

THE VERTEBRATE FAUNA OF THE CLEVELAND MEMBER (FAMENNIAN) OF THE OHIO SHALE

by
Robert K. Carr and Gary L. Jackson



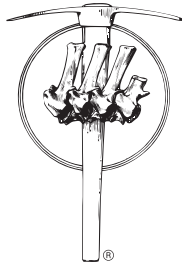
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CHAPTER 5, THE VERTEBRATE FAUNA OF THE CLEVELAND MEMBER (FAMENNIAN) OF THE OHIO SHALE

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INTRODUCTION

The Devonian represents a time of complex biotic and abiotic events. Rocks recording these events offer a unique and important view of this time period because they represent the largest estimated volume and geological map area for Paleozoic systems (Dineley, 1984). The Old Red Sandstone Continent developed during this period and was associated with a number of tectonic events. The environment of deposition for the sediments of the Old Red Sandstone Continent (fresh water river and lakes versus marine or marginal marine) is still actively debated. At the beginning of the Late Devonian, a major facies shift occurred within the North American marine carbonate basins, characterized by widespread deposition of anoxic black shales. The Late Devonian further represents a time of change with orogenic events associated with the early suturing of Pangaea (McMillan and others, 1988). Paralleling the geological changes at this critical time are biological changes; for example, shifts from provincialism to cosmopolitanism, changes in species diversity, and global extinction events. The patterns of change in species numbers associated with the extinction events differ between invertebrates and vertebrates and even varies when comparing subgroups of vertebrates. The rock layers of northern Ohio, especially the Cleveland Member of the Ohio Shale, help to tell the biological story of the Late Devonian.

CAST OF CHARACTERS (CRANIATE SYSTEMATICS)

Living craniates include four groups (fig. 5-1A). The hagfish and lampreys are members of a larger paraphyletic group that includes agnathan or jawless fishes. Gnathostomes (jawed vertebrates) include the chondrichthyans (sharks, skates, rays, and holocephalans) and osteichthyans (a group of bony fishes consisting of the ray-finned fishes, which we often see on the dinner table, and the lobe-finned fishes and their descendents, which include humans).

The craniates are recognized by the development of paired external sense organs associated with the evolutionary origin of a predator with improved sensory modalities and improved locomotor capabilities (Northcutt and Gans, 1983). Vertebrates (lampreys and gnathostomes) further enhance their sensory modalities with the origin of electroreception in the extinct osteostracans (an agnathan group most closely related to jawed vertebrates). The appearance of pectoral fins is an obvious asset for improved maneuverability. Finally, the gnathostomes add to this improved locomotor and sensory pattern with the origin of pelvic fins and jaws capable of capturing, manipulating, and processing food items.

Among the gnathostomes there are two extinct groups, the placoderms and acanthodians (figs. 5-1B and C, 5-2). The placoderms, representing 43.1% of the Cleveland Member vertebrate fauna, are a diverse group known from the Late Silurian through the Devonian (fig. 5-3). They span a wide

range of body forms (fig. 5-2) ranging from dorsoventrally flattened ray-like taxa to laterally compressed taxa. Their interpreted life styles range from bottom-living forms to free-swimming cruisers and they occupy habitats from the marine-influenced deltaic environment to the pelagic realm of open waters in epicontinental basins. Their presence in freshwater habitats (for example, fluvial or lacustrine) is currently debated (see "Other vertebrate faunas of the Late Devonian" below).

The acanthodians (figs. 5-1–5-3, 5-4) are known from the Upper Ordovician to the Lower Permian based on microremains, with articulated remains known from as early as the Lower Devonian (early records from Hanke and Wilson, 2004, p. 189; latest record from Denison, 1979, p. 1). Historically, the acanthodians were subdivided into three major groups based, in part, on the presence of scales or tesseræ (fig. 5-4) on the head and dermal bones associated with the shoulder region and the presence of one or two dorsal fins with spines (fig. 5-2). However, recent work on Lower Devonian forms has blurred these boundaries (Hanke and Wilson, 2004).

The chondrichthyans, characterized by their cartilaginous skeleton (fig. 5-5A), are often considered to have a limited fossil record. However, the presence of teeth and/or scales (fig. 5-5B and C) is now recognized from as early as the Late Ordovician (Turner, 2004, p. 73). Adding significantly to our early understanding of sharks is the excellent preservation of whole bodies seen in the Cleveland Member fauna (fig. 5-2). Two living groups of chondrichthyans are recognized: the holocephalans (ratfish or chimaerids) and the elasmobranchs (sharks, skates, and rays). With the addition of newly discovered fossils, however, inter-group boundaries become blurred (refer to Coates and Sequeira, 2001, for a review of chondrichthyan phylogenies and contrast that with the analysis of Lund and Grogan, 2004).

The osteichthyans, known from the Late Silurian to the Recent, are traditionally subdivided into two clades based on the presence or absence of body musculature extending into the paired appendages (fins). These two groups are known as lobe-finned (sarcopterygian) fishes and ray-finned (actinopterygian) fishes. Living sarcopterygian fishes include the three genera of lungfishes and *Latimeria*, the only living coelacanth (two species are now recognized, *L. chalumnae* and *L. menadoensis*; Thomson, 1991). Living actinopterygians are represented by over 23,000 species (Kent and Carr, 2001, p. 54) and range in form from the seahorse and eel to the gar and bowfin. In the Devonian, the number of species in these two large groups was inverted from today's findings with actinopterygians known from less than 20 species and sarcopterygians known from over 180 species (Cloutier and Arratia, 2004, p. 217). The variety of forms for the actinopterygians is limited in the Devonian and is represented by the paleoniscids (figs. 5-2, 5-6).

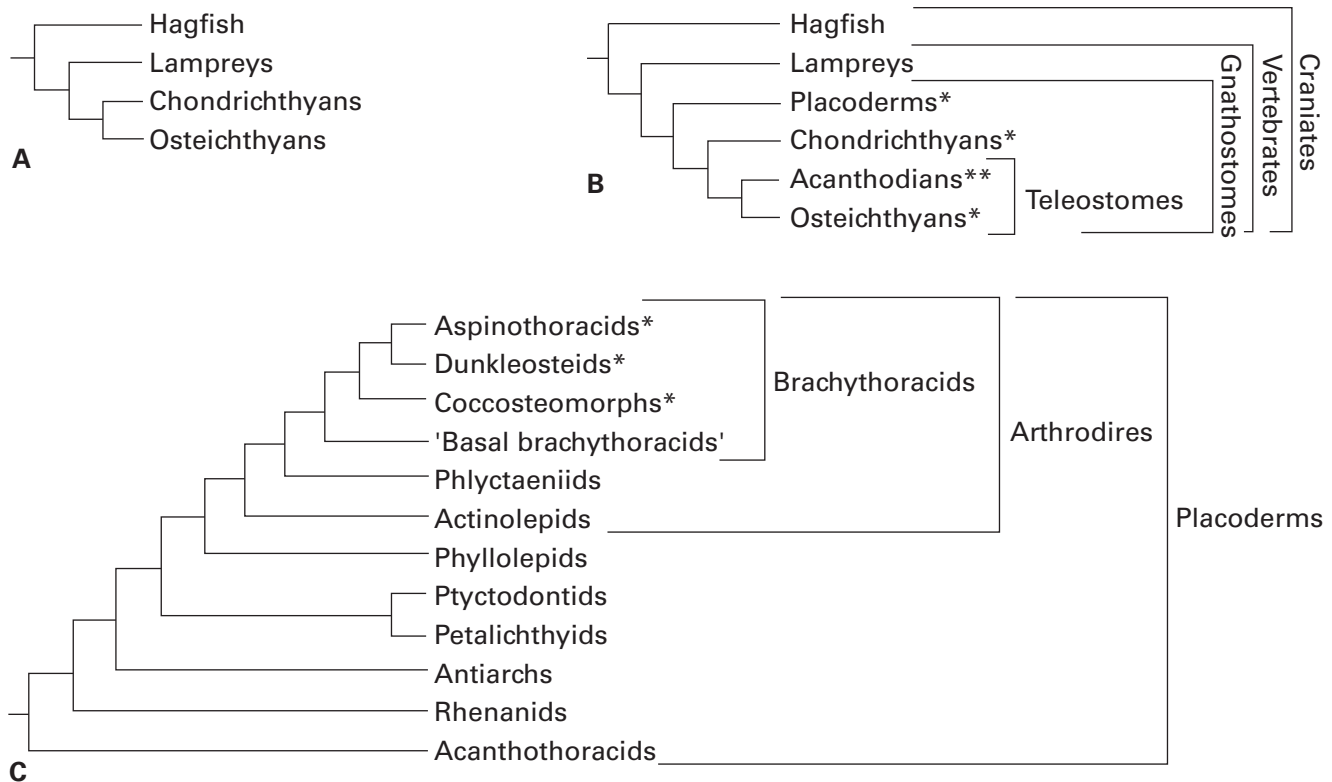


FIGURE 5-1.—A, a cladogram (or graphic representation of relationships) of the living craniates. The hagfish and lampreys form a paraphyletic group (a group that shares a common ancestor, but excludes its descendants, the jawed vertebrates). Based on molecular data, some systematists unite the living jawless fishes within a single clade (a group sharing a common ancestor and includes all its descendants). B, a cladogram of living and fossil groups. C, a cladogram of the major groups of placoderms. Only the arthrodires are represented within the Cleveland Member, although antiarchs, phyllolepid, and other arthrodires are known from the Famennian of the Appalachian Basin. An asterisk indicates groups represented within the Cleveland Member fauna. A double asterisk indicates that an acanthodian has been reported, but unpublished information (see text) suggests that it may be a shark. Of the 28 species of placoderms in the Cleveland Member fauna, one is a coccosteomorph, one (possibly two) is a dunkleosteid, three are considered arthrodires *incertae sedis* (arthrodires of uncertain relationships), and the remaining 22 species are represented by aspinothoracid arthrodires.

AN INTRODUCTION TO ANATOMY IN THE FIELD

Recognizing fossil fishes in the field requires an understanding of their basic anatomy and the various processes that have altered the organism from the time of its death to its discovery as a fossil. The study of this process is known as taphonomy (refer to the “Taphonomy” section below for details of this process as it relates to the Cleveland Member). A key consideration in the process of fossilization is the possession of elements that are likely to be preserved and recovered as fossils. In most cases, these are the “hard parts” or skeleton and bony scales.

Chondrichthyans

The chondrichthyans lack large dermal plates with their outer covering consisting mainly of a shagreen of dermal denticles (placoid scales; fig. 5-5B and C). The endoskeleton is characterized by cartilage that is often uniquely ossified in the form of prismatic cartilage (Williams, 1990, fig. 237B). The skeleton, therefore, consists of the axial skeleton (chondrocranium in fig. 5-5A and axial vertebral column), visceral

skeleton (gill arches including the jaws; fig 5-5A), and the appendicular skeleton (pectoral and pelvic endoskeletal girdle and fin and median fins). The median dorsal fins of some chondrichthyans possess a spine (e.g., *Cladoselache* in fig. 5-2, although the spine in this species is believed to be completely covered by skin). Prismatic cartilage usually does not survive taphonomic processes, and the only fossil remains often consist of isolated dermal denticles, teeth, or spines. However, the mode of preservation in the Cleveland Member is exceptional, often preserving whole shark specimens, some with traces of soft tissue (Williams, 1990; refer to the “Taphonomy” section below for a discussion of why such exceptional preservation may occur).

Osteichthyans

The osteichthyans (bony fishes) possess the same skeletal elements as sharks, but the endoskeletal elements of osteichthyans may be fully ossified. Additionally, there are numerous dermal plates covering the head and jaws and encircling the pectoral girdle (figs. 5-2, 5-6A and B). The body is often covered by a series of scales differing from those

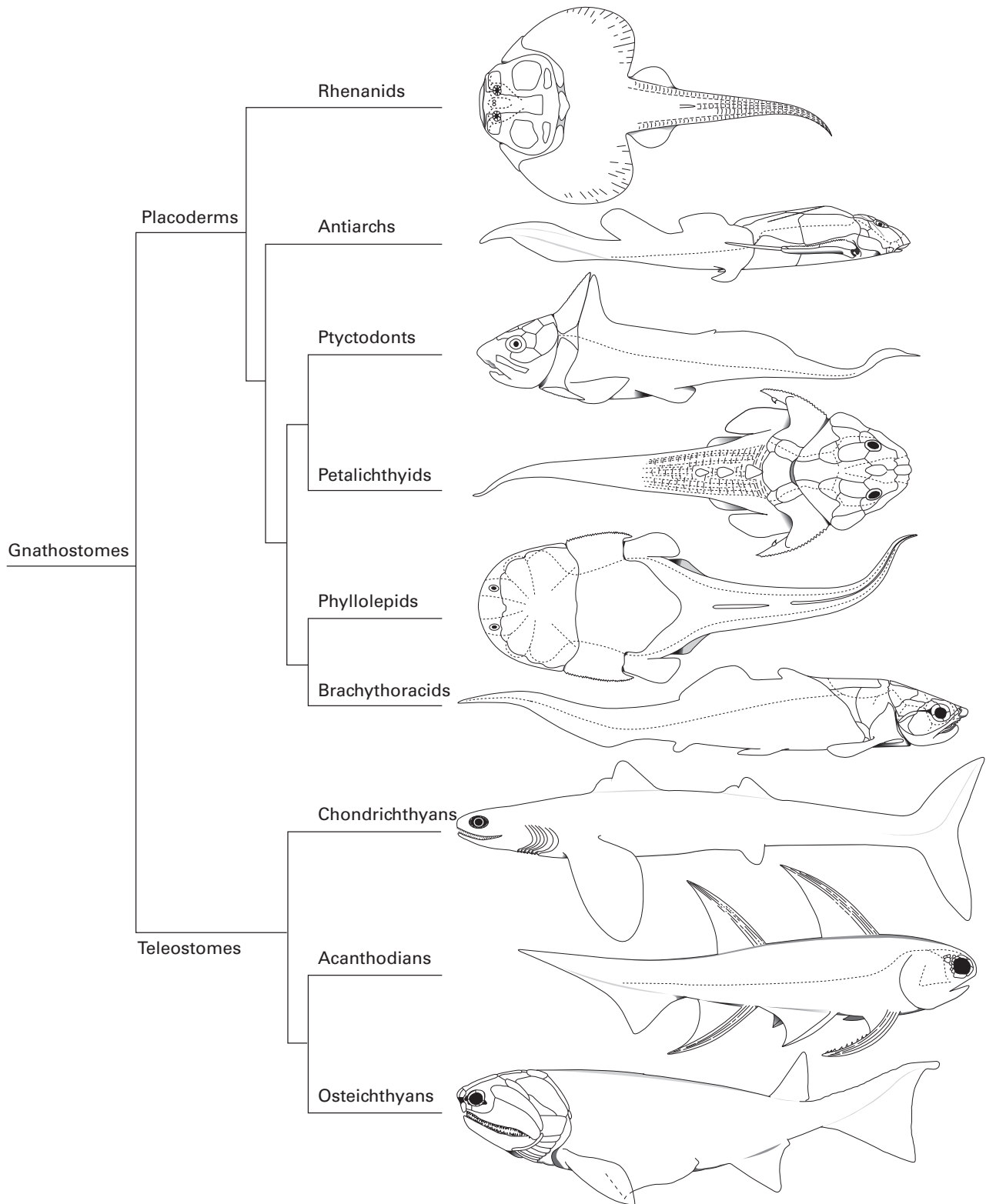


FIGURE 5-2.—Reconstructions (not to scale) of representative taxa placed on a cladogram. From top to bottom: *Gemuendina stuerzi*, a rhenanid, in dorsal view; *Bothriolepis canadensis*, an antiarch, in lateral view; *Ctenurella gladbachensis*, a ptyctodont, in lateral view; *Lunaspis broilii*, a petalichthyid, in dorsal view; *Phyllolepis orvini*, a phyllolepid, in dorsal view; and *Cocosteus cuspidatus*, a brachythoracid arthrodire, in lateral view (original figures from Stensiö, 1963, redrawn from Carr, 1995); *Cladoselache fylleri*, a chondrichthyan, in lateral view (redrawn from Zangerl, 1981); *Diplacanthus elli*, an acanthodian, in lateral view (after Gagnier, 1996); and *Cheirolepis canadensis*, a paleoniscid osteichthyan, in lateral view (after Arratia and Cloutier, 1996).

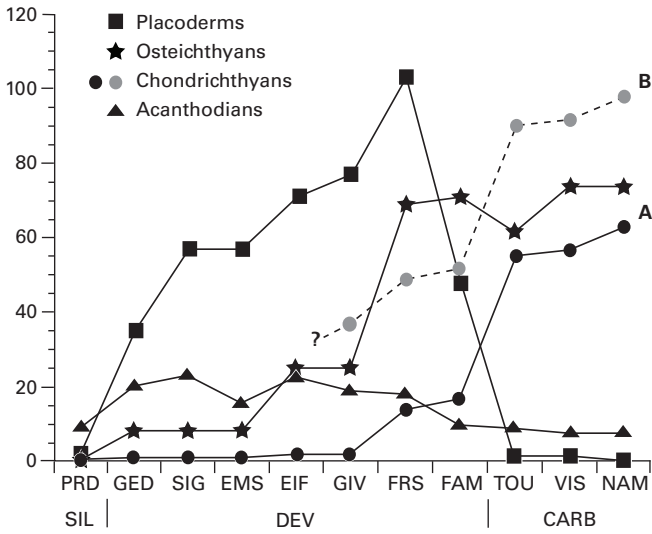


FIGURE 5-3.—A comparison of stage-level generic (genus-level) diversity for major gnathostome groups (clades, after Carr, 1995): placoderms (squares), osteichthyans (stars), chondrichthyans (black circles, line A), and acanthodians (triangles). Line B (gray circles) represents the Givetian-Namurian record for chondrichthyans proportionally increased to reflect the Famennian relative diversity between placoderms and chondrichthyans in the Cleveland Member fauna. Would the sampling bias for osteichthyans also suggest an unreported higher diversity?

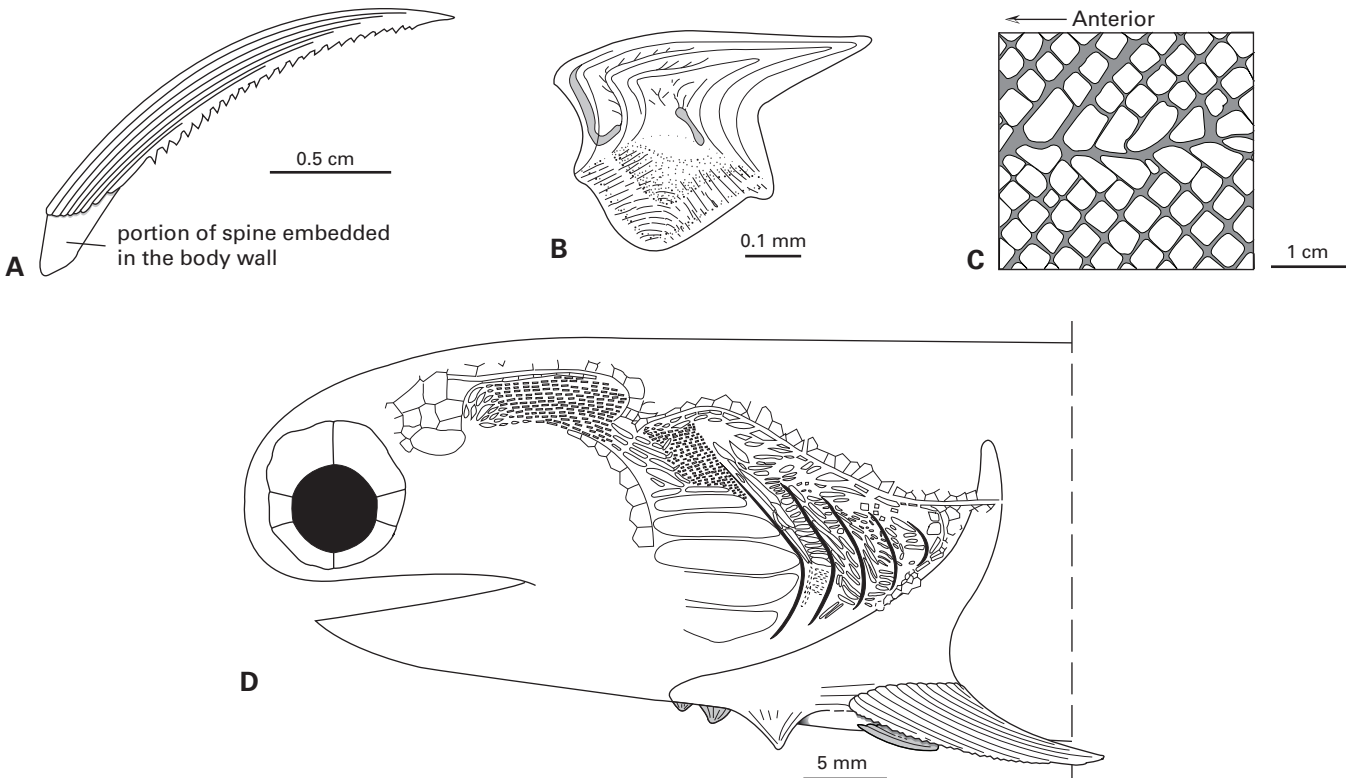


FIGURE 5-4.—A, *Homacanthus gracilis*, dorsal spine. B, *Cheiracanthus splendens*, cross-section of a single scale. C, *Eupleurogmus cresswelli*, a sample pattern of scales. (A, B, and C after Denison, 1979.) D, *Climatius reticulatus*, head and shoulder region of a climatiid acanthodian showing details of scales, tesserae, and dermal bones (composite after Miles, 1973, and Denison, 1979). Anterior is to the left.

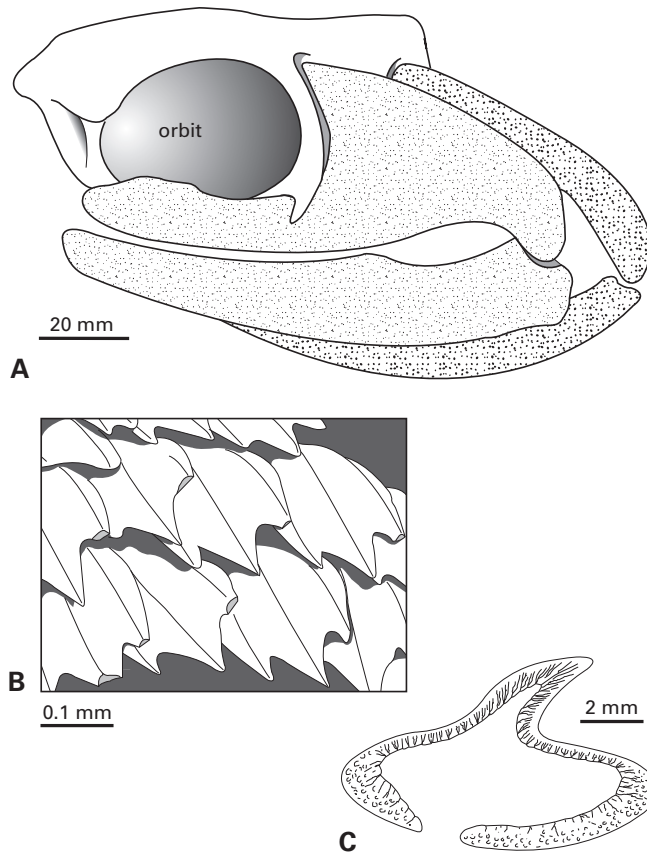


FIGURE 5-5.—A, *Cobelodus aculeatus*, cartilages of the upper and lower jaw (lightly stippled, palatoquadrate and Meckel's cartilages, respectively), upper and lower hyoid arch elements (heavily stippled, hyomandibular and ceratohyal, respectively), and braincase (chondrocranium; after Zangerl and Williams, 1975, redrawn from Zangerl, 1981). B, *Carcharodon carcharias*, a sample of shagreen of scales in the skin (drawing after photo by S. Lindsay, <www.amonline.net.au>, Australian Museum, Sydney, 2005). C, *Raja blanda*, a placoid scale in cross-section (after Goodrich, 1909). Anterior to left (upper-left in B).

found on sharks and consisting of two forms: the ganoid scales of paleoniscids and the cosmoid scales of sarcopterygian fishes (fig. 5-6C and E, respectively). Ganoid scales are characterized by their rhomboid shape and glossy enamel coating (ganoid scales; fig. 5-6C and D). This is the pattern of scales for the subdivision of bony fishes (paleoniscids) that are found in the Cleveland Member. The cosmoid scales (fig. 5-6E and F) of the lobe-finned fishes (sarcopterygians), which differ in shape and histology, are not found in the Cleveland Member, although *Chagrinia* (a coelacanth) is known from the shallower, laterally equivalent Chagrini Member. As members of the osteichthyan clade, both humans and these Paleozoic fishes share bone names (for example, parietals and dentaries [fig. 5-6A and B]).

Acanthodians

The acanthodians, considered the sister group to osteichthyans (fig. 5-1B), have apparently retained a primitive pattern (fig. 5-4D) of a mosaic of dermal scales and small bones (tesseræ) rather than the derived, fused, dermal elements of their sister group (bony fishes). The scales of the body are characterized by a unique histology showing a pattern of concentric growth (fig. 5-4B).

The endoskeleton, in many cases, is only partially ossified and poorly preserved. The best-preserved endoskeletal fossil material is not seen until the Carboniferous to Permian (for example, *Acanthodes*; Denison, 1979, figs. 1–3, 5, 6).

Characteristic of the acanthodians are the series of dermal spines (figs. 5-2, 5-4A and D) associated with the paired and median fins (also seen to a lesser extent in chondrichthyans, which, as noted, are restricted to the median dorsal fins). Like the shagreen of dermal placoid scales in sharks, the elements covering the head and body often disarticulate, thus the common fossil find for acanthodians is isolated scales, tesseræ, or spines (fig. 5-4). Newberry (1875) described a single acanthodian spine in the Cleveland Member, but it is now considered to represent an undescribed shark (table 5-2, note 5).

Placoderms

Like the osteichthyans, the placoderms are covered with dermal armor (fig. 5-7A and B). It is believed that the pattern of dermal bones in placoderms and osteichthyans have independently evolved (fig. 5-1B [note the disjunct presence of dermal bone suggesting an independent origin]), thus one encounters an entirely different nomenclature for the bones of the two groups.

Although most geology researchers working in the field are not familiar with placoderms, the nomenclature is easily adopted because most bone names represent their position on the body. For example, the bones that encircle the thorax include a dorsal midline bone, the medial dorsal plate (MD; fig. 5-7). The lateral sides of placoderms have two pairs of bones, a dorsal set and lateral set. These are the anterior and posterior dorsolateral plates, and anterior and posterior lateral plates, respectively (ADL and PDL, and AL and PL; fig. 5-7). A similar nomenclature is applied throughout the dermal skeleton (fig. 5-7).

The preservation of the endoskeleton is limited to occasional perichondral ossification of cartilaginous endoskeletal elements. The often-thick dermal bones of the placoderms make them a common vertebrate fossil find in Devonian sediments (fig. 5-7C). They represent the most commonly found fossil fish in the Cleveland Member.

HISTORICAL CONTEXT

The fishes of the Cleveland Member represent a single epicontinental basin characterized by the deposition of black shales, but they are not an isolated biological entity—they represent part of a larger story. For example, the brachiopods of the Middle Devonian demonstrate a shift from provincialism to cosmopolitanism associated, in part,

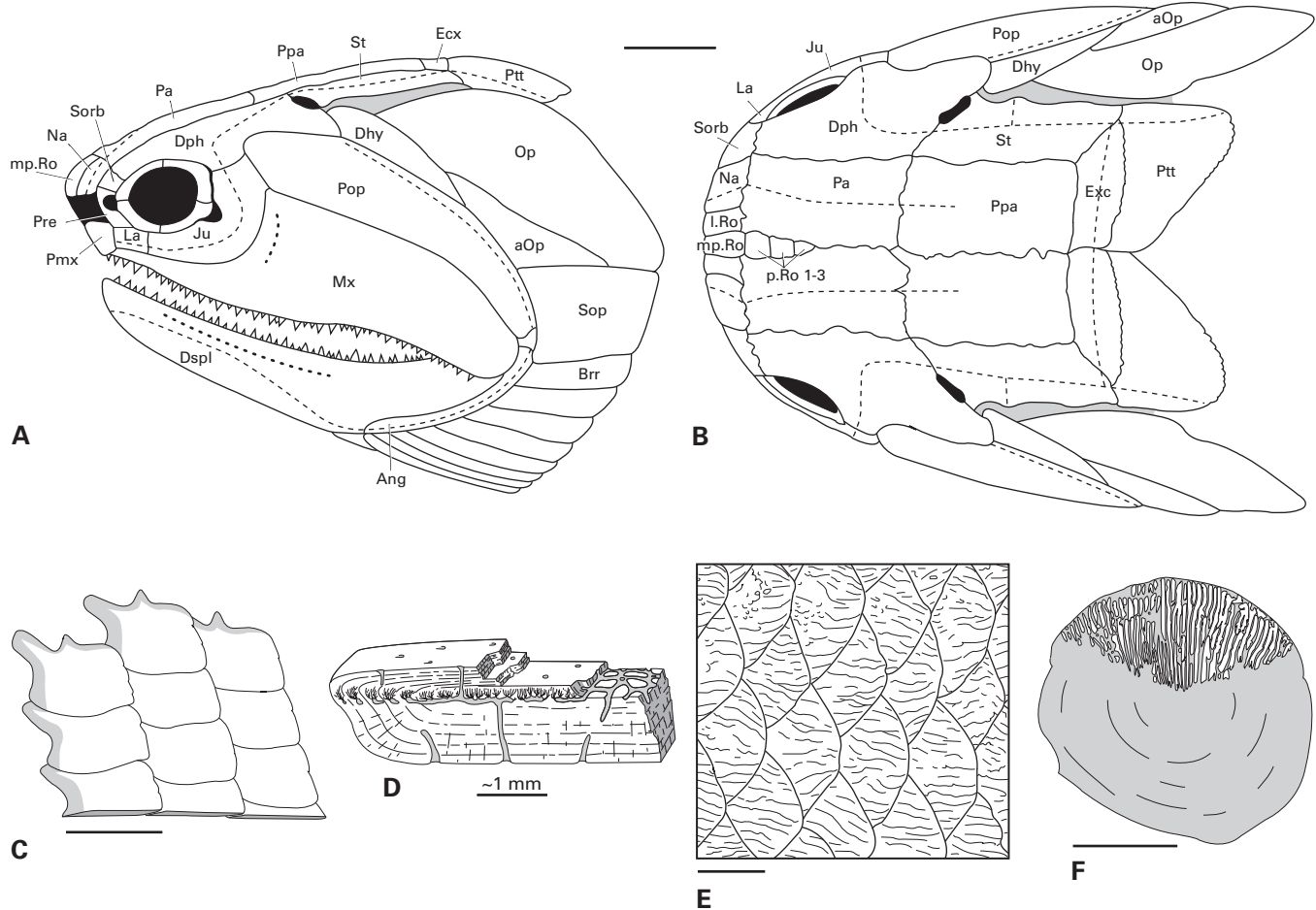


FIGURE 5-6.—A and B, *Cheirolepis canadensis*, dermal bones of the head in lateral (A) and dorsal (B) views (after Arratia and Cloutier, 1996). C, *Lepidosteus osseus*, a sample pattern of ganoid scales (after Goodrich, 1909). D, *Eurynotus crenatus*, ganoid scale in cross-section (after Goodrich, 1909). E, *Holoptychius jarviki*, a sample pattern of cosmoid scales from a sarcopterygian fish (after Schultze and Cloutier, 1996a). F, *Miguashaia bureaui*, a single cosmoid scale (composite after Cloutier, 1996); the exposed ornament can be quite variable. Scale bars equal 1 cm unless otherwise indicated. Anterior is to the left. See table 5-1 for abbreviations.

with the Upper Givetian onlap (relative sea-level rise) that effectively lowered the North American continental arch (Johnson, 1970). Among the ammonoids (cephalopods), eight separate extinction events have been described (House, 1985) with six ranging from the Upper Givetian to Lower Tournasian (Taghanic, Frasnian, Kellwasser, Enkeberg, Annulata, and Hangenberg Events). Of these, three are considered “substantial” (Sepkoski, 1986, p. 290) on a global scale (Frasnian or Givetian-Frasnian, Kellwasser or Frasnian-Famennian, and Enkeberg or Famennian-Tournasian extinction events). Of greatest importance here is the Frasnian-Famennian extinction event, for it sets the stage for what we see in the Famennian deposits of the Cleveland Member.

The extinction pattern for many invertebrate animals is well documented (McGhee, 1996), but the fishes tell a different story when considering their diversity patterns for the three globally important extinction episodes (Carr, 1995). During the Givetian-Frasnian event, a generic-level (genus-

level) decline is only seen in petalichthyids (placoderms) and acanthodians. The actinopterygians (ray-finned bony fishes), sarcopterygians (lobe-finned bony fishes and their descendants), chondrichthyans, arthrodires, and phyllolepid (the latter two placoderms) all demonstrate a generic increase, while other clades maintain stable levels. At the Frasnian-Famennian event, all placoderm groups except phyllolepid (the latter two placoderms) show a generic-level decline (a 52.5% or 53.1% decline, depending on the level of analysis to stage or substage, respectively; Carr, 1995, table 1). Of the seven placoderm orders recognized prior to the Famennian, five survive the Frasnian-Famennian event (Antiarcha, Arthrodira, Petalichthyida, Ptyctodontida, and Phyllolepida, although the latter group may be a subdivision within the arthrodires; Goujet and Young, 2004). At the Famennian-Tournasian event, there is an effective 100% decline in placoderms (fossil records in the Tournasian may represent reworked fossils), while the chondrichthyans and osteichthyans, in general, demonstrate an overall increase in genera.

Table 5-1.—*Morphological abbreviations*

ADL	anterior dorsolateral plate
AL	anterior lateral plate
Ang	angular
aOp	accessory operculum
ASG	anterior superognathal
AVL	anterior ventrolateral plate
Brr	branchiostegal rays
C	central plate
Dhy	dermohyoid
Dph	dermosphenotic
Dspl	dentalosplenic
Ecx	extrascapular
IG	inferognathal
IL	interolateral plate
Ju	jugal
l.Ro	lateral rostral
La	lacrimial
M	marginal plate
MD	median dorsal plate
mp.Ro	medial middle postrostral
Mx	maxillary
Na	nasal
Nu	nuchal plate
Op	operculum
p.Ro1-3	posterior postrostral 1-3
Pa	parietal
PDL	posterior dorsolateral plate
Pi	pineal plate
PL	posterior lateral plate
PM	postmarginal plate
Pmx	premaxilla
PN	postnasal plate
PNu	paranuchal plate
Pop	preoperculum
Ppa	postparietal
Pre	preorbital
PrO	preorbital plate
PSG	posterior superognathal
PSO	posterior suborbital plate
PtO	postorbital plate
Ptt	post-temporal
PVL	posterior ventrolateral plate
R	rostral plate
SM	submarginal plate
SO	suborbital plate
Sop	suboperculum
Sorb	supraorbital
SP	spinal plate
St	supratemporal

Models for these extinction events may differ, but the biological effect of the events is often reported as a complete trophic collapse (a collapse throughout the entire food chain). This is not the case among gnathostomes, as noted above, which raises questions from the scientific community about the validity of the model itself or its assumptions of uniform and global effects. Ecological correlates for the organisms showing patterns different from a complete trophic collapse have yet to be worked out (for example, are there different extinction patterns between open water and bottom-living species or between species feeding on invertebrates and top predators eating other fishes?).

Following the Frasnian-Famennian extinction event, there was a shift in the relative proportions of individual taxa. This period represents a time of ecological recovery from the extinction event and demonstrates such ecological interactions as competitive and opportunistic replacement (respectively, the displacement of one species by another through active competition, or an independent reduction in the presence of a species with a new species expanding its range or territory to fill the void). The Cleveland Member offers a snapshot of this time period leading up to the Famennian-Tournasian extinction event, where there was a 100% extinction rate for placoderms (as noted above, Carboniferous records for placoderms in fig. 5-3 potentially represent reworked fossils).

TAPHONOMY

Taphonomic processes include those that might impact the preservation of an organism from its time of death until burial (e.g., decomposition, transport, scavenging, and disarticulation) and post-burial processes (e.g., chemical and physical alteration during diagenesis). The accumulative effect of taphonomic processes has resulted in the rarity of fossils. Raup and Stanley (1971, p. 11) estimate that only 0.013% or less of species in the past 600 million years have been preserved as fossils. Compounding the rarity of fossils are sampling biases by collectors (e.g., accessibility to fossiliferous strata or that small, flattened, or fossils lacking color contrast with the surrounding rock are easily overlooked).

Many of the fossils from the Cleveland Member are found within flattened carbonate concretions. Due to the size of the concretions, their relatively high fossil content, and their distinct appearance, researchers in the field are biased toward sampling them. The distribution of carbonate concretions is discontinuous, both laterally (Hlavin, 1976, the Big Creek concretionary zones, p. 76) and vertically within the shale (George Kampouris, personal communication, 2005). The concretions are restricted to what appear to be mapable horizons across river basins. In the concretions, there is typically an organic object at its core (fish or plant). Another field indicator that is often associated with fossils, though to a relatively lesser extent, is a carbonate cone-in-cone layer.

In both of these instances (concretions and cone-in-cone), there is a sampling bias due to the visibility of the matrix enclosing the fossil; however, fossils are not limited to these structures. Careful examination of concretion layers reveal isolated bones in the Cleveland Member (George Kampouris, personal communication, 2005). Bones can be recovered elsewhere within the shale; however, the recognition of black flattened bones (in cross-section) against a background of black shale is difficult if not impossible to discern (although larger species would be preferentially collected due to the larger cross-section of individual bones). One of the best collections of placoderms was from a quarried section of shale that exposed a large surface area of one of the more fossiliferous horizons, an atypical exposure in the Cleveland Member that is usually limited to river cuts (Carr, 1991, p. 352).

One of the interesting findings in the Cleveland Member is that sharks are the only fishes that have their soft tissues

Table 5-2.—List of taxa found within the Cleveland Member and their reported geographic ranges (endemic and limited ranges are recorded). Eighty-three percent of the fishes are endemic to the Cleveland Member. Selected references are provided. Abbreviations: AP, Appalachian Basin; CL, Cleveland Member only; EA, a Euramerican distribution.

Taxa	Ranges	References
Arthrodires		
<i>Brontichthys clarki</i> Claypole, 1894	CL	Claypole, 1894
<i>Bungartius perissus</i> Dunkle, 1947	CL	Dunkle, 1947
<i>Callognathus regularis</i> Newberry, 1889	AP	Hlavin, 1976
<i>Coccosteus cuyahogae</i> Claypole, 1893b	CL	Hlavin, 1976
<i>Diplognathus mirabilis</i> Newberry, 1878	AP	Newberry, 1878
<i>Dunkleosteus terrelli</i> (Newberry, 1873)	EA ¹	Heintz, 1932
<i>Glyptaspis verrucosus</i> Newberry, 1889	CL	Newberry, 1889
<i>Gorgonichthys clarki</i> Claypole, 1892	CL	Claypole, 1893c
<i>Gymnotrachelus hydei</i> Dunkle and Bungart, 1939	CL	Carr, 1994
<i>Heintzichthys gouldii</i> (Newberry, 1885)	CL	Carr, 1991
<i>Holdenius holdeni</i> Dunkle and Bungart, 1942	CL	Dunkle and Bungart, 1942
<i>Hussakofia minor</i> (Newberry, 1878)	CL	Claypole, 1903
<i>Mylostoma eurhinus</i> (Dunkle and Bungart, 1945)	CL	Hlavin and Boreske, 1973
<i>Mylostoma newberryi</i> Eastman, 1907	CL	Eastman, 1907
<i>Mylostoma variabile</i> Newberry, 1883	EA	Hlavin and Boreske, 1973
<i>Paramylostoma arcualis</i> Dunkle and Bungart, 1945	CL	Dunkle and Bungart, 1945
paramylostomid new species	CL	(authors' personal observations)
selenosteid new genus and species	CL	Hlavin, 1976
<i>Selenosteus brevis</i> (Claypole, 1896)	CL	Dean, 1901
<i>Stenosteus angustopectus</i> Carr, 1996	CL	Carr, 1996
<i>Stenosteus glaber</i> Dean, 1901	CL	Dean, 1901
<i>Titanichthys agassizii</i> Newberry, 1885	CL	Newberry, 1885
<i>Titanichthys attenuatus</i> Wright in Claypole, 1893b	CL	Wright in Claypole, 1893b
<i>Titanichthys clarkii</i> Newberry, 1887	CL	Newberry, 1887
<i>Titanichthys hussakofi</i> Hay, 1929 [<i>Brontichthys clarki</i> , in part, Claypole, 1894]	CL	Claypole, 1894
<i>Titanichthys rectus</i> Wright in Claypole, 1893b	CL	Claypole, 1893b
<i>Trachosteus clarki</i> Newberry, 1889	CL	Newberry, 1889
type "T" arthrodire	CL	(field identification, Cleveland Museum of Natural History Interstate-71 salvage project)
Chondrichthyans		
<i>Ctenacanthus (Cladodus) terrelli</i> (Newberry, 1889)	CL	Ginter (in press)
<i>Ctenacanthus (Cladodus) tumidus</i> (Newberry, 1889)	CL	Ginter (in press)
<i>Cladoselache acanthopterygius</i> Dean, 1909	CL	Dean, 1909
<i>Cladoselache brachypterygius</i> Dean, 1909	CL	Dean, 1909
<i>Cladoselache clarki</i> Claypole, 1893a	CL	Claypole, 1893a
<i>Cladoselache desmopterygius</i> Dean, 1909	CL	Dean, 1909
<i>Cladoselache fylleri</i> (Newberry, 1889)	CL	Newberry, 1889
<i>Cladoselache magnificus</i> Claypole, 1894	CL	Claypole, 1894
<i>Cladoselache newberryi</i> Dean, 1894	CL	Dean, 1894
cladoselachian, new genus and species ²	CL	Williams, M. E., before 2003
cochliodont	CL	Williams, M. E., before 2003
<i>Ctenacanthus concinnus</i> (Newberry, 1875)	CL	Ginter (in press)
<i>Ctenacanthus vetustus</i> ? ³ Newberry, 1873	CL	Williams, M. E., before 2003
<i>Diademodus hydei</i> Harris, 1950	CL	Harris, 1950
eugeneodontid	CL	(field identification, Cleveland Museum of Natural History Interstate-71 salvage project)
new genus and species	CL	Williams, M. E., before 2003., CMNH 5965, "unique spine"
hybodont	CL	Williams, M. E., before 2003.
<i>Monocladodus</i> Claypole, 1893a, species	CL	Williams, M. E., before 2003.
<i>Orodus</i> Agassiz, 1838, species ⁴	CL	Williams, M. E., 1990, fig. 243
<i>Orodus</i> Agassiz, 1838, species "B"	CL	Michal Ginter (personal communication, 2005)
<i>Orodus</i> Agassiz, 1838, species "C"	CL	Michal Ginter (personal communication, 2005)
<i>Phoebodus politus</i> Newberry, 1889	CL	Ginter and Ivanov, 1992
shark with cephalic head spines ⁵	CL	M. E. Williams (personal communication, before 2003.)
<i>Sphenacanthus</i> Agassiz, 1837 (tentative identification)	EA	Williams, M. E., before 2003
stethacanthid new genus	CL	Hlavin, 1976
<i>Stethacanthus altonensis</i> (St. John and Worthen, 1875)	EA	Williams, M. E., before 2003

Table 5-2.—List of taxa found within the Cleveland Member and their reported geographic ranges—continued

Taxa	Ranges	References
Chondrichthyans (continued)		
<i>Stethacanthus carinatus</i> (St. John and Worthen, 1875)	CL	Williams, M. E., before 2003
<i>Stethacanthus</i> Newberry, 1889, new species	CL	Hlavin, 1976
<i>Tamiobatis vetustus</i> Eastman, 1897	?	Williams, 1998
<i>Tamiobatis</i> cf. <i>succinctus</i> (St. John and Worthen, 1875)	CL	Michal Ginter (personal communication, 2005)
type A ⁶	CL	Williams, M. E., before 2003
type B ⁷	CL	Williams, M. E., before 2003
Osteichthyans		
<i>Kentuckia hlavini</i> Dunkle, 1964	CL	Dunkle, 1964
<i>Kentuckia</i> Rayner, 1952, species ⁸	CL	Terry Martin (personal communication, 2005)
paleonisoid cf. <i>Mesopoma</i> Traquair, 1890	EA	Terry Martin (personal communication, 2005)
<i>Proceratodus wagneri</i> (Newberry, 1889)	CL	Newberry, 1889
<i>Tegeolepis clarki</i> (Newberry, 1888)	CL	Dunkle and Schaeffer, 1973

¹*Dunkleosteus terrelli* is reported from Morocco (M. Rutlan, personal communication, 2005) extending its range to the western shores of the Old Red Sandstone Continent.

²This undescribed new genus and species is based on Williams (before 2003), who distinguished two morphologies within the Cleveland Member cladoselachians.

³Williams recognizes the presence of *Ct. vetustus*, although the type for *Ct. vetustus* (AMNH 351) is synonymized by Hlavin (1976) with his stethacanthid new genus, based on other material.

⁴Interestingly noted, in one case, as the putative stomach contents of *Dunkleosteus terrelli*, CMNH 8735 (Williams, 1990, fig. 243). Michal Ginter (personal communication, 2005) recognized three potential species of *Orodus* (his species “A–C”) although it is difficult to equate the identifications of Hlavin (1976), Williams, and Ginter, which are based in part on different specimens. Two specimens identified as *O. turgidus* or *daedaleus* by Williams represent sp. “B” and “C” of Ginter.

⁵An isolated spine was formerly recognized as *Homacanthus parvulus* (Newberry, 1875), an acanthodian.

⁶A potentially new undescribed shark with ctenacanthid-like scales.

⁷A potentially new undescribed shark with acanthodian-like scales.

⁸Terry Martin (personal communication, 2005) reports the presence of at least one additional species of paleonisoid based on isolated bones of a distinct morphology differing from *Kentuckia hlavini*.

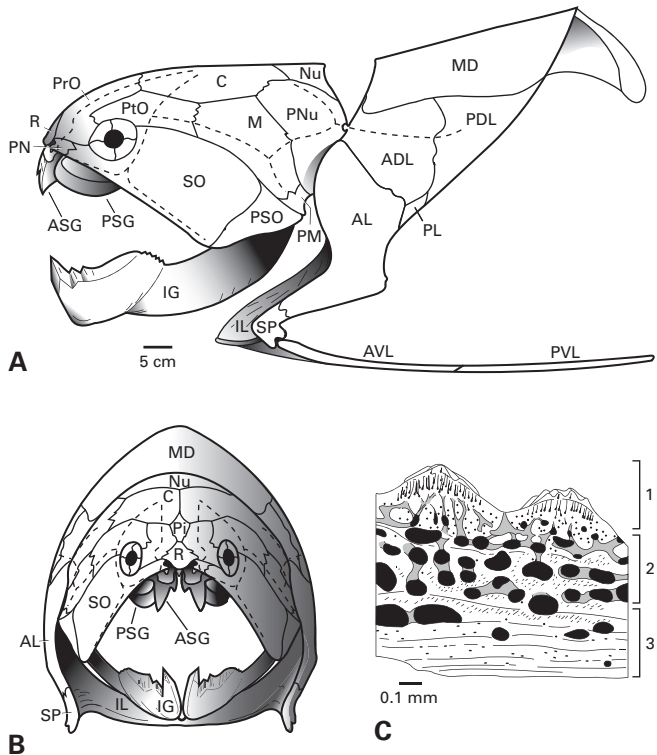


FIGURE 5-7.—A, *Dunkleosteus terrelli*, dermal bones in right lateral view and B, anterior view (composite after Heintz, 1932 and 1968). C, *Phlyctaenaspis acadica*, cross-section of the dermal bone in an arthrodire (after Gross, 1957; unlike *Dunkleosteus terrelli*, the surface of the bone in *P. acadica* is covered with tubercles and in *D. terrelli*, parts of individual bones can exceed 10 cm in thickness); 1, superficial tubercles with semidentine (the latter is characteristic of placoderms); 2, layer of spongy bone (vascular layer); 3, compact or lamellar bone. See table 5-1 for abbreviations.

preserved (Williams, 1990, p. 277). One difference among modern taxa may lend itself to explain why this occurs: The living sharks and the sole surviving coelacanth retain urea (a form of nitrogenous waste retained in sharks to maintain an osmotic balance with the marine environment). It can be speculated that the taphonomic geochemistry of the decomposition of Cleveland Member sharks and their urea in effect “pickles” them. The future discovery of *Chagrinia* (a Chagrín Member coelacanth) within the sediments of the Cleveland Member might support this explanation.

Another preservational difference between sharks and other fishes is the completeness of preservation. Many shark fossils show body and fin outlines with little or no disturbance of the shagreen of placoid scales and the relatively delicate prismatic cartilage (both highly susceptible to scavenging and currents; Williams, 1990, p. 277, notes the presence of 150 articulated shark specimens with soft tissue preservation in the Cleveland Museum of Natural History collection). This pattern suggests little postmortem time between death, settling, and eventual burial (Williams, 1990). In contrast, only 5.1% of the *Dunkleosteus* specimens (a large placoderm) have more than 25% of their ossified skeleton preserved. Even though a large amount of dermal bone is typical for *Dunkleosteus* species, their preservational patterns suggest a period of floatation with loss of elements (Carr, 2008).

ECOLOGY OF THE PLACODERMS

It is common knowledge that there is a high level of diversity in form and habitat range of living chondrichthyans and bony fishes; however, this knowledge does not transfer to extinct placoderms. With what is described as their heavy dermal armor, placoderms are often portrayed as bottom living or restricted to a life near the bottom (Denison, 1978, p. 17). Analogous to this misinterpretation is the historical portrayal of dinosaurs as slow and cumbersome cold-blooded beasts that could barely support their own immense weight. What is emerging today is an understanding of placoderms as a dynamic group of active predators that ruled the seas in the “Age of Fishes.” Their greatest species diversity was during this time (fig. 5-3) and in many cases, as seen in the Cleveland Member (table 5-2), these species were an important component of the fauna (table 5-3). Less than 5% of the 720 reported placoderm taxa preserve portions of the pectoral fin (Carr and others, in press). Our understanding of the caudal fin is equally limited. For the pectoral fin, it is the proximal elements that are preserved and the tail likewise preserves proximal elements, so that the actual span of these appendages is speculative. As such, the locomotor pattern for placoderms has been assumed to be an eel-like (sinusoidal) undulation of a slow, cumbersome bottom-living fish (see Moy-Thomas and Miles, 1971, or Denison, 1978, for a review of early interpretations of placoderm ecology). A recent discovery of radials in *Dunkleosteus*, and the presence of an organic film outlining the remains of the fin in *Dunkleosteus* (CMNH 8982) as well as in a related taxon, demonstrate a fin span (lateral extent relative to width) more like that seen in sharks. If distal elements have not been detected in the pectoral fin for this length of time (since the

recognition of placoderms over 150 years ago), it is conceivable that a similar story holds for the caudal fin. We are now faced with a much wider potential for locomotor styles in placoderms. This is supported in part by the analysis of *Dunkleosteus* using taphonomic evidence that it was a pelagic cruiser of the waters overlying the future Cleveland Member (Carr, 2008). The analysis of *Dunkleosteus* makes placoderm extinction all the more interesting because it means a dominant placoderm group consisting of some of its top predators did not survive the Famennian-Tournasian extinction event.

THE VERTEBRATE FAUNA OF THE CLEVELAND MEMBER

There are 40 vertebrate taxa recorded in the literature for the Cleveland Member (24 placoderms, 14 sharks, and 2 osteichthyans; Hlavin, 1976), but this number is an underestimate. At present there is evidence for 65 taxa (table 5-2) represented by the placoderms (28), chondrichthyans (32), and osteichthyans (5). Although the placoderms are represented by five orders that survived the Frasnian-Famennian extinction event, only arthrodires are recognized in the open water habitat associated with the Cleveland Member. Other placoderm groups (phyllolepid and antiarchs) and teleostome groups (acanthodians, sarcopterygians) are present within the Appalachian Basin, but most appear either to be restricted to shallower or near-shore environments or are more sensitive to taphonomic processes and are therefore not preserved.

A single acanthodian, *Homacanthus parvulus*, has been reported from the Cleveland Member (Newberry, 1875); however, M. Williams (personal communication before 2003) noted a single chondrichthyan specimen with several cephalic spines of the “homacanthid” type. With the association of these spines with a chondrichthyan specimen and the fact that no isolated acanthodian scales have ever been reported from the Cleveland Member, it is reasonable to tentatively remove “*Homacanthus parvulus*” from the faunal list of the Cleveland Member.

Placoderms represent the largest portion of the collection, but this volume is overly represented by a single species, *Dunkleosteus terrelli*. Its large size and thick, visible bones may represent a size bias during collecting. Other species of placoderms are often represented by limited numbers of specimens (for example, *Bungartius perissus* is only known from two specimens [CMNH 7573, the holotype, and CMNH 6666]), and *Holdenius holdeni* only from isolated jaws.

Sharks represent the largest number of species in the Cleveland Member vertebrate fauna, but their relatively small number of specimens is again representative of relative taphonomic and sampling biases (their delicate prismatic cartilage skeleton and difficult detection in the field except when found in concretions). Williams (1990, p. 277) noted the presence of 150 Cleveland Museum of Natural History shark specimens that preserve traces of soft tissue. Of these, he records 53 with evidence of stomach contents. It is interesting to note that the genus *Cladoselache* represents 71.4% of these latter specimens. Among the sharks, it appears that *Cladoselache* is the numerically dominant

Table 5-3.—Famennian vertebrate faunas of the world. All faunas, except Cleveland and Red Hill, Pennsylvania, were compiled from Lelièvre (2003). Abbreviations: ACN, number of acanthodians; ACT number of actinopterygians; CH, number of chondrichthyans; PL, number of placoderms; SAR, number of non-tetrapod sarcopterygians; TE, number of tetrapods; and TOT, total number of taxa.

Locality	Facies	TOT	PL	ACN	CH	ACT	SAR	TE
Cleveland Member, Ohio ¹	deep-marine basin clastics	65	28 (43.1%)		33 (49.2%)	4 (6.2%)	1 (1.5%)	
Red Hill, PA (Catskill Delta) ²	fluvial clastics	15	3 (20%)	1 (6.7%)	2 (13.3%)	1 (6.7%)	6 (40%)	2 (13.3%)
Witpoort Formation, South Africa	shallow-marine clastics	10	4 (40%)	1 (10%)	2 (20%)		3 (30%)	
Worange Point Formation, NSW, Australia	clastics (origin?) ³	4	3 (75%)				1 (25%)	
Bumberry Formation., NSW, Australia	marine clastics ³	11	4 (36.4%)	1 (9.1%)	4 (16.7%)	1 (4.2%)	6 (54.5%)	
Belgium (Fa 2d age deposits)	marine clastics	24	5 (20.8%)	2 (8.3%)			12 (50%)	
Zhongning Formation, Ningxia Province, China	shallow-marine clastics ³	6	5 (83.3%)				1 (16.7%)	
Magunao Formation, Hunan Province, China	shallow-marine carbonates	11		2 (18.2%)	7 (63.6%)	1 (9.1%)	1 (9.1%)	
Daihua Formation, Guizhou Province, China	Marine	10		1 (10%)	7 (70%)	1 (10%)	1 (10%)	
Cuche Fm., Columbia	marine clastics ³	9	3 (33.3%)	1 (11.1%)	1 (11.1%)	1 (11.1%)	3 (33.3%)	
Aina Dal and Britta Dal Formation, Greenland	marine clastics ³	17	4 (23.5%)	1 (5.9%)	2 (11.8%)		8 (47.0%)	2 (11.8%)
Dura Den, Scotland	shallow-marine clastics ³	11	4 (36.4%)				7 (63.6%)	
Ketleri Formation, Latvia	marine clastics ³	10	1 (10%)	2 (20%)		1 (3.1%)	5 (50%)	2 (20%)
Tafilalt, Morocco	marine basin clastics	32	13 (40.6%)	2 (6.3%)	13 (40.6%)		3 (9.4%)	
St. Croix Mountains, Poland	margin of carbonate platform	15	7 (46.7%)	2 (15.4%)	8 (53.3%)		6 (46.1%)	2 (15.4%)
Khovanschina Formation, Russia	marine basin	13	2 (15.4%)	2 (15.4%)	5 (71.4%)	1 (7.7%)	1 (4.3%)	
Mae Sam Lap, Thailand	Marine	7		1 (7.7%)	4 (30.8%)	2 (15.4%)	5 (38.4%)	
Yiginli Formation and Köprülü black shales, Turkey	shallow-marine clastics ³	13	1 (7.7%)					

¹Note that 83.1% represent endemic species.

²Data compiled from <<http://www.devoniantimes.org/who/pages/who.html>>.

³A marine interpretation is based on the vertebrate faunal assemblage (Lelièvre, 2003).

member of the shark fauna, assuming there were minimal to no sampling biases and that similar taphonomic processes existed among the sharks (unlike *Dunkleosteus* among the placoderms with its easily recognizable large bones).

Recognizing the true diversity of sharks in the Cleveland Member fauna remains an active endeavor. The unfinished work of the late M. Williams suggests the presence of a number of undescribed forms. There is also much work left to be done in analyzing the cladoselachians from the material collected and described in the late Nineteenth and early Twentieth centuries, as noted by Zangerl (1981, p. 68). This opinion is supported by more recent analyses of Michal Ginter (for example, his synonymy of ctenacanthid species in Ginter [in press] and through personal communication [2005] suggests the potential synonymy of at least two species of *Cladoselache*). The size of the Cleveland Member shark collections and their distribution in multiple institutions hinders a concise comparison of this dispersed material. The descriptions of the shark fauna by Hlavin (1976), Williams (before 2003), and Michal Ginter (personal communication, 2005) each use a different subset of total specimens, so agreement on the presence or absence of a particular species is difficult to discern by the outside reader. Much work remains to be done on this important collection. However, what is clear is that the species diversity for sharks in the Cleveland Member is under-represented in the literature.

Unlike the sharks and placoderms, the remains of osteichthyans are often limited to isolated scales or individual dermal bones. It is rare to find articulated specimens. One rare find of three articulated specimens is exceptionally unusual in that it was part of the stomach contents of a cladoselachian shark (*Cladoselache fylei*; Williams, 1990; fig. 242).

Of the 65 species reported from the fauna, greater than 83% are endemic to the Cleveland Member (table 5-2). This could represent a taphonomic or sampling bias, as it seems doubtful that fish species of the open basin did not cross into the waters of the basin slope and more shoreward or that they are limited to a single basin. The number of species reported from the Chagrin Member is extremely limited and, typically, paleoichthyologists have considered the Chagrin Member to be practically barren of specimens. (However, fish have been reported from the Chagrin by Hannibal [1990, p. 285, fig. 4], and M. Williams and others have collected small articulated arthrodire placoderms in the Chagrin Member in Ashtabula County during the last three decades.) This disparity in numbers between faunas that represent adjacent environments clearly points to the unique nature of the Cleveland Member and its fauna (based on preservation and history of collecting). The importance of endemism should be evaluated in light of whether comparisons are being made between equally sampled basins or localities. For example, the Cleveland Member fauna and the Tafilalt fauna of Morocco (the second most diverse Famennian fauna with 32 species; table 5-3) show interesting faunal similarities. Other black shales with limited faunas appear to under-represent the true regional fauna, which is exemplified by the Antrim Shale of Michigan where recent fieldwork indicates a much larger fauna than previously reported (Carr and Jackson, 2005).

OTHER VERTEBRATE FAUNAS OF THE LATE DEVONIAN

Lelièvre (2003) summarizes the vertebrate faunas of the Late Devonian. In the Famennian, he records 18 vertebrate faunas (table 5-3) and assumes a marine influence for all of these faunas (refer to the “Freshwater versus marine habitats” section below).

The Cleveland Member represents the most diverse fauna (65 species), but this may reflect the long history of collecting in the shales of northern Ohio (Hlavin, 1976; Hannibal, 2008) and hints at the potential diversity of other faunas that have yet to be closely studied. The next most-diverse fauna is the Moroccan Tafilalt fauna (32 species). In both faunas, the placoderms represent a major portion of the fauna (43.1% and 40.6% in the Cleveland and Tafilalt faunas, respectively). The chondrichthyans are the largest portion of species represented in the Cleveland Member fauna (49.2%). However, the arthrodires have the largest number of individual specimens (with *Dunkleosteus terrelli* represented by hundreds of specimens). The large number of chondrichthyan species in the Cleveland Member compared to other faunas is most likely a sampling bias (as noted above) in that the sharks are often well preserved in easily detectable carbonate concretions. The relatively large number of *Dunkleosteus* specimens is due to both their preservation in concretions and cone-in-cone and (unlike with the sharks) the ease of finding them in cross-section within the shale, as float on talus piles, and even within river sediments. This has given researchers the impression that the placoderms were the dominant taxon in the Late Devonian (Carr, 1995; Lelièvre, 2003; fig. 5-3). In five additional faunas, the chondrichthyans represent the greatest proportion of species (40.6–71.4%; Lelièvre, 2003; table 5-3).

An application of a rare-fraction analysis to the Cleveland Member fauna, with its long history of collection and large number of specimens, might provide a reasonable picture of the actual fauna in the Famennian (especially compared to lesser collected faunas). However, this assumes that different taxa contribute equally to the taphonomic process, have equal chances of preservation, and are equally likely to be collected.

Carr (1995), in his comparison of simple diversity curves for reported species and genera of gnathostomes, noted low diversity levels for the chondrichthyans and osteichthyans in the Late Devonian with a rapid increase after the Famennian-Tournasian extinction of the placoderms (fig. 5-3 [note plot line A for chondrichthyans and the plot line for osteichthyans]). This form of comparison does not take into account disparities in sampling. If we assume that the specimens from the Cleveland Member are indicative of the Famennian, then the diversity curves for the chondrichthyans and osteichthyans would reflect higher values. Carr (1995) assumed, based on the evidence at the time, that the Late Devonian and, especially, the Carboniferous increases in chondrichthyan and osteichthyan diversity were consistent with a pattern of opportunistic replacement. With a clearer picture of diversity patterns, it is possible that competition may have played a greater role in the extinction of placoderms than previously suspected (Miles, 1969; Carr, 1995;

Also, compare fig. 5-3, plot line B for chondrichthyans with the plot line for placoderms in the Late Devonian. Note the diversity pattern after the Frasnian peak diversity for the placoderms, the “double-wedge pattern” of Benton [1987, p. 318], which is more consistent with an interpretation of competitive displacement).

To better document these patterns, it is important to renew efforts to document Late Devonian vertebrate faunas, including microvertebrates. Elliot and others (2000) note that this latter effort has been a weak point in North American vertebrate paleontology. In the study of chondrichthyans, Ginter (2004, p. 473) notes that there is a wealth of microvertebrate information associated with the vast amount of conodont stratigraphic washings (“about 40 already named and probably many more yet undescribed Devonian tooth-based species from all over the world”). One pathway to a better understanding of the evolution and diversity of Paleozoic vertebrates is a cooperative effort among palynologists, biostratigraphers, microvertebrate paleontologists (coordinated with those who work with macro-fossils), and members of any discipline processing washings of Paleozoic sediments.

Freshwater versus marine habitats

The Cleveland Member and its lateral equivalent, the Chagrin Member (representative of more proximal slope deposits within the Appalachian Basin), clearly represent sediments deposited in a marine environment, as demonstrated by their invertebrate faunas that indicate the presence of marine species (for the Cleveland Member refer to Hannibal and others, 2008; for the Chagrin Member, Hannibal, 1990, table 20). Fossil fishes found in the Cleveland Member represent either fishes living within the marine basin, post-mortem allochthonous accumulations of floating carcasses, or a mixture of both (Brett and Baird, 1993, p. 254). The former hypothesis is clearly demonstrated for *Dunkleosteus terrelli* (Carr, 2008, a basin-wide distribution is based on a statistical analysis of the distribution of fossil remains). A marine basin distribution can be extended to the sharks and most of the placoderms based on evidence of minimal transport prior to burial (a lack of disarticulation within the fossils). Lelièvre (2003) assumes that all of the Famennian vertebrate faunas represent marine or marginal marine habitats. He bases this interpretation on new evidence for the presence of marine invertebrates, a marine geochemical signal in the deposits, or in the absence of other evidence on the assemblage of vertebrates present (some members of each assemblage are from undisputed marine habitats). This interpretation is debated, though, when considering the Catskill Delta Red Hill fauna (Sevon, 1985; Woodrow and others, 1995) and the historic Old Red Sandstone faunas of Scotland (for example, Schmitz and others, 1991). Conversely, a number of faunas that have historically been interpreted as freshwater are now reinterpreted as marine or marginal marine based on either new fossil evidence (for example, presence of marine invertebrates) or geochemical analyses (for example, Spitsbergen [Goujet, 1984], the Baltic region and Podolia [Mark-Kurik, 1991], and Escuminac Formation, Quebec [Chidiac, 1989; Vézina, 1991]). Freshwater interpretations are often associated with arguments of negative evidence,

for example, the lack of acritarchs (marine algal spores) or easily detected marine invertebrates; a fluvial interpretation is often supported by sedimentological studies, specifically the recognition of paleosols (for example, as noted for the Red Hill, PA, locality).

In the argument of a freshwater or marine habitat for the fishes found as fossils in Devonian deposits, it is difficult to explain the global distribution of fish species, for example, *Groenlandaspis*, when they are assumed to be restricted to freshwater habitats. *Groenlandaspis* (fig. 5-8) is known from East Greenland, Antarctica, Ireland, Turkey, South Africa, Pennsylvania (U.S.A.), Belgium, Iran, England (Cornwall Basin), Australia, Falkland Islands, and Columbia, South America (Janvier and Clément, 2005; the latter location was based on a questionable identification, but additional fossil finds confirm their presence [Janvier, personal communication, 2005]). In many of these localities it is undisputed that the sediments are marine and not freshwater; it is difficult to argue for the global dispersal of a freshwater taxon across all of Gondwana and Euramerica (fig. 5-8). This argument is not limited to a single species, but can be expanded to numerous taxa (lungfishes, sarcopterygians, antiarchs, and phyllolepis and additional arthrodires other than *Groenlandaspis*; Schultze and Cloutier, 1996b; Lelièvre, 2003).

The disparity between established habitat classifications and the contrary evidence at hand raises a challenge to sedimentologists and paleontologists to clarify the distinction between fluvial systems and the unparalleled epicontinental deltaic margins under a marine influence that may have typified ancient coastlines.

CONCLUSION

The fishes of the Cleveland Member offer one of the best pictures of vertebrate life in the Famennian. This is the result of the exceptional preservation of many of the fossils and nearly 150 years of fossil collecting. This collection can be improved with studies of the microfauna of the Cleveland Member and other Paleozoic vertebrate localities.

The three global extinction events associated with the Late Devonian (Givetian-Frasnian, Frasnian-Famennian, and Devonian-Mississippian) differ in their effect on invertebrate and vertebrate diversity. Among vertebrates, each event is characterized by different patterns of extinction, stasis, and diversity increases for different subgroups (Carr, 1995). The improved picture of Late Devonian diversity based on the Cleveland Member fauna provides valuable information for understanding the causal mechanisms associated with the extinction of all placoderms by the end of the Devonian.

The greater proportion of chondrichthyan species (49.2%) than placoderm species (43.1%) in the Cleveland Member suggests that if this diversity pattern is similar in other lesser-known faunas, our understanding of the extinction of placoderms may be that their extinction was the result of competitive displacement by the chondrichthyans and, by extension, the osteichthyans. Part of the reason for this displacement may be that the chondrichthyans and osteichthyans have demonstrated evolutionary adaptations associated with more effective locomotor patterns and feeding (Carr, 1995).

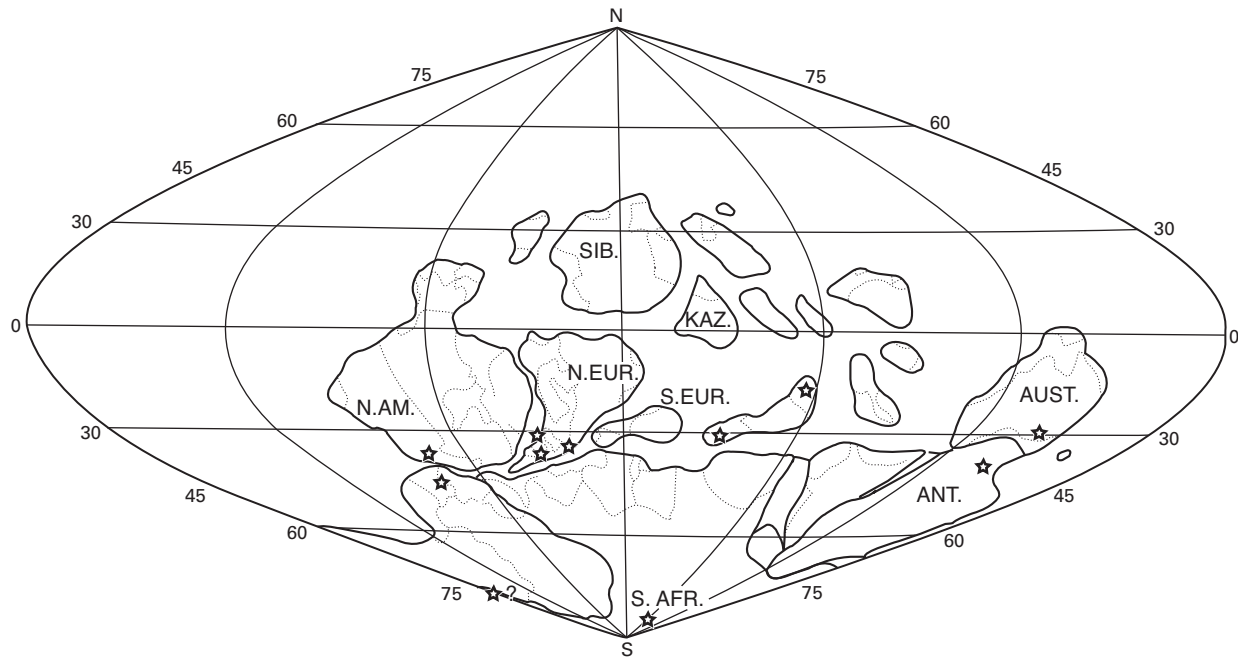


FIGURE 5-8.—A global paleogeographic reconstruction for the Middle-Late Devonian after Streel and others (2000) indicating the localities (stars) for *Groenlandaspis* (an arthropod often found in putative freshwater sediments, but also known from marine deposits).

The vertebrate faunas of the Late Devonian (Givetian-Frasnian; Schultze and Cloutier, 1996b; Famennian, Lelièvre, 2003) are suggestive of a marine or marginal marine interpretation for the sediments in which they are preserved. This is an important consideration since it implies that tetrapods originated in a marine influenced habitat and that fully freshwater faunas are a product of the Carboniferous Period. This information is part of the continuing debate about whether the depositional environments for sediments of the Old Red Sandstone Continent represent freshwater or marine habitats. The cooperative efforts of sedimentologists and paleontologists should lead to a better understanding of these and other paleoenvironments of the Paleozoic.

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As outlined in Hlavin's (1976) dissertation, the volume of the collection of fishes is the product of a long history of combined professional and amateur collectors (see also Hannibal, 2008). Often neglected in these commentaries are the current crop of collectors and volunteers. We would like to extend our sincerest appreciation to all those contributors that continue to make the vertebrate paleontology collections at the Cleveland Museum of Natural History a global standard for the study of fossil fishes. Listed alphabetically, they include: Doug Dunn, Steve Green, George Kampouris, Joe Klunder, Terry Martin, Wally Moll, Doris and George Reich and sons Kurt and Mark, Robert Schwarz and sons Eric and Karl, Verna Vander Kooi, and Dale Zelinski.

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