*). These forms have been assigned to *Gerastos* (*Gerastos*) Goldfuss, 1843, and good discussions of this genus are given in Lutke (1990) and Snajdr (1980). Other forms clearly belonging to the genus *Gerastos* and the "*G. cuvieri* species group" are listed in Lutke (1990), Alberti (1969, 1970), Snajdr (1980), Kielan (1954), and Ellermann (1992). This species group probably persists from the Lochkovian (Helderbergian of New York State) to the Eifelian (Alberti, 1969; Lutke, 1990; Snajdr, 1980). Some species closely related to *G. cuvieri* are shown in figure 8.

All of these taxa essentially agree on the condition of the characters utilized in this phylogenetic analysis. For character 46 this species was coded as having the prosopon smooth or with very small granules, although some of the species within the "*Gerastos cuvieri* species group" do develop tubercles (e.g., *G. akrechanus*, *G. prox*, and *G. tuberculatus*). However, the condition of this character does not alter the relationships depicted in the cladogram.

It also appears that at least one member of the "*G. cuvieri* species group" appears in ENA. The species *G. stenopyge* (Hall and Clarke, 1888) consists of a single pygidium known from the Bois Blanc Formation (upper Emsian of Oliver [1966, 1976, 1989]; Kirchgasser et al., [1985], etc.) of Garden Island, Lake Michigan. It is equivalent to *G. protuberans* (Hall, 1859) (fig. 8.7) from the New Scotland Formation of the Helderberg Group, with the hallmark pygidial characteristics (i.e., pygidial axis as wide as pleurae, dorsoventrally flattened, with flat posterior terminus, and steeply curved in sagittal section). These attributes strongly suggest that it is a member of the "*G. cuvieri* species group." This species is discussed in more detail below in the section on the Emsian Proetinae faunule of Eastern North America.

PUDOPROETUS HESSLER, 1963

TYPE SPECIES: *Proetus fernglenensis* Weller, 1909.

DIAGNOSIS: See Hessler (1963).

DISCUSSION: This genus is based on several species known from the Lower Carboniferous of the North American continental interior and the Ural Mountains. The species used to code character states for the genus *Pudoproetus*, *P. missouriensis* (Shumard, 1855) was chosen because it provided the best-preserved material that could be easily obtained.

Pudoproetus missouriensis
(Shumard, 1855)

Proetus missouriensis Shumard, 1855: 20, pl. B, fig. 13a, b.

Phillipsia obesa Branson and Andrews, 1938: 114, pl. 15, fig. 21.

Proetus (*Pudoproetus*) *missouriensis* Shumard. Hessler, 1963: 548–549, pl. 59, figs. 9–16, 18–20.

DIAGNOSIS: Anterior brim of cephalon rounded ledge; margin of glabella near eyes bulging at midline of eye; intraoccipital lobes posteriorly not separated from L0; anterolateral portion of L0, anterior of lateral occipital lobes straight; posterior portion of glabella elevated far above L0; anterior border developed as narrow ledge; dorsal pygidial border present; pygidial axis of even dorsoventral height.

MATERIAL: AMNH 6661/1 (four specimens), 6661/2 (three specimens), 39357, 39358.

DISCUSSION: This species is known from the Lower Mississippian Waverley Group, Licking County, Ohio, and the Waverley or Kinderhook Group, Hannibal, Missouri. Although this species appears in the fossil record in the early Carboniferous, long after the origination of the Proetinae, it lacks several derived characters shared by many other species of Siluro-Devonian proetids. Because of this, it maps as primitive on the phylogeny. The disconcordance between phylogenetic position and stratigraphic occurrence of this taxon is also implied in the discussion of Owens (1973: 10) where he recognized the retention of primitive characteristics in the genus *Pudoproetus*.

Owens (1973) suggested that the relationships of *Pudoproetus* (for him, a subgenus of *Proetus*) lay with *Gerastos* (which he also treated as a subgenus of *Proetus*). Although *Pudoproetus missouriensis* and *Gerastos cuvieri* share similar morphological characteristics, these similarities appear to be primitive retentions that are not necessarily phylogenetically informative. However, in referring to the close relationship between *Gerastos* and *Pudoproetus*, Owens (1973) actually commented on the affinity he recognized between *Pudoproetus* and *Proetus* (*Gerastos*) *tenuimargo*, which is referred to herein as *Longiproetus tenuimargo* (Richter, 1909). Owens (1973) suggested that *Pudoproetus* may be derived from *L. tenuimargo*, a relationship also suggested by Lutke (1990). Both authors held that *Pudoproetus* was derived from *Longiproetus*, which itself was derived from *Gerastos*. If we avoid the obvious paraphyletic groupings these discussions introduce and concentrate instead on essentials, it is clear that both authors propounded a close relationship between *Longiproetus tenuimargo* and *Pudoproetus*. The phylogeny derived herein confirms this close relationship. However, conclusions about a relationship between *Gerastos* and *Longiproetus* are not supported.

Hessler (1963) also briefly treated the relationships of *Pudoproetus*. He hypothesized that the ancestry of this genus lay either with *Basidechenella* Richter, 1912, or *Coniproetus bohemicus* (Hawle and Corda, 1847). There appear to be few or no unique derived traits that *Basidechenella* (which is discussed below) and *Pudoproetus* share. However, *Pudoproetus* and *Coniproetus bohemicus* do share a common ancestor to the exclusion of several other genera of the Proetinae. Using the earliest known occurrence of *Coniproetus ryckholti* (Barrande, 1846), a taxon that is discussed below, and following the procedures of Hennig (1966) and Norell (1992), the chain of lineal descent between *C. boh-*

emicus and *Pudoproetus* must have been severed at the latest by the Ludlow.

Also clear from the cladogram in figure 1 is that *Pudoproetus* is one of a series of stem taxa that forms part of a paraphyletic grade if assigned to the genus *Proetus*. The phylogenetic positioning of this species suggests that some of the early forms of the Proetinae may have managed to survive the elevated extinction intervals at the end of the Devonian, and they underwent new episodes of minor diversification in the Carboniferous.

LONGIPROETUS CAVET AND PILLET, 1958

TYPE SPECIES: *Longiproetus tenuimargo* (Richter, 1909).

DIAGNOSIS: For diagnoses see Cavet and Pillet (1958) and Lutke (1990).

DISCUSSION: This genus may be a taxonomic grab bag as presently construed. Lutke (1990) has argued on the basis of the unique rostral plate and subcephalic sutural plan of *L. tenuimargo* that several of the taxa that have been assigned to *Longiproetus* in the past should instead be placed in other genera, such as *Coniproetus* and *Proetus*. He claims that the only valid species of this genus is the type; however, it must be recognized that autapomorphies reveal nothing about relationship. In this analysis only the phylogenetic position of the type of the genus was considered.

Longiproetus tenuimargo (Richter, 1909)

Proetus cornutus (Goldfuss). Beyrich, 1846: 28, pl. 3, fig. 9, non Goldfuss, 1843.

Proetus tenuimargo R. Richter, 1909: 14.

Proetus (*Euproetus*) *tenuimargo* (Richter). Richter and Richter, 18: 69, text-fig. 4a–c.

Proetus (*Proetus*) *tenuimargo* Richter. Richter and Richter, 1921: 164; Erben, 1951: 8; Richter and Richter, 1952: 109, pl. 4, figs. 25–27.

Proetus (*Longiproetus*) cf. *tenuimargo* (Richter). Cavet and Pillet, 1958: 25, 27, pl. 3, fig. 6, 6a, text-fig. 1b.

Proetus (*Longiproetus*) *tenuimargo* (Richter). Ormiston, 1967: 57, 59; Pillet, 1972: 107–108, pl. 1, fig. 2, pl. 2, fig. 2.

Proetus (*Gerastos*) *tenuimargo* (Richter). Owens, 1973: 10, fig. 3e, f.

Gerastos (*Longiproetus*) *tenuimargo* (Richter). Snajdr, 1980: 62.

?*Proetus* (*Gerastos*) sp. aff. *tenuimargo* (Richter). Morzadec, 1983: 113, pl. 2, figs. 4, 7.

?*Proetus* (*Gerastos*) cf. *tenuimargo* (Richter). Morzadec, 1983: 113–114, pl. 2, figs. 5, 6, 8, 10.

Longiproetus tenuimargo (Richter). Lutke, 1990: 30–1, pl. 6, figs. 37–39.

DIAGNOSIS: S1 flexes transversely posteriorly and anteriorly; S0 and L0 straight medially with slight posterior kink of S0 medially; intraoccipital lobes posteriorly not separated from L0; glabella anteriorly steeply arched; mushroom-shaped rostral plate; prosopon covered with large tubercles; dorsal pygidial border absent; pygidial axis of even dorsoventral height; pygidial axis with flat posterior terminus; pygidial axis in sagittal section steeply curved.

DISCUSSION: Several authors (e.g., Owens, 1973; Lutke, 1990; Snajdr, 1980) have suggested close affinity between *Gerastos cuvieri* and *Longiproetus tenuimargo*. However, the phylogeny in figure 1 suggests that this species is not related to *Gerastos*, and any similarities it shares with this species are primitive retentions. It appears to be closely related to *Pudoproetus*, as discussed above, and several members of the genus *Coniproetus*, as discussed below. Therefore, the classifications that suggested *tenuimargo* was a species of *Gerastos* (e.g., Owens, 1973; Snajdr, 1980; Morzadec, 1983) are not supported herein.

Several other species that probably belong to the genus *Longiproetus* are presented in Cavet and Pillet (1958), Pillet (1972), and Snajdr (1980). However, these will have to be incorporated into phylogenies in order to determine if they make *Longiproetus* paraphyletic.

Originally Ormiston (1967) suggested that *Longiproetus* Cavet and Pillet, 1958, might be connected with the origination of the genus *Dechenella* Kayser, 1880. However, the species he originally considered to play a key role as an evolutionary intermediate, *Longiproetus sverdrupi* (Tolmachoff, 1926), he later (Ormiston, 1975a) assigned to the genus *Prodrevermannia* Alberti, 1964. This species is probably not related to either *Dechenella* or any other species within the Proetinae, and appears to belong with the cyrtosymbolinids (Cyrtosymbolinae Hupe, 1953), a group whose relationships are not considered in this paper. They possess several characters that suggest exclusion from the ingroup Proetinae. In particular, the pygidial pleural ribs are developed behind the axis, the anterior portion of the pygidial pleural fields lack the structures serially homologous to the Fulcrum-Forsatz of the thoracic pleurae, L0 is long medially, etc.

Longiproetus tenuimargo differs from *Basidechenella* Richter, 1912, and *Dechenella* by the absence of several charaters, and these taxa appear to be nested far up the tree relative to *L. tenuimargo*.

The mushroom-shaped rostral plate of *Longiproetus tenuimargo* (Richter, 1909) discussed in Lutke (1990) is very unusual in the Proetinae, and the only other proetine taxon from which a similar structure is known is *Kegeliella* Lutke, 1990. However, this character was not utilized for phylogenetic analysis herein. Further analysis might suggest that these shared characters are evidence of close phylogenetic relationship, although Lutke (1990) does not support this conclusion. Because of the ambiguity of relationship between *Longiproetus*, *Pudoproetus*, and *Coniproetus*, these generic names were retained, and although strictly phenetic arguments for classification are not argued herein, this seems permissible in light of certain autapomorphic traits that each of these genera appears to possess.

The affinity between *Longiproetus tenuimargo* and *Coniproetus bohemicus* (Hawle and Corda, 1847) and the other species of the genus *Coniproetus* Alberti, 1966, had not been remarked on previously. However, it appears that the monophyly of this clade may be established on the basis of the following characters: posterior portion of glabella elevated above L0; glabella steeply arched, developed as a vertical wall (neither of these characters is found in *Coniproetus ryckholti*).

CONIPROETUS ALBERTI, 1966

TYPE SPECIES: *Proetus* (*Proetus*) *condensus* Pribyl, 1965 [= *Proetus* (*Proetus*) *novaki* Pribyl, 1964, fide Snajdr, 1980: 68, 70].

DIAGNOSIS: Longitudinal lineations on anterior border rim of cephalon closely packed and linear; posterior edge of librigenae posterior of eyes flexing anteriorly, then posteriorly; S0 and L0 straight medially; genal spine furrow deflects about 10° exsagittally from course followed by lateral edge of anterior border furrow; S1 flexes transversely posteriorly and anteriorly; anterior branch of facial suture does not deflect sharply laterally, only about 20° or less from sagittal line drawn from inner edge of eye; anterolateral portion of L0 anterior of intraoccipital lobes flexes strongly anteriorly; posterior edge of librigenae posterior of eyes flexing anteriorly, then posteriorly; longitudinal lineations on anterior border rim of cephalon closely packed and linear; dorsal pygidial border present; pygidial axis of even dorsoventral height.

DISCUSSION: Alberti (1969) recognized a morphological transition between what he termed the *bohemicus* group, signified by what he termed *Proetus* (*Proetus*) *bohemicus*, here *Coniproetus bohemicus*, and the rest of the genus *Coniproetus*. Lutke (1990) also recognized a shared body plan between these groups, and divided the genus *Coniproetus* into two subgenera, *Coniproetus* and *Bohemiproetus*, the latter with *C.* (*Bohemiproetus*) *bohemicus* as the type species. Lutke (1990) also presented additional diagnostic features of the genus. He strongly advocated a subgeneric classificatory scheme for this genus, and although such a scheme may be warranted, it is not pursued herein. Snajdr (1980) also recommended additional subgeneric categories that are not considered herein, although they may be valid. However, not enough taxa were considered in the cladogram in figure 6 to make any conclusions along these lines. Three species considered in the analysis herein are classified in the genus *Coniproetus*: *C. folliceps* (Hall and Clarke, 1888), *C. ryckholti* (Barrande, 1846), and *C. bohemicus* (Hawle and Corda, 1847). Several additional species that belong to this genus are listed in Snajdr (1980), Alberti (1969), Pillet (1972), Lutke (1990), and Ellermann (1992). It is recommended that the generic appellation *Coniproetus* be used to refer to those taxa that define a monophyletic group to the exclusion of both *Longiproetus tenuimargo* and *Pudoproetus missouriensis*.

Ormiston (1975a) also refers to specimens that are certainly allied with this genus. One of these, his *Proetus* cf. *P. affinis* (pl. 4, figs. 20, 21, 25), is very similar to *Coniproetus affinis affinis* (Boucek, 1933) shown in Snajdr

(1980: pl. 9, figs. 3–11) from the basal Lochkovian (early Gedinnian), Lochkov Formation of Czechosolovakia. The cephalon and pygidium figured by Ormiston (1975a) from the late Lochkovian of the Yukon differ principally from the Old World species *C. affinis* by a slightly narrower axis, and the glabella, which is slightly more expanded anteriorly. The same species is also shown in Ormiston (1971: pl. 5, fig. 7–14). The presence of these very similar forms, as well as his *P.* (*Coniproetus*) sp. discussed below with *C. bohemicus* (Hawle and Corda), was used by Ormiston (1975a) to argue for the close relationship between Arctic faunas and those of the Old World in the Lochkovian and particularly Pragian. Ormiston's (1967) *Proetus* cf. *bohemicus*, although not directly allied with *Coniproetus bohemicus*, appears to belong to the genus *Coniproetus* on the basis of its dorsal pygidial border, equally incised pleural and interpleural furrows, and 10 pygidial axial rings. However, this taxon also differs from *C. bohemicus* in the state of several of its characters, such as its pygidial border developed as a flattened shelf; its relationship is therefore enigmatic. It is herein tentatively assigned to the genus *Coniproetus*.

Some species that should be assigned to *Coniproetus* on the basis of characters presented in this analysis show convergence with species of the Proetinae known from the Middle Devonian of Eastern North America. They were presented as species of *Proetus* in Hall and Clarke (1888) and discussed in detail by Stumm (1953a, 1953b, etc.). This can lead to considerable confusion when one tries to assess the evolutionary relationships of certain taxa known from the Schoharie Grit and Bois Blanc Formation (Emsian), and the Onondaga Limestone (Eifelian), of New York State and Canada. Particularly, in the Schoharie Grit and Bois Blanc Formation proetid trilobites are often preserved as isolated pygidia or cephala, and it can be very difficult to ascertain taxonomic affinity without an entire specimen. Taxa that should be assigned to *Coniproetus* Alberti, 1966, show the greatest convergence on *Crassiproetus* Stumm, 1953a, and forms assigned to *Basidechenella* Richter, 1912, by Stumm (1953a, 1953b, etc.), which are revised herein. Taxa showing the greatest convergence toward forms such as *Crassiproetus crassimarginatus* (Hall, 1843) are discussed in the section on *Coniproetus folliceps* (Hall and Clarke, 1888). These convergences are primarily in features of cephalic morphology.

Prominent convergences can be recognized between the morphology of *Basidechenella*, particularly *B. clara* (Hall, 1861) and *B. rowi* (Green, 1838), and species of *Coniproetus* that appear to be closely related to *C. ryckholti*. In particular, the isolated pygidium in Ormiston (1975a: pl. 4, fig. 25) that he assigned to *Proetus* cf. *P. affinis*, and is assigned herein to *Coniproetus*, bears a strong resemblance to *Basidechenella rowi* (Green, 1838) and *B. clara* (compare fig. 4.1 with Ormiston's [1975a] pl. 4, fig. 25). Pygidia of species related to *Coniproetus* can be discriminated from *Basidechenella rowi* by the former's slightly broader pygidial axis; pygidial axial rings deflecting more weakly posteriorly medially; Fulcrum-Forsatz on the pygidial pleural fields lying closer to the axis then they are in *B. rowi* or *B. clara* (they typically have two fewer pygidial axial rings than *B. clara* or *B. rowi*); and pygidial pleural segments deflecting more weakly posteriorly in *Coniproetus* sp. aff. *affinis* and more weakly arched pygidial segments in posterior view in *C.* sp. aff. *affinis* (compare figs. 24.9, 24.10, and 24.12 with fig. 24.11).

Similarities between *Basidechenella* and *Coniproetus* are also found in features of the cephalon. For instance, Pillet (1972) concluded that several poorly preserved specimens recovered from the Late Emsian and Early Eifelian of the Massif Armoricain belonged to the genus *Pseudodechenella* Pillet, 1972. This genus was also to contain the ENA species of *Basidechenella* that Stumm (1953a, 1953b, etc.) discussed. However, on the basis of the phylogenetic analysis performed herein, the species from the Massif Armoricain that were assigned to *Pseudodechenella* appear to be more closely related to *Coniproetus*, particularly *C. ryckholti* (Barrande, 1846). This conclusion is based on the following character evidence: both *C. ryckholti* and the Massif Armoricain species figured in Pillet (1972) lack the bulging glabellar margins near the eyes, which species of *Basidechenella* have; they have the anterior portion of L0 and S0 medially straight, whereas in *Basi-*

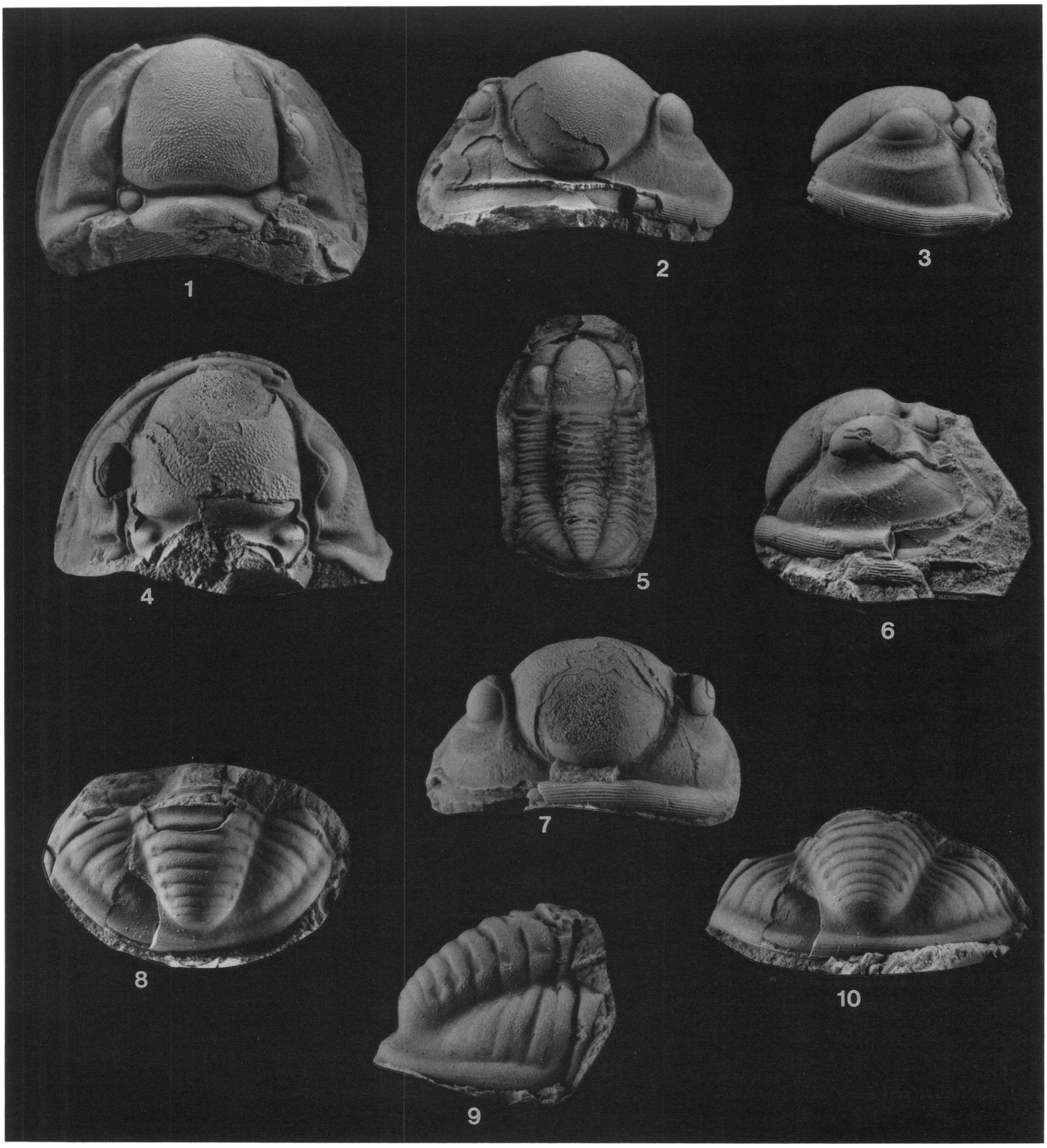

Fig. 9. *Coniproetus bohemicus* (Hawle and Corda, 1847). Koneprusy Limestone, Pragian (Siegenian), Bohemia, the Czech Republic. **1-3.** YPM 33798, dorsal, anterior and lateral views of cephalon, ×2.75 except 3, ×2.5. **4, 6, 7.** YPM 33794, dorsal, lateral, and anterior views of cephalon, ×2.5. **5.** YPM 33796, dorsal view of entire specimen, ×2. **8-10.** YPM 33797, dorsal, lateral, and posterior views of pygidium, ×2.7.

dechenella medially the posterior portion of the glabella first flexes posteriorly and then anteriorly; they have the intraoccipital lobes not fully isolated from L0, whereas they are isolated in most, although not all species of *Basidechenella*; they have a preglabellar field that is absent in *Basidechenella*; they have the facial suture not deflected sharply anterior of the eye (i.e., diverging at about 20° anterior of the eyes), whereas in *Basidechenella* this divergence is approximately 45°; and they have the facial sutures immediately anterior of the eyes diverging, whereas immediately in front of the eyes the facial sutures parallel each other in *Basidechenella*. (On the basis of these diagnostic characteristics, what Alberti [1967, 1969] referred to as *Proetus* (*Coniproetus*) *maurus* should instead be assigned to the genus *Basidechenella*. This species is discussed in greater detail in the section on the origin of the Eastern North American proetid fauna, where a phylogenetic analysis of species of the genus *Basidechenella* is presented.)

Pillet (1972) recovered no pygidia associated with the cephala he assigned to *Pseudodechenella*. However, he did assign several isolated pygidia to this taxon. It is hard to comment on the affinities of these pygidia as they are so poorly preserved. *Pseudodechenella incerta* (Oehlert) (see Pillet, 1972: pl. 15, fig. 7) appears to lack the Fulcrum-Fortsatz on the anteriormost pygidial pleurae, and it also has pygidial pleurae developed behind the axis and therefore does not belong to the Proetinae. Pillet's other figured specimens of *P. incerta* are too poorly preserved to comment on. Pillet's (1972: pl. 15, fig. 5) ?*Pseudodechenella chauffouri* lacks a dorsally expressed posterior border and it instead appears to belong to *Gerastos chauffouri* Pillet, 1972.

In addition to convergence between *Basidechenella* and *Coniproetus* from Armorica, Bohemia, and the Yukon, superficial similarities can also be found between *Basidechenella* and taxa restricted to the Schoharie Grit (Emsian, Sawkillian) of New York State. The species *Coniproetus angustifrons* (Hall, 1861) and *C. conradi* (Hall, 1861) have traditionally been assigned to *Proetus* or *Dechenella*, but they belong with *Coniproetus*. They can be discriminated from *Basidechenella* as follows: *C. conradi* and *C. angustifrons* have a poorly developed pygidial border; margins of the glabella in these two species do not bulge near the eyes; in *Basidechenella* the anterior border of the cephalon is developed as a flattened shelf parallel to an imaginary plane perpendicular to the dorsoventral axis, but in *C. conradi* the anterior border roughly parallels the angle formed by the arc of the librigenae; in *Basidechenella* the medial glabellar impressions intersect S1, whereas in *C. conradi* and *C. angustifrons* they do not intersect; in *Basidechenella* S0 medially deflects posteriorly and immediately laterally it deflects anteriorly, whereas in *C. conradi* and *C. angustifrons* S0 is straight; in *C. angustifrons* and *C. conradi* the facial sutures do not parallel each other anterior of the eye, but in *Basidechenella* they do; in *C. conradi* and *C. angustifrons* a preglabellar field is present, whereas it is absent in *Basidechenella*; and in *C. conradi* and *C. angustifrons* there are 10 pygidial axial rings present, but in *Basidechenella rowi* there are 12. The two species of Sawkillian *Coniproetus* also have a slightly broader pygidial axis, with the pygidial axial rings deflecting more weakly posteriorly medially, and the triangular projections on the anterior portions of the pygidial pleural fields (the Fulcra-Fortsatz) lie closer to the axis compared to those of *Basidechenella*.

These characters not only exclude these two species from *Basidechenella*, but they also emphasize their affinity with *Coniproetus*. Synonymies, diagnoses, and discussions of the species of *Coniproetus* that these two species are related to are given in the section on the origin of the Middle Devonian proetid fauna of ENA in which the Sawkillian (upper Lower Devonian) proetids are considered. Note that there are at least four species of *Coniproetus* found in the Emsian and Eifelian, but not Givetian, strata of ENA. In addition to the two species from the Schoharie Grit (*C. angustifrons* and *C. conradi*) there are two species known from the Onondaga Formation and its equivalents (Erian Series), and these are discussed under *Coniproetus folliceps* and in the section on the origin of the Middle Devonian proetid fauna of ENA.

Coniproetus bohemicus
(Hawle and Corda, 1847)
Figure 9

Proetus bohemicus Hawle and Corda, 1847: 73, pl. 4, fig. 43.

Proetus (*Proetus*) *bohemicus* Hawle and Corda. Erben, 1951: 6–8, pl. 2, fig. 2; Alberti, 1969: 63, 72–74.

Gerastos (*Bohemiproetus*) *bohemicus* (Hawle and Corda). Pillet, 1972: 126, fig. 53.

Proetus (*Coniproetus*) *bohemicus* (Hawle and Corda). Owens, 1973: 8–10.

Gerastos (*Bohemiproetus*) *bohemicus* (Hawle and Corda). Snajdr, 1980: 58-60, text fig. 7a, 19, pl.

6, figs. 1–14, pl. 61, fig. 4, pl. 63, fig. 6 (with synonymy); Snajdr, 1990: 70–71, 150, fig. on p. 151.

Coniproetus (*Bohemiproetus*) *bohemicus* (Hawle and Corda). Lutke, 1990: 23–24, pl. 3, fig. 18.

DIAGNOSIS: Intraoccipital lobes posteriorly separated from L0 and topographically elevated; anterior brim of cephalon rounded ledge; posterior portion of glabella elevated far above L0; eye sits on pedestal on free cheek, which is broad flat space bounded distally by ridge; glabella steeply arched anteriorly, developed as vertical wall; posterior edge of lateral occipital lobes straight, paralleling posterior border furrow; anterior border developed as narrow ledge; pygidial pleural furrows and interpleural furrows incised to equal depths.

MATERIAL: AMNH 44767, 44768; YPM 33791–33800.

DISCUSSION: This species is known from the Koneprusy Limestone, Pragian (Siegenian), the Czech Republic. *Coniproetus bohemicus* and closely related forms have been assigned by several authors to the genus *Gerastos*, e.g., Pillet (1972), Snajdr (1980, 1990), and Ellermann (1992). However, most of the characters *C. bohemicus* shares with species of *Gerastos* are plesiomorphic retentions, and the species shares several unique features with the genus *Coniproetus* Alberti, 1967. On the basis of the monophyly criterion, *bohemicus* cannot be assigned to *Gerastos*. It could be placed in its own genus and also in its own subgenus as some (e.g., Lutke, 1990) have advocated, but this classificatory scheme is not adopted herein. Instead, *bohemicus* is placed in the genus *Coniproetus*.

The phylogenetic relationships for the genus *Coniproetus* advocated herein are congruent with some of the phylogenetic schemes advocated by earlier authors. For example, Alberti (1969), Owens (1973), and Lutke (1990) all recognized the close relationship between *bohemicus* and *Coniproetus* as originally defined by Alberti (1966). This relationship is suggested on the basis of the following characters: dorsal pygidial border present; posterior edge of librigenae posterior of eyes flexing anteriorly, then posteriorly; and furrow on genal spine has a dogleg (indeterminate in *C. folliceps*).

A specimen figured by Ormiston (1975a: pl. 5, fig. 22) which he refered to as *P.* (*Coniproetus*) sp. from the Yukon, Prongs Creek Formation, late Lochkovian, is very similar to *Coniproetus bohemicus*, differing only by possessing a smoother prosopon and a less dorsomedially arched pygidial axis.

Ellermann (1992) assigned several specimens to the new subspecies *Gerastos* (*Bohemiproetus*) *bohemicus similis*, which she held was closely related to *C. bohemicus*. However, on the basis of her figures (pl. 1, figs. 17, 18) it appears that the pygidia she shows are closely related to *Gerastos cuvieri*. These pygidia differ from *C. bohemicus* and resemble *Gerastos cuvieri* because of the following: they lack a border, they possess eight axial rings with a very broad axis, the axis flattens posteriorly, and is steeply curved in sagittal section. The cephala, however, are similar to *C. bohemicus*.

Coniproetus folliceps
(Hall and Clarke, 1888)
Figure 10.1–10.6

Proetus folliceps Hall and Clarke, 1888: 101–104, pl. 23, figs. 3–8.

Proetus (*Proetus*) *folliceps* Hall and Clarke. Stumm, 1953b: 15, pl. 2, fig. 1.

DIAGNOSIS: Glabella strongly elevated with posterior portion flat and far above L0; anterior branches of facial suture parallel; space between posterior portion of S1 and S0 large; longitudinal lineations on anterior border closely packed and linear; eyes small with anterior end between distal tips of S1 and S2; intraoccipital lobes posteriorly not separated from L0; anterior border developed as narrow ledge; anterior edge of pygidial axis narrow, about 50–65% width pleural field.

TYPES: NYSM 4722, from the Onondaga Limestone, near Leroy, New York (NY), formerly a syntype, is designated the lectotype. NYSM 4721 and 4723, formerly syntypes, become paralectotypes.

MATERIAL: AMNH 39336; NYSM 4721–4723.

DISCUSSION: This species is known from the upper Onondaga Limestone, Leroy, NY, from the Jeffersonville Limestone (Eifelian), the Falls of the Ohio, Kentucky, and possibly also from drift of the the Amherstburg Do-

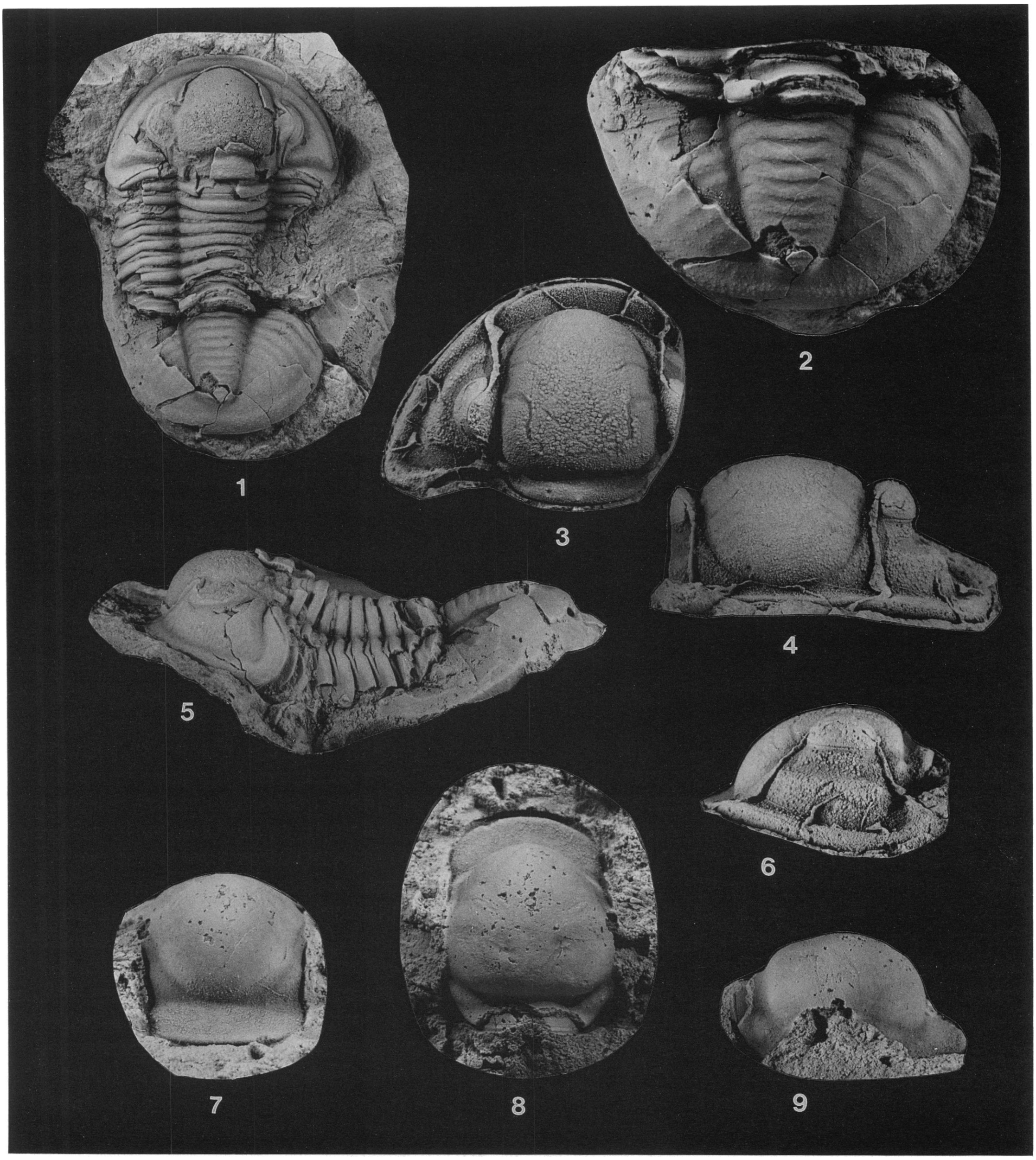

Fig. 10. *Coniproetus* spp. **1, 2, 5.** *Coniproetus folliceps* (Hall and Clarke, 1888). Upper Onondaga Limestone, Eifelian, Leroy, New York, NYSM 4722, lectotype, dorsal view of entire specimen, dorsal view of pygidium, and lateral view of entire specimen, × 1.5 except 2, × 2.5. **3, 4, 6.** *Coniproetus folliceps* (Hall and Clarke, 1888). Upper Onondaga Limestone, Southwoodian (Eifelian), Leroy, New York, NYSM 4723, paralectotype, dorsal, anterior, and lateral views of cephalon, × 2.5 except 4, × 2.75. **7-9.** *Conipreotus tumidus* (Hall and Clarke, 1888). Lower Onondaga Limestone, Southwoodian (Eifelian), Port Colborne, Ontario, UMMP 29516, anterior, dorsal, and lateral views of cephalon, × 2.6.

momite, Ann Arbor, Michigan (MI) (Hall and Clarke, 1888: 101). There appears to be marked morphological convergence between *Coniproetus folliceps* and *Crassiproetus crassimarginatus* (Hall). The genus *Crassiproetus* is discussed at greater length in both the *Crassiproetus* portion of this section on higher level phylogeny and in the discussion on the origins of the Middle Devonian proetid trilobite fauna of ENA. However, commentary on this convergence is necessary here. Both species possess dramatically dorsally ballooned glabellas with facial sutures that are roughly parallel anterior of the eyes. In addition, both have a shelflike anterior border. This convergence is manifested by the incorrect assignment of specimens of *Crassiproetus crassimarginatus* to *Coniproetus folliceps* in the literature. For instance, Stumm (1953b) assigned the cranidium (AMNH hypotype 2897/6, now a paralectotype, AMNH 39330) from the Jeffersonville Limestone to *Proetus* (*Proetus*) *folliceps*. This specimen is illustrated in Hall (1876: pl. 20, fig. 20) and Hall and Clarke (1888: pl. 20, fig. 20) and Stumm (1953b: pl. 2, figs. 7, 8). Cephala of this species and other species of *Crassiproetus* can be easily discriminated from *Coniproetus folliceps* by the following criteria: when viewed anteriorly, the middle region of the glabella is strongly arched in *Crassiproetus crassimarginatus* (Hall) and in all other species of *Crassiproetus* (Stumm, 1953a), although in *C. alpenensis* it is less strongly arched and it is flat in *Coniproetus folliceps*; when viewed dorsally the facial sutures deflect weakly anterior of the eyes in species of *Crassiproetus*, approximately 10° from a sagittal line through the eyes, and they are parallel in *Coniproetus folliceps*; the lateral border at the edges of the cephalon is developed as a rounded cylinder circumscribed by longitudinal lineations in *Crassiproetus*, whereas it is a flattened ledge in *C. folliceps*; and anteriorly, the lateral margins of the glabella converge slightly more strongly in *C. folliceps* than in *Crassiproetus*.

Stumm (1953b) also confused pygidia belonging to species of *Crassiproetus* with those of *Coniproetus folliceps*. Stumm (1953b) depicted a pygidium (pl. 2, fig. 2) that he assigned to *Proetus folliceps*. This specimen, UMMP 29519, from the Bois Blanc Formation of Trout Island, Lake Michigan, actually appears to belong to *Crassiproetus stummi*, new species. The pygidial pleural segments of *Crassiproetus stummi* deflect sharply posteriorly distally (see fig. 15). They are only weakly deflected posteriorly distally in *Coniproetus folliceps* (see figs. 10.1, 10.2). In addition, the pygidial border is developed as a thick brim in true *Coniproetus folliceps*, whereas it is a thin ridge in *Crassiproetus stummi*. Furthermore, the pygidial axial rings are much wider transversely (tr.) relative to the pygidial pleural fields in *Crassiproetus* than in *Coniproetus*. Finally, the posterior portion of the pygidium of *Coniproetus folliceps* roughly parallels a transverse line when viewed dorsally. In *Crassiproetus stummi* the posterior portion of the pygidium is rounded. A more detailed discussion of this species is given in the section dealing with the origin of the Middle Devonian proetid fauna.

The single specimen designated as *Dechenella* (*Basidechenella*) *tumida* by Stumm (1953b: 24, pl. 4, fig. 11), and referred to as *Proetus tumidus* by Hall and Clarke (1888: p. 111, pl. 23, fig. 9), is probably a member of the genus *Coniproetus*, closely related to *C. folliceps*. It has the portions of the facial suture anterior of the eye parallel, the sides of the glabella slightly converging anteriorly, a broad, flat anterior border, the anterior portions of the intraoccipital lobes deflecting anteriorly laterally, the glabella strongly ballooned dorsally, and the anterior portion of the glabella, when viewed laterally, developed as a wall (see figs. 10.7–10.9). However, when viewed anteriorly, the medial portion of the glabella is arched, not flattened, and the anterior border ledge is much longer (sag.) than in *C. folliceps*. Thus, there is some convergence on *Crassiproetus crassimarginatus*. *Coniproetus tumidus* is known from the lower Onondaga Limestone, Port Colborne, Ontario, Canada.

Ormiston (1975a) assigned several specimens of Pragian trilobites from the Prongs Creek Formation of the Royal Creek Area, Yukon Territory, Canada, to *Basidechenella inflecta* [nomen nudum]. These specimens appear to belong to a series of taxa. Some of these specimens are assigned to a taxon described herein as *Arcticormistonia edgecombei*, new species. This species is not closely related to *Coniproetus*. However, one of the specimens that Ormiston (1975a) informally designated (pl. 5, fig. 24) appears closely related to *Coniproetus* and possibly *C. tumidus*, and is referred to as *C.* sp. aff. *tumidus* on the basis of its dorsally expanded glabella, its facial sutures (which are roughly parallel anterior of the eyes), its short, flattened anterior border, and the slight convergence of the sides of its glabella anteriorly. However, this specimen does have a small space between S0 and the distal tips of S1. This space is large in the members of *Coniproetus* subjected to character analysis herein. The specimen shown by Ormiston (1975a: pl. 5, fig. 24) is certainly a new species, and may be closely related to the specimen shown in figures 18.9, 18.10, and 18.12 where it is presented along with specimens of *Basidechenella clara* for comparison.

It appears that the three Eifelian species *C. folliceps*, *C. tumidus*, and *C.* sp. aff. *tumidus* are closely related to such taxa as the Bohemian *Coniproetus affinis* (Boucek, 1933) and the Moroccan *C. foucauldi* (Alberti, 1967), which are both known from the Lochkovian (Gedinnian). Phylogenetic analyses of this genus are not pursued herein. Such analyses might provide elucidation of Lower Devonian paleobiogeography and they will be pursued in detail at a later date. Both *Coniproetus folliceps* and *C. tumidus* are discussed briefly in the section on the origin of the Middle Devonian proetid fauna of ENA.

Coniproetus ryckholti
(Barrande, 1846)

Proetus Ryckholtii Barrande, 1846: 63.

Proetus (*Unguliproetus*) *ryckholti* (Barrande). Erben, 1951: 13–15, pl. 3, fig. 9.

Proetus (*Coniproetus*) *ryckholti* (Barrande). Alberti, 1969: 93.

Proetus (*Coniproetus*?) *ryckholti* (Barrande). Alberti, 1970: 36.

Proetus (s.l.) *ryckholti* Barrande. Owens, 1973: 24, pl. 2, fig. 9.

Coniproetus (*Ryckholtia*) *ryckholti* (Barrande). Snajdr, 1980: 76–77, pl. 10, figs. 1–18, text fig. 7e; Snajdr, 1990: 152, fig. on p. 153.

DIAGNOSIS: Intraoccipital lobes bulge significantly exsagittally beyond margin of glabella, reaching visual surface of eyes, not separated from L0; anterior brim of cephalon flattened ledge; preglabellar field present; anterior border developed as long ledge; posterior edge of lateral occipital lobes flexes anteriorly laterally; posterior portion of glabella at same level as L0; pygidial pleural furrows as deep as interpleural furrows (see Snajdr [1980] for more).

DISCUSSION: This species is known from the Ludlow of the Czech Republic. Owens (1973) originally suggested that it may be related to *Falcatoproetus falcatus* (Owens, 1973); however, the shared characteristics, such as the weakly developed occipital lobes, appear to be primitive similarities. Owens (1973) also claimed on the basis of these primitive retentions that *C. ryckholti* did not belong in the subgenus *Coniproetus*. His conclusion is not followed herein. Instead, the evolutionary affinities of *ryckholti* appear to lie with *Coniproetus* on the basis of the presence of a dorsal pygidial border, the furrow on the genal spine is developed as a dogleg, the posterior edge of the librigenae posterior of the eyes flexes anteriorly, then posteriorly, and the longitudinal lineations on the anterior border rim of the cephalon are closely packed and linear. Snajdr (1980) also recognized the close relationship between this species and other members of the genus *Coniproetus*. He designated it the type species of a new subgenus, *C.* (*Ryckholtia*). Such subgeneric classifications are not recognized in this analysis because not enough taxa were considered to assess their status as true genealogical entities.

PLESIOWENSUS, NEW GENUS

TYPE SPECIES: *Proetus obconicus* (Lindstrom, 1885).

ASSIGNED TAXA: *Proetus* (*Lacunoporaspis*) *confossus* Owens, 1973, *P.* (*L.*) *oppidanus* Thomas, 1978, and *L. chlupaci* Snajdr, 1980.

DIAGNOSIS: Genal spine furrow intersects posteriormost midpoint of genal spine; posterior edge of lateral occipital lobes flexes anteriorly laterally; S2 and S3 flexing posteriorly; longitudinal lineations on anterior border rim of cephalon generally straight but wavy and separated; dorsal pygidial border absent; pygidial axis of even dorsoventral elevation, axis with rounded terminus.

ETYMOLOGY: Compounding *plesio*, Greek for near or close to, in recognition that this genus forms part of a primitive grade group that are stem taxa to several proetine taxa, and *owensus* for Dr. R. M. Owens, who has done important work on proetid trilobites.

DISCUSSION: On the basis of the type species of *Lacunoporaspis* designated by Yolkin (1966), it appears that the two taxa Owens (1973) discussed as *Proetus* (*Lacunoporaspis*) *confossus* and *P.* (*L.*) *obconicus* differ from the original conception of the genus in the condition of several characteristics. A translation of this original diagnosis of Yolkin (1966) is given in Ormiston (1971), and paraphrased it is: glabella tapers anteriorly, three lateral furrows present, weak constriction opposite anterior extremity of palpebral lobe is developed, preglabellar field short, L0 with intraoccipital lobes and median tubercle, pygidium moderately convex, rounded, having 9 to 12 axial segments and five to eight pleurae. This diagnosis needs to be emended to contain more morphological features that will better constrain the evolutionary position of *Lacunoporaspis*. A detailed diagnosis of *Lacunoporaspis* is presented in the section on this genus given herein. However, certain key diagnostic features of *Lacunoporaspis* are: dorsal pygidial border present, pygidial axis of even dorsoventral height, margin of glabella bulging near eyes, posterior border furrow flexes posteriorly laterally, longitudinal lineations on the anterior border rim of the cephalon closely packed and linear, and the facial sutures anterior of the eyes parallel each other.

Because the taxa here assigned to *Plesiowensus* lack these features and several others, they are separated from *Lacunoporaspis norrisi* Ormiston, 1971, by several nodes occupied by different genera of Proetinae. A total of 17 unambiguous synapomorphies separate *Plesiowensus* from *Lacunoporaspis norrisi*. Because *Lacunoporaspis norrisi* fits the original diagnosis of the genus, and because it has a similar morphology to the type species, *Lacunoporaspis contermina* Yolkin, 1966, it appears to be a clear choice for representing the *Lacunoporaspis* clade in the phylogeny shown in figure 6. Therefore, if the entire genus *Lacunoporaspis* is not to be made polyphyletic, it is necessary to place *obconicus* and *confossus* in new genera.

In addition to the taxa *obconicus* and *confossus* considered in the phylogenetic analysis performed herein, a few additional taxa have been assigned to *Proetus* (*Lacunoporaspis*) by Owens (1973) and Thomas (1978). Among these are *P.* (*L.*) *oppidanus* Thomas, 1978, and *P.* (*L.*) aff. *oppidanus* discussed in Thomas (1978) and *P.* (*L.*) cf. *confossus* discussed in Owens (1973). A new genus is created to accommodate these species, *Plesiowensus*. The shutter mark convention of Wiley (1979) is used for some of the species in recognition that this genus is paraphyletic. The species *Plesiowensus obconicus* (Lindstrom, 1885) is defined provisionally as the type of the new genus because it contains more morphological information than its probable congeners, "*Plesiowensus*" *confossus* and "*P.*" *oppidanus*. In addition to these better known taxa, Snajdr (1980: 172–3, pl. 32, figs. 5–9, pl. 64, fig. 1) described a new species, *Lacunoporaspis chlupaci*, from the Pridoli of Bohemia that should be placed in "*Plesiowensus*" on the basis of its wavy and separated longitudinal lineations on the anterior brim of the cephalon, absent dorsal pygidial border, pygidial axis dorsoventrally flattened posteriorly, and several other characters. The taxa placed in this genus are not well represented, and it is possible that a wide range of other morphologies could be present as part of this primitive plexus, which is designated as "*Plesiowensus*." Because of this, and because of the state of the material, I am hesitant to erect at least two new monotypic genera. Moreover, additional studies with higher resolution and more taxa studied might be able to recognize closer relationship between these species. It does appear that all the members of this genus are Silurian and from Baltica and Armorica.

Although the taxa comprising this genus were originally considered to belong to a subgenus of *Proetus*, it appears that several discrete characters separate them from *Proetus concinnus*. Moreover, the species that comprise this grade group are also derived relative to the genera *Coniproetus*, *Longiproetus*, and *Pudoproetus*. *Plesiowensus*, along with some other Wenlock taxa, represent some of the key forms requisite to deduce the evolutionary history of the Proetinae. By the time they had appeared, it seems that all the major groups of the Proetinae had become established. These groups represent a link between the Silurian Proetinae and the Devonian forms that have often been classified in separate subfamilies, the Dechenellinae and the Schizoproetinae. Continuity between Silurian Proetinae such as *Proetus concinnus* and *Coniproetus ryckholti* and many Devonian forms assigned to *Dechenella* and *Basidechenella* is mediated by *Plesiowensus*, and this demonstrates the fundamental genealogical unity of the Proetinae recognized by Owens (1973). (Although Owens assigned some of these Devonian forms to separate subfamilies, he recognized their continuity with the earlier Silurian forms.) In addition, the documentation of these forms by Owens (1973) indicates that the radiation of the entire range of proetine morphological diversity had already been completed by the Wenlock.

Plesiowensus obconicus
(Lindstrom, 1885)

Proetus latifrons (McCoy). Salter, 1848: 337 pl. 6, fig. 1a–c.

Proetus obconicus Lindstrom, 1885: 78, pl. 15, figs. 22–24.

Proetus? sp. Lindstrom. Alberti, 1969: 368, pl. 46, fig. 8.

Proetus (*Coniproetus*) *obconicus* (Lindstrom). Alberti, 1969: 446.

Proetus (*Lacunoporaspis*) *obconicus* (Lindstrom). Owens, 1973: 11, 17–19, pl. 4, figs. 11–19, pl. 5, fig. 1; Thomas, 1978: 37.

Lacunoporaspis obconicus (Lindstrom). Snajdr, 1980: 173.

Diagnosis: Genal spine furrow deflects about 10° laterally from course followed by lateral edge of anterior border furrow, has dogleg, deflects sharply laterally near anterior border furrow, intersects midpoint of genal spine; genal spines extend back to third or fourth thoracic segment; anterior brim of cephalon flattened ledge; facial suture anterior of eye deflects sharply laterally, at about 45° angle from sagittal line drawn from inner edge of eye; anterior border developed as long ledge, 1.5 times as long (sag.) as L0 medially; posterior edge of librigenae posterior of eyes straight; longitudinal lineations on anterior border rim of cephalon generally straight, but wavy and separated; dorsal pygidial border absent; 10 pygidial axial rings; pygidial axial rings flex anteriorly medially, flex posteriorly laterally; pygidial axis of even dorsoventral height, in lateral section steeply curved (see Owens [1973] for more).

Discussion: This species is known from the Ludlow of Gotland, Sweden, and the Wenlock and Ludlow of the British Isles. It was chosen as the type because it is better preserved than the other taxa assigned to "*Plesiowensus*."

"*Plesiowensus*" *confossus*
(Owens, 1973)

Proetus (*Lacunoporaspis*) *confossus* Owens 1973: 15–17, pl. 4, figs. 1–8; Thomas, 1978: 38, pl. 9, figs. 10, 14.

Diagnosis: Genal spine furrow follows course of lateral edge of anterior border furrow; intraoccipital lobes do not bulge significantly laterally beyond margin of glabella; genal spines extend back to third thoracic segment; anterior brim of cephalon rounded; S1 flexes transversely posteriorly and anteriorly; facial suture anterior of eye does not deflect sharply, about 20° or less from sagittal line drawn from inner edge of eye; genal spine furrow straight, intersects midpoint of genal spine; anterior border very thin, ledge developed only farthest anteriorly with length equal to sagittal length of L0 medially; genal spine triangular lappet curving sagittally posteriorly; S3 flexing posteriorly, inclined at 45° angle relative to transverse line; S2 flexing posteriorly; longitudinal lineations on anterior border rim of cephalon generally straight but wavy and separated; glabella anteriorly, in lateral view, inclined at 40° angle; dorsal pygidial border absent; 10 pygidial axial rings; pygidial axial rings flex posteriorly, axis of even dorsoventral height, with rounded terminus (see Owens [1973] for more).

Discussion: This species is known from the Wenlockian, Dudley, United Kingdom.

ARCTICORMISTONIA, NEW GENUS

Type Species: *Basidechenella inflecta*, new species [nomen nudum] (Ormiston, 1975a), now *Arcticormistonia edgecombei*, new species.

Assigned Taxa: *Dechenella* (*Basidechenella*) *laticaudata* Ormiston, 1967, and possibly *Dechenella* (*Basidechenella*) *dombrowiensis* Sobolew, 1909.

DIAGNOSIS: Intraoccipital lobes posteriorly not separated from L0, flex strongly anteriorly; margin of glabella near eyes straight; facial suture deflects sharply laterally past exsagittal margin of inner edge of eye; posterior edge of librigenae posterior of eyes flexing anteriorly, then posteriorly; anterior brim of cephalon developed as flattened ledge; anterior border narrow ledge; longitudinal lineations on anterior border rim of cephalon closely packed and linear; anterior portion of pygidial axial rings flexes anteriorly.

ETYMOLOGY: Compounding Arctic, for the paleobiogeographic province that this genus occurs in, with Ormiston, for Dr. A. Ormiston who has done the seminal work on Devonian proetids and the paleobiogeography of the Canadian Arctic.

DISCUSSION: This genus is erected to contain the taxa *Arcticormistonia edgecombei*, new species and *A. laticaudata* (Ormiston, 1967). Ormiston (1967) recognized a new species, *Dechenella* (*Basidechenella*) *laticaudata*, based on two cranidia and pygidia from late Lower or early Middle Devonian strata of Prince of Wales Island (Ormiston, 1967: 101, pl. 13, figs. 12–15). He assigned the species to this genus on the basis of its indistinct intraoccipital lobes, its well-developed interpleural furrows, and the facial suture anterior of the eyes that deflects laterally. Although these traits are developed in some of the species assigned herein to *Basidechenella*, these characters appear to be primitive for the Proetinae. Therefore, they may not be good features to deduce the generic affinities of specific forms. This species and *Arcticormistonia edgecombei*, new species bear the following characters that set them apart from *Basidechenella*: intraoccipital lobes do not bulge exsagittally significantly beyond the margin of the glabella, genal spines extend back only to the third or fourth thoracic segment (not known for *A. edgecombei* but coded this way based on their condition in *A. laticaudata*), margin of the glabella near the eyes is straight, intraoccipital lobes posteriorly not separated from L0 (derived in all except *Basidechenella maura* and *B. kayseri*), interpleural furrows relatively deep, anterior border developed as a narrow ledge, posterior edge of librigenae posterior of eyes flexing anteriorly, then posteriorly (indeterminate in *A. laticaudata*), and S3 is transverse, inclined at 10° angle measured from a line through the anterior end of S3 and parallel to the posterior border, intraoccipital lobes flex strongly anteriorly, and L0 flexes strongly posteriorly medially. The condition of the genal spines could not be determined in *Arcticormistonia edgecombei*, new species, and *A. laticaudata* (Ormiston, 1967) was used to code these characters.

Arcticormistonia edgecombei, new species

Basidechenella inflecta Ormiston, 1975a: 398, pl. 4, fig. 17 (nomen nudum), non pl. 5, figs. 24, 25.

DIAGNOSIS: Same as for genus and, in addition, glabella contacts anterior border furrow, anterior end of eyes opposite lateral edge of S2.

TYPES: Holotype complete specimen except for distal tips of genal spines, Ormiston (1975a: pl. 4, fig. 17) from GSC locality C-8225, Prince of Wales Island, the Canadian Arctic.

ETYMOLOGY: This species is named for Gregory D. Edgecombe, who introduced me to systematic analysis of trilobites, and with whom I have quaffed many a Rolling Rock.

DESCRIPTION: Cephalic length (sag.) 55% of width; anterior border short (equal to length of L0 medially), sloping dorsally posteriorly; anterior border furrow deep and narrow; longitudinal lineations on anterior border rim of cephalon closely packed and linear; fixigena smoothly decline to anterior border furrow. Prosopon of small granules. Anterior margin of glabella barely contacts anterior border furrow. Anterior portion of glabella conical. Facial sutures moderately divergent anteriorly at approximately 40° angle from exsagittal line. Glabellar furrows developed as faint markings. S3 nearly transverse, deflected posteriorly about 10° from exsagittal line; S2 medially directed posteriorly, deflected about 45 degrees from transverse line; S1 flexes weakly transversely at posterior and anterior ends, S1 and S2 laterally contact axial furrows. Maximum length and width of glabella equal. Glabella constricted more sharply anterior of S2. S0 well incised, anterolateral portion of L0 straight. Intraoccipital lobes flex strongly anteriorly laterally, not separated posteriorly from L0, do not deflect strongly beyond lateral margins of glabella. Tubercle developed on posteromedian portion of L0. L0 flexes strongly posteromedially. Posterior portion of eye adjacent to lateral portion of L0 anterior of intraoccipital lobes, extending to point opposite distal tips of S2. Eye sits on broad flat pedestal developed on free cheek. Palpebral lobes broadest at point less than 50% along length (exsag.) of eye. Librigena shallowly sloping medially, more steeply curved near lateral border furrow. Posterior border furrow laterally first flexes anteriorly, then posteriorly, narrow and deep.

Thorax with 10 thoracic segments. Axis 32% width of thorax. Fulcra-Fortsatz developed on anterior portion of thoracic pleural segments, about halfway between axis and lateral edges of pleural tips.

Pygidial length 45% width; pleural furrows prominently incised, interpleural furrows moderately incised; apodemes present; axis of even height, with rounded terminus, in sagittal section steeply curved; anterior edge of axis narrow (tr.), about 60% width of pleural field; axial rings flex anteriorly medially and posteriorly around medial bulge; 11 axial rings present, nine pleural segments. Border prominently developed, parallels pleurae, narrow, posteriorly narrower or equal to width anterolaterally; pleurae gently rounded, slightly curving ventrally laterally; anterior margin of pleurae convex, transitions between pleural bands and pleural furrows gradual. Axis with rounded terminus, in sagittal section steeply curved.

DISCUSSION: This species closely resembles *Arcticormistonia laticaudata* (Ormiston, 1967). The chief differences between them are the slightly larger eyes of *A. laticaudata*, whose anterior ends extend to a point between the lateral tips of S2 and S3, one additional pygidial axial ring in *A. laticaudata*, the relation of the glabella to the anterior border furrow, the anterior border furrow is narrower and deeper in *A. edgecombei*, and the slightly weaker transverse flexure of S1 both at its anterior and posterior ends. There appear to be taxonomic representatives from several diverse phyletic lines present in the Arctic, and this new species appears to represent one of the important transitional forms in the evolution of the morphologically diverse Proetinae.

This taxon bears a strong resemblance to some members of a monophyletic *Basidechenella*. It also lacks a series of derived characteristics that serve to distinguish it from *Basidechenella*, *Lacunoporaspis*, and *Dechenella*. Ormiston (1967) commented that the closely related *A. laticaudata* was related to Richter's (1912: 281, pl. 18, figs. 9–14) and Kielan's (1954: 21, pl. 2, fig. 8) "*Dechenella (Basidechenella)*" *dombrowiensis* (Sobolew, 1909). This conclusion seems correct; however, because specimens of "*D.* (*B.*)" *dombrowiensis* could not be obtained for this study, these conclusions cannot be corroborated. However, based on the type species, "*D.* (*B.*)" *dombrowiensis* differs from a monophyletic *Basidechenella* in the same features that *A. laticaudata* and *A. edgecombei* do. Therefore, *dombrowiensis* may also be a member of the genus *Arcticormistonia*. However, the poor quality of Richter's (1912) and Kielan's (1954) figures makes this difficult to ascertain. These phylogenetic issues are not pursued further because the purpose of this study is to explicitly discuss the origins of the Middle Devonian proetid fauna of ENA in light of a higher level phylogeny of the Proetinae. Although issues such as the biogeographic affinites and shifting area relationships of the genus *Arcticormistonia* are of interest, they are ancillary to this analysis and will be pursued at a later date.

Some specimens figured by Ormiston (1975a: pl. 5, figs. 24, 25) as *Basidechenella inflecta* must be excluded from *Arcticormistonia edgecombei* as they differ from the type specimen. The cranidium (shown as pl. 5, fig. 24) has a prominently expanded glabella, the facial sutures are parallel anterior of the eye, the anterior border is developed as a narrow, flattened ledge, L0 does not deflect significantly posteriorly medially, and the anterior edge of the glabella is prominently separated from the anterior border furrow. In these respects the cranidium figured by Ormiston (1967) is very similar to *Coniproetus tumidus* (Hall and Clarke) from the Eifelian of the Appalachian, Illinois, and possibly Michigan Basins, and it may be a form closely related to that species but occurring in the Pragian of the Arctic Faunal Province. As discussed above under the section on *Coniproetus folliceps*, this species is referred to as *C.* sp. aff. *tumidus*. The pygidium (shown in pl. 5, fig. 25) differs from that of the type of *A. edgecombei* in the condition of a few characters. In particular, the pygidial pleurae deflect more strongly posteriorly than in *A. edgecombei*, and there are 13 (rather than 11) pygidial axial rings. However, the structure of the pygidial axial rings and the depth of the interpleural furrows are very similar to what is found in *A. edgecombei*, and this pygidium may be another species of *Arcticormistonia* closely related to the species placed in that genus herein.

A new specific name was used rather than *inflecta* to avoid confusion, as Ormiston's (1975a) nomen nudum contains some specimens that appear to differ in the state of several characters when compared to the type of the species.

CRASSIPROETUS STUMM, 1953A

TYPE SPECIES: *Crassiproetus traversensis* (Stumm, 1953a).

DIAGNOSIS: Prominent anterior border ridge; small space between glabella and anterior border ridge; S0 curves forward anteriorly; L0 short medially; genal spines very small or absent, glabella large, comprising most of width of cephalon; anterior of eyes, facial sutures weakly divergent; librigenal field next to eyes strongly expanded and steeply arched; preglabellar field absent; S3 flexing posteriorly; glabella anteriorly steeply arched, developed as a vertical wall in lateral aspect; longitudinal lineations on anterior border rim of cephalon closely packed and linear; large pygidium, nearly equal in length to thorax; pygidial axis strongly arched, of constant width back to at least third axial ring; at least 13 axial rings; anterior portion of pygidial axial rings medially flex anteriorly and then distally first posteriorly, then anteriorly, then posteriorly; interpleural furrows faint or absent.

DISCUSSION: This genus is treated extensively in the section on the origin of the Middle Devonian proetid fauna. However, some comments are necessary here. Stumm (1953a) introduced *Crassiproetus* as a new subgenus of *Proetus*. Here it is elevated to generic status, as it is clearly genealogically distinct from the genus *Proetus*. In the section on the origin of the Middle Devonian proetid fauna in Eastern North America, all known species of *Crassiproetus* are subjected to a detailed phylogenetic analysis. However, taxa incorrectly assigned to this genus and the basis for their exclusion are discussed here. In addition, taxonomic considerations regarding the status of *Crassiproetus* are treated here. The oldest complete known species of *Crassiproetus*, *C. globosus* Maximova, 1960, from the Pragian or Emsian of central Kazakhstan (Maximova, 1960, 1968) (using the stratigraphic conceptions of Kirchgasser et al., [1985]), was used for character analysis in the higher-level phylogeny of the Proetinae. There are, however, some characters used in this higher-level analysis that do show variation within the genus. These characters are 1, 2, 10, 17, 18, 20, 24, 25, 29, 33, and 35 (see table 1), and they were coded on the basis of their condition in *C. globosus*.

Several authors have suggested that *Crassiproetus* should be placed in a higher taxonomic category to document its distinctness from the remainder of the Proetinae. Such taxonomic decisions have been made for at least two chief reasons. The first is based on taxonomy in the evolutionary systematics mode. Several authors have used the presence of certain distinctive autapomorphic traits in *Crassiproetus* as justification for elevating the group to a high taxonomic level. These traits include the globose cephalon and the long, prominently arched pygidium. Conclusions on the taxonomically distinct status of *Crassiproetus* have also been propounded on the basis of traits shared by species of *Crassiproetus* and *Schizoproetus*. Both of these arguments are rejected herein.

Autapomorphous traits were first used to justify classifying *Crassiproetus* at a high level of the taxonomic hierarchy by Osmolska (1970a). She erected a new subfamily, the Crassiproetinae, to accommodate the genera *Crassiproetus* Stumm, 1953a, and *Conophillipsia* Roberts, 1963. Osmolska (1970a) diagnosed this subfamily on the basis of its strongly arched, globose cephalon and its vaulted, long pygidium. *Conophillipsia* was originally defined on the basis of a single species, *C. brevicaudata*, by Roberts (1963: 25–

27; pl. 6, figs. 13–20). This taxon was demonstrated to be synonymous with *C. breviceps* (Mitchell, 1918) by Engel and Morris (1984), and they described several other closely related species. The species treated by Engel and Morris (1984) as *Conophillipsia breviceps* and by Roberts (1963) as *C. brevicaudata* appears to lack the derived traits of the Proetinae. In particular, it lacks the triangular projection, or Fulcrum-Fortsatz, on the anterior portion of the anteriormost pygidial pleural segment; it has pygidial pleurae developed behind the pygidial axis; the lineations on the anterior brim of the cephalon are also visible in dorsal view on the interior edge of the genal spine; L0 is long medially; the librigenae lacks a flattened pedestal circumscribing the eye; and the preannulus is absent from the articulating half-rings of the thorax. The limited material of this species does share some characteristics with members of the "*Thebanaspis* clade"— in particular, the genus *Monodechenella* (Stumm, 1953a)— such as the prominent lineations on the pygidial doublure, the weakly divergent facial sutures anterior of the eye, and the faint or absent pygidial interpleural furrows. This relationship is substantiated in a detailed manner in the section on the origin of the Eastern North American proetid fauna that treats the "*Thebanaspis* clade." The affinity between *C. breviceps* and *Crassiproetus* is rejected on the basis of the latter's possession of the morphological hallmarks of the Proetinae, which are absent in the former. Similarities between the two genera appear to be convergences rather than homologous characters. In particular, apparent convergent traits are the weakly incised pygidial interpleural furrows of *Conophillipsia* (which actually characterize only the derived members of *Crassiproetus* and not *C. globosus*, which has moderately incised pygidial interpleural furrows), its weakly divergent facial sutures anterior of the eye, and its short genal spines. Other traits of *C. breviceps*, such as L0 deflected posteriorly medially, appear to have no homologue in *Crassiproetus*. Therefore, the association of *Conophillipsia* and *Crassiproetus* in a subfamily to the exclusion of other taxa is rejected. A similar conclusion was reached by Owens (1973).

The two unique traits of *Crassiproetus* recognized by Osmolska (1970a), and used to justify elevation of this taxon to distinct subfamilial status, are listed among the characteristics Stumm (1953a) used to diagnose *Crassiproetus* as a new subgenus of *Proetus*. Thus, Stumm (1953a) concluded that these unique traits conferred subgeneric status on *Crassiproetus*, whereas Osmolska (1970a) concluded that they were subfamilial characters. Until a more objective way of using such gestalt phenetic conclusions emerges, such approaches are not followed. To elevate *Crassiproetus* to a new subfamily on the basis of these autapomorphies would make the Proetinae paraphyletic. In addition, this would obscure the pattern of stepwise evolution manifested between the genera *Proetus* and *Dechenella*. Therefore, this solution is rejected. To keep *Crassiproetus* as a subgenus of *Proetus* would make *Proetus* polyphyletic. Such a solution is also untenable.

Lutke (1990) proposed that *Crassiproetus* be placed within a monotypic tribe, the Crassiproetini. He suggested that the similarities between the pygidia of *Schizoproetus* and *Crassiproetus* were convergences. He also recognized the clear affinities of *Crassiproetus* with the rest of the Proetinae. His rationale for elevating the genus to a distinct tribe was based on its unique features that he related to "divergency and taxonomic importance" (Lutke, 1990: 47). However, Lutke (1990) also suggested that the affinities of this taxon might lie with *Hedstroemia* (Pribyl and Vanek), which is referred to herein as part of the "*Thebanaspis* clade." This relationship is not suggested herein because, as discussed above, this clade does not belong to the Proetinae sensu stricto. Therefore, any similarities between *Crassiproetus* and this clade are viewed as convergences.

Similarly, Holloway (1980) claimed that the affinities of *Crassiproetus* lay with a member of a group that is herein considered part of the "*Thebanaspis* clade." This group is considered in greater detail in the section on *Monodechenella* that deals explicitly with the origin of the Middle Devonian Proetid fauna. Holloway (1980) asserted that the pygidium of *Crassiproetus globosus* closely resembled what is referred to herein as *Hedstroemia delicata* (Hedstrom, 1923), and its close relative, figured in Owens (1973) as "*Schizo-*

proetus" aff. *delicatus* but referred to herein as *Milesdavis eldredgei*, new species. *Milesdavis eldredgei* is known only from two pygidia. The chief similarity between *Milesdavis eldredgei* and *Crassiproetus* is the form of the pygidial axial rings, which flex anteriorly medially and posteriorly laterally. *Milesdavis eldredgei* appears related to *Hedstroemia delicata* on the basis of its anterior portion of the pygidial pleural bands, which are elevated significantly above the posterior portion of the pleurae. In addition, *M. eldredgei* lacks the Fulcra-Fortsatz on the anterior pleural bands of the pygidium, and it has pleurae developed behind the pygidial axis. Hence, it is excluded from the Proetinae and placed in the "*Thebanaspis* clade." However, in *H. delicata* the pygidial axial rings are straight medially. In *Milesdavis eldredgei* and the related *Monodechenella* the medial portion of the pygidial axial rings deflects posteriorly. The chief reason for Holloway's (1980) assertion that *Crassiproetus globosus* and *H. delicata* are related was the structure of the pygidial axial rings. Because these characters appear to be variable within the Proetinae and the "*Thebanapsis* clade," presuming affiliation on the basis of this character does not seem justified; instead, these taxa appear to belong to two different genealogical groups.

Other authors, such as Ormiston (1967) and Owens (1973) (although both with some reservations), suggested that *Crassiproetus* should be excluded from the Proetinae on the basis of what they thought was an affinity with *Schizoproetus* Richter, 1912. Both authors united these taxa on the basis of their multisegmented pygidium. Owens (1973) also suggested that they both shared a smooth glabella. Owens (1973) used these two features to unite *Schizoproetus* in the subfamily Schizoproetinae Yolkin, 1968. (The status of Schizoproetinae as a valid subfamilial name is not accepted herein and this is discussed below under the heading of the genus *Schizoproetus*.) A multisegmented pygidium appears to have evolved several times in different proetine genera. The pygidium of exponents of *Schizoproetus*, such as *S. onyx* Richter, 1912, is considerably larger than that found in the primitive members of *Crassiproetus*, such as *C. globosus* and *C. stummi*, new species (discussed below). Similarities between the pygidia of *Crassiproetus traversensis* Stumm, 1953a, the type of the genus, and *Schizoproetus* do not outweigh the many morphological traits that unite *Crassiproetus* as a monophyletic unit and that group *Schizoproetus* with the genus *Dechenella*. In addition, a smooth glabella is shared by several other taxa (e.g., *Gerastos cuvieri*, *Proetus concinnus*, and *Coniproetus folliceps*), and it is probably primitive for the Proetinae. Moreover, it does not even appear to characterize *Schizoproetus*. However, there are some additional convergences between *Crassiproetus* and *Schizoproetus* that need to be pointed out. For instance, in both taxa the margin of the glabella near the eyes is straight and the posterior border furrow is straight (variable for derived members of *Crassiproetus*). In addition, several derived members of *Crassiproetus* have faintly incised interpleural furrows, a common trait of the sister taxon of *Schizoproetus*, *Schizoproetoides* Ormiston, 1967. However, all members of *Crassiproetus* lack the following traits (see table 1) developed in *Schizoproetus*: 6, 9, 21, 26, 43, 46, 47, and 50. Therefore, the close evolutionary affinity of *Schizoproetus* and *Crassiproetus*, which both Ormiston (1967) and Owens (1973) questioned, is not supported herein.

Richter and Struve (1959: 385) did, however, recognize the affinity *Crassiproetus* shared with other members of the genus *Proetus*, and accordingly they designated it a subgenus of *Proetus*. Although this overall evolutionary affinity is supported on the basis of the phylogeny herein, *Crassiproetus* is not construed as a subgenus of *Proetus* in order to retain the monophyly of *Proetus*. Ludvigsen (1987) also briefly discussed *Crassiproetus*. He was correct in noting that "the long, multisegmented pygidium has been a source of considerable confusion in the classification of *Crassiproetus*" (Ludvigsen, 1987: 681). Ludvigsen (1987) also concluded that the affinities of *Crassiproetus* lie with *Proetus*, and if the length and convexity of the *Crassiproetus* pygidium are ignored, it is very similar to pygidia typical of *Proetus*. Ludvigsen (1987) further noted that *Cummingella* Reed, 1942, and *Bollandia* Reed, 1943, are probably related to *Crassiproetus*. These two genera certainly belong to the Proetinae as discussed above, but their relationships are not assessed in detail herein.

There is another important species that is not closely related to *Crassiproetus*, but which has been assigned to this genus by Owens (1973). ?"*Crassiproetus*" *curtisi* Owens, 1973, was assigned to *Crassiproetus* on the basis of its ovate, smooth glabella and large pygidium by Owens (1973). This specimen is poorly preserved, and it is hard to make definitive phylogenetic conclusions with the available material, British Geological Survey GSb 4687. However, it appears that the condition of the thorax and pygidium is unlike that which characterizes the Proetinae. For instance, the preannulus on the thoracic articulating half-rings is absent, as is the Fulcrum-Fortsatz. For this reason, ?"*Crassiproetus*" *curtisi* is excluded from the Proetinae, and is therefore not considered to be related to true *Crassiproetus*. Pribyl (1970) concluded that it might be related to *Latiproetus* Lu, 1962, but Owens (1973) disputed this claim. As mentioned above, *Latiproetus* may be related to the "*Thebanaspis* clade."

Using the conception of *Crassiproetus* advocated herein, the range of this genus is Upper Silurian–Givetian. All taxa known are from Eastern North America except *C. globosus*, which is from central Kazakhstan. However, there is the intriguing mention of *Crassiproetus*, new species from the Lower Devonian (Onesquethaw) of Western Canada in Corgan (1963), but this specimen is not figured or described and it could not be obtained. Therefore, this potentially interesting geographic range expansion for this genus cannot be accepted at this time. The pygidia from the Upper Silurian West Point Formation of Gaspe, Quebec, shown in Northrop (1939: pl. 26, figs. 8, 9) and assigned to *Proetus turgidus* bear a strong resemblance to *Crassiproetus*. In particular, the pygidial axis is strongly arched in lateral and posterior views, there are 13 axial rings, the axis is of roughly constant breadth across the first 3 rings, and the interpleural furrows are faint. However, in this species the anterior portion of the pygidial axial ring does not medially flex anteriorly and then distally first posteriorly, then anteriorly, then posteriorly, which is characteristic of *Crassiproetus*. These specimens are tentatively placed in *Crassiproetus*. Although more material needs to be collected to be sure, the present range of the genus is extended to the Upper Silurian. Northrop's figured cranidium (pl. 26, fig. 10) may also belong to *Crassiproetus*, but it is too poorly preserved to make a positive identification. *Crassiproetus turgidus* is discussed in greater detail under the section on the phylogeny of *Crassiproetus* in the section dealing with the biogeographic origin of the Middle Devonian proetid fauna of ENA.

Crassiproetus globosus Maximova, 1960

Proetus (*Crassiproetus*) *globosus* Maximova 1960: 256, pl. 54, fig. 3; Maximova, 1967: 782, pl. 3, figs. 1, 2; Maximova, 1968: 17–18, pl. 1, figs. 2–5.

DIAGNOSIS: Same as for genus and, in addition, anterior brim of cephalon rounded ledge; posterior border furrow straight; posterior edge of lateral occipital lobes straight; posterior portion of glabella in anterior view flat; anterior border very thin ledge, developed only farthest anteriorly; pygidial interpleural furrows weakly incised; 14 axial rings; axis steeply curved.

DISCUSSION: This taxon was used to represent the genus *Crassiproetus* because it is the oldest member of that genus excluding the incomplete *C. turgidus* (Northrop, 1939). (See the discussion on the origin of the Middle Devonian Eastern North American proetid fauna for more discussion on this.) In addition, *C. globosus* has a number of primitive retentions that appear to be lost by the younger members of this genus. It appears that even the earliest member of this genus was quite morphologically distinct from other members of the Proetinae. Perhaps intermediate forms may be discovered from Kazakhstan or Laurentia that may shed more light on the early relationships of *Crassiproetus*. However, on the basis of the phylogeny herein, it does appear to be derived relative to a series of Arctic and Baltic taxa. The origins of this genus appear far less clear than its subsequent evolutionary history in Eastern North America.

VALIDITY OF SUBFAMILY DECHENELLINAE

Several authors have argued that all or most of the taxa discussed below be assigned to the subfamily Dechenellinae or family Dechenellidae Pribyl, 1946. For instance, Pribyl (1946), Richter and Richter (1950), Stumm (1953a, 1953b, etc.), Richter and Struve (1959), Ormiston (1967, 1971, 1975a, 1975b, 1976), Pillet (1972), Owens (1973), Lutke (1980), Cooper (1982), and others advocate that some or all of the following genera: *Basidechenella*, *Lacunoporaspis*, *Ormistoniella*, *Dechenella*, *Pedinodechenella*, *Humeia*, *Camsellia*, *Fuscinipyge*, *Schizoproetus*, *Schizoproetoides* should be placed in a subfamily or family separate from the Proetinae. In addition, all of these authors recognized that the "Dechenellinae" were clearly derived from the Proetinae (e.g., see Ormiston [1967: fig. 7] or Owens [1973: text fig. 12]). Because of these suggested evolutionary relationships, and those also manifest in this analysis, this taxonomic decision is not advocated herein because it violates the monophyly criterion of Hennig (1966). To preserve the monophyly of the Proetinae, the subfamily Dechenellinae Pribyl, 1946, is not accepted. Therefore, all the genera listed below that were traditionally assigned to the Dechenellinae are instead placed in the Proetinae. Another possible taxonomic solution would be to erect the subfamily Dechenellinae along with several subfamilies each based on single genera that had traditionally been assigned to the Proetinae. This solution is not followed here because it would require the creation of several monotypic subfamilies.

In addition to the taxonomic problems with the subfamily Dechenellinae, certain taxa have been vaguely assigned to the Dechenellinae that need to be excluded not only from this taxonomic category, which is rejected herein, but also from the rest of the Proetinae. Chief among these taxa is the genus *Benesovella* Chlupac, 1969. Species in this genus such as *B. emarginata* (Barrande, 1852), shown in Snajdr (1980: 170–172, pl. 32, figs. 10–15), lack the Fulcrum-Fortsatz on the anteriormost pygidial pleurae, have very long (sag.) L0, and S2 is concave (not convex) anteriorly, and therefore it does not satisfy the characters for Proetinae group membership. Instead, its affinities probably lie with *Koneprusites* Pribyl, 1964, as Pribyl (1965) suggested. This group is probably closely related to the Proetinae, but is not treated herein. In addition, Yolkin and Sheltonogowa (1974) assigned several taxa to the Dechenellidae that belong to the genus *Warburgella*. As the members of this genus fail to satisfy the criteria for Proetinae group membership, and because the dechenellids are a group that is nested within the Proetinae, these taxa cannot be assigned to the Dechenellinae. Instead, they should be placed in the Warburgellinae Owens, 1973. As discussed above, *Monodechenella*, a member of the "*Thebanaspis* clade," also does not belong in the Proetinae, and any similarities it shares with *Dechenella* are convergences. This has important implications for the taxonomy generated by Pillet (1972). He erected a new subfamily of the Dechenellidae, the Mondechenellinae, to encompass the genus *Monodechenella*. This taxonomic decision is not valid because the family Dechenellidae is not valid, and more importantly, *Monodechenella* is not a member of, nor is it derived from, the Proetinae.

BASIDECHENELLA RICHTER, 1912

TYPE SPECIES: *Basidechenella kayseri* Richter, 1912.

DIAGNOSIS: Margin of glabella bulging at midline of eye; genal spine extends posteriorward to fifth thoracic segment; S1 flexes transversely posteriorly and anteriorly; anterior border developed as long ledge; facial sutures anterior of eyes parallel each other for short distance; S3 flexing posteriorly, inclined at 45° angle; tubercle on L0 present; glabella at anterior end, in lateral view, inclined at 40°; facial sutures anterior of eyes smoothly convex laterally anterior of portion of facial suture, which parallels sagittal line; S0 flexes anteriorly; 10–14 pygidial axial rings; medially, anterior margin of axial rings weakly deflected posteriorly, weakly deflected forward distally; pygidial interpleural furrows weakly incised.

DISCUSSION: There has been considerable confusion regarding the evolutionary relationships of what is here referred to as *Basidechenella*. Originally, this genus was classified as a subgenus of *Dechenella* Kayser, 1880. However, the species included in *Basidechenella* lack several of the features shared by the type of the genus *Dechenella*, *Dechenella verneuili* (Barrande, 1852), and its close relatives. For instance, in *Basidechenella* the posterior border furrow does not flex backward distally, S0 and L0 do not curve prominently anteriorly medially, the pygidial axis is not flat in sagittal section, the pygidial border is not developed as a flattened shelf and is not shorter posteriorly than anterolaterally, the posterior edge of the intraoccipital lobes does not flex anteriorly laterally, and the lateral glabellar bulge near the midline of the eye is significantly smaller than its condition in *Dechenellla* Kayser, 1880. On the basis of the condition of these characters, either *Basidechenella* must be excluded from the genus *Dechenella* or a very large genus *Dechenella* needs to be defined. The latter option is not recommended.

Several authors have commented on the relationship between those European forms assigned to *Basidechenella* by Richter (1912) and Richter and Richter (1950) (e.g., *B. kayseri* and *B. dombrowiensis*) and those North American forms subsequently assigned to *Basidechenella* by Stumm. Stumm (1953a and subsequent publications) assigned several species to *Basidechenella*. He remarked that these species differed chiefly from the type of the subgenus on the basis of the intraoccipital lobes not being fully separated posteriorly from L0, the intraoccipital lobes not bulging as far laterally, and the glabella not being as constricted anteriorly in *B. kayseri*. These differences are evident in Richter's (1912) illustrations of *Basidechenella kayseri* (pl. 18, figs. 1–8). The diagnosis that Richter and Struve (1959: 388) presented of *Dechenella* (*Basidechenella*) stated that the glabella tapers gradually, the lateral furrows are faint, the intraoccipital lobes are not separated, and the pygidial axis has 12 or 13 rings (should be 14). There are certain forms herein assigned to the genus *Basidechenella* that fit this diagnosis, but other taxa that do not entirely conform to this diagnosis. If these species were to be excluded from *Basidechenella*, this genus would be paraphyletic. Instead of creating a paraphyletic *Basidechenella*, the generic diagnosis is slightly emended. It appears that some members of *Basidechenella*, particularly the Eastern North American species, do have their intraoccipital lobes separated from L0 and bulging significantly exsagittally whereas others do not. Therefore, Stumm's (1953a) diagnosis of *Basidechenella* in which he stated that the large, prominent occipital lobes are one of the diagnostic characters of the genus (subgenus) is either incorrectly translated from Richter (1912), or it is an altered diagnosis of *Basidechenella* that is also not a valid characterization of the genus. In order to treat the genus *Basidechenella* as an actual phylogenetic unit, the diagnosis given above is appropriated as the new diagnosis of this genus. Specimens of *Basidechenella dombrowiensis* (Sobolew, 1909) could not be obtained for study, and thus it could not be determined if this species actually belonged to the genus *Basidechenella*. However, specimens of this species figured in Richter (1912: pl. 18, figs. 9–14) and Kielan (1954: pl. 2, fig. 8) suggest that it may lack some of the features diagnostic of the genus. In particular, the pygidial axial rings appear to be straight in their transverse course rather than flexing posteriorly, S0 and the posterior margin of the glabella does not arch anteriorly medially, and the lateral margins of the glabella near the eye do not appear to bulge laterally. This is suggestive of a possible relationship with *Schizoproetus* rather than *Basidechenella*.

The detailed evolutionary relationships of species of *Basidechenella* are considered in the section on *Basidechenella* that deals with the origin of the Middle Devonian Eastern North American Proetid fauna. However, a comment on the phylogenetic relationships of this genus is necessary here.

Hessler (1963) made a few brief comments on *Basidechenella* in his treatment of Lower Missippian trilobites that are worthy of mention. He suggested that there was a close evolutionary relationship between *Basidechenella* and the Carboniferous *Pudoproetus* Hessler, 1963. This affinity is dubious, as any features shared by these taxa are primitive retentions. However, Hessler (1963) was correct in recognizing the important role that

Basidechenella plays as a form transitional between *Proetus* and what were viewed as subgenera of *Proetus*, but are here treated as genera (e.g., *Coniproetus*, *Longiproetus*, *Gerastos*, and *Pudoproetus*) and taxa assigned to the genus *Dechenella* Kayser, 1880. *Basidechenella* is positioned centrally in a phylogeny of the Proetinae, possessing some, but not all, of the traits that characterize *Dechenella*. (*Dechenella* is discussed in greater detail below.) However, the important morphological characteristics developed in *Basidechenella*, which indicate that they share a more recent common ancestry with *Dechenella* than with *Proetus*, include the effacement of the pygidial interpleural furrows, the lateral bulging of the margins of the glabella, the anterior brim of the cephalon developed as a flattened ledge, and the facial sutures briefly paralleling each other anterior to the eyes.

Ormiston (1967) also considered the phylogenetic placement of *Basidechenella*. In his phylogeny of the "Dechenellinae," Ormiston (1967: 70, fig. 7) placed *Basidechenella* as the sister taxon of *Cyrtodechenella* Richter and Richter, 1950, and *Cyrtosymbole*, and he held that these two genera were in turn sister to *Dechenella*. *Cyrtodechenella* and *Cyrtosymbole* are not treated herein, as the "cyrtosymbolinids" are rampantly polyphyletic (Fortey and Owens, 1975) and in need of substantial revision. They also appear not to be directly related to the evolution of the Proetinae. The relationship between *Basidechenella* and *Dechenella* appears less ambiguous. Ormiston (1967) was correct in noting that these two taxa do appear to be related, although they do not appear to be as closely related as he suggested. There are several other genera that appear to be more closely related to *Dechenella* than *Basidechenella*, and these are both shown in the cladogram in figure 6 and discussed below. For the same reason, Lutke's (1980: fig. 26) phylogeny, which places *Basidechenella* and *Dechenella* as sister taxa, is not supported.

The phylogenetic analysis herein also does not support Ormiston's (1967) contention that *Basidechenella* is derived from, or closely related to, *Longiproetus*. These taxa differ by the absence of the derived state for several characters in *Longiproetus*. These characters include 0, 1, 10, 11, 14, 15, 16, 19, 20, 36, and 37 (see table 1).

Ormiston (1967, 1975a) also introduced several species from the Lower Devonian of the Canadian Arctic that he placed in the genus *Basidechenella*. However, as discussed above, these taxa belong both to a new genus, *Arcticormistonia*, and to *Coniproetus* Alberti, 1966. These taxa can be distinguished from species of *Basidechenella* on the basis of several characters, which are presented above in the sections on these genera. The pygidium of another species from the Lower Devonian (Onesquethawan) of the Yukon has been assigned to *Basidechenella* by Corgan (1963: 153, fig. 4). The specimen is too poorly preserved to ascertain with certainty the accuracy of this assignment. However, the pygidial interpleural furrows appear to be too deeply incised for *Basidechenella*, and it is tentatively placed in *Lacunoporaspis* (see below).

Stumm (1953b) suggested that his "?*Dechenella* (*Dechenella*)" *angustifrons* (Hall, 1861), here termed *Coniproetus angustifrons*, might belong to *Basidechenella*. However, it differs in the state of several characters, as discussed under *Coniproetus*, and is very distantly related to *Basidechenella*. (This species is discussed further in the section on the Emsian–Eifelian proetids of ENA.) Stumm (1953b) also suggested that his "*Dechenella* (*Dechenella*)" *halli* (Hall, 1861) might be a species of *Basidechenella*. This species has since been designated *Mannopyge halli* by Ludvigsen (1987). As discussed above, it is a member of the "*Thebanaspis* clade," and therefore does not satisfy many of the criteria for Proetinae group membership. Instead, this species is treated as a species of *Monodechenella* Stumm, 1953a, which is no longer a subgenus of *Dechenella*, and which is outside of the subfamily Proetinae.

Stumm (1953a: 122–123, pl. 5, fig. 3) figured a cephalothorax that he designated *Dechenella* (*Basidechenella*) sp. C from the Thunder Bay Limestone (upper Givetian, Taghanic). This specimen is interesting but poorly preserved; however, the anterior portion of the thoracic pleural segments are straight and lack a Fulcrum-Fortsatz. For the other diagnostic features of the Proetinae the condition of the characters could not be ascertained. Another specimen is known from the Tully Limestone (AMNH unnumbered collections [upper Givetian, Taghanic] that closely resembles this new species). This specimen may be an early phillipsiid, but more material is required before any definitive statement can be made. It is excluded from *Basidechenella* and from the Proetinae on the basis of the condition of the thoracic pleurae.

Pillet (1972) discussed several taxa that he assigned to the new genus *Pseudodechenella*, which he formerly assigned to *Basidechenella*. However, as discussed in the section on the genus *Coniproetus*, phylogenetic analysis based on the character evidence presented herein indicates that these taxa should be assigned to *Coniproetus*.

Fagerstrom (1961) assigned a series of cephala and pygidia to *Dechenella* (*Basidechenella*) *formosensis*. These forms are conspecific with *Monodechenella halli* (Stumm, 1953b) (see Ludvigsen [1987] for detailed illustrations), and therefore do not belong to *Basidechenella* or to the Proetinae but rather to the "*Thebanaspis* clade."

Basidechenella rowi (Green, 1838)

Figure 4.1, 4.3

Calymene rowi Green, 1838: 406.

Proetus rowi (Green). Hall, 1861: 75; Hall, 1876: pl. 21, fig. 2–6; Hall and Clarke, 1888: 119–121, pl. 21, figs. 2–6, 24–26, pl. 23, fig. 20–23, 27–28; Shimer and Shrock, 1944: 653, pl. 274, fig. 10; Ellison, 1965: 158, pl. 18, fig. 1.

Dechenella (subgen?) *rowi* (Green). Richter and Richter, 1926: 24.

Dechenella (*Basidechenella*) *rowi* (Green). Stumm, 1953a: 120, pl. 3, fig. 11, pl. 4, figs. 1, 2.

Dechenella rowi (Green). Speyer and Brett, 1986: fig. 2c; Speyer, 1987: figs. 7c, d, 12f.

?*Proetus rowi* (Green). Hall and Clarke, 1888: 119–121, pl. 23, fig. 29.

DIAGNOSIS: Intraoccipital lobes separated from L0, topographically elevated and bulging beyond lateral margins of glabella; furrow in front of eye deep; median glabellar impressions anterior of S1 developed as long lineaments running into S1; faint furrow separates series of latitudinal striations on anterior end of cephalic border into two ridges; anterior brim of cephalon flattened ledge; anterolateral portion of L0 anterior of lateral occipital lobes flexes strongly anteriorly; anterior branches of facial sutures parallel each other; 12 pygidial axial rings; posterior portion of pygidium notched in posterior view; tubercles on pygidium absent; pygidial axis with rounded terminus; interpleural furrows faint.

MATERIAL: AMNH 5505/3 (four specimens), 5505/4, 5809/1 (two specimens), 5809/2 (two specimens), 39340, 44755, 44756, 44763, 44674; BMS E5433, E8440; CU 18869; YPM 26159, 32969, 33773–33775, 33790, 33814–33817, 33848, 33861, 33864–33866.

DISCUSSION: The evolutionary relationships of this species and the other species of *Basidechenella* are considered in detail in the section that deals with the origin of the Middle Devonian Eastern North American Proetid fauna. *Basidechenella rowi* was chosen as the species to be used in the higher level phylogenetic analysis of the Proetinae because it is both the most commonly recovered and best-preserved species of *Basidechenella* known from North America. Employing other species of *Basidechenella* would not alter the determination of character polarity states except for the condition of the prosopon and the number of pygidial axial rings.

ORMISTONIELLA COOPER, 1982

TYPE SPECIES: *Ormistoniella malaca* (Lake, 1904).

DIAGNOSIS: Posterior border furrow flexes posteriorly laterally; intraoccipital lobes not developed; glabella bulges laterally next to eyes; nine thoracic segments; pygidial border with same slope as inner part of pleural field; posterior portion of pygidium pointed; pygidial pleural furrows very faint. (See Cooper [1982] for more).

DISCUSSION: This generic name was originally applied to a single species. However, there is a species known from what is probably Carboniferous strata, most likely the Pennsylvanian Coal measures of Texas or Missouri, that is very similar to the type of *Ormistoniella*. It is tentatively treated as *Ormistoniella longicauda* (Hall, 1862). The holotype by monotypy is AMNH 5507. As for *O. malaca*, this species has nine thoracic segments, prominently bulging margins of the glabella near the eye, a triangular pygidium

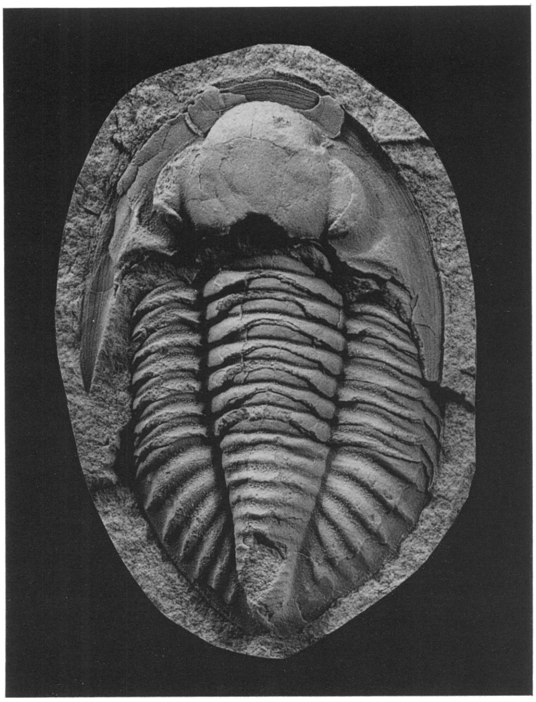

Fig. 11. *Ormistoniella malaca* (Lake, 1904). Gydo Formation, Bokkeveld Group, upper Emsian, South Africa, SAM K559, holotype, dorsal view of entire specimen, internal mold, ×1.5.

that is pointed posteriorly, weakly developed intraoccipital lobes, and a rounded anterior cephalic border. However, this species does differ in the condition of several traits, including a significantly greater number of pygidial axial rings, 22 versus 11–12 in *O. malaca*. This species will be treated in detail in a future work.

Ormistoniella malaca (Lake, 1904)
Figure 11.1

Ormistoniella malaca. Cooper, 1982: 6–14, fig. 1–4, 5c, 6b, 7c.

MATERIAL: SAM K559, K4203.

DIAGNOSIS: Same as for genus.

DISCUSSION: This species is known from the Gydo Formation (treated as upper Emsian on the basis of Cooper [1982, 1986]), the Bokkeveld Group, South Africa. The genus *Ormistoniella* may be monotypic, with *O. malaca* occurring in the Lower Devonian of South Africa, and this species is the only member of the Proetinae treated herein that has 9 thoracic segments instead of the typical 10. Cooper (1982) commented on what appear to be two distinct pygidial morphologies in this taxon, and he concludes that these differences probably reflect sexual dimorphism. The exact meaning of these differences in pygidial morphology is not clear because of the paucity of available material, and the Type I pygidia of Cooper (1982), which bear a relatively broader pygidial axis, were used to code the pygidial characters in this taxon.

Cooper (1982) suggested that *Ormistoniella* was very closely allied to *Dechenella*, and he originally favored calling it a new subgenus of that genus. However, he chose to assign this taxon a new generic name on the basis of its unique number of thoracic segments. He is correct in suggesting that these taxa share a close relationship, but other genera appear to be more closely related to *Dechenella*.

According to the cladogram in figure 6 this taxon, known exclusively from the Malvinokaffric Faunal Province in the Devonian, is transitional between two distinct series comprised of Arctic, North American, and European taxa. Although this form is most likely not ancestral to the taxa *Dechenella*, *Lacunoporaspis*, and *Schizoproetus*, it clearly represents an interesting biogeographic puzzle involving a temporary change in area relations. Perhaps future collecting will reveal the extent to which the Malvinokaffric Realm played a role in the evolution of *Dechenella*, *Lacunoporaspis*, *Schizoproetus*, and other genera, as it has not typically been ascribed any role. For now, the issue must remain unresolved.

AAYEMENAYTCHEIA, NEW GENUS

TYPE SPECIES: *Dechenella paragranulata* (Ormiston, 1967).

ETYMOLOGY: Pronounced A-M-N-H-ia, for the American Museum of Natural History, which has funded my research for the past few years.

DIAGNOSIS: Posterior edge of lateral occipital lobes flexes anteriorly laterally; eye sits on pedestal of free cheek that is flat space bounded distally by ridge; facial sutures anterior to eyes parallel each other; pygidial border widest posteriorly; pygidial axis in dorsal view with weakly pointed terminus; pygidial pleurae steeply arched laterally, medially forming flattened shelf (see Ormiston [1967] for more).

DISCUSSION: As it is currently conceived, this genus contains a single species, *Aayemenaytcheia paragranulata*, which was originally assigned to the genus *Dechenella*. Ormiston (1967) claimed that *A. paragranulata* was closely related to Richter's (1912: 309, pl. 21, fig. 9) *Dechenella granulata* (also illustrated in Richter and Richter [1956], which Ormiston [1967] incorrectly cited). However, according to the evolutionary schema developed herein, these taxa do not actually appear to be related. Although their cephalic morphology is broadly similar, they differ in several important respects. The posterior margin of the intraoccipital lobes flexes much more strongly anteriorly in *A. paragranulata* than in *D. granulata*. *Aayemenaytcheia paragranulata* also lacks two of the characteristic features of the genus *Dechenella* as it is conceived of herein. For instance, in *Aayemenaytcheia* the pygidial axis is not of even dorsoventral height and does not appear flattened in transverse profile. In addition, S1 in *D. granulata* is a rounded arc, whereas in *A. paragranulata* S1 flexes transversely posteriorly and anteriorly. *Dechenella* has the secondarily derived primitive state for the characters 12, 32, and 47, with this secondarily derived state characterizing a few other genera, whereas in *A. paragranulata* these characters are not present in their secondarily derived state. In order to maintain the generic name *Lacunoporaspis*, and to avoid making the genus *Dechenella* polyphyletic, a new monotypic genus is erected to accommodate this taxon.

Aayemenaytcheia paragranulata (Ormiston, 1967)

Dechenella paragranulata Ormiston, 1967: 86–88, pl. 10, figs. 13–15, pl. 11, figs. 1–5, 7; Ormiston, 1975a: pl. 4, fig. 3.

DIAGNOSIS: Same as for genus.

DISCUSSION: This species is known from the Emsian and Eifelian of Bathurst Island in the Canadian Arctic. The morphology of this species points out the confusing array of diversity that accompanied the radiation of those taxa traditionally termed the "dechenellids." The chief synapomorphies separating *Aayemenaytcheia paragranulata* from the genus *Dechenella* are a set of reversals and two characters of the pygidium. Thus, the transition between *Basidechenella* and *Dechenella* is marked by a series of evolutionary intermediates with some homoplasy developed. Ormiston's (1967) phylogeny of the "Dechenellinae" depicts *A. paragranulata* as sister to the rest of the genus *Dechenella*. According to the phylogeny in figure 6, this view is not completely correct, as *Lacunoporaspis* shares a more recent common ancestry with *Dechenella* than *A. paragranulata*. However, Ormiston did not consider *Lacunoporaspis* in his 1967 bulletin. *Aayemenaytcheia paragranulata* is treated as the sister taxon of the clade (*Lacunoporaspis*, *Dechenella*, *Schizoproetus*, and *Schizoproetoides*).

LACUNOPORASPIS YOLKIN, 1966

TYPE SPECIES: *Lacunoporaspis contermina* Yolkin, 1966.

DIAGNOSIS: Longitudinal lineations on anterior border rim of cephalon closely packed and linear; margin of glabella near eyes bulging; anterior branches of facial sutures parallel each other; preglabellar field present; S1 developed as rounded arc; posterior border furrow flexes posteriorly laterally; posterior edge of lateral occipital lobes flexes anteriorly laterally; pygidial pleurae gently rounded, slightly curving ventrally laterally; dorsal pygidial border present, thickest posteriorly. See translation of Yolkin (1966) given in Ormiston (1971) for additional diagnostic characters.

DISCUSSION: This genus is a diverse taxon containing several Devonian species from the Canadian Arctic and Siberia. Because *Lacunoporaspis norrisi* Ormiston, 1971, provided the best available material for this genus, and because of the morphological verisimilitude of the various species in this genus, this was the species used to code for character analysis. The phylogenetic position of *Lacunoporaspis* suggested herein accords well with Ormiston's (1971) prediction that *Lacunoporaspis* and *Dechenella* are very closely related. However, it also suggests that the assignment of several Silurian species to this genus by Owens (1973) and Thomas (1978), that are discussed above under "*Plesiowensus*," must be reevaluated. Several other taxa appear to be more closely related to both *Lacunoporaspis contermina*, the type of the genus, and *L. norrisi*. Because these taxa lack the characters of the type of the genus that are presented in the emended diagnosis of the genus above, they must be excluded from *Lacunoporaspis*. Ormiston (1971), provided a translation of the diagnosis of *Lacunoporaspis* given by Yolkin (1966). As discussed in the section on "*Plesiowensus*," this diagnosis of *Lacunoporaspis* does not provide enough morphological characters to constrain the evolutionary position of this genus, and therefore the diagnosis of *Lacunoporaspis* is emended here. Snajdr (1980: 172–173, pl. 32, figs. 5–9, pl. 64, fig. 1) describes and figures a new species, *Lacunoporaspis chlupaci*, from the Pridoli of Bohemia, and the affinities of this taxon also appear to lie with "*Plesiowensus*" on the basis of the absent dorsal pygidial border, the longitudinal lineations on the anterior border rim of the cephalon being wavy and separated, and other characteristics.

Therefore, all Silurian species that have been assigned to *Lacunoporaspis* in the past can no longer be comfortably contained within this genus, and *Lacunoporaspis* becomes exclusively Devonian and Siberian/Canadian Arctic in its distribution.

In addition, as discussed below, counter to Owens' (1973) and Lutke's (1980) suggestions, *Schizoproetus* Richter, 1912, appears to be more closely related to *Dechenella* Kayser, 1880, than is *Lacunoporaspis* Yolkin, 1966. Still, as Owens (1973) suggested, *Lacunoporaspis*, *Dechenella*, *Schizoproetus*, and *Schizoproetoides* Ormiston, 1967 do appear to represent a monophyletic group to the exclusion of several other genera. This group is defined by four characters. For two of these characters, a reversion to the primitve state is the synapomorphous trait. These characters are S1 developed as a rounded arc (has the derived state for *Schizoproetoides richteri* Ormiston, 1967, and a different derived state for some members of *Dechenella*) and the pygidial pleurae gently rounded, slightly curving down abaxially (has the derived state for *S. richteri*). This implies that some homoplasy is concentrated at the node that contains the clade *Lacunoporaspis*, *Dechenella*, *Schizoproetus*, and *Schizoproetoides*. However, these primitive characters, which help to define this clade, remained invariant from the Wenlock through the Eifelian, implying 45 million years of evolutionary stability. Thus, it seems safe to view the reacquisition of the primitive condition of these characters as a unique evolutionary event. In addition, the distribution of these characters suggests that *Schizoproetoides richteri* differs from some of the other species within this clade in the condition of some of the key defining characters.

Both Owens (1973) and Lutke (1980) recognized a close relationship between *Lacunoporaspis* and *Dechenella*. However, both concluded that *Lacunoporaspis* was more closely related to *Dechenella* than *Schizoproetus*. As discussed under the sections on *Dechenella* and *Schizoproetus*, some homoplasy is concentrated at the node that unites *Dechenella* and *Schizoproetus/Schizoproetoides* to the exclusion of *Lacunoporaspis*. Therefore, it would be unwise to strongly emphasize the relationship of *Schizoproetus/Schizoproetoides* and *Dechenella* to the exclusion of *Lacunoporaspis*. Obviously all four genera are closely related, with particularly subtle differences developed between *Lacunoporaspis* and *Dechenella*.

Because of these close evolutionary relationships, there has been some confusion regarding the assignment of certain specimens to particular genera. Corgan (1963: 153, fig. 4) assigned a single pygidium from the Lower Devonian (Onesquethawan) questionably to *Basidechenella* that Ormiston (1971) suggested belongs to *Lacunoporaspis*. Although it is too poorly preserved to make definitive statements about its evolutionary relationships, the interpleural furrows appear to be more deeply incised than what is typically seen in *Basidechenella*. It is possible that this pygidium belongs to *Arcticormistonia*, new genus. However, in this genus, the lateral portions of the pygidium appear to deflect slightly posteriorly whereas the pleurae follow a rounded arc in *Lacunoporaspis*. The pygidium figured by Corgan (1963) displays the latter pleural morphology and accords well with other features of *Lacunoporaspis*, including the incision of the interpleural furrows. Therefore, it may belong to *Lacunoporaspis*. As Ormiston (1971) stated, *Dechenella* sp. indet. (Ormiston, 1967: 108, pl. 17, fig. 10) appears to actually belong to *Lacunoporaspis*. The pygidial pleural furrows appear too long and the interpleural furrows too deeply incised for *Dechenella*.

Pillet (1972) erected a new subfamily of the Dechenellidae, the Lacunoporaspinae, to encompass *Lacunoporaspis* and several other genera. This subfamilial designation is not accepted for the same reason that Dechenellidae Pribyl, 1946, or Dechenellinae is not accepted; that is, because it would make the Proetinae paraphyletic or require the erection of several new subfamilies. The first option runs counter to the ambitions of phylogenetic analysis, and the latter seems unjustified.

Owens (1973) suggested that both *Khalfinella* Yolkin, 1968, and *Ganinella* Yolkin, 1968, belonged in the genus *Lacunoporaspis* Yolkin, 1966. Both taxa, particularly *Ganinella*, do appear to be closely related to *Lacunoporaspis*. However, *Ganinella* and *Khalfinella* were not considered in this phylogenetic analysis, and therefore this proposition cannot be evaluated in detail.

Lacunoporaspis norrisi
Ormiston, 1971

Lacunoporaspis norrisi Ormiston, 1971: 31–33, pl. 3, figs. 1–7, 9–15. Ormiston, 1975a: pl. 2, figs. 7, 8.

MATERIAL: GSC 24255–24258, 24262–24263.

DIAGNOSIS: Same as for genus.

DISCUSSION: This species is known from the Michelle Formation (Emsian) of the Yukon Territory, Canada. The chief character that presents some ambiguity in its coding is the condition of S1 (character 12). The states of character 12 are rounded arc (0), or anterior and posterior ends flex transversely (1). In most specimens of *L. norrisi*, S1 is developed as a rounded arc. However, the arc of S1 is not as smoothly rounded as it is in species of the genus *Dechenella*. In a few specimens of *L. norrisi* (e.g., GSC 24255; Ormiston, 1971: pl. 3, fig. 1), the anterior and posterior ends of S1 do appear to flex slightly transversely. *Lacunoporaspis norrisi* was coded as having state 0 for this character, but the coding of this character does not affect the phylogenetic conclusions herein.

DECHENELLA KAYSER, 1880

TYPE SPECIES: *Phillipsia verneuili* Barrande, 1852.

DIAGNOSIS: Anterior branch of facial sutures diverging from margin of glabella; S0 and L0 curve prominently anteriorly; posterior edge of lateral occipital lobes flexes anteriorly laterally; margins of glabella bulging prominently near eyes; posterior border furrow flexes posteriorly laterally; pygidial axis flattened in sagittal section, of even dorsoventral height; pygidial pleural furrows very faint; pygidium with at least 14 axial rings.

DISCUSSION: This genus certainly represents one of the most prominent Devonian proetid morphotypes. Because of this it has become something of a taxonomic grab bag, with several taxa assigned either to the genus *Dechenella* (*Dechenella*) or to various subgenera of *Dechenella*. For this reason, to undertake a taxonomic study of *Dechenella* requires consideration of several taxa. The morphological criteria that can be used to discriminate this genus from others can be subtle, indicating the prominent range of intermediates that exist between this taxon and Silurian and Devonian genera of the Proetinae. Because of this series of intermediates, there is no reason to recognize *Dechenella* or its close relatives as part of a subfamily separate from the Proetinae.

On the basis of morphological studies and the phylogeny shown in figure 6, it appears that certain taxa that have been classified as subgenera of *Dechenella* must be excluded from this genus and accorded full generic status. The most prominent of these taxa is *Basidechenella* Richter, 1912. Richter (1912), Richter and Richter (1950), Stumm (1953a, 1953b, etc.), Richter and Struve (1959), Ormiston (1967), Chatterton and Perry (1977), and others considered *Basidechenella* to be a subgenus of *Dechenella*. However, the phylogeny in figure 6 suggests that these taxa are distantly related. Characters that are primitive in *Basidechenella* and derived in *Deche-*

nella include 17, 22, 26, 27, 29, 43, and 48. Keeping *Basidechenella* as a subgenus of *Dechenella* would make *Dechenella* polyphyletic, and therefore this subgenus is removed from *Dechenella*.

Stumm (1953a) proposed *Monodechenella* as a new subgenus of *Dechenella*. As discussed above, *Monodechenella* is not a member of the Proetinae, and instead should be placed in what is informally termed here the "*Thebanaspis* clade." Therefore, this subgenus must also be removed from *Dechenella*; otherwise, the latter would become significantly polyphyletic. *Dechenella* (*Pedinodechenella*) Ormiston, 1967, is believed to be closely related to *Dechenella*, and it is elevated to generic status. A new species of *Pedinodechenella*, *P. modelli*, is included in the phylogenetic analysis of the genus *Dechenella* that is presented below in the section that deals with the origins of the Middle Devonian proetid fauna of Eastern North America. The genera *Humeia* Ormiston, 1975b, and *Camsellia* Ormiston, 1976, are considered to be closely related to *Dechenella*. However, their relationships were not considered in detail herein.

The species Stumm (1953b) designated as "*Dechenella* (*Dechenella*)" *angustifrons* is here placed in the genus *Coniproetus* and it is not closely related to *Dechenella*. It differs in the state of several characters, including glabella margins not bulging near eyes, S1 flexing transversely at its anterior and posterior ends, intaoccipital lobes not separated from L0, and the pygidium having five fewer axial rings.

Cyrtodechenella is not considered to be closely related to *Dechenella*. There appear to be substantial problems regarding the phylogenetic placement of this genus and the other closely aligned members of the Cyrtosymbolinae Hupe, 1953. As discussed above, this taxon seems to suffer from particularly high levels of polyphyly (Fortey and Owens, 1975). The entire group requires substantial revision before its relationships can be considered. Because most members appear to lack several of the characters defining the Proetinae, as mentioned above, this group was not considered here.

Allan (1935) designated a new species, *Dechenella* (*Eudechenella*) *mackayi*, based on a single pygidium from the Lower Devonian Reefton Beds of New Zealand. From the drawing of this specimen it is difficult to ascertain its exact affinity. The specimen has about 17 pygidial axial rings and a granulose prosopon with a raised tubercle on the medial portion of the axis. It is possible that this speces belongs to *Dechenella*, although the tubercle on the medial portion of the pygidial axis is characteristic of certain species of the genus *Monodechenella* Stumm, 1953a. However, it could not be discerned if this taxon possessed the criteria for group membership in the Proetinae. Until better specimens are recovered, the exact affinities of this pygidium remain equivocal.

Pek and Vanek (1991) described a new genus and species, *Xenodechenella chacomaensis*, on the basis of a few isolated pygidia from the upper Belen Formation at Chacoma, Bolivia, possibly Emsian or Eifelian (Lieberman et al. [1991] and refs. therein). The specimens have 15 pygidial axial rings, well-incised pygidial interpleural furrows, and a prominent pygidial posterior border. From these poorly preserved specimens, it is impossible to say with certainty whether or not these pygidia belong to *Dechenella*. They do bear a resemblance to *Dechenella perscheii*, new species from the Eifelian of Ellesmere Island. Edgecombe (personal commun.) suggested that this genus may be synonymous with *Ormistoniella*.

Two species of *Dechenella* were used to ascertain the phylogenetic position of this genus relative to the other major generic groups of the Proetinae. These species are *D. perscheii*, new species from the Canadian Arctic Islands and *D. alpenensis* Stumm, 1953a, from ENA.

The genus *Dechenella* is diverse and taxonomically widespread and occurs in Eifelian and Givetian strata. Species are known from Morocco and Germany (Armorica), the Canadian Arctic Islands, the Yukon, and ENA (Laurussia sensu Ziegler, 1991). The evolutionary relationships and biogeographic affinities of most of the species that comprise this genus are considered in detail in the section on the origin of the Middle Devonian Proetid fauna of ENA.

Dechenella perscheii, new species

Basidechenella sp. Tolmachoff, 1926: 25, pl. 1, fig. 10.

Dechenella (*Dechenella*) *spaekassensis* (Tolmachoff). Ormiston, 1967: 94–96, pl. 12, figs. 11–17 non 9, 10.

Diagnosis: Glabella contacts anterior border furrow; S1 in dorsal view relatively smoothly arched; facial suture meets on dorsal portion of anteromedian edge of eye forming a right angle; facial suture at lateralmost point of eye displaced as far abaxially as most laterally deflected point of suture on anterior border; prosopon of coarse granules; intraoccipital lobes most expanded laterally anteriorly; anterior cephalic border furrow narrow; S3 inclined posteriorly medially; S2 rounded curve, convex anteriorly; anteromedian portion of eye opposite distal tip of S2; anterior edge of pygidial axis transversely thick, width of pleural field; 15 pygidial axial rings; pygidial border developed as rounded lip, convex up dorsally; posterior portion of pygidial border long, flat region, with length equal to first two axial rings; dorsal surface of pygidial posterior border flattened, parallel to dorsal plane.

Types: Holotype cranidium GSC 18198 (Ormiston, 1967: pl. 12, figs. 14–16), Blue Fiord Formation, Blue Fiord, Ellesmere Island.

Etymology: Named for Per Schei, who collected specimens of this species during the Second Norwegian Arctic Expedition (1898–1902).

Description: Cephalic length (sag.) 150% maximum glabellar width; anterior border developed as long ledge (1.5 times length of L0 medially), inclined posteriorly and convex dorsally; anterior border furrow deep and narrow; longitudinal lineations on anterior border of cephalon closely packed and linear. Prosopon of coarse granules. Anterior edge of glabella contacts anterior border furrow. Anterior portion of glabella conical. Facial sutures moderately divergent anteriorly at an approximately 40° angle, meeting on anteromedian edge of eye forming right angle, displaced as far laterally at lateral edge of eye as at maximum lateral deflection on anterior border. Lateral margins of glabella opposite S4 parallel, and between S3 and S4 parallel. Space between anteromedian portion of eye and anterior border furrow equal to orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1. Glabellar furrows faintly impressed. S3 flexing posteriorly, inclined at 45° angle to transverse line, convex anteriorly; S2 rounded curve medially directed posteriorly, deflected about 45° from exsagittal line; S1 rounded arc, posterior tips follow a straight course, does not contact S0; S1 and S2 laterally contact the axial furrows; space between distal tips of S1 and S2 1.5 times distance between distal tips of S2 and S3. Median glabellar furrow directed posteromedially. Maximum length and width of glabella equal. Glabella constricted more sharply anterior to S4, with lateral margins converging at same angle between S1 and S2 as between S2 and S3; maximum glabellar bulge posterior to distal tip of S1. S0 well incised. Anterior margins of intraoccipital lobes follow a constant line from S0 to axial furrow, expanded dorsally, at posterior margin flexed more strongly anterolaterally, deflected anteriorly beyond transverse line tangent to anteromedian portion of S0, separated posteriorly from L0; lateral margins deflect beyond lateral margins of glabella. Tubercle not developed on L0. L0 flexed forward medially. L0 elevated to level of posterior region of glabella. Posterior portion of glabella anterior to medial portion of L0 flexes forward distally; posteromedian portion of glabella flattened in transverse profile. Posterior portion of eye adjacent to lateral portion of L0 anterior to intraoccipital lobes, extending to point opposite distal tips of S2. Palpebral lobes broadest at point less than 50% length (exsag.) of eye. Posterior portion of palpebral ridge anterior of point where it deflects sharply posteriorly opposite point about one-third length (exsag.) between anterior end of S1 and anterior portion of intraoccipital furrow. Fixigenae in course from lateral margins of glabella at S3 to anterior border are posteriorly less steeply inclined, then have moderately abrupt break in slope and anteriorly are more steeply inclined. Eye sits on pedestal of free cheek, which is flat space. Genal spine furrow deflects 10° exsagittally from course followed by lateral edge of anterior border furrow, intersects outer edge of genal spine, genal spines extend back to approximately third or fourth thoracic segment.

Pygidial length 65% width; pleural furrows prominently incised, interpleural furrows weakly incised; apodemes faint; axis of even dorsoventral height; axial rings flex posteriorly medially, laterally are roughly straight; 15 axial rings; axis with rounded terminus, in sagittal section flattened, anterior edge of axis as wide as pleural field; 10 pygidial pleural segments. Border prominently developed as flattened shelf, wide, posteriorly wider, reaches point of constant and greatest length (exsag.) opposite fifth pleural segment; posterior portion of border in dorsal aspect appears rounded; dorsal surface of pleurae gently rounded, slightly curving ventrally laterally; anterior margin of pleurae convex anteriorly, transitions between pleural bands and pleural furrows gradual.

DISCUSSION: Ormiston (1967) concluded that material D. J. McLaren collected from east of Blue Fiord, Ellesmere Island, was identical to *Basidechenella spaekkassensis* Tolmachoff, 1926, and he redescribed this material as *D.* (*D.*) *spaekkassensis*. There appear to be significant morphological differences between Tolmachoff's *Basidechenella spaekkassensis*, his *Basidechenella* sp., and some of the specimens Ormiston (1967) figured as *D. spaekkassensis*. These differences include: in *Dechenella spaekkassensis* the pygidial border becomes a very narrow strip anteriorly, whereas in *D. perscheii*, new species it is distinctly developed anteriorly. In *D. spaekkassensis* (Tolmachoff, 1926) the pygidial interpleural furrows are more deeply incised laterally than medially on the first four pleurae. In *D. perscheii*, new species these furrows are of constant depth. In *D. spaekkassensis* the posterior portion of the pygidial border is transverse in dorsal view, whereas in *D. perscheii* the posterior portion of the border is smoothly rounded. In addition, *D. spaekassensis* has 17 pygidial axial rings and 11 pleural segments whereas *D. perscheii* has 15 axial rings and 10 pleural segments. Thus, the new GSC material and the pygidium PMO A28838 should be placed in a new species. Another pygidium, GSC 18199/3, which Ormiston (1967) assigned to *D. spaekkassensis*, has not been observed by the author; however, it is believed to belong to *D. perscheii*. This species is known from the Blue Fiord Formation at Ellesmere Island, Eifelian (Ormiston, 1967) and possibly upper Emsian (Yolkin and Ormiston, 1985). Ormiston (1967) figures several specimens of trilobites, including the specimens that Tolmachoff (1926) originally figured and assigned to *Basidechenella spaekassensis*. It appears that in the original series of syntype pygidia housed at the Paleontologisk Museum of Oslo there are at least two species. PMO A28845 from Spaekassen, Ellesmere Island, shown in Ormiston (1967: pl. 12, figs. 9, 10) differs from PMO A28838, recovered from Goose Fiord, Ellesmere Island, and from those specimens that Ormiston (1967) figured from near Blue Fiord, Ellesmere Island. The pygidium from Blue Fiord, GSC 18196, is identical to the syntype pygidium from Goose Fiord, and a series of cephala and a free cheek are associated with the pygidium from Blue Fiord. Therefore, these are all treated as belonging to a single species, *D. perscheii*, new species. As PMO A28845 is from the type locality at Spaekeassen, it is treated as the lectotype of *D. spaekassensis*, and one of the former syntypes of this species is assigned to the new species *D. perscheii*. The complete cranidium, GSC 18198 from the Blue Fiord Formation (upper Emsian or Eifelian) at Blue Fiord, Ellesmere Island, is treated as the holotype of the new species *D. perscheii* as it is the most complete of the specimens figured by Ormiston (1967). Tolmachoff (1926) also figured a single pygidium, which he assigned to *Basidechenella* sp. Ormiston (1967) claimed that this specimen, PMO A28837, was identical with those of *D. spaekassensis*. However, it could not be ascertained if this specimen was identical to *D. spaekassensis* (Tolmachoff, 1926) or the other species in the series of specimens that Ormiston (1967) assigned to *D. spaekassensis*, *D. perscheii*.

Dechenella perscheii is also treated in the section on the origin of the Middle Devonian Proetid fauna of ENA.

Dechenella alpenensis
Stumm, 1953a

Dechenella (*Dechenella*) *alpenesis* Stumm, 1953a: 116–117, pl. 2, figs. 1–15; Stumm, 1967: 116, pl. 2, figs. 1, 2; Chlupac, 1992:142.

?*Dechenella* (*Dechenella*) sp. A Stumm, 1953a: 117, pl. 5, figs. 1, 2.

DIAGNOSIS: Preglabellar field absent; S3 transverse; tubercle on L0 absent; sides of glabella anterior to S3 are parallel; pygidial interpleural furrows absent; anteromedian portion of eye opposite point between distal tips of S2 and S3; cephalic axial furrows between S1 and S2 converging at same angle as between S2 and S3; space between facial suture along anteromedian portion of eye and glabellar furrow small, not displaced as far exsagittally as maximum lateral glabellar bulge; posterior portion of S1 does not contact S0; space between anteromedian portion of eye and anterior border furrow equal to 1.5 times orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1; pygidial axial rings flex anterolaterally; pygidial border flattened posteriorly in dorsal aspect; anterior edge of pygidial axis about 50–65% width (tr.) of pleural field; transition between pygidial pleural bands and pleural furrows abrupt; pleurae flattened, elevated blocks; pygidial posterior border flattened dorsally in lateral view.

MATERIAL: UMMP 54155; USNM 117867, 117870, 117873, 123569.

DISCUSSION: The specimen that Stumm (1953a) identified as *D.* (*Dechenella*) sp. A is treated questionably as *D. alpenensis*. This decision cannot be reached with certainty because *D.* sp. A is too poorly preserved; however, it does not differ in any of the morphological criteria used for phylogenetic analysis. This species is discussed more extensively in the section that deals with the origin of the Middle Devonian proetid fauna of ENA.

SCHIZOPROETUS RICHTER, 1912

TYPE SPECIES: *Proetus celechovicensis* Smycka, 1895.

DIAGNOSIS: Cephalic posterior border furrow straight; prosopon of large tubercles; facial suture at anterior edge of eye forms a right angle directed laterally; S1 rounded arc; S3 flexing posteriorly, inclined 45°; posterior edge of lateral occipital lobes flexes anteriorly laterally; anterior border very narrow ledge equal to length of L0 medially, developed only farthest medially; pygidial axis with straight posterior terminus; pygidial posterior border thick posteriorly, wider than anterolaterally.

DISCUSSION: Some authors (Yolkin, 1968; Pillet, 1972; Ormiston, 1972, 1976; Owens, 1973) have suggested that this genus be classified in a separate subfamily, the Schizoproetinae Yolkin, 1968. Other authors suggest that *Schizoproetus* and the closely related *Schizoproetoides* Ormiston, 1967 should be assigned to the Dechenellinae (Richter and Struve, 1959; Ormiston, 1967). As discussed above, the validity of the Dechenellinae is not accepted herein, as erection of this subfamily would make the Proetinae paraphyletic. For similar reasons, the validity of the subfamily Schizoproetinae cannot be accepted.

Both Ormiston (1967) and Owens (1973) suggested that *Crassiproetus* and *Schizoproetus/Schizoproetoides* were sister taxa. This affinity was principally propounded on the basis of their shared, large, multisegmented pygidium. This relationship does not appear to be supported for several reasons. First, primitively the pygidium of *Crassiproetus* Stumm, 1953a, exemplified by *Crassiproetus globosus* and *C. turgidus* (Northrop, 1939), does not appear to be large and multisegmented, so this characteristic shared by some members of *Crassiproetus* and *Schizoproetus* is evidence of convergence, not homology. In addition, *Crassiproetus* and *Schizoproetus* differ in the condition of several characters. *Crassiproetus* lacks the derived state for several characters that are derived for *Schizoproetus*, including 20, 21, 24, 26, 46, 47, and 48, and several taxa appear to be more closely related to *Schizoproetus* than is *Crassiproetus*.

Ormiston (1967) and Owens (1973) also suggested that certain subgenera of *Proetus*, *Longiproetus* and *Lacunoporaspis*, respectively, are more closely related to *Dechenella* than is *Schizoproetus*. As argued above, *Longiproetus* appears to be only distantly related to *Dechenella*, and its affinities instead appear to lie with *Coniproetus* and *Pudoproetus*. However, a close relationship is advocated herein between *Lacunoporaspis* and *Dechenella*. Instead of *Lacunoporaspis* being the sister taxon of *Dechenella* as Owens (1973) proposed, here *Schizoproetus* and *Schizoproetoides* are treated as sister taxa, and these two genera are the sister taxa of *Dechenella*.

However, this relationship is not strongly supported by the phylogeny herein. On the basis of the character evidence used, *Dechenella* and *Schizoproetus* are both highly derived members of the Proetinae, but their close relationship is supported by only a single synapomorphy. This synapomorphy is a reversion to the primitive state in character 32, which concerns the condition of the anterior branch of the facial suture.

Schizoproetus and *Schizoproetoides* are united by three characters. For two of these characters, the derived state supports the affinity of these genera. These are prosopon of large tubercles and the facial sutures at the anterior edge of the eyes forming a right angle directed laterally. In addition, one reversal to the primitive condition characterizes this node, as in both *Schizoproetus* and *Schizoproetoides* the posterior border furrow is straight. Therefore, some of the enigma surrounding the relationship of *Schizoproetus* concerns what appear to be reversions to the primitive state for two characters that, in their derived state, define nodes farther down the tree. Unlike reversals that characterize the *Lacunoporaspis* node of the cladogram, the derived state of characters 17 and 32 is acquired around the same putative time that the reacquisition of the primitive state occurs. The bulk of the character evidence does support the derived status of *Dechenella*, *Schizoproetus*, and *Schizoproetoides* relative to most other members of the Proetinae. However, the derived status of these taxa relative to *Lacunoporaspis* and *Aayemenaytcheia* cannot be advocated with the utmost confidence.

As discussed above in the section on the "*Thebanaspis* clade," Hedstrom (1923: 4, pl. 1, figs. 1–15) described and figured *Proetus delicatus* from the late Wenlock of Gotland, here treated as *Hedstroemia delicata*. Owens (1973: 37, pl. 15, figs. 16, 17) figured and described a pygidium from the Wenlock Limestone, Dudley, Worcestershire, which he recognized was very similar to *H. delicata*. He claimed that this pygidium was referrable to *Schizoproetus*, and he called it *S.* aff. *delicatus*. As recognized by Pribyl and Vanek (1978) and reiterated by Lutke (1990), Hedstrom's (1923) *P. delicatus* should be assigned to a new genus, which they named *Hedstroemia* Pribyl and Vanek, 1978. The members of this genus lack several of the characters used to define the Proetinae. Therefore, *Hedstroemia delicata* and "*Schizoproetus*" aff. *delicatus*, here treated as *Milesdavis eldredgei*, cannot be related to *Schizoproetus*. However, they may be important phylogenetic links between the Proetinae and other proetid subfamilies. By removing these Wenlock taxa from *Schizoproetus*, the genus is restricted to the Lower and Middle Devonian of Armorica.

Ormiston (1967) proposed that *Paradechenella* Richter, 1912, was closely related to *Schizoproetus*. Material of *Paradechenella* could not be obtained for this study; therefore, this proposition could not be evaluated. *Fuscinipyge* Ormiston, 1972, is clearly closely related to *Schizoproetus* and *Schizoproetoides*. However, its exact phylogenetic position was not considered.

Among taxa considered here, *Schizoproetus* is sister to *Schizoproetoides*, a genus known from the Eifelian of the Canadian Arctic Islands and the Yukon Territory. Again, as discussed under *Dechenella*, a close biogeographic affinity is recognized between the Armorican forms and those forms from the Yukon and the Canadian Arctic.

Schizoproetus onyx Richter, 1912

Dechenella Kayseri Richter, 1909: 29, 34.
Dechenella (aff. *Basidechenella*) *onyx* Richter, 1912: 286, pl. 18, figs. 15, 16.
Schizoproetus onyx (Richter). Richter and Richter, 1950: 162–165, pl. 2, figs. 14–17.

DIAGNOSIS: Same as for genus.

DISCUSSION: This species is known from the Eifelian and Emsian of Germany. It was chosen for this phylogenetic analysis because it provided the best material that could be viewed. Other species seem to differ little in the essential features of their morphology.

SCHIZOPROETOIDES ORMISTON, 1967

TYPE SPECIES: *Cyrtosymbole richteri* Tolmachoff, 1926.

DIAGNOSIS: Margin of glabella near eyes straight; posterior border furrow straight; preglabellar ridge present; facial sutures at anterior edge of eye form a right angle; prosopon of large tubercles; S0 and L0 straight medially, with slight posterior kink of S0 medially; S1 flexes transversely at its posterior and anterior ends; pygidial axis of even height, with rounded or pointed terminus (see Ormiston [1967] for more).

DISCUSSION: This genus consists of at least four species, two formally designated, from the Siegenian, Emsian, and Eifelian of the Yukon and the Canadian Arctic Islands. One of the chief differences between this genus and *Schizoproetus* is the condition of the margin of the glabella near the eyes. It is bulging in *Schizoproetus* and straight in *Schizoproetoides*. This character state marks another reversion to the primitive condition around the *Dechenella*, *Schizoproetus*, and *Schizoproetoides* node. As mentioned above under *Schizoproetus*, there appears to be some homoplasy associated with the definition of this clade. Other differences between *Schizoproetus* and *Schizoproetoides* are the condition of the pygidial pleural furrows, which appear to be somewhat more deeply incised in the former, and the presence of a prominent, transverse, preglabellar ridge in *Schizoproetoides*.

Schizoproetoides richteri
Tolmachoff, 1926

Cyrtosymbole richteri Tolmachoff, 1926: 26, pl. 1, fig. 14.

Dalmanites sp. Tolmachoff, 1926: 22, pl. 1, figs. 3, 4.

Schizoproetoides richteri (Tolmachoff). Ormiston, 1967: 111–115, pl. 14, figs. 15–18, pl. 15, figs. 1–6; Ormiston, 1971: 33.

MATERIAL: PMO A28835, A28847.

DIAGNOSIS: Same as for genus.

DISCUSSION: This species is known from the Eifelian Blue Fiord Formation of Ellesmere Island. This species of *Schizoproetoides* was analyzed because it is the most morphologically complete of the genus.

BIOGEOGRAPHIC ORIGIN OF MIDDLE DEVONIAN PROETID FAUNA OF EASTERN NORTH AMERICA

One of the goals of this analysis was to use information on the evolutionary histories and geographic distributions of fossil taxa to infer the relationship between macroevolutionary patterns and processes and changes in paleogeography and environment caused by the movements and collisions of plates and transgressions and regressions. Phylogenetic patterns during the upper Lower and Middle Devonian were concentrated on to assess macroevolutionary patterns and processes operating on at least two different hierarchical levels. Emphasized was how biogeographic (plate tectonic) and environmental factors affect the origin, diversification, and extinction of major evolutionary fossil faunas.

The Paleozoic fossil record of New York State consists of about 13 major evolutionary fossil faunas. Each of these persists for about 5–10 million years, consists of about 200 largely unique species, and occupies a relatively broad geographic region. Several hypotheses have been promulgated about the evolution of these fossil faunas by Eldredge (1985, 1989). For instance, it has been suggested that the sudden appearance of a fauna in the fossil record is associated with the immigration of taxa from different paleogeographic regions, and that once a fauna is established, relatively small amounts of diversification transpire. Furthermore, faunas are generally terminated by large extinction events, and species lineages tend to change relatively little during the persistence of a fauna (Eldredge, 1985). (The last hypothesis is assessed elsewhere [Lieberman and Brett, in press].) To test these hypotheses the proetid trilobite taxa in the faunas of the Onondaga Limestone and the Hamilton Group were emphasized.

The higher-level phylogeny of the Proetinae presented in the first part of the study can be used to recognize that there are three genera of this subfamily that are known to occur in both the Eifelian and Givetian strata of ENA (Eastern North America). In addition, a set of species that belongs to the "*Thebanaspis* clade" also occur in strata from this interval.

The reason for concentrating on these taxa and this interval is that these species lived during the onset and intensification of the

Acadian Orogeny. This orogeny induced a drastic change in paleoenvironment and involved a major restructuring of the contiguous relationship of the earth's cratonic plates. The Acadian Orogeny may have been caused by either the collision between Armorica, Laurentia, and the intervening Traveler Terrane (Kent, 1985), by the oblique convergence of Avalonia and Laurentia (Ettensohn, 1985), or by collision between Armorica and Avalonia with subsequent effects on Laurentia (Soper et al., 1992).

The first signs of the Acadian Orogeny are present in the upper Lower Devonian (Emsian) of New York, Pennsylvania, Virginia, and West Virginia (Ettensohn, 1985). The orogeny has been related to deposits referred to as the Esopus Shale in New York and the Needmore Shale in the central Appalachians. After a brief interval of tectonic quiescence during the Eifelian, the Acadian Orogeny reintensified at the start of the Givetian (Ettensohn, 1985). Associated with this reintensification was the nearly complete restriction of the calcareous lithofacies that had become widespread in the Eifelian of ENA to the Michigan and Illinois Basins, and the concomitant development of detrital clastic deposition and muddy-bottom type conditions in the Appalachian Basin (Brett and Baird, 1986; Brett, 1986). Around the time of the post-Eifelian reintensification of the orogen, there appears to be a change in the faunal affinities of the taxa recovered from deposits in ENA (Burton and Eldredge, 1974; Bailey, 1983; Boucot, 1975; Eldredge, 1985, 1989; Oliver, 1976, 1977). In the Eifelian many of the taxa in the ENA province appear to be endemic and are derived from earlier ENA taxa. However, in the Hamilton Group fauna of the Givetian, there appears to be a dramatic incursion of taxa with Old World–Rhenish affinities from Armorica into ENA.

First, the primitive biogeographic condition of each of these generic clades is considered to ascertain their biogeographic origin. In particular, the question of whether or not these clades were endemic to ENA prior to the deposition of the Onondaga Limestone and the Hamilton Group, or rather that they undergo a prominent change in area relationships associated with the appearance of the Hamilton Group fauna and the reintensification of the Acadian Orogeny is examined. This information will be used to test hypotheses about the origin of faunas. In addition, detailed phylogenies are constructed for each of these four clades. We can use our understanding of the evolution of these taxa, in conjunction with their geographic and stratigraphic distributions, to assess patterns of diversification and extinction. Special attention is paid to the role that changes in environment mediated by the Acadian Orogeny played in influencing the evolution of these organisms. The occurrences, diversification, and extinction of taxa will also be integrated into the transgressive–regressive cycles developed by Johnson et al. (1985). The causes of transgressive–regressive cycles are consigned to eustatic and/or tectonic factors, and it is only the cycles, not their causes, that are considered herein.

In addition to the large-scale biogeographic patterns potentially relating to the origin of faunas, the ENA faunal province is divided into a series of partially isolated topographic basins or depressions that were centers of sedimentary deposition. Each of these basins possessed a subtly differentiated fauna (Imbrie, 1959; Eldredge, 1972, 1973, 1974). Using the phylogenetic relationships and biogeographic and stratigraphic distributions of the intra-ENA members of these clades, I assess how this smaller-scale geography relates to the evolution of these clades. This information will also be used to test the amount of diversification that occurs during the persistence of particular fossil faunas, and to examine the relative extent to which extinction is concentrated at the end of faunal boundaries.

In addition to the consideration of macroevolutionary patterns and processes associated with the Middle Devonian fossil faunas of ENA, a method is also developed to adapt the phylogenetic information from all four clades to biogeographic patterns. An analysis is conducted to assess how the different sedimentary basins of ENA and the Arctic and Armorican biogeographic regions are related.

To avoid simple scenario building, and for the purposes of introducing an element of rigor into evolutionary and geographic analyses of the fossil record, an objective method of formulating and testing biogeographic hypotheses must be employed. The best prospects for such methods lie in the recently burgeoning field of cladistic vicariance biogeography. However, there remain certain aspects of this field that require fine-tuning in order to deal with the geological processes governed by plate tectonics and the geographic distributions we find in the fossil record. Although an overhaul of vicariance biogeography is not advocated, a new way of applying it is suggested.

Traditionally, the development of vicariance biogeography has been viewed as a byproduct of the reformulation of plate tectonics in the 1960s (see Jardine and McKenzie, 1972; Cracraft, 1974; Nelson and Platnick, 1981; Wiley, 1988a, 1988b; Wiley et al., 1991). However, the bulk of biogeographic literature has concentrated on the splitting apart of land masses or areas engendered by rifting and other geological processes. This may be because most vicariance biogeographic studies focused on extant organisms. The distributions and evolutionary relationships of these organisms, if related at all to geological processses, would largely be the product of the breaking up of Pangaea and the subsequent dispersal of the various continents throughout the late Mesozoic and Cenozoic. The continents are more split apart now than they have been at any time in the last 400 million years (Flessa, 1975; Schopf, 1979; Valentine, 1973). Thus, for at least the last 180 million years, since the breakup of Pangaea, plate tectonics has acted to produce a configuration of the earth's cratons that one might predict would be compatible in many cases with a vicariance biogeographic perspective; that is, if the earth and its life forms do evolve together, as Croizat (1958) so strongly stated.

When authors such as Wiley (1988a, 1988b) and Nelson and Platnick (1981) focused on the relationship between vicariance biogeography and plate tectonics they only emphasized half of the picture. Only the fissioning effect of plate tectonics was appreciated, although Rosen (1979) did comment on reticulation in area cladograms. Of course, plate tectonics need not always mediate the splitting of larger land masses into smaller. Much of the post-Cambrian Paleozoic and early Mesozoic was characterized by the collision of cratonic blocks and the fusion of smaller cratons into successively larger land masses. For instance, during this greater than 250 million year stretch, first Gondwana, then Laurussia, and finally Pangaea formed. The legacy of such great geologists as James Hall and Marshall Kay teaches us that the history of North America in the Paleozoic is nothing but a series of progressive orogenic events that have since been related to the amalgamation of cratons, plates, and arcs. We thus must recognize that areas do not necessarily have any cohesion through time. This is further emphasized when the additional effects of rising and falling sea-levels are factored in.

If we seek a deeper understanding of the relationship between plate tectonics and the evolution of life, particularly Paleozoic life, we must consider both of the paleogeographic effects that plate tectonics can mediate. Only through a holistic appreciation of geological processes can we hope to construct a naturalistic method of formulating biogeographic hypotheses and conducting analyses. A new way of dealing with the other sorts of prominent changes in geographic area relationships produced by plate tectonics, the agglomeration of continents, is developed. This paper presents a way of dealing with both the agglomerative and disassociative aspects of plate tectonics by means of a case study. The biogeographic method used here is termed naturalistic biogeography.

This section of the paper consists of three parts. First, the phylogenetic analyses of proetid clades are presented, along with discussions of the biogeographic origins and the patterns of extinction and diversification for each clade. New diagnoses are presented for all taxa, and in the case of newly recognized taxa, descriptions are also given. Then, the new biogeographic method that is to be used herein is presented. This method is applied to the evolutionary histories gleaned from analysis of these four clades. A discussion integrating macroevolutionary patterns and process is also given. Finally, a comment is given on the depauperate proetid trilobite fauna that appears to largely predate the appearance of most of the members of the four clades that were intensely studied herein. This comment includes a brief discussion of this depauperate fauna's possible evolutionary affinities, along with an elaboration of the evolutionary implications of the existence of distinct faunas recognized in the rock record.

PHYLOGENY OF *CRASSIPROETUS* STUMM, 1953A

For diagnosis and discussion of taxa to be excluded from this genus see above. A phylogeny for this genus was generated using 33 characters and 14 taxa. The characters used are given in table 3, and the character codings for these taxa are given in table 4. One most parsimonious tree (fig. 12) was produced using the **ie*** option of Hennig86 (Farris, 1988) (equivalent to the exhaustive search of PAUP) and the heuristic search using stepwise random addition with 10 replications of Paup 3.0q (Swofford, 1990). The tree was 81 steps long with a consistency index of .49 and a retention index of .51. *Crassiproetus turgidus* (Northrop, 1939) is treated as the outgroup. This species is known from the Upper Silurian of the Gaspe region from pygidia only, although there is a poorly preserved cranidium from this locality that may belong to this species. Because of this, only the pygidial characters were treated as polarizable, with the other characters treated as missing data. This taxon was treated as the outgroup on the basis of the following criteria: it significantly predates the other members of the genus (Upper Silurian vs. Pragian); it lacks one of the characters shared by all the other members of *Crassiproetus*; the pygidial axial segments medially only arch anteriorly, whereas in all other species the pygidial axial segments arch first anteriorly, then laterally first posteriorly, then anteriorly, then posteriorly; and it has a unique structure of the pygidial border. A taxon outside of the genus *Crassiproetus* was not employed as the outgroup because most members of this genus develop unique structures that make it difficult to discern homologous character transformations and polarities.

A bootstrap analysis was run using PAUP 3.0q (Swofford, 1990) in order to assess the confidence one can have in this phylogeny. One hundred bootstrap replications were performed. For each replication a heuristic search was employed that searched for the most parsimonious tree created by substitution and replacement of the data matrix. This heuristic search used the simple stepwise addition option. Confidence intervals from the bootstrap analysis were obtained by retaining groups compatible with the 50% majority-rule consensus trees. The nodes that appeared in the tree in figure 12 that are supported by the bootstrap analysis are the *C. alpenensis/canadensis* node with a .28 value, the ((*calhounensis*)(*alpenensis/canadensis*)) node with a .28 value, the *C. norwoodensis/sibleyensis* node with a .38 value, and the *neoturgidus/halliturgidus* node with a .80 value. Obviously none of these values are statistically significant at the .05 level.

Phylogenetic position and stratigraphic first occurrence of taxa are congruent except for *Crassiproetus schohariensis*, new species. This species is hypothesized to be one of the more derived members of *Crassiproetus* analyzed herein, yet it appears early (Upper Emsian) in the ENA fossil record of the group. This means that the clade containing *C. crassimarginatus* (Hall, 1843), *C. sibleyensis* Stumm, 1953b, and *C. norwoodensis* Stumm, 1953a and the clade containing *C. traversensis* Stumm, 1953a, must have already begun to differentiate by this time. *Crassiproetus crassimarginatus* and *C. traversensis* appear in the earliest Eifelian. Therefore this means that there is only minor incongruence between the stratigraphic and phylogenetic data bases. Because we are dealing with species, which for the limits of resolution of this type of character analysis can potentially be ancestral taxa (that is, we cannot discriminate between separate populations of a species), we need not conclude that the clade containing *C. micrograniulatus* Stumm, 1953a, or the clade containing *C. calhounensis* (Cooper and Cloud, 1938), *C. alpenensis* Stumm, 1953a, and *C. canadensis* Stumm, 1953a, must have begun differentiating.

Four new species of *Crassiproetus* are recognized. These species are known only from pygidia, and thus had to be coded as missing for a large number of the characters employed in the phylogenetic analysis of this genus. When the character codings for these taxa were included in phylogenetic analysis, one tree was obtained. When these more fragmentary taxa were removed, two trees were

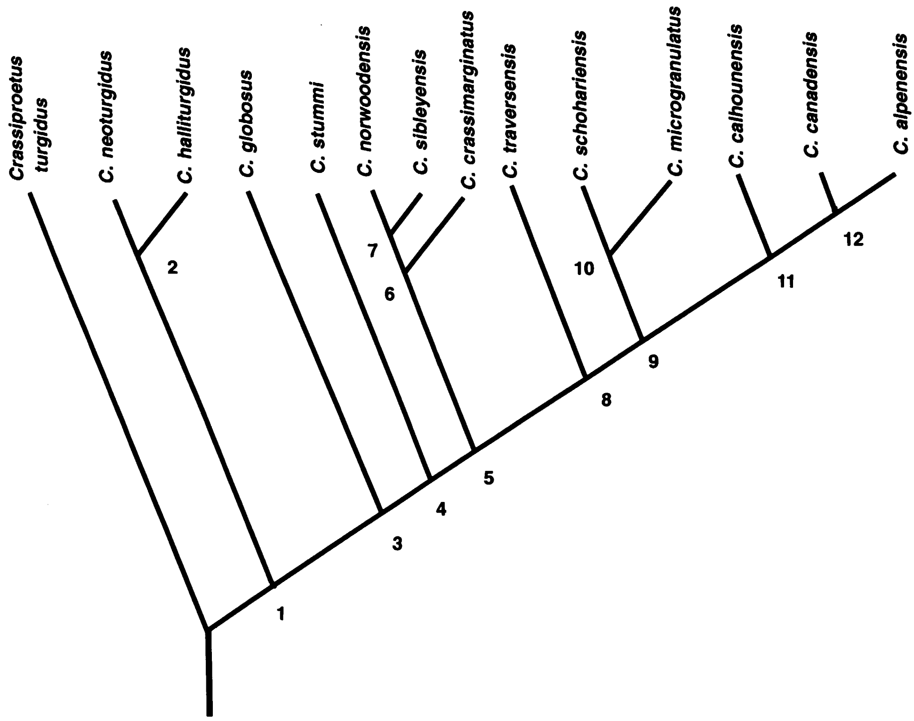

Fig. 12. The single most parsimonious cladogram depicting the phylogeny generated for taxa from the genus *Crassiproetus* using the data matrix given in table 4. This single most parsimonious tree was generated using the **ie*** option (exhaustive search) of Hennig86 (Farris, 1988) and an heuristic search using PAUP 3.0q with stepwise random addition and 10 replications (Swofford, 1990). The tree has a length of 81 steps, a consistency index of .49, and a retention index of .51. All multistate characters were treated as unordered, nonadditive. Characters were optimized using ACCTRAN and are shown for each node with unambiguous apomorphies depicted by parentheses, ( ), and ambiguous apomorphies, either due to missing data or multiple equally parsimonious resolutions, depicted by brackets, [ ]. Node 1: 5[0,1], 6[0,1], 9[0,1], 14[0,1], 19[0,2], 21[0,1], 23(2), 30[0,1]; Node 2: 22(1), 30(1), 32(1); Node 3: 25(2), 27(1), 28(2); Node 4: 30(0), 31(1); Node 5: 6(1), 9(1), 14(1), 19(2), 22(1), 26[1,2], 29(1); Node 6: 2[0,1,2], 15(1), 16(1), 17(1), 20[0,1], 25(1); Node 7: 2(2), 8(1), 12[0,1], 18(1), 19[1,2], 21(0), 30[0,1]; Node 8: 4(1), 5(1), 21(1), 23(1); Node 9: 7(1), 10(1), 18[0,1], 26(1), 27[0,1]; Node 10: 15[0,1], 20[0,1], 22(0), 27(0), 30(1); Node 11: 0[0,1], 1[0,1], 3(1), 8[0,1], 13(1), 19(1); Node 12: 5(0), 6(0), 12(1), 18(0), 27(0).

obtained, and these differed only in the placement of a single taxon. This is analogous to the phenomenon recognized by Donoghue et al. (1989) and Novacek (1992). Poorly preserved fossil taxa can alter schemes of relationship when added to a phylogeny that incorporates only completely preserved recent taxa. In this case, poorly preserved fossil taxa, when added to a data matrix, can improve the resolution obtained from an analysis of well-preserved fossil taxa.

Another taxon, *C. brevispinosus* Fagerstrom, 1961, is elevated from the rank of subspecies to species. It is not considered in the phylogenetic analysis, but it is treated as very closely related to *Crassiproetus crassimarginatus* (Hall). Two of the new species, *C. neoturgidus* and *C. halliturgidus*, share a unique feature with *Crassiproetus turgidus* (Northrop, 1939), the prominent arching and elevation of the pygidial axis, particularly posteriorly; however, this character is treated as primitive in phylogenetic analysis because *C. turgidus* was employed as the outgroup.

We must use caution when using a higher-level phylogeny to deduce the biogeographic origins of a clade, particularly when we recognize that large disjunctions in geography

TABLE 3

Characters Used in Phylogenetic Analysis of the Genus *Crassiproetus*

"0" is the plesiomorphic state. Character matrix is given in Table 4

0. Anterior cephalic border ridge: (0) long, (1) short.

1. Anterior portion of frontal glabellar lobe in dorsal view: (0) rounded, (1) pointed.

2. Striations on anterior border ridge developed: (0) anteriorly, (1) ventrally, (2) dorsally.

3. Anterior ledge between frontal glabellar lobe and striated anterior border ridge: (0) visible in dorsal view, (1) not visible in dorsal view.

4. Genal field near posterior and lateral border furrows: (0) pointed, (1) rounded.

5. Genal angle deflected: (0) posteriorly, (1) anteriorly.

6. Genal angle: (0) long and pointed, (1) meeting as a long line directed exsagittaly, (2) smoothly rounded.

7. Eye sits on: (0) small socle, (1) wide, flat socle or palpebral pedestal.

8. Eyes: (0) small, anterior end between S2 and S3, posterior end at or in front of anterior edge of intraoccipital lobe, (1) large, anterior end at or beyond S3, posterior end at anterior edge of intraoccipital lobe.

9. Eyes positioned: (0) far forward, posterior end of eye in front of anterior edge of intraoccipital lobe, (1) far backward, posterior end of eye at anterior edge of intraoccipital lobe.

10. Facial suture circumscribing eye: (0) asymmetrical, reflexes exsagittally (out laterally) in posterior half, gently curves sagittally anteriorly, (1) suture symmetrical, equally curved around anterior and posterior halves of the eye.

11. S0, at anterior edge of the intraoccipital lobe: (0) follows a straight, linear course distally to axial furrow, (1) flexes sharply laterally anterior of medial portion of S0.

12. Librigena: (0) slightly arched lateral of eye socle, (1) steeply arched lateral of eye socle.

13. Size of librigenal field between the eye socle and the lateral border furrow: (0) relatively large, twice the width (tr.) of the eye, (1) small, equal to the width (tr.) of the eye.

14. Posterior region of glabella: (0) at same level as L0, (1) elevated significantly above L0.

15. Posterior region of glabella: (0) planar, (1) inflated.

16. S0 at midline: (0) weakly incised, (1) well incised.

17. Posterior border furrow lateral to an exsagittal line drawn from the distal end of the eye: (0) straight, (1) kinked anteriorly, then flexed posteriorly.

TABLE 3—(*Continued*)

18. Anterior of eye, facial suture: (0) directed laterally at 20°, (1) straight, paralleling or inclined at 5° angle from an imaginary exsagittal line.

19. Lineations on front of glabella: (1) roughly convex and parallel, (2) roughly straight, parallel to a dorsal plane cutting the glabella, and discontinuous.

20. Lateral margins of glabella, posterior of eyes, due to conformation of intraoccipital lobes: (0) parallel to an imaginary sagittal line, (1) posteriorly flexes laterally.

21. Anterior of the eye, between S3 and S4, the sides of the glabella: (0) are parallel, (1) converge slightly.

22. Shape of pygidium: (0) broad, width 1.5 times length, (1) long, width 1.2 times length.

23. Pygidial border: (0) developed as a rounded, laterally splayed ridge, (1) developed as a steep, near vertical plane.

24. Pygidial axis: (0) reaches the border, (1) separated from the border by a small space.

25. Pygidial axis: (0) low and flattened, (1) arched.

26. Number of pygidial axial rings: (0) 14, (1) 15–16, (2) 17–18, (3) 13.

27. Pygidial pleurae: (0) laterally curving sharply posteriorly, (1) laterally weakly deflected posteriorly.

28. Medial kinks on pygidial axial rings visible: (0) on all but the rings back more than 75% of the sagittal length of the pygidium, (1) on the rings back to 50% the sagittal length of the pygidium.

29. Interpleural furrows: (0) present, (1) faint to invisible.

30. Pygidial pleurae in lateral view: (0) rounded, (1) flat.

31. Pleural furrows: (0) broad, approximately the width of the pleural bands, (1) narrow and faint.

32. Pygidial axial furrows: (0) converge posteriorly, (1) do not converge until posterior of eighth or ninth axial ring.

may be present within genera or even species over time. However, it is still instructive to consider the biogeographic origins of the genus *Crassiproetus*. We can first use Fitch optimization (Fitch, 1971), treating biogeographic regions as unordered multistate characters to deduce the ancestral biogeographic state of the *Crassiproetus* clade. This is analogous to mapping characters onto the terminal taxa of a tree and then determining, on the basis of parsimony, the optimal state for a character at any interior node. It is clear that biogeographic states can change significantly within any different phylogeny, suggesting that biogeographic area relationships of taxa are not parsimonious. However, this does not mean that parsimony should not be used as an arbiter to choose between competing biogeographic hypotheses.

Other methods of character optimization aside from Fitch's could have been used. For instance, characters could be optimized via DELTRAN (Swofford and Maddison, 1987) using most parsimonious reconstruction sets. However, this requires the assumption of ordered character states. As this analysis is being employed in an exploratory fashion to ascertain the possible biogeographic affinities of genera without prior assumptions of a particularly likely set of area relationships, Fitch optimization, which considers multistate characters to be unordered, appears to be the least assumption-laden. The geographic distributions of genera from the phylogeny of figure 6 were treated as Arctic, Eastern North America, Armorican, and Baltic. These paleocontinental regions are defined as shown in figure 13, which follows Van der Voo (1988) and Kent (1985). Only taxa in the clade sister to "*Plesiowensus*" *confossus* were considered, as this part of the phylogeny of the Proetinae contained the best representation in terms of geographic realms and number of species sampled (see fig. 14). This analysis indicates that the ancestral biogeographic state of the genus *Crassiproetus* is in Eastern North America and/or the Arctic. This accords well with the observation that all but one of the species in this genus are known from ENA; however, none of the species in this genus are known to occur in the Arctic.

The earliest known species of this genus, *C. turgidus*, discussed below, is known from the Upper Silurian of Quebec, which is treated as ENA following Oliver (1977). Because the earliest species of this genus is known from ENA, and indeed no species of this genus are known to occur in the Arctic, the biogeographic affinities of this genus are treated as primitively belonging to ENA. Thus, *Crassiproetus* was a genus endemic to ENA that survived in that region over several faunal intervals. There is not a prominent change in area relationships associated with the reintensification of the Acadian Orogeny at the Eifelian–Givetian transition in this genus. Howerver, there was a brief period of cosmopolitanism in this genus during the Emsian when it attained a relatively broad distribution with species in ENA and Kazakhstan. This craton probably lay somewhere to the right (east) of where Baltica is in figure 13 (Pedder and Oliver, 1990). As discussed above, during the early Emsian the initial minor effects of the Acadian Orogeny were felt in ENA and this plate tectonic event may be related to the interval of relative cosmopolitanism in *Crassiproetus*. A similar pattern is found for *Basidechenella* and is discussed below.

TABLE 4

Character State Distribution for Species Used in Phylogenetic Analysis of *Crassiproetus*

Characters and states are listed in table 3. Missing data are indicated by "?"

		1	11111	11112	22222	22223	33
	012345	67890	12345	67890	12345	67890	12
Crassiproetus turgidus	??????	?????	?????	?????	?0000	00000	00
C. globosus	000000	00000	00000	00000	00202	31201	00
C. alpenensis	100110	01011	01100	000?0	10102	10210	10
C. crassimarginatus	001000	10010	10011	11021	11211	21210	10
C. traversensis	000011	10011	10010	00020	11102	21210	10
C. canadensis	010100	01111	11110	00010	11112	20110	10
C. microgranulatus	000011	11011	00011	00121	10212	10111	10
C. sibleyensis	002101	10111	01011	11111	01201	11211	10
C. calhounensis	110111	11111	0011?	10110	01102	11210	10
C. norwoodensis	0020??	??110	0??11	1?1?0	0????	?????	?0
C. stummi	??????	?????	?????	?????	?0212	01200	10
C. schohariensis	??????	?????	?????	?????	?0101	302?1	10
C. neoturgidus	??????	?????	?????	?????	?1200	000?1	?1
C. halliturgidus	??????	?????	?????	?????	?1200	100?1	?1

If we consider the complete diversity of the genus through time and space we recognize

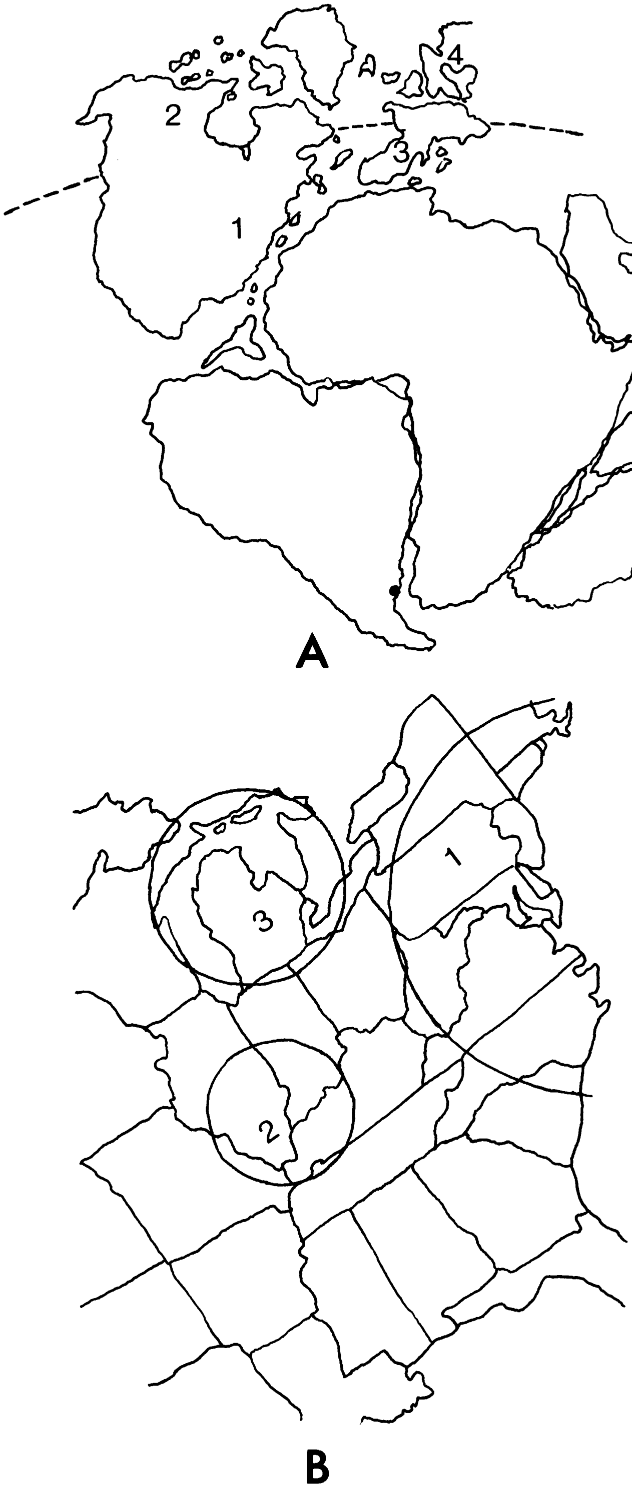

Fig. 13. **A.** Reconstruction of earth's paleogeography during the Middle Devonian emphasizing the regions considered in this study. The reconstruction is based on Kent (1985) and Van der Voo (1988).

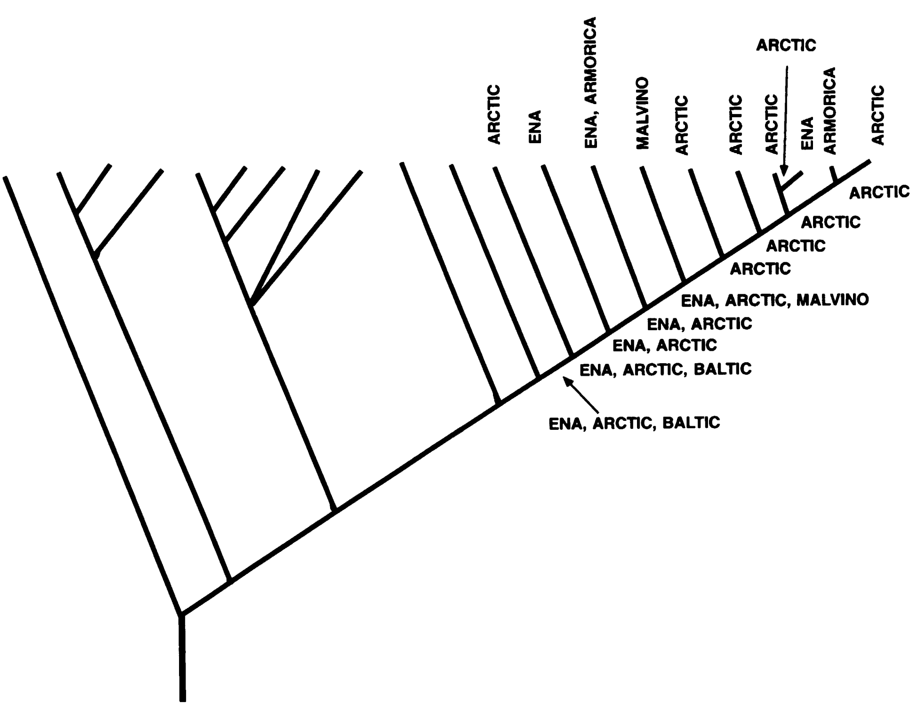

Fig. 14. Biogeographic states are mapped on the terminal taxa and the nodes for the best represented portions of the higher-level phylogeny of the Proetinae (i.e., those taxa sister to *Plesiowensus obconicus*). Nodes are optimized parsimoniously using Fitch optimization, which allows unordered transformations between multistate characters. ENA = Eastern North America. The other biogeographic conditions are self-explanatory. The biogeographic distributions for each of the terminal taxa were determined using the distributions of the two most basal members phylogenetically within each terminal taxon except for the two species of *Dechenella*. These species were coded following their biogeographic distributions, which gives the optimization for their ancestral node as ENA, ARCTIC in the preliminary phase of Fitch optimization. However, the addition of the ARMORICA biogeographic state, common for some of the derived species of *Dechenella*, would not affect the optimization produced during the final phase of Fitch optimization for any of the nodes considered.

that one species of *Crassiproetus*, *C. turgidus*, is known from the Upper Silurian of the Gaspe Peninsula, one species is known from the Pragian–Emsian of Kazakhstan, *C. globosus*, and in ENA two species of *Crassiproetus* are known from the upper Emsian, *C. stummi* and *C. schohariensis*. The latter two species also occur in the Eifelian. There are seven more species that occur in the Eifelian of ENA: *C. brevispinosus*, *C. crassimarginatus*, *C. sibleyensis*, *C. schohariensis*, *C. neoturgidus*, *C. hallituridus*, and *C. traversensis*. One of these species, *C. traversensis*, persists into the Givetian. In addition to this species, there

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The dot in southern South America is the paleopole and the dashed line through Laurentia is the paleoequator. Numbers are placed on important paleobiogeographic regions: Eastern North America = 1, the Arctic = 2, Armorica = 3, and Baltica = 4. **B.** Reconstruction of Eastern North America with the approximate outer bounds of the major tectonic basins in this region during the Middle Devonian demarcated by circles. Shown are the Appalachian Basin (1), the Illinois Basin (2), and the Michigan Basin (3). Figure based on Beaumont et al. (1988).

are four species known exclusively from the Givetian: *C. microgranulatus*, *C. calhounensis*, *C. alpenensis*, and *C. norwoodensis*.

No species of *Crassiproetus* is known to occur in strata younger than the late Givetian Taghanic Stage (strata coeval with the Thunder Bay and Tully Limestones). (See comments on *Crassiproetus* in the section on higher-level phylogeny to see those taxa that have been incorrectly assigned to this taxon that occur in Carboniferous strata.) Therefore, this genus is held to go extinct near the end of the Givetian at the end of the Taghanic Stage, along with most of the rest of the Hamilton Group fauna.

Population densities of species in this genus are typically low relative to such trilobites as *Phacops rana* (Green, 1832) (e.g., Eldredge, 1972); however, locally such densities may be relatively high (Ludvigsen, 1987). This may make it difficult to develop with certainty any explanations for their extinction. Of course, chance could be a factor (Raup, 1991). However, an important contributing factor may be the disappearance of environment. This genus is always associated with reefal or carbonate, shallow-water deposits, as are many proetids (Fortey and Owens, 1975; Snajdr, 1980; Ludvigsen, 1987). This is not to say that *Crassiproetus* occurs in all carbonate deposits in ENA during the Middle Devonian. However, in the Eifelian, when carbonate deposition was nearly ubiquitous in ENA, the genus (and one species, *C. crassimarginatus*) was widespread.

The beginning of the Givetian is accompanied by a marked deepening in the Appalachian Basin, referred to as transgressive–regressive cycle Ie (Johnson et al., 1985). In the Appalachian Basin carbonates of the Onondaga Limestone are replaced by the anoxic black shales of the Marcellus Formation in the manner described by Griffing and ver Straeten (1991). The Marcellus is the oldest formation in the lithostratigraphic package of shales and occasional limestones that make up the Hamilton Group. (Interestingly, *Crassiproetus* has never been recovered from these limestones in the Appalachian Basin.) After this time, species of *Crassiproetus* are only found in areas of nearly continuous limestone deposition (e.g., the Michigan Basin and the Illinois Basin).

A prominent deepening or transgressive event marks the end of the Taghanic Stage of the Upper Givetian (taken to be at the top of the Tully Limestone following Kirchgasser et al. [1985]) that is termed transgressive–regressive cycle IIa by Johnson et al. (1985). Associated with this deepening is the replacement of carbonates by shales in the stratigraphic record; for example, the Geneseo Shale in New York State replaces the Tully Limestone, the Antrim Shale in the Michigan Basin replaces the Traverse Limestone (Catacosinos et al., 1991), and the New Albany Group in the Illinois Basin replaces the Cedar Valley Limestone (Treworgy and Devera, 1991). No species of *Crassiproetus* are known to postdate this transition. Thus, this bespeaks a possibly clearcut case of environmental extirpation mediating the extinction of a clade. It seems that species will broadly track their habitats or zones of environmental tolerance (Coope, 1978; Eldredge, 1989). Once these habitats disappear, species must change or face extinction. The species of *Crassiproetus* that persisted into the upper Givetian apparently could not change.

We can combine stratigraphic information with the results from phylogenetics and information about rising and falling sea-levels (either eustatic or tectonic) to obtain a more detailed understanding of the relationship between changing area relationships, diversification, extinction, and transgressive–regressive cycles. The bulk of the diversification of *Crassiproetus* in the Eifelian can be related to the effects of transgressive–regressive cycle Ic of Johnson et al. (1985) although these cycles do need to be better integrated with Rickard's (1989) and Kirchgasser et al.'s (1985) correlation charts. During this time, species of this genus occur in the Michigan, Illinois, and Appalachian Basins. In the Givetian, species of *Crassiproetus* are restricted to the Michigan and Illinois Basins. During this time, if the evolutionary history of the group is not caused by much earlier geological events, it may be related to the effects of transgressive–regressive cycles Ie, If, and IIa of Johnson et al. (1985).

For the taxa considered herein, this approach can be further refined to the species level (see table 5). (Most of the species from the Illinois Basin could not be obtained be-

TABLE 5
Species of Trilobites in the Subfamily Proetinae and in the "*Thebanaspis* Clade"
Species are divided up by genus, showing their representation in each of the three major basins in Eastern North America in the Middle Devonian.[a]

	APP	IL	MI
Upper Emsian/Sawkillian			
Crassiproetus schohariensis	X		
C. stummi			X
Basidechenella clara			X
B. sp. aff. *clara*	X		
B. hesionea	X		
Eifelian/Southwoodian			
Crassiproetus traversensis		X	X
C. brevispinosus	X		X
C. crassimarginatus	X	X	X
C. halliturgidus		X	
C. neoturgidus	X		
C. schohariensis	X		
C. sibleyensis			X
C. stummi	X		X
Basidechenella canaliculata	X	X	
B. clara	X	X	X
B. eriensis			X
B. nodosa			X
B. lucasensis		X	
Dechenella planimarginata			X
D. welleri		X	X
Monodechenella halli	X		X
M. curvimarginata		X	
Late Eifelian and Givetian/Cazenovia, Tioughniogan, and Taghanic[b]			
Crassiproetus traversensis			X
C. alpenensis			X
C. calhounensis		X	
C. canadensis			X
C. microgranulatus			X
C. norwoodensis			X
C. arietinus		X	
C. bumastoides		X	
C. occidens		X	
Basidechenella arkonensis	X		X
B. cartwrightae			X
B. elevata		X	
B. lucasensis			X
B. nodosa			X
B. pulchra			X
B. reimanni			X
B. rowi	X		X
B. witherspooni			X
B. prouti		X	
Dechenella alpenensis			X
D. haldemani	X		
D. valentini			X
Monodechenella macrocephala	X		
M. legrandsmithi			X

[a] Abbreviations: APP = the Appalachian Basin (primarily New York State and Pennsylvania, although *Basidechenella clara* is also known from the Needmore Shale of West Virginia and Virginia), IL = the Illinois Basin, and MI = the Michigan Basin.

[b] Three species of *Dechenella* known from the latest portion of the Eifelian in the Cazenovian are listed in this section.

cause they were under study. However, information from Walter [1923], Hickerson [1992] and Hickerson [personal commun.] could be used to add to table 5 three species of *Crassiproetus*, *C. arietinus* (Walter, 1923), *C. bumastoides* (Walter, 1923), and *C. occidens* (Hall, 1861). These species are known from late middle and late Givetian times according to Hickerson [1992].) Differences are evident in the number of widespread taxa (occurring in two or more of the major basins in ENA) in the Eifelian and Givetian. In the Eifelian, *Crassiproetus crassimarginatus* (Hall, 1843) is known to occur in the Appalachian, Michigan, and Illinois Basins, *C. brevispinosus* Fagerstrom, 1961, is known from the Appalachian and Michigan Basins, and *C. traversensis* Stumm, 1953a, occurs in the Michigan and Illinois Basins. *Crassiproetus traversensis* is restricted to the Michigan Basin in the Givetian. Thus, there are three widespread species in the Eifelian. One species, *C. stummi*, new species, apparently moves from the Michigan Basin in the Upper Emsian Bois Blanc Formation to the Appalachian Basin in the Eifelian Onondaga Limestone of New York State. Two species, *C. schohariensis*, new species and *C. neoturgidus*, new species, are restricted to the Appalachian Basin in the Eifelian (the former also occurs there in the Upper Emsian). One species, *C. halliturgidus*, new species is restricted to the Illinois Basin in the Eifelian, and one, *C. sibleyensis* Stumm, 1953b, is restricted to the Michigan Basin in the Eifelian.

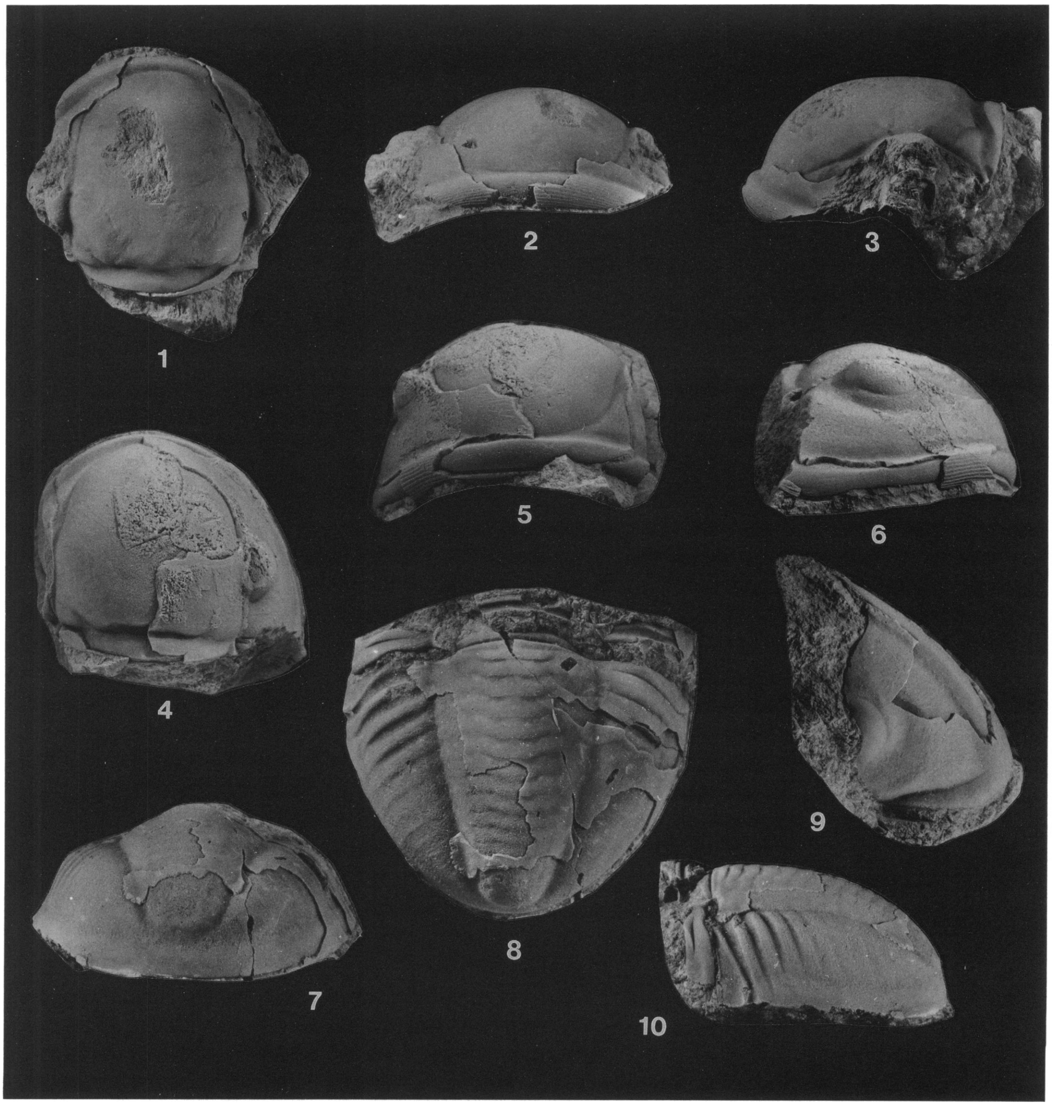

Fig. 15. *Crassiproetus traversensis* Stumm, 1953a. **1-3.** Four Mile Dam Limestone, Traverse Group, Tioughniogan (Givetian), Four Mile Dam on Thunder Bay River, 3 mi. northwest of Alpena, Alpena County, Michigan, UMMP 28673, paratype, dorsal, anterior, and lateral views of cephalon, ×2. **4-6.** Jeffersonville Limestone, Southwoodian (Eifelian), Waverley, Morgan County, Indiana, YPM 33828, dorsal, anterior, and lateral views of cephalon, ×2.5. **7, 8, 10.** Horizon and locality same as **1-3.** UMMP 28674, paratype, posterior, dorsal, and lateral views of pygidium, ×2. **9.** Horizon and locality same as **1-3.** UMMP, 25446, external view of librigenae, ×2.

In the Givetian, four species are restricted to the Michigan Basin: *C. microgranulatus* Stumm, 1953a, *C. alpenensis* Stumm, 1953a, *C. canadensis* Stumm, 1953a, and *C. norwoodensis* Stumm, 1953a. Of species that could be analyzed here, one species was restricted to the Illinois Basin, *C. calhounensis* (Cooper and Cloud, 1938), although several other species are endemic to this basin. Thus, by Givetian times there were no remaining widespread species in ENA. These results do need to be bolstered by comparison to the Illinois Basin *Crassiproetus* fauna to ascertain if any of the distinct species from this

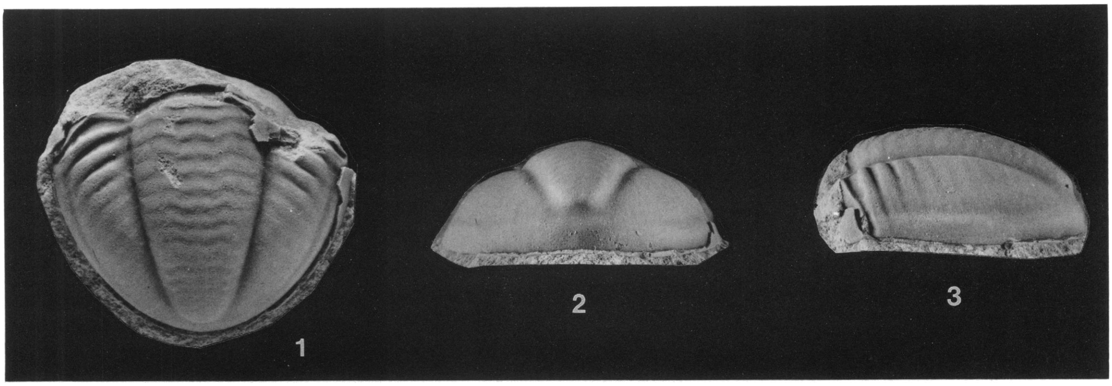

Fig. 16. *Crassiproetus traversensis* Stumm, 1953a. 1-3. Jeffersonville Limestone, Southwoodian (Eifelian), Morgan County, Indiana, YPM 33827, dorsal, posterior, and lateral views of pygidium, ×2.5.

basin are actually synonymous with species found in the Michigan Basin. However, at present, these results indicate that species of *Crassiproetus* in the Givetian underwent a moderate reduction in the size of their geographic distributions. This could have conceivably made them more susceptible to extinction, as species with narrower geographic distributions are more likely to succumb to the vicissitudes of environmental change (e.g., Scheltema, 1986).

CRASSIPROETUS STUMM, 1953A

Crassiproetus traversensis Stumm, 1953a

Figures 15, 16

Proetus crassimarginatus (Hall). Howell, 1951: 271, pl. 5, fig. 3.

Proetus (*Crassiproetus*) *traversensis* Stumm, 1953a: 112, pl. 1, figs. 1–2, 10–15.

Proetus (*Crassiproetus*) sp. *A*. Stumm, 1953a: 114, pl. 1, fig. 16.

Proetus (*Crassiproetus*) *crassimarginatus glabrus*. Stumm, 1953b: 17, pl. 2, fig. 11.

Proetus crassimarginatus (Hall). Stumm, 1964: 3, pl. 1, figs. 7–12.

Crassiproetus traversensis Stumm. Kesling et al., 1974: pl. 3, fig. 17.

DIAGNOSIS: Genal angle deflected posteriorly, with lateral edge directed straight back; posterior region of glabella planar; S0 at midline weakly incised; facial suture symmetrical around eye, evenly curves around anterior and posterior halves of eye; striations on anterior border developed anteriorly; intraoccipital lobes weakly incised; 17–18 pygidial axial rings; axis low and flattened; pygidial border developed as rounded lateraly splayed ridge; pygidial pleurae laterally curving sharply posteriorly, relatively steeply arched, with dorsal surface in lateral view flat; pygidial axis reaches border.

MATERIAL: AMNH 44701, 44702; SDSNH 10693, 10694; UMMP 4897, 4897R, 25446, 25447, 25547, 25549, 28673–28675, 41790–41792; YPM 33807, 33810, 33812, 33826, 33827, 33830, 33831, 33841.

DISCUSSION: This species was designated the type of the subgenus *Crassiproetus* by Stumm, 1953a. It is known from the Columbus Limestone (Eifelian), Kelley's Island, Lake Erie, Ohio; the Jeffersonville Limestone (lower Eifelian) from the Falls of the Ohio, near Louisville, Kentucky; and from Clark and Morgan Counties, Indiana; from the Traverse Group, Ferron Point Formation (lower Givetian), Presque Isle County, Michigan (MI); the Gravel Point Formation (lower Givetian), Petoskey, MI; the 4-mile Dam Formation (middle Givetian), Alpena, MI; and the Dock Street Clay (middle Givetian), Alpena, MI. This species appears to have differing distributional patterns in the Eifelian and the Givetian. It is restricted to southern Indiana and Ohio in the Eifelian, and to northern Michigan in the Givetian. During the Eifelian its distribution appears to partially overlap that of *Crassiproetus crassimarginatus* (Hall) in Indiana, Ohio, and Kentucky. Thus, it is associated with deposits of transgressive–regressive cycles Ic, Ie, and If. It occurs in the basal transgression of cycle Ie and possibly also If.

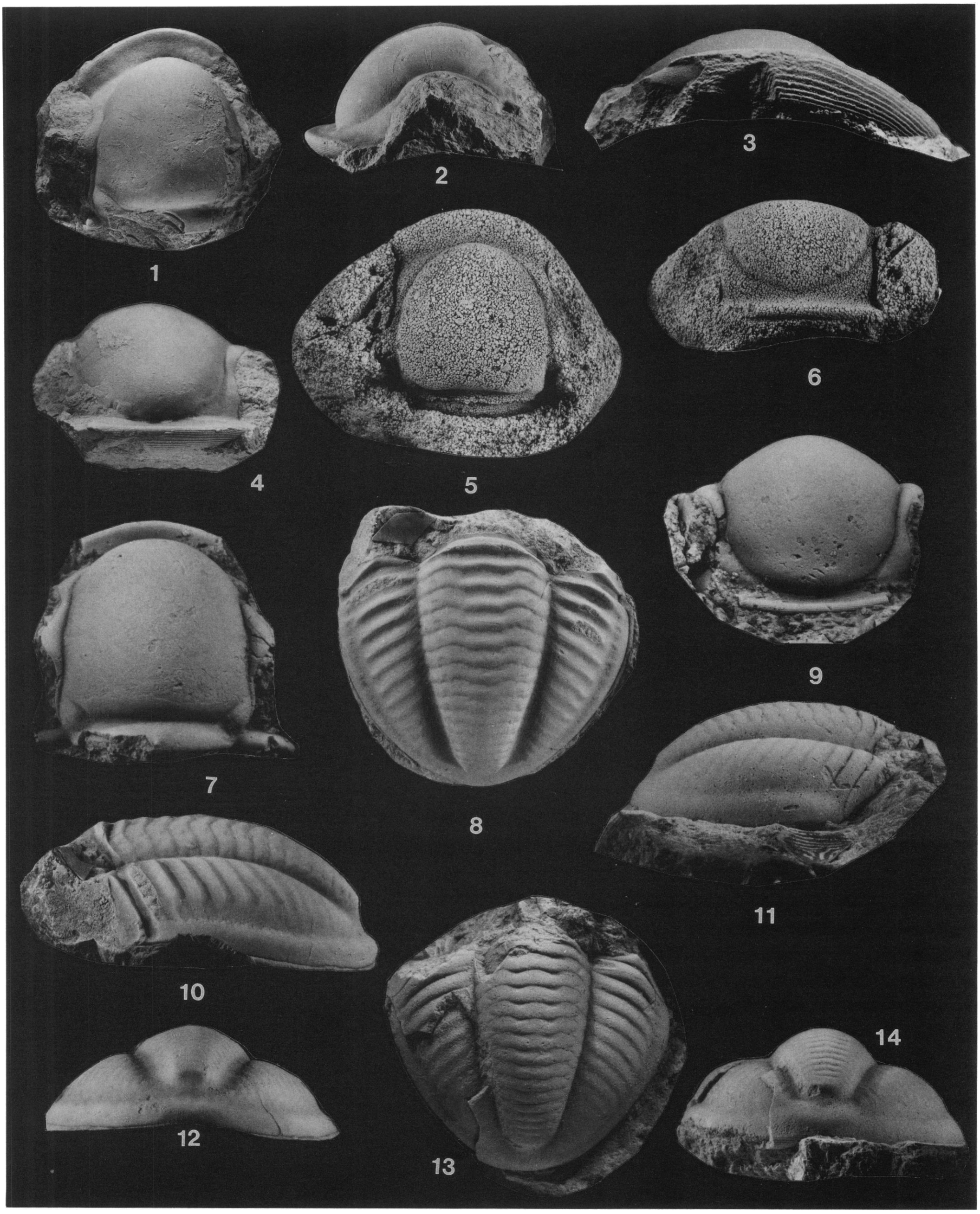

Fig. 17. *Crassiproetus* spp. **1-4.** *Crassiproetus crassimarginatus* (Hall, 1843). Formosa Reef Limestone, lower Amherstburg Formation, early Southwoodian (Eifelian), Highway Roadcut 2.5 mi. north of Formosa, Ontario, UMMP 29538, dorsal, lateral, ventral, and anterior views of cephalon, × 1.25. **5, 6.** *Crassiproetus crassimarginatus* (Hall, 1843). Springvale Sandstone, basal Onondaga Limestone, earliest Southwoodian (Eifelian), Springvale, Ontario, BMS E11987, dorsal and anterior views of cephalon, × 1.25. **7, 9.** *Crassiproetus brevispinosus* Fagerstrom, 1961. Horizon and locality same as 1–4. ROM 35387, dorsal and anterior views of cephalon, × 2.5. **8, 10, 12.** *Crassiproetus crassimarginatus* (Hall, 1843). Edgecliff Member, lower Onondaga Limestone, early Southwoodian (Eifelian), Williamsville, NY,

There are two distinct pygidial morphologies of species of *Crassiproetus* that are known from the Jeffersonville Limestone of southern Indiana. One of these can assuredly be assigned to *C. crassimarginatus*. However, the other pygidial morphotype is only associated with cephala that have been designated as *C. traversensis*. These pygidia are assigned to *C. traversensis* by the process of elimination and using the assumption that there is not another species of Proetinae occurring in southern Indiana whose cephala are never preserved. This logic is supported by the trilobite fauna in the Middle Devonian of Michigan. There pygidia and cephala are found associated that are identical to those from southern Indiana that are placed in *C. traversensis*.

It is probably because of this overlap in geographic ranges that authors have confused *C. traversensis*, particularly when only isolated pygidia are preserved, with *C. crassimarginatus*. For instance, Howell (1951) and Stumm (1964) misidentified pygidia of *C. traversensis*, calling them *C. crassimarginatus*. However, in these cases the pygidial axis extends to the pygidial border and it is flattened posteriorly (both characteristic of *C. traversensis*). In addition, the pygidial pleurae are more steeply arched than is typical of *C. crassimarginatus*, and the pygidial pleurae are typically steeply arched in *C. traversensis*.

There are other specimens that have been assigned to different species that should be assigned to *C. traversensis*. For instance, Stumm (1953a) remarks that *Crassiproetus* sp. A is similar to *Crassiproetus traversensis*, but they differ in the condition of the pleural segments. However, no such differences could be detected, partly because this specimen is too poorly preserved. Thus, *Crassiproetus* sp. A is treated as a synonym of *C. traversensis*. In addition, Stumm (1953b) described a new subspecies, *C. crassimarginatus glabrus*, from the Columbus and Jeffersonville Limestones of Ohio and Indiana, respectively, on the basis of pygidia that are treated here as synonymous with *C. traversensis*. For instance, the pygidium has the axis extending to the posterior border (and flattened posteriorly) and the more steeply arched pleural segments characteristic of *C. traversensis*.

Stumm (1953a) suggested that *Crassiproetus traversensis* might be closely related to *C. bumastoides* (Walter, 1923). The material of *C. bumastoides* could not be obtained because it is under study by another author. However, from figured material, the two taxa appear to differ in several features, including the condition of the pygidium. In *C. traversensis* the pygidial axis proceeds to the border. In *C. bumastoides* there is a small space between the axis and the border. In addition, the intraoccipital lobes are not separated from the glabella in *C. bumastoides*, but in *C. traversensis* the anterior portion of S0 is weakly incised such that the intraoccipital lobe is separated from the glabella. *Crassiproetus traversensis* may be closely related to *C. arietinus* (Walter, 1923). In particular, on the basis of figured material, these species appear to possess the same number of pygidial axial rings, and in *C. arietinus* the pygidial axis does appear to proceed to the border. However, as this material also could not be obtained because it was under study, such decisions await further investigation.

Crassiproetus traversensis is the only species of *Crassiproetus* that crosses the transition from the Onondaga Limestone to the Hamilton Group that does not go extinct. However, on the basis of the phylogeny in figure 12, clearly several other lineages must have survived this transition.

Crassiproetus crassimarginatus (Hall, 1843)

Figures 17.1–17.6, 17.8, 17.10–17.14, 18

Calymene crassimarginata Hall, 1843: 172, fig. 5.
Proetus crassimarginatus (Hall). Hall, 1859: 88.
Phillipsia crassimarginata (Hall). Billings, 1861: 362.

←

AMNH 39328, lectotype, dorsal, lateral, and posterior views of pygidium, × 1.25. **11, 13, 14.** *Crassiproetus crassimarginatus* (Hall, 1843). Jeffersonville Limestone, Southwoodian, Falls of the Ohio River, Kentucky, AMNH 39332, paralectotype, lateral, dorsal, and posterior views of pygidium, ×2.5.

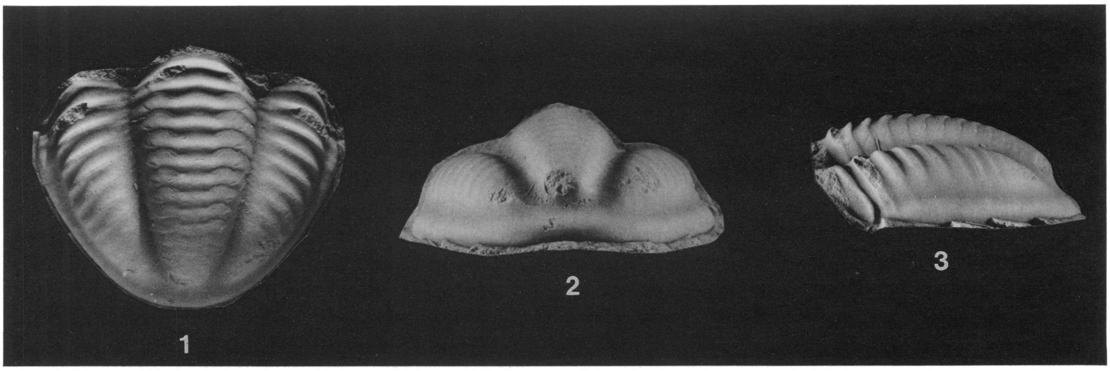

Fig. 18. *Crassiproetus crassimarginatus* (Hall, 1843). **1-3.** Jeffersonville Limestone, Southwoodian (Eifelian), Jefferson County, Kentucky, YPM 33808, dorsal, posterior, and lateral views of pygidium, ×2.25.

Proetus crassimarginatus (Hall). Hall, 1861: 72; Hall, 1862: 100; Hall, 1876: pl. 20, figs. 20–23, 26–31; Hall and Clarke, 1888: 99–101, pl. 20, figs. 20–22, 25, 26, 29–31, pl. 22, figs. 22, 26; Bassett, 1935: 453, pl. 38, figs. 12, 13; Shimer and Shrock, 1944: 651, pl. 274, fig. 19; Howell, 1951: 271.

Proetus (*Crassiproetus*) *crassimarginatus* (Hall). Stumm, 1953b: 15–17, pl. 1, figs. 2–6, 9–11, pl. 2, figs. 9, 10; Fagerstrom, 1961: 41–42, pl. 14, figs. 8–10.

Proetus (*Proetus*) *folliceps* (Hall and Clarke). Stumm, 1953b: 15, pl. 2, figs. 7, 8.

?*Proetus crassimarginatus* (Hall). Hall and Clarke, 1888: pl. 22, figs. 24, 25.

?*Proetus* (*Crassiproetus*) sp. aff. *P.* (*C.*) *crassimarginatus* (Hall). Stumm, 1953b: 17, pl. 2, figs. 3–5.

DIAGNOSIS: Genal spines absent; S0 at anterior edge of intraoccipital lobe flexes sharply outward; genal angle deflected posteriorly; S0 at midline weakly incised; posterior border furrow kinks anteriorly distal to eye, then flexes posteriorly; length (sag.) of anterior cephalic border to length of cephalon 0.15–0.16; pleurae laterally curving sharply posteriorly; top of pleural segments in lateral view flattened; medial kinks on pygidial axial rings visible on all but 25% most posterior rings; ratio of pygidial width–length 1.1–1.23; pygidial axis separated from border by small space.

TYPES: Lectotype, AMNH 39328 (fig. 17.8, 17.10, 17.12) from the Onondaga Limestone, Williamsville, New York (NY), equals Hall and Clarke (1888: pl. 20, figs. 29, 31). Paralectotypes in the AMNH collections are: 39330, Hall and Clarke (1888: pl. 20, fig. 20); 39331, Hall and Clarke (1888: pl. 20, fig. 6); 39332, Hall and Clarke (1888: pl. 20, fig. 5); 39333, Hall and Clarke (1888: pl. 20, fig. 22); 39335, Hall and Clarke (1888: pl. 25, fig. 8).

MATERIAL: AMNH 39328, 39330–39333, 39335, 39337, 39338, 44698, 44726, 44733; BMS E12345, E12896; SDSNH 849; UMMP 29536, 29538, 29540, 29543, 29546; YPM 33808, 33809, 33811.

DISCUSSION: This species is known from the Edgecliff Member of the Onondaga Limestone (lower Eifelian), western New York State; the Upper Onondaga Limestone, western New York State; the Columbus Limestone (Eifelian), Kelly's Island, Lake Erie, Ohio; the Jeffersonville Limestone (middle Eifelian) at the Falls of the Ohio River, Jefferson County, Kentucky, and Clarke County, Indiana; the Amherstburg Dolomite (lower Eifelian), Monroe County, southern Michigan; and the Formosa Reef Limestone (a member within the Amherstburg Dolomite, lower Eifelian), southern Ontario. Thus, it appears to be a widespread species, occupying several different basins in ENA and it is associated with transgressive–regressive cycle Ic. It first occurs at the base of the Onondaga and its equivalents in the Appalachian and Michigan Basins in deposits associated with the second prominent transgression in cycle Ic. This species and its sister taxon (discussed below) *C. brevispinosus* are fairly abundant in the Eifelian-age limestones of ENA, and taken together these species are certainly the most common species of *Crassiproetus*.

Stumm (1953b) incorrectly treated Hall's (1843: 172, fig. 5) specimen as the holotype of the species. Hall's original figured specimens were syntypes, and a lectotype must be designated. AMNH 39328, a pygidium, formerly one of the series 2897/3 from the Onondaga Limestone (probably Edgecliff Member), Williamsville, Erie County, NY, is designated herein as the lectotype of this species based on its better state of preservation then the specimen figured by Stumm (1953a: pl. 1, fig. 9).

Because of its broad geographic distribution, there is some confusion regarding the delineation of this species. As discussed above, specimens of *Crassiproetus traversensis* from Ohio and Indiana have been incorrectly assigned to this species. However, consideration of material originally assigned to *C. crassimarginatus* from New York State and southern Ontario indicates that there are two closely related species found in these locales. Fagerstrom (1961) described a new subspecies, *C. crassimarginatus brevispinosus*, from the Formosa Reef Limestone in southern Ontario on the basis of a cephalon that had slightly pointed genal spines. Genal spines are typically flattened in *C. crassimarginatus*. Here this taxon is treated as a distinct species, *Crassiproetus brevispinosus* Fagerstrom, 1961, sister to *C. crassimarginatus*. There exist additional characteristics that allow us to distinguish between *C. crassimarginatus* and *C. brevispinosus*. For instance, the prominently projecting anterior cephalic border is a synapomorphy that is uniquely shared by these two species. However, this anterior cephalic border is slightly shorter in *C. brevispinosus* than in *C. crassimarginatus*. For instance, the ratio of the length of the anterior border to the entire length of the cephalon is roughly 11–13% for *C. brevispinosus*, whereas in *C. crassimarginatus* this value is 15–16%. (These measurements are based on less than five specimens for each species.) However, using the small sample t-distribution to distinguish between the means of two different samples, the differences between means were found to be significant at the 95% level of confidence. The difference between means was found to be .033 ± .017. In addition, the width–length ratio of the pygidia in *C. brevispinosus* is slightly smaller than in *C. crassimarginatus*, 1–1.05 vs. 1.1–1.23 (based on measurements from three and six specimens, respectively). The small sample t-distribution was also used to discover if the differences in the means of these two putative species were significant. The difference between means was found to be .155 ± .086 at the 95% level of confidence. On the basis of these three characteristics, the two closely related species can be distinguished.

Stumm (1953b) recognized a pygidium that he claimed was distinct from *Crassiproetus crassimarginatus*, and he erected a new subspecies, *C. crassimarginatus glabrus*, to accommodate this pygidium. He was correct in recognizing that it differed from *C. crassimarginatus*. However, this pygidium should actually be assigned to *C. traversensis* as indicated above, and it is not considered a valid subspecies of *C. crassimarginatus*.

Stumm (1953b: pl. 2, figs. 3–6) figured and discussed specimens that he referred to *Crassiproetus* sp. aff. *C. crassimarginatus* from the Amherstburg Dolomite in southeastern Michigan. These specimens are too poorly preserved to make any exact taxonomic assignations. However, because they appear to be similar to *C. crassimarginatus* and lack the steeply arched pygidial pleural fields of *C. brevispinosus*, they are treated as conspecific here.

Crassiproetus brevispinosus Fagerstrom, 1961

Figure 17.7, 17.9

Proetus crassimarginatus (Hall). Hall, 1876: pl. 20, fig. 20; Hall and Clarke, 1888: 99, pl. 20, figs. 20, 27, 28.

Proetus (*Proetus*) *folliceps* (Hall and Clarke). Stumm, 1953b: 15, pl. 2, fig. 1.

Proetus (*Crassiproetus*) *crassimarginatus* (Hall). Stumm, 1953b: 15, pl. 1, figs. 7, 12, 13.

Proetus (*Crassiproetus*) *crassimarginatus brevispinosus* Fagerstrom, 1961: 42, pl. 14, figs. 6, 7, 11, 12.

Crassiproetus crassimarginatus (Hall). Ludvigsen, 1979: 82, fig. 55d, e; Ludvigsen, 1987: 681–682, figs. 4, 5, 6a–i.

?*Proetus crassimarginatus* (Hall). Bassett, 1935: 453.

DIAGNOSIS: Same as for *Crassiproetus crassimarginatus* except small genal spines present; ratio of length (sag.) of anterior cephalic border to length of cephalon 0.11–0.13; ratio of pygidial width–length 1.0–1.07.

MATERIAL: AMNH 39329, Hall and Clarke's (1888: pl 20, figs. 28, 30), 39337, 44700, 44707–44713; BMS E11987; UMMP 4897, 29536, 29540, 29541; ROM 35386, 35387.

DESCRIPTION: Hypostome roughly trapezoidal in outline, maximum width across anterior tips of anterior wings 120% length (sag.); anterior wings deflect anterolaterally at about 10° angle from exsagittal line; medially course of anterior margin (hypostomal suture) gently convex. Lateral margin convex, bulging laterally at point about 65% sagittal length of hypostome, width at this point 75% of maximum length. Middle body U-shaped, broadest anteriorly; lateral margins defined by furrow; border furrow deepest posteriorly. Anterior wing and middle body both moderately arched. Maculae long, thin protuberances, positioned back about 60% sagittal length of hypostome, inclined posteriorly at 40° angle to exsagittal line. Margin of posterolateral border straight, inclined at 45° angle to sagittal line; posterior border flattened, straight in dorsal view. Posterolateral and posterior border of equal length, about 10% sagittal length of hypostome.

Pygidium roughly parabolic in outline, length about 95–100% of width; border developed as laterally splayed ridge, flattened laterally. Axial furrow narrow, straight, converging backward at about 20°. Axis about 35% of pygidial width anteriorly, prominently arched in lateral and posterior aspect, moderately elevated posteriorly, with 18 rings; rings flex anteriorly, medially posteriorly, and then slightly anteriorly. Ring furrows shallow. Small space developed between axial terminus and border. Fifteen pleural segments, prominently arched, strongly deflected backward distally, top of segments appear flat when viewed in lateral aspect; interpleural furrows faint to invisible. Pleural furrows narrow and faint, more deeply incised anteriorly.

DISCUSSION: This species is known from the Onondaga Limestone (probably Edgecliff Member [lower Eifelian]) of western New York; the Onondaga Limestone (Eifelian), the Oneida Lime and Sand Company Quarry, Haldimand County, Ontario; the Onondaga Limestone, Albany County, New York; and the Formosa Limestone Member of the Amherstburg Dolomite (lower Eifelian), Formosa, southern Ontario. Thus, it appears to partially overlap the distribution of *C. crassimarginatus* and is associated with transgressive–regressive cycle Ic. In parts of the Appalachian and Michigan Basins it occurs in the base of the Onondaga Limestone and its equivalent, which are associated with the second prominent transgression in cycle Ic. Because *C. brevispinosus* does not occur in several of the localities where *C. crassimarginatus* occurs (e.g., Indiana, Ohio, and Michigan), the differences between these two taxa are not considered to be due to sexual dimorphism. Fagerstrom (1961) included a description of this taxon. However, he did not have access to the pygidium or the hypostome, which were later figured by Ludvigsen (1987) as *C. crassimarginatus*. Therefore, a description of these is included above. Pygidia of this species are only found associated with cephala. There are no complete, articulated specimens of *C. brevispinosus*, although such do exist for *C. crassimarginatus*. However, only two species of trilobites belonging to the Proetinae are known from the Formosa Reef Limestone. Both of these species are the most common trilobites in this member of the Amherstburg Dolomite, and a pygidium can be definitely assigned to *C. crassimarginatus* on the basis of complete, articulated specimens. Therefore, it is concluded that the distinct pygidia, which are very similar in morphology to the pygidia of *C. crassimarginatus*, belong to the same species as the cephala that are morphologically distinct, yet closely resemble *C. crassimarginatus*.

Bassett (1935) presciently recognized that some of the forms that had been called *C. crassimarginatus* from western New York might differ from *C. crassimarginatus* from southern Indiana. The specimens in question are most likely *C. brevispinosus*.

Crassiproetus microgranulatus
Stumm, 1953a
Figure 19.1–19.6

Proetus (*Crassiproetus*) *microgranulatus* Stumm, 1953a: 111, pl. 1, figs. 8, 19.

Proetus (*Crassiproetus*) sp. B Stumm, 1953a: 115, pl. 1, fig. 9.

DIAGNOSIS: Eye sits on relatively broad, flat pedestal; posterior region of glabella inflated pygidial axis separated from border by small space; anterior branch of facial suture running straight forward; medial kinks on pygidial axial rings visible on half of axial segments; typically 16 rings; top of pygidial pleural segments, in lateral view, rounded; pygidium broad, width 1.5 times length; pygidial border developed as rounded, laterally splayed ridge.

MATERIAL: BMS E13351; UMMP 25448, 28676.

DISCUSSION: This species is known from the Newton Creek Limestone (lower Givetian), Alpena, Michigan; and the Genshaw Formation (lower Givetian), Thunder Bay Island, MI. Thus it is associated with the upper portion of transgressive–regressive cycle Ie. The first occurrence of this species in the stratigraphic record is at odds with its position in the phylogeny of *Crassiproetus* shown in figure 3. Assuming that the phylogeny is correct, and that neither *C. traversensis* nor *C. crassimarginatus* is ancestral to *C. microgranulatus*, we must conclude that *C. microgranulatus* or the lineage that gave rise to *C. micrograpulatus* split off during the early Eifelian. *Crassiproetus micrograpulatus* is quite rare, with only three specimens discovered; therefore, it is it not entirely implausible to think that it would not have been recovered from Eifelian sediments, even if it had occupied Eifelian environments.

Stumm (1953a) discovered a pygidium from the Genshaw Formation of Thunder Bay Island, MI, that he called *Crassiproetus* sp. B. He concluded that this species was similar to *C. micrograpulatus*, but differed by having the axis more elevated posteriorly and bearing more distinct segmentation. However, these differences appear to be due to the fact that the pygidium is preserved as an internal mold. This specimen accords with all the character codings for *C. micrograpulatus* used in this analysis, and they are treated as conspecific.

Stumm (1953a) suggested that *C. micrograpulatus* was closely related to *C. calhounensis*, although he does not provide any morphological evidence to substantiate this claim. The only prominent morphological trait that these species share, the presence of a broad flat socle that the eye sits on, appears to be convergent on the basis of parsimony analysis.

Crassiproetus calhounensis (Cooper and Cloud, 1938)

Cornuproetus calhounensis Cooper and Cloud, 1938: 455–457, pl. 55, figs. 9, 13–15, 18, 19, 23.

Crassiproetus calhounensis (Cooper and Cloud). Stumm, 1953a: 111–112; Hickerson, 1992: 131.

DIAGNOSIS: Eye sits on relatively broad, flat pedestal on librigena; librigenal field small, width equal to width (tr.) of eye; lineations on front of glabella roughly convex and parallel; anterior ledge between frontal glabellar lobe and striated anterior border not visible in dorsal view; S0 at anterior edge of intraoccipital lobe follows a straight, linear course abaxially; posterior border furrow straight distal to eye; anterior of eye, for short distance anterior of S3, margins of glabella parallel; anterior portion of frontal glabellar lobe pointed (in dorsal view); anterior cephalic border ridge thin.

DISCUSSION: This species appears in a limestone bed from the base of the Devonian system in Calhoun County, west central Illinois. Originally (Cooper and Cloud, 1938) these strata were thought to be equivalent to the Tully Limestone (upper Givetian) of New York State. It is now believed that these strata may be equivalent to the Solon Member of the Little Cedar Formation (upper Givetian) of central and Eastern Iowa (Hickerson, 1992). Thus, it is probably associated with transgressive–regressive cycle IIa and the Taghanic onlap.

Cooper and Cloud (1938) remarked that this species may be closely related to *Crassiproetus bumastoides* or *C. searighti*. Specimens of these taxa could not be obtained because they were under study elsewhere. However, on the basis of figured material, the two taxa appear to differ in several features, including the condition of the pygidium. In both *C. traversensis* and *C. calhounensis* the pygidial axis proceeds to the border. In *C. bumastoides* there is a small space between the axis and the border. However, the condition of the intraoccipital lobes in *C. bu-*

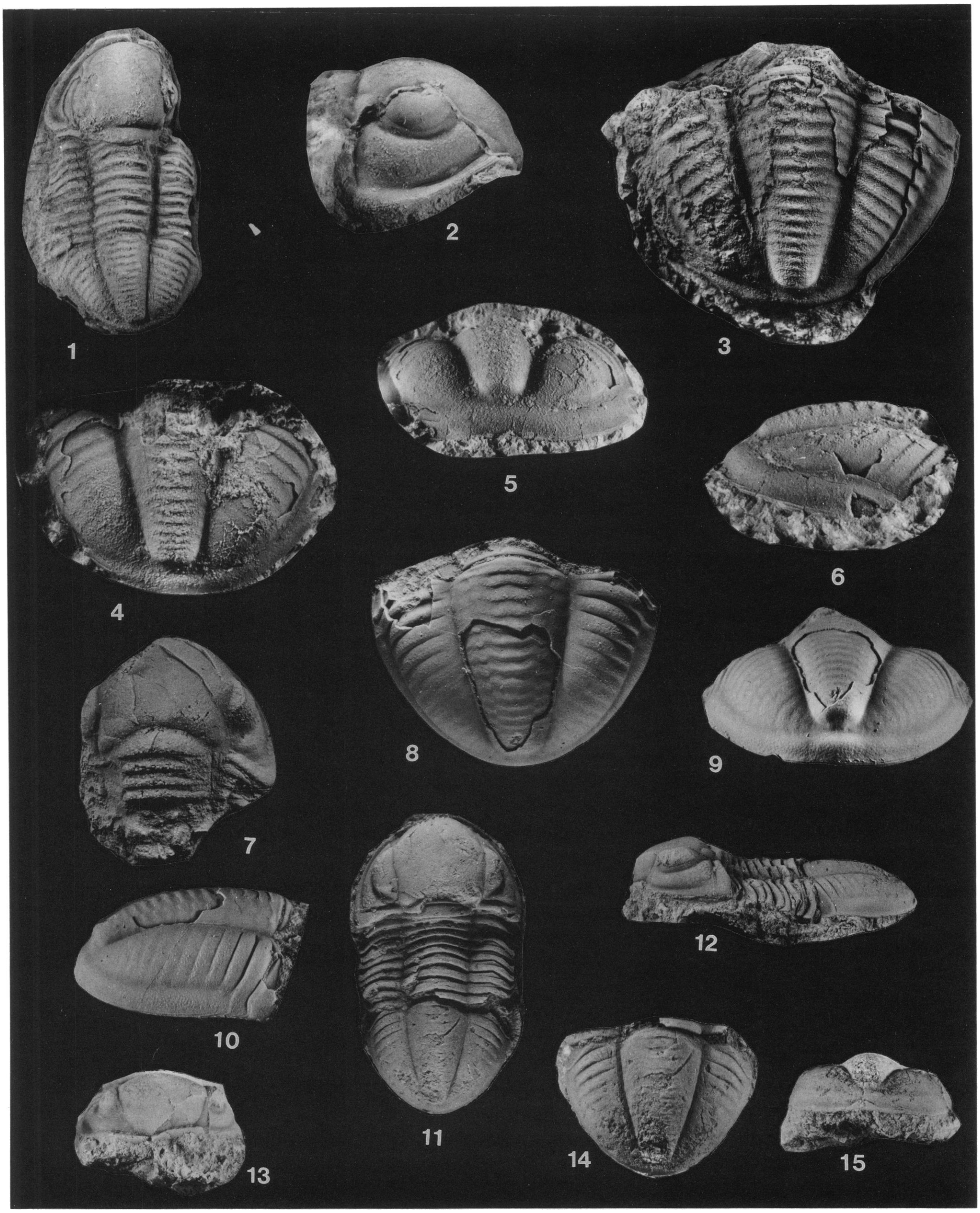

Fig. 19. *Crassiproetus* spp. **1, 2.** *Crassiproetus microgranulatus* Stumm, 1953a. Newton Creek Limestone, Cazenovian (Givetian), Alkali Quarry, Alpena, Michigan, BMS E13351. **1**, Dorsal view of entire specimen, ×2.5; **2**, lateral view of cephalon, ×3.75. **3.** *Crassiproetus microgranulatus* Stumm, 1953a. Genshaw Formation, Cazenovian (Givetian), Thunder Bay Island, Alpena County, Michigan, UMMP 25448, dorsal view of pygidium, ×2.5. **4-6.** *Crassiproetus microgranulatus* Stumm, 1953a. Horizon and locality same as 1, 2. UMMP 28676, paratype, dorsal, posterior, and lateral views of pygidium, ×3.5. **7.** *Crassiproetus alpenensis* Stumm, 1953a. Thunder Bay Limestone, Taghanic (Givetian), Partridge Point on Thunder Bay, Lake Huron, four mi. south of Alpena, Michigan, UMMP 25501, holotype, dorsal view of cephalon and partial thorax, ×3. **8-10.** *Crassiproetus alpenensis* Stumm, 1953a. Horizon and locality same as **1, 2.** UMMP 27080, dorsal, posterior, and lateral views of pygidium, ×2.5. **11-15.**

mastoides and *C. calhounensis* is similar. In *C. bumastoides* they are not at all separated from the glabella, and in *C. calhounensis* the anterior portion of S0 anterior of the intraoccipital lobe is so weakly incised that the intraoccipital lobe is only slightly separated from the glabella. *Crassiproetus calhounensis* may be closely related to *C. arietinus* (Hickerson, 1992), as it is closely related to *C. traversensis* and the latter shares several features with *C. arietinus*. On the basis of figured material, in both *C. calhounensis* and *C. arietinus* the pygidial axis appears to proceed to the pygidial border. However, *C. calhounensis* appears to have consistently fewer pygidial axial rings than either *C. traversensis* or *C. arietinus*.

Crassiproetus alpenensis
Stumm, 1953a

Figure 19.7–19.10

Proetus (*Crassiproetus*) *alpenensis* Stumm, 1953a: 113–114, pl. 1, figs. 4, 5, 20; Stumm, 1967: 115, pl. 2, figs. 8, 9.

Proetus (*Crassiproetus*) *microgranulatus* Stumm, 1953a: 111, pl. 1, fig. 3.

Diagnosis: Genal angle deflected posteriorly; genal spine long and pointed; S0 at anterior edge of intraoccipital lobe follows a straight linear course distally; S0 at midline weakly incised; librigena steeply arched; librigenal field narrow, equal to transverse width of eye; anterior cephalic border short (sag., exsag.); pygidial border developed as flat, vertical flange; pygidial axis contacts border; pygidial pleurae laterally weakly deflecting posteriorly.

Material: UMMP 25501, 27080, 27088, 27089.

Discussion: This species is known from the Newton Creek Formation (lower Givetian), Alpena, MI; the Potter Farm Formation (upper Givetian), Alpena, MI; and the Thunder Bay Limestone (upper Givetian), Alpena, MI. Thus it is associated with transgressive–regressive cycles Ie and IIa, possibly occurring in the upper portion of cycle Ie and in the basal transgression of cycle IIa.

Stumm (1953a) suggested that this species could conceivably be related to *Crassiproetus bumastoides* because in both taxa the intraoccipital lobes are not separated from the glabella. The anterior portion of S0 anterior to the usual position of the intraoccipital lobe is very faint in both taxa, and in *C. alpenensis* it appears to follow a straight abaxial course. The condition of this character in *C. bumastoides* could not be assessed because material of this species is under study by another author. However, as Stumm (1953a) noted, the glabella is much more steeply arched in *C. bumastoides* than in *C. alpenensis*.

Stumm (1953a) assigned a pygidium from the Newton Creek Formation of Michigan to *Crassiproetus microgranulatus* that appears to belong to *C. alpenensis*. In particular, in this specimen the pygidial border is developed as a flat, vertical flange, a condition characteristic of *C. alpenensis*. In *C. microgranulatus* this flange is generally a rounded, laterally splayed ridge. In addition, in this specimen the pygidial axis contacts the border, which is characteristic of *C. alpenensis*. In *C. microgranulatus* there is a small space between the axis and the border. This specimen, UMMP 27080, was originally designated the paratype of *C. microgranulatus*, and this designation can no longer be considered valid.

Crassiproetus canadensis
Stumm, 1953a

Figure 19.11–19.15

Proetus (*Crassiproetus*) *canadensis* Stumm, 1953a: 113, pl. 1, figs. 6, 7.

Crassiproetus canadensis Stumm. Ludvigsen, 1979: 84, fig. 55c.

Diagnosis: S0 at anterior edge of intraoccipital lobe flexes sharply laterally exsagittally; anterior portion of frontal glabellar lobe

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←

Crassiproetus canadensis Stumm, 1953a. Lower Widder Formation, Tioughniogan (Givetian), Hungry Hollow on the Aux Sable River, .75 miles north and 2 mi. east of Arkona, Ontario, UMMP 27090, holotype, dorsal and lateral views of entire specimen, anterior view of cephalon, and dorsal and posterior views of pygidium, all ×2.5 except 14, ×3.

in dorsal view pointed; medial kinks on pygidial axial rings visible back to 50% sagittal length of pygidium; pygidial pleurae do not deflect sharply posteriorly laterally; space present between pygidial axis and border; pygidial pleural segments in lateral view flat.

MATERIAL: UMMP 28672, 27090.

DISCUSSION: This species is known from the lower Widder Formation (middle Givetian [Rickard, 1989] or late middle Givetian [Sparling, 1992]) of Arkona, southern Ontario. Thus, it is associated with transgressive–regressive cycle If, possibly with the base of the fourth transgression in cycle If.

Stumm (1953a: pl. 1, fig. 6) illustrated a librigena of *C. canadensis* and described the genal angle as broadly rounded. However, relative to the genal angle of other species of *Crassiproetus*, the genal angle is long and pointed (see fig. 19 and Stumm, 1953a: pl. 1, fig. 7). The perception of pointed depends on the correct orientation of the librigena. Stumm (1953a: pl. 1, fig. 6) inadvertently rotated the distal portion of the free cheek ventrally and counterclockwise such that the genal angle appeared rounded. However, in its proper orientation, the true nature of the genal angle can be ascertained. The condition of the genal angle in *C. canadensis* resembles that found in *C. alpenensis*.

Crassiproetus sibleyensis
Stumm, 1953b
Figure 20.1–20.7

Proetus crassimarginatus (Hall). Bassett, 1935: 453, pl. 38, figs. 12–17; Shimer and Shrock, 1944: 653, pl. 274, fig. 18.
Proetus (*Crassiproetus*) *sibleyensis* Stumm, 1953b: 18, pl. 2, figs. 12–14, 16.

DIAGNOSIS: Striations on anterior border visible in dorsal view; anterior ledge between frontal glabellar lobe and anterior border not visible in dorsal view; S0 at anterior edge of intraoccipital lobe follows a straight course abaxially; lineations on front of glabella convex and parallel; genal angle meeting as long line parallel to sagittal line; posterior region of glabella inflated; pygidial axis separated from pygidial border by small space; 16 pygidial axial rings present; top of pygidial pleurae in lateral view appear rounded.

MATERIAL: UMMP 15127–15130, 15175.

DISCUSSION: This species is known from the Dundee Limestone (upper Eifelian), Sibley, MI. Thus, it is known from the upper portion of transgressive–regressive cycle Ic. Specimens are known from at least two lithologies, a buff to yellowish brown biomicrite and a white, more crystalline micrite. Remains of the cranidium, the librigena, and the pygidium are not found articulated. Because each of these sclerites is discrete from those of all other species of *Crassiproetus*, and because they are all known from the same locality, they are treated as conspecific. However, according to Bassett (1935), specimens similar to these have been reported to occur 50 mi. southwest of Sibley in the Columbus Limestone from the Whitehouse Quarry in Lucas County, Ohio. These reports could not be verified, and Stumm (1953a, 1953b) did not discuss them. The specimens in question may be *C. crassimarginatus*, which is known to occur in the Columbus Limestone in northern Ohio.

Pygidia of this species are very similar to those of *C. crassimarginatus*, but pygidia of *C. sibleyensis* can be distinguished on the basis of the condition of the top of their pleural segments, which in lateral view appear rounded in *C. sibleyensis*. In addition, the pygidial border is splayed slightly farther laterally in *C. crassimarginatus* than in *C. sibleyensis*.

Crassiproetus norwoodensis
Stumm, 1953a
Figure 20.8–20.10

Proetus (*Crassiproetus*) *norwoodensis* Stumm, 1953a: 114, pl. 1, fig. 18.
Crassiproetus norwoodensis Stumm. Kesling et al., 1974: pl. 3, fig. 26.

DIAGNOSIS: Striations on anterior border developed dorsally; facial suture circumscribing eye asymmetrical, reflexes exsagittally in posterior half, gently curves sagittally anteriorly; S0 at midline well incised; posterior region of glabella inflated; anterior branch of facial suture straight, parallel to sagittal line; S0 at anterior edge of intraoccipital lobe follows linear course abaxially; intraoccipital lobes very reduced.

MATERIAL: UMMP 25444.

DISCUSSION: This species is known from a single cranidium from the *Schizophoria* bed in the upper part of the Petoskey Formation

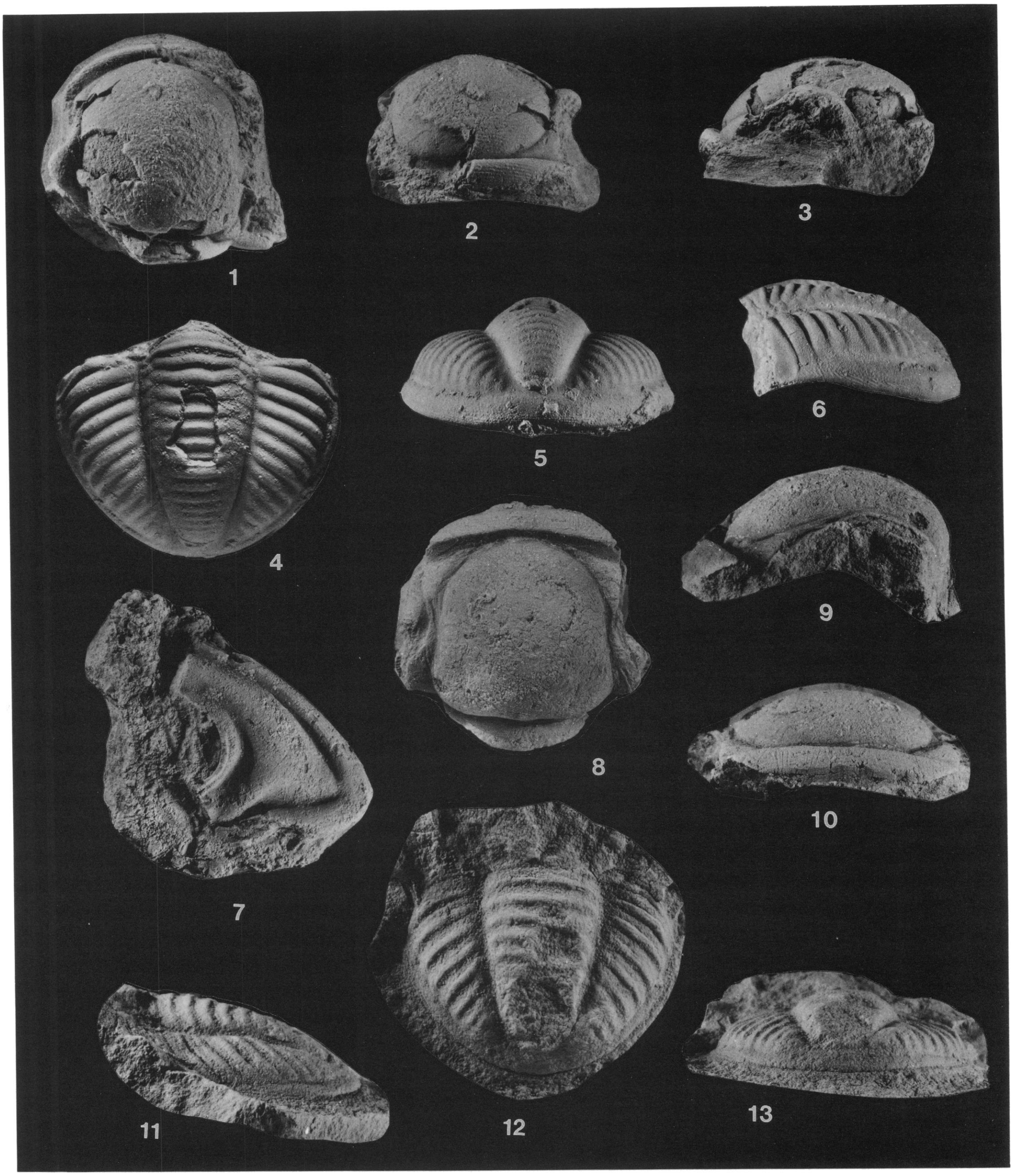

Fig. 20. *Crassiproetus* spp. **1-3.** *Crassiproetus sibleyensis* Stumm, 1953b. Dundee Limestone, Southwoodian (Eifelian), quarry of Solvay Processing Company, at Sibley, 2 mi. north of Trenton, Wayne County, Michigan, UMMP 15130, holotype, dorsal, anterior, and lateral views of cephalon, ×2.5. **4-6.** *Crassiproetus sibleyensis* Stumm, 1953b. Horizon and locality same as 1–3. UMMP 15128, paratype, dorsal, posterior, and lateral views of pygidium, ×2.5. **7.** *Crassiproetus sibleyensis* Stumm, 1953b. Horizon and locality same as **1-3.** UMMP 15175, paratype, dorsal view of librigenae, ×2.5. **8-10.** *Crassiproetus norwoodensis* Stumm, 1953a. Upper part of Petoskey Formation, *Schizophoria* bed, Taghanic (Givetian), Lake Michigan shore, 1.1 mi. north of Norwood, Charlevoix County, Michigan, UMMP 25444, holotype, dorsal, lateral, and anterior view of cephalon, ×2.5. **11-13.** *Crassiproetus stummi*, new species. Bois Blanc Formation, Sawkillian (upper Emsian), south side of Trout Island, Lake Michigan, Charlevoix County, Michigan, UMMP 29519, holotype, lateral, dorsal, and posterior view of pygidium, ×2.5.

(upper Givetian), Norwood, Charlevoix County, MI. Thus, it is associated with transgressive–regressive cycle IIa. This species is particularly closely related to two taxa, *C. crassimarginatus* and *C. sibleyensis*, that are known only from the Eifelian. Therefore, there is a substantial gap separating its first, and only, appearance and the last known report of its two successive putative sister taxa.

This species had to be coded as missing for more than half of the characters used in phylogenetic analysis. Thus, in terms of numbers of characters it is almost as poorly known as the two taxa discussed below. However, in this analysis, cephalic characters appear to contain more phylogenetic information than pygidial characters.

***Crassiproetus stummi*, new species**

Figure 20.11–20.13

Proetus (*Crassiproetus*) *crassimarginatus* (Hall). Stumm, 1953b: 15, pl. 1, fig. 8.

Proetus (*Proetus*) *folliceps* (Hall and Clarke). Stumm, 1953b: 15, pl. 2, fig. 2.

?*Proetus crassimarginatus* (Hall). Hall and Clarke, 1888: 99, pl. 20, fig. 6, pl. 22, fig. 21.

?*Proetus* sp. Goldring and Flower, 1942: 676.

DIAGNOSIS: Pygidial axis separated from border by small space; 13 axial rings; medial kinks on axial rings visible back to 75% of sagittal length of pygidium; pleural furrows visible; top of pleural segments in lateral view flattened; pleurae distally curve sharply posteriorly; border developed as rounded, laterally splayed ridge.

TYPES: Holotype UMMP 29519 (fig. 20.11–20.13), Bois Blanc Formation (upper Emsian/Sawkillian), Trout Island, Lake Michigan, MI.

ETYMOLOGY: Named for Erwin C. Stumm, who contributed so much to our knowledge of the Middle Devonian trilobites of Eastern North America.

MATERIAL: AMNH 44703, 44704; UMMP 29519, 29537.

DESCRIPTION: Pygidium roughly U-shaped in outline, length about 80% of width; border developed as laterally splayed ridge, flattened laterally. Axial furrows narrow, straight, converging backward at about 30°. Axis about 35% of pygidial width anteriorly, weakly arched in lateral and posterior aspect, not elevated posteriorly, with 13 rings, rings flex anteriorly medially and weakly flex posteriorly around this anteromedial flexion. Ring furrows very shallow. Small space developed between axis and posterior border. Ten pleural segments present; segments moderately arched, deflect strongly posteriorly distally when viewed dorsally; tops of segments appear flattened when viewed in lateral aspect; interpleural furrows visible. Pleural furrows narrow and faint, more weakly incised posteriorly.

DISCUSSION: This species is known from the Bois Blanc Formation (upper Emsian) of Trout Island, Lake Michigan, MI, and the Schoharie Grit (upper Emsian) and/or Onondaga Limestone (Eifelian), Schoharie County, New York. It may occur in the Schoharie Grit (upper Emsian) of Albany County, NY. Thus, it is associated with several of the transgressions in transgressive–regressive cycle Ic. The holotype was designated as the best preserved of the specimens that Stumm (1953b) examined. Using this criterion, the specimen Stumm (1953b) figured and assigned to *Proetus folliceps* was chosen as the holotype.

The species is only known from pygidia, and perhaps because of this it has consistently been assigned to different taxa. Accordingly, a description is presented above.

Crassiproetus stummi is one of the oldest members of the genus known from Laurentia, and it is thus unfortunate that more complete specimens do not exist. In terms of gestalt similarity it does closely resemble the pygidium of *C. globosus*. It also appears to be similar to *C. schohariensis*, new species. However, *C. schohariensis* differs from *C. stummi* in having one more pygidial axial ring, a more arched pygidial axis in lateral and posterior view, the pygidial pleural segments not deflecting prominently posteriorly laterally, and in having the pygidial border developed as a steep, near-vertical plane instead of a rounded, laterally splayed ridge.

It was difficult to ascertain the lithostratigraphic horizon to which the specimens of *C. stummi* from New York State should be assigned. On the basis of lithology, they appear to come from the Schoharie Grit, but this awaits further work. On the basis of this, the pygidia that Goldring and Flower (1942)

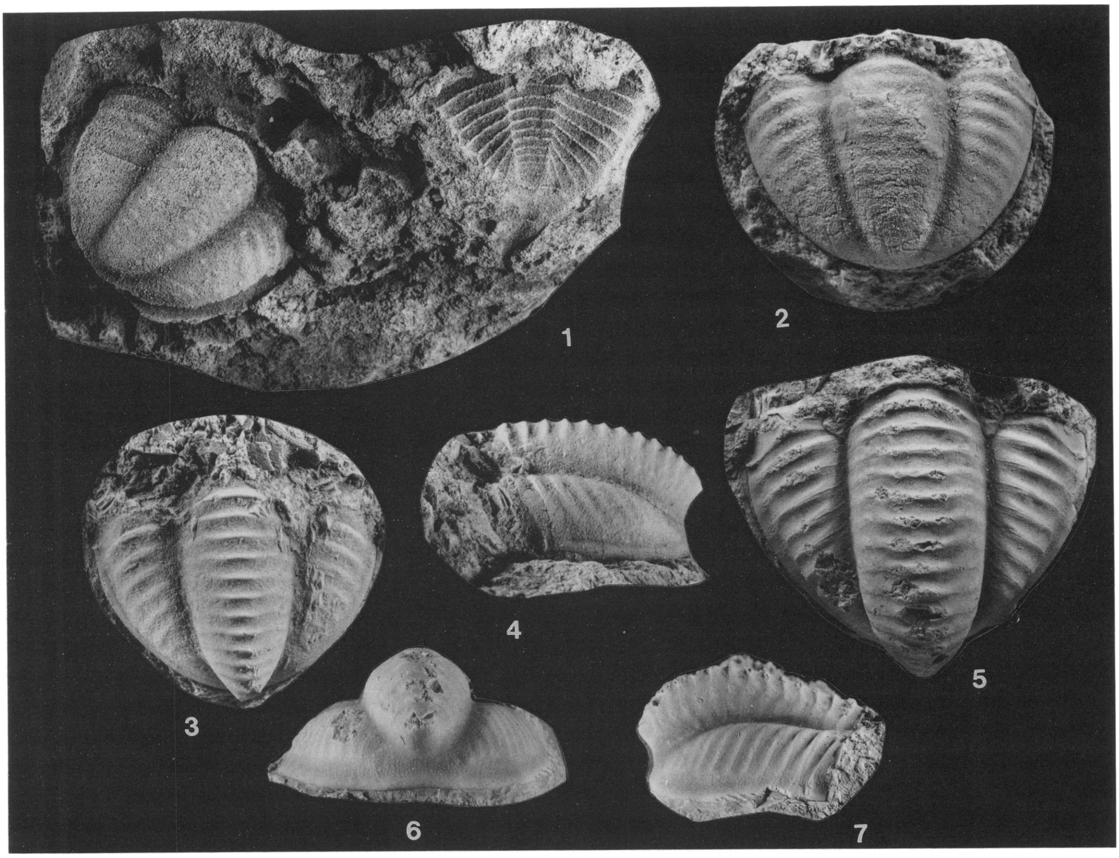

Fig. 21. *Crassiproetus* spp. **1.** *Crassiproetus schohariensis*, new species. Schoharie Grit, Sawkillian (upper Emsian), loose at Goshen, Orange County, New York, AMNH 44699, holotype, dorsal view of pygidium, associated with pygidium of *Anchiopsis anchiops* (Green), × 2. **2.** *Crassiproetus schohariensis*, new species. Horizon same as above, Schoharie, New York, AMNH 44724, dorsal view of pygidium, × 2. **3, 4.** *Crassiproetus neoturgidus*, new species. Onondaga Limestone, Southwoodian (Eifelian), Schoharie, New York, AMNH 44720, holotype, dorsal and lateral views of pygidium, × 2.4. **5–7.** *Crassiproetus halliturgidus*, new species. Jeffersonville Limestone, Southwoodian (Eifelian), Jefferson County, Kentucky. YPM 33825, holotype, dorsal, posterior, and lateral views of pygidium, all × 1.25 except 5, × 1.75.

recovered from the Schoharie Grit and called *Proetus* sp. may belong to *C. stummi*. It could also be *C. schohariensis*, new species.

Crassiproetus schohariensis, new species

Figure 21.1, 21.2

?*Proetus crassimarginatus* (Hall). Hall and Clarke, 1888: 99, pl. 20, figs. 7, 8, pl. 22, fig. 20.

?*Proetus* sp. Goldring and Flower, 1942: 676.

DIAGNOSIS: Pygidial axis arched in lateral and posterior views; pygidial border developed as steep, near vertical plane; 14 axial rings; pleural segments do not deflect sharply posteriorly distally.

TYPES: Holotype AMNH 44699, from the Schoharie Grit (late Emsian), Orange County, NY.

ETYMOLOGY: This species is named for its occurrence in the Schoharie Grit.

MATERIAL: AMNH 44699, 44705, 44706, 44714, 44724, 44725.

DESCRIPTION: Pygidium roughly U-shaped in outline, length about 80% of width; border developed as laterally splayed ridge, flattened laterally. Axial furrows narrow, straight, converging backward at about 35°. Axis about

45% of pygidial width anteriorly, moderately arched in lateral and posterior aspect, not prominently elevated posteriorly, with 14 rings; rings flex anteriorly medially and weakly flex posteriorly around this anteromedial flexion. Ring furrows shallow. Small space developed between axis and posterior border. Twelve pleural segments present; segments moderately arched, do not deflect strongly posteriorly distally when viewed dorsally; top of segments when viewed in lateral aspect appear rounded; interpleural furrows not visible due to poor preservation. Pleural furrows narrow and faint, more weakly incised posteriorly.

DISCUSSION: This species is known from the Schoharie Grit (upper Emsian) of Orange County, NY, and the Schoharie Grit and/or Onondaga Limestone of Albany and Schoharie Counties, NY. Thus, it is associated with transgressive–regressive cycle Ic. The holotype was designated as an external mold of the pygidium from the Onondaga Limestone or Schoharie Grit of Schoharie County. The holotype is better preserved than either of the specimens that Hall and Clarke (1888) figured and assigned to *C. crassimarginatus*.

As with *Crassiproetus stummi*, it was difficult to ascertain the lithostratigraphic horizon to which specimens of *C. schohariensis* should be assigned. On the basis of lithology, they appear to come from the Schoharie Grit. If this assignation is correct, the specimens Flower and Goldring (1942) referred to as *Proetus* sp. may be specimens of *C. schohariensis*. They also could be specimens of *C. stummi*.

Crassiproetus turgidus
(Northrop, 1939)

Proetus turgidus Northrop, 1939: 233, pl. 26, figs. 8, 9.

?*Proetus* cf. *turgidus* Northrop, 1939: 233, pl. 26, fig. 10.

DIAGNOSIS: Thirteen pygidial axial rings; axis prominently arched and elevated posteriorly, prominently pointed posteriorly; axial segments weakly convex anteriorly interpleural furrows faint; 10 pleural segments; distally pleural segments moderately deflected posteriorly; border developed as flattened ledge.

DISCUSSION: A diagnosis is only presented for the pygidium, as this is the only part that can be unambiguously assigned to *Crassiproetus turgidus*. This species is known from the upper Silurian West Point Formation of the Gaspe Peninsula, Quebec. It is tentatively placed in the genus *Crassiproetus*, but it does lack the structure of the pygidial axial rings that is generally characteristic of *Crassiproetus* (their medial flexure anteriorly and distally, first deflecting posteriorly, then anteriorly, and then posteriorly). In addition, the pygidial border is developed as a thin flattened ledge, and this is unique for the genus *Crassiproetus*.

This species is only known from carbonate deposits (the West Point Formation [Northrop, 1939] being largely made up of limestones), which is typical of *Crassiproetus*. Pygidia similar to *Crassiproetus turgidus* are known from the Eifelian of ENA. These two new species are described and discussed below.

***Crassiproetus neoturgidus*, new species**
Figure 21.3–21.4

DIAGNOSIS: Thirteen pygidial axial rings; axial furrows do not converge until posterior of 8th axial ring; axis prominently arched and elevated, particularly posteriorly, in lateral aspect wall from axial furrows ascends dorsally, wall concave posteriorly; anterior axial rings straight; posterior rings flex anteriorly, then distally posteriorly, then anteriorly, then posteriorly; axial terminus pointed; border developed as small rounded, laterally splayed ledge; 10 pleural segments, segments moderately deflected posteriorly distally.

TYPES: Holotype AMNH 44720 (fig. 21.3, 21.4), Onondaga Limestone (Eifelian), Schoharie County, NY.

ETYMOLOGY: This species is named by combining Neo for new with turgidus for the resemblance this taxon bears with the older *Crassiproetus turgidus*.

MATERIAL: AMNH 44720, 44721.

DESCRIPTION: Pygidium parabolic in outline, length about 90% width; border developed as small rounded ridge, flattened laterally. Axial furrows narrow, straight back to eighth axial ring, then converging backward at about 45°. Axis about 45% of pygidial width anteriorly, strongly arched in lateral and posterior aspect, and very prominently elevated posteriorly, with 13 rings; rings in anterior portion of axis are straight, then in posterior portion of axis, flexing anteriorly medially and weakly flexing posteriorly, then anteriorly, and then posteriorly; lateral margins of axis from posteriormost segment to eighth axial segment diverge at 35° angle; anterior of eighth axial ring lateral margins parallel. Ring furrows deep. In dorsal view axis projects past posterior margin of pygidium. Postaxial region steep, concave backward. No space developed between wall ascending to pygidial axis and the posterior border. Ten pleural segments, prominently arched, do not deflect strongly posteriorly distally when viewed dorsally, top of segments when viewed in lateral aspect appear rounded.

DISCUSSION: This species is known from the Onondaga Limestone, NY, and is thus associated with transgressive–regressive cycle Ic. It is very rare, known only from a few scrappy internal molds of pygidia. The holotype was designated using the best preserved of these internal molds.

This species is similar to *Crassiproetus turgidus*, particularly in the elevation of the pygidial axis posteriorly; however, the species differ in the development of the axial rings. In the posterior portion of the axis of *C. neoturgidus* the axial rings are developed as they typically are in *Crassiproetus*, although the anterior and posterior flexure is less marked. In addition, *C. turgidus* and *C. neoturgidus* differ in the condition of the pygidial border. The border is a flattened ledge in *C. turgidus*, and it is a rounded, laterally splayed ridge in *C. neoturgidus*. Finally, in *C. neoturgidus* the axial furrows do not converge until posterior of the eighth axial ring. The axial furrows converge posterior of the third axial ring in *C. turgidus*. The condition in *C. turgidus* is that characteristic of all species of *Crassiproteus* except *neoturgidus* and *halliturgidus*.

Crassiproetus neoturgidus, new species is nearly identical to *C. halliturgidus* from the Jeffersonville Limestone, at the Falls of the Ohio River, KY. They differ only in the greater elevation of the posterior portion of the pygidial axis in *C. halliturgidus* and the presence of two additional segments in the pygidial axis of *C. halliturgidus*.

***Crassiproetus halliturgidus*,**
new species

Figure 21.5–21.7

Proetus crassimarginatus (Hall). Hall and Clarke, 1888: 99, pl. 22, fig. 23.

DIAGNOSIS: Same as for *Crassiproetus neoturgidus*, except 15 pygidial axial rings; axial furrows do not converge until posterior of ninth axial ring; 12 pygidial pleural segments present.

TYPES: Holotype YPM 33825 (fig. 21.5–21.7), Jeffersonville Limestone, Jefferson County, Falls of the Ohio River, KY.

ETYMOLOGY: This species was named by compounding Hall, who, along with Clarke, figured a pygidium of this species with turgidus, for its resemblance to *Proetus turgidus*.

MATERIAL: YPM 33825.

DESCRIPTION: Same as *C. neoturgidus*, except axial furrows converging backward at about 45° behind ninth axial ring; anterior of ninth axial ring sides parallel. Axis about 35% of pygidial width anteriorly, with 15 rings; 12 pleural segments.

DISCUSSION: This species is known from the Jeffersonville Limestone (Eifelian) of Kentucky and thus is associated with transgressive–regressive cycle Ic. The holotype is a complete pygidium (internal mold). It is better preserved than Hall and Clarke's (1888) figured specimen, which they assigned to *C. crassimarginatus*.

PHYLOGENY OF *BASIDECHENELLA* RICHTER, 1912

For diagnosis and discussion of taxa to be excluded from this genus see above. A phylogeny for this genus was generated using 25 characters and 16 taxa. The characters used are given in table 6, and the character codings for these taxa are given in table 7. One most parsimonious tree (fig. 22) of length 59, consistency index .54, and retention index .61 was produced using the **ie*** option of Hennig86 (Farris, 1988) (equivalent to the exhaustive search option of PAUP) and the heuristic search using random addition with 10 replications of PAUP 3.0q (Swofford, 1990). All taxa considered were from the Lower and Middle Devonian except *Basidechenella timwhitei*, new species, which is

TABLE 6

Characters Used in Phylogenetic Analysis of the Genus *Basidechenella*

"0" is the plesiomorphic state. Character matrix is given in table 7

0. Posterior of pygidium in dorsal view: (0) pointed, (1) straight, transverse, (2) rounded.
1. Number of pygidial axial rings: (0) 14, (1) 13, (2) 11, (3) 10.
2. Number of pleural segments: (0) 7, (1) 9, (2) 8.
3. Anterior cephalic border: (0) short, equal to the length (exsag.) between the distal tips of S1 and S2, (1) long, equal to the length (exsag.) between distal tip of S1 and point midway between S2 and S3, and concave dorsally.
4. Intraoccipital lobes: (0) even with the lateral margins of the glabella, (1) bulging beyond the glabella.
5. Prominent furrow separating series of latitudinal striations on anterior end of cephalic border into two ridges: (0) absent, (1) present but faint, (2) prominent.
6. Glabella bulges adjacent to eyes: (0) weak, (1) well developed.
7. Pygidial border in posterior view: (0) rounded, (1) notched.
8. Posterior border furrow behind eyes: (0) straight, (1) flexes anteriorly.
9. Posterior border furrow at distal end: (0) straight, (1) flexes slightly anteriorly.
10. Glabellar furrows: (0) shallowly impressed, (1) developed as patches of pigment.
11. Genal spine projects back to thoracic segment number: (0) 5, (1) 6.
12. Median glabellar impression anterior of S1: (0) longer lineament running into S1, (1) short lineation.
13. Prosopon: (0) smooth or covered with very fine granules, (1) covered with coarse granules.
14. Furrow in front of eye: (0) shallow, (1) deep.
15. S4: (0) long and straight marking, (1) short and intersecting S3 to form a triradiate structure.
16. Sides of glabella: (0) parallel between anterior edge of eye and S3, (1) parallel between anterior edge of eye and point beyond S3 equal to distance between S2 and S3.
17. Anterior edge of glabella in dorsal view: (0) curved, (1) flat or straight.
18. Tubercles on thorax: (0) absent, (1) present on all thoracic axial rings (2) present on first and six posteriormost thoracic segments.
19. Tubercles on pygidium: (0) absent, (1) on anteriormost axial rings, (2) on all axial rings.
20. Glabella posterior of eyes: (0) curving inward, (1) flexing slightly laterally.
21. Anterior border furrow: (0) intersects glabella at its anterior edge, (1) contacts anterior edge of glabella.

TABLE 6—(*Continued*)

22. S0 between the intraoccipital lobes: (0) straight, (1) flexes anteriorly.
23. Intraoccipital lobes: (0) wide (tr.), extending medially past point where glabella starts to flex anteriorly, (1) narrow (tr.) do not extend far medially.
24. S0 medially: (0) smoothly arching anteriorly, (1) directed posteriorly next to anterior deflections.

known from the Carboniferous, Osagean (upper Tournaisian) Lower Mississippian Keokuk Limestone of Indiana. This species is about 25 million years younger than all other known species of *Basidechenella* (using the chronostratigraphic assignations of Treworgy and Devera [1991]). *Basidechenella timwhitei* appears to be related to the Givetian species *B. arkonensis* known from the Appalachian and Michigan Basins. In this analysis *Ormistoniella malaca* from the Lower Devonian of South Africa was treated as the outgroup on the basis of the higher-level phylogeny shown in figure 6. It was chosen as the outgroup instead of a species of *Crassiproetus* because of the unique morphological traits developed in some members of this genus. However, when *C. globosus* was used as the outgroup taxon, with *O. malaca* treated as part of the ingroup, the same topology was obtained as that shown in figure 22 except *O. malaca* was part of a basal polytomy with *Basidechenella maura* (Alberti, 1967) that was sister to the rest of *Basidechenella*.

When *B. timwhitei* was removed, the topology of the tree produced is identical to that shown in figure 22. The tree was 57 steps long with a consistency index of .56 and a retention index of .60. The tentative phylogeny presented herein is the one including *Basidechenella timwhitei*. However, it would be informative to recover species of this genus from the late Devonian and early Mississippian. Note that Owens (1990) recognized that there is often a strong degree of similarity between the proetid fauna of the Middle Devonian and the early Carboniferous.

When *Basidechenella hesionea* (Hall, 1861), known from two pygidia, is removed from the phylogenetic analysis nine most parsimonious trees are obtained of length 58, consistency index of .55 and retention index of

.60. A strict consensus of these trees is moderately well resolved, but the relationships among some of the Givetian taxa in the Michigan Basin are unresolved. The addition of this poorly preserved or fragmentary taxon can be considered as somewhat analogous to adding a poorly preserved fossil taxon to a data set consisting of extant taxa. As has been recognized by several studies (e.g., Donoghue et al., 1989), the addition of such taxa often improves phylogenetic resolution. This result reiterates the value of fossil taxa in phylogenetic analysis. In this case, however, the argument that such fossil taxa retain plesiomorphies absent in extant taxa is clearly not relevant.

A bootstrap analysis was run using PAUP 3.0q (Swofford, 1990) to assess the confidence one can have in this phylogeny. One hundred bootstrap replications were performed. For each replication, a heuristic search was employed which searched for the most parsimonious tree created by substitution and replacement of the data matrix. This heuristic search used simple stepwise addition. Confidence intervals from the bootstrap analysis were obtained by retaining groups compatible with the 50% majority-rule consensus trees. The nodes that appeared in the tree in figure 22 that are supported by the bootstrap analysis are (*clara* /*eriensis*) = .39, (*arkonensis*/*timwhitei*) = .53, (*elevata*/ *witherspooni*) = .59, and (*lucasensis*/*cartwrightae*) = .64. None of these values are significant at the .95 level of confidence.

TABLE 7

Character State Distribution for Species Used in Phylogenetic Analysis of *Basidechenella*

Characters and states are listed in table 6. Missing data are indicated by "?"

		1	11111	11112	2222
	012345	67890	12345	67890	1234
Ormistoniella malaca	000000	10000	00000	00000	00?0
Basidechenella maura	???000	1???0	?01?0	00??1	1100
B. canaliculata	232012	10??1	?10?1	10?20	0111
B. clara	222110	01100	10001	10001	1111
B. rowi	222011	11001	00011	10001	0111
B. arkonensis	211011	11001	00011	10111	0111
B. nodosa	122011	11000	??111	10121	0111
B. elevata	122011	11010	??001	00?11	0111
B. eriensis	2?0112	1?001	11001	10001	1111
B. witherspooni	122011	11011	?10??	00211	1111
B. lucasensis	230110	11001	11111	10120	0111
B. pulchra	122012	11011	11111	10121	0111
B. reimanni	122010	11011	?0111	11111	0111
B. hesionea	211???	?0???	??0??	???0?	????
B. cartwrightae	???110	1???0	?11?1	10??0	0111
B. timwhitei	?11111	1???1	?01??	10?11	0111

Phylogenetic position and stratigraphic first occurrence of taxa do show some incongruence in this genus. The chief conflict between phylogenetic position and stratigraphic first occurrence is caused by the phylogenetic position of *B. hesionea* (Hall, 1861). This species is known from two pygidia in the Schoharie Grit. One pygidium occurs in the black, calcareous portion of the upper Emsian Schoharie Grit, and an internal mold of another specimen is known from the gritty brown, spongy weathered Schoharie Grit material. Lithological evidence seems to support, though not guarantee, this stratigraphic assignation. This stratigraphic setting is coeval with that of the relatively more basal *B. maura* (Alberti, 1967) and with the earliest occurrence of *B. clara* (Hall, 1861), which survives into the Eifelian. The sister taxon of *B. clara*, *B. eriensis* Stumm, 1953b, is known from the late Eifelian upper Delaware Limestone of Ohio, and thus does not introduce substantial incongruence to this scheme. In addition, *B. lucasensis* Stumm, 1965, and *B. canaliculata* (Hall, 1861), both relatively more derived than *B. hesionea*, are known from the red clay layer of the middle Jeffersonville Limestone at the Falls of the Ohio, Kentucky (Stumm, 1964) (possibly middle Eifelian). Again, these stratigraphic ranges and phylogenetic positions are not substantially incongruent. However, at least two taxa with a more basal position than *B. hesionea*, *B. rowi*

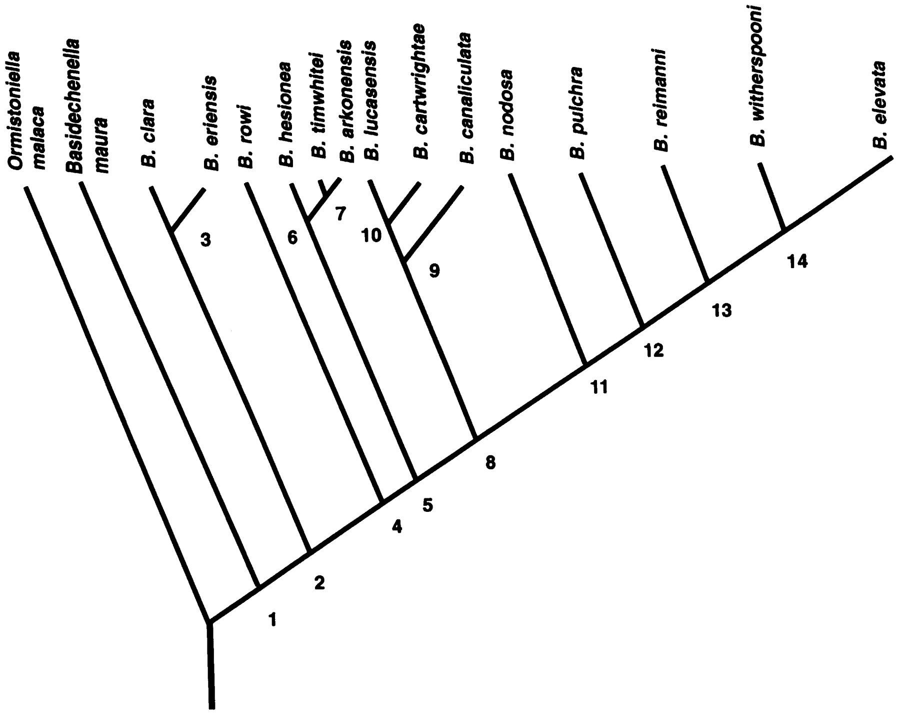

Fig. 22. The single most parsimonious cladogram showing phylogenetic relationships of species in the genus *Basidechenella* generated using the data matrix given in table 7. This most parsimonious tree has a length of 59 steps, a consistency index of .54, and a retention index of .61 and was produced using the **ie*** option (exhaustive search) of Hennig86 (Farris, 1988) and a heuristic search using random addition with 10 replications of PAUP 3.0q (Swofford, 1990). All multistate characters were treated as unordered, nonadditive. Characters were optimized using ACCTRAN and are shown for each node with unambiguous apomorphies depicted by parentheses, ( ), and ambiguous apomorphies, either due to missing data or multiple equally parsimonious resolutions, depicted by brackets, [ ]. Node 1: 0[0,2], 1[0,2], 2[0,2], 6(1), 7[0,1], 20(1), 21[0,1], 22(1), 23[0,1]; Node 2: 0(2), 1(2), 4(1), 7(1), 10[0,1], 15(1), 16(1), 23(1), 24(1); Node 3: 11(1), 21(1); Node 4: 2(2), 5(1), 10(1), 14(1), 21(0); Node 5: 18(1); Node 6: 1(1), 2(1); Node 7: 19(1); Node 8: 11(1), 12(1), 13[0,1], 19(2); Node 9: 1(3), 5[0,1,2], 20(0); Node 10: 2[0,2], 3(1), 5(0), 13(1); Node 11: 0(1), 13(1); Node 12: 9(1); Node 13: 19(1); Node 14: 13(0), 14[0,1], 16(0), 18[1,2].

(Green, 1838) and *B. arkonensis* Stumm, 1953a, do not appear until the middle Cazenovian of the lower Givetian (using the chronostratigraphic assignments of Rickard [1989] and Kirchgasser et al. [1985]). One would predict, on the basis of the occurrences of *B. clara*, *B. hesionea*, *B. canaliculata*, and *B. lucasensis*, that lineages giving rise to *B. rowi* and *B. arkonensis* should be recovered from the Eifelian even if not from the relatively meager upper Emsian record.

At least four possibilities could explain these irregularities. First, the fossil record of some of these species, particularly *B. rowi* and *B. arkonensis*, must be substantially obscured. This is troubling, particularly since *B. rowi* appears to be one of the more common and more abundant members of this genus. Second, the evolutionary history and diversification of this genus could substantially predate its appearance in the fossil record of ENA. Third, *B. clara* could be the ancestor of *B. rowi*, and *B. hesionea* could be the ancestor of *B. arkonensis*. As the operational taxonomic units being treated here are held to be species, it is conceivable that they could function as ancestral forms since populations of these species could have given rise to daughter taxa; however, because of our limits of resolution, we would not be able to distinguish these populations of *B. clara* and *B. hesionea* (it is recognized that *B. hesionea* is known from two specimens, making it impossible to speak of populations of species) from those of the rest of the species. Finally, the phylogenetic scheme developed herein may prove to be incorrect. The first explanation certainly seems likely (the other subjects will not be broached here), particularly when we recognize the strong control that transgressions and limestone belts have on the distribution of these taxa.

In addition to *B. timwhitei*, new species one new species of *Basidechenella* is recognized. This species, *B. cartwrightae*, is known from a single cranidium, and descriptions of both new species are presented below.

Using the method employed for the genus *Crassiproetus*, the biogeographic origins of the genus *Basidechenella* will be considered. Geographic distributions of taxa from the phylogeny of figure 2 were treated as unordered multistate characters having the following states: Arctic, Eastern North America, Armorica, and Baltica. These characters were optimized using Fitch optimization (Fitch, 1971). Only taxa in the clade sister to "*Plesiowensus*" *confossus* were considered, as this part of the phylogeny of the Proetinae contained the best representation in terms of geographic realms and number of species sampled (see fig. 14). This analysis indicates that the ancestral biogeographic state of the genus *Basidechenella* is in Eastern North America or the Arctic. This accords well with the observation that all but one of the species in this genus are known from ENA. However, as in *Crassiproetus*, no species of this genus are known from strata in the Canadian Arctic.

These data must be considered in light of additional stratigraphic and phylogenetic evidence. The most basal species in this genus, as discussed below and illustrated in the phylogeny in figure 22, is *B. maura* (Alberti, 1967). It is also one of the first species to appear in the fossil record, being known from the upper Emsian of Morocco. (However, two other basal species, *B. clara* and the more derived *B. hesionea*, are known from the upper Emsian of the Michigan Basin of ENA and the upper Emsian Schoharie Grit of the Appalachian Basin in New York State.) These singular facts may provide evidence that the genus *Basidechenella* originated in the Old World faunal realm (treated as Armorica). In order to ascertain the true biogeographic affinities of the genus, one must decide which set of data shall be the arbiter, the most parsimonious solution, or evidence on the basis of chronologically calibrated distributions of taxa. The continually changing area relationships in this family clearly indicates that anything but parsimony governs its evolution and patterns of dispersal. However, parsimony can be a good preliminary exploratory technique when comparing competing hypotheses. As both aspects of the data conflict, they are presented as two possible solutions that can be tested by future collection of fossil taxa. In the biogeographic analysis of species of the genus *Basidechenella*, the genus is treated as primitively ENA/Arctic.

Thus, this genus may be an endemic element of ENA whose appearance in the Onondaga Limestone and the Hamilton Group was not associated with immigration from a distinct paleobiogeographic region, or it may have entered ENA from the Arctic paleobiogeographic region during the upper Emsian, although no species from this region are known to exist. As with *Crassiproetus*, this genus may have experienced a brief period of relative cosmopolitanism during the Emsian, and this change in areas occupied may be associated with the initial development of the Acadian Orogeny. Alternatively, phylogenetic position of the basal species in the genus, *B. maura*, might indicate an Armorican origin for this genus with subsequent invasion into ENA in the upper Emsian.

If we consider the complete diversity of the genus through time and space, we recognize that one species of *Basidechenella*, *B. maura*, is known from the upper Emsian of western Morocco, and three species are known from the upper Emsian of ENA, *B. hesionea*, *B. clara*, and *B.* sp. aff. *clara*. *Basidechenella clara* persists into the Eifelian. Four other species are known from the Eifelian of ENA, *B. canaliculata*, *B. eriensis*, *B. lucasensis*, and *B. nodosa*, with the last two taxa carrying over into the Givetian. Seven other species are known from the Givetian of ENA, and one is known from the Lower Mississippian Osagean Stage of southern Indiana.

As with *Crassiproetus*, the interval following the late Givetian Taghanic Stage (strata coeval with the Thunder Bay and Tully Limestones) appears to have had a profound impact on the evolutionary history of *Basidechenella*. Unlike *Crassiproetus*, this genus does not go extinct near the end of the Givetian at the end of the Taghanic Stage; however, the apparent absence of any species of *Basidechenella* from Givetian to Osagean times, about 25 million years using the Decade of North American Geology (DNAG) time scale, is notable. Species in this genus are almost always associated with reefal or carbonate, shallow-water deposits, and are known from almost all the significant carbonate deposits in the late Early and Middle Devonian of New York State (along with the carbonate-rich Wanakah Shale), the Michigan Basin, and the Illinois Basin. However, the species are absent from the Selinsgrove Limestone of Pennsylvania and the Cherry Valley Limestone of New York, implying that this genus does not occur in all of the Middle Devonian carbonate deposits known from ENA. When most carbonate environments disappeared from Laurentia with the extensive development of black shales at the end of the Taghanic Stage, all of the discovered species of *Basidechenella* went extinct. However, some species of *Basidechenella* must have established themselves in refugia, which for some reason may have been inaccessible to *Crassiproetus*, and *Basidechenella timwhitei*, new species later appeared in ENA when limestone environments were reestablished there in the Lower Mississippian.

Unlike *Crassiproetus*, species of *Basidechenella* are known from Givetian deposits in the Appalachian Basin in New York State. However, the strong control that limestone lithofacies exert on distribution that was witnessed for *Crassiproetus* is also evident in *Basidechenella*. *Basidechenella rowi* exemplifies this pattern particularly well, as it appears in several of the limestone pulses in the Hamilton Group that were deposited in the Appalachian Basin. Specimens of *B. rowi* are very rare in the Stafford Limestone Member of the lower Skaneateles Formation during the Cazenovian Stage of the Erian Series. Thus, this species' first occurrence is probably associated with the transgression during transgressive–regressive cycle Ie of Johnson et al. (1985). Species of *Basidechenella* are uncommon at this time in the Appalachian Basin but are more frequently recovered from slightly older rocks in the Michigan Basin (based on Rickard [1989], but the correlations of Cooper et al. [1942] suggest they may be slightly younger).

The most prominent concentrations of specimens during this time are found in strata from the Tioughniogan Stage of the Erian Series. *Basidechenella rowi* (Green, 1838) is known from the Tioughniogan Stage Centerfield Limestone in central and western New York and from the coeval Stone Mill Limestone of eastern New York, and *B. arkonensis* Stumm and particularly *B. rowi* occur in moderate abundance in event beds or epibole deposits from the slightly younger Wanakah Shale, which is a calcareous shale (Speyer and Brett, 1986; Speyer, 1987). *Basidechenella rowi* is also known from the Taghanic Tully Limestone in moderate numbers. Species of *Basidechenella* and particularly *B. rowi* attain prominence in the Appalachian during the transgressive stages of transgressive–regressive cycles If and IIa of Johnson et al. (1985), although their cycles need to be better integrated with Rickard's (1989) correlation chart. They are also known from the Michigan and Illinois Basins during this period. During transgressive–regressive cycle Id, species of *Basidechenella* are restricted to the Michigan and Illinois Basins, whereas in transgressive–regressive cycle Ic species occur throughout ENA.

For the taxa considered herein, these data can be further refined to the species level (see table 5). (Most of the species from the Illinois Basin could not be obtained because they were under study. However, information from Walter [1923], Hickerson [1992] and Hickerson [personal commun.] could be used to add to table 5 a single species, *Basidechenella prouti* (Shumard, 1863),which is known from the late middle Givetian.) When the existence of geographically widespread species is considered, only one species, *B. clara*, is found to occur in roughly coeval strata from all three basins. The species is known from the Onondaga Limestone of New York State (Appalachian Basin), the Jeffersonville Limestone from Kentucky (Illinois Basin), the Port

Colborne Limestone of southwestern Ontario, the Columbus and Delaware Limestones of Ohio, and the Amherstburg Dolomite of Michigan (Michigan Basin). Only one species occurs in both the Appalachian and Illinois Basins, *Basidechenella canaliculata*, which is quite rare, but is known from the Eifelian (probably cycle Ic) of New York State and Kentucky. Two species are known to co-occur in roughly coeval strata (probably cycle If) from the Appalachian and Michigan Basins, *Basidechenella rowi* (from the Tioughniogan 4-Mile Dam Formation in the Michigan Basin, the Centerfield Limestone in New York State, and the slightly younger Wanakah Shale of New York) and *B. arkonensis* (from the Tioughniogan Hungry Hullow Formation in southwestern Ontario, the Stone Mill Limestone in New York State, and the slightly younger Wanakah Shale of New York). In the Taghanic, *B. rowi* is restricted to the Tully Limestone in the Appalachian Basin. All of the other species studied were restricted to the Michigan Basin.

Thus, in the Eifelian, there were at least two widespread species (in at least two of the three major basins of ENA) of *Basidechenella* in ENA. In the Givetian there were also two widespread species. Thus, species of *Basidechenella* do not undergo the relative reduction in geographic distribution in the Givetian that was recognized for *Crassiproetus*. However, they do undergo cycles of appearance and disappearance in different basins associated with the development and contraction of limestone facies. Individual species can be seen to appear, disappear, and reoccur in the same basins in different limestone deposits. This pattern is epitomized by *Basidechenella rowi* in the Appalachian Basin. The species is found during the Cazenovian Stage in the Stafford Limestone during the prominent transgression associated with transgressive–regressive cycle Ie, during the Tioughniogan Stage in the Centerfield and Stone Mill Limestones and the Wanakah Shale during the prominent transgression(s) associated with transgressive–regressive cycle If, and during the Taghanic Stage in the Tully Limestone during the prominent transgression associated with transgressive–regressive cycle IIa. However, it has not been recovered from intervening deposits.

BASIDECHENELLA RICHTER, 1912
Basidechenella maura
(Alberti, 1967)

Proetus (*Coniproetus*) *maurus* Alberti, 1967: 483–484, pl. 1, fig. 3.
Proetus? (*Coniproetus*?) *maurus* Alberti. Alberti, 1969: 99, pl. 4, fig. 1.

DIAGNOSIS: Furrows between intraoccipital lobe and glabella and between intraoccipital lobe and main body of L0 faint; intraoccipital lobe does not project beyond lateral margin of glabella; prosopon of dense granules; anterior border furrow contacts anterior edge of glabella; S0 not directed posteriorly medially.

DISCUSSION: This species is known from the upper Emsian Kalkmergel of western Morocco (Alberti, 1967, 1970). It is thus, along with *B. clara* and *B. hesionea*, one of the three eldest species in the genus, although Richter and Richter (1950) suggested that there may be a cranidium of a new species of *Basidechenella* known from the Lower Devonian in the Harz Mountains of Germany. Its appearance may be associated with the initiation of transgressive–regressive cycle Ic.

Although Alberti (1967) assigned this species to *Proetus* (*Coniproetus*), he commented on its possible relationship to species in the genus *Dechenella*. Later Alberti (1970) suggested that it might be related to *Basidechenella*. The close relationship with *Basidechenella* is supported by several characters, and this species can no longer be assigned to *Coniproetus*. In particular, *B. maura* has the bulging glabellar margins near the eyes that are characteristic of *Basidechenella*, but are not found in *Coniproetus*. In addition, in *B. maura* the anterior portion of L0 and S0 medially flexes anteriorly, which is typical of *Basidechenella*. In *Coniproetus* the anterior portion of L0 and S0 is straight. In *B. maura* the preglabellar field is not developed, whereas it typically is developed in *Coniproetus*. In *Coniproetus* the facial suture is not deflected sharply anterior of the eyes (i.e., it diverges at an angle of about 20° anterior of the eyes), whereas in *Basidechenella* and *B. maura* this angle of divergence is approximately 45°. In addition, in *Coniproetus* the facial sutures immediately anterior of the eyes diverge, whereas in *B. maura* and all other species of

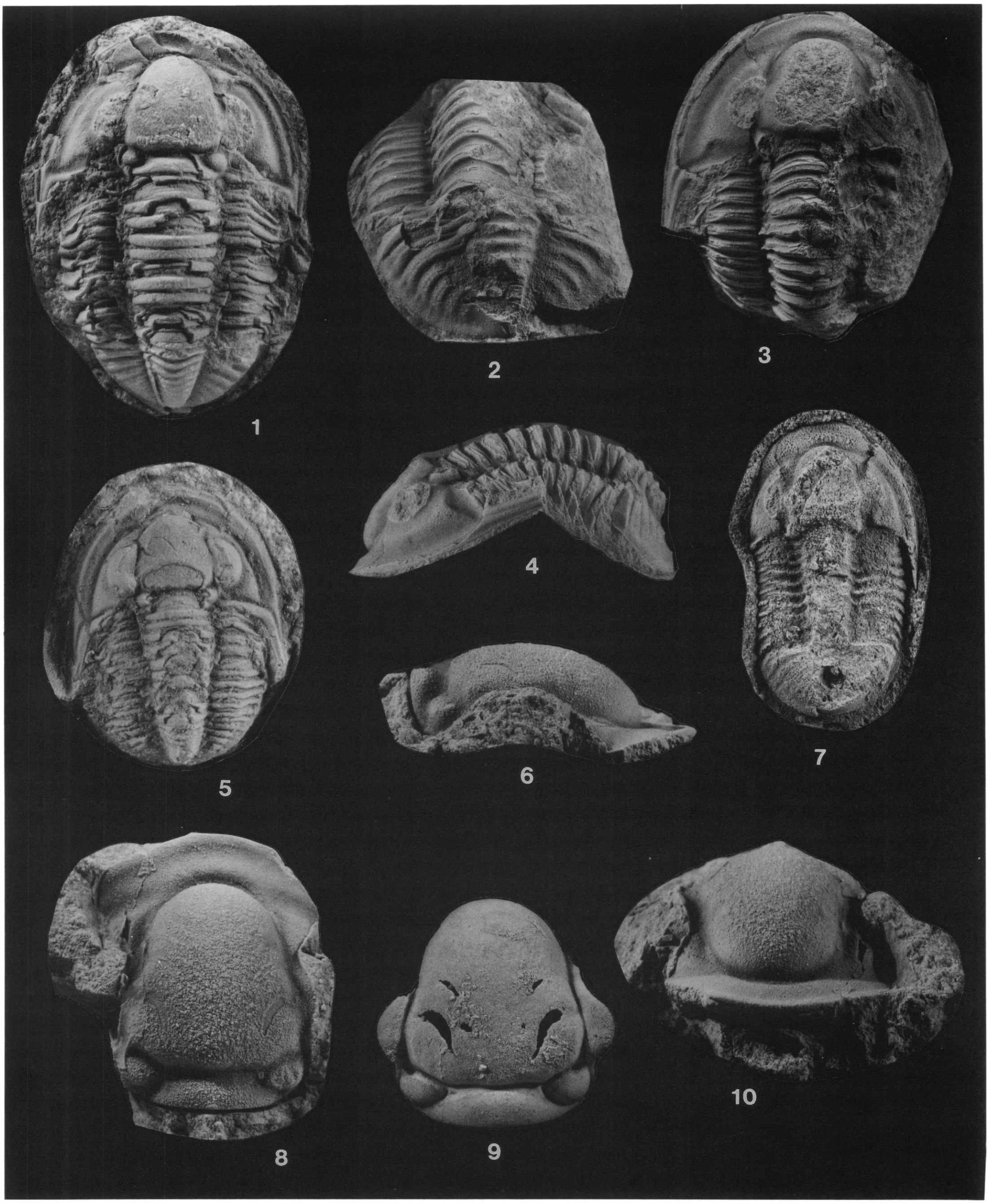

Fig. 23. *Basidechenella clara* (Hall, 1861). **1.** Onondaga Limestone, Southwoodian (Eifelian), Stafford, New York, AMNH 39326, lectotype, dorsal view of entire specimen, ×2.5. **2–4.** Jeffersonville Limestone, Southwoodian (Eifelian), Falls of the Ohio River, near Louisville, Kentucky, UMMP 29509, dorsal view of pygidium and thorax, dorsal view of cephalothorax, and lateral view of entire specimen, ×2.5. **5.** Horizon and locality same as 1. AMNH 39327, paralectotype, dorsal view of entire specimen, ×4. **6, 8, 10.** Columbus Limestone, Southwoodian (Eifelian), abandoned quarry, 1.5 mi. southwest of Castalia, Erie County, Ohio, UMMP 29510, lateral, dorsal, and anterior views of cephalon, ×3.5. **7.** Onondaga Limestone, Southwoodian (Eifelian), Leroy, New York, YPM 33821, dorsal view of entire specimen,

Basidechenella immediately in front of the eyes the facial sutures parallel each other.

Some controversy exists regarding the aptness of Stumm's (1953a, 1953b) assignment of several species of ENA proetids to *Basidechenella*. Several authors claimed that these species could not belong to *Basidechenella* because they all had intraoccipital lobes well separated from the middle body of L0 and from the glabella. Although the Senckenberg Museum would not allow the type species of *Basidechenella*, *B. kayseri*, to be borrowed, examination of illustrations suggests that this species is very similar to *B. maura*. The only difference appears to be the greater lateral displacement of the intraoccipital lobes in *B. maura*. Both species lack the prominently developed intraoccipital lobes, and this happens to be the primitive condition of this character for the subfamily Proetinae. *Basidechenella maura* (and by the same token, *B. kayseri*) shares several features with the ENA proetids Stumm assigned to *Basidechenella* to the exclusion of all other species in the Proetinae. Therefore, at present, it is advocated that the generic name *Basidechenella* be maintained and applied to the Old World–Rhenish species *B. kayseri* and *B. maura* and to the ENA species discussed herein. The diagnosis is emended such that this genus is no longer defined on the basis of its prominently developed intraoccipital lobes.

Basidechenella maura is separated from a clade of ENA *Basidechenella* by several characters. In particular, it lacks the posteromedial flexure of the anterior portion of S0, the anterior border furrow contacts but does not intersect the glabella, and the intraoccipital lobes are not prominently developed. This indicates that there may be a gap in our knowledge of the evolution of *Basidechenella*, particularly when we consider that all other nodes in the cladogram in figure 1 are diagnosed by relatively few synapomorphies.

On the basis of its earlier occurrence in Morocco, this genus may have had its origins in the Old World Faunal Realm. However, as mentioned above, the primitive biogeographic affinities of the genus are in ENA and/or the Arctic. If specimens of *B. kayseri* could be obtained to permit incorporation of this species into phylogenetic analysis, these affinities could change. In particular, if *B. kayseri* were sister to the clade (*maura*(ENA *Basidechenella*)), or *B. maura* were sister to the clade (*kayseri*(ENA *Basidechenella*)), then *Basidechenella* is primitively Arctic. This is because the node occupied by the genus *Basidechenella* in figure 14 would be characterized as Armorican instead of ENA/Armorican.

Basidechenella clara (Hall, 1861)

Figures 23, 24.1–24.8

Proetus clarus Hall, 1861: 71; Hall, 1862: 99; Hall, 1876: pl. 20, figs. 12–14; Hall and Clarke, 1888: pl. 20, figs. 12–14, pl. 22, figs. 28–30; Howell, 1951: 271.

Dechenella (*Basidechenella*) *clara* (Hall). Stumm, 1953b: 23, pl. 4, figs. 1–9; Stumm, 1964: 4, pl. 2, figs. 7–9, 13–16.

?*Dechenella* (*Basidechenella*) *rowi sanduskiensis* Stumm, 1953b: 25, pl. 4, figs. 15–16.

Dechenella (?*Basidechenella*) sp. A. Stumm, 1964: 5, pl. 3, fig. 10.

Diagnosis: Facial suture straight between anterior edge of eye and anterior border furrow, diverging anteriorly at roughly 15°; genal spine projects back to sixth thoracic segment; anterior cephalic border long, equal to length between distal tip of S1 and point midway between S2 and S3, concave dorsally; 11 pygidial axial rings; prominent notch developed on pygidium in posteromedian margin.

Types: Lectotype was AMNH 4075/1, renumbered 39326 (fig. 23.1), Hall and Clarke's (1888: pl. 20, figs. 12, 13), designated by Stumm (1953b).

Material: AMNH 39326, 39327, 44738–44748; SDSNH 10696; UMMP 29509–29515, 47200, 47201, 47203, 47204, 47212; YPM 33183, 33821.

Discussion: This species is known from the following units: Bois Blanc Formation (upper Emsian), Mackinaw City, Michigan; the Needmore Shale (Eifelian), Hayfield, Vir-

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←

×2.5. **9.** Jeffersonville Limestone, Southwoodian (Eifelian), Falls of the Ohio River, Jeffersonville, Clark County, Indiana, UMMP 47212, dorsal view of silicified cranidium, ×2.5.

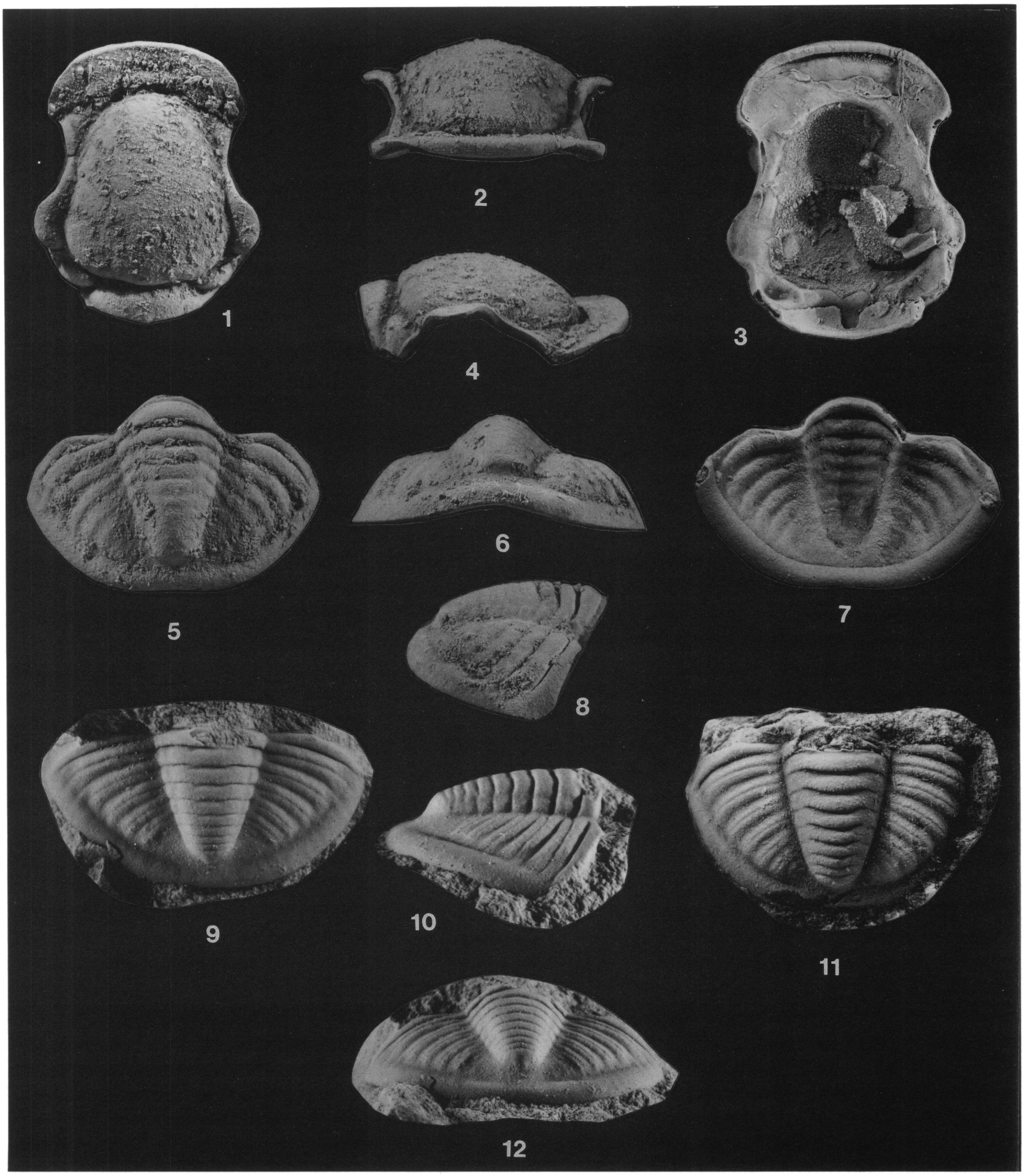

Fig. 24. *Basidechenella* and *Coniproetus* spp. **1-4.** *Basidechenella clara* (Hall, 1861). Jeffersonville Limestone, Southwoodian (Eifelian), Falls of the Ohio River, Jeffersonville, Clark County, Indiana, UMMP 47203, dorsal, anterior, ventral, and lateral views of silicified cranidium, ×2.5. **5-8.** *Basidechenella clara* (Hall, 1861). Horizon and locality same as 1–4. UMMP 47201, dorsal, posterior, ventral, and lateral views of silicified pygidium, ×2.5. **9, 10, 12.** *Coniproetus* sp. aff. *affinis* (Boucek, 1933). Grand Greve Limestone, Pragian (Siegenian), east end of Gaspe Peninsula, Quebec, YPM 33873, dorsal, lateral, and posterior views of pygidium, ×3.4. **11.** *Basidechenella* sp. aff. *clara* (Hall, 1861). Schoharie Grit, Sawkillian (upper Emsian), Schoharie County, New York, AMNH 44730, dorsal view of pygidium, ×3.

ginia, AMNH locality 3099, (see Eldredge, 1972, 1973), intersection of U.S. 50 and Virginia 600; the Onondaga Limestone, Leroy and Stafford, New York State, and Port Colborne, Ontario; the Jeffersonville Limestone, the Falls of the Ohio River, near Louisville, Kentucky; the Columbus Limestone, Marion County, Ohio, and Castalia, Erie County, Ohio; upper Delaware Limestone, Wagner Quarry, N & W Railroad, Sandusky, Erie County, Ohio; and the Amherstburg Dolomite, Cummin's Quarry, Petersburg, Monroe County, Michigan. Thus, this species is a widespread form found in all major basins of ENA in the Eifelian. It is probably associated with several of the transgressions in transgressive–regressive cycle Ic.

Because of its wide distribution and plesiomorphic appearance, *B. clara* has occasionally been confused with other taxa. Stumm (1953b) described a new subspecies, *B. rowi sanduskiensis*, that appears to be identical to typical *B. clara*. In particular, the anterior border furrow contacts the anterior edge of the glabella, rather than intersecting the glabella as in *B. rowi* (Green, 1838). In addition, the pygidium is relatively short and wide when compared to *B. rowi*, which is characteristic of *B. clara*. This species is most likely *B. clara* rather than *B. eriensis* Stumm, 1953b, as there appear to be eight pygidial pleural segments rather than seven. However, many of the cephalic characters that would allow one to discriminate between *B. clara* and *B. eriensis* are absent. Unfortunately, the specimen that Stumm (1953b) assigned to *B. rowi sanduskiensis*, (OCGM 7538c) is lost (K. Meldahl, personal commun.).

Stumm (1964) assigned a series of silicified pygidia and cephala from the Jeffersonville Limestone to *B. clara*. He stated that two of these pygidia (his pl. 2, figs. 11, 12) might indeed belong to *B. canaliculata* (Hall, 1861). On the basis of the pygidial axial nodes and the absence of the posteromedian pygidial notch, these specimens must be assigned to *B. canaliculata*. The librigena that Stumm (1964) assigned to *B. clara* probably belongs to that species rather than *B. canaliculata* because the prominent furrow with associated elevated ridges on the anterior end of the anterior cephalic border is absent, whereas it is prominent in *B. canaliculata*. In addition, as these librigena appear identical to typical free cheeks of *B. clara* they are tentatively assigned to that taxon.

Stumm (1964) figured a cranidium that he called *Dechenella* (?*Basidechenella*) sp. A. He commented that the palpebral lobes, occipital lobes, and occipital ring are similar to those of typical *B. clara*. No criteria could be recognized that would allow one to distinguish between this cranidium and those typical of *B. clara*, and they are treated as conspecific.

There are several specimens of pygidia from the Schoharie Grit, at Albany and Schoharie Counties, NY, that are nearly identical to typical *B. clara*, differing only from that species by possessing one fewer pygidial axial ring and one fewer pleural segment. These specimens are too poorly preserved to merit a description. The possibility also exists that specimens of *B. clara* known from overlying Eifelian strata may possess 10 or 11 pygidial axial rings, as several of these are too poorly preserved to make definitive ring counts. This would imply that this species showed some variability, and recognizing a new species presumably sister to *B. clara* would be inappropriate. These specimens are herein assigned to *B.* sp. aff. *clara* (see fig. 24.11). They are AMNH 39324, 39325, 44727, 44730, 44731, and 44737 and have been figured as *Proetus angustifrons* by Hall and Clarke (1888: pl. 20, figs. 2–5). (The cephalon that Hall and Clarke [1888: pl. 20, fig. 1] illustrated as *Proetus angustifrons* (Hall, 1861) almost certainly does not belong to the same species as the pygidia do, which is discussed more fully in the section on the Emsian trilobite fauna of ENA.) These specimens are somewhat similar to *Coniproetus* sp. aff. *affinis* (fig. 24.9, 24.10, 24.12), which is shown for comparative purposes.

Specimens of cranidia of *B. clara* are known from rocks correlative with the Schoharie Grit, but they are only known to occur in the Michigan Basin. These cranidia cannot be distinguished from cranidia from the Eifelian of the Appalachian or Illinois Basins, but apparently no pygidia have been recovered from these strata, leaving open the possibility that

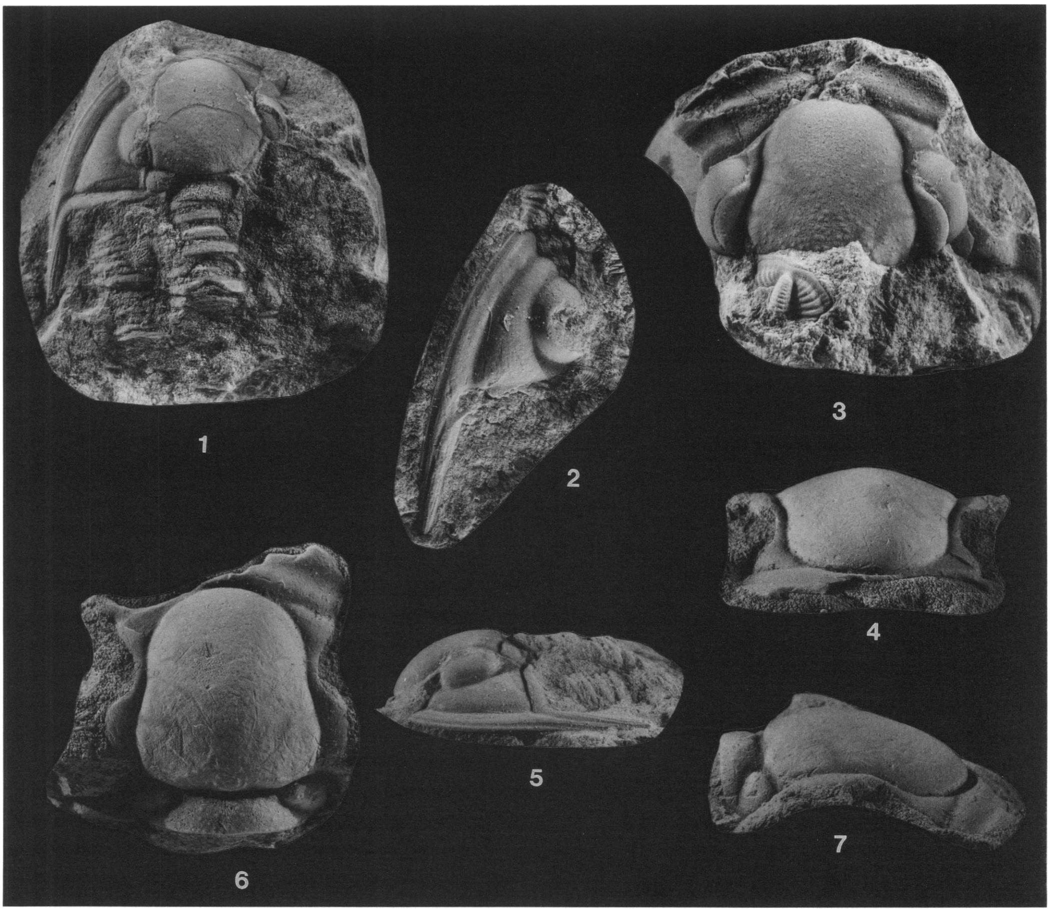

Fig. 25. *Basidechenella eriensis*. **1, 5.** Upper part of the Delaware Limestone, Southwoodian (Eifelian), abandoned Wagner Quarry west of Norfolk and Western Railroad yards, 2 mi. south of Sandusky, Erie County, Ohio, OCGM 7538b, paratype, dorsal and lateral views of partial cephalothorax, ×2. **2, 3.** Horizon and locality same as 1, 5. OCGM 7538b, paratype. **2**, Dorsal view of librigena, ×2.5; **3**, dorsal view of partial cephalon with associated pygidium of juvenile, ×3.75. **4, 6, 7.** Horizon and locality same as 1, 5. UMMP 29517, paratype, anterior, dorsal, and lateral views of cephalon, ×2.5.

their pygidia may differ from upper Emsian *B. clara* in the Appalachian Basin and resemble *B.* sp. aff. *clara*. Such conclusions await further collecting.

Basidechenella eriensis
Stumm, 1953b
Figure 25

Dechenella (*Basidechenella*) *eriensis* Stumm, 1953b: 24–25, pl. 4, figs. 12–14.

DIAGNOSIS: Posterior border furrow behind eyes straight; glabellar furrows developed as patches of pigment; median glabellar impression short lineation; furrow in front of eye shallow; glabellar bulges adjacent to eye present; tubercles on thorax absent; S4 intersects S3 to form triradiate structure.

MATERIAL: OCGM 7538b; UMMP 29517.

DISCUSSION: This species is known from the upper Delaware Limestone (Eifelian) at the abandoned Wagner Quarry just west of the N&W Railroad yards, 2 mi. south of Sandusky, Erie County, Ohio. Thus, it is associated with the upper part of transgressive–regressive cycle Ic.

It appears to be closely related to *B. clara* on the basis of their shared long genal spines that extend back to the sixth thoracic segment, their anterior border furrow that contacts but does not intersect the glabella, and their relatively long anterior cephalic border.

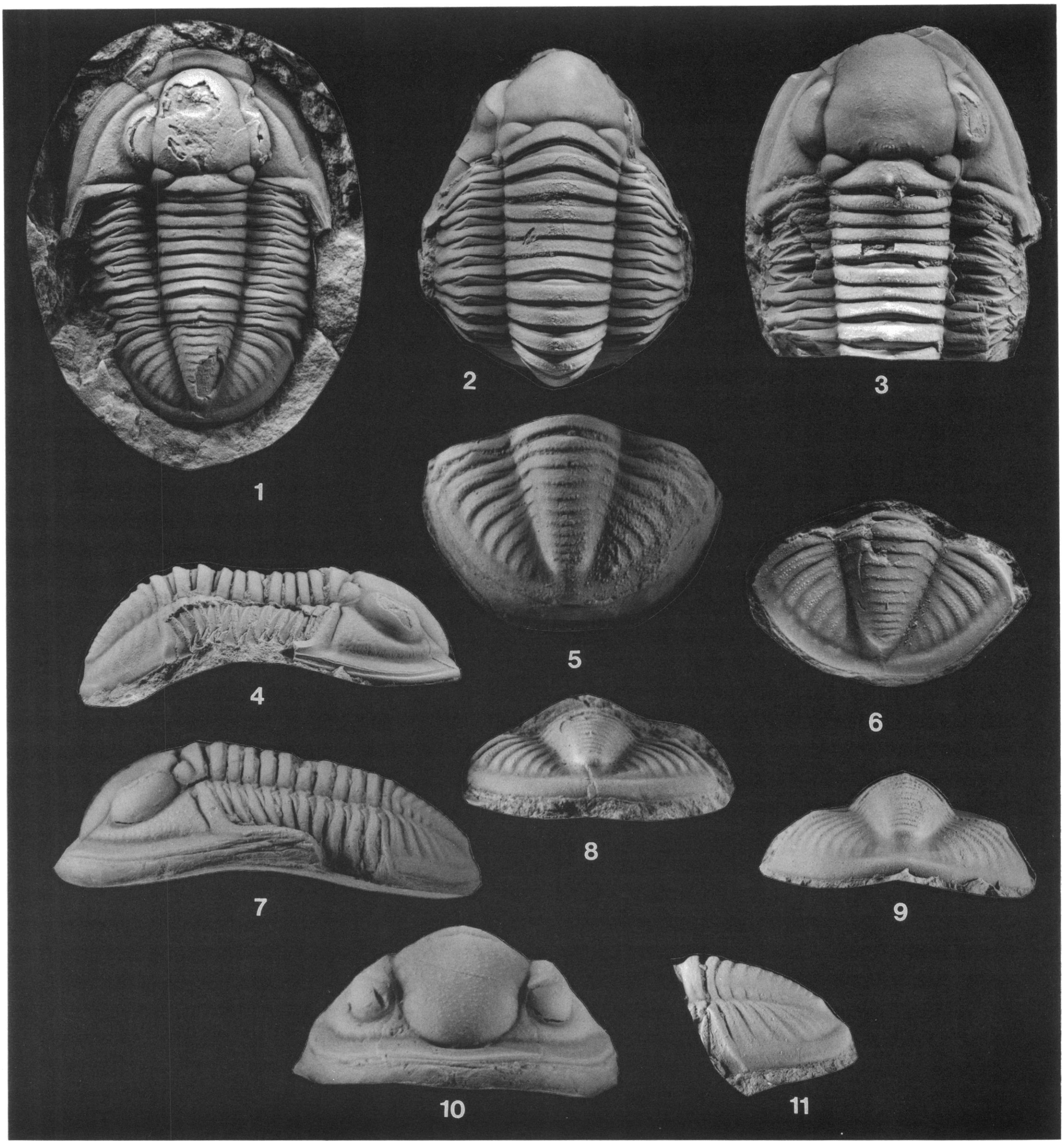

Fig. 26. *Basidechenella rowi* (Green, 1838). **1.** Wanakah Shale, trilobite beds, Ludlowville Formation, Tioughniogan (Givetian), Wanakah cliff beach, Wanakah, New York, BMS E8440, dorsal view of entire specimen, ×2. **2.** Horizon and locality probably the same as 1. YPM 33814, dorsal view of cephalothorax, ×2. **3, 4, 9, 11.** Horizon and locality probably the same as 1. YPM 33816, dorsal and lateral views of entire specimen, and posterior and lateral views of pygidium, all ×2 except 11, ×3. **5, 7, 10.** Centerfield Limestone, Ludlowville Formation, Tioughniogan (Givetian), East Bethany, New York, BMS E5433, dorsal view of pygidium, lateral view of entire specimen and anterior view of cephalon, all ×3 except 7, ×2.4. **6, 8.** Wanakah Shale, Ludlowville Formation, Tioughniogan (Givetian), 18 Mile Creek, shores of Lake Erie, New York, YPM 33773, dorsal and posterior views of pygidium, ×3.5.

Basidechenella rowi (Green, 1838)
Figures 4.1, 4.3, 26

DISCUSSION: For synonymies and diagnosis see the section on the phylogeny of the Proetinae. This species is known from the Appalachian Basin in the Cazenovian Stage from the Stafford Limestone, lower Skaneateles Formation, 6 mi. east of Batavia, NY; the Tioughniogan Stage, Ludlowville Formation, from the Centerfield Limestone, East Bethany, Genesee County, NY, and the Wanakah Shale, at 18 Mile Creek, Erie County, Murder Creek, Darien, NY, and Jaycox Run, the upper part of the Frame Shale Member of the Mahantango Formation at Huntingdon, Pennsylvania; the Taghanic Stage from the Tully Limestone near Penn Yan, NY; and from the Michigan Basin in the Tioughniogan Stage, Four Mile Dam Limestone, Alpena County, Michigan, the Traverse Group. It is the most commonly recovered species of the genus. Thus, its distribution is related to at least two transgressions in transgressive–regressive cycle If, the basal transgression and the fourth transgression in the cycle, and also to the major transgressions associated with transgressive–regressive cycles Ie and IIa.

Hall and Clarke (1888) suggested that this species is closely related to *B. clara*. Indeed, they claimed that *B. rowi* is the Hamilton representative or descendant of *B. clara*. However, several synapomorphies serve to distinguish *B. rowi* from *B. clara*, and it is unlikely that they share an ancestral–descendant relationship, particularly since *B. clara* is the sister taxon of *B. eriensis*.

As Hall and Clarke (1888) suggested, *Proetus marginalis* (Conrad, 1839) is synonymous with *B. rowi*, and this species name is thus no longer valid.

Basidechenella arkonensis Stumm, 1953a, occurs in strata roughly coeval to those in which *B. rowi* is found. In particular, it occurs in the Stone Mill Limestone, which is chronostratigraphically equivalent to the Centerfield Limestone from which *B. rowi* is known, and both species are recovered from the Wanakah Shale. These taxa can be differentiated on the basis of two additional axial rings and one additional pleural segment in *B. arkonensis* and the absence of tubercles on the pygidial and thoracic axial rings in *B. rowi*. In addition, the glabella of *B. arkonensis* tapers more sharply anteriorly such that it has a more conical appearance.

Specimens of *Basidechenella* from the Centerfield Limestone were lumped into a single species by several authors, particularly Hall and Clarke (1888). Hall and Clarke (1888: pl. 23, figs. 20–29) figured several specimens of "*Proetus*" *rowi*. Some of these should be assigned to *B. arkonensis* Stumm, 1953a. In particular, specimens figured on plate 23, figures 23–26 of Hall and Clarke (1888) all have the more prominently tapering glabella and the development of median tubercles on the thoracic and pygidial axial rings characteristic of *B. arkonensis*. These are therefore assigned to this species rather than to *B. rowi*. In addition, a hypostome is known from these sediments that Hall and Clarke (1888: pl. 23, fig. 29) assigned to *B. rowi*. Although probabilistically this assignation may be correct, as the number of specimens of *B. rowi* recovered from strata in New York State do substantially outnumber *B. arkonensis* (by about five to one based on personal assay of museum specimens), this hypostome could conceivably belong to *B. arkonensis*. Therefore, it is only tentatively assigned to *B. rowi*.

Basidechenella arkonensis
Stumm, 1953a
Figure 27

Proetus rowi Green. Hall and Clarke, 1888: pl. 23, figs. 23–26.

Dechenella (*Basidechenella*) *arkonensis* Stumm, 1953b: 120–121, pl. 3, figs. 9, 10.

Proetus arkonensis Stumm. Ludvigsen, 1979: 84, fig. 58b, c.

DIAGNOSIS: Posterior border furrow straight; glabellar furrows developed as patches of pigment; median glabellar impression long lineaments running into S1; anterior border furrow intersects glabella at its anterior edge; prosopon smooth; tubercles developed on thoracic axial rings and anteriormost pygidial axial rings; 13 pygidial axial rings; nine pygidial pleural segments.

MATERIAL: AMNH 44749–44752, 44757, 44759; ROM 1067; UMMP 25541, 28682; YPM 33849, 33860.

DISCUSSION: This species is known from the following units: the Gravel Point Formation (upper Cazenovian), Penn Dixie Cement Company, west quarry lower level, Petoskey, MI; the Arkona Shale, (upper Cazenovian), at Hungry Hollow, Arkona, Ontario; the Ludlowville Formation, Tioughniogan Stage in the Stone Mill Limestone, Roberts Road, West Eaton, New York; the Wanakah Shale, 18 Mile Creek, NY, shore of Lake Erie (the possibility could not be eliminated that these may come from another locality in western NY); the Hungry Hollow Limestone and Widder Shale, Arkona, Ontario; and possibly the Centerfield Limestone from Canandaigua, Ontario County. The species appears to be developed roughly contemporaneously in two of the major tectonic basins in ENA (the Michigan and Appalachian Basins) during the major transgression at the opening of Tioughniogan times (referred to as the fourth transgression in transgressive–regressive cycle If of Johnson et al. [1985]), and is present in the Michigan Basin at the end of transgressive–regressive cycle Ie. Thus, its distribution during the Tioughniogan, though not in the Cazenovian, broadly mirrors that of *B. rowi*. *Basidechenella arkonensis* and *B. rowi* are found in close proximity, at times co-occurring, but in some instances they occur at outcrops in different lithologic units (but with similar lithologies) that are in close proximity. For instance, *B. arkonensis* is known from the Stone Mill Limestone of eastern New York, but it is not found in the Centerfield Limestone, which is developed in central and western New York. In addition, its occurrence in the Michigan Basin, in Arkona, Ontario, is close to the position of the outcrop where *B. rowi* is known to occur in the Michigan Basin, Alpena County, MI. However, because there are no intervening outcrops between these two localities, we cannot be sure of the significance of this. They do appear to occur together in the Wanakah Shale at 18 Mile Creek.

As discussed above, this species is very similar to *B. rowi*, differing chiefly in the number of pygidial axial rings and in the development of tubercles on the thoracic and pygidial axial rings. It is also closely related to a species described on the basis of a single pygidium, *Basidechenella hesionea* (Hall, 1861). *Basidechenella arkonensis* can be distinguished from this species on the basis of the posterior portion of its pygidium, which is notched, and the presence of tubercles on the anteriormost pygidial axial rings. However, the putative sister taxon of *B. arkonensis*, *B. hesionea*, significantly predates the appearance of *B. arkonensis* in the fossil record (upper Emsian as compared to middle Givetian). This incongruence is not as problematic if we recognize that the relatively more derived *B. lucasensis* and *B. canaliculata* (Hall, 1861) are known from the early Eifelian, indicating that some of the history of diversification in this clade is obscured.

Basidechenella hesionea
(Hall, 1861)
Figure 28.1–28.3

Proetus hesione Hall, 1861: 70; Hall, 1862: 98; Hall, 1876: pl. 20, figs. 15, 16; Hall and Clarke, 1888: 93, pl. 20, figs. 15, 16.

DIAGNOSIS: Posteromedian margin of pygidial border not notched; 13 pygidial axial rings; nine pygidial pleural segments, no tubercles on pygidial axial rings.

TYPES: Holotype (by monotypy) AMNH 2898 (fig. 28.1–28.3), figured by Hall and Clarke (1888: pl. 20, figs. 15, 16), from the Schoharie Grit, Schoharie County, Schoharie, NY.

MATERIAL: AMNH 2898, 44723.

DISCUSSION: This species is known from two pygidia. It was originally reported from the Schoharie Grit at Schoharie, NY, by Hall and Clarke (1888). One of the specimens, AMNH 44723 (formerly 2897/2), certainly comes from this horizon. The assignment could be incorrect for the other specimen. However, tentatively, on the basis of lithological evidence, this specimen is assigned to strata of the Schoharie Grit until additional specimens are recovered. An associated unidentified gastropod, possibly *Ruedemannia*, might provide additional stratigraphic resolution. According to this limited evidence, this species occurrence can be associated with the early part of transgressive–regressive cycle Ic.

As mentioned above, because this species is only known from pygidia it had to be coded as missing for several of the character states employed in phylogenetic analysis. However, removal of this species from analysis served to reduce resolution. Associated with the internal mold of the pygidia (AMNH 44723), there is a poorly preserved internal mold of a cephalon that appears to resemble those of *Basidechenella*, and it has a short anterior cephalic border. However, it is too poorly

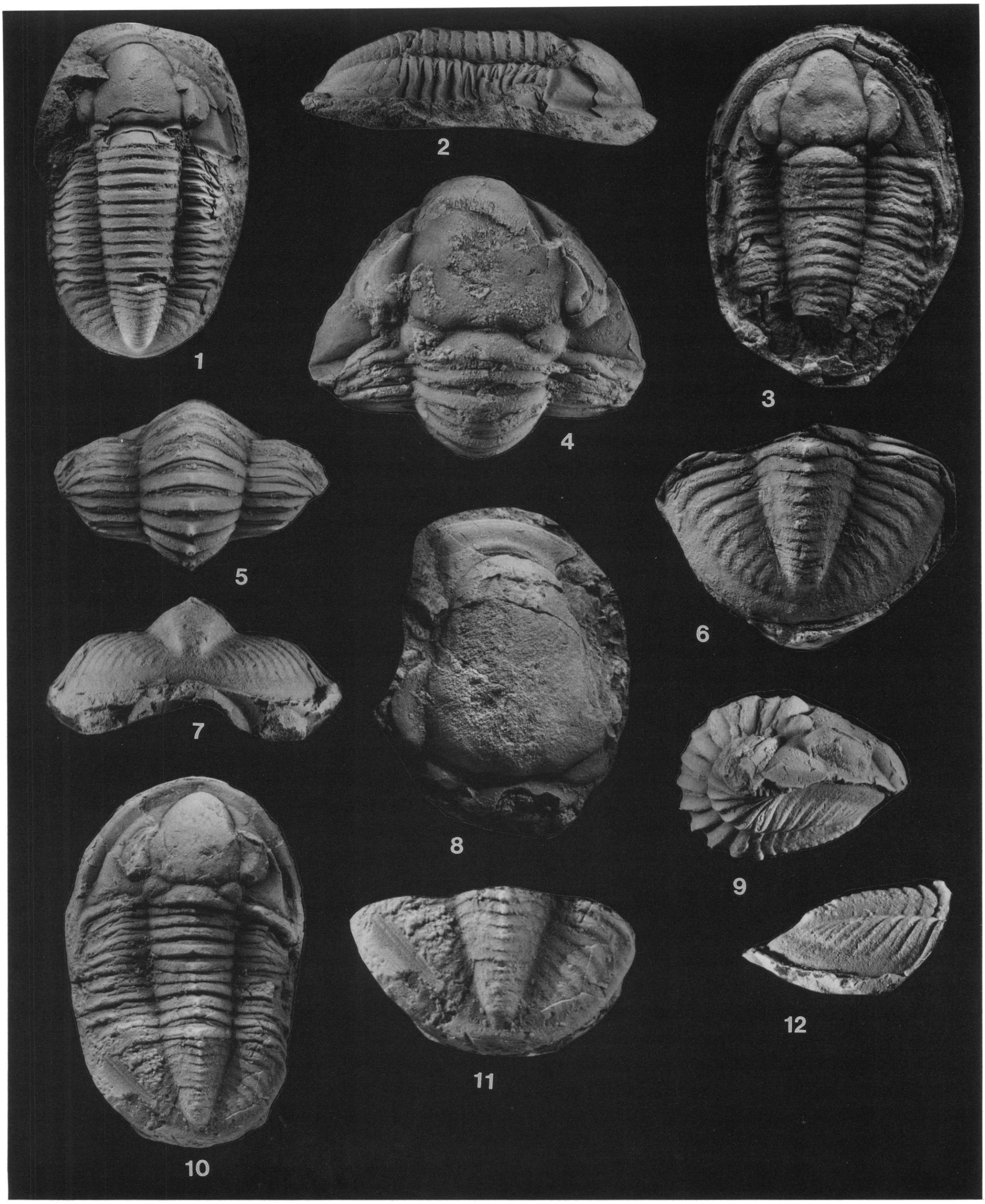

Fig. 27. *Basidechenella arkonensis* Stumm, 1953a. **1, 2.** Wanakah Shale, Trilobite Beds, Tioughniogan (Givetian), ?Wanakah, New York, YPM 33860, dorsal and lateral views of entire specimen, ×1.8. **3.** Hungry Hollow Formation, Coral Bed, Tioughniogan (Givetian), Hungry Hollow on the Aux Sable River, 2 mi. east and .75 mi. north of Arkona, Canada, UMMP 28682, holotype, dorsal view of entire specimen, ×2.5. **4-7, 9.** Horizon and locality same as **3.** UMMP 28682, paratype, dorsal view of cephalon, dorsal view of thorax, dorsal and posterior views of pygidium, lateral view of entire specimen, all ×2.5 except **4, 6,** ×3. **8.** Arkona Shale, Cazenovian (Givetian), Hungry Hollow, Arkona, Ontario, AMNH

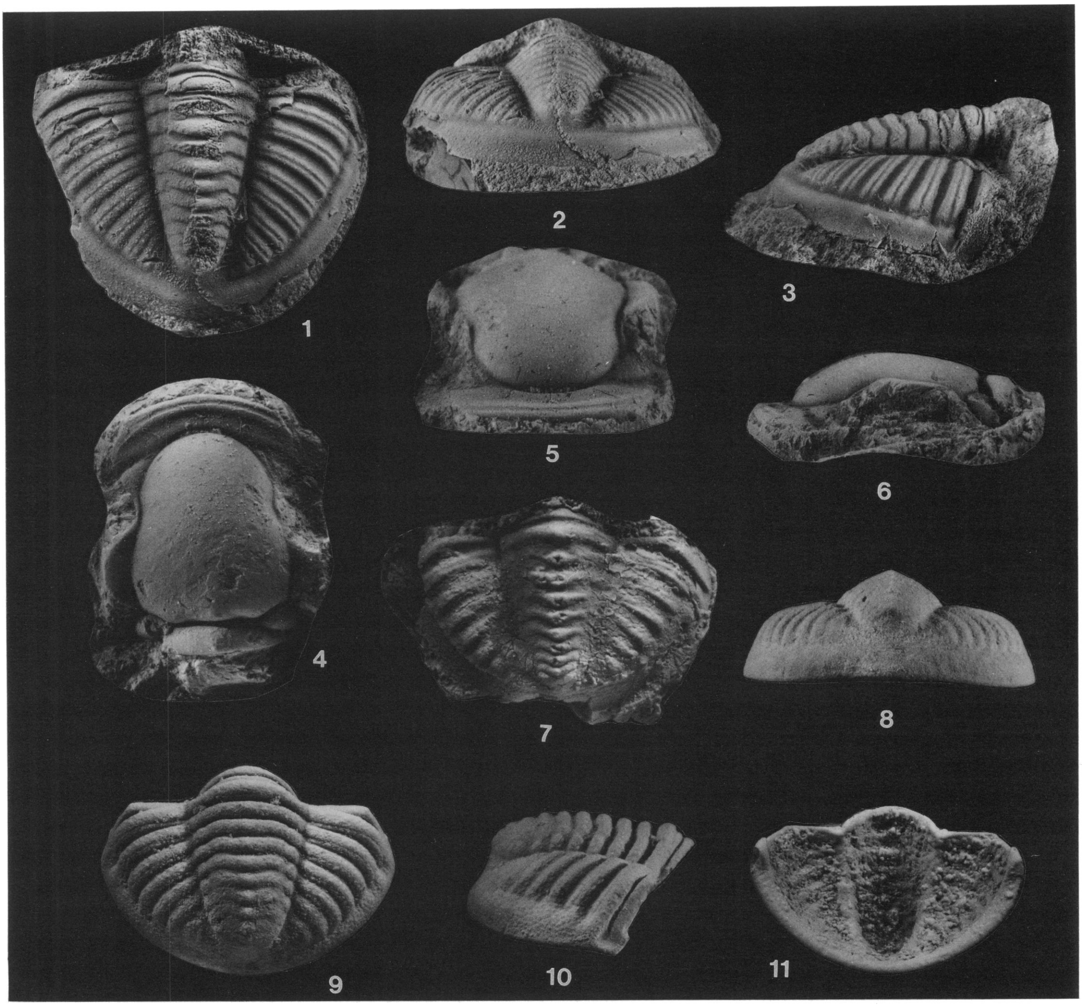

Fig. 28. *Basidechenella* spp. **1-3.** *Basidechenella hesionea* (Hall, 1861). Schoharie Grit, Sawkillian (upper Emsian), Schoharie, New York, AMNH 2898, holotype, dorsal, posterior, and lateral views of pygidium, all ×2.1 except 1, ×2.4. *Basidechenella canaliculata* (Hall, 1861). **4-6.** Jeffersonville Limestone, Southwoodian (Eifelian), Falls of the Ohio River, near Louisville, Kentucky, AMNH 4253, holotype, dorsal, anterior, and lateral views of cranidium, ×3.75. **7.** ?Onondaga Limestone, Southwoodian (Eifelian), Cherry Valley, New York, YPM 33777, dorsal view of pygidium, ×5. **8-11.** Jeffersonville Limestone, Southwoodian (Eifelian), Falls of the Ohio River, Jeffersonville, Clark County, Indiana, UMMP 47198, posterior, dorsal, lateral, and ventral views of silicified pygidium, ×4.

preserved to say for sure, and, in addition, it might not belong to the same species as the pygidium. At present, it appears to be sister to *B. arkonensis* on the basis of the shared number of pygidial axial rings and pleural segments. Therefore, its sister taxon, known from the Cazenovian and Tioughniogan Stages of the Erian Series (Givetian), does not

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←

44751, dorsal view of cranidium, ×2.5. **10-12.** Horizon and locality same as 3. ROM 1067, **10**, dorsal view of entire specimen, ×2, **11**, dorsal view of pygidum, ×2, **12**, lateral view of pygidium, ×3.

appear in the fossil record until substantially after the first occurrence of *B. hesionea*. However, the relatively more derived *B. lucasensis* and *B. canaliculata* are known to occur by the middle Jeffersonville Limestone from the red clay layer (Stumm, 1964), possibly middle Eifelian.

Basidechenella canaliculata
(Hall, 1861)
Figure 28.4–28.11

Proetus canaliculatus Hall, 1861: 73; Hall, 1876: pl. 20, figs. 10, 11; Hall and Clarke, 1888: 107–108, pl 20, figs. 10, 11, pl. 23, figs. 10, 11.

Dechenella (*Basidechenella*) *canaliculata* (Hall). Stumm, 1953b: 24, pl. 4, fig. 10; Stumm, 1964: 4, pl. 2, figs. 4, 17, 18.

Dechenella (*Basidechenella*) *clara* (Hall). Stumm, 1964: pl. 2, figs. 11, 12.

Diagnosis: Prominent furrow separates series of latitudinal striations on anterior end of cephalic border into two ridges; anterior cephalic border short, length (sag.) equal to that between distal tips of S1 and S2; median glabellar impression anterior of S1 short lineation; margins of glabella posterior of eyes flexing slightly medially; anterior border furrow intersects glabella at its anterior edge; 10 pygidial axial rings, all with medial tubercles; pygidial border in posterior view appears rounded.

Types: AMNH 4253, the holotype, by monotypy (fig. 28.4–28.6), from the Jeffersonville Limestone at the Falls of the Ohio River, Kentucky, was designated by Stumm (1953b) on the basis of Hall (1876) and Hall and Clake (1888: pl. 20, figs. 10, 11).

Material: AMNH 4253 (holotype); UMMP 47198; YPM 33773.

Discussion: This species is known from the red clay layer, middle of the Jeffersonville Limestone at the Falls of the Ohio, Kentucky. It is also known from at least one other unit of the Jeffersonville Limestone at this locality, although the exact stratigraphic position could not be obtained. It also may be known from the Onondaga Limestone, Cherry Valley, NY. This locality is based on the label from YPM 33773. Lithologically this assignment seems reasonable, although it may also be compatible with the stratigraphically problematic Cherry Valley Limestone (see Griffing and ver Straeten [1991] for detailed discussion of stratigraphy of this unit). If from the Onondaga Limestone in New York State, it can only be associated with transgressive–regressive cycle Ic. If it occurs in the Cherry Valley Limestone, it would be associated with transgressive–regressive cycle Id. Three species of proetids in ENA are associated with this cycle, all in the genus *Dechenella* Kayser, 1880 (discussed below). Tentatively, the stratigraphic assignment is treated as the Onondaga Limestone rather than the Cherry Valley Limestone since only one species of proetid has ever been reported from the Cherry Valley Limestone.

Stumm (1953b) commented that this species was very similar to *B. clara*. However, *B. canaliculata* can be confidently distinguished from *B. clara* on the basis of its prominent furrow on the anterior cephalic border, possession of tubercles on the pygidial axial rings, and a shorter pygidium lacking a notch in the posterior border. On the basis of these features it can be recognized that the two pygidia Stumm (1964: pl. 2, figs. 11, 12) assigned to *B. clara* instead belong to *B. canaliculata*, a possibility that Stumm (1964) mentioned.

Basidechenella lucasensis
Stumm, 1965
Figure 29.1–29.7

Dechenella (*Basidechenella*) *lucasensis* Stumm, 1965: 164–165, pl. 1, figs. 1–8; Stumm, 1967: 116, pl. 2, fig. 3, Stumm, 1968: 33–34, pl. 1, fig. 1; Kesling and Chilman, 1975: 153, pl. 31, fig. 8, pl. 51, figs. 1, 2, pl. 120, fig. 7.

Dechenella (*Basidechenella*) *canaliculata* (Hall). Stumm, 1964: pl. 2, fig. 4.

Dechenella (*Basidechenella*) sp. A Stumm, 1953a: pl. 5, figs. 9, 10.

Diagnosis: Anterior cephalic border long, equal to length between distal tip of S1 and point midway between S2 and S3; no furrow separating series of latitudinal striations on anterior end of cephalic border; prosopon of dense granules; lateral margins of glabella posterior of eyes curving inward; anterior border furrow intersects glabella at its anterior edge; tubercles on six posteriormost thoracic axial rings; 10 pygididal axial rings.

Material: AMNH 44772–44776; UMMP 25506, 47232, 49757, 49759–49763, 54158.

Discussion: This species is known from the following units: the red clay unit of the

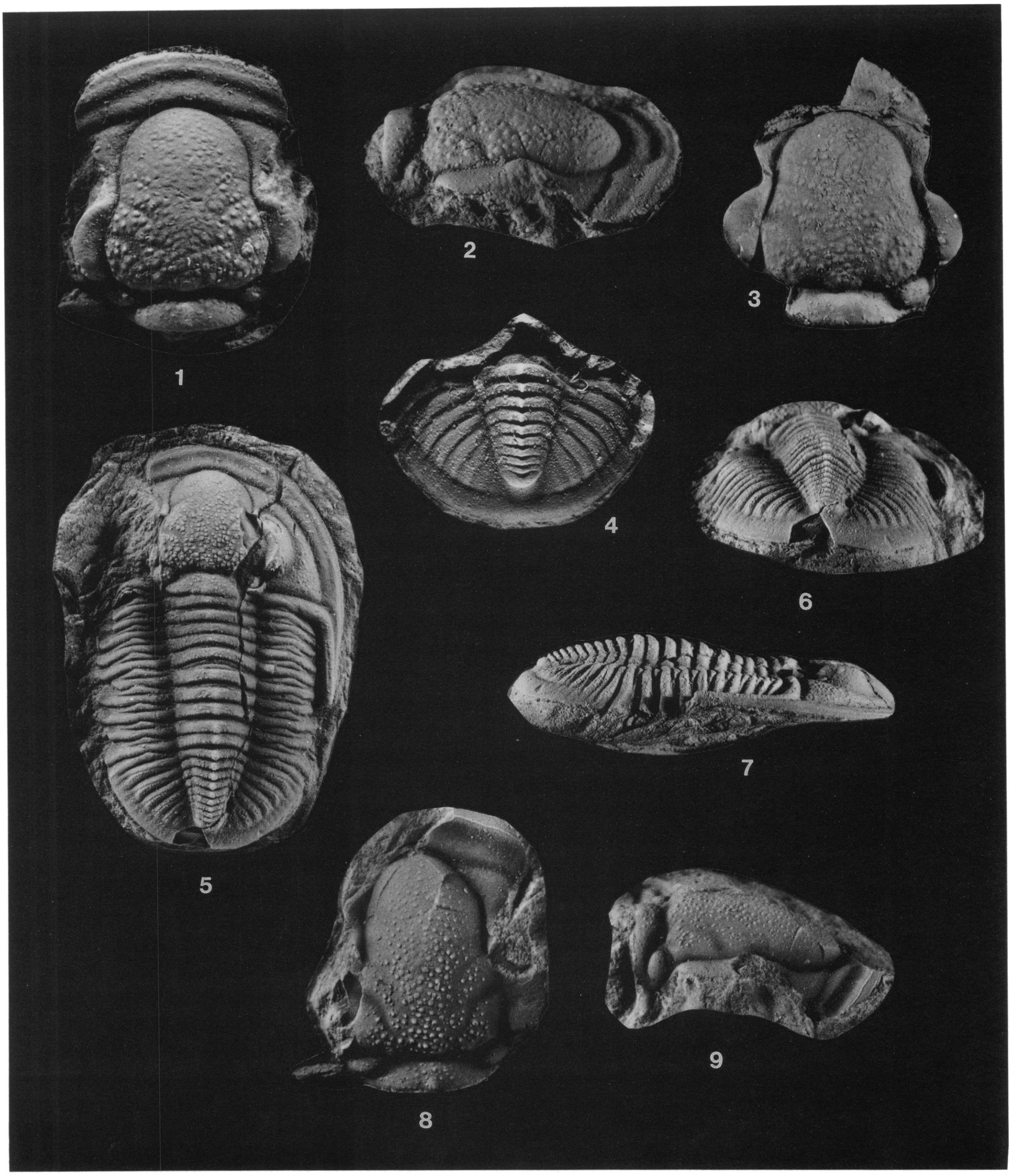

Fig. 29. *Basidechenella* spp. **1, 2.** *Basidechenella lucasensis* Stumm, 1965. Silica Shale, Cazenovian (Givetian), north quarry of the Medusa Portland Cement Company at Silica, 1.5 mi. southwest of Sylvania, Lucas County, Ohio, UMMP 49762, paratype, dorsal and dorsolateral views of cranidium, ×4. **3.** *Basidechenella lucasensis* Stumm, 1965. Jeffersonville Limestone, Southwoodian (Eifelian), Falls of the Ohio River, Jeffersonville, Clark County, Indiana, UMMP 47232, dorsal view of cranidium, ×5. **4.** Horizon and locality same as 1, 2. UMMP 49761, paratype, dorsal view of pygidium, ×5. **5-7.** Horizon and locality same as 1, 2. UMMP 49757, holotype, dorsal, posterior, and lateral views of entire specimen, ×3. **8, 9.** *Basidechenella cartwrightae*, new species. Traverse Group, Gravel Point Formation, *Longispina emmetensis* zone, Cazenovian (Givetian), Gravel Point, Pine River Point, South Point, 1.5 mi. west of Charlevoix, Michigan, UMMP 25514, holotype, dorsal and dorsolateral views of cranidium, ×5.5.

Jeffersonville Limestone, possibly middle Eifelian (Southwoodian), Falls of the Ohio, Jeffersonville, Clark County, Indiana; the Silica Shale, lower Givetian (Cazenovian), Medusa Portland Cement Company at Silica, Lucas County, Ohio; and the Norway Point Formation (Tioughniogan), Alpena, Alpena County, MI. Thus, the species occurs in the Illinois Basin in the Eifelian, transgressive–regressive cycle Ic, and the Michigan Basin in the Givetian, transgressive–regressive cycles Ie and If. It is found in the lower portion of cycle Ie and in the fourth prominent transgression of cycle If.

Stumm (1953a) identified several isolated cranidia and pygidia as *Basidechenella* sp. A from the Norway Point Formation at Alpena, MI. He claimed that they may be similar to *B. pulchra* Stumm, 1953a. For some of the specimens this appears to be correct. However, two of the cranidia lack the prominent furrow with two distinct ridges on the anterior portion of the anterior cephalic border, characteristic of *B. pulchra*, and the lateral margins of the glabella posterior of the eyes deflect medially, characteristic of *B. lucasensis*. Stumm (1964) assigned a cranidium from the Jeffersonville Limestone to *B. canaliculata* that appears instead to belong to *B. lucasensis*. This specimen lacks the prominent furrow on the anterior cephalic border, and it has a prosopon of coarse granules. These two cephalic characters can be used to distinguish between *B. canaliculata* and *B. lucasensis*. However, *B. canaliculata* and *B. lucasensis* are closely related and are part of a clade that includes *B. cartwrightae*, new species. This clade is defined by 10 pygidial axial rings (indeterminate in *B. cartwrightae*) and the lateral margins of the glabella posterior of the eyes deflect medially.

This species attains its greatest abundance in the Silica Shale, and it is the only species of *Basidechenella* known from this horizon. In the other horizons it is very uncommon.

***Basidechenella cartwrightae*,**
new species

Figure 29.8, 29.9

Dechenella (*Basidechenella*) *pulchra* Stumm, 1953a: 119, pl. 3, fig. 4; Kesling et al., 1974: pl. 12, fig. 27.

DIAGNOSIS: Anterior cephalic border long, length equal to distance between distal tip of S1 and point midway between S2 and S3, without prominent furrow; glabellar furrows shallow; prosopon of dense granules; lateral margins of glabella posterior of eyes curve medially; anterior border furrow intersects glabella at its interior edge.

TYPES: Holotype UMMP 25514 (fig. 29.8, 29.9), from the Gravel Point Formation (Cazenovian, correlative with the upper Marcellus Formation), *Longispina emmetensis* zone, ½ mi. west of Charlevoix, MI.

ETYMOLOGY: Named for Ms. Paulyn Cartwright.

MATERIAL: UMMP 25514.

DESCRIPTION: Cephalic length (sag.) 130% maximum width of glabella; anterior border long, length equal to distance between distal tip of S1 and point midway between S2 and S3, prominently concave dorsally; anterior border furrow shallow; longitudinal lineations on anterior border rim of cephalon closely packed and linear. Prosopon of coarse granules. Anterior border furrow intersects glabella. Anterior portion of glabella conical. Facial sutures moderately divergent anteriorly at approximately 40° angle. Glabellar furrows faint. S3 flexing posteriorly at 45° angle from transverse line; S2 medially directed posteriorly, deflected about 45° from sagittal line from inner edge of eye; S1 flexes weakly transversely at posterior and anterior ends; S1 and S2 laterally contact axial furrows. Median glabellar impression anterior of S1 short lineament. Maximum length and width of glabella equal. Lateral margins of glabella between anterior edge of eye and point beyond S3 parallel, posterior of eyes flex medially. S0 well incised, anterolateral portion of L0 straight. Intraoccipital lobes flex strongly anteriorly laterally, separated posteriorly from L0, deflect strongly beyond the lateral margins of the glabella. Tubercle developed on posteromedian portion of L0. L0 flexes anteriorly medially. S0 between intraoccipital lobes flexes anteriorly except medially where it flexes slightly posteriorly. Posterior portion of eye adjacent to lateral portion of L0 anterior of intraoccipital lobes, extending to point opposite distal tips of S2. Palpebral lobes broadest at point 50% length (exsag.) of eye.

DISCUSSION: This species is based on a single cranidium from the Gravel Point Formation (Cazenovian, correlative with the upper Marcellus Formation), *Longispina emmetensis* zone, ½ mi. west of Charlevoix, MI. Thus, it occurs during the early portion of transgressive–regressive cycle Ie.

Originally, Stumm (1953a) assigned this cranidium to *Basidechenella pulchra*. However, this assignment is untenable. The specimen lacks the prominent furrow separating the two ridges on the anterior portion of the anterior cephalic border. In addition, *B. cartwrightae* has a long anterior cephalic border. In *B. pulchra* Stumm, 1953a, this border is generally relatively short. In addition, the glabellar furrows are shallow in *B. cartwrightae* whereas they are developed as patches of pigment in *B. pulchra*. Finally, the lateral margins of the glabella posterior of the eyes flex medially in *B. cartwrightae* whereas they deflect laterally in *B. pulchra*. This species appears to be closely related to *B. lucasensis* Stumm, 1964, on the basis of their shared long anterior cephalic border, their densely granulose prosopon, and the absence of a prominent furrow on the anterior cephalic border.

Basidechenella nodosa Stumm, 1953a
Figure 30.1–30.7

Dechenella (*Basidechenella*) *nodosa* Stumm, 1953a: 118–119, pl. 2, figs. 16–20.

Phacops ohioensis Stumm, 1954: 214–215, pl. 4, figs. 14, 17.

DIAGNOSIS: Faint furrow separating series of latitudinal ridges on anterior end of cephalic border; posterior border furrow at distal end straight; prosopon of dense granules; furrow in front of eye deep; sides of glabella parallel between anterior edge of eye and point beyond S3; anterior border furrow intersects glabella at anterior edge; tubercles on all axial rings of pygidium and thorax; posterior portion of pygidium in dorsal view straight, transverse; eight pygidial pleural segments.

MATERIAL: UMMP 15172, 25509, 25445, 28678, 31333.

DISCUSSION: This species is known from the Dundee Limestone (upper Eifelian), west quarry of France Stone Company at Silica, 1.5 mi. southwest of Sylvania, Lucas County, Ohio (OH), and at the abandoned quarry of the Solvay Process Company, Sibley, 2 miles north of Trenton, Wayne County, MI. It is also known from Ferron Point Formation (lower Givetian), the abandoned shale pit of the Alpena Portland Cement Company, 6 mi. north of Alpena, MI, and the Genshaw Formation (also lower Givetian), Rabiteau Farm and Black Lake, Presque Isle County, MI. Thus, it is associated with transgressive–regressive cycle Ic and and the basal transgression in cycle Ie.

Stumm (1954) recognized a new species, *Phacops ohioensis*, on the basis of two pygidia. He commented that this species is distinct from other species of *Phacops* in many structures of the pygidium. He is correct, as these were misassigned at the ordinal level, but *Phacops* and *Basidechenella* do share certain gestalt similarities in pygidial morphology. However, these pygidia certainly belong to *Basidechenella* on the basis of their well-developed border, the depth and course of the pleural furrows, and the relative anterior displacement of the interpleural furrows. The pygidia of *Phacops ohioensis* are identical with those of *B. nodosa* in terms of the pygidial characteristics used in this analysis. However, it is conceivable that their cephalothoraxes might serve to differentiate them. In addition, the medial axial regions of these two pygidia are strongly weathered, making it impossible to ascertain if they have the complement of axial tubercles typical of *B. nodosa*. Thus, the assigment to *B. nodosa* is tentative and awaits the recovery of additional material.

Although Stumm (1953a) compared this species to *Proetus curvimarginatus* (Hall, 1861) this comparison is not apt, as this appears to be a species of *Monodechenella* and is discussed below in the section on the phylogeny of the "*Thebanaspsis* clade."

Basidechenella pulchra Stumm, 1953a
Figures 30.8–30.12, 31.1–31.7

Dechenella (*Basidechenella*) *pulchra* Stumm, 1953a: 119–120, pl. 3, figs. 1–8; Kesling et al., 1974: pl. 12, fig. 28.

Dechenella (*Basidechenella*) sp. A Stumm, 1953a: 121–122, pl. 5, figs. 8, 11.

Dechenella (*Basidechenella*) sp. B Stumm, 1953a: 122, pl. 5, figs. 4, 5.

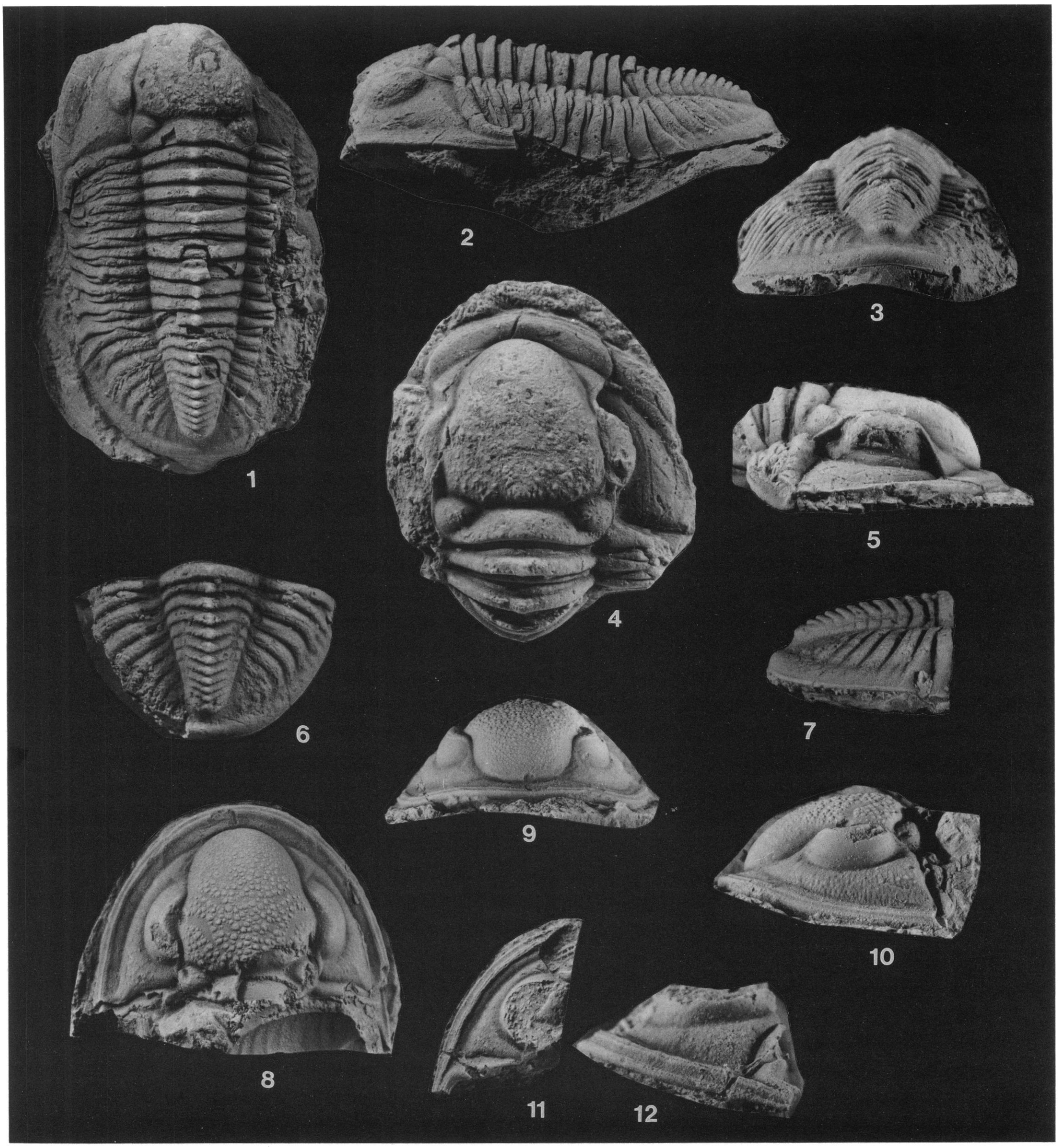

Fig. 30. *Basidechenella* spp. **1-3.** *Basidechenella nodosa* Stumm, 1953a. Traverse Group, Genshaw Formation, Cazenovian (Givetian), Rabiteau Farm, Presque Isle County, Michigan, UMMP 28678, holotype, dorsal, lateral, and posterior views of entire specimen, ×2. **4-7.** *Basidechenella nodosa* Stumm, 1953a. Horizon and locality same as 1–3. UMMP 25509, paratype. **4**, Dorsal view of cephalon and partial thorax, ×3; **5**, lateral view of cephalon and partial thorax, ×2.75; **6, 7,** dorsal and lateral views of pygidium, ×2.5. *Basidechenella pulchra* Stumm, 1953a. **8-10.** Traverse Group, Alpena Limestone, Cazenovian (Givetian), abandoned quarry of the Thunder Bay Limestone Company, Alpena, Michigan, UMMP 28680, holotype, dorsal, anterior, and lateral views of cephalon, ×2.75. **11, 12.** Traverse Group, Potter Farm Formation, Taghanic (Givetian), shale pit on the west side of Evergreen Cemetery, western city limits of Alpena, Michigan, UMMP 28717. **11**, Dorsal view of librigena, ×3, **12**, lateral view of librigena, ×3.5.

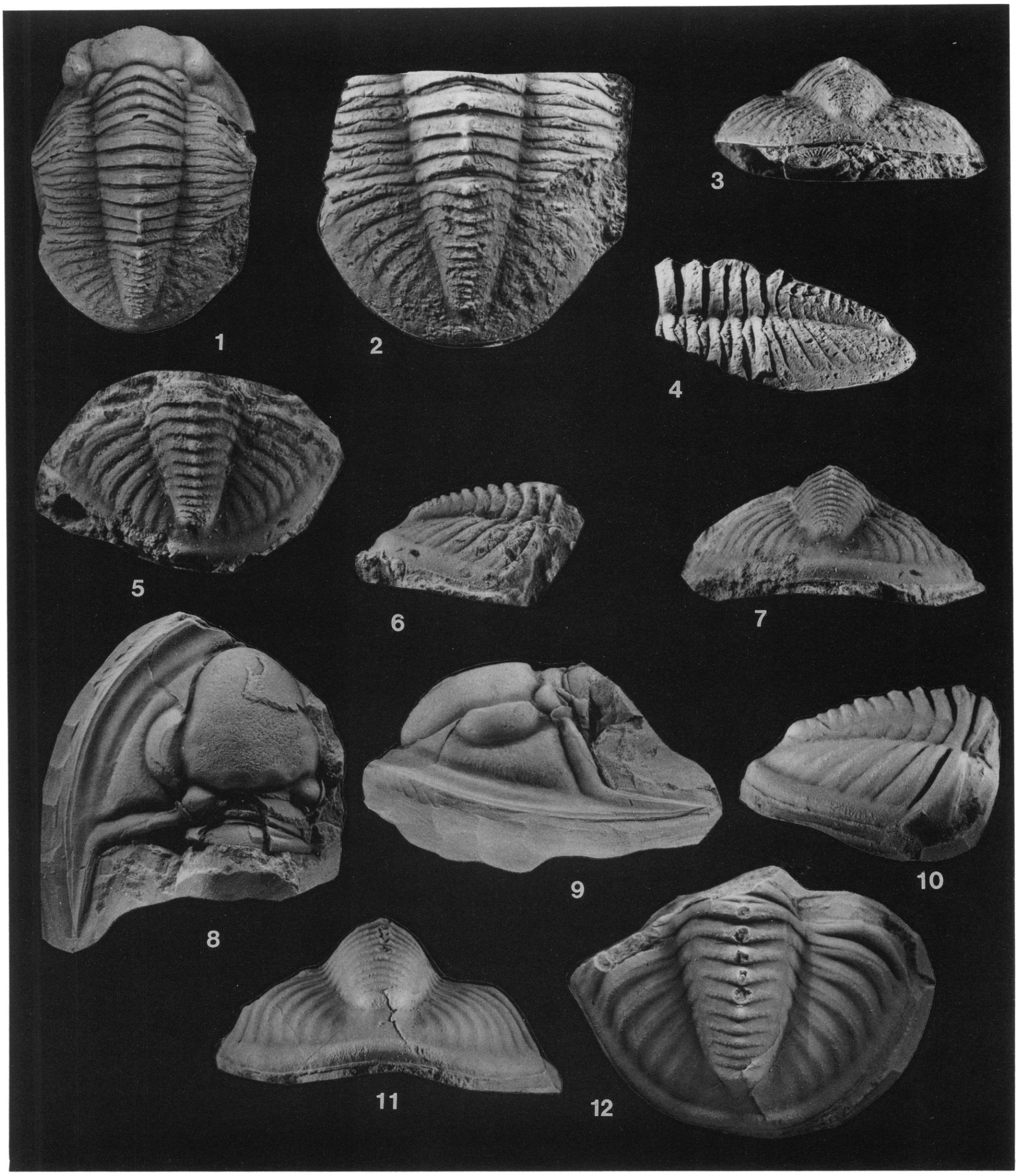

Fig. 31. *Basidechenella* spp. **1-4.** *Basidechenella pulchra* Stumm, 1953a. Dock Street Clay, Cazenovian (Givetian), abandoned quarry of the Thunder Bay Quarry Company, Alpena, Michigan, UMMP 28681, paratype, dorsal view of entire specimen and dorsal, posterior, and lateral views of pygidium and thorax, all × 3.2 except 1, × 2.4. **5-7.** Norway Point Formation, Tioughniogan (Givetian), ledges on south bank of Thunder Bay River, just below 7 Mile Dam, 5 mi. northwest of Alpena, Michigan, UMMP 28721, dorsal, lateral, and posterior views of pygidium, × 4.5. *Basidechenella elevata* (Cooper and Cloud, 1938). **8, 9.** Taghanic (Givetian), Kritesville, Calhoun County, Illinois, USNM 95200j, paralectotype, dorsal and lateral views of cephalon, × 2. **10-12.** Horizon and locality same as 8–9. USNM 95200d, paralectotype, lateral, posterior, and dorsal views of pygidium, × 2.5.

DIAGNOSIS: Posterior border furrow at distal end flexes slightly anteriorly; prosopon of dense granules; prominent furrow separates two well-developed ridges on anterior portion of cephalic border; anterior edge of glabella in dorsal profile curved; glabella posterior of eyes flexing slightly laterally; median glabellar impression developed as short line that does not contact S1; posterior margin of pygidium in dorsal view straight, transverse; 11 pygidial axial rings; medial tubercles on all pygidial axial rings.

MATERIAL: AMNH 44769–44771; UMMP 25505, 28680, 28681, 28683, 28717, 28719, 28721.

DISCUSSION: This species is known from the following units: the *Longispina emmetensis* zone of the Gravel Point Formation (Cazenovian), Penn Dixie Cement Company, west quarry lower and upper levels, Petoskey, MI; the Norway Point Formation (middle Givetian, Tioughniogan), Thunder Bay River, Alpena, Alpena County, MI; the Potter Farm Formation (upper Givetian, Taghanic), Evergreen Cemetery, Alpena, Alpena County, MI; and the Dock Street Clay and the Alpena Limestone (both lower Givetian, Cazenovian), Thunder Bay Quarry, Alpena. Thus this species is associated with transgressive–regressive cycles Ie, If, and IIa. It occurs in the upper portion of cycle Ie and in the fourth prominent transgression of cycle If.

Stumm (1953a) figured a few specimens that he assigned to *Basidechenella* sp. A. He claimed that these were quite similar to *B. pulchra*. The cephala belonging to the set that Stumm (1953a) designated, as mentioned above, appear to be more properly assigned to *B. lucasensis*. However, the other specimens, that is, a single pygidium and left librigena, are indistinguishable from those characterizing *B. pulchra*. Stumm (1953a) also figured a few specimens that he assigned to *B.* sp. B. He claimed that these were very similar to *B.* sp. A but differed in having a relatively narrow concave brim. This is correct, as the cephala assigned to *B.* sp. A have a long anterior border and this trait is characteristic of *B. lucasensis*. These specimens should be assigned to *B. lucasensis*. The specimens assigned to *B.* sp. B have a short anterior cephalic border relative to *B. lucasensis*, which is characteristic of *B. pulchra*. In addition, they possess the prominent furrow that demarcates two prominent ridges on the anterior cephalic border and the margins of the glabella are parallel between the anterior edge of the eye and a point beyond S3 equal to the distance between S2 and S3.

Stumm (1953a) commented that *B. pulchra* was very similar to *B. nodosa*. He was correct in recognizing their close affinity; however, they can be distinguished by several characters, including the anterior flexure of the posterior border furrow at its distal end in *B. pulchra*, the more deeply incised glabellar furrows in *B. nodosa*, and the condition of the furrow on the anterior cephalic border.

This species belongs to a monophyletic group including *B. reimanni* Stumm, 1953a, *B. elevata* (Cooper and Cloud, 1938), and *B. witherspooni* Stumm, 1968, to the exclusion of all other species of *Basidechenella* considered herein. This clade is defined by the anterior flexure of the posterior border furrow distally.

Basidechenella reimanni
Stumm, 1953a

Figure 32.1–32.5

Dechenella (*Basidechenella*) *reimanni* Stumm, 1953a: 121, pl. 5, figs. 6, 7.

DIAGNOSIS: Furrow not developed on anterior cephalic border; posterior margin of pygidium in dorsal view straight, transverse; posterior border furrow at distal end flexes slightly anteriorly; median glabellar impression developed as long line running into S1; anterior edge of glabella in dorsal view transverse; median tubercles developed on anteriormost pygidial axial rings.

MATERIAL: UMMP 27075, 28718.

DISCUSSION: This species is known from the Thunder Bay Limestone, Partridge Point, Alpena, Alpena County, MI (upper Givetian, Taghanic). Thus, it is associated with transgressive-regressive cycle IIa. It is part of a clade including *B. elevata* (Cooper and Cloud, 1938) and *B. witherspooni* Stumm, 1968, and this clade is defined by the presence of tubercles on the anteriormost pygidial axial rings.

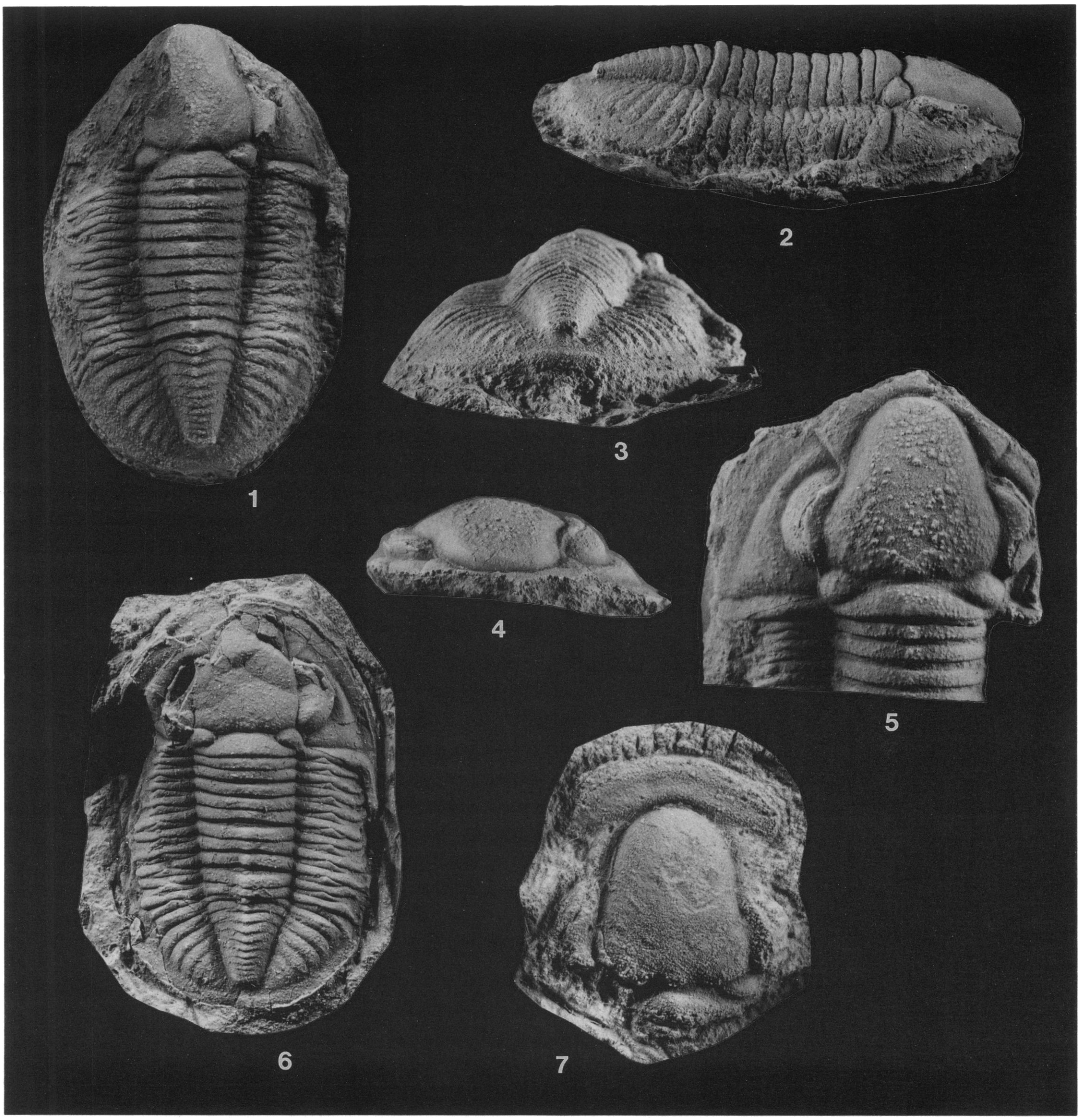

Fig. 32. *Basidechenella* spp. **1-3.** *Basidechenella reimanni* Stumm, 1953a. Thunder Bay Limestone, Taghanic (Givetian), north side of Partridge Point, 4 mi. south of Alpena, Michigan, UMMP 27075, holotype, dorsal, lateral, and posterior views of entire specimen, ×2. **4, 5.** *Basidechenella reimanni* Stumm, 1953a. Horizon and locality same as 1–3. UMMP 28718, paratype, anterior and dorsal views of cephalon and partial thorax, ×2. **6.** *Basidechenella witherspooni* Stumm, 1968. Alpena Limestone, Cazenovian (Givetian), quarry of the Huron Portland Cement Company, Alpena, Michigan UMMP 56620, holotype, dorsal view of entire specimen, ×2.5. **7.** *Basidechenella timwhitei*, new species. Keokuk Limestone, Lower Mississippian (Osagean), Crawfordsville, Indiana, YPM 25594, holotype, dorsal view of cranidium, ×3.

Basidechenella elevata (Cooper and Cloud, 1938)

Figure 31.8–31.12

Dechenella elevata Cooper and Cloud, 1938: 453–455, pl. 55, figs. 20–22, 24–27.

Dechenella (subgen. nov.) *elevata* Hickerson, 1992: 133.

DIAGNOSIS: Anterior border furrow intersects glabella; sides of glabella parallel between anterior edge of eye and S3; furrow in front of eye shallow; anterior cephalic border short, length (sag.) equal to that between distal tips of S1 and S2; faint furrow on anterior cephalic border present separating two ridges; posterior border furrow at distal end flexes slightly anteriorly; posterior margin of pygidium in dorsal view transverse; tubercles on anteriormost pygidial axial rings.

TYPES: Lectotype cephalon USNM 92500a, formerly the syntype, from the base of the Devonian, "Cedar Valley Limestone" in Calhoun County, Illinois (IL). All other syntypes (92500b–j) become paralectotypes.

MATERIAL: USNM 95200a–j.

DISCUSSION: This species is known from the base of the Devonian in Calhoun County, IL, which may be correlative with the *varcus* zone in the Little Cedar Formation (Hickerson, 1992) implying a middle to late Devonian age. Cooper and Cloud (1938) suggested that the strata this species is known from are correlative with the Tully Limestone (Taghanic) of New York State. This would imply that it is associated with transgressive–regressive cycle IIa, although the stratigraphic decisions need to be bolstered.

Hickerson (1992) comments that *B. elevata* may be synonymous with *B. prouti* (Shumard, 1863). However, Cooper and Cloud (1938) rejected this on the basis of differences in the size of the genal spine. As the original materials of this species are in the possession of Hickerson, neither of these assertions could be verified.

This species is sister to *Basidechenella witherspooni* Stumm, 1968. The node defining this clade is supported by two unambiguous synapomorphies that happen to be reversals to the primitive state. In both taxa the prosopon is smooth and the lateral margins of the glabella are not parallel anterior of S3. This indicates that a moderate amount of homoplasy is concentrated at this node.

Basidechenella witherspooni Stumm, 1968

Figure 32.6

Dechenella (*Basidechenella*) *witherspooni* Stumm, 1968: 33, pl. 1, fig. 2.

DIAGNOSIS: Posterior border furrow at distal end flexes slightly anteriorly; prosopon smooth; glabellar furrows developed as pigment patches; faint furrow separates two ridges on anterior cephalic border; anterior edge of glabella in dorsal view appears transverse; tubercles only on anteriormost pygidial axial rings and the anteriormost and six posteriormost thoracic axial rings; posterior margin of pygidium in dorsal view is transverse; 11 pygidial axial rings present.

MATERIAL: UMMP 56620.

DISCUSSION: This species is known from one specimen in the Alpena Limestone (lower Givetian, Cazenovian, equivalent to the upper Marcellus Formation in NY), quarry of the Huron Portland Cement Company, Alpena, Alpena County, MI. Thus it is associated with the upper portion of transgressive–regressive cycle Ie.

Stumm (1968) suggested that this species was most closely related to *B. reimanni* Stumm, 1953a. *Basidechenella witherspooni* shares several characters with *B. reimanni*, and they are closely related. In particular, they share the transverse anterior portion of the glabella (also found in *B. elevata*); however, *B. witherspooni* appears to be most closely related to *B. elevata* on the basis of the two shared reversals to the primitive condition.

Basidechenella timwhitei, new species

Figure 32.7

DIAGNOSIS: Anterior cephalic border long, equal to exsagittal length between distal tip of S1 and point midway between S2 and S3; no prominent furrow on anterior end of anterior cephalic border; glabellar furrows shallowly impressed; prosopon of dense granules; anterior edge of glabella in dorsal view rounded; lateral margins of glabella behind eyes deflect medially; anterior border furrow intersects glabella at anterior edge; anterior edge of eyes opposite point between distal tips of S1 and S2; 12 pygidial axial rings.

TYPES: Holotype YPM 25594 (fig. 32.7),

from the Keokuk Limestone, Lower Carboniferous, Osagean, Crawfordsville, IN.

ETYMOLOGY: This species is named for Tim White, Invertebrate Paleontological Collections Manager at the YPM, who brought the specimens of this taxon to my attention.

MATERIAL: YPM 25594, 25595, 26868.

DESCRIPTION: Cephalic length (sag.) 140% maximum width of glabella; anterior border long, prominently concave dorsally; longitudinal lineations on anterior border of cephalon closely packed and linear. Prosopon of coarse granules. Anterior border furrow intersects glabella. Anterior portion of glabella conical. Facial sutures moderately divergent anteriorly at approximately 40° angle. Glabellar furrows faint. S3 flexing posteriorly at 45° angle from transverse line; S2 medially directed posteriorly, deflected about 45° from sagittal line from inner edge of eye; S1 flexes weakly transversely at its posterior and anterior ends; S1 and S2 laterally contact axial furrows. Median glabellar impression anterior of S1 long line running into S1. Maximum width of glabella equal to 90% maximum length of glabella. Lateral margins of glabella between anterior edge of eye and point beyond S3 parallel, posterior of eyes flexing medially. S0 well incised, anterolateral portion of L0 straight. Intraoccipital lobes flex strongly anteriorly laterally, separated posteriorly from L0, deflect strongly beyond lateral margins of glabella. Tubercle developed on posteromedian portion of L0. L0 flexes anteriorly medially. S0 between intraoccipital lobes flexes anteriorly, except medially where it flexes slightly posteriorly. Posterior portion of eye adjacent to lateral portion of L0 anterior of intraoccipital lobes, extending to point between distal tips of S1 and S2. Palpebral lobes broadest at point 50% length (exsag.) of eye.

Twelve pygidial axial rings, nine pleural segments; tubercles present on at least first three axial rings; border prominent and convex dorsally.

DISCUSSION: This species is known from the Keokuk Limestone, the Osagean Stage of the Lower Mississippian, Crawfordsville, Montgomery County, IN. Three specimens were available—the complete holotype cranidia (fig. 32.7), a fragmentary cranidia, and a fragmentary pygidium.

As mentioned above, this species, when included in the phylogenetic analysis of *Basidechenella*, appears to be the sister taxon of *B. arkonensis*. The existence of this species in the Lower Mississippian indicates that there is a substantial gap in the known stratigraphic record of the genus. Its representation in the Carboniferous, first recognized by J. Cisne and noted in a drawer at YPM, significantly extends the history of the genus. In addition, it indicates that species of *Basidechenella* must have survived in refugia, probably carbonate-rich environments, that thus far have not been sampled.

There is also a pygidium, YPM 26868, from the same locality as the cephala of the species *B. timwhitei* that appears to have the morphology typical of *Basidechenella*. Neither of the cephala are associated with this pygidium, but tentatively it is assigned to the same species. The specimen is too poorly preserved to be completely described, and it could not be coded for all pygidial characters. However, the states of character 1, 2, and 19 could be determined.

PHYLOGENY OF *DECHENELLA* KAYSER, 1880

A phylogeny of *Dechenella* and one species of the closely related genus *Pedinodechenella* Ormiston, 1967, was generated using 49 characters and 19 taxa. The characters used are given in table 8, and the character codings for these taxa are given in table 9. One most parsimonious tree (fig. 33) was produced using the **ie*** option of Hennig86 (Farris, 1988) (equivalent to the exhaustive search of PAUP) and the heuristic search using random addition with 10 replications of PAUP 3.0q (Swofford, 1990). The tree was 202 steps long with a consistency index of .35 and a retention index of .42. *Lacunoporaspis norrisi* Ormiston, 1971, is treated as the outgroup. This species is known from the Lower Devonian of the Canadian Arctic. This taxon was treated as the outgroup on the basis of the phylogeny shown in figure 6 and the fact that the members of the *Schizoproetoides/Schizoproetus* clade develop several unique morphological traits.

A bootstrap analysis was run using PAUP 3.0q (Swofford, 1990) to assess the confidence one can have in this phylogeny. One hundred bootstrap replications were per-

TABLE 8

Characters Used in Phylogenetic Analysis of the Genus *Dechenella*

"0" is the plesiomorphic state. Character matrix is given in table 9

0. Anterior portion of intraoccipital lobe: (0) flexes anteriorly beyond anterior portion of S0, (1) behind transverse line tangent to anteromedian portion of S0.

1. Glabella: (0) does not contact anterior border furrow, (1) contacts anterior border furrow.

2. Posterior tip of S1: (0) deflects medially, (1) follows a straight course.

3. Number of pygidial axial rings: (0) 14–15, (1) 21, (2) 18, (3) 16, (4) 19–20, (5) 17.

4. Number of pygidial pleural segments: (0) 9, (1) 12–13, (2) 10, (3) 11.

5. Pygidial border reaches point of constant, and greatest length (exsag.) opposite pleural segment: (0) 6 or 7, (1) 4–5, (2) 3, (3) 9.

6. Pygidial border posteriorly: (0) poorly developed, (1) well developed.

7. Pygidial border posteriorly: (0) flattened dorsally, (1) rounded lip, convex dorsally.

8. Medial portion of pygidial axial rings: (0) flex posteriorly, then anteriorly, medially, (1) straight medially, (2) flex posteriorly medially, (3) flex anteriorly medially.

9. Pygidial border posteriorly, in dorsal aspect: (0) rounded, (1) transverse.

10. S1, in dorsal view: (0) relatively smoothly arched, (1) doglegged kink of two straight lines.

11. Posterior portion of glabella anterior of medial portion of L0: (0) flexes anteriorly laterally, posteriorly medially, (1) smoothly arches anteriorly, (2) straight.

12. S3: (0) straight, (1) roughly convex anteriorly.

13. S4: (0) straight, roughly parallel to L0, (1) posterior end inclined posteriorly.

14. Sides of glabella anterior of S3: (0) converging, (1) parallel.

15. Glabellar bulges proximal to eyes: (0) weak, (1) prominent.

16. Facial suture meets on dorsal portion of anteromedian edge of eye and: (0) forms a right angle, (1) for a portion circumscribing the anteromedian part of the eye, then directed straight forward, forming an obtuse angle laterally, (2) suture meets at anteromedian edge of eye forming an acute angle laterally.

17. Anterior cephalic border: (0) flattened, (1) raised broad ledge, convex, (2) concave.

18. Interpleural furrows: (0) prominently developed, (1) faint, (2) very faint to absent.

19. Facial suture anterior of the anterior border furrow: (0) proceeds for a short distance anterior of furrow, then deflects sharply medially, (1) proceeds for a long distance, slightly rounded, and weakly diverging medially, then deflects more strongly medially.

20. Anterior border: (0) long, length (sag.) equal to 1.5 times length (exsag.) between distal tips of S1 and S2, (1) short, equal to exsagittal length between distal tips of S1 and S2, (2) very long, equal to two to three times exsagittal length between distal tips of S1 and S2.

21. Posterior portion of S1: (0) does not contact S0, (1) does contact S0.

22. Space between distal tips of S1 and S2: (0) 1.5 times length (exsag.) between distal tips of S2 and S3, (1) two times length between distal tips of S2 and S3.

23. Facial suture at most lateral point of eye: (0) displaced further laterally than on anterior border, (1) displaced as far laterally as its most abaxial point on the anterior border, (2) displaced further laterally on anterior border than on lateral most point where it circumscribes the eye.

24. Medial portion of L0: (0) elevated above posterior portion of glabella when viewed in lateral aspect, (1) at level of posterior portion of glabella, (2) beneath level of posterior portion of glabella.

25. Prosopon: (0) smooth or with small granules, (1) large granules.

26. Posterior portion of pygidial border: (0) short region, equal to the length of first axial ring, (1) long, flat region, with length equal to the length of first two pygidial axial rings.

27. Dorsal surface of pygidial border next to the pleurae: (0) flattened, parallel to the dorsal plane, (1) inclined at the angle of the pleurae.

28. Anterior border furrow: (0) faint, diffuse, marked by gradual change in slope between gena and preglabellar field and border, (1) narrow, marks prominent change in cephalic topography between gena and anterior border, preglabellar field, and anterior border.

29. Median glabellar furrows medially: (0) directed posteriorly, (1) directed anteriorly.

30. Anteromedian portion of eye opposite: (0) point between distal tips of S2 and S3, (1) distal tip of S2, (2) distal tip of S3.

31. Lateral margins of glabella between distal tips of S1 and S2: (0) converging more sharply than during their course between S2 and S3, (1) converging at the same angle as between S2 and S3.

32. Maximum glabellar bulge laterally: (0) opposite distal tip of S1, (1) posterior of distal tip of S1.

33. S2: (0) straight, (1) rounded curve, convex anteriorly.

TABLE 8—(*Continued*)

34. Space between facial suture along anteromedian portion of eye and S3: (0) large, not displaced as far as sagittal line tangent to maximum lateral glabellar bulge, (1) small, not displaced as far as sagittal line tangent to maximum lateral glabellar bulge.

35. Space between anteromedian portion of eye and anterior border furrow: (0) equal to orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1, (1) equal to 1.5 times orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1, (2) equal to two times orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1.

36. Sides of glabella opposite S4: (0) converging, (1) parallel.

37. S3: (0) directed posteromedially, (1) transverse.

38. Posteromedian portion of glabella, in anterior and posterior view: (0) arched, medially, (1) flattened.

39. Intraoccipital lobes: (0) not deflected beyond margins of posterior portion of glabella, (1) deflected laterally beyond margins of the glabella.

40. Intraoccipital lobes: (0) flattened, (1) expanded dorsally.

41. Intraoccipital lobes: (0) evenly expanded laterally, (1) most expanded laterally anteriorly, (2) most expanded laterally posteriorly, (3) most expanded medially.

42. Furrow anterior of intraoccipital lobe: (0) follows a constant line from S0 to the axial furrow, (1) laterally, deflected more strongly laterally, (2) laterally deflected more strongly anteriorly.

43. Pygidial axial rings expand medially (in dorsal view) back to a ring that is, proceeding from the anterior to the posterior portion of the axis (rounding down to nearest even number) (posterior of this ring, the lateral margins of the axial rings are straight): (0) half the value of the total number of axial rings, (1) numerically farther than halfway back, (2) numerically less than halfway back.

44. Fixigenae, in their anterior course from the lateral margins of the glabella at S3 to the anterior border, are: (0) evenly sloping, (1) posteriorly more shallowly inclined, then have an abrupt break in slope, and they are anteriorly more sharply inclined.

45. Anterior margin of the pygidial pleurae, in dorsal view is: (0) a smoothly arched curve, convex laterally, (1) sinusoidally shaped.

46. Posterior portion of palpebral ridge, anterior of point where it deflects sharply posteriorly is opposite: (0) point about one-third of way between anterior end of S1 and anterior portion of intraoccipital furrow, (1) opposite anterior portion of the intraoccipital furrow.

47. Pygidial axial rings: (0) flex anterolaterally, (1) straight.

48. Pygidial pleurae, in cross section: (0) rounded, (1) flattened.

formed. For each replication an heuristic search was employed that searched for the most parsimonious tree created by substitution and replacement of the data matrix. This heuristic search used the branch and bound option with tree-bisection and reconnection. Confidence intervals from the bootstrap analysis were obtained by retaining groups compatible with the 50% majority-rule consensus trees. The nodes that appeared in the tree in figure 33 that are supported by the bootstrap analysis are (*planimarginata/bathurstensis/welleri/perscheii/alpenensis/valentini/haldemani/carvalhoae/polonica/verneuili/osborni/algida/struvei/maclareni/setosa/rittbergensis/gigouti*) = .56, (*struvei/maclareni*) = .39, (*valentini/haldemani*) = .39, (*gigouti/rittbergensis*) = .52, (*polonica/carvalhoae*) = .13. Obviously none of these values exceed .95.

One new species of *Dechenella* and one new species of *Pedinodechenella* are presented, which are included in phylogenetic analysis and described herein. These are *Pedinodechenella modelli* and *Dechenella carvalhoae*. Another new species, *D. perscheii*, is described in the section on the higher-level phylogeny of the Proetinae. There is not substantial incongruence between stratigraphic position and phylogenetic placement for the cladogram shown in figure 33 except possibly for *Pedinodechenella modelli*, new species. This species may be known from the Frasnian, yet it has a basal position in the phylogeny. This is not a serious problem, however, as it appears closely related to several other species of *Pedinodechenella* that were not considered but that are known to occur in the Eifelian and Givetian, implying that *Pedinodechenella* and *Dechenella* had diverged by the Eifelian. In addition, this stratigraphic assignment for *P. modelli* is not made

TABLE 9

Character State Distribution for Species Used in Phylogenetic Analysis of *Dechenella*

Characters and states are listed in table 8. Missing data are indicated by "?"

	1	11111	11112	22222	22223	33333	33334	44444	444
012345	67890	12345	67890	12345	67890	12345	67890	12345	678
Lacunoporaspis norrisi									
000000	00000	00000	00000	00000	00000	00000	00000	00000	000
Pedinodechenella modelli									
111000	110?1	21?00	10100	00010	11111	01110	01100	12201	001
Dechenella perscheii									
011021	11200	01011	01100	00111	10101	11110	10111	00112	000
D. bathurstensis									
001112	11210	01011	10200	11210	01001	10110	00111	21211	110
D. algida									
001232	10100	01010	21201	11110	00110	01111	10111	10011	110
D. osborni									
001322	11100	01011	10200	11110	00001	00112	10111	30011	110
D. maclareni									
001410	10301	11101	20101	01010	00100	00110	00101	11111	110
D. haldemani									
101530	11100	21?11	01100	01110	01100	01111	01111	2?201	101
D. alpenensis									
001530	10210	11111	00200	01110	10110	11110	01111	31201	101
D. valentini									
001430	11200	11?01	01100	011?0	011?0	11110	0??1?	?02?1	101
D. setosa									
001413	11201	11011	20212	11110	00101	01110	10111	10211	101
D. rittbergensis									
001413	10111	10111	20212	10110	10101	10010	00101	10211	111
D. verneuili									
001020	11100	11011	21200	011?0	11100	00110	0??01	3221?	110
D. struvei									
001210	10101	11001	21101	110?0	11110	01010	00?01	?0101	110
D. gigouti									
?01413	11100	?0111	01112	011?0	11102	11011	001??	??201	?11
D. planimarginata									
001321	11200	01011	12102	112?0	01110	10102	1????	?1111	101
D. welleri									
101001	00210	21?11	10112	11100	11000	11110	000??	??210	101
D. polonica									
101020	11110	11?01	20110	011?0	10111	01100	1??01	01101	111
D. carvalhoae									
001?20	10100	11?11	20100	011?0	11110	11110	1??01	10?01	111

with complete confidence. Additional incongruence between phylogenetic position and stratigraphic occurrence emerges due to the relatively derived positions of the Eifelian taxa *D. osborni* Ormiston, 1967, *D. algida* Ormiston, 1967, and *D. maclareni* Ormiston, 1967, which are nested among a few Givetian species of *Dechenella*.

The biogeographic origins of this genus have been considered by several authors (e.g., Ormiston, 1967; Richter and Richter, 1950). Ormiston (1967) suggested that the genus originated in the Canadian Arctic rather than in Europe (Armorica) on the basis of its earlier occurrence in Arctic sediments. However, specimens are also known from ENA in early Eifelian sediments, and on the basis of Ormiston's (1967) criterion it would be difficult to distinguish between an Arctic or ENA origin. Although the early appearance

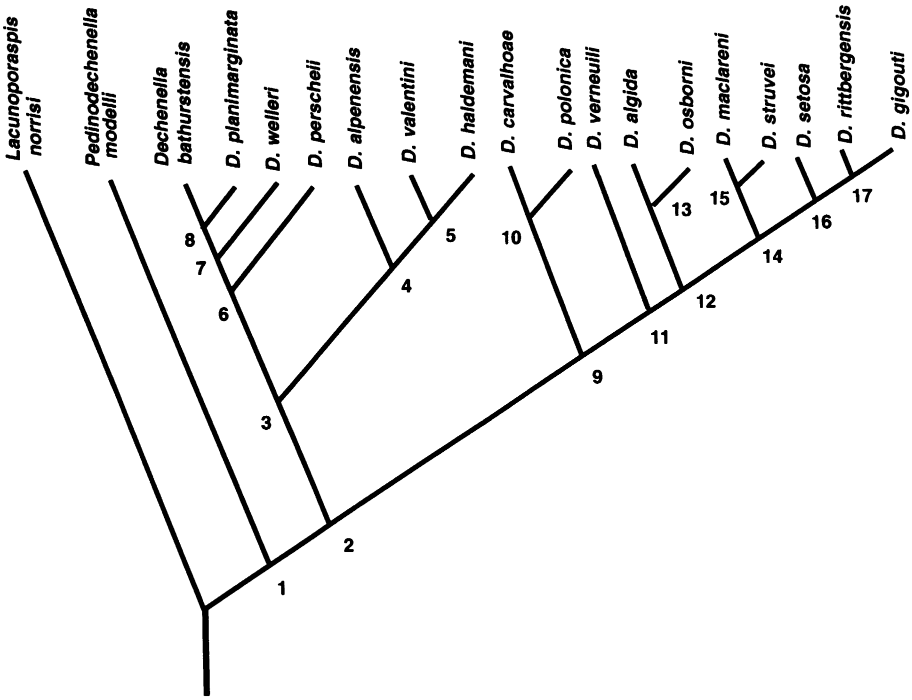

Fig. 33. The single most parsimonious cladogram showing phylogenetic relationships of species in the genus *Dechenella* generated using the data matrix given in table 9. This most parsimonious tree has a length of 202 steps, a consistency index of .35, and a retention index of .42 and was produced using the **ie*** option (exhaustive search) of Hennig86 (Farris, 1988) and an heuristic search using random addition with 10 replications of PAUP 3.0q (Swofford, 1990). All multistate characters were treated as unordered, nonadditive. Characters were optimized using ACCTRAN and are shown for each node with unambiguous apomorphies depicted by parentheses, ( ), and ambiguous apomorphies, either due to missing data or multiple equally parsimonious resolutions, depicted by brackets, [ ]. Node 1: 2(1), 6(1), 7(1), 11[0,1,2], 12(1), 18(1), 24(1), 26(1), 27[0,1], 28(1), 32(1), 33(1), 34(1), 38(1), 41(1), 43(2), 45(1), 48(1); Node 2: 4(2), 8[0,1,2], 11[0,1], 14(1), 15(1), 22(1), 23(1), 40(1), 46(1); Node 3: 8(2), 31(1), 39(1), 41(2); Node 4: 3(5), 4(3), 11(1), 13[0,1], 37(1); Node 5: 17(1), 27(1); Node 6: 5(1), 11(0); Node 7: 9[0,1], 16(1), 20[0,2], 21(1), 27(1), 28[0,1], 42[0,1], Node 8: 3[0,1,3], 20[0,1], 23(2), 26(0), 32(0), 42(1); Node 9: 8(1), 11(1), 16(2), 47(1); Node 10: 29(1), 36(1), 43[1,2]; Node 11: 18(2), 44(1), 48(0); Node 12: 3[0,2,3,4], 20[0,1], 21(1), 26[0,1], 27(0); Node 13: 3[0,2,3], 5(2), 11(0), 26(0), 35[0,1,2], 36(1), 39(1), 43(0); Node 14: 3[2,4], 4(1), 10(1), 20[0,1,2]; Node 15: 7(0), 14(0), 18(1), 20(1), 23(0), 43(1); Node 16: 3(4), 5(3), 19(1), 20(2), 30(1), 48(1); Node 17: 12(0), 13(1), 26(1), 33(0).

of *Dechenella* in the Canadian Arctic and ENA may provide inferential support for a Laurussian rather than Armorican origin of the genus, other sources of data, particularly evolutionary histories, need to be considered. Fitch optimization (Fitch, 1971), using biogeographic states mapped on the phylogeny in figure 6 as unordered characters (shown in fig. 14), suggests that this genus originated in the Arctic. This accords well with the basal position of the Arctic taxon *Pedinodechenella modelli* in the phylogeny in figure 33. On the basis of the phylogeny in figure 33 it appears that there were at least two independent invasions of the genus *Dechenella* into ENA from the Arctic paleogeographic regions. Thus, unlike *Crassiproetus* and *Basidechenella*, this genus was not endemic to ENA for a long period before the deposition of the Hamilton Group. One of the invasions from the Arctic must have occurred in the Eifelian, whereas one took place at the very end of the Eifelian. Thus there may be some change in area relationships that occurred in this genus during the reintensification of the Acadian Orogeny.

The phylogeny of *Dechenella* suggests that there is a large Old World–Rhenish or Armorican clade with a few species of Arctic species nested within it and another large clade containing several Arctic and ENA taxa.

This genus is characterized by a persistently much broader geographic range than the two other genera of Proetinae considered in detail in this analysis. The stratigraphic ranges are presented for those species considered in this analysis with the best representation attained for species occurring in ENA. For additional species belonging to *Dechenella*, and closely related genera occurring in the Canadian Arctic, interested readers should consult Ormiston (1967, 1975a, 1976). Stratigraphic assignments used here are based on information from Rickard (1989), Kirchgasser et al., (1985), Ormiston (1967), Yolkin and Ormiston (1985), Chlupac (1992), Uyeno (1991), and Snajdr (1980). Four species are known from the lower–middle Eifelian—*D. planimarginata* (Meek, 1871), *D. maclareni* Ormiston, 1967, *D. perscheii*, new species, and *D. welleri* (Stauffer, 1909)—with the first three persisting into the upper Eifelian. If we use the stratigraphic correlations of Yolkin and Ormiston (1985) instead of Ormiston (1967), then *D. maclareni* and *D. perscheii* would also be known from the upper Emsian. Two additional species are known from the upper Eifelian, *D. osborni* Ormiston, 1967, and *D. algida* Ormiston, 1967. For two species, *D. setosa* (Whidborne, 1889) and *D. rittbergensis* Zimmermann, 1892, it could not be ascertained if they belonged to late Eifelian or early Givetian strata (Chlupac, 1992). Seven species are known from the latest Eifelian and lower Givetian—*D. alpenensis* Stumm, 1953a, *D. valentini* Stumm, 1953b, *D. haldemani* (Hall, 1861), *D. carvalhoae*, new species, *D. polonica* Gurich, 1896, *D. verneuili* (Barrande, 1852), and *D. bathurstensis* Ormiston, 1967—with the latter persisting throughout the Givetian. The stratigraphic ranges of two species, *D. struvei* Richter and Richter, 1950, *D. gigouti* Richter and Richter, 1950, could not be localized within the Givetian. *Pedinodechenella modelli*, new species may occur in Frasnian strata, but it is part of a lineage that must have shared a last common ancestor with *Dechenella* no later than the Eifelian.

Of the species considered, seven belong to the Old World–Rhenish faunal realm and are treated as Armorican taxa, five are treated as Canadian Arctic taxa, and five are treated as ENA taxa. Further paleobiogeographic resolution is attempted for the taxa occurring in ENA, and in addition their appearance in relation to the transgressive–regressive cycles of Johnson et al. (1985) is presented.

In the Eifelian two species are known from the Michigan Basin, with one of these also occurring in the Illinois Basin. Two species are known from the latest Eifelian (basal Cazenovian) of the Michigan Basin and one species is known from the latest Eifelian of the Appalachian Basin. One species that occurs in the latest Eifelian of the Michigan Basin is found throughout the lower part of the Givetian in much of the Cazenovian, and also in the upper Givetian Taghanic. Thus it is probably also associated with transgressive–regressive cycles Ie and IIa. (There are also at least two additional species of *Dechenella* in the Illinois Basin that occur in strata of the late middle Givetian [Hickerson, 1992]. One of these species was assigned to *D. haldemani* by Walter [1923]. However, specimens of this species could not be obtained because they were under study by another author. A cursory glance of the poor available figures indicates that these two forms most likely are not conspecific. The other species in the Illinois Basin was referred to as "*Proetus*" *nortoni*, new species by Walter [1923]. It certainly belongs to the genus *Dechenella*, but its phylogenetic placement also could not be ascertained.)

These stratigraphic data indicate that the occurrence of three species of *Dechenella* in ENA is associated with cycle Ic of Johnson et al. (1985). Three other species are associated with cycle Id. Thus, species of the genus *Dechenella* are the only species of proetid trilobites (probably true for all trilobites) whose distribution in ENA appears to be related to transgressive–regressive cycle Id. This is the transgression associated with the initiation of the deposition of the Hamilton Group, although not necessarily the first appearance of the Hamilton Group fauna, in New York State, which largely follows this interval. At this time we witness the first manifestation of detrital products from Acadian source terranes after a period of tectonic quiescence (Ettensohn, 1985; Anderson et al., 1988).

Two of the species in ENA are only known from the basal portion of the Marcellus Formation. As their persistence in ENA seems so ephemeral, it is difficult to suggest an environmental or facies control for the disappearance of this genus in ENA. However, it is interesting to note that only one of the species in this genus, *D. welleri* (Stauffer), attains a widespread geographic distribution (more than one basin), and it is exceedingly rare and known only from the Eifelian. This is contrary to the pattern found for *Crassiproetus* and *Basidechenella* (discussed above) and *Monodechenella* (discussed below). Thus, the disappearance of species of *Dechenella* from ENA is probably not comparable to what is seen in the three other proetid genera simply because they were never permanently established in ENA over geologic time scales.

PEDINODECHENELLA ORMISTON, 1967

TYPE SPECIES: *Dechenella* (*Pedinodechenella*) *melvillensis* Ormiston, 1967.

DIAGNOSIS: See Ormiston (1967).

DISCUSSION: This genus consists of a series of species treated in detail by Ormiston (1967, 1976) that are known from the Eifelian and Givetian of the Canadian Arctic Islands and British Columbia. If the stratigraphic assignment for the sole specimen of *P. modelli*, new species is correct, the range of this genus extends into the Frasnian. *Pedinodechenella* was originally referred to as a subgenus of *Dechenella*; however, here it is treated as a distinct genus in order to avoid introducing additional taxonomic categories where they are not needed.

***Pedinodechenella modelli*, new species**

Figure 34.1–34.4

DIAGNOSIS: Anterior portion of intraoccipital lobe straight and behind transverse line tangent to anteromedian portion of S0; sides of glabella anterior of S3 converging; glabellar bulges proximal to eyes weak; length (exsag.) between distal tips of S1 and S2 1.5 times length between distal tips of S2 and S3; anteromedian portion of eye opposite distal tip of S2; posterior portion of palpebral lobe, anterior of point where it deflects sharply posteriorly, opposite point about one-third of way between anterior end of S1 and anterior portion of intraoccipital furrow; pygidial pleurae in cross section appear flattened; anterior edge of pygidial axial rings flex posteriorly, then anteriorly, medially; 15 pygidial axial rings; posterior portion of pygidial border broad, flat region, equal to length of first two pygidial axial rings.

TYPES: Holotype YPM 33762 from either the Ramparts or Beavertail Limestone, at the Ramparts of the Mackenzie River in northern British Columbia, Canada.

ETYMOLOGY: Named for the excellent photographer at the AMNH who provided all of the photographs used in this paper, Mr. Andrew Modell.

MATERIAL: YPM 33762.

DESCRIPTION: Cephalic length (sag.) 55% width; anterior border developed as long ledge (1.5 times length of L0 medially), sloping dorsally posteriorly and flattened; anterior border furrow deep and narrow; longitudinal lineations on anterior border of cephalon closely packed and linear. Prosopon smooth. Anterior edge of glabella contacts anterior border furrow. Anterior portion of glabella weakly rounded. Anterior branch of facial sutures moderately divergent anteriorly at approximately 25° angle, meet on anteromedian edge of eye, circumvent anteromedian part of eye, then run sagittaly and form an obtuse angle, displaced farther laterally at lateral edge of eye than at maximum lateral deflection on the anterior border. Lateral margins of glabella converging anterior of S3. Length (exsag.) between anteromedian portion of eye and anterior border furrow equal to orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1. Glabellar furrows faintly impressed. S3 roughly transverse, inclined at 10° angle to transverse line, convex anteriorly; S2 rounded curve medially directed posteriorly, deflected about 45° from exagittal line from inner edge of eye; S1 dog-legged kink of two intersecting straight lines, does not contact S0; S1 and S2 laterally contact axial furrows; length (exsag.) between distal tips of S1 and S2 1.5 times length between distal tips of S2 and S3. Median glabellar furrow medially directed anteriorly. Maximum width of glabella equal to maximum length. Glabella constrict-

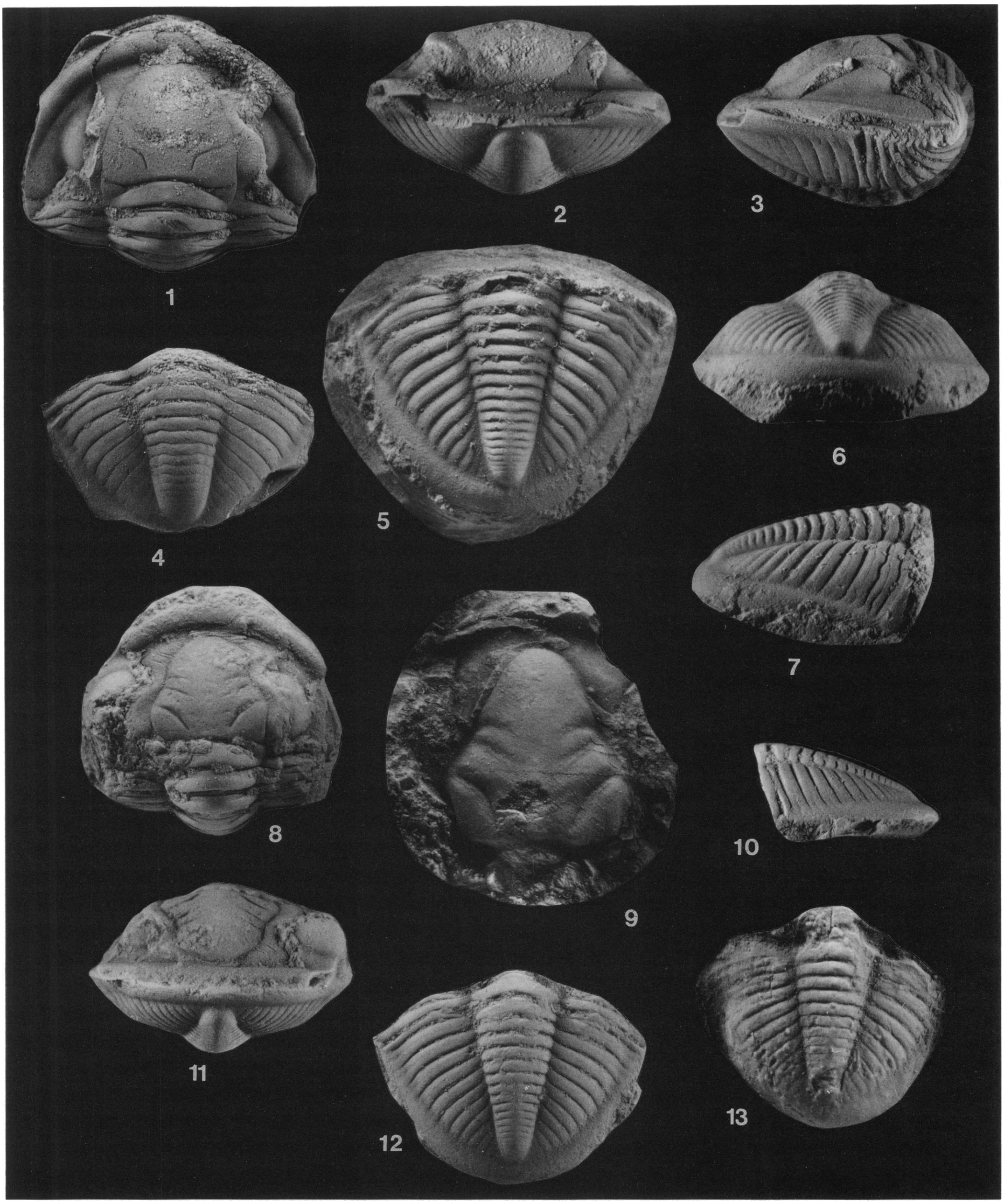

Fig. 34. *Pedinodechenella* and *Dechenella* spp. **1-4.** *Pedinodechenella modelli*, new species. ?Ramparts or Beavertail Limestone (Frasnian), Ramparts of the Mackenzie River, northern British Columbia, Canada, YPM 33762, holotype, dorsal, anterior, and lateral views of entire enrolled specimen and dorsal view of pygidium, ×5. **5-7.** *Dechenella valentini* Stumm, 1953b. Rogers City Limestone, Cazenovian (latest Eifelian), shore of Lake Huron, 0.5 mi. north of Rockport, Alpena County, Michigan, UMMP 29776, paratype, dorsal, posterior, and lateral views of pygidium, all ×4.5 except 5, ×5. **8, 10-12.** *Dechenella haldemani* (Hall, 1861). Stony Hollow Member, basal Marcellus Formation, Cazenovian (latest Eifelian), "*Agoniatite*" limestone/"*Proetus*" *haldemani* beds, New York State, SDSNH 850, dorsal view of cranidium and anterior thoracic segments, lateral view of pygidium, anterior view of entire enrolled specimen, and dorsal view of pygidium, ×3.75. **9.** Horizon same as 8, 10–12. Locality Herkimer

ed more sharply anterior of S3, lateral margins converging more sharply between S2 and S3 than between S1 and S2; maximum glabellar bulge posterior of distal tip of S1. S0 moderately well incised. Intraoccipital lobes laterally deflected more strongly anteriorly, flattened dorsally, not deflected anteriorly beyond transverse line tangent to anteromedian portion of S0, not deflected beyond margins of posterior portion of glabella, moderately separated posteriorly from L0. Tubercle not developed on L0. L0 flexes anteriorly medially, elevated at level of posterior region of glabella. Posterior portion of glabella anterior of medial portion of L0 is transverse. Posteromedian portion of glabella in anterior and posterior view is flattened. Posterior portion of eye adjacent to lateral portion of L0 anterior of intraoccipital lobes, extends to point opposite distal tips of S2. Palpebral lobes broadest at point less than 50% length (exsag.) of eye. Posterior portion of palpebral ridge anterior of point where it deflects sharply posteriorly is opposite point about one-third of way between anterior end of S1 and anterior portion of intraoccipital furrow. Fixigenae in course from lateral margins of glabella at S3 to anterior border flat. Eye sits on pedestal of free cheek, which is narrow, flat space.

Thorax with 10 segments. Dorsal surface of thoracic segments flattened. Axis 45% width of thorax. Fulcrum-Fortsatz developed at approximately 35% width (tr.) of pleura.

Pygidial length 60% width; pleural furrows moderately incised; interpleural furrows very weakly incised; apodemes on lateral fields of axis present and faint; axis of even dorsoventral height, rings flex posteriorly medially, laterally roughly straight; 15 axial rings; 10 pleural segments. Border prominently developed as rounded lip, convex dorsally, longer posteriorly than width anterolaterally, reaches point of constant and greatest width opposite sixth pleural segment; pleura flattened, slightly curving ventrally laterally, anterior margin of pleura convex; transitions between pleural band and pleural furrow gradual. Axis with rounded terminus, in sagittal section flattened, lateral margins diverging at 15°; anterior edge of axis equal to width (tr.) of pleural field.

DISCUSSION: This species cannot be localized with absolute certainty. However, it may come from either the Ramparts or Beavertail Limestone, at the Ramparts of the Mackenzie River in northern British Columbia, Canada. If this is correct, that would put this species in the Frasnian, using Uyeno's (1991) stratigraphic correlations. The holotype of this species was designated using the only known specimen, a complete, enrolled cuticular specimen.

This species appears to be closely related to those that Ormiston (1967, 1976) refers to as *Dechenella* (*Pedinodechenella*) Ormiston, 1967. In particular, *P. modelli* has the diagnostic traits of this genus, including the flattened pygidial pleural segments, low pygidial axis, S1 developed as two intersecting lines, glabella tapering anterior of S1, intraoccipital lobes not bulging laterally beyond the lateral margins of the glabella, and the flattened posterior portion of the glabella. This subgeneric category is elevated to generic status in this analysis. This genus is separated from *Dechenella* by the absence of the derived state for seven characters, and thus there does appear to be a prominent morphological split between these two genera. According to the bootstrap analysis conducted, the node of the cladogram defining the dichotomous branching of *Pedinodechenella* and *Dechenella* is the best supported of all the nodes shown in the phylogeny in figure 33. Other species in this genus were not evaluated in detail, but *P. modelli* and *P. holoccipitis* Ormiston, 1976, share the condition of the anterior portion of the intraoccipital lobe lying behind a transverse line tangent to the anteromedian portion of S0.

DECHENELLA KAYSER, 1880

For diagnosis and discussion of taxa to be excluded from this genus, see the section on the phylogeny of the Proetinae.

←

County, New York, YPM 33838, dorsal view of cranidium, ×3.75. **13.** Horizon same as 8, 10–12. Locality western New York, AMNH 5504, lectotype, dorsal view of pygidium, ×4.

Dechenella valentini Stumm, 1953b
Figure 34.5–34.7

Dechenella (*Dechenella*) *valentini* Stumm, 1953b: 19–20, pl. 3, figs. 1, 2.

DIAGNOSIS: Posterior portion of glabella smoothly arches anteriorly; anterior cephalic border developed as raised broad ledge, convex; S3 roughly transverse, inclined at 10° angle to transverse line; length (exsag.) between anteromedian portion of eye and anterior border furrow equal to orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1; pygidial pleurae in cross section flattened; dorsal surface of pygidial border inclined at angle of pleurae; interpleural furrows faint; 17 pygidial axial rings.

MATERIAL: UMMP 29776.

DISCUSSION: This species is known from the Rogers City Limestone (treated as latest Eifelian) at the US Steel quarry at Rogers City, Presque Isle County, and along the shore of Lake Huron, ½ mi. north of Rockport, Alpena County, MI. It is thus associated with the initial transgressive pulse of transgressive–regressive cycle Id that initiated the Hamilton Group. The range of this species is roughly coeval with some of the taxa found in the regionally correlatable units named after their dominant constituent species in the lower Marcellus Formation of the Appalachian Basin. Species such as the proetid *D. haldemani* (Hall, 1861) and certain agoniatite ammonoids briefly appear in the record and then vanish, apparently unable to establish long-lived populations (Anderson et al., 1988; Griffing and ver Straeten, 1991). It appears that two closely related proetid species, *D. valentini* and *D. haldemani*, appear in the record at about the same time but in different tectonic basins and they both persist in the record for a geological instant. This indicates that there may have been two closely related source populations persisting in environments that generally were not sampled that invaded two separate regions, perhaps facilitated by transgression. It may also imply that a single widespread species that was typically unsampled entered ENA and underwent rapid differentiation in the two separate tectonic basins.

Dechenella haldemani (Hall, 1861)
Figure 34.8–34.13

Proetus haldemani Hall, 1861: 74; Hall, 1862: 102; Hall, 1876: pl. 21, figs. 7, 9; Hall and Clarke, 1888: 113–116, pl. 21, figs. 7, 9, pl. 23, figs. 13–15; Shimer and Shrock, 1944: 653, pl. 274, fig. 6; Howell, 1951: 272, pl. 5, figs. 4, 5; Anderson et al., 1988: 123; Griffing and Ver Straeten, 1991: 211.

DIAGNOSIS: Anterior cephalic border raised broad ledge, convex; anterior portion of intraoccipital lobe straight behind transverse line tangent to anteromedian portion of S0; sides of glabella immediately anterior of S4 parallel; lateral margins of glabella between S1 and S2 converging more sharply than during their course between S2 and S3; length (exsag.) between anteromedian portion of eye and anterior border furrow equal to 1.5 times orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1; 17 pygidial axial rings; dorsal surface of pygidial border inclined at angle of pleura; posterior portion of pygidial border short, equal to length of first axial ring; anterior portion of axial rings straight medially before flexing posteriorly.

TYPES: Hall's (1876) and Hall and Clarke's (1888: pl. 21, fig. 9) pygidium, AMNH 5504, is designated the lectotype of the species. AMNH 39339a and b, pl. 21, figures 7 and 8, become the paralectotypes.

MATERIAL: AMNH 5504, 39339a, b; SDSNH 850; YPM 33838–33840.

DISCUSSION: This species is known from the Chestnut Street Beds found in the Stony Hollow and Union Springs Members of the basal Marcellus Formation (latest Eifelian) in a belt of outcrops across New York State at several localities including Herkimer County; Judd's Falls between Cherry Valley and Sharon Springs, Otsego County; Manlius, Onondaga County; and others that are listed in Griffing and ver Straeten (1991). Hall and Clarke (1888) also reported that this species is known from the southwestern part of Pennsylvania. It also might eventually be recovered from the south-central part of the state where *Agoniatites* beds have been found in what appears to be the basal Marcellus (author and C. ver Straeten, personal obs.), and in New York State these overly the "Proetid" or Chestnut Street Beds in which *D. haldemani* is typically found (Griffing and Ver Straeten, 1991).

This species, like *D. valentini*, occurs in strata that are associated with transgressive–regressive cycle Id, possibly during a brief period of regression after the initial transgressive pulse of the cycle. This cycle and the facies that *D. haldemani* appears associated with can be related to the reactivation of the Acadian Orogeny at the end of the Eifelian and the start of the Givetian (Anderson et al., 1988; Griffing and ver Straeten, 1991). Its occurrence in the Appalachian Basin appears to be short-lived even though it is found over a broad geographic range.

Although this species has traditionally been assigned to the genus *Proetus*, first by Hall and then by almost all subsequent authors, it has all of the characterstics typical of the genus *Dechenella*. In addition, Hall assigned almost every member of the order Proetida to the genus *Proetus*, and thus effaced the phylogenetic meaning of this appellation.

Dechenella alpenensis
Stumm, 1953a
Figure 35.1–35.4

Dechenella (*Dechenella*) *alpenensis* Stumm, 1953a: 116–117, pl. 2, figs. 1–15; Stumm, 1967: 116, pl. 2, figs. 1, 2.
Dechenella alpenensis Stumm. Ludvigsen, 1979: 84; Chlupac, 1992: 142.
Dechenella (*Dechenella*) sp. A Stumm, 1953a: 117, pl. 5, figs. 1, 2.

DIAGNOSIS: Sides of glabella anterior of S1 parallel for short distance; anterior cephalic border flattened; anterior border long, equal to 1.5 times length (exsag.) between distal tips of S1 and S2; posterior portion of S1 does not contact S0; S2 rounded curve, convex anteriorly; S3 roughly transverse, inclined at 10° angle to transverse line; intraoccipital lobes most expanded medially; 17 pygidial axial rings; pygidial interpleural furrows absent; posterior portion of pygidial border equal to length of first two axial rings.

MATERIAL: UMMP 51982, 54155; USNM 117867, 117870, 117873, 123569.

DISCUSSION: This species is known from the Bell Shale, Rogers City, Presque Isle County, and Rockport, Alpena County, MI; the Ferron Point Formation, Rockport, Alpena County, MI; the Genshaw Formation, Alpena, Presque Isle, and Cheboygan Counties, MI; the Arkona Shale, Thedford–Arkona region, southwestern Ontario, Canada, all lower Cazenovian, latest Eifelian, and early Givetian; the Potter Farm Formation, Alpena County, MI, upper Givetian (Taghanic). Thus, it is associated with transgressive–regressive cycles Id (the basal transgressive pulse), Ie (the basal transgressive pulse), and IIa. It is the only species of the genus *Dechenella* occurring in ENA in the latest Eifelian that is not restricted to the lowermost portion of that stage.

Stumm (1953a) commented that this species was similar to *Dechenella verneuili* (Barrande, 1852) from the lower Givetian of Germany. However, it appears that whatever similarities these species share are the result of primitive retentions or convergences, and they differ in the condition of several characters. Ormiston's (1967) suggestion that *D. alpenensis* might be a synonym of *D. verneuili* must be rejected on the grounds that type material of each of these species differs in the condition of the following characters: 3, 4, 7, 8, 9, 13, 16, 17, 27, 29, 31, 32, 39, 42, 44, 47, and 48. Stumm (1953b) also suggested that *D. alpenensis* was closely related to *D. valentini* Stumm, 1953b. The phylogeny in figure 33 corroborates his statement. It appears that there is a small clade of three closely related ENA species of *Dechenella*. These are uniquely grouped by several characters, including the possession of 17 pygidial axial rings and 11 pygidial pleural segments, the similar anterior arching of the posteromedial portion of the glabella, and the roughly transverse development of S3. All but one of these species, *D. alpenensis*, appear to have either moved elsewhere or gone extinct. Only *D. alpenensis* established a successful population in ENA or continued to be successful at recolonizing ENA from an outside source.

Stumm (1953a) assigned two specimens, an incomplete cephalon and pygidium, to *Dechenella* sp. A, and he concluded that they are closely related to *D. alpenensis*. No differences could be discerned between these specimens and those typical of *D. alpenensis*, and they are treated as conspecific. This implied that after a long hiatus occupying part

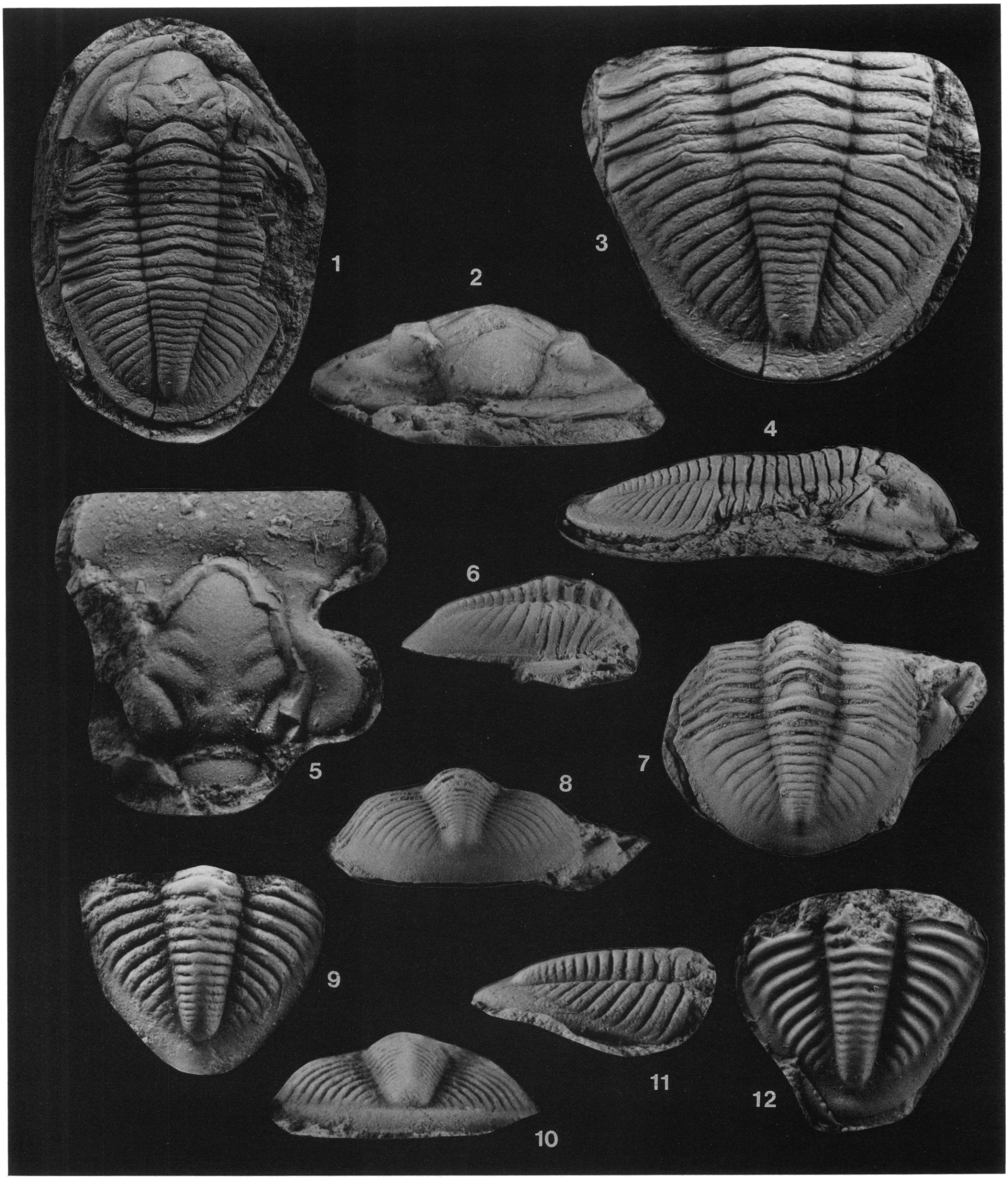

Fig. 35. *Dechenella* spp. **1-4.** *Dechenella alpenensis* Stumm, 1953a. Ferron Point Formation, Cazenovian (Givetian), Ocqueoc Falls, Presque Isle County, Michigan, USNM 123569, dorsal view of entire specimen, anterior view of cephalon, dorsal view of pygidium and thorax, and lateral view of entire specimen, all ×2 except 2, 3, ×3. **5-8.** *Dechenella welleri* (Stauffer, 1909). Columbus Limestone, Southwoodian (Eifelian), south of Venice, Ohio, OSU 16976, holotype, dorsal view of cranidium, lateral view of pygidium and partial thorax, dorsal view of pygidium and partial thorax, and posterior view of pygidium, all ×2.75 except 5, ×5. **9-12.** *Dechenella verneuili* (Barrande, 1852). **9-11.** Eifel Limestone, Eifelian, between Pelm and Gerolstein, Eifel, Germany, YPM 33852, dorsal, posterior, and lateral views of pygidium, ×6. **12.** Horizon and locality same as 9–11. YPM 33854, dorsal view of pygidium, ×3.5.

of the Cazenovian and all of the Tioughniogan, *D. alpenensis* returned to ENA after a sojurn elsewhere. Ironically, the only species of Proetinae with a temporal distribution reminiscent of this species is similarly named. *Crassiproetus alpenensis* Stumm, 1953a, is known to occur in strata assigned to transgressive–regressive cycles Ie and IIa.

Dechenella perscheii, new species

DISCUSSION: A diagnosis, a synonymy list, and a description of this species are presented in the section on the higher-level phylogeny of the Proetinae. Ormiston (1967) suggested that *D. spaekassensis* was closely related to *D. haldemani*. The pygidia of *D. spaekassensis* shares with *D. haldemani* a similar form of the border and they both have the same number of axial rings. However, the exact phylogenetic affinities of *D. spaekassensis* were not considered. On the other hand, *Dechenella perscheii* is part of a large clade including *D. haldemani* and several other Arctic and ENA species, and the similarities these species share are primitive characters.

Dechenella welleri
(Stauffer, 1909)
Figure 35.5–35.8

Proetus welleri Stauffer, 1909: 195–196.
Proetus planimarginatus Meek. Bassett, 1935: 454, pl. 39, figs. 5–7.
Dechenella (*Dechenella*) *welleri* (Stauffer). Stumm, 1953b: 21, pl. 3, figs. 3–5.
Cyrtodechenella welleri (Stauffer). Stumm, 1964: 5-6, pl. 1, figs. 14, 15, pl. 2, fig. 10.

DIAGNOSIS: Anterior portion of intraoccipital lobe straight behind transverse line tangent to anteromedian portion of S0; lateral margins of glabella converging at same angle between S1 and S2 and S2 and S3; posterior portion of glabella transverse; facial suture meets on dorsal portion of anteromedian edge of eye for portion circumscribing anteromedian part of eye, then running sagittally and forming an obtuse angle; pygidial border reaches point of constant thickness opposite pleural segment four, poorly developed and flattened dorsally, long flat region equal to length of first two axial rings; pleural segments flat.

MATERIAL: OSU 16976; UMMP 47194, 47205.

DISCUSSION: This species is known from the Columbus Limestone (Eifelian), Venice, Erie County, OH, and in the Jeffersonville Limestone, middle red clay layer (probably middle Eifelian), at the Falls of the Ohio, Jeffersonville, Clarke County, IN. Thus, it is a widespread species, although undoubtedly very rare, and it occurs in the Michigan and Illinois Basins during a roughly coeval interval for the limits of resolution available with the data base for this species. Its distribution is related to transgressive–regressive cycle Ic. Stumm (1953b) suggested that this species is closely related to *D. planimarginata* (Meek), particularly on the basis of its long anterior cephalic border. He is correct in recognizing their close relationship. They share the following synapomorphous characters: the dorsal surface of the pygidial border is inclined at the same angle as the pleurae; facial suture meets on dorsal portion of anteromedian edge of eye for a portion circumscribing the anteromedian part of the eye, then running sagittally, and forming an obtuse angle; and the posterior portion of S1 contacts S0. However, *D. bathurstensis* Ormiston, 1967, appears to be more closely related to *D. planimarginata* than *D. welleri*. Bassett (1935) suggested that *D. welleri* was conspecific with *D. planimarginata* (Meek). However, they do differ in several characters, including the number of the pygidial axial rings (14 as opposed to 16) and in the degree of the anterior flexure of the intraoccipital lobes.

Stumm (1964: 5, pl. 1, figs. 13–15, pl. 2, fig. 10) assigned a few specimens to what he called *Cyrtodechenella welleri* and claimed these were conspecific with *D. welleri*. However, one of these specimens seems to differ significantly from Stauffer's (1909) original *D. welleri* in the condition of several characters. In particular, the anterior portion of the anterior cephalic border is deflected ventrally, with lineations visible dorsally. These are not concentric but are irregular and spaced relatively far apart in the glabella that Stumm (1964) assigned to *C. welleri*, and this character is typical of some species that have been assigned to the Cyrtosymbolinae Hupe, 1953. *Cyrtodechenella welleri* also shares other features of the glabella characteristic of many of the species assigned to the Cyrtosymbolinae such as the prominently converging lateral margins of the glabella anterior of the maximum glabellar bulge and S0 being very short (sag.). Therefore, this specimen certainly belongs to a new species, is not conspecific with *D. welleri*, and probably belongs to an entirely different taxonomic category at the subfamilial level. By contrast, *Dechenella welleri* (Stauffer) has all the characteristics typical of the Proetinae and diagnostic of the genus *Dechenella*. In addition, the pygidia that Stumm (1964) figured appear to be nearly identical with that of the holotype. They have the same number of axial rings, an identical structure of the axial ring, and a pygidial border of the same shape and conformation.

As mentioned above, the subfamily Cyrtosymbolinae is certainly polyphyletic and is not treated in detail here. As this group and the species within it are probably not at all related to the members of the Proetinae considered herein, their phylogenetic affinities do not have an important bearing on this study. However, a brief comment on the specimen figured by Stumm (1964) is worthwhile. This species is provisionally treated as *Cyrtodechenella*, new species (without character analysis) as it appears to be quite similar to several species from the Givetian of the Eifel district of Germany that Richter and Richter (1950) figure and assign to the genus *Cyrtodechenella*. Thus, as recognized with *Basidechenella* and *Dechenella*, there appears to be another genus of proetid trilobites that has closely related species occupying both the Old World–Rhenish faunal realm (treated as Armorica) and ENA, implying a significant interchange of taxa between these two regions during the Eifelian and Givetian.

Dechenella bathurstensis
Ormiston, 1967

Dechenella (*Dechenella*) *bathurstensis* Ormsiton, 1967: pl. 7, figs. 11–18, pl. 8, figs. 1–4.

Diagnosis: Facial suture at lateralmost portion of eye not displaced as far laterally as on anterior border; maximum glabellar bulge opposite distal tip of S1; anterior portion of intraoccipital furrow laterally deflected more strongly laterally; intraoccipital lobes most expanded laterally posteriorly; 21 pygidial axial rings; pygidial border reaches point of constant and greatest width opposite pleural segment three; border with relatively transverse course posteriorly.

Material: GSC 18146–18150, 18152, 18153.

Discussion: This species is known from the Bird Fiord Formation (Givetian), Bathurst Island. Ormiston (1967) commented that it closely resembled *D. setosa* Whidborne, 1888, from the late Eifelian/early Givetian of England. These two species do share several characters, but according to the phylogeny in figure 33 these are primitive retentions. They differ in the condition of several characters, including 3, 5, 9, 10, 11, 16, 17, 18, 22, 26, 31, 41, 43, 45, 47, and 48.

Dechenella planimarginata
(Meek, 1871)

Proetus planimarginatus Meek, 1871: 89; Meek, 1873: 233, pl. 23, fig. 3a, b; Bassett, 1935: 453–454, pl. 39, figs. 1–4, 8.

?*Proetus planimarginatus* Meek. Hall and Clarke, 1888: 112–113, pl. 23, fig. 12.

Dechenella (*Dechenella*) *planimarginata* (Meek). Stumm, 1953b: 20–21, pl. 3, figs. 8–13; Ormiston, 1967: 91.

Dechenella planimarginata (Meek). Ludvigsen, 1979: 84, fig. 57c.

Proetus delphinulus Hall and Clarke, 1888: 111–112, pl. 23, figs. 1, 2; pl. 25, fig. 6.

Dechenella (*Dechenella*) *delphinula* (Hall and Clarke). Stumm, 1953b: 21–22, pl. 3, fig. 6.

Dechenella delphinula (Hall and Clarke). Ludvigsen, 1979: 84.

Diagnosis: Anterior portion of intraoccipital lobe flexes anteriorly beyond anterior portion of S0; space between anteromedian portion of eye and anterior border furrow equal to twice orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1; anterior cephalic border concave dorsally; facial suture anterior of anterior border furrow proceeds anteriorly for short distance anterior of furrow, then deflects sharply medially; anterior margin of pygidial pleurae in dorsal view sinusoidally shaped; laterally pygidial axial rings in dorsal view flex anteriorly before flexing posteriorly; 16 axial rings; border reaches point of constant width opposite pleural segment five.

Material: NYSM 4720.

DISCUSSION: This species is known from the lower Onondaga Limestone (lower Eifelian), Port Colborne and North Cayuga, Welland County, Ontario; the Dundee Limestone (upper Eifelian), at Whitehouse and Silica, Lucas County, OH, and Sibley, Wayne County, MI. Thus it is associated with transgressive–regressive cycle Ic and is restricted to the Michigan Basin.

Stumm (1953b) recognized two distinct species of *Dechenella* from the Eifelian of the Michigan Basin, *D. delphinula* (pl. 3, fig. 6) and *D. planimarginata* (pl. 3, figs. 8–12). However, there do not appear to be any valid criteria for discriminating between these two species. Instead, they are taken to be a single species, and the name *planimarginata* is retained on the basis of priority. Stumm (1953b) was correct in recognizing that his *Dechenella delphinula* and Hall and Clarke's (1888) *Proetus delphinulus* were identical.

Ormiston (1967) suggested that *D. planimarginata* was identical to *D. gigouti* Richter and Richter, 1950, from the Givetian of Morocco, and he regarded the latter as a junior subjective synonym. The chief feature that these two taxa share is the relatively long anterior border. These taxa appear to be only distantly related and differ in the condition of several characters, including 3, 4, 5, 8, 11, 12, 16, 17, 20, 21, 23, 26, 29, 30, 32, 33, 34, 35, 36, 43, 44, and 47.

Dechenella carvalhoae, new species

Dechenella (*Dechenella*) cf. *verneuili* (Barrande, 1852). Kielan, 1954: 17, pl. 3, figs. 8, 9.

TYPES: Holotype specimen shown on pl. 3, figure 9a, b, Kielan (1954) from the Givetian (possibly upper Givetian) of Grzegorzowice-Skaly in the Ste-Croix Mountains of Poland. Repository Museum Ziemi, Warsaw, Poland.

ETYMOLOGY: This species is named for Maria da Gloria Pires de Carvalho of the Universidade Federal Rio de Janeiro who has done important work on the Devonian trilobites of the Malvinokaffric Faunal Realm.

DIAGNOSIS: Anterior portion of intraoccipital lobe flexes anteriorly beyond anterior portion of S0; posterior portion of glabella anterior of medial portion of L0 smoothly arches anteriorly; S3 roughly convex anteriorly; sides of glabella anterior of S3 parallel for short distance; glabellar bulges proximal to eyes prominent; facial suture meets on dorsal portion of anteromedian edge of eye and forms acute angle; anterior border furrow narrow; dorsal surface of pygidial border inclined at angle of pleurae; pygidial border flattened dorsally; anterior portion of axial rings straight medially and laterally.

DESCRIPTION: Cephalic length (sag.) 150% maximum glabellar width, anterior border developed as long, flattened ledge (1.5 times length of L0 medially); anterior border furrow deep and narrow; longitudinal lineations on anterior border of cephalon closely packed and linear. Prosopon of very fine granules. Anterior edge of glabella does not contact anterior border furrow such that preglabellar field is developed. Anterior portion of glabella conical. Facial sutures moderately divergent anteriorly at approximately 40° angle from sagittal line drawn from inner edge of eye, meet on anteromedian edge of eye forming an acute angle, displaced as far laterally at lateral edge of eye as at maximum lateral deflection on anterior border. Lateral margins of glabella opposite S4 parallel, and between S3 and S4 parallel. Space between anteromedian portion of eye and anterior border furrow equal to orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1. Glabellar furrows faintly impressed. S2 rounded curve directed posteromedially, deflected about 45° from exsagittal line from inner edge of eye; S1 rounded arc, posterior tips follow straight course, does not contact S0; S1 and S2 laterally contact axial furrows; length (exsag.) between distal tips of S1 and S2 twice that between distal tips of S2 and S3. Median glabellar furrow directed anteromedially. Maximum length and width of glabella equal. Glabella constricted more sharply anterior of S4; lateral margins of glabella converging at same angle between S1 and S2 as between S2 and S3; maximum glabellar bulge posterior of distal tip of S1. S0 well incised. Anterior margins of intraoccipital lobes follow constant line from S0 to axial furrow, expanded dorsally, flex more strongly anteriorly laterally, deflected anteriorly beyond transverse line tangent to anteromedian portion of S0, separated posteriorly from L0, deflect strongly beyond lateral margins of glabella. Tubercle not developed on L0. L0 flexes anteriorly medially. L0 elevated to level of posterior region of glabella. Posterior portion of glabella anterior of medial portion of L0 flexes anteriorly medially. Posterior portion of eye adjacent to lateral portion of L0 anterior of intraoccipital lobes, extends to point between distal tips of S2 and S3. Posterior portion of palpebral ridge anterior of point where it deflects sharply posteriorly opposite anterior portion of intraoccipital furrow. Fixigena flat in course from lateral margins of glabella at S3 to anterior border. Eye sits on pedestal of free cheek that is narrow flat space.

Pygidial length 80% width; pleural furrows prominently incised, interpleural furrows faint; apodemes faint; axis of even height; axial rings flex anteriorly medially, laterally flex anteriorly; at least 17 rings present, and at least 11 pleural segments. Pygidial border prominently developed as flattened shelf, wide, posteriorly wider than anterolaterally, reaches point of constant and greatest length opposite sixth pleural segment; posterior portion of border in dorsal aspect appears rounded; dorsal surface of pleurae gently rounded, slightly curving ventrally laterally; anterior margin of pleurae sinusoidal; transitions between pleurae and pleural furrows relatively abrupt. Axis with rounded terminus, flattened in sagittal section; anterior edge of axis as wide (tr.) as pleural field; lateral margins of axis diverging from posterior to anterior at 10° angle.

DISCUSSION: This species is known from the Givetian (possibly upper Givetian) of Grzegorzowice-Skaly in the Ste-Croix Mountains of Poland. The specimen designated the holotype was the most morphologically complete and best preserved of Kielan's (1954) figured material. When contacted, the repository of this material, the Museum Ziemi in Warsaw, would not allow the loan of specimens. Therefore the description given above is based on photographs.

Kielan (1954) concluded that this species was closely related to *Dechenella verneuili*; however, she listed several differences between the two species. In addition to these, the species differ in the condition of characters 7, 17, 18, 31, 32, 36, 41, 42, 44, and 48. The species *D. carvalhoe* appears to be most closely related to *D. polonica* Gurich, 1896. These species are united by the condition of characters 29 and 36. However, these characters do display some homoplasy, and are found in several other taxa, including *D. planimarginata*.

Dechenella polonica Gurich, 1896

Dechenella polonica Gurich, 1896: 371, pl. 15, fig. 2a, b; Sobolew, 1904: 100–107, pl. 7, fig. 27; Sobolew, 1909: 392, 527; Chlupac, 1992: 142.
Dechenella (aff. *Eudechenella*) *polonica* Gurich. Richter, 1912: 316–319, pl. 21, figs. 6–8.
Dechenella (aff. *Dechenella*) *polonica* Gurich. Richter and Richter, 1950: 178.
Dechenella (*Dechenella*) *polonica* Gurich. Kielan, 1954: 17–18, pl. 2, fig. 1–5.

DIAGNOSIS: Anterior portion of intraoccipital lobe behind transverse line tangent to anteromedian portion of S0; posterior portion of glabella anterior of medial portion of L0 smoothly arches anteriorly; sides of glabella converging anterior of S3; facial suture on dorsal portion of anteromedian edge of eye forming an acute angle, proceeds for long distance anterior to anterior border furrow, slightly rounded, and weakly diverging medially, then deflects more strongly medially; posterior portion of S1 does not contact S0; prosopon of small granules; lateral margins of glabella converging more sharply between S1 and S2 than between S2 and S3; intraoccipital lobes most expanded laterally anteriorly; pygidial border reaches point of constant width opposite pleural segment seven, developed as rounded lip posteriorly, convex up dorsally; pygidial axial rings straight abaxially.

DISCUSSION: This species is known from the Givetian (probably the middle and upper Givetian) of Grzegorzowice-Skaly in the Ste-Croix Mountains of Poland. Kielan (1954) presents a table giving differences between this species and *D. verneuili*. The chief areas of departure between these two species are as follows: the greater anterior flexure of the anterior portion of the intraoccipital lobe in *D. verneuili*; the more strongly converging lateral margins of the glabella anterior of S3 in *D. polonica*; the anterior cephalic border developed as a raised broad ledge in *D. verneuili* as opposed to a flattened ledge; the dorsal surface of the pygidial border is inclined at the angle of the pleurae in *D. verneuili* but it is flattened in *D. polonica*; and the maximum glabellar bulge is farther forward in *D. verneuili*. The species *D. polonica* appears to be most closely related to *D. carvalhoae*, but the character evidence for this relationship is not very robust.

Dechenella verneuili (Barrande, 1852)

Figure 35.9–35.12

Phillipsia verneuili Barrande, 1852: 478.

Dechenella verneuili (Barrande). Kayser, 1880: 705–706, pl. 37, figs. 1–5; Richter, 1909: 23, 34; Howell, 1951: 295. Chlupac, 1992: 142.

Dechenella (*Eudechenella*) *verneuili* (Barrande). Richter, 1912: 289, pl. 19, figs. 1–13.

Dechenella (*Dechenella*) *verneuili* (Barrande). Richter and Richter, 1950: 153–154, pl. 1, figs. 1, 2, pl. 3, fig. 27; Kielan, 1954: 16–17, pl. 3, figs. 6, 7; Richter and Struve, 1959, O388, fig. 297, 1; Selwood, 1965: 323, 332; Ormiston, 1967: 19, 84–85, 104.

DIAGNOSIS: Anterior portion of intraoccipital lobe flexes anteriorly beyond anterior portion of S0; posterior portion of glabella anterior of medial portion of L0 smoothly arches anteriorly; facial suture on dorsal portion of anteromedian edge of eye forms an acute angle; length (exsag.) between distal tips of S1 and S2 twice length between distal tips of S2 and S3; anteromedian portion of eye opposite point between distal tips of S2 and S3; lateral margins of glabella converging more sharply between S1 and S2 than during their course between S2 and S3; S2 straight; space between facial suture along anteromedian portion of eye and glabellar furrow small, not displaced past exsagittal tangent to maximum lateral glabellar bulge; lateral margins of glabella at S4 converging; intraoccipital lobes most expanded medially; anterior portion of S0 anterior of intraoccipital lobe distally deflected more strongly laterally; pygidial pleurae rounded in cross section; border rounded lip posteriorly, convex up dorsally; anterior portion of axial rings straight medially.

MATERIAL: SDSNH 10562; YPM 33850–33852, 33854.

DISCUSSION: This species is the type of the genus *Dechenella*. It is known from the Givetian of Grzegorzowice-Skaly in the Ste-Croix Mountains of Poland and from the Fleringer Schichten, lower Givetian from the Eifel district, possibly between Pelm and Gerolstein, Germany.

Dechenella osborni Ormiston, 1967

Dechenella (*Dechenella*) *osborni* Ormiston, 1967: 76–78, pl. 8, figs. 12–18.

DIAGNOSIS: S3 roughly convex anteriorly; facial suture circumscribes anteromedian part of eye, then parallels sagittal line forming an obtuse angle; posterior portion of S1 contacts S0; anterior border furrow faint, diffuse, marked by gradual change in slope between fixigenae and preglabellar field and anterior cephalic border; median glabellar furrows medially directed posteriorly; anteromedian portion of eye opposite distal tip of S2; pygidial interpleural furrows absent; anterior portion of pygidial axial rings straight medially; border rounded lip, convex up dorsally, reaches point of constant and greatest thickness opposite pleural segment three; 16 pygidial axial rings.

MATERIAL: GSC 18158–18160.

DISCUSSION: This species is known from the middle of the Bird Fiord Formation (middle Eifelian), Twilight Creek, Bathurst Island. Ormiston (1967) suggested that it was closely related to *D. bathurstensis*, with that species probably derived from *D. osborni*. The characters shared by these taxa appear to be either due to primitive retention or convergence as these taxa are separated by several nodes on the cladogram shown in figure 33. *Dechenella osborni* does appear to be closely related to *D. algida*, which is discussed below.

Dechenella algida Ormiston, 1967

Dechenella (*Dechenella*) *algida* Ormiston, 1967: 74–76, pl. 8, figs. 5–11.

DIAGNOSIS: Posterior portion of glabella anterior of medial portion of L0 flexes anteriorly laterally, posteriorly medially; sides of glabella parallel for short distance anterior of S4; facial suture meets on dorsal portion of anteromedian edge of eye and forms an acute angle; anteromedian portion of eye opposite point between distal tips of S2 and S3; anterior border furrow narrow; S3 inclined posteriorly medially; anterior portion of intraoccipital furrow follows constant line from S0 to axial furrow; pygidial pleurae rounded in cross section; posterior portion of pygidial border short, equal to length of first pygidial axial ring; pygidial border reaches point of constant and greatest width opposite pleural segment three, border flattened dorsally; pygidial interpleural furrows absent.

MATERIAL: GSC 18154, 18155, 18157.

DISCUSSION: This species is known from the upper Bird Fiord Formation (upper Eifelian), Twilight Creek, Bathurst Island. Ormiston (1967) remarked that this species is quite dissimilar from *D. bathurstensis*, which is true; however, he commented that *D. bathurstensis* was closely related to *D. osborni*. The phylogeny in figure 33 suggests that this is not the case. Instead, *D. algida* is closely related to *D. osborni*. The clade formed by these two species is defined by the following characters: the lateral margins of the pygidial axial rings expand medially (when viewed dorsally) back to a ring (rounding down to the nearest even number) that is half the value of the total number of rings; the intraoccipital lobes are deflected laterally beyond the margins of the glabella; the sides of the glabella opposite S4 are parallel; the posterior portion of the pygidial border is short, equal to the length of first pygidial axial ring; and the posterior portion of the glabella anterior of the medial portion of L0 flexes anteriorly laterally, posteriorly medially. All but two of these characters happen to be reversals to the primitive state, indicating that there is a fair amount of homoplasy concentrated at this node.

Dechenella struvei
Richter and Richter, 1950

Dechenella (*Dechenella*) *struvei* Richter and Richter, 1950: 154–158, pl. 1, figs. 3–10; Ormiston, 1967: 98–99.

DIAGNOSIS: Pygidial border flattened dorsally; 18 pygidial axial rings; S1 in dorsal view dog-legged kink of two straight lines; sides of glabella anterior of S3 converging; interpleural furrows faint; posterior portion of S1 contacts S0; lateral margins of glabella between S1 and S2 converging at same angle as between S2 and S3; laterally axial rings in dorsal view appear straight; pleurae rounded in cross section; anterior border short, equal to length (exsag.) between distal tips of S1 and S2.

DISCUSSION: This species is known from the Bellerophon Limestone (middle Givetian) of the Eifel District, Germany. It appears to be most closely related to *Dechenella maclareni* Ormiston, 1967, from the Eifelian of the Canadian Arctic. These two taxa are united by the possession of the following characters: pygidial border flattened dorsally; sides of glabella anterior of S3 converging; interpleural furrows faint; anterior border short; facial suture at most lateral point of eye displaced farther laterally than on anterior border; and the lateral margins of the pygidial axial rings expand medially back to a ring number that is farther than halfway back. Three of these characters appear to be reversals to the primitive state, again indicating some homoplasy is concentrated in this portion of the tree.

Ormiston (1967) figured two cranidia that he called *Dechenella* aff. *struvei* from the Melville Island Formation (possibly Givetian), Ibbet Bay, Melville Island. He claimed that this species was very closely related, though not conspecific, to *D. struvei* of Germany. These taxa do share several similarities, including the following: S1 developed as a dog-legged kink of two straight lines, intersecting S0; glabella not contacting anterior border furrow; anterior cephalic border raised ledge, short, convex up; glabella converging anterior of S3; and facial sutures deflected farther laterally at lateral margin of the eyes than on anterior border. However, the taxa do differ in the condition of several characters. In particular, S3 is straight in *D.* aff. *struvei* and it is convex anteriorly in *D. struvei*, the anterior edge of the eye reaches a point between the distal tips of S2 and S3 in *D. struvei* but it reaches S3 in *D.* aff. *struvei*, the glabellar bulges are pointed in *D.* aff. *struvei* but they are rounded in *D. struvei*, and the anterior portion of the intraoccipital lobe flexes anteriorly beyond a transverse line tangent to the anteriormost portion of S0 in *D. struvei* whereas in *D.* aff. *struvei* it lies behind such a line. The exact evolutionary affinities of *D.* aff. *struvei* are not considered herein, but the species is probably closely related to *D. struvei*. Although *D.* aff. *struvei* is known from the Canadian Arctic and *D. struvei* is known from

Germany, this is not implausible as the phylogeny in figure 33 indicates that the Arctic *D. maclareni* and *D. struvei* share a sister relationship.

Dechenella maclareni
Ormiston, 1967

Dechenella (*Dechenella*) *maclareni* Ormiston, 1967: 82–85, pl. 9, fig. 17, pl. 10, figs. 1–10; Chlupac, 1992: 142.

Diagnosis: Facial suture meets on dorsal portion of anteromedian edge of eye and forms an acute angle; posterior portion of S1 does not contact S0; length (exsag.) between distal tips of S1 and S2 twice length between distal tips of S2 and S3; anterior border furrow narrow; glabellar furrows between S1 and S2 converging more sharply than during their course between S2 and S3; maximum glabellar bulge opposite medial tip of S1; S3 inclined posteriorly medially; anterior portion of furrow anterior of intraoccipital lobe laterally deflected more strongly laterally; medial portion of pygidial axial rings flex anteriorly; pygidial posterior border reaches point of constant and greatest thickness opposite pleural segment seven, 19–20 pygidial axial rings; posterior portion of pygidial border short, equal to length of first pygidial axial ring, flattened and parallel to dorsal plane, reaches point of constant and greatest width opposite pleural segment seven.

Discussion: This species is known from the Blue Fiord Formation (Givetian) at Twilight Creek, Bathurst Island. Ormiston (1967) commented that this species was closely related to *D. verneuili*. However, these taxa differ in the condition of several characters, including 3, 4, 7, 8, 10, 13, 14, 15, 17, 18, 22, 26, 27, 41, 42, and 43. Although they are not distantly related, they can be clearly differentiated. Ormiston (1967) also suggested that this species was closely related to *D. alpenensis*. This suggestion is related to Ormiston's conclusion that *D. alpenensis* and *D. verneuili* were closely related or perhaps synonymous. These taxa are not especially closely related, and differ in the condition of several characters, as discussed above. *Dechenella alpenensis* differs from *D. maclareni* in the condition of several characters, including 3, 4, 8, 9, 10, 14, 16, 18, 20, 23, 26, 29, 31, 32, 37, 39, 41, 43, 44, 47, and 48.

Dechenella setosa
Whidborne, 1889

Dechenella setosa Whidborne, 1889: 29, pl. 2, figs. 15–17; Richter, 1912: 310, pl. 20, fig. 8; Selwood, 1965: 326–333, pl. 1, figs. 1–4, 8, 12, 14, 15.

Dechenella rittbergensis Richter, 1912: pl. 20, figs. 4–7; Chlupac, 1992: 138–142, pl. 3, figs. 1–12, pl. 4, figs. 2–8, pl. 5, figs. 1, 2, 4–12.

Diagnosis: S3 roughly convex anteriorly; facial suture meets on dorsal portion of anteromedian edge of eye and forms an acute angle; anterior cephalic border flattened; length (exsag.) between distal tips of S1 and S2 twice length between distal tips of S2 and S3; prominent tubercle on L0; anteromedian portion of eye opposite distal tip of S3; maximum glabellar bulge posterior of distal tip of S1; S2 rounded curve, convex anteriorly; sides of glabella opposite S4 parallel; intraoccipital lobes deflected laterally beyond margins of glabella; laterally, pygidial axial rings in dorsal view flex anteriorly, medially flex posteriorly; 19–20 axial rings; posterior border reaches point of constant and greatest thickness opposite pleural segment nine, rounded lip, convex up dorsally, rounded and short posteriorly; interpleural furrows very faint.

Material: BMNH I.5039, IT.105; GSM 6987.

Discussion: This species is known from the black limestones, either late Eifelian or early Givetian, at the Chercombe Bridge Quarry, near Newton Abbot, Devon, England, and from the Celechovice Limestone, probably either late Eifelian or early Givetian, Celechovice, Prerov, and Grygov, Moravia, the Czech Republic. Although there is certainly controversy about the configuration of the cratonic fragments at this time, these occurrences indicate that for a species of *Dechenella* this species had a relatively broad geographic distribution.

There has been considerable confusion regarding the alpha taxonomy of *Dechenella setosa* and *D. rittbergensis* Zimmerman, 1892. It appears that specimens of *D. setosa* have at times been incorrectly assigned to *D. rittbergensis* and vice versa. The principal source of confusion probably arises because both species are very similar and are known from the same locality. This raises the possibility that these two different species may represent a single sexually dimorphic species, as Selwood (1965) suggested. This is of course possible; however, similar patterns of variation are not found in other species of *Dechenella*. In addition, this does not present a significant problem for the phylogeny of *Dechenella* adopted herein as the two species or sexual dimorphs come out as sister taxa. (This assumes of course that sexual dimorphs are not likely to be wildly disparate taxa that differ in several character states and are found in dramatically different localities, but rather those forms that are very similar and are recovered from the same localities.) Therefore, *D. setosa* and *D. rittbergensis* are treated as two separate but closely related species.

Assignment of the appropriate cephala and pygidia was made possible by information in several references. These include Selwood (1965) who designated a lectotype for *Dechenella setosa* (Selwood, 1965: pl. 1, fig. 14) and Richter and Richter (1950) who designated a lectotype for *D. rittbergensis*; Richter and Richter (1950) designated the specimen shown in Richter (1912: pl. 20, fig. 2). In addition, figures of an articulated specimen and of specimens with preserved genal angles displayed in Chlupac (1992) provided useful information. Chlupac (1992: pl. 4, fig. 1) showed a typical specimen of *D. rittbergensis* with the following states: straight S2, S3, and S4 all deflected posteriorly; intraoccipital lobes not deflected beyond the lateral margins of the posterior portion of the glabella; space between distal tips of S1 and S2 1.5 times distance between distal tips of S2 and S3; lateral margins of glabella between S1 and S2 converging at roughly same angle between S2 and S3 (not shown as well on this specimen as others in Selwood [1965]); maximum glabellar bulge opposite distal tip of S1; and sides of glabella opposite S4 converging. In addition, the lateral margin of the cephalon flexes slightly laterally, caused by a slight lateral deflection of the genal spine. In forms having characteristics typical of *D. setosa*, the genal spine does not deflect laterally from the arch of the smoothly curving outline of the anterior cephalic border.

Chlupac (1992: pl. 3, fig. 8) figured an enrolled specimen preserving a pygidium and a fraction of the cephalon with the genal spine. The genal spine does not deflect laterally, but follows the smoothly curving outline of the anterior cephalic border, indicating that the cephalon and pygidium must have belonged to *D. setosa*. The pygidium is characterized by having the following characters: 12–13 pleural segments; the posterior border well developed as a rounded lip, flattened, parallel to the dorsal plane, convex up dorsally, and reaching a point of constant and greatest width opposite pleural segment three; 19–20 axial rings; the anterior portion of the pygidial axial rings flex posteriorly medially; the axial rings expand medially at lateral margins back to ring number eight; laterally the axial rings in dorsal view flex anteriorly; the anterior margin of the pleurae in dorsal view are sinusoidally shaped; the interpleural furrows are very faint; and the pleurae are flattened in cross section.

This recovery of an associated cephalon and pygidium allowed the accurate identification and character coding for the pygidia, the cephala, and the free cheek that Selwood (1965) discussed and figured. Selwood (1965) defined four varieties of *D. setosa*, two different cephalic types and two different pygidial types. For the most part, Selwood's Groups A and C correspond to *D. setosa* and Groups B and D correspond to *D. rittbergensis*. However, for a few specimens his group classification scheme appears to be inconsistent. For instance, Selwood assigned BMNH IT.103 (Selwood, 1965: pl. 1, fig. 13) to group C (held herein to be true *D. setosa*) when it has the characteristics of *D. rittbergensis* (Selwood's [1965] group D). In addition, he assigned the pygidium BMNH I.1110a (pl. 1, fig. 8) to group B; however, the pygidium appears to have the morphological traits characteristic of *D. setosa* (Group A). The free cheek, BMNH IT.105, shown by Selwood (1965: pl. 1, fig. 15) appears to be identical to that typical of *D. setosa*, and therefore it is assigned to that species. The groupings suggested by this analysis, Group A with Group C and Group B with Group D, do not follow what Selwood (1965) predicted. He speculated that cranidium D and pygidium A belonged to the same species or form and cranidium C and pygidium B belonged to the same species or form. Note that when the character data from pygidia were switched to what are argued here to be the incorrect cephala, the phylogeny remained unchanged.

Selwood (1965) suggested that the bivariate analyses he conducted indicated the verisimilitude of what he referred to as the different groups of *Dechenella setosa*. However, it is unlikely that such tests would have significant resolving power considering the number and types of measurements that were taken. It is possible that the forms herein divided into two distinct species represent a single species. However, there does not appear to be a significant amount of intergradation between what are treated here as *D. setosa* and *D. rittbergensis* in the traits for which they differ. That is, they seem to be distinct morphological entities rather than points of a continuum. The species ontology used here follows that of Eldredge and Cracraft (1980) and Cracraft (1989) with a species being defined as the smallest diagnosably distinct cluster of organisms. Therefore, these different clusters are defined as distinct species.

Selwood (1965) also suggested that pygidium A and cranidium D showed characters typical of those found in *Dechenella verneuili*, whereas cranidium C and pygidium B showed characters typical of *D. rittbergensis*. This suggestion is not consistent with the type material of *D. setosa* and *D. rittbergensis*. In addition, all cranidia and pygidia substantially differ from those of *D. verneuili*. The phylogeny in figure 31 indicates that *D. setosa* and *D. rittbergensis* are closely related, although not sister taxa, and form a clade of three species with *D. gigouti* Richter and Richter, 1950, which is known from the Givetian of Morocco. Richter and Richter (1950) suggested that *D. setosa* and *D. gigouti* might be closely related, although Selwood (1965) disagreed with this conclusion. Selwood (1965) suggested that the possession of a granulose prosopon by *D. setosa* was a trait that served to differentiate it from *D. rittbergensis*. This trait appears to be no longer valid, as some of the specimens Selwood (1965) had assigned to *D. setosa*, which possess granulose prosopons, appear to belong to *D. rittbergensis*. The character appears to be controlled by depositional habitus.

Ormiston (1967) suggested that *D. setosa* may be closely related to *D. bathurstensis*. However, the phylogeny in figure 33 suggests that they are distantly related, with any shared characters being either symplesiomorphies or homoplasies.

Dechenella rittbergensis
Zimmermann, 1892

Dechenella rittbergensis Zimmermann, 1892: 119, pl. 1, fig. 4;
Chlupac, 1992: 138–142, pl. 1, fig. 1, pl. 2, fig. 1, pl. 3, fig. 3.
Dechenella (*Eudechenella*) *rittbergensis* Zimmermann. Richter, 1912: 307–310; pl. 20, figs. 1–3.
Dechenella (*Dechenella*) *rittbergenis* Zimmermann. Richter and Richter, 1950: 177.
Dechenella (*Eudechenella*) *setosa* Whidborne. Richter, 1912: 310–13, pl. 20, fig. 9.
Dechenella (*Dechenella*) *setosa* Whidborne. Selwood, 1965: 326–333, pl. 1, figs. 5–7, 9–11, 13.

DIAGNOSIS: S3 straight, directed posteriorly medially; anterior branch of facial forms an acute angle laterally; posterior portion of S1 contacts S0; space between distal tips of S1 and S2 1.5 times length (exsag.) between distal tips of S2 and S3; prominent tubercle on L0; lateral margins of glabella between S1 and S2 converging at same angle as between S2 and S3; maximum glabellar bulge opposite medial tip of S1; S2 straight; sides of glabella opposite S4 converging; anterior margin of pygidial pleurae sinusoidal; laterally axial rings straight, medially flexing posteriorly; 20 axial rings; border flattened, reaches point of constant and greatest width opposite pleural segment nine; posterior portion of border transverse in dorsal view and long.

MATERIAL: BMNH I.1110a, IT.104.

DISCUSSION: This species is known from the same horizons as *Dechenella setosa*. As discussed above, the existence of an articulated specimen of *D. setosa* preserving the genal angle and the pygidium allowed determination of those pygidia that should be assigned to *D. setosa*. In the Chercombe Bridge Quarry, Selwood (1965) recognized two types of cephala and two types of pygidia. As one variety of cephalon and one variety of pygidium were shown to belong to the species *Dechenella setosa*, and by recognizing that the other variety of cephalon is demonstrably *D. rittbergensis*, we can assign the other pygidium (clearly of *Dechenella* character) found associated with this cephalon both at Chercombe Bridge Quarry and in the Celichovice Limestone in Moravia to *D. rittbergensis*. This assignment suggests that the pygidium of *D. rittbergensis* is characterized by the following traits: 20 axial rings; border well developed, flattened dorsally; medial portion of axial rings straight; posteriorly, border in dorsal view appears flattened, with length equal to length of the first two axial rings, and parallel to a dorsal plane; interpleural furrows very faint; axial rings expand medially at lateral margins back to ring number eight, laterally straight; 12–13 pleural segments; and the pygidial pleurae in cross section are flattened.

Chlupac (1992) suggested that *Dechenella rittbergensis* and *D. setosa* are closely related. He was correct in recognizing the close relationship of these two taxa even though the majority of the specimens he considered to be *D. rittbergensis* were actually *D. setosa*.

Dechenella gigouti
Richter and Richter, 1950

Dechenella (*Dechenella*) *gigouti* Richter and Richter, 1950: 158–160, pl. 2, figs. 11–13; Ormiston, 1967: 91; Selwood, 1965: 332–333.

Diagnosis: S3 straight, directed posteriorly; anterior branch of facial suture forms a right angle directed laterally; anterior cephalic border flattened, very long, length equal two to three times length between distal tips of S1 and S2; posterior portion of S1 does not contact S0; median glabellar furrows medially directed posteriorly; anteromedian portion of eye opposite distal tip of S3; maximum glabellar bulge posterior of distal tip of S1; sides of glabella opposite S4 converging; fixigenae from lateral margins of glabella to anterior border evenly sloping; pygidial border developed as rounded lip, convex up dorsally, reaches point of constant and greatest width opposite pleural segment number nine; 19–20 axial rings.

Discussion: This species is known from the Givetian of Morocco. Ormiston (1967) suggested that it was closely related to *Dechenella planimarginata* (Meek); however, as mentioned above, these two taxa differ in the condition of several characters. Selwood (1965) suggested that this species was closely related to *D. setosa*. This conclusion seems to be upheld by the phylogeny in figure 33. These two species and *D. rittbergensis* comprise a clade to the exclusion of all the other species of *Dechenella* considered, which can be defined on the basis of the following characters: 19–20 pygidial axial rings; pygidial border attains point of constant and greatest width oppposite pleural segment number nine; facial suture anterior of anterior border furrow proceeds for a long distance slightly rounded and weakly diverging, then deflects more strongly medially; anterior border very long, length equal to two to three times length between distal tips of S1 and S2; and pygidial pleurae in cross section flattened. All of these characters show some homoplasy. *Dechenella gigouti* appears to be more closely related to *D. rittbergensis* than to *D. setosa* on the basis of the shared possession of the following characters: S3 straight; medial end of S1 inclined posteriorly; posterior portion of pygidial border long flat region, as long as first two pygidial axial rings; and S2 developed as a straight impression. Two of these characters are reversions to the primitive condition, implying some homoplasy is concentrated at this node of the cladogram.

PHYLOGENY OF THE "*THEBANASPIS* CLADE"

A phylogenetic analysis of the four genera in the "*Thebanaspis* clade" was conducted. Characters demonstrating that the members of this clade do not belong to the Proetinae sensu stricto are elaborated above in the section on the higher-level phylogeny of the Proetinae. Characters used to define the clade herein as follows: the length (exsag.) of the anterior portion of the pygidial pleural bands increases distally; when pairs of adjacent pleural segments are considered, the anterior pleural bands elevate distally relative to the posterior bands (treated as a special case of Owens' [1973] imbricate pygidial structure); the posterior portion of the thoracic pleural band arches strongly posteriorly distally; and the posterior portion of the eye is rotated laterally relative to a sagittal line through the anteromedian edge of the eye. To diagnose this clade, these characters can be combined with some of the characters that indicate these taxa belong outside of the Proetinae. How-

TABLE 10

Characters Used in Phylogenetic Analysis of the Genus *Monodechenella*

"0" is the plesiomorphic state. Character matrix is given in table 11

0. Lateral margins of glabella between S1 and S2: (0) converging, (1) parallel.

1. Anterior and posterior portion of palpebrum, interior to margins of eye: (0) equal such that the palpebrum is of a symmetrical, half-moon shape, (1) posterior portion larger such that palpebrum in dorsal view is half pear-shaped.

2. Anterior portion of glabella: (0) does not contact anterior border furrow, (1) contacts anterior border furrow.

3. Anteromedian portion of pygidial axial rings in dorsal view: (0) straight, (1) deflected posteriorly.

4. Prominent tubercle on medial portion of pygidial axial rings: (0) absent, (1) present.

5. S1: (0) does not contact S0, (1) contacts S0.

6. Portion of S0 anterior of intraoccipital lobe: (0) is straight from S0 to axial furrow, (1) deflects more sharply laterally anteriorly.

7. Pygidial interpleural furrows: (0) faint, (1) absent.

8. Pygidial pleurae in lateral section: (0) flattened, (1) strongly arched.

9. Posterior portion of eye: (0) lies opposite anterior margin of S0 anterior of intra-occipital lobe, (1) displaced far anterior of anterior margin of S0, anterior of intraoccipital lobe.

10. Sagittal length of pygidial border posteriorly: (0) long flat region, equal to sagittal length of first 1.5 axial rings, (1) very short, less than sagittal length of first pygidial axial ring.

11. Anterior branch of facial suture: (0) divergent to anterior border, (1) parallel for distance equal to distance between distal tips of S1 and S2, then diverging to anterior border.

12. Space on pygidium between anterior margin of pygidial border and posterior of axis: (0) small, pygidial axis practically contacts posterior border, (1) large, length of at least the last two pygidial axial rings.

13. Anterior cephalic border: (0) long (anteroposteriorly), equal to distance between lateral tips of S1 and S2, (1) short, one-third distance between lateral tips of S1 and S2.

14. Prosopon: (0) of fine granules, (1) of coarse granulation.

15. Topographic elevation of L0: (0) constant, (1) increases posteriorly.

16. Posterior margin of glabella, anterior of S0, in dorsal view: (0) straight, (1) curving slightly posteriorly.

TABLE 10—(*Continued*)

17. Number of pygidial axial rings: (0) 11, (1) 15, (2) 9, (3) 13, (4) 12, (5) 14.

18. Number of pygidial pleural segments: (0) 8, (1) 10, (2) 11, (3) 9, (4) 12.

19. Pygidial pleurae laterally, relative to arc of pleurae medially: (0) deflected posteriorly, (1) deflected anteriorly, (2) equivalently arching.

ever, in some of the taxa considered, the pygidial pleural furrows are effaced. Instead of a prominent difference between anterior and posterior pygidial pleural segments, we must rely on what seem to be homologous structures. In taxa with effaced interpleural furrows (i.e., some species of *Monodechenella*), there are two parallel bands of tubercles surrounding a faint black line on the pygidial pleural segments. Distally the region posterior of this black line (i.e., behind the interpleural furrow, making it the anterior portion of each pygidial pleural segment) lengthens anteroposteriorly (sagittally) and weakly elevates dorsally. If we accept the zone of tubercles as the positional trace of the interpleural furrow demarcating the expression of the anterior portion of the pleural band, then these forms do have the typical structure of the pygidial pleural ribs developed in most members of the "*Thebanaspis* clade."

The genera used in the phylogenetic analysis of this clade were *Monodechenella* (Stumm, 1953a), *Hedstroemia* Pribyl and Vanek, 1978, *Thebanaspis* (Weller, 1907), and *Milesdavis*. The phylogeny was generated using 20 characters and 10 taxa. The characters used are given in table 10, and the character codings for these taxa are given in table 11. Three most parsimonious trees of length 36 were produced using the **ie*** option of Hennig86 (Farris, 1988) and the exhaustive search of PAUP 3.0q (Swofford, 1990). A strict consensus of these trees is shown in figure 36. The tree is 36 steps long with a consistency index of .77 and a retention index of .75. In the analysis, *Thebanaspis thebana* Lutke, 1990, is treated as the outgroup. This species is known from the Early Llandovery Edgewood Limestone, near Thebes, Illinois. This taxon was treated as the outgroup on the basis of its early occurrence in the fossil record, its relatively generalized appearance,

TABLE 11

Character State Distribution for Species Used in Phylogenetic Analysis of *Monodechenella*

Characters and states are listed in table 10. Missing data are indicated by "?"

		1	11111	1111
	012345	67890	12345	6789
Thebanaspis thebana	000000	00000	00000	0000
Hedstroemia pachydermata	000000	00100	00011	0110
Milesdavis eldredgei	???10?	?01?1	?1?0?	?000
"*M.*" *zlichovianus*	???10?	?11?1	?1?1?	?410
Monodechenella boteroi	???11?	?01?1	?1?1?	?412
Monodechenella halli	011110	10111	01111	0231
M. macrocephala	111111	11110	11111	0541
M. legrandsmithi	011111	11110	11111	1521
M. curvimarginata	011110	11111	11111	1321
M. breviceps	0?1000	10101	11111	1521

and its possession of the traits required for ingroup membership in the "*Thebanaspis* clade." In addition, in *T. thebana* the pygidial pleurae in lateral section are flattened and L0 is of constant elevation. All other members of the clade have the derived state for these two characters, implying a clear outgroup relationship between this taxon and the rest of the clade.

A bootstrap analysis was run using PAUP 3.0q (Swofford, 1990) in order to assess the confidence one can have in this phylogeny. One hundred bootstrap replications were performed. For each replication an heuristic search was employed that searched for the most parsimonious tree created by substitution and replacement of the data matrix. This heuristic search used the branch and bound option with nearest neighbor interchanges, and no more than 20 trees were saved for each replication. Confidence intervals from the bootstrap analysis were obtained by retaining groups compatible with the 50% majority-rule consensus trees. The nodes that appeared in the tree in figure 36 that are supported by the bootstrap analysis are ("*Milesdavis*"/*Monodechenella*) = .68, (*Monodechenella macrocephala/M. curvimarginata/M. legrandsmithi*) = .56, and (*Monodechenella macrocephala/M. legrandsmithi*) = .73. Although none of these values exceed .95, they are higher than values attained from the other analyses, partly because fewer taxa were considered. This indicates a reasonably robust phylogeny with most nodes supported by a moderate amount of character evidence.

An attempt was also made to discriminate between phylogenetic signal and random noise in the data set shown in table 11. This type of analysis could not be applied to the other data sets because of the large numbers of taxa they employed, which required prohibitive amounts of computer time. Although this analysis has generally been applied to DNA sequence data (e.g., Hillis, 1991), it can also be applied to morphological data. To do this, we can treat morphological evolution as a Markovian process independent of phylogeny that can be modeled in the way described by Raup and Gould (1974). We know that if all tree topologies are equally optimal for a set of sequences or morphological data, then the phylogeny would be an unresolved polytomy. However, Hillis (1991) argued that by chance alone, random variation in DNA sequences would result in some trees being shorter than others, and the distribution of trees would include some topologies shorter, and others longer, than average. He suggested that the result would be a largely symmetrical distribution of tree lengths. Only data with a strong phylogenetic signal (i.e., nonrandom) in it would produce highly asymmetrical tree-length distributions (Hillis, 1991). We can extrapolate these results to morphological data, and conclude that for those data sets that only departed from an unresolved polytomy due to random differences in morphology we would obtain a tree-length distribution that was highly symmetrical. The exhaustive search of PAUP 3.0q (Swofford, 1990) gives a measure of skewness for tree-length distributions, g_1. The g_1 value obtained for the phylogeny of the "*Thebanaspis* clade" was-1.14. This value departs significantly from randomly generated data and normally distributed data at the .01 level (Hillis, 1991). Thus the information in this

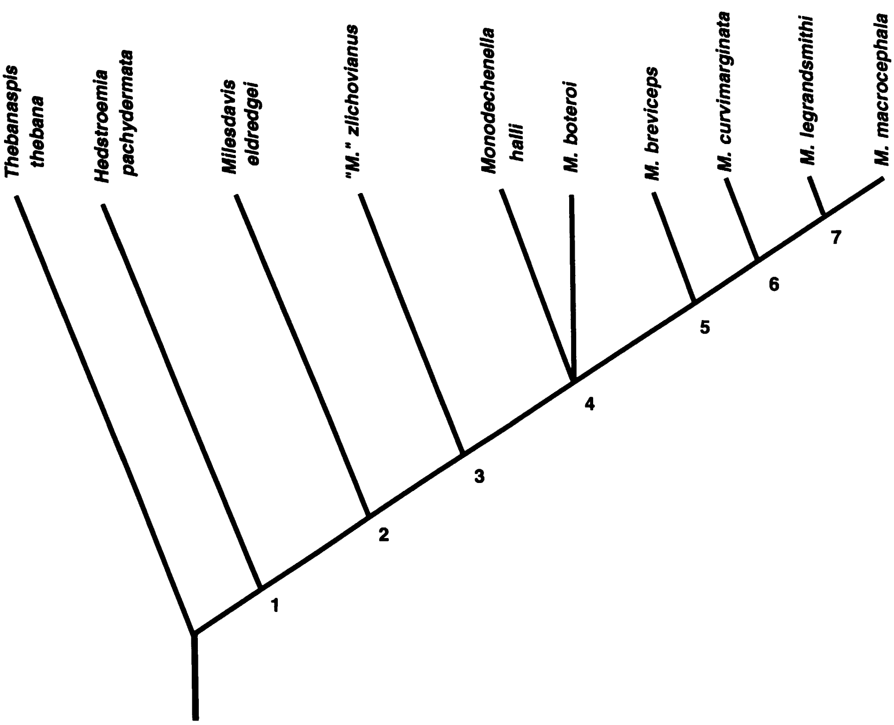

Fig. 36. A strict consensus cladogram showing phylogenetic relationships of species in the "*Thebanaspis* clade" generated using the data matrix given in table 11. The consensus cladogram was generated using the three most parsimonious trees of length 36 steps, consistency index .77, and retention index .75 and was produced using the **ie*** option (exhaustive search) of Hennig86 (Farris, 1988) and the exhaustive search of PAUP 3.0q (Swofford, 1990). All multistate characters were treated as unordered, nonadditive. Characters were optimized using ACCTRAN and are shown for each node with unambiguous apomorphies depicted by parentheses, ( ) and ambiguous apomorphies, either due to missing data or multiple equally parsimonious resolutions, depicted by brackets, [ ]. Node 1: 8(1), 14[0,1], 15(1), 18[0,1]; Node 2: 1[0,1], 2[0,1], 3(1), 6[0,1], 9[0,1], 10(1), 12(1), 13[0,1]; Node 3: 14(1), 17(4), 18(1); Node 4: 1(1), 2(1), 4(1), 6(1), 13(1), 19(1); Node 5: 11(1), 16(1), 17(5), 18(2); Node 6: 7(1), 9(1); Node 7: 5(1), 10(0).

phylogeny departs significantly from the information that is usually produced by random data.

The taxa used in the phylogenetic analysis of the "*Thebanaspis* clade" are presented and discussed here. One new species of *Milesdavis* and one new species of *Monodechenella* are described.

The phylogenetic analysis shows moderate congruence between phylogenetic position and stratigraphic first occurrence. The most basal species in the phylogeny, *Hedstroemia pachydermata* (Barret, 1878), first occurs in the Pridolian of New Jersey and the Helderbergian of Maryland, and the more derived *Milesdavis eldredgei*, new species is known from the Wenlockian of England. "*Milesdavis*" *zlichovianus* is, according to Pribyl (1966), known from the Zlichovian (Emsian) of Bohemia. However, Snajdr (1980) disputed this age claim, instead arguing that the specimen must have been derived from an unspecified locality outside of Bohemia of Carboniferous age. Thus, the age of first appearance of this species must for the present remain uncertain. *Monodechenella boteroi* (Caster and Richter *in* Richter and Richter, 1950) is known from the Floresta Series of Colombia; however, Caster (1939) was unable to date specimens of this species except by bracketing them between Lower Devonian (Lochkovian/Gedinnian) and Middle Devonian (Givetian). *Monodechenella halli* (Stumm, 1953b) is known from the Middle

Devonian (Eifelian) Onondaga Limestone of New York State and the Formosa Reef Limestone (Eifelian) of southern Ontario. *Monodechenella halli* and *M. boteroi* are sister to a clade of Eifelian and Givetian species from ENA and also a species known from the Lower Carboniferous, upper Tournaisian of New South Wales, Australia, *M. breviceps* (Mitchell, 1918). The phylogenetic position of the Australian species causes the most serious incongruence between phylogenetic position and stratigraphic appearance, assuming that Pribyl's (1966) age assignation for "*Milesdavis*" *zlichovianus* is correct. This result may indicate a period before the Lower–Middle Devonian during which the genus attained a cosmopolitan distribution.

The biogeographic origins of this clade could not be considered because it is not placed in a broader phylogenetic context. However, the putative outgroup, *Thebanaspis thebana* Lutke, 1990, and all the species in that genus are restricted to Laurentia. *Hedstroemia* is known from eastern Laurentia, Baltica, and the Canadian Arctic. When the stratigraphic and geographic ranges of the other taxa in this clade outside of ENA are considered, one species is known from the Wenlockian of England, one species is known from the Lower Devonian or Carboniferous of central Europe, one species is known from the Lower or Middle Devonian of Colombia, and one species is known from the Lower Carboniferous of Australia (with several other species known to exist from Australia, but these are not treated herein). In addition, when we view species from ENA sensu stricto in detail, we find that one species is known from the late Silurian, Pridolian of New Jersey, and the Lower Devonian of Maryland, two species are known from the Eifelian, and two species are known from the Givetian. Of the Eifelian taxa, one species is known from the Michigan Basin (southern Ontario), and this species also occurs in the Appalachian Basin, and one species is known from the Illinois Basin. In the Givetian, one species is known from the Appalachian Basin (Tioughniogan and Taghanic) and one species is known from the Michigan Basin (Tioughniogan) (see table 5). Note that the fauna recovered from Colombia, along with the trilobite *M. boteroi*, appears to be a depauperate representative of the ENA realm fauna in South America (Eldredge and Ormiston, 1979). Therefore, this distributional pattern is not so unusual.

These biogeographic patterns indicate that the species in ENA belonged to a cosmopolitan clade, and this interval of cosmopolitanism may have significantly predated the Eifelian. Thus, there was not a prominent change in the area relationships of this clade associated with the Eifelian–Givetian transitional interval. However, within ENA during the time of the Onondaga and Hamilton faunas, there may have been some vicariant differentiation within this clade following the lines of the major sedimentary basins.

Using the distribution of taxa in ENA we can deduce the relationship between transgressive–regressive cycles and the distribution of taxa. Two species are known to appear during transgressive–regressive cycle Ic. Two species are known to appear in transgressive–regressive cycle If, with one of these also known to be associated with strata deposited during transgressive–regressive cycle IIa.

The major reorganization of facies belts in ENA precipitated by tectonic factors and/or changes in global sea-level may have caused the demise of the two species of *Monodechenella* known from the Givetian. This induced extinction rate is as high as that associated with the Eifelian for that genus (possibly the end of the Eifelian), when there was a major reduction in the size of the limestone belts in ENA. However, *M. macrocephala* does not appear to be restricted to the limestone belts in the Michigan Basin during the Givetian, and it also occurs in the Appalachian Basin during some of the intervals of prominent limestone and shaley limestone deposition. The occurrence of *M. breviceps* in mudstones from the Carboniferous of Australia, the greater prevalence of *Monodechenella macrocephala* in the upper Tioughniogan shales and limey shales relative to all other proetid taxa considered, and the relatively low magnitude of whatever extinctions may have occurred at the end of the Givetian (a maximum of three species assuming that *M. macrocephala*, *M. legrandsmithi*, and *M. boteroi* could have been affected) diminishes the prominent role that environmental restriction might have played in the extinction of this genus.

THEBANASPIS LUTKE, 1990

TYPE SPECIES: *Thebanaspis thebana* Lutke, 1990.

DISCUSSION: For diagnosis see Lutke (1990). The genus consists of at least four species known from the Upper Ordovician–Lower Silurian of Laurentia.

Thebanaspis thebana
Lutke, 1990

Proetus determinatus Foerste, 1919: 389, pl. 19, fig. 14a–d.

Thebanaspis thebana Lutke, 1990: 42–43, pl. 9, figs. 60–64.

DIAGNOSIS: Anterior and posterior portion of palpebrum interior to margins of eye equal such that palpebrum is of symmetrical, half-moon shape; anterior portion of glabella does not contact anterior border furrow; S1 does not contact S0; portion of S0 anterior of intraoccipital lobe is straight from S0 to axial furrow; 11 pygidial axial rings; pygidial pleural segments laterally, relative to their arc medially, are deflected posteriorly.

DISCUSSION: This species was employed as the outgroup in this analysis. It is known from the Edgewood Limestone, early Llandoverian, near Thebes, Illinois. It was chosen as the outgroup on the basis of its relatively early stratigraphic occurrence relative to other members of the genus *Thebanaspis*, and because it was the best preserved species of the genus that could be examined. In addition, it satisfied the criteria of "*Thebanaspis* clade" ingroup membership, and all members of this genus are separated from other members of the clade by the presence of the primitive state for two characters, the condition of the pygidial pleurae and the elevation of L0.

HEDSTROEMIA
PRIBYL AND VANEK, 1978

TYPE SPECIES: *Hedstroemia delicata* (Hedstrom, 1923).

DISCUSSION: For diagnosis see Pribyl and Vanek (1978) and Lutke (1990). Lutke (1990) advocated that the genus *Hedstroemia* be divided into two subgenera, *Pachyproetus* Lutke, 1990, and *Hedstroemia* Pribyl and Vanek, 1978. Lutke (1990) suggested that *H. pachydermata* be assigned to *Pachyproetus*. The validity of these subgenera is not considered herein.

The genus *Hedstroemia* appears to have a wide geographic distribution. It is known from the Silurian of almost all continental blocks except Gondwanaland (Lutke, 1990). J. M. Adrain (personal commun., 1992) has recovered a new species of this genus from the Wenlock of the Canadian Arctic. There are also species in the Mackenzie Mountains of the Northwest Territories of Canada. Lutke (1990) suggested that Ormiston's (1975a) unidentified tropidocoryphinid genus from the Lower Devonian (Gedinnian) of Nevada (pl. 1, figs. 13–16) belonged to the genus *Hedstroemia*. The structure of the pygidial pleurae certainly indicates an affinity with the "*Thebanapsis* clade." In addition, the cephalic characters appear to fit those diagnostic of the "*Thebanapis* clade." However, as Lutke (1990) stated, these specimens are too poorly preserved to make a definitive assignment.

Lutke (1990) and Holloway (1980) suggested that *Crassiproetus globosus* Maximova, 1960, and *C. turgidus* (Northrop, 1939) were closely related to *Hedstroemia* on the basis of the muscle scars on the pygidial axis. However, as discussed above in the section on the higher level phylogeny of the Proetinae under the genus *Crassiproetus*, this relationship is not supported by character evidence. In particular, these two taxa satisfy the criteria of Proetinae ingroup membership, whereas *Hedstroemia* of course does not.

Hedstroemia pachydermata
(Barret, 1878)

Proetus pachydermatus Barret, 1878: 371; Weller, 1903: 248, pl. 22, figs. 16–21; Ohern and Maynard, 1913: 489–490, pl. 89, fig. 1.

Hedstroemia (*Pachyproetus*) *pachydermata* (Barret). Lutke, 1990: 50–51, pl. 11, figs. 75–79.

DIAGNOSIS: Anterior and posterior portion of palpebrum interior to margins of eye equal such that palpebrum is of symmetrical, half-moon shape; anterior portion of glabella does not contact anterior border furrow; topographic elevation of L0 increases posteriorly; portion of S0 anterior of intraoccipital lobe is straight from S0 to axial furrow; prosopon of coarse granules; pygidial interpleural furrows faint; pygidial pleurae in lateral section strongly arched; border posteriorly flat region, length equal to sagittal length of first 1.5 pygidial axial rings; 15 pygidial axial rings.

DISCUSSION: This species is known from the Decker Formation, Pridolian, Nearpass Quarry, Montague, New Jersey, and the Keyser Member, Lochkovian (Helderbergian), Helderberg Formation, Cumberland, MD. It appears to be closely related to *Hedstroemia delicata* (Hedstrom, 1923) and a new species J. Adrain has recovered from the Canadian Arctic. This species was analyzed rather than others in the genus because it was the one for which the best and most complete material could be obtained. The monophyly of this genus was therefore not evaluated in this analysis.

MILESDAVIS, NEW GENUS

TYPE SPECIES: *Milesdavis eldredgei*, new species.

ASSIGNED TAXA: *Milesdavis eldredgei* and *Dechenella* (*Monodechenella*) *zlichoviana* Pribyl, 1966.

ETYMOLOGY: Named for Miles Davis, the great musician.

DIAGNOSIS: Anteromedian portion of pygidial axial rings, in dorsal view, deflected posteriorly; prominent tubercle on medial portion of axial rings absent; interpleural furrows faint to absent, pleurae in sagittal section strongly arched; pygidial border posteriorly very short, less than sagittal length of first axial ring; space on pygidium between anterior margin of pygidial border and posterior of axis equal to length of at least last two pygidial axial rings; pleurae laterally, relative to arc of pleurae medially, deflected posteriorly.

DISCUSSION: A portion of this genus is recognized as paraphyletic, and the shutter mark convention of Wiley (1979) is used to denote this. A separate generic name could have been erected for each of the species contained in this genus. However, because of the paucity of material, and the lack of any preserved cephala or thoraxes, this was not done. An alternative taxonomic decision would have been to place both species in the genus *Hedstroemia*, making this genus paraphyletic. This also was not done, as there appears to be several species from several different localities that could probably be assigned to a monophyletic *Hedstroemia*.

Recovery of cephala for both species based only on pygidia might cause both species of *Milesdavis* to group with *Hedstroemia*. This possibility is most likely for *M. eldredgei*, the type of the genus, which Owens (1973) considered to be very similar to *Hedstroemia delicata*, the type of *Hedstroemia*.

Milesdavis eldredgei, new species

Schizoproetus aff. *delicatus* (Hedstrom, 1923). Owens, 1973: 37, pl. 15, figs. 16, 17.

TYPES: Holotype GSM 33122, from the Wenlock Limestone Formation, Dudley, United Kingdom.

ETYMOLOGY: Named for Niles Eldredge, who has done some of the fundamental work in formulating macroevolutionary theory.

MATERIAL: GSM 33122.

DIAGNOSIS: Same as for genus; also, prosopon of fine granules; pygidial interpleural furrows faint; 11 axial rings; eight pleural segments.

DESCRIPTION: Pygidial length 95% width; pleural furrows prominently incised, interpleural furrows faint; apodemes faint; axis of relatively even height, axial rings flex anteriorly medially, abaxially first flex posteriorly, then anteriorly, then posteriorly; 11 axial rings; eight pleural segments. Pygidial border prominently developed as flat projection, dorsoventrally thin, of uniform length posteriorly and anterolaterally, posterior portion of pygidial border in dorsal aspect appears rounded; pleurae of imbricate structure, strongly arched, with anterior margin convex; pleurae laterally, relative to arc of pleurae medially, deflected more strongly posteriorly; transitions between pleural bands and pleural furrows abrupt. Sagittal length of anterior portion of pleural bands increases distally; anterior pleural band elevates distally relative to posterior band. Axis with rounded terminus, flattened in sagittal section; short space between anterior portion of pygidial posterior border and posterior portion of axis, length less than sagittal length of first axial ring; anterior edge of axis wide (tr.), 120% width of pleural field; lateral margins of axis diverging anteriorly at 30° angle.

DISCUSSION: This species is known from the Wenlock Limestone, Dudley, England. The specimen designated the holotype is the morphologically most complete referable to this species, and is figured in Owens (1973: pl. 15, fig. 17). It appears to be very closely related to *Hedstroemia delicata* (Hedstrom, 1923), differing principally from this species in having one fewer pygidial axial ring (12 as opposed to 11 based on the drawings in Pribyl and Vanek [1978]). (My procedure for counting axial rings produces different results from that of Owens [1973].) The cephalic morphology of *Milesdavis eldredgei* may have been very similar to that of *H. delicata* (i.e., nearly identical to *H. pachydermata*, which was analyzed herein). However, because material of the cephalon was missing for *M. eldredgei* these characters were coded as missing. The large amount of missing data coded for this taxon does not appear to have a significant effect on the phylogeny produced herein, as removal of this taxon from analysis results in an identical tree topology to that shown in figure 36.

As discussed above, this species possesses the characters of the "*Thebanaspis* clade." Thus, it is not a member of the Proetinae and cannot be included within the genus *Schizoproetus*, as was done by Owens (1973).

"*Milesdavis*" *zlichovianus*
(Pribyl, 1966)

Dechenella (*Monodechenella*)? *zlichoviana* Pribyl, 1966: 51, pl. 1, fig. 9; Snajdr, 1980: 283–284.

DIAGNOSIS: Same as for genus; also, prosopon of coarse granules; pygidial interpleural furrows absent; 12 axial rings; 10 pleural segments.

DISCUSSION: This species is of disputed age and provenance. It is from either the Lower Devonian (Zlichovian) of Bohemia (Pribyl, 1966) or the Carboniferous of an unknown locality (Snajdr, 1980). It is known from a single pygidium. Although a precise stratigraphic position for this specimen would not change the phylogeny shown in figure 36, it might allow us to make predictions about the propinquity of this species to its sister group, the genus *Monodechenella*. In addition, it might elucidate the aptness of using this specimen as one of the sole representatives of the genus in phylogenetic analysis, especially since this portion of the paper focuses on the biogeographic origin of the Middle Devonian proetid fauna of ENA. An important tenet of this paper is that the biogeographic area relationships of taxa are subject to change over geologically rapid intervals, and the uncertainty associated with the age and provenance of this species certainly caution against using it in the biogeographic analysis of this genus.

MONODECHENELLA STUMM, 1953A

TYPE SPECIES: *Monodechenella macrocephala*, designated by Stumm (1953a).

DIAGNOSIS: Same as for "*Thebanaspis* clade"; also, anterior and posterior portions of palpebrum, interior to margins of eye, asymmetrical with posterior portion larger such that palpebrum is half pear-shaped; anterior portion of glabella contacts anterior border furrow; portion of S0 anterior of intraoccipital lobe deflects more sharply laterally anteriorly; posterior portion of eye displaced far anterior of anterior margin of S0, anterior of intraoccipital lobe; anterior cephalic border short, sagittal length one-third length between distal tips of S1 and S2.

DISCUSSION: Stumm (1953a) designated *Monodechenella* as a new subgenus of *Dechenella*, and several authors, including Richter and Struve (1959), treated it in this manner. However, on the basis of character evidence presented herein, this hypothesis of phylogenetic relationship seems strongly contradicted. Character analysis performed herein suggests that species of *Monodechenella* belong to the "*Thebanaspis* clade." Therefore, *Monodechenella* cannot be a valid subgenus of *Dechenella*, and it is instead elevated to full generic rank and removed from the Proetinae sensu stricto.

Some of the characters diagnostic of the genus *Monodechenella* are based on the condition of the cephalon, and one of the species considered, *M. boteroi* (Caster and Richter *in* Richter and Richter, 1950), could only be coded for pygidial characteristics. Thus, it is conceivable that this taxon's phylogenetic position and/or the diagnosis of this genus could change upon recovery of a cephalon of *M. boteroi*.

The generic concept of *Monodechenella* is enlarged to encompass *Mannopyge* Ludvigsen, 1987. This genus name could be preserved; however, this would require the erection of a monotypic genus for *Monodechenella boteroi*, known only from pygidia.

As discussed above, in some species of *Monodechenella*, particularly *M. macrocephala*, *M. legrandsmithi*, and *M. curvimarginata*, the pygidial interpleural furrows are effaced. This makes it difficult to recognize one of the homologies of the "*Thebanaspis* clade," the difference in length (exsag.) and dorsal elevation between anterior and posterior pygidial pleural bands. In these taxa there are two parallel bands of tubercles surrounding a faint dark line on the pygidial segment that can be used to demarcate the zone of the anterior and posterior pygidial pleural bands and also the position of the interpleural furrow. This allows recognition of the trait developed in the other members of the "*Thebanaspis* clade," but there is less difference between the dorsal elevation of the different portions of the pleural bands in these taxa.

This genus appears to consist of species restricted to ENA, northern South America, and Australia, implying that it is found in Laurentia and parts of Gondwana. However, these widespread occurrences are not coeval. As for the other generic clades considered from ENA, almost all of the species in this genus occur solely in limestones or calcareous shales. In the Middle Devonian, species appear to be restricted to limestones and limy shales of ENA and northern South America, which is part of the ENA Realm. In the Carboniferous, a single species is known from brown mudstone, and it occurs only in Australia. The phylogenetic placement of this species suggests that species ancestral to it must have differentiated from most of the species of *Monodechenella* that appear in ENA by the Middle Devonian.

Monodechenella halli
(Stumm, 1953b)

Figure 37

Proetus verneuili Hall, 1861: 73; Hall, 1862: 101; Hall, 1876: pl. 20, figs. 18, 19; Hall and Clarke, 1888: pl. 20, figs. 18, 19; non *Proetus verneuili* Barrande, 1852: 119.

Dechenella (?*Dechenella*) *halli* Stumm, 1953b: 23; Fagerstrom, 1961: 42–43, pl. 14, figs. 18, 19.

"*Dechenella*" *halli* (Stumm). Ludvigsen, 1979: 77, fig. 52c.

Dechenella (*Basidechenella*) *formosensis* Fagerstrom, 1961: 42, pl. 14, figs. 4, 5, 20.

Mannopyge halli (Stumm). Ludvigsen, 1987: 683, 685, fig. 6j–o, 7, 8, 10a, b.

?*Proetus ovifrons* Hall and Clarke, 1888: 110–111, pl. 22, figs. 31, 32.

?*Dechenella* (*Monodechenella*) *ovifrons* (Hall and Clarke). Fagerstrom, 1961: 42.

Diagnosis: Lateral margins of glabella between S1 and S3 converging; S1 weakly sinusoidal, does not contact S0; pygidial interpleural furrows faint; anterior branch of facial suture divergent to anterior border; posterior margin of glabella, anterior of S0, in dorsal view transverse; nine pygidial axial rings; nine pleural segments; pygidial pleurae laterally deflected anteriorly relative to arc of pleurae medially; prominent nodes equivalent in position to extensions of pygidial pleurae developed on border and separated from medial portions of pleurae by effacement of pleural segments; prominent tubercle on medial portion of pygidial axial rings; pygidial border posteriorly very short, less than sagittal length of first pygidial axial ring.

Types: Stumm (1953b) designated Hall's (1876) and Hall and Clarke's pygidium AMNH 4074 (1888: pl. 20, figs. 18, 19), from the Edgecliff Member of the Onondaga Limestone (lower Eifelian) at Williamsville, New York, the holotype of the species by monotypy.

Material: AMNH 4074, 44719; ROM 35397.

Discussion: This species is known from the Onondaga Limestone, probably Edgecliff Member (lower Eifelian), Williamsville, and possibly Phelps and Canandaigua, Ontario County, western New York State, and the Formosa Reef Limestone (lower Eifelian), Formosa, Ontario. Thus, it is associated with the second transgression at the base of the Eifelian in transgressive–regressive cycle Ic.

Originally this species was assigned to *Proetus verneuili*. However, it differs fundamentally from *Dechenella verneuili* (Barrande, 1852), originally *Proetus verneuili*, which belongs to the Proetinae and is treated above. Hall and Clarke's (1888) *Proetus ovif-*

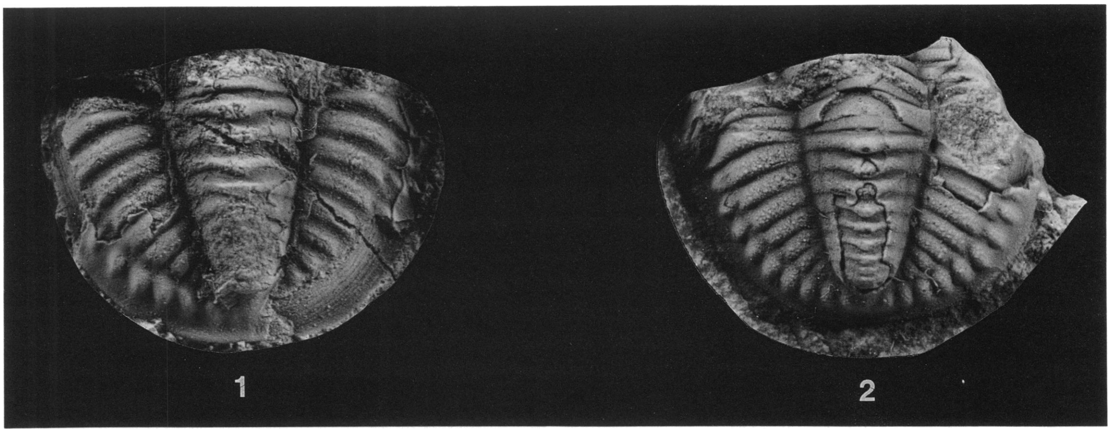

Fig. 37. *Monodechenella halli* (Stumm, 1953b). **1.** Onondaga Limestone, Southwoodian (Eifelian), Williamsville, New York, AMNH 44719, dorsal view of pygidium, ×4. **2.** Horizon and locality same as 1. AMNH 4074, holotype, dorsal view of pygidium, ×5.

rons appears to be identical to *Monodechenella halli*. However, their figured specimens of this species, known from the Onondaga Limestone of Canadaigua, have only a portion of the cranidium preserved. These cranidia could belong to *M. macrocephala*, agreeing particularly with this species in the more rounded aspect of S1. Indeed, Hall and Clarke (1888) argued for a very close relationship between *ovifrons* and *macrocephala*. However, S1 has a more sigmoidal appearance in *M. halli*. Figured *ovifrons* appears to have the lateral margins of the glabella converging between S1 and S2 (which is characteristic of *M. halli*), whereas they are generally parallel in *M. macrocephala*. These cranidia come from stratigraphic horizons and geographic localities typical of *M. halli*. Tentatively, these cranidia are treated as *M. halli*, and the more rounded aspect of S1 is treated as a byproduct of the very small size of the specimens in question.

Fagerstrom (1961) described a new species, *Dechenella* (*Basidechenella*) *formosensis* that he suggested was very similar to *Monodechenella ovifrons* (Hall and Clarke) but differed in having sigmoidal S1 and larger intraoccipital lobes. The size of the intraoccipital lobes appears to be identical in the species Fagerstrom figured and that which he referred to *M. ovifrons*, but the state of the material for *ovifrons* makes it very difficult to discern this. Fagerstrom's *D.* (*B.*) *formosensis* cannot be distinguished from *M. halli*, and the two are treated as conspecific.

Ludvigsen (1987) suggested that this species should be placed in a new genus, *Mannopyge*, in the subfamily Warburgellinae. As discussed above, there is considerable controversy regarding the higher-level relationships of the Proetidae and whether or not the Warburgellinae is a subfamily of the Proetidae or the Brachymetopidae. Such issues are beyond the scope of this paper. However, *Mannopyge halli* has all of the synapomorphies of the "*Thebanapsis* clade," and, as discussed above, this group shares some morphological features with the Tropidocoryphinae/ Cornuproetinae and others with the Proetinae, all of course, members of the Proetidae. In particular, *M. halli* appears to have imbricate pygidial structure, rather than flat-topped (as Ludvigsen [1987] suggested) which is typical of the Warburgellinae. It also has all of the characters diagnostic of *Monodechenella*. Herein, it is treated as a species in that genus, and the senior generic name *Monodechenella* is appropriated instead of keeping *Mannopyge*. This prevents erecting a monotypic generic name for *Monodechenella boteroi*, known only from isolated pygidia, and preserves the well-known name *Monodechenella* for such species as *M. macrocephala*.

An important, diagnostic characteristic of *M. halli* is the nodes developed on the margins of the pygidium, which are extensions of the pleural segments. These are treated as homologous to the hallmark traits of the "*Thebanaspis* clade," the exsagittally lengthening and distally elevating pleural tips. This trait is prominently developed in *Thebanapsis*, "*Milesdavis*," *Hedstroemia*, and *Monodechenella halli*, but much less so in some of the other species of *Monodechenella*. This structure of the pygidial pleurae is treated as imbricate following Owens' (1973) definitions.

Monodechenella boteroi
(Caster and Richter *in* Richter and Richter, 1950)

?*Dalmanites* cf. *patacamayaensis* Kozlowski. Caster, 1939: 181, pl. 14, figs. 3–6.

Dechenella (?*Basidechenella*) *boteroi* Caster and Richter *in* Richter and Richter, 1950: 161–162.

Dechenella boteroi Caster and Richter. Eldredge and Ormiston: 1979, 164.

DIAGNOSIS: Anteromedial portion of pygidial axial rings deflected posteriorly; prominent tubercle on medial portion of axial rings; interpleural furrows faint; pleurae strongly arched in lateral section; pygidial border posteriorly very short, length less than sagittal length of first axial ring; space on pygidium between anterior margin of border and posterior of axis, large, equal to sagittal length of last two axial rings; prosopon of coarse granules; 12 axial rings; 10 pleural segments; pleurae laterally, relative to arc of pleurae medially, equivalently arching.

MATERIAL: A pygidium loaned to Dr. Niles Eldredge from Stephen Barrett, formerly at the University of Chicago.

DESCRIPTION: Pygidial length 75% width; pleural furrows prominently incised, interpleural furrows faint; apodemes faint; axis of relatively even dorsoventral height; axial rings flex posteriorly medially, abaxially first flex anteriorly, then posteriorly; 12 axial rings; 10 pygidial pleural segments. Border dorsoventrally thin, short, less than length of first axial ring, of uniform length posteriorly and anterolaterally; posterior portion of pygidial border in dorsal aspect appears rounded; pleurae of imbricate structure, strongly arched; anterior margin of pleurae convex; pleurae evenly arching, transitions between pleurae and pleural furrows abrupt. Pygidial axis with rounded terminus, in sagittal section flattened; large space between anterior portion of posterior border and posterior portion of axis equal to sagittal length of first two rings; anterior edge of axis 105% width of pleural field; lateral margins of axis diverging at 20° angle.

DISCUSSION: This species is known from the Floresta Beds of Colombia (either Lower or Middle Devonian), in a limy, shaly, argillaceous unit. The lithology of the unit from which the examined specimen of this species is derived is similar to samples of the Needmore Shale (Lower–Middle Devonian) from West Virginia and Virginia. It occurs outside of ENA but in a region that contains a fauna that has typically been described as Appalachian or Eastern North American (Oliver, 1976, 1977; Eldredge and Ormiston, 1979). This species was originally assigned to the genus *Dalmanites*; however, the condition of the pleural and interpleural furrows, the development of the pygidial border, and the expression of the axial rings clearly demonstrate its proetid character. Indeed, Caster (1939) commented that some paleontologists had suggested that this species recalls the genus *Dechenella* more than *Dalmanites*.

Richter and Richter (1950) questionably assigned this species to the subgenus *Basidechenella*. This assignment appears to be mistaken on the basis of the absence of the Fulcrum-Fortsatz from the anteriormost pleural segments, the prominent incision of the interpleural furrows, and the dorsoventally thin pygidial border, which lies parallel to the dorsal plane. Although difficult to ascertain because of poor preservation, the structure of the pygidial pleural segments may be imbricate. These characters, and the close resemblance *M. boteroi* bears to other species of *Monodechenella* in all the traits considered, strongly indicate that this assignment to *Monodechenella* is correct. However, it can clearly be difficult to determine the phylogenetic position of isolated pygidia.

Note that Eldredge and Ormiston (1979) also suggested that the species might be related to *Monodechenella macrocephala* (Hall). Better material, particularly with associated cephala, needs to be examined before the assignment to *Monodechenella* can be verified, but for the present this species is placed in *Monodechenella*. In the phylogeny shown in figure 34 it forms part of a polytomy with *M. halli* and the other species of *Monodechenella*.

Monodechenella breviceps (Mitchell, 1918)

Phillipsia breviceps Mitchell, 1918: 449, pl. 45, figs. 11, 12, pl. 51, figs. 2, 3.

Conophillipsia brevicaudata Roberts, 1963: 26–27, pl. 6, figs. 13–20.

Conophillipsia breviceps breviceps (Mitchell). Engel and Morris, 1984: 31–35, figs. 4, 5.

DIAGNOSIS: Same as for genus; also, lateral margins of glabella between S1 and S2 converging; S1 does not contact S0; interpleural furrows faint; posterior portion of eye lies opposite anterior margin of S0 anterior of intraoccipital lobe; anterior cephalic border short, length equal to one-third exsagittal length between distal tips of S1 and S2; posterior margin of glabella, anterior of S0, curving slightly posteriorly; anteromedial portion of pygidial axial rings in dorsal view straight; prominent tubercle on median portion of pygidial axial rings absent; pygidial border posteriorly very short, length less than sagittal length of first axial ring; 14 axial rings; 11 pleural segments.

DISCUSSION: This species is known to occur in brown mudstone of the Bingleburra Formation (Lower Carboniferous, upper Tournaisian), at Lewinsbrook, New South Wales, Australia. The characters used in phylogenetic analysis for these taxa were coded on the basis of examination of photographs. For all characters considered (except 9 and 15), the assessment of character states appeared unambiguous. For character 1, the palpebra were too poorly preserved to allow determination of the correct character coding.

As mentioned above, the occurrence of this species in a Gondwanan locality is particularly unusual, as the bulk of the species of the "*Thebanaspis* clade" are known from ENA. Of course, *Monodechenella boteroi* discussed above is known from northern South America. Note that Roberts (1963) suggested similarities between the fauna *M. breviceps* is associated with and the Kinderhook fauna of America. *Monodechenella breviceps* is also the only species of the genus *Monodechenella* and of the "*Thebanaspis* clade" that is known to persist into the Carboniferous that was treated here. However, Engel and Morris (1984) figured and discussed several other specimens from the Lower Carboniferous of eastern Australia and Japan that they assigned to *Conophillipsia* and which are very similar to *M. breviceps*. Therefore, there may exist a moderately diverse fauna of *Monodechenella* in the Lower Carboniferous. Engel and Morris (1984) also concluded that Roberts' *Conophillipsia brevicaudata* is identical to Mitchell's (1918) *Phillipsia breviceps*, and following their conclusions these taxa are treated as identical and they are henceforth designated as *Monodechenella breviceps* (Mitchell).

Roberts (1963) assigned this species to the genus *Conophillipsia*, which he placed in the family Phillipsiidae Oehlert, 1886. As developed briefly in the section on the higher-level phylogeny of the Proetinae that deals with the post-Devonian proetid trilobite fauna, there may be important similarities shared between species assigned to the Phillipsiidae and those placed in the "*Thebanaspis* clade." Whether these similarities are due to convergence or are evidence for descent cannot be evaluated yet, for the evolutionary relationships of the phillipsiids, and the validity of this family, are at present controversial and are under study by Dr. R. M. Owens (personal commun., 1992). Because these similarities do not bear directly on the problem at hand, they are not discussed further.

Monodechenella breviceps has all of the characters diagnostic of the genus, and, in addition, it appears to bear the diagnostic characters of the "*Thebanaspis* clade." In particular, it clearly lacks the Fulcrum-Fortsatz on the anteriormost pygidial pleural segments, has a relatively long (sag.) S0, lineations on the internal margins of the genae, pygidial pleural segments developed posterior of the axis, anterior bands of the pygidial pleurae lengthening (sag.) distally and elevating dorsally, a flattened narrow shelf around the eye that is not expanded posteriorly and laterally, and lacks the prominent development of the pygidial articulating half-ring.

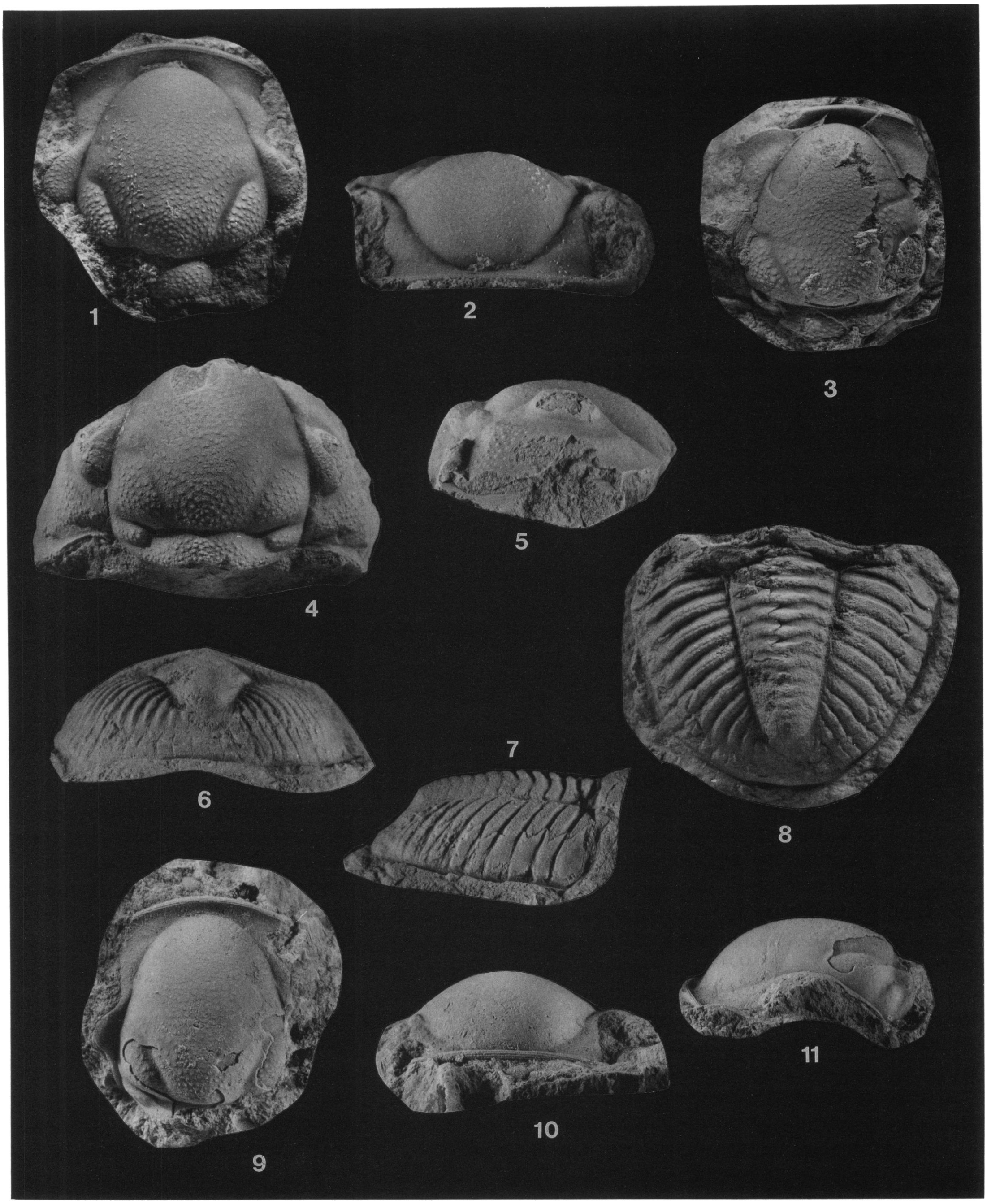

Fig. 38. *Monodechenella* spp. **1, 2.** *Monodechenella curvimarginata* (Hall and Clarke, 1888). Jeffersonville Limestone, Southwoodian (Eifelian), Morgan County, Indiana, YPM 33837, dorsal and anterior views of cranidium, ×4. **3.** *Monodechenella curvimarginata* (Hall and Clarke, 1888). Horizon and locality same as 1, 2. YPM 33836, dorsal view of cranidium, ×2.5. **4, 5.** *Monodechenella curvimarginata* (Hall and Clarke, 1888). Horizon and locality same as 1, 2. YPM 33835, dorsal and lateral views of cephalon, ×3. **6-8.** *Monodechenella curvimarginata* (Hall and Clarke, 1888). YPM 33832, posterior, lateral, and dorsal views of pygidium, ×3. **9-11.** *Monodechenella legrandsmithi*, new species. Four Mile Dam

Monodechenella curvimarginata (Hall and Clarke, 1888)

Figure 38.1–38.8

Proetus curvimarginatus Hall and Clarke, 1888: 94–97, pl. 22, figs. 13–19.

DIAGNOSIS: Same as for genus; also, S1 does not contact S0; posterior margin of glabella, anterior of S0 in dorsal view, curving slightly posteriorly; lateral margins of glabella between S1 and S2 converging; pygidial border very short, sagittal length less than that of first axial ring; 13 pygidial axial rings; 11 pleural segments; pleurae laterally, relative to arc of pleurae medially, deflected anteriorly.

TYPES: Hall and Clarke's (1888) plate 22, figure 13 from probably the Jeffersonville Limestone (called Schoharie Grit), Pendleton, IN, is designated as the lectotype.

MATERIAL: YPM 33832, 33834–33837.

DISCUSSION: This species is known from the Jeffersonville Limestone (Southwoodian/Eifelian), Waverly and Pendleton, Morgan County, IN. Although Hall and Clarke (1888) report this species from the Schoharie Grit, they are most likely referring to Onondagan equivalents such as the Jeffersonville Limestone. Thus, its distribution is related to transgressive–regressive cycle Ic. Hall and Clarke (1888) suggested that this species was closely related to *Monodechenella macrocephala* (Hall), known from the Hamilton Group of New York State. This conclusion appears to be correct. A clade of three species of *Monodechenella* from ENA in the Illinois, the Michigan, and Appalachian Basins are united by the possession of the following characters: pygidial interpleural furrows absent and posterior portion of eye displaced far anterior of anterior margin of S0.

This species uniquely shares a single trait with *Monodechenella legrandsmithi*, new species. They both have a similar form of the posterior margin of the glabella, anterior of S0, which in dorsal view curves slightly posteriorly medially. This evidence for evolutionary relationship is outweighed, however, by the two traits shared by *M. legrandsmithi* and *M. macrocephala*. They share the following unique traits: S1 contacts S0 and there are 14 pygidial axial rings.

Monodechenella legrandsmithi, new species

Figures 38.9–38.11, 39

Dechenella (*Monodechenella*) *macrocephala* (Hall). Stumm, 1953a: 123, pl. 4, figs. 4–6.

TYPES: Holotype UMMP 27079 from the Four Mile Dam Limestone, Alpena, Alpena County, MI.

ETYMOLOGY: This species is named for LeGrand Smith, who has greatly contributed to our knowledge of Devonian Malvinokaffric trilobites.

MATERIAL: UMMP 27079, 28715.

DIAGNOSIS: Same as for genus; also, anterior branch of facial suture parallel for distance equal to distance between distal tips of S1 and S2, then diverging to anterior border; pygidial interpleural furrows absent; posterior portion of eye displaced far anterior of anterior margin of S0; posterior margin of glabella curving slightly posteriorly; 14 pygidial axial rings; 11 pleural segments; S1 contacts S0; pygidial border posteriorly flat with sagittal length equal to length of first 1.5 axial rings.

DESCRIPTION: Cephalic length (sag.) 125% maximum glabellar width; anterior border developed as short dorsoventrally thin ledge (60% length of L0 medially), flattened; thin trace of concentric longitudinal lineations visible on anteriormost portion of cephalon; anterior border furrow nearly effaced; longitudinal lineations on anterior border rim of cephalon closely packed and linear. Prosopon of coarse granules. Anterior edge of glabella contacts anterior border furrow. Anterior portion of glabella conical. Anterior branches of facial sutures parallel for distance equal to length between distal tips of S1 and S2, then diverging to anterior border at an approxi-

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Limestone, Tioughniogan (Givetian), Four Mile Dam, Thunder Bay River, 3 mi. northwest of Alpena, Michigan, UMMP 27079, holotype, dorsal, anterior, and lateral views of cranidium, ×2.5.

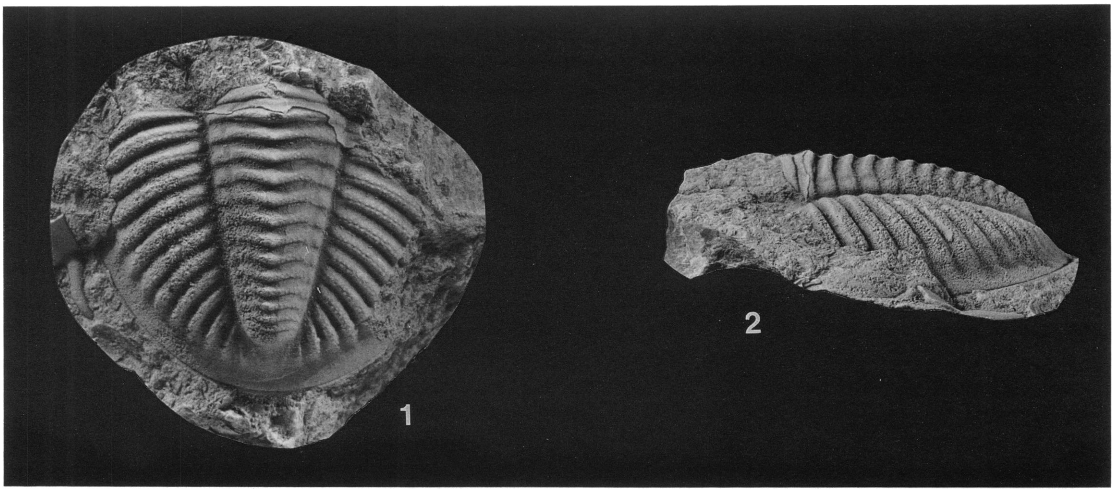


Fig. 39. *Monodechenella legrandsmithi*, new species. **1, 2.** Four Mile Dam Limestone, Tioughniogan (Givetian), Four Mile Dam, Thunder Bay River, about 3 mi. northwest of Alpena, Michigan, UMMP 28715, dorsal and lateral views of pygidium, ×2.5.

mately 15° angle, displaced farther laterally at lateral edge of eye than at maximum lateral deflection on the anterior border. Lateral margins of glabella anterior of S1 converging. Space between anteromedian portion of eye and anterior border furrow equal to orthogonal distance between anterolateral portion of intraoccipital furrow and distal tip of S1. S1 faintly impressed, other glabellar furrows developed as patches of pigment. S3 faint, nearly transverse, moderately sinusoidal; laterally convex portion of furrow directed posteriorly; medially convex portion of furrow directed anteriorly. S2 sinusoidal, laterally convex portion of furrow directed posteriorly, medially convex portion of furrow directed anteriorly, rounded curve medially directed posteriorly, deflected about 10° from transverse line from inner edge of eye. S1 moderately sinusoidal, anterior edge of furrow developed as transverse line; posterior tips deflect medially relative to medial portion, follows a straight course, contacting S0; S1, S2, and S3 laterally contact axial furrows; space between distal tips of S1 and S2 twice length between distal tips of S2 and S3. Median glabellar furrow very faint, medially directed posteriorly, inclined at 45° angle from sagittal line. Maximum width of glabella equal to 90% maximum length. Lateral margins of glabella converging at same angle between S1 and S2 as between S2 and S3; maximum glabellar bulge posterior of distal tip of S1. S0 moderately incised. Anterior portion of S0 anterior of intraoccipital lobe deflects more sharply laterally anteriorly, expanded dorsally; lateral margins of intraoccipital lobes flex laterally anteriorly, deflected anteriorly beyond transverse line tangent to anteromedian portion of S0, separated posteriorly from L0, deflect strongly beyond lateral margins of glabella. Tubercle not developed on L0. L0 straight medially, below level of posterior region of glabella, elevates posteriorly. Posterior portion of glabella medially flexes posteriorly, then laterally anteriorly, then posteriorly, then anteriorly. Posterior portion of eye adjacent to lateral portion of S0 anterior of the intraoccipital lobes, extending to point between distal tips of S1 and S2. Posterior portion of palpebral lobe larger than anterior portion such that palpebral lobe in dorsal view is half pear-shaped. Fixigenae in course from lateral margins of glabella at S3 to anterior border evenly inclined.

Pygidial length 65% of width; pleural furrows prominently incised, interpleural furrows absent; apodemes faint; axis of relatively even dorsoventral height; axial rings flex posteriorly medially, abaxially first flex anteriorly, then posteriorly; 14 axial rings; 11 pleural segments present. Pygidial border dorsoventrally thin, flat, sagittal length equal to length of first 1.5 axial rings, of uniform length posteriorly and anterolaterally; posterior portion of border in dorsal aspect appears rounded; pleurae of imbricate structure, strongly arched; anterior margin of pleurae convex; pleurae evenly arching, transitions between pleural bands and pleural furrows abrupt; laterally pleurae deflect anteriorly relative to arc of pleurae medially. Axis with rounded terminus, flat in sagittal section flat, arched in lateral section; anteromedial tubercles developed on axial rings; large space between anterior portion of border and posterior portion of axis, sagittal length equal to length of first two axial rings; anterior edge of axis 110% width of pleural field; lateral margins of axis diverging at 30° angle.

DISCUSSION: This species is known from the Four Mile Dam Limestone (Tioughniogan), Thunder Bay River, Alpena, Alpena County, MI. Thus, its distribution is related to transgressive–regressive cycle If. The specimen designated as the holotype is an external mold of the cephalon. The only pygidium available was an internal mold.

Stumm (1953a) originally suggested that specimens similar to *Monodechenella macrocephala* occurring in the Michigan Basin were conspecific to those found in the Appalachian Basin. However, the two taxa can be differentially diagnosed by the condition of three characters. The first is the condition of the lateral margins of the glabella between S1 and S2. These converge in *M. legrandsmithi* and are parallel in *M. macrocephala*. They also differ in the condition of the posterior margin of the glabella anterior of S0 (straight in *M. macrocephala*, converging in *M. legrandsmithi*) and in the number of pygidial pleural segments. There are 11 pleural segments in *M. legrandsmithi* and 12 in *M. macrocephala*.

As mentioned above, two characters are uniquely shared by *M. legrandsmithi* and *M. macrocephala*. These characters are S1 contacts S0 and 14 pygidial axial rings. They also share a reversal to the primitive condition for character 10. These two taxa clearly are very closely related, perhaps originating due to the vicariance of an ancestral population present in both the Michigan and Appalachian Basins.

Monodechenella macrocephala
(Hall, 1861)
Figures 40, 41

Proetus macrocephalus Hall, 1861: 77; Hall and Clarke, 1888: 116–119, pl. 21, figs. 10–21, pl. 23, figs. 30, 31.

Dechenella (subgen.?) *macrocephala* (Hall). Richter and Richter, 1926: 24.

Dechenella (*Monodechenella*) *macrocephala* (Hall). Stumm, 1953a: 123, pl. 4, fig. 3; Richter and Struve, 1959: 388, fig. 297, 2; Ellison, 1965: 158–159, pl. 18, figs. 2, 3; Eldredge and Ormiston, 1979: 164.

Dechenella macrocephala (Hall). Speyer and Brett, 1986: 316, 318–319, 321; Speyer, 1987: fig. 12g.

DIAGNOSIS: Same as for genus; also, lateral margins of glabella between S1 and nearly S2 parallel; S1 contacts S0; posterior margin of glabella anterior of S0, in dorsal view, straight; pygidial interpleural furrows absent; border posteriorly long flat region, equal to length (sag.) of first 1.5 axial rings; 14 axial rings; pleurae laterally deflected anteriorly relative to arc of pleurae medially; 12 pleural segments.

TYPES: Stumm (1953a) treated NYSM 13994/1-5, now 4733–4737, as the syntypes. To this list must be added AMNH 39342, 39343, and 39345. NYSM 4734 (Hall and Clarke, 1888: pl. 21, fig. 14), a cephalon from the Hamilton Group (probably the Middle Windom Shale, Moscow Formation), Canandaigua Lake (probably Menteth Gully, west shore of the lake), NY, is here designated as the lectotype. Thus NYSM 4733, 4735–4737 and AMNH 39341, 39342, 39343, 39345, 44777 become paralectotypes. These are, respectively, Hall and Clarke's (1888, pl. 20, figs. 10, 17, 18, 19, 11, 13, 15, 16, 12).

MATERIAL: AMNH 5503/6 (2 specimens), 5503/7, 5503/8 (8 specimens), 5503/9 (4 specimens), 5503/10 (2 specimens), 5503/11 (11 specimens), 39341–39343, 39345, 44715, 44758, 44760, 44761, 44777; BMS E4253; NYSM 4733–4737; YPM 33766, 33768, 33769, 33771, 33824.

DISCUSSION: This species is known from the Deep Run Shale, Moscow Formation, Jaycox Run, near Geneseo, NY; the Middle Windom Shale, Moscow Formation, Menteth Gully, west shore of Canadaigua Lake; the Kashong Shale, Moscow Formation, Bowen Brook, near Attica, 2 mi. northwest

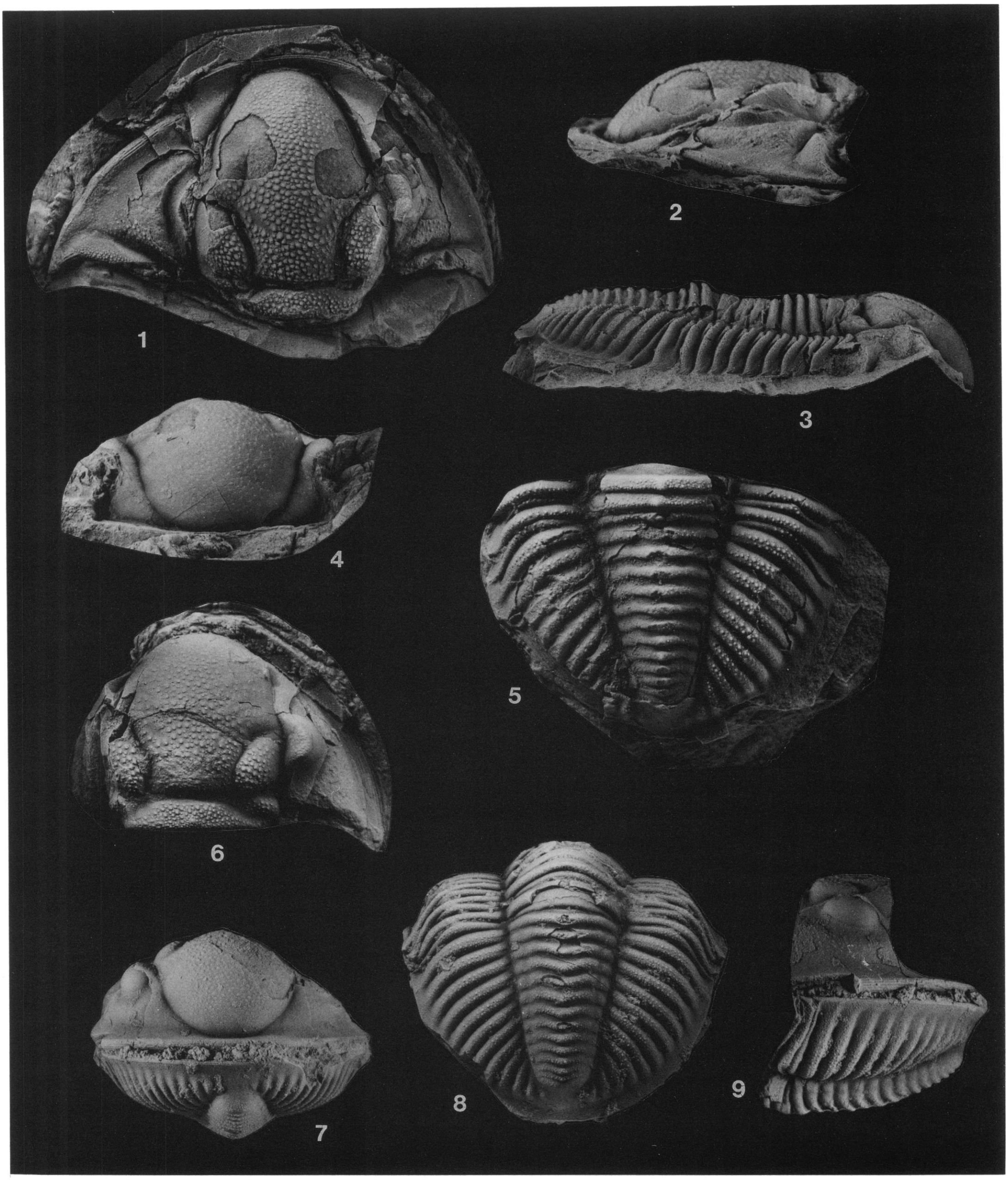


Fig. 40. *Monodechenella macrocephala* (Hall, 1861). **1, 2.** Wanakah Shale or King Ferry Shale, Tioughniogan (Givetian), west shore of Canadaigua Lake, NYSM 4734, lectotype, dorsal and lateral views of cephalon, ×2.25. **3-5.** Kashong Shale, Moscow Formation, Tioughniogan (Givetian), Bowen Brook, near Attica 2 mi. northwest of Alexander, New York, BMS E4253. **3**, Lateral view of entire specimen; ×2, **4**, anterior view of cranidium, ×1.8; **5**, dorsal view of pygidium, ×2.5. **6.** ?Moscow Formation, Tioughniogan (Givetian), Cayuga Lake. NYSM 4733, paralectotype, dorsal view of cephalon, ×2.5. **7-9.** ?Windom Shale, Encrinal Limestone, Tioughniogan (Givetian), 18 Mile Creek, New York, AMNH 44715, anterior view of entire enrolled specimen, dorsal view of pygidium, and lateral view of part of entire enrolled specimen, ×2.5.

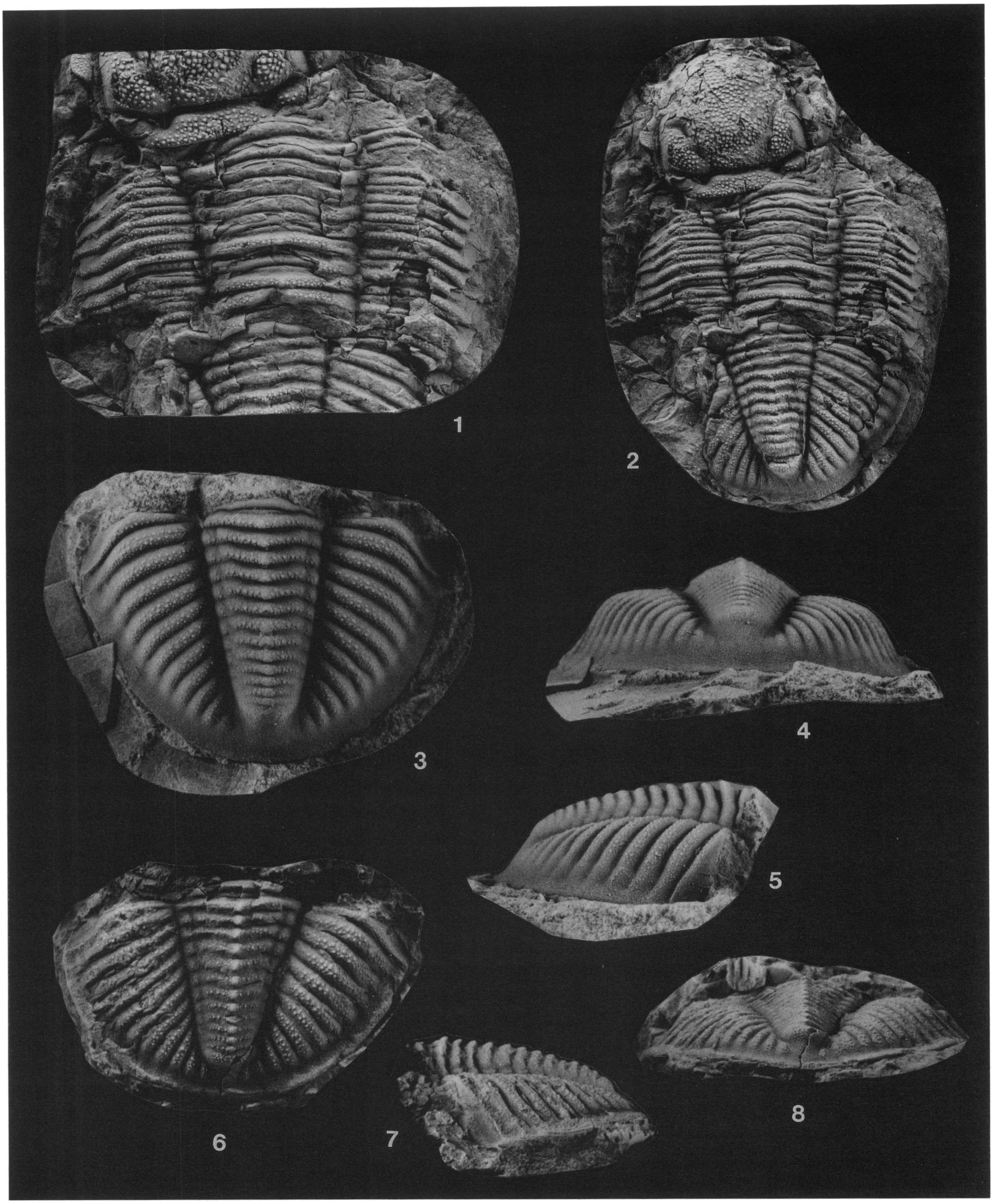


Fig. 41. *Monodechenella macrocephala* (Hall, 1861). **1, 2.** Jaycox Shale, Tioughniogan (Givetian), Jaycox Run, near Geneseo, New York, AMNH 39341, paralectotype, dorsal views of entire specimen, 1, ×2.5, 2, ×1.25. **3-5.** Hamilton Group, western New York, AMNH 39343, paralectotype, dorsal, posterior, and lateral views of pygidium, ×4. **6-8.** Hamilton Group, New York, NYSM 4736, paralectotype, dorsal, lateral, and posterior views of pygidium, ×2.7.

of Alexander, NY; the Wanakah Shale, Ludlowville Formation; from unspecified horizons in the Hamilton Group, probably the Moscow Formation, at Cayuga Lake, North Bristol, and York; from the Tully Limestone, Carpenter Road, 1 mi. from "T" intersection with NY 80, south of Sheds, NY; AMNH Loc. 3067—"Centerfield" Member, Mahantango Formation, county road between Pennsylvania Rt. 209 and Saylorsburg, PA; AMNH Loc. 3072—Frame Member, upper Mahantango Formation, roadcut along U.S. Rt. 22, opposite Huntingdon, PA; upper part of Crooked Creek Shale, Mahantango Formation at Martins Gap, PA, and possibly the Windom Shale, 18 Mile Creek, shore or Lake Erie. It is also known from York, NY, and Skaneateles Lake, NY unknown horizons, certainly Wanakah or Windom equivalents. Thus, it occurs in the Tioughniogan, particularly the late portion of this stage, and the Taghanic of the Appalachian Basin, and its distribution is associated with transgressive–regressive cycles If (the uppermost transgression) and IIa.

Hall and Clarke (1888) commented on what they claimed was the variable development of the axial row of tubercles in this species. They designated a variety *Proetus macrocephalus*, var. *a*, to distinguish specimens with tubercles from those without. There does seem to be some variation in the development of tubercles in this species. In certain specimens, the medial portions of the pygidial axial rings are V-shaped and thicken dorsally, whereas in others small tubercles are present. The differences seem to be attributable to the type of preservation of each specimen. Small discrete tubercles are developed in specimens preserved as external molds or those with cuticles intact, whereas those specimens that are internal molds show thickenings in the medial regions of the axial rings. In this study, these differences are not taken as phylogenetically significant, the variety is not treated as valid, and the taxon is coded as having anteromedial tubercles on the pygidial axial rings.

Hall and Clarke (1888) commented that this species was very similar to *Monodechenella curvimarginata*. Ellison (1965) also recognized the close affinity between these two taxa. As stated above, both authors are correct, although *M. legrandsmithi* appears to share a sister group relation with *M. macrocephala* to the exclusion of *M. curvimarginata*.

Stumm (1953a) originally designated this species the type of the subgenus *Monodechenella*. This generic name is no longer a valid subgenus of *Dechenella*. However, the subgeneric name is elevated to generic rank, and the type species of the genus is of course retained.

BIOGEOGRAPHY OF THE ENA PROETID FAUNA

The biogeographic method used to evaluate patterns in the Devonian trilobite clades studied is explained and discussed here. It was developed because of what were perceived to be inadequacies of the vicariance biogeographic method when it is applied to patterns witnessed in the fossil record and in the extant biota. The method of analysis used is based on the parsimony method developed by Brooks (1985) and Wiley (1988a, 1988b). However, the method used herein is based on coding the biogeographic state at nodes and terminal taxa in a different manner than that employed by Brooks (1985) and Wiley (1988a, 1988b). Component methods are rejected as inadequate candidates for biogeographic analysis on the basis of the cogent arguments developed by Wiley (1988a, b). Such methods do not produce most parsimonious solutions because they are based on a consensus technique (Miyamoto, 1985; Wiley, 1988a, 1988b). In addition, Assumptions 1 and 2 of the component method essentially force the scientist to invent aspects of a taxon's distribution to obviate incongruence (Wiley, 1988a, 1988b). Such a procedure cannot be accepted, as it violates the very tenets of phylogenetic analysis formulated by Hennig (Wiley, 1988b).

The assumption of an a priori relationship between speciation, evolution, and a *single* event of vicariance throughout a clade's persistence is not followed in this analysis, and this is the chief difference between this methodology and that developed by Brooks and Wiley. However, if a clade followed a strictly vicariant pattern of phylogenetic and biogeographic evolution, it would be scored in a manner identical to that developed by Brooks and Wiley and the results of the two methods would be identical. The results from these analytical methods only differ when frequent expansions or alterations in range occur through time, a situation commonly encountered in the fossil record engendered by, among other things, rising and falling sea-levels (e.g., Lieberman et al., 1991; Lieberman, 1993). The new method of analysis can handle situations when frequent dispersal occurs, with concomitant change in the ancestral ranges of species-level taxa (or other taxa, but only species are treated here).

This appears to be a strength of this method. It can handle the ideal biogeographic situation outlined by several authors, when there is an analytically clean pattern of evolution with vicariance (e.g., those examples elaborated by Grande [1985]); however, the method also can handle the much more common patterns found in the fossil record. The key is to assume that vicariance can be used to discover the relatedness of geological areas, but also to recognize that there may be several intervals of vicariance preceded by sudden range expansion throughout a clade's history. We can still discern the relatedness of areas by considering the relationship between phylogeny and the biogeographic distributions of taxa, but this relationship can be taken at face value. By means of coding the nodes of cladograms, we can recognize intervals when there were prominent changes in the relationships of two areas. Such instances will be recognized as a shift in the biogeographic distributions of taxa.

The procedure to code taxa is relatively straightforward and is illustrated by means of the data sets considered herein. Absence in an area is to be scored as "0" rather than "?", based on the assumption that the geological record reasonably reflects the actual evolutionary and distributional history of species. The joint occurrence of a taxon in two areas is taken as evidence of geological relationship between these areas, and a species occurring in regions A and B is treated as a character present in Areas or Taxa A and B, with their presence scored as a "1". Because this method was developed to avoid looking for a single episode of vicariance in all phylogenetic hypotheses, the objection that distribution of a taxon in two areas could be due to a failure to respond to vicariance is not valid.

The procedure involves five simple steps. First, phylogenies are generated for all groups that are deemed salient to this analysis. The phylogenies are assumed to represent taxa evolving during the same time interval. This is based on the recognition that the geological history of a region can change substantially over time, with particular geographic regions related to each other in significantly different ways over time. Second, the geologic or geographic regions to be analyzed are recognized. Third, the occurrence of each taxon in an area is determined and mapped on the terminal taxa of the cladogram. Some taxa can occur in different areas through time. Only those areas associated with the time of diversification between sister taxa are treated at this stage. This is because subsequent changes in area of occurrence do not have relevance if we wish to ascertain the geographic region that characterizes the ancestral node of two or more taxa. Fourth, the nodes on the cladogram are optimized using Fitch Optimization (Fitch, 1971), which is used for multistate characters, with all transformations between characters treated as unordered. This is done because a priori we must assume that all transformations between different areas are equiprobable, as the relationship between these areas is of course what we wish to discern. Fifth, all terminal taxa and all ancestral nodes are now coded into the format of a data matrix, such as those used in phylogenetic analysis. The areas are treated following the methodology of Brooks Parsimony Analysis (BPA), and the distributions of taxa are scored as the characters of these taxa.

All ancestral nodes and all terminal taxa are treated as characters and are scored in the following manner. Presence in a particular area is denoted by a "1" in the appropriate taxon. However, the axis of the cladogram must also be examined. Certain instances of changes in area occupied between adjacent ancestral nodes and between an ancestral node and its associated terminal taxon will be recognized that require special coding. When one proceeds up a tree from an ancestral to a descendant node and there is a change in area of occurrence that is either a range contraction, expansion, or shift, then the descendant node is coded as an ordered multistate character, with presence in the ancestral area coded by "1" and presence in the descendant area(s) coded by a "2"', and so on. The same procedure is followed when a terminal taxon differs in area of occurrence from its immediately ancestral node. In addition, certain taxa will be recognized to occur first in one area, then in another through time, particularly for taxa that persist over long periods. These changes in area relationship will also be coded as ordered multistate transformations. For instance, if the ancestral geographic occurrence of a terminal taxon is area A and at time t_1 the terminal taxon occurs in area B and at time t_2 it occurs in area C, this terminal taxon would be coded as an ordered multistate character, with a "1" in the row for Area A, a "2" in the row for Area B, and a "3" in the row for Area C.

This procedure is shown for the phylogenies deduced for the genera *Crassiproetus*, *Basidechenella*, *Dechenella*, and *Monodechenella*. All ancestral nodes are optimized using Fitch optimization and the characters for the terminal taxa are also shown (see fig. 42a–d). The ancestral biogeographic conditions for the three genera of Proetinae were determined from the optimization of biogeographic data to the higher-level phylogeny of the Proetinae shown in figure 14. For the "*Thebanaspis* clade" only the taxa *Monodechenella curvimarginata*, *M. legrandsmithi*, and *M. macrocephala* were considered because this genus is the only portion of that clade for which detailed phylogenetic analyses on many taxa were performed. The biogeographic state of the last common ancestor of these three taxa was deduced in the same manner as presented above. 0 is the ARCTIC Faunal Realm, 1 is the APPALACHIAN BASIN, 2 is the ILLINOIS BASIN, 3 is the MICHIGAN BASIN, and 4 is ARMORICA, which is treated as synonymous with the Old World/Rhenish–Bohemian Faunal Realm. OUTGROUP is the hypothetical ancestral biogeographic realm. (One taxon, *Crassiproetus globosus* occurs in the Pragian-Emsian of Kazakhstan. As this is obviously an autapomorphous distribution, which will have no affect on the biogeographic conclusions if it is included, other than placing Kazakhstan sister to the other biogeographic regions considered, its terminal coding and the coding of its ancestral node are left out.) All taxa (characters) are coded as 0 or primitively absent from the OUTGROUP or ancestral biogeographic realm. To illustrate the use of this method, a detailed discussion for coding the data matrix using the genus *Basidechenella* is presented below. In the phylogeny of *Basidechenella* the species *B. timwhitei* has been removed because it is Carboniferous in age and thus significantly postdates whatever biogeographic processes may have been associated with diversification in this clade. In addition, the intervening Late Devonian through Early Carboniferous history of this genus has been effaced.

The ancestral biogeographic state of *Basidechenella* is represented by character 0. It is coded as present in 0, 1, 2, 3 and absent in 4 and OUTGROUP or 0, 1, 1, 1, 1, 0. The transition between the ancestral condition and the basal node on the phylogeny is treated as a transition from present in 0, 1, 2, 3 to present in 0, 1, 2, 3, 4. This is depicted by character 17, which is coded as an ordered multistate character, with the states 0, 1, 1, 1, 1, 2.

Other characters (taxa) will also be coded as multistate using this method. *Basidechenella lucasensis* is known from the Illinois Basin in the Eifelian and from the Michigan Basin in the Givetian. Thus, this taxon (character 7) is coded as a multistate ordered character, with the coding 0, 0, 0, 1, 2, 0. This is because the transition from the Eifelian to the Givetian involved a transition in area relationships, which can be informative for questions of biogeographic propinquity among areas. In addition, *B. lucasensis* needs to be coded with an extra character, as the transition from the last common ancestor of *B. lucasensis* involves a change in areas occupied. In particular, there was a contraction in range possibly associated with vicariant splitting, with the ancestor of *B. lucasensis* primitively present in areas 1, 2, and 3, but as a species it is only recovered from 2, the Illinois Basin. Thus this species (character) is coded as 0, 0, 1, 2, 1, 0.

Other characters are treated as simple binary characters. For instance, *Basidechenella arkonensis* is known from the Appalachian

(1) and Michigan Basins (3). The ancestral state for this taxon, character 20, is also to be present in 1 and 3 (see fig. 42a). Thus, both of these characters (taxa) are coded as 0, 0, 1, 0, 1, 0.

The data matrix that shows how all cladograms were coded is given in table 12. The optimizations for each genus-level phylogeny were taken from figure 42b for *Crassiproetus*, figure 42c for *Dechenella*, and figure 42d for the "*Thebanaspis* clade." Characters 0–27 are the codings for *Basidechenella*, 28–55 are the codings for *Crassiproetus*, 56–91 are the codings for *Dechenella*, and 92–97 are the codings for the "*Thebanaspis* clade." As mentioned above, for the "*Thebanaspis* clade," only the biogeographic states of three of the species of the genus *Monodechenella* (*M. curvimarginata*, *M. legrandsmithi*, and *M. macrocephala*) and their ancestral states were coded.

When these data were analyzed using the exhaustive search option of PAUP 3.0q (Swofford, 1990), a single most parsimonious tree was produced. It is shown in figure 43 and has a length of 233, a consistency index of .84, and a retention index of .70. It suggests that the ARCTIC and ARMORICAN faunal realms share a sister relationship and that these taxa are sister to the different biogeographic basins in ENA. In ENA, the MICHIGAN and APPALACHIAN BASINS are sister taxa. The tree frequency distribution indicates several salient features. First, the most parsimonious tree is five steps shorter than the next most parsimonious tree. In addition, it takes 20 additional steps to break the APPALACHIAN BASIN–MICHIGAN BASIN sister relationship and put the MICHIGAN and ILLINOIS BASINS as sister taxa.

The tree frequency distribution for this data set only has a moderate amount of negative skewness, indicating phylogenetic information, with a g_1 statistic of-.28 (Hillis, 1991). According to Hillis (1991), this value differs from the range of tree length distributions produced by random data, but at a value that is not significant at the .05 level. Thus, the phylogenetic signal in the data is not very strong. We can employ additional analytical techniques to ascertain what components of the data base may be contributing to the appearance of randomness in the data. To do this, a bootstrap analysis was run on the data to assess how well supported the statements about biogeographic area relationships are. One hundred bootstrap replications were used in an heuristic search with a simple addition sequence and tree-bisection–reconnection branch-swapping performed. A 50% majority-rule consensus tree was produced from the results of the bootstrap analysis. The bootstrap tree was identical to the single most parsimonious tree produced by the exhaustive search. The ARCTIC/ARMORICA node was reproduced in 83% of the replicates. The ENA relationship was reproduced in 100% of the replicates, and the APPALACHIAN BASIN/MICHIGAN BASIN sister relationship was reproduced in 98% of the replicates. The ENA Realm and the close relationship of the APPALACHIAN and MICHIGAN BASINS are particularly well supported by the phylogenetic and distributional evidence.

The biogeographic method developed here suggests the following patterns that can be related to geological processes, changes in sea-level, and/or distance between geographic basins. The Michigan and Appalachian Basins are most closely related to the exclusion of the Illinois Basin. This follows the predictions of Beaumont et al.'s (1988) model, in which uplift of the Findlay and Kankakee Arches during and after the Middle Devonian left a thin linkage between the Michgan and Appalachian Basins but isolated the Illinois Basin from the Appalachian and Michigan Basins. This result is further reinforced by, though of course it is also influenced by, the distributions of individual species of proetids in the Eifelian and Givetian. However, we must be careful to recognize the pattern of environmental and spatial restriction that most of the proetid taxa show, and compare only relative numbers of taxa shared between different basins in ENA. Excluding taxa found in all basins, in the Eifelian, one species is shared by the Appalachian and Illinois Basins, three species are shared by the Appalachian and Michigan Basins, and two species are shared by the Illinois and Michigan Basins. In the Givetian, no species are shared by the Appalachian and Illinois Basins, two species are shared by the Appalachian and Michigan Basins, and no species are shared

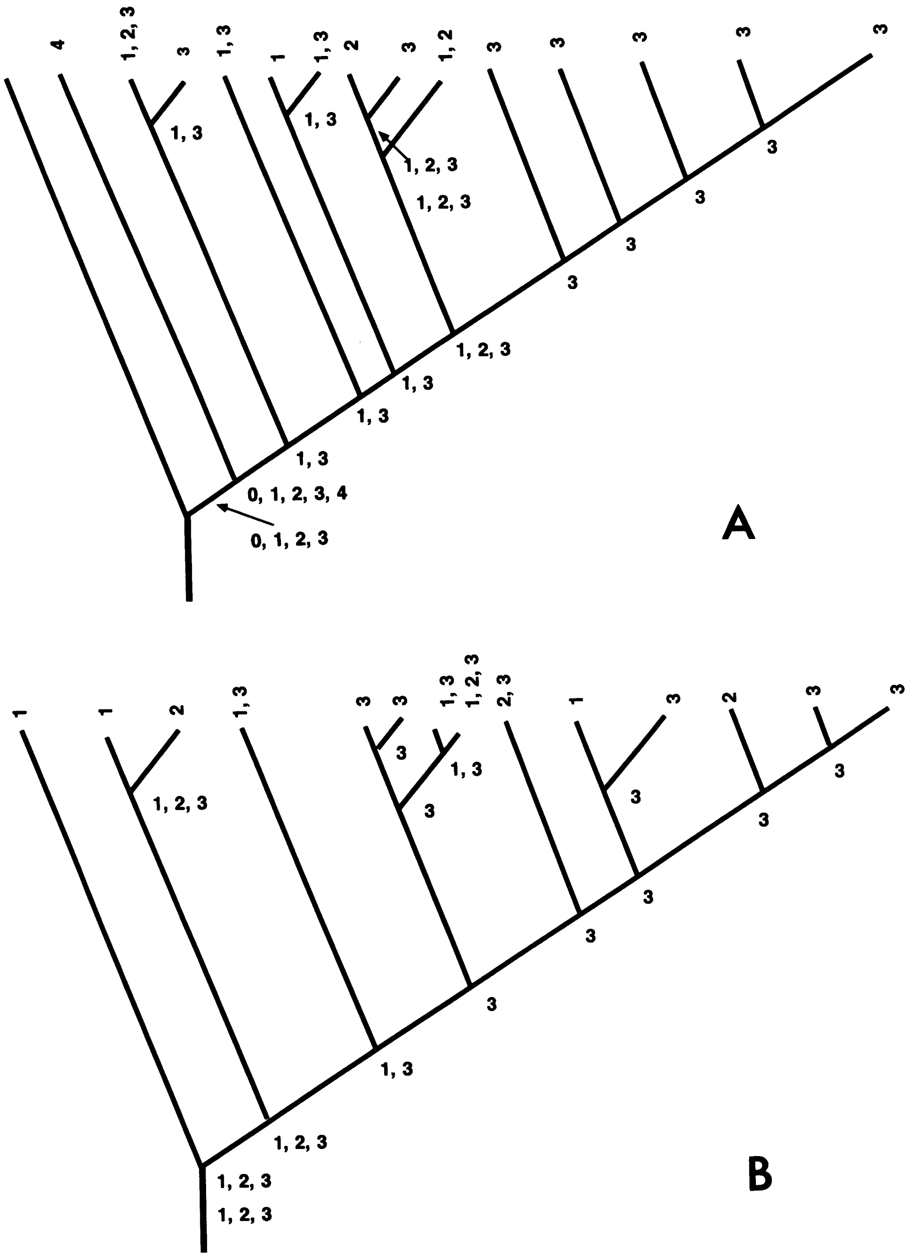
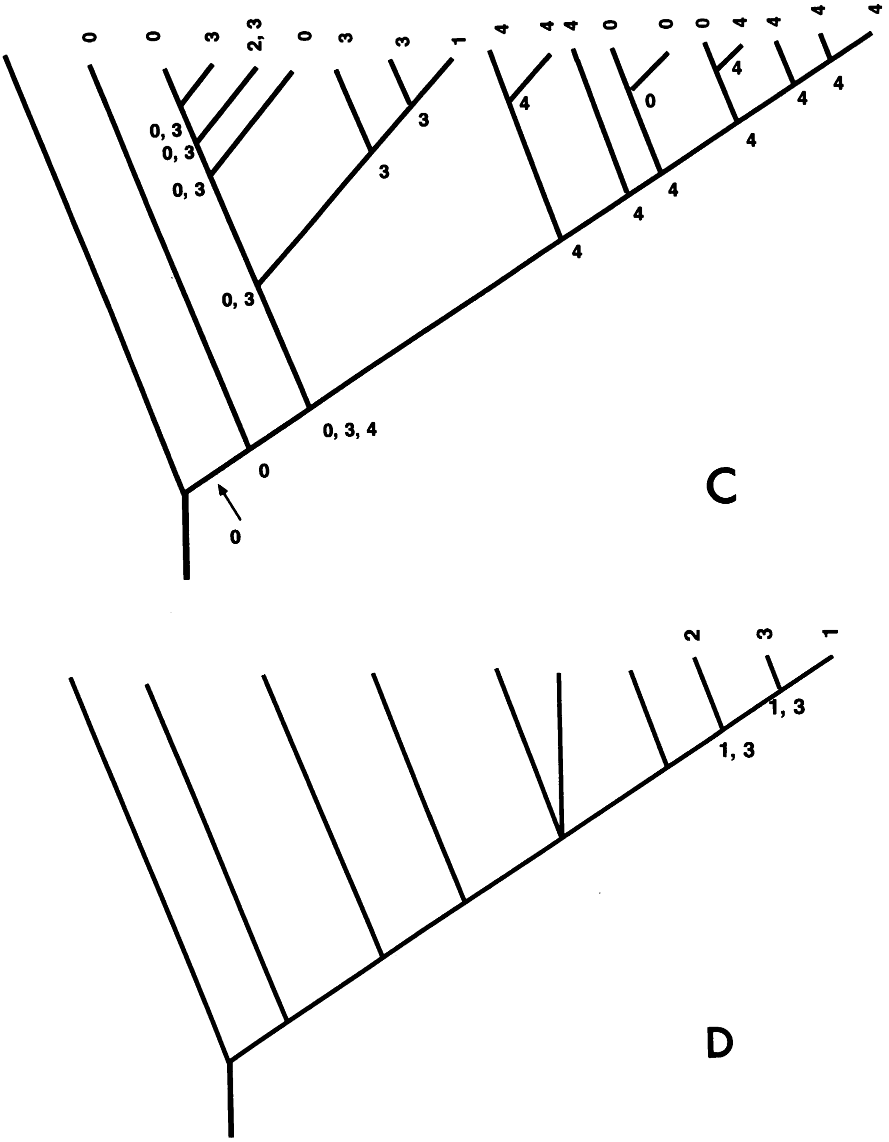


Fig. 42. Biogeographic states optimized to nodes on the phylogenies that were produced via the parsimony analyses given herein. Fitch optimization, which treats transitions between multistate characters as unordered, was used. The biogeographic character states for nodes and terminal taxa are shown. Optimizations for basal node were obtained using the higher-level phylogeny with the biogeographic states optimized given in figure 14. "0" is the Arctic Faunal Realm, "1" is the Appalachian Basin, "2" is the Illinois Basin, "3" is the Michigan Basin, and "4" is Armorica, which is treated as equivalent to the Old World/Rhenish–Bohemian Faunal Realm. Outgroups are not included in the optimizations except in the case of the phylogeny of *Crassiproetus*. **A.** Optimizations to the phylogeny for *Basidechenella* shown in figure 22. The sole Carboniferous taxon, *Basidechenella timwhitei*, new species, has been deleted from the phylogeny. **B.** Optimizations to phylogeny for *Crassiproetus* given in figure 12. The



taxon with the autapomorphous distribution in Kazakhstan, *Crassiproetus globosus* Maximova, 1960, has been deleted from the phylogeny. In addition, *Crassiproetus brevispinosus* Fagerstrom, 1961, is treated as sister to *Crassiproetus crassimarginatus* (Hall, 1843). **C.** Optimizations to phylogeny given for *Dechenella* in figure 33. **D.** Optimizations to phylogeny given for the "*Thebanaspis* clade" in figure 36. Only the taxa with adequate representation in Eastern North America, *Monodechenella curvimarginata* (Hall and Clarke, 1888), *M. legrandsmithi*, new species, and *M. macrocephala* (Hall, 1861), and the nodes associated with these taxa are optimized.

by the Illinois and Michigan Basins. In spite of environmental restriction in many proetid taxa, a progressive isolation of the Illinois Basin may be recognizable; however, these results need to be qualified. There are taxa from the Illinois Basin that could not be obtained in this study, but which must be considered to verify if they are all endemic species as Hickerson (1992) has claimed.

The bigeographic method developed herein also suggests that the ARCTIC and ARMORICAN biogeographic realms are most

TABLE 12

Character State Distribution for Biogeographic Analysis

Areas are treated as taxa; taxa and ancestral nodes in phylogenies are treated as characters[a]

		1	11111	11112	22222	22223	33333	33334	44444	44445	55555	55556	66666	66667	77777	77778	88888	88889	99999	99
	012345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67
Ancestor	000000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00
Arctic	100000	00000	00000	10000	00000	00000	00000	00000	00000	00000	00000	11211	20000	00111	10001	12111	11100	00000	00000	00
Appalachian Basin	101112	11012	00000	12111	11110	00122	11001	02000	01111	10000	00012	00000	00020	00000	00000	00000	00000	00000	01112	11
Illinois Basin	102000	02112	00001	11000	02110	00111	20002	20020	01110	00000	00000	00002	00000	00000	00000	00000	00000	00000	00200	00
Michigan Basin	101211	11221	11110	12111	11111	11111	11111	11111	11111	21111	11111	00121	11110	00000	00000	22221	11100	00000	01121	11
Armorica	010000	00000	00000	21000	00000	00000	00000	00000	00000	00000	00000	00000	00001	11000	21110	21000	00211	11111	10000	00

[a] "0" implies that a taxon is absent in an area; "1" and "2" imply that a taxon is present. All multistate characters are treated as additive (ordered). Ancestor refers to the ancestral biogeographic state of all species, treated as absent from all regions; Arctic refers to the Canadian Arctic Islands, Alaska, the Yukon Territory, and the Northwest Territories; Armorican refers to taxa from the German Eifel District, Bohemia, Morocco, and southern England. The basins of ENA follow their designation in Beaumont et al. (1988) and Leighton et al. (1991) and refer to their boundaries in the Middle Devonian.

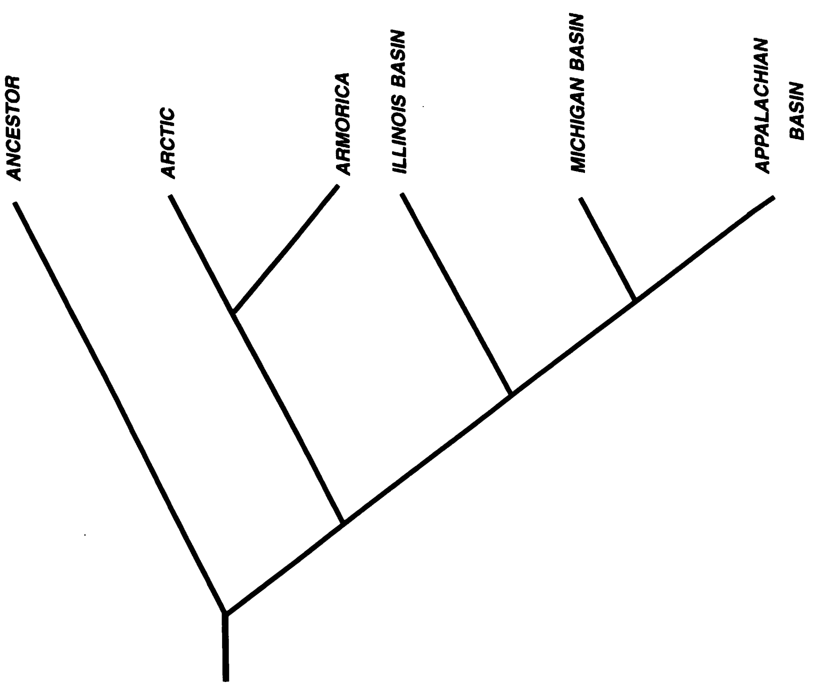


Fig. 43. A cladogram showing the relationships during the Middle Devonian for the biogeographic areas considered in this analysis. The cladogram was generated using the data matrix given in table 12. It is the single most parsimonious tree produced using the exhaustive search option of PAUP 3.0q (Swofford, 1990). The tree has a length of 233 steps, a consistency index of .84, and a retention index of .70. The data matrix was coded using the biogeographic methodology discussed in the text, which allows for multiple instances of range expansion with subsequent vicariance in each clade considered.

closely related to each other to the exclusion of the ENA realm. These two realms are sister to the basins in ENA, and this is consistent with data from several avenues that indicate that the ENA realm contains elements from both the ARCTIC and ARMORICAN faunal realms. This may have implications for plate tectonic reconstructions of the paleogeography of the Middle Devonian. For instance, the reconstructions presented in Ziegler (1991) suggest that geologically it would be difficult to argue for significant interactions between ARMORICA and ENA to the exclusion of the ARCTIC faunal realm. These reconstructions are not refuted by the data presented herein. Unfortunately, these data cannot test the reconstructions of Van Der Voo (1988) or Kent and Van Der Voo (1990) that advocated a possible sister group relationship between ENA and north Africa or ENA and northern South America, respectively, because too few taxa treated herein occur in either northern South America or northern Africa. Studies underway (Lieberman and Kloc, in review) may clarify this issue.

MACROEVOLUTIONARY PATTERNS AND PROCESSES

Patterns of Diversification

In order to perform a detailed analysis of the relationship between phylogenetic patterns and biogeographic and environmental changes, a few procedures must be utilized and a few assumptions must be made. First, we assume that the phylogenies generated reasonably reflect the evolutionary histories of the groups being considered. Second, we must assume that there is a relationship between patterns of evolution and biogeographic/environmental controls. Third, we assume that for the limits of resolution of this analysis, species can be ancestral taxa, although

TABLE 13
Speciation Events in the Proetid Trilobites Considered for Different Geologic Stages of the Latest Lower and Middle Devonian[a]

	Speciation events
Latest Sawkillian/Southwoodian	
Crassiproetus	8
Basidechenella	7
Dechenella	2
Monodechenella	1
Total	18
Cazenovian	
Dechenella	3
Crassiproetus	3
Basidechenella	5
Total	11
Tioughniogan	
Crassiproetus	1
Total	1
Cazenovian or Tioughniogan	
Basidechenella	1
Monodechenella	2
Total	3
Cazenovian, Tioughniogan, or Taghanic	
Crassiproetus	1
Basidechenella	1
Total	2

[a] New Yorkian stage names are used. Their possible European equivalents have been discussed in the text. The latest Sawkillian Bois Blanc Limestone/Schoharie Grit and the Southwoodian are treated as a single unit for analysis.

we will not recognize individual species as such. This is because we cannot distinguish between different populations of a species. Thus, species-level taxa are treated like quantum particles in a manner analogous to the wave–particle duality of electrons (e.g., Feynman, 1965). The act of observation affects conclusions about the nature of electrons. The same appears to hold true for species. When we observe species as taxa they cannot be ancestral, whereas when we do not observe them as indivisible taxa, recognizing that species could be paraphyletic but we are unable to differentiate among separate populations for these types of fossil species, then the possibility exists that they could be ancestral. Phylogenetic reconstruction of taxa obviates the role of these taxa as ancestral, but their existence as species may allow them to be ancestral. This will affect conclusions made about minimum ages of divergence, and thus it has some relevance.

The geologic stage in which the ENA species of proetids first appeared was determined using stratigraphic first occurrence and the phylogenetic topology of the species in each genus. The Sawkillian and Southwoodian Stages are treated as a single stage because only the last portion of the Sawkillian, when the Bois Blanc Limestone and Schoharie Grit were deposited, was considered. The other stages considered were the Cazenovian, the Tioughniogan, and the Taghanic. Discordance between stratigraphic first occurrence and phylogenetic position is manifest in only four cases. The first concerns the phylogenetic position of *Crassiproetus globosus*. It is purported to be Pragian–Emsian (Maximova, 1968). If this stratigraphic assignation is correct, then we must conclude that the lineage leading to *C. neoturgidus* and *C. halliturgidus* must have appeared before the Eifelian/Southwoodian. In addition, *Crassiproetus calhounensis* (or the lineage leading to this species), known from the Taghanic Stage, must have evolved by the Cazenovian. *Basidechenella rowi* (or the lineage leading to this species), known from the Cazenovian, the Tioughniogan, and the Taghanic, must have evolved by the Eifelian/Southwoodian. Finally, *Basidechenella elevata* (or the lineage leading to it), known from the Taghanic Stage must have evolved by the Cazenovian.

These data can be adapted to develop minimum levels of diversification during these times (see table 13). We can consider species to be potentially ancestral to other taxa, although not polyphyletic. Thus, we can treat our phylogenies as evolutionary trees sensu Eldredge and Cracraft (1980) and map out patterns of ancestral–descendant relationship. When we do this for the late Sawkillian and Southwoodian Stages we come up with a minimum of eight speciation events in the genus *Crassiproetus*, seven in the genus *Basidechenella*, two in the genus *Dechenella*, and one in the genus *Monodechenella*. Thus, assuming the fossil record of these proetids is reasonably complete, there were a minimum of 18 diversification events in the latest Emsian and early to late Eifelian in the genera of the Middle Devonian proetids in ENA considered here. In the Cazenovian, Tioughniogan, and Taghanic Stages of the latest Eifelian and Givetian, we recognize a minimum of 17 speciation events, at least 5 in *Crassiproetus*, 7 in *Basidechenella*, 3 in *Dechenella*, and 2 in *Monodechenella*.

When these data from the latest Eifelian and Givetian are broken down by stages (see table 13) we recognize 11 speciation events during the Cazenovian, one during the Tioughniogan, three during the Cazenvoian or Tioughniogan, and two during the Cazenovian, Tioughniogan, or Taghanic. In the genus *Basidechenella* one speciation event occurs during the Cazenovian or Tioughniogan, five during the Cazenovian, and one during the Cazenovian, Tioughniogan, or Taghanic. In the genus *Crassiproetus* three speciation events occur during the Cazenovian, one speciation event occurs during the Cazenovian, Tioughniogan, or Taghnic, and one speciation event occurs during the Tioughniogan. In the genus *Dechenella* three speciation events occur during the Cazenovian, and in the genus *Monodechenella* two speciation events occur during the Cazenovian or Tioughniogan.

If we use approximate time values gleaned from the DNAG time scale we can relate these diversification events to the duration of stages to see if there was a difference between the diversification rate of these groups during periods of widespread limestone deposition (the Sawkillian, Southwoodian, and Taghanic) versus periods of restricted limestone deposition (the Cazenovian and Tioughniogan). The duration of the Southwoodian is considered to be 387–380 Ma. We extend this lower boundary down another 2.33 million years to include the late Sawkillian to the base of the Bois Blanc Limestone and the Schoharie Grit in the upper Emsian, thereby totaling 9.33 million years of recorded widespread limestone deposition in the Emsian and Eifelian of ENA. This value was obtained by using the DNAG time scale, which treats the length of the Emsian as 7 million years. The Schoharie and Bois Blanc, largely coeval deposits, represent one of three formations consigned to the Emsian in ENA, using Kirchgasser et al. (1985). These formations are treated as of equal length (one-third of seven is 2.33). Again, following the DNAG time scale, the boundaries of the Givetian are treated as 380–374 Ma, and the end of the Taghanic is treated as 375 Ma (C. Brett, personal commun.). However, the base of the Cazenovian does not exactly correspond to the base of the Givetian, but rather appears to precede it (Kirchgasser et al., 1985; Griffing and ver Straeten, 1991; Rickard, 1989). In particular, only the portion of the Cazenovian above the Union Springs Member and the Cherry Valley Limestone can be assigned to the Givetian. Three of the speciation events (all for *Dechenella*) during the interval of restricted limestone deposition were placed in the basal portion of the Cazenovian, immediately below the Cherry Valley Limestone. Thus, they occur in the very latest Eifelian. It is difficult to ascertain for sure what length of time this interval represents; thus a technique for estimation must be employed. The length of this interval is taken as roughly equivalent to the length of the Tully Limestone, which has a duration of approximately 1 million years (C. Brett, personal commun.). Therefore, the interval of restricted limestone deposition during the Cazenovian and the Tioughniogan is assumed to occupy 6 million years.

Eighteen diversification events in the 9.33 million years of the Southwoodian and Sawkillian translates to 1.93 speciation events per million years. In the Cazenovian and Tioughniogan there were 15 speciation events. In addition, two speciation events occurred in either the Cazenovian, the Tioughniogan, or the Taghanic. Treating the Cazenovian and Tioughniogan as being of equal duration for the 5 million-year span of the Hamilton Group, excluding the Taghanic, then these two stages represent five-sixths of Hamilton time. Thus, assuming that these events occurred with equal probability within any of these stages, the chance that these two speciation events actually occurred during the restricted limestone deposition interval of the Hamilton Group (the Cazenovian and the Tioughniogan) is five-sixths for each event; therefore, a total of 1.67 speciation events can be consigned to this interval from these ambiguously placed events. Using these estimations, a total of 16.67 speciation events occurred in the 6 million-year span of the Cazenovian (not counting the Seneca Limestone) and the Tioughniogan. This is equivalent to a rate of 2.78 speciation events per million years. This value suggests that speciation rate had increased by 44% in the upper Cazenovian and the Tioughniogan relative to the Sawkillian/Southwoodian. In addition, by the Taghanic Stage, when widespread limestone deposition had returned, speciation rates again clearly declined, with approximately .67 speciation events per million years.

These data first indicate an increase in speciation rate during the period of limestone restriction engendered by the Acadian Orogeny. This pattern of increased speciation rate during geographic and environmental restrictions can be related explicitly to macroevolutionary hypotheses about diversification in clades and their relation to levels of endemism. In particular, Vrba (1985, 1992) developed the turnover-pulse hypothesis to explain a phenomenon of diversification in the South American and African tropical mammalian faunas of the Neogene that appears analogous to the pattern seen here. The Acadian Orogeny largely restricted most proetid trilobite taxa to more isolated regions of ENA due to changes in environment and the tracking of preferred environment by taxa. This is similar to the restriction of the tropical mammalian fauna of South America and Africa to refugia during the Neogene in the glacial portions of the glacial–interglacial cycles (Vrba, 1985, 1992). Glacial climates restricted the preferred environment of many tropical mammalian taxa, and, in turn, as these taxa tracked their preferred environment, they became more highly endemic and restricted geographically. This appears to have led to elevated diversification rates in this fauna, following the predictions of the allopatric model of speciation (Vrba, 1985, 1992; Eldredge, 1989). The Acadian Orogeny, by producing changes in the environment, largely restricted the preferred environment of proetid trilobite taxa. In addition, it appears that the endemism and geographic restriction of the proetids, with concomitant reduction in population size, led to elevated speciation rates in these groups during the latest Eifelian and most of the Givetian (relative to intervals in which their preferred environment was widespread, both in the Sawkillian/Southwoodian and the Taghanic. This follows the predictions of Vrba's (1985, 1992) turnover-pulse hypothesis. In addition to this analysis of diversification levels based strictly on lumped trilobite taxa, a study is underway that considers how diversification levels are related to the number of lineages extant at any one time.

Patterns of Extinction

Although diversification levels fit the tenets of Vrba's turnover-pulse hypothesis, clearly something had happened to these trilobite clades by the Taghanic such that they were no longer diversifying at the level they were when similar environments were widespread in the Eifelian. In particular, only two species, *Basidechenella rowi* and *Monodechenella macrocephala*, are found in the Appalachian Basin when widespread limestones occur there again. When limestone deposition was widespread in the Sawkillian and Southwoodian Stages, there were substantial numbers of proetid species in the Appalachian Basin. As discussed above under the genera *Crassiproetus*, *Basidechenella*, *Dechenella*, and *Monodechenella*, there is a strong association between restriction of environment, decline of diversity, and extinction of species in these four clades. It was hypothesized that the restriction of limestone environments at the end of the Eifelian in ENA, and then elimination of limestone environments at the end of the Taghanic in ENA, first decimated and then extinguished populations of these species. The actual levels of extinction are briefly elucidated here. Taxonomic analysis and data on stratigraphic distributions can be combined to develop provisional levels of extinction (see table 14). These are based on the assumption that the last interval of occurrence approximates the interval of extinction. They indicate that by the end of the Eifelian (Southwoodian) one species of *Monodechenella*, four species of *Basidechenella*, five species of *Crassiproetus*, and two species of *Dechenella* went extinct, totaling 12 species extinctions during or at the end of the Eifelian. It is impossible to discern with the available evidence if the Kacak-Otomari Event (Walliser, 1985) at the end of the Eifelian played a prominent role in these extinctions. This event is hypothesized to have played an important role in the extinction of several trilobite subfamilies (Feist, 1991). During or at the end of the Taghanic three species of *Crassiproetus*, four species of *Basidechenella*, one species of *Dechenella*, and one species of *Monodechenella* went extinct. It cannot be discerned whether or not these extinctions are associated with House's (1985) Taghanic Event or the synonymous *Pharciceras* Event of Walliser (1985).

In addition, by the Taghanic, speciation rates had clearly declined following the predictions of the turnover-pulse hypothesis. As discussed above, during the Taghanic, limestone environments had once again spread across ENA, and these environments appear to be the preferred environment for members of the proetid genera studied herein. Reduction in endemism should be associated with declining speciation rates if Vrba's (1985, 1992) turnover-pulse hypothesis is correct. The decline of speciation rates during the Taghanic mirrors these predictions. However, at the end of the Taghanic, there was widespread deposition of black shales and the elimination of the preferred environment of the proetids not only in the Appalachian Basin, but across all of ENA. This spread of black shales after the end of the Taghanic Stage has been referred to as the Taghanic Event by House (1985) or the *Pharciceras* Event by Walliser (1985), and probably played an important role in the extinction of the bulk of species diversity in these genera. Thus, this appears to be a clear case of environmental extirpation mediating the extinction of a clade. However, the mode of extinction at the end of the Taghanic Stage (late Givetian) may not only have been precipitated by the Taghanic Event or environmental extirpation, but it also may fit the signature pattern of the Frasnian–Famennian extinction events that McGhee (1988a, 1988b, 1989) recognized in brachiopod taxa. McGhee recognized that during the Frasnian and Famennian a putative mass-extinction event was actually being generated not solely by an elevated extinction rate, but also by a declining diversification rate. Extrapolating from Vrba's turnover-pulse hypothesis, the disappearance of barriers creating endemism may have contributed to the declining diversification rate.

The applicability of McGhee's (1988a, 1988b) model to data on proetid trilobites from the Givetian can be quantified by a more detailed consideration of actual patterns of extinctions during particular stages (see table 14). During the early Cazenovian two species of *Dechenella* became extinct, during the middle or at the end of the Cazenovian four species became extinct (one species of *Crassiproetus* and three species of *Basidechenella*) and during or at the end of the Tioughniogan five species became extinct (two species of *Crassiproetus*, two species of *Basidechenella*, and one species of *Monodechenella*). During the entire interval of the Taghanic three species of *Crassiproetus*, four species of *Basidechenella*, one species of *Dechenella*, and

TABLE 14

Species-level Extinction Events for Different Geologic Stages Classified by Genera

	Extinction events
Southwoodian	
Crassiproetus	6
Basidechenella	4
Dechenella	2
Monodechenella	1
Total	13
Cazenovian	
Crassiproetus	1
Basidechenella	3
Dechenella	2
Total	6
Tioughniogan	
Crassiproetus	2
Basidechenella	2
Monodechenella	1
Total	5
Taghanic	
Crassiproetus	3
Basidechenella	4
Dechenella	1
Monodechenella	1
Total	9

one species of *Monodechenella* became extinct. These extinction levels for the Cazenovian, Tioughniogan, and Taghanic 6, 5, and 8 must be put in perspective by realizing that the Taghanic was probably of far shorter duration than the Cazenovian or the Tioughniogan. This implies a significantly elevated extinction rate in the Taghanic. Thus, both declining speciation rates and elevated extinction rates contributed to the demise of the proetid trilobite fauna of ENA; the extinction of the proetids at the end of the Taghanic is associated with an extinction event of considerable magnitude, the demise of the rest of the Hamilton fauna.

The analysis of speciation and extinction presented above does require certain caveats. In particular, the role of the environment was assayed using a simple distinction between limestone environments and clastic environments. This was done because of the consistent association of proetid taxa with limestones. However, obviously a more detailed refinement of environment could provide additional illumination, but at this time isotopic evidence is not available to conduct a more detailed analysis. The role of environmental extirpation in mediating the extinction of clades also needs qualification. In particular, environments should not simply disappear, but rather they should migrate. If taxa prefer certain environments, then they should track those facies belts. Thus, we should be able to laterally trace migrating environments and migrating taxa. However, because of the nature of the fossil record, and also possibly because the nature of this extinction event, this does not appear to be possible.

Other caveats that must be mentioned include the difficulty of quantifying the durations of the stratal intervals being studied. Because several of the stratigraphic units being analyzed did not begin or terminate at the Eifelian or Givetian boundaries, estimations had to be made about the lengths of these units. In addition, even the dates for the initiation and termination of the Eifelian and the Givetian have significant error bars associated with them. These dates were used to calculate speciation rates. In this context, an elevation of speciation rate by nearly 50% seems substantial, but of what significance is another matter. Other potential problems when this type of data base is employed include possible discrepancies between the actual evolution of taxa and their occurrence in the fossil record, and, finally, the fact that phylogenies may not accurately reflect evolutionary history.

Although this discussion on speciation and extinction events has been presented in a largely qualitative manner it is important that it be bolstered by quantitative methods. In particular, how confident can we be that range truncation represents actual extinction? Several methods have been developed to perform such an analysis, and Marshall (1990) presents an excellent exposition of these. The method used here to establish confidence intervals on stratigraphic ranges follows the equation that he presents. The α value equals the confidence interval expressed as a fraction of the stratigraphic range. This value is calculated using the number of known fossiliferous horizons for a taxon.

On the basis of the collections available it was difficult to discern the number of horizons from which a specimen was recovered. The following method was used to calculate horizons. Each locality was treated as a separate horizon except in the case of *Dechenella haldemani*, which is known to occur in two closely spaced (often condensed to one) geographically widespread event beds or epiboles that are taken to be coeval (e.g., Anderson et al., 1988; Griffing and ver Straeten, 1991). Every formation a specimen is known from is taken as a single horizon, with first occurrences placed at the base of the formation and last occurrences placed at the top of the formation. Although this may appear to artificially emphasize appearances and extinctions at the bases and tops of the formations respectively, in the calculation of confidence intervals it actually does the reverse. This is because it lengthens the range of a taxon, and confidence intervals are expressed as a fraction of the taxon's total range.

Marshall (1990) also discusses some of the assumptions necessary to apply the method. One assumption is that the fossil horizons are randomly distributed, with sedimentation rates and fossilization potential stochastically constant. In addition, collection intensity also must not vary across localities if the method is to be applied. With the state of collections available, it is difficult to ascertain if these assumptions are satisfied. The important control that sedimentary facies such as calcareous deposits exert on the distribution of species of proetids was recognized above, and this suggests that at least in the Appalachian Basin, where limestone deposition is not continuous during the Givetian, fossil horizons are not randomly distributed. However, in the Michigan Basin limestone deposition appears to be continuous at least up to the end of the Taghanic stage, and there the requirement of randomly distributed fossil horizons appears to be satisfied for the Eifelian and most of the Givetian.

Results are expressed in terms of 50% confidence intervals on entire ranges, with the number of horizons used given in parentheses next to each taxon, and the α values given expressed next to each taxon. The smaller the α value, the more confident we can be that the range truncation represents an actual extinction. The values equal the amount of "horizons" the range of a taxon needs to be extended. A taxon must be known from at least two horizons to calculate confidence intervals. Values are from Marshall (1990: table 1); they are: *Crassiproetus traversensis* (9) = 0.16, *C. crassimarginatus* (8) = 0.19, *C. brevispinosus* (4) = 0.46, *C. microgranulatus* (2) = 1.78, *C. calhounensis* (1), *C. alpenensis* (3) = 0.74, *C. canadensis* (1), *C. sibleyensis* (2) = 1.78, *C. norwoodensis* (1), *C. stummi* (3) = 0.74, *C. schohariensis* (3) = 0.74, *C. neoturgidus* (1), *C. halliturgidus* (2) = 1.78, *Basidechenella clara* (10) = 0.14, *B. eriensis* (1), *B. rowi* (6) = 0.26, *B. arkonensis* (6) = 0.26, *B. hesionea* (1), *B. canaliculata* (3) = 0.74, *B. lucasensis* (3) = 0.74, *B. cartwrightae* (1), *B. nodosa* (4) = 0.46, *B. pulchra* (5) = 0.34, *B. reimanni* (1), *B. elevata* (1), *B. witherspooni* (1), *Dechenella planimarginata* (5) = 0.34, *D. valentini* (1), *D. haldemani* (2) = 1.78, *D. welleri* (2) = 1.78, *Monodechenella halli* (4) = 0.46, *M. curvimarginata* (2) = 1.78, *M. legrandsmithi* (1), and *M. macrocephala* (11) = 0.13. These values indicate that for many of the taxa under study we can be confident at a 50% level that the extinction and first appearance data reflect times reasonably close to the actual times of extinction and appearance. When α values are 0.3 or less we can state that there is a 50% chance that the extinction occurred at a point bracketed at the bottom by the known range truncation and at the top by a point lying above this truncation by a distance of 15% of the total depositional thickness of the species range in a composite or single section. This seems to be a reasonably well-constrained interval. However, for several taxa that are known from one or two horizons, we must be very cautious about extrapolating patterns of extinction and first appearance to causal statements about geological and environmental processes.

In conjunction with this discussion of the diversification and extinction of the ENA proetid fauna, it is necessary to briefly discuss the depauperate proetid fauna of the upper Emsian Schoharie Grit because it bears on the way we view the evolution of faunas.

THE EMSIAN–EIFELIAN PROETID TRILOBITES OF ENA AND THE ORIGIN OF MAJOR EVOLUTIONARY FAUNAS

As mentioned above, most of the proetid trilobites discussed above are restricted to the Eifelian and Givetian in ENA. However, two species of *Crassiproetus* and at least two (possibly three) species of *Basidechenella* are known from the upper Emsian Bois Blanc Formation and the Schoharie Grit. There also exist a few additional poorly preserved species of proetids known from enigmatic remains in the Bois Blanc Formation, the Schoharie Grit, and the Onondaga Limestone that have been variably assigned to the genera *Proetus* and *Dechenella*. The affinities of these taxa appear not to lie with either of these genera but rather with *Gerastos* and *Coniproetus*. Most of the Schoharie Grit taxa do not occur in the overlying Onondaga Limestone except for a single species, and this species is also known to occur in the Helderbergian New Scotland Limestone (probably

Lochkovian according to Kirchgasser et al. [1985]). In addition, two species occur in the Onondaga Limestone (Eifelian) that are not known from the upper Emsian of ENA. These taxa, *Coniproetus folliceps* (Hall and Clarke, 1888) and *Coniproetus tumidus* (Hall and Clarke, 1888), are closely related to each other, but probably not closely related to the other species of *Coniproetus* known from the upper Emsian of ENA. All of these species are closely related to species known from Bohemia and Morocco, implying that there was a faunal link between ENA and Armorica before mass exchange between these regions got underway in the Givetian. This also indicates that there was a separate, but depauperate, fauna of Proetinae occupying ENA before or around the time when several proetid taxa began to undergo diversification in ENA. This fauna and the proetid fauna considered in detail herein have largely separate origins. In addition, one of these faunas enjoyed moderate evolutionary success whereas the other was first very rare and then became extinct.

The very rare fauna was composed principally of members of the genus *Coniproetus*. There were probably two species of *Coniproetus* in the upper Emsian and two species of *Coniproetus* in the Eifelian. The two Emsian taxa were closely related to each other, as may have been the two Eifelian taxa. However, the Emsian and Eifelian taxa were not closely related to each other, differing in the condition of several characters. The two Emsian taxa appear to be related to such taxa as *Coniproetus eurysthenes* (Chlupac and Vanek, 1965) and *C. alamar* Snajdr, 1980. These taxa are known from the Slivenec Limestone, Pragian (Siegenian) of Bohemia (Snajdr, 1980). Ormiston (1975a) suggested that there may have been a close relationship between the Siegenian trilobites of the Canadian Arctic and the Old World, Bohemian, and Armorican Faunal Realms. One of the patterns used to bolster his argument was the distributions and evolutionary relationships of species of the genus *Coniproetus*. The elucidation of the relationships of *Coniproetus angustifrons* (Hall, 1861) and *C. conradi* (Hall, 1861) might provide additional evidence at some level for a link between the ENA fauna and those of the Arctic and Old World Faunal Realms in the Pragian and Emsian. In addition, the Eifelian taxa *Coniproetus folliceps* and *C. tumidus* also appear to be closely related to other trilobite taxa known from the Lochkovian (Gedinnian), such as *C. affinis* (Boucek, 1933) from Bohemia, *C. foucauldi* from Morocco, and *C.* sp. aff. *tumidus* from the Siegenian of the Yukon Territory, Canada. Finally, *Gerastos protuberans* (Hall, 1859), known from Lochkovian and Emsian strata, also appears to have a close relative in the Pragian through Eifelian strata of the Eifel district of Germany. Thus, in the Lower Devonian of ENA there was a depauperate and largely cosmopolitan fauna that consisted of a few species of Proetinae.

Brief discussions are given here of *Gerastos protuberans*, *Coniproetus angustifrons*, and *C. conradi*, which, because of their typically poor preservation and the dearth of their remains, have in the past received relatively little coverage. A comment on the origins of major evolutionary faunas is given after these discussions.

Gerastos protuberans (Hall, 1859)
Figure 8.6

Proetus protuberans Hall, 1859: 351, pl. 73, figs. 6, 7.

Proetus cf. *protuberans* Hall. Ohern and Maynard, 1913: 490–491, pl. 89, figs. 3, 4.

Proetus stenopyge Hall and Clarke, 1888: 110, pl. 22, fig. 27.

Proetus (*Proetus*) *stenopyge* Hall and Clarke. Stumm, 1953b: 14–15, pl. 1, fig. 1.

?*Proetus* cf. *protuberans* Hall. Ohern and Maynard, 1913: 490–491, pl. 89, fig. 2.

DIAGNOSIS: Eight or nine pygidial axial rings; axial rings flex posteriorly; pygidial border notched, border well developed; interpleural furrows present; axis very wide (tr.), equal to 1.5 times width of pleural field; axis dorsoventrally flattened posteriorly; axis in lateral section arched; axial terminus flat posteriorly; border posteriorly equal to width anterolaterally; pleurae gently rounded, slightly curving ventrally laterally.

TYPES: The pygidium discussed in Hall (1859), plates published in (Hall, 1861: pl. 73, fig. 7), AMNH 35239, originally a syntype, is designated the lectotype of this species. All figured specimens in Hall (1861), formerly syntypes, become paralectotypes.

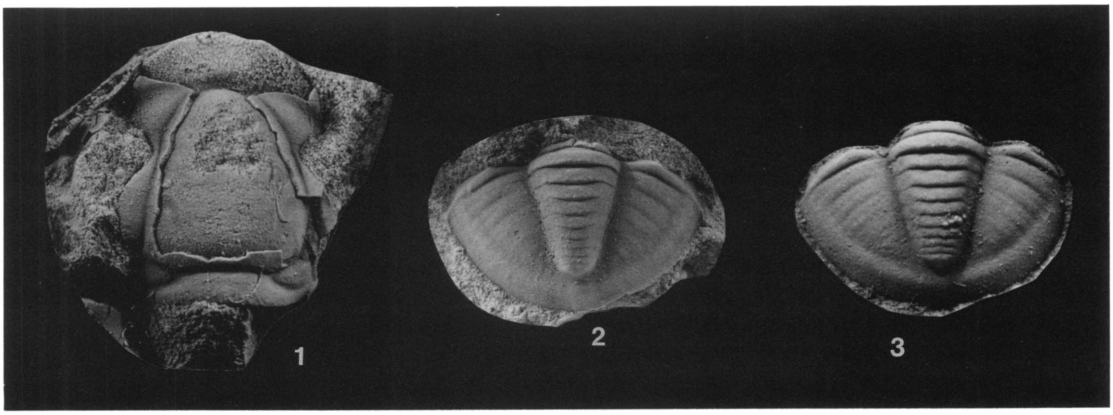


Fig. 44. *Coniproetus* spp. **1.** *Coniproetus angustifrons* (Hall, 1861). Schoharie Grit, Sawkillian (upper Emsian), Albany County, New York, AMNH 2900, lectotype, dorsal view of partly exfoliated cranidium, ×3.5. *Coniproetus conradi* (Hall, 1861). **2.** Schoharie Grit, Sawkillian (upper Emsian), Schoharie, New York, AMNH 39321, lectotype, dorsal view of pygidium, ×2.5. **3.** Horizon and locality same as **2.** AMNH 44729, dorsal view of pygidium, ×4.5.

The syntype of "*Proteus stenopyge*," NYSM 4761, is a valid type of a junior subjective synonym.

MATERIAL: AMNH 35239; NYSM 4761.

DISCUSSION: This species is known from pygidia from the New Scotland Formation, Helderberg Group, Helderbergian (Lochkovian), the Bois Blanc Formation (upper Emsian), Garden Island, Lake Michigan, and the Onondaga Limestone, Phelps, NY. This species is very similar to the other members of the "*Gerastos cuvieri* species group." These species are known principally from the Pragian–Emsian of Germany, Bohemia, and Morocco. Thus, an exponent of this group appears in strata slightly older than the strata it appears in its main distributional area. However, this information needs to be corroborated with phylogenetic information before its relevance is apparent. This species differs principally from *Gerastos cuvieri* by having a more prominently developed pygidial border, a more steeply arched axis, and by possessing one or two fewer pygidial axial rings.

Hall and Clarke (1888) recognized that *Proetus stenopyge*, here treated as conspecific with *Gerastos protuberans*, was closely related to some species known from Germany and Bohemia that are treated here as members of the "*Gerastos cuvieri* species group." Stumm (1953b) concurred with Hall and Clarke's conclusions.

Although a cephalon of this species has been figured (e.g., Ohern and Maynard, 1913), the illustration does not match specimens of the "*Gerastos cuvieri* species group." In particular, the cephalon assigned to *G. protuberans* has the lateral margins of the glabella converging and the facial sutures diverging. As actual specimens of cephala of this species could not be observed, the specimen figured in Ohern and Maynard (1913) is only tentatively assigned to this species, as it may belong to an unrelated form. Another possibility is that the species has a pygidial morphology very similar to members of the "*G. cuvieri* species group," but the cephalic morphology is very different.

Coniproetus angustifrons
(Hall, 1861)
Figure 44.1

Proetus angustifrons Hall, 1861: 70; Hall, 1862: 98; Hall, 1876: pl. 20, fig. 1; Hall and Clarke, 1888: 91–93, pl. 20, fig. 1.

Dechenella (*Dechenella*)? *angustifrons* (Hall). Stumm, 1953b: 22, pl. 3, fig. 7.

?*Proetus* sp. Hall and Clarke, 1888: 94, pl. 22, fig. 6.

DIAGNOSIS: Anterior cephalic border very long, length equal to sagittal distance between distal tips of S1 and S2, weakly sloping ventrally anteriorly; lateral margins of glabella converging anterior of S0, not bulging near eyes; intraoccipital lobes do not bulge laterally beyond margin of glabella; eye extends from anterior portion of intraoccipital lobe to point between distal tips of S2 and S3; medial portion of S0 straight; S1 flexes transversely at posterior and anterior ends; glabellar furrows developed as patches of pigment; S2 and S3 expand medially, S3 transverse, S2 directed posteriorly at approximately 40° angle measured from transverse line through anterior edge; intraoccipital lobes weakly separated from L0 posteriorly, dorsally flattened; S0 anterior of intraoccipital lobe straight from medial portion of S0 to lateral margins of glabella; S0 prominently incised; glabella weakly arched in anterior view; facial sutures anterior of anteromedian portion of eye immediately diverge at 40° angle from sagittal line, smoothly and gently recurve medially one-third of distance along anterior cephalic border; prosopon of fine granules.

TYPES: Most of the specimens designated syntypes of *angustifrons* are actually not synonymous with this species and are thus not valid type specimens. The only valid type, AMNH 2900, a lectotype, was designated by Stumm (1953a).

MATERIAL: AMNH 2900 (lectotype) and 44718.

DISCUSSION: This species is known from the Schoharie Grit at Albany County, New York.

Stumm (1953b) recognized that several of the specimens originally assigned to *Coniproetus angustifrons* by Hall and Hall and Clarke actually belonged to a different species, *C. conradi*. The gena that Hall and Clarke (1888) figured (pl. 22, fig. 2) also appear identical to *C. conradi* and herein they are regarded as belonging to that taxon. Thus, the only samples that belong to *C. angustifrons* are two cranidia, and the descriptions of the pygidia and free cheeks provided by Hall and Clarke (1888: 91–92) are not valid for this species. However, a single poorly preserved pygidium is known from the Schoharie Grit, AMNH 44717, which generally resembles *Coniproetus conradi* (Hall, 1861), but differs in having a somewhat more prominent dorsal pygidial border and also two fewer pygidial axial rings. It may belong to *C. angustifrons*, but this assignment is not made definitively and requires further work and collection.

Stumm (1953b) suggested that this species may belong to *Basidechenella* on the basis of the condition of the intraoccipital lobes. However, the intraoccipital lobes are quite dissimilar from those found in the specimens that Stumm (e.g., 1953a, 1953b, etc.) assigned to this genus, as they are not prominently isolated or dorsally expanded in *C. angustifrons*. They do bear more resemblance to the intraoccipital lobes of taxa like *B. maura* (Alberti, 1967); however, the cranidia of *C. angustifrons* differ in several characters from those of *B. maura*, and this species lacks many of the criteria that are diagnostic of the genus *Basidechenella*. In particular, these include the prominent bulges of the glabella near the eye, the facial sutures anterior of eyes do not parallel each other for a short distance, and S3 does not flex posteriorly.

A proposed generic assignment for *angustifrons* was made by coding the character states for the cephala of these taxa. It appears that the species shares many aspects of its morphology with some of the members used in the higher-level phylogenetic analysis of the Proetinae, particularly *Coniproetus ryckholti* (Barrande, 1846). It also bears a close resemblance to some taxa that have been assigned to *Coniproetus*, but that could not be obtained for phylogenetic analysis. These taxa are *Coniproetus eurysthenes* (Chlupac and Vanek, 1965) and *C. alamar* Snajdr, 1980, and they are known from the Slivenec Limestone, Pragian (Siegenian) of Bohemia (Snajdr, 1980). In particular, they share the long (sag.) preglabellar field, the medial expansion of S2 and S3, the weakly separated intraoccipital lobes, the tubercle on L0 absent (present in *C. alamar*), facial sutures diverge immediately anterior of eye at about a 40° angle, S0 is straight medially, S1 flexes transversely at anterior and posterior ends, the long L0, S0 anterior of the intraoccipital lobes straight from medial portion of S0 to the lateral margins of the glabella, the lateral margins of the glabella converging, S2 deflected posteriorly at 45° angle, S3 transverse, and glabella weakly arched. On the basis of these shared characteristics this taxon is tentatively assigned to the genus *Coniproetus*. However, it is difficult to make taxonomic assignments without a pygidium or librigena, and it must be stated that *C. angustifrons* is also similar morphologically to *Arcticormistonia edgecombei*, new species. These species differ in the condition of the intraoccipital lobes (which are not isolated at all in *A. edgecombei*), the presence of a tubercle on L0 in *A. edgecombei*, a relatively short anterior cephalic border in *A. edgecombei*, S2 and S3 do not expand medially in *A. edgecombei*, and S3 is directed posteriorly in *A. edgecombei*. In addition, although the condition of the facial sutures anterior of the eye in *C. angustifrons* appears to match that of other specimens in the genus *Coniproetus* (e.g., *C. eurysthenes*), the facial sutures in all species of *Coniproetus* considered herein in phylogenetic analysis (e.g., *C. bohemicus*, *C. folliceps*, and *C. ryckholti*) were found to be weakly divergent anterior of the eyes.

This species bears many similarities with *Coniproetus conradi* (Hall, 1861), which is also known from the Schoharie Grit and is discussed below. In particular, they both share the long anterior cephalic border smoothly sloping ventrally; the facial sutures diverging immediately anterior of the anteromedian portion of the eye at a 45° angle, then smoothly and gently recurving medially; and the lateral margins of the glabella not bulging near the margins of the eye. The structure of the glabellar furrows also appears to be similar; however, the glabella of all known specimens of *C. conradi* are too poorly preserved to ascertain this.

Coniproetus conradi (Hall, 1861)

Figure 44.2, 44.3

Proetus conradi Hall, 1861: 69; Hall, 1862: 97; Hall, 1876: pl. 20, fig. 6; Hall and Clarke, 1888: 89–91, pl. 20, fig. 9, pl. 21, figs. 27, 28, pl. 22, fig. 4.

Proetus angustifrons Hall. Hall and Clarke, 1888: pl. 20, figs. 2–5, pl. 22, figs. 1–3.

Proetus marginalis Hall. Hall, 1876: pl. 21, figs. 27, 28.

DIAGNOSIS: Anterior cephalic border long, equal to twice length (exsag.) between distal tips of S1 and S2; margins of glabella converging; anterior portion of eye reaches point between distal tips of S2 and S3; facial sutures anterior of anteromedian portion of eye immediately diverge at 45° angle to sagittal line, smoothly and gently recurve medially one-third of distance along anterior cephalic border; prosopon of fine granules; lineations on anterior margin of cephalon closely packed, parallel and linear; anterior margin of S1 flexes transversely (posterior margin could not be discerned); pygidial axis 130% width pleurae; pygidium 1.8 times as wide as long; pygidium with 10 axial rings; border not developed, but trace parallels the pleurae; pleural furrows very faint, almost as shallow as interpleural furrows; axial rings weakly flex posteriorly medially; axis and pleurae moderately arched in lateral section; axis low, margins diverge at 35° angle.

TYPES: Lectotype pygidium (designated here), AMNH 39321, figured by Hall (1876: pl. 20, fig. 6) and Hall and Clarke (1888: pl. 20, fig. 9), from the Schoharie Grit, near Clarksville, Albany County, NY. The following specimens in the AMNH collections become paralectotypes: 39334, 44716.

MATERIAL: AMNH 39321–39323, 39334, 44716, 44718, 44722, 44728, 44729, 44732, 44734–44736, 44766.

DISCUSSION: This species is known from several pygidia and a few poorly preserved complete specimens from the Schoharie Grit at Schoharie, Schoharie County, and near Clarksville, Albany County, eastern New York. As mentioned above, the cephalon of this species bears several similarities to that of *C. angustifrons*, and these taxa differ chiefly in the condition of the glabella, which is relatively broader in *C. conradi*. *Coniproetus conradi* was assigned to *Coniproetus* on the basis of the same character evidence used to assign *C. angustifrons*. As with *C. angustifrons*, the facial sutures are more strongly divergent in *C. conradi* than is typical of some of the members of *Coniproetus*.

This species can easily be distinguished from such taxa as *Basidechenella clara* and *B. rowi* by the possession of one less pygidial axial ring, a broader pygidium relative to its length, and the absence of the dorsal pygidial border. *Coniproetus conradi* and *Basidechenella* sp. aff. *clara* both have 10 pygidial axial rings, but they differ in the condition of the border, in the possession of a relatively broader pygidium by *C. conradi*, in the condition of the axial rings (which medially arch farther posteriorly in *B.* sp. aff. *clara*), and in the further posterior deflection of the pleurae laterally in *B.* sp. aff. *clara*.

THE EVOLUTION OF FOSSIL FAUNAS

It appears that the origin of the Middle Devonian proetid fauna of ENA can be viewed as an event that began at the end of the Emsian, if not earlier, and that this fauna took over from, and possibly replaced or displaced, the earlier, depauperate cosmopolitan fauna. By upper Emsian time, two of the genera that comprised the Middle Devonian proetid fauna, *Basidechenella* and *Crassiproetus*, had undergone a small amount of diversification. The other two genera that comprise this fauna, *Monodechenella* and *Dechenella*, began to diversify in the Eifelian. The genera *Basidechenella* and *Crassiproetus* are mostly restricted to ENA, and they only have two and one species, respectively, that occur outside of ENA. Their Emsian through Givetian diversity in ENA totals at least 27 species. The genus *Monodechenella* has at least two species known from outside ENA, and the genus *Dechenella* has several members that occur in Armorica in the Old World Faunal Realm and in the Arctic Faunal Province in Alaska, the Yukon Territory, and the Canadian Arctic Islands. The geographic distributions and stratigraphic ranges of most of the species of *Dechenella* suggest that they were only established in the Appalachian Basin of ENA for a short amount of time. The total diversity of these two genera in ENA from the Eifelian to the Givetian totals at least nine species. Thus, the proetid fauna of the Middle Devonian of ENA, excluding members of the depauperate fauna of earlier evolutionary origins, contained at least 36 valid species. This does not include such species as *Cyrtodechenella* sp. (discussed along with *Dechenella welleri*) and many aulacopleurid and "mystrocephalid" taxa. Therefore this fauna did attain levels of moderate diversity.

The Acadian orogeny may have played a dual role in the evolution of the Middle Devonian proetid fauna of ENA. The first members of the fauna appear in the upper Emsian, after the initial stages of the Acadian Orogeny, although they may have been endemic to ENA for a long interval preceding the upper Emsian. In addition, at least two of the proetid genera studied herein undergo significant expansions in their range at this time. This may be caused either by a relative sea-level rise associated with the Acadian Orogeny, or by the coming into contact of formerly disjunct plates. In some unknown manner the Acadian Orogeny may have engendered either the initial appearance or diversification of this proetid fauna.

Then, during a period of tectonic quiescence in the Eifelian (Southwoodian), this proetid fauna underwent moderate diversification with low levels of extinction. The Acadian Orogeny was reactivated at the end of the Eifelian, leading to increased rates of clastic deposition throughout ENA, particularly in the Appalachian Basin. Concomitantly, widespread black shales were deposited, which are associated with several transgressions in the late Eifelian and early Givetian. These could have possibly been mediated by the flexural response of the lithosphere to tectonic loading and the subsidence of intra-cratonic basins (Beaumont et al., 1988). These areally widespread black shale deposits, with associated restricted limestone deposition, significantly reduced what appears to be the proetids preferred habitat. From this time on, the proetid genera studied herein were largely excluded from the Appalachian Basin, where limestone deposition remained sporadic throughout the Givetian. Elevated extinction rates were witnessed in the proetid genera studied at this time. In addition, the pattern of geographic restriction led to elevated speciation rates in these clades in a manner similar to that predicted by Vrba's (1985, 1992) turnover-pulse hypothesis.

At the end of the Givetian another period of widespread black shale deposition occurred, this time terminating carbonate deposition not only in the Appalachian Basin but also in the Illinois and Michigan Basins. All species of proetid genera studied herein vanished from ENA at this time. Thus, in the long term, the Acadian Orogeny appears to have had a significantly negative impact on the Middle Devonian proetids in ENA, chiefly because this orogen reduced and then eventually eliminated the size of their preferred environment, leading to extinction. However, the orogen is associated with the proetids initial development in ENA, and also appears to have at least temporarily mediated elevated speciation rates in these clades.

Unlike other groups, such as the homalonotid (Lieberman, in prep.) and phacopid trilobites (Eldredge, 1972, 1973, 1985; Burton and Eldredge, 1974), the rugose corals (Oliver, 1977), the bivalves (Bailey, 1983), and the brachiopods (Boucot, 1975), the Givetian boundary does not mark a time of significant faunal invasion from Armorica into ENA. However, according to the phylogeny in figure 22, the most basal member of the genus *Basidechenella*, *B. maura*, is known from Morocco, and it is probably closely related to *B. kayseri* from the Eifel district of Germany. This roughly fits the pattern Burton and Eldredge (1974) described for *Phacops* with a clade of ENA species of trilobites sister to a clade of Armorican species; however, optimization of biogeographic distributions suggests that the origin of *Basidechenella* was in ENA or the Arctic, contrary to the pattern recognized by Burton and Eldredge (1974). The phylogeny of the genus *Dechenella* in figure 33 indicates that this genus had species distributed throughout the Arctic, Old World, and ENA Faunal Realms. In this clade, the species known from ENA appear to be most closely related to Arctic taxa, and there appear to have been two independent invasions from the Arctic into ENA. For the genus *Monodechenella*, the stratigraphic data may be ambivalent, particularly regarding "*Milesdavis*" *zlichovianus*. However, if Pribyl's (1966) stratigraphic assignation is correct, then the genus *Monodechenella*, first appearing in ENA in the Eifelian, is derived from a series of Armorican and Baltic taxa. Some members of the genus *Monodechenella* also occur in northern South American (Gondwanan) strata. *Crassiproetus* appears to be almost exclusively ENA in occurrence, with a single species known from Kazakhstan, and its origin appears to be in ENA or in the Arctic on the basis of phylogenetic evidence and in ENA on the basis of stratigraphic evidence.

The phylogenetic results from the analysis herein suggest that the changes in the Middle Devonian trilobite fauna in ENA may have come in at least two pulses. Eldredge (1972), Burton and Eldredge (1974), and Eldredge (1985) have already documented the prominent invasive pulse that occurred around the Givetian. The results from the proetid taxa considered herein suggest that there may have been additional pulses during the upper Emsian and at the start of the Eifelian that had an influence on part of the Middle Devonian trilobite fauna. Additional work on Hamilton Group trilobites (Lieberman and Kloc, in review) indicates additional invasive events. These results suggest that rather than constituting a single evolutionary event influenced by one or a few biogeographic and environmental factors, the origin of the Hamilton Group fossil fauna appears to have occurred piecemeal. There seem to be several different biogeographic source areas for the taxa that comprise the trilobites of the Hamilton fauna. In addition, some lineages do appear to pass through from underlying faunas into the Hamilton Group such that there is evolutionary connectivity between fossil faunas in synjacent geographic regions. However, very few "species-level" taxa pass through such faunal boundaries, and no species are shared between the different major biogeographic realms recognized in the Lower and Middle Devonian. Thus, this study is a partial refutation of the "catastrophist" pattern of faunal evolution, as the Hamilton Group fauna did not originate during a narrowly (temporally) constrained interval, nor is it derived from a single biogeographic region, nor do all taxa in underlying faunas fail to cross faunal boundaries. However, it is difficult to pin down the precise time of origination and extinction, but at least in the case of extinction events, these may be associated with faunal and/or stage boundaries. Finally, these results point out the contingent nature of such evolutionary events. Whether or not such patterns of piecemeal faunal evolution can be generalized to other fossil faunas remains to be tested.

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