An examination of the Devonian fishes of Michigan (#28497)

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An examination of the Devonian fishes of Michigan

Jack Stack Corresp., [1] , **Lauren Sallan** Corresp. [1]

[1] Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA, United States

Corresponding Authors: Jack Stack, Lauren Sallan
Email address: stackj@sas.upenn.edu, lsallan@upenn.edu

We surveyed the taxa, ecosystems, and localities of the Devonian fishes of Michigan to provide a framework for renewed study, to learn about the diversity and number of these fishes, and to investigate their connection to other North American faunas. Twenty genera of fishes have been found in diverse Middle and Late Devonian formations in Michigan, of which thirteen are placoderms represented by material ranging from articulated cephalic shields to ichthyoliths. As expected from the marine nature of these deposits, placoderms are overwhelmingly arthrodire in nature, but two genera of ctenodonts have been reported along with rarer antiarch and petalichthyid material. The remaining fish fauna consists of fin-spines attributed to "acanthodians," two genera of potential crown chondrichthyans, an isolated dipnoan, and onychodont teeth/jaw material. There was an apparent drop in fish diversity and fossil abundance between Middle and Late Devonian sediments. This pattern may be attributed to a paucity of Late Devonian sites, along with a relative lack of recent collection efforts at existing outcrops. It may also be due to a shift towards open water pelagic environments at Late Devonian localities, as opposed to the near-shore reef fauna preserved in the more numerous Middle Devonian localities. The Middle Devonian vertebrate fauna in Michigan shows strong connections with same-age assemblages from Ohio and New York. Finally, we document the presence of partially articulated vertebrate remains associated with benthic invertebrates, an uncommon occurrence in Devonian strata outside of North America. We anticipate this new survey will guide future field work efforts in an undersampled yet highly accessible region that preserves an abundance of fishes from a critical interval in marine vertebrate evolution.

An Examination of the Devonian Fishes of Michigan

Jack Stack[1] and Lauren Sallan[1]

[1]Department of Earth and Environmental Science, University of Pennsylvania, 240 S. 33rd Street, Philadelphia, PA, USA 19104-6316

Corresponding Authors:

Jack Stack[1]

stackj@sas.upenn.edu

Lauren Sallan[1]

lsallan@upenn.edu

Abstract —We surveyed the taxa, ecosystems, and localities of the Devonian fishes of Michigan to provide a framework for renewed study, to learn about the diversity and number of these fishes, and to investigate their connection to other North American faunas. Twenty genera of fishes have been found in diverse Middle and Late Devonian formations in Michigan, of which thirteen are placoderms represented by material ranging from articulated cephalic shields to ichthyoliths. As expected from the marine nature of these deposits, placoderms are overwhelmingly arthrodire in nature, but two genera of ptyctodonts have been reported along with rarer antiarch and petalichthyid material. The remaining fish fauna consists of fin-spines attributed to "acanthodians," two genera of potential crown chondrichthyans, an isolated dipnoan, and onychodont teeth/jaw material. There was an apparent drop in fish diversity and fossil abundance between Middle and Late Devonian sediments. This pattern may be attributed to a paucity of Late Devonian sites, along with a relative lack of recent collection efforts at existing outcrops. It may also be due to a shift towards open water pelagic environments at Late Devonian localities, as opposed to the nearshore reef fauna preserved in the more numerous Middle Devonian localities. The Middle Devonian vertebrate fauna in Michigan shows strong connections with same-age assemblages from Ohio and New York. Finally, we document the presence of partially articulated vertebrate remains associated with benthic invertebrates, an uncommon occurrence in Devonian strata outside of North America. We anticipate this new survey will guide future field work efforts in an undersampled yet highly accessible region that preserves an abundance of fishes from a critical interval in marine vertebrate evolution.

INTRODUCTION

The Devonian Period (419-359 Ma), the so-called "Age of Fishes," was marked by major transitions in vertebrate biodiversity, including the takeover of ecosystems by jawed fishes, the first appearance of tetrapods, and several group-specific and global extinctions (Friedman and Sallan, 2012). Despite the evolutionary importance of this interval, Devonian vertebrates from the U.S. have been undersampled and understudied in the last 50 years relative to specimens of the same age from the U.K., China, Australia and even Antarctica (Long, 1994), with possible exceptions being select very Late Devonian faunas such as the Cleveland Shale and Red Hill (Carr and Jackson, 2008; Daeschler and Cressler, 2011). Fishes are common in fossil-bearing Paleozoic strata throughout the midwestern U.S., with many outcrops discovered over a century ago (Newberry, 1889; Eastman, 1907; Eastman, 1908). The Devonian-aged fauna from Michigan is both abundant and neglected in the scientific literature relative to similar strata in Ohio, Pennsylvania and elsewhere, despite heavy, ongoing collection efforts by amateurs. We undertook this survey of Devonian fishes from Michigan, the first since 1970, as a result of new discoveries by one of us (J.S.) with the assistance of avocational paleontologists and to motivate new fieldwork.

During the Devonian, the Michigan Basin was located between, and connected to, the better described Illinois (Hussakof, 1913; Cluff, 1980; Brusatte, 2007) and Appalachian Basins (Newberry, 1873; Claypole, 1883; Carr and Jackson, 2008; Carr and Hlavin, 2010; Downs et al., 2011; Daeschler and Cressler, 2011), yet it has been largely ignored by researchers for over a century. Most of the handful of studies on Devonian vertebrates from Michigan are descriptions of single taxa (e.g. Stevens, 1964; Miles, 1966; Schultze, 1982; Carr and Jackson, 2005). Only

one study from the last century attempted to survey Devonian fossil fishes from Michigan, but was limited in scope to arthrodires (Case, 1931). Several decades later, an additional summary of vertebrate fossils from the University of Michigan Museum of Paleontology was published by Dorr and Eschman (1970), accompanied by a description of the Devonian ecosystems in Michigan, including information on collecting sites, geologic history, and invertebrate faunae. However, many of their identifications were incorrect, and some of their figured and described specimens are currently missing from the UMMP collections.

Recent fieldwork in Michigan, undertaken mostly by amateur collectors, has revealed a diverse and in many ways distinct Devonian vertebrate fauna containing taxa not reported by Case (1931) and Dorr and Eschman (1970). New sites have produced an abundance of relatively well-preserved vertebrate skeletal remains, including articulated material. 118 of 200 catalogued Michigan Devonian specimens were collected after the previous survey. Here, we provide an updated and comprehensive summary of what is known about the Devonian fish fauna from Michigan. We also compare the Devonian fish fauna of Michigan to similarly aged marine faunas from New York and Ohio, placing it within the larger regional context of Devonian North America.

MATERIALS AND METHODS

We surveyed Michigan Devonian fish specimens in the collections of the University of Michigan (UMMP), the Michigan History Museum (BV, JS, M, or a date), Michigan State University Museum (VP), the Cleveland Museum of Natural History (CMNH), and the literature, which

contains records for other specimens from the Michigan State University Museum, the Cleveland Museum of Natural History, and the Great Lakes Area Paleontological Museum. We also performed surveys of known outcrops as described in text. Collections from localities on public lands were approved by the State of Michigan, State Historic Preservation Office Permit AE2016-10, and collections deposited in the Michigan Historical Museum. We compiled and organized information including type specimen, specimen counts, geologic setting and localities (Tables 1-4). A full list of examined specimens is available as a supplement. Below, we describe the occurrence and distribution of vertebrate remains by formation alongside information on associated invertebrate remains, depositional environment, and the locations of vertebrate-bearing fossil sites. We also summarize the characteristics of Devonian vertebrates resident in Michigan. We then synthesized temporal patterns, ecology, and faunal similarities with other marine Devonian localities.

MIDDLE DEVONIAN GEOLOGICAL DISTRIBUTION

Middle Devonian Formations

Pre-Traverse Group

The oldest vertebrate bearing Devonian localities in Michigan are from the Eifelian (Middle Devonian) (Swezey, 2002; Brett et al., 2011; Fig. 1). These occur in the Dundee Limestone and the Rogers City Limestone formations, which also produce numerous invertebrates (Dorr and Eschman, 1970; Ehlers and Kesling, 1970). The fish found in the Dundee Limestone include the onychodont *Onychodus sigmoides* Newberry, 1873, the acanthodian *Machaeracanthus* Newberry, 1873, the chondrichthyan *Acondylacanthus*

gracillimus St. John and Worthen, 1875, the presumptive arthrodire ?*Titanichthys* Newberry, 1885, the ptyctodont *Ptyctodus* Pander 1858, and the petalichthyid ?*Macropetalichthys* Norwood and Owen, 1846 (Dorr and Eschman, 1970; Fig. 2). ?*Titanichthys* (UMMP 26114), *A. gracillimus* (UMMP 26523), and *Machaeracanthus* (UMMP 26111, UMMP 26112) and a jaw (UMMP 26113) from *Onychodus* are known from Sibley Quarry, Wyandotte, Wayne County (Dorr and Eschman, 1970). An isolated fin spine from *Machaeracanthus* (UMMP 3521) and an isolated tooth from *Onychodus* (UMMP 22006) are documented from a site in London Township, Monroe County (Dorr and Eschman, 1970). One specimen of two articulated armor plates (UMMP 14320) from ?*Macropetalichthys* and another specimen of *Ptyctodus* (UMMP 14321) are documented from a locality near Trenton, in Wayne County (Dorr and Eschman, 1970). It is important to note that the geological source of the *Ptyctodus* specimen is uncertain and cannot be verified based on the matrix (Dorr and Eschman, 1970). Despite this taxonomic diversity, vertebrate abundance and perhaps preservation potential within the Dundee Limestone appears to be very poor (Ehlers and Kesling, 1970).

The Traverse Group

The Traverse Group encompasses all but three of the known vertebrate-bearing formations from Michigan (Dorr and Eschman, 1970), and is referred to with different names in different parts of the state (Fig. 3). It was deposited in the Givetian, or the Erian regional series (Swezey, 2002; Fig. 1). Six separate depositional environments or zones have been sampled from the Traverse group, representing different water depths: a lagoonal zone, the zone of turbulence, the stromatoporid-coral zone, the coral-brachiopod zone, the diverse fauna zone, and a bioherm

(Ehlers and Kesling, 1970). These zones were identified and described by Ehlers and Kesling (1970), and are briefly summarized here for future reference. The stromatoporid-coral zone was nearshore, shallow, and contained invertebrates such as brachiopods and crinoids (Ehlers and Kesling, 1970). The coral-brachiopod zone represents deeper water coincident with the lowest limit of stromatoporoids, with fossil material consisting mostly of brachiopods, corals, and bryozoans (Ehlers and Kesling, 1970). Rocks from both of these zones are abundant in the Traverse Group, and tend to be medium to fine grained limestones that can grade down into calcareous shales (Ehlers and Kesling, 1970). The diverse fauna zone was reefal with abundant vertebrates, brachiopods, trilobites, and crinoids with less common corals, bryozoans, and mollusks (Ehlers and Kesling, 1970). The rocks from the diverse fauna zone tend to be thick claystones or shale beds, with low calcareous content (Ehlers and Kesling, 1970). It is also possible to find fish and invertebrate fossils in the lagoonal sediments, but these may have been the result of marine incursions rather than distinct faunas (Stevens, 1964; Ehlers and Kesling, 1970). The rocks from the lagoonal zone are lithographic limestone (Ehlers and Kesling, 1970).

Vertebrate Distribution in Early Erian (Givetian) Deposits

Bell Shale.— One tooth plate (UMMP 14460) from *Ptyctodus* has been reported from the Bell Shale of Rogers City, Presque Isle County (Dorr and Eschman, 1970). Invertebrate material suggests that the Bell Shale was deposited in the diverse fauna zone (Pohl, 1930; Ehlers and Kesling, 1970).

Rockport Quarry Limestone.— The fishes found in the Rockport Quarry Limestone

include the arthrodires *Protitanicthys rockportensis* Case, 1931, ?*Holonema rugosum* Claypole, 1883, *Holonema* sp., *Dunkleosteus* sp. Lehman, 1956, *Mylostoma* sp. Newberry, 1883 and *Dinomylostoma* sp. Hussakof, 1913, the ptyctodont *Ptyctodus* sp., the acanthodian ?*Machaeracanthus* sp., and the chondrichthyan ?*Tamiobatis* sp. Eastman, 1897 (Dorr and Eschman, 1970; personal observation; Fig. 4). There are also two specimens (14M, VP. 522) of placoderms of unknown affinity. One of these specimens (14M) consists of armor fragments distinguishable from other resident taxa by a lack of tubercles (Fig. 4(B)), but further material is required to make an exact attribution. Also, a single specimen (UMMP 3898) was given an uncertain designation as ?*Holonema rugosum* by Dorr and Eschman (1970).

The Rockport Quarry Limestone is the most diverse fossil fish fauna in Michigan (Dorr and Eschman, 1970; Sallan and Coates, 2010). The main vertebrate-bearing outcrop is at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County (Dorr and Eschman, 1970). The degree of preservation is often good, with partially articulated armor plates frequently observed in the field, but mining operations have damaged many of the accessible fossils. Fortunately, this locality is the most productive vertebrate site in Michigan by far (personal observation), and better specimens are likely to be recovered in the future. Despite the relatively high diversity and abundance of fish material and collection efforts by amateurs, little material has been accessioned in state museums. The UMMP contains only single specimens of ?*Machaeracanthus* sp. (UMMP 13047), *Dunkleosteus* sp. (UMMP 16152), *Mylostoma* sp. (UMMP 13612), *Ptyctodus* sp. (UMMP 13045), and ?*Tamiobatis* sp. (UMMP 13147). *P. rockportensis* and *Holonema* sp. are represented by 58 and 40 specimens, respectively, in UMMP, MSU and the MHM, many more recently recovered fossils reside in

176 private collections (personal observation). The large numbers of stromatoporoids and corals,
177 alongside less common brachiopods, trilobites, and crinoids, suggests that the vertebrate
178 bearing rocks were deposited in the stromatoporoid-coral zone (Ehlers and Kesling, 1970). In
179 contrast to most Devonian sites elsewhere, articulated vertebrate remains are often preserved
180 in conglomerates with invertebrate specimens from these groups (personal observation). It is
181 notable that the abundance and diversity of coincident invertebrates is considerably lower than
182 the underlying Bell Shale, most likely because of the difference in depositional zone (Ehlers
183 and Kesling, 1970).

184 *Genshaw Formation.*— A single specimen of an anterior ventrolateral plate (UMMP
185 4169) of the antiarch *Bothriolepis* sp. Eichwald, 1840 has been documented from the Genshaw
186 Formation near Posen, Presque Isle County (Dorr and Eschman, 1970). While this specimen
187 belongs to one of the most globally abundant and widespread placoderm genera (Friedman and
188 Sallan, 2012), it remains the sole confirmed antiarch specimen of any kind found in the state
189 (Dorr and Eschman, 1970). In addition, a specimen of ?*H. rugosum* (UMMP 3899) has been
190 reported from the Killians member of the Genshaw Formation, at a locality referred to as
191 French Road near Long Lake, near Rockport Quarry, Alpena County (Dorr and Eschman,
192 1970). Invertebrates found in this formation are typical of the diverse fauna zone (Ehlers and
193 Kesling, 1970).

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195 Vertebrate Distribution in Middle Erian (Givetian) Deposits
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198 *Newton Creek Limestone.*— A single specimen of the lungfish (dipnoi) *Chirodipterus*
199 *onawayensis* (unnumbered) Schultze, 1982, along with two specimens of *Machaeracanthus*

(UMMP 47691 and UMMP 47692), two specimens of *Holonema farrowi* Stevens, 1964 (UMMP 46647, UMMP 46648), two specimens of ?*H. ragosum* (UMMP 46647 and UMMP 46648), and one unattributable *Holonema sp.* (UMMP 3130), are documented from the Newton Creek Limestone (Stevens, 1964; Schultze, 1982; Dorr and Eschman, 1970). These fossils were collected from the north edge of the Onaway Stone Quarry (Crawford's Quarry), Presque Isle County, where the Newton Creek Limestone is referred to as the Koehler Limestone (Dorr and Eschman, 1970; Ehlers and Kesling, 1970). While these fishes were recovered from the lagoonal zone (Stevens, 1964), some may have been deposited during a deeper marine incursion (Ehlers and Kesling, 1970).

Gravel Point Formation.— This formation has produced single catalogued specimens of *Gyracanthus* sp. Woodward, 1906 (UMMP 1329) Newberry, 1883, ?*Onychodus* sp. (UMMP 14370) (Dorr and Eschman, 1970), and a holonemid (UMMP 1329) (Dorr and Eschman, 1970). These specimens were found at South Point (Gravel Point), Little Traverse Bay, Charlevoix County (Ehlers and Kesling, 1970; Newberry, 1883). The invertebrate fossils from this formation are typical of the diverse fauna zone (Pohl, 1930; Ehlers and Kesling, 1970).

Alpena Limestone Formation.— This formation was deposited contemporaneously with the Gravel Point Formation (Ehlers and Kesling, 1970). Single specimens of *Dunkleosteus* sp. (UMMP 16152) and *Ptyctodus* sp. (UMMP 16157), along with four specimens of ?*Mylostoma* (BV3, BV7, BV6, and BV4) (Fig. 5) comprise the catalogued vertebrate material from the Alpena Limestone (Dorr and Eschman, 1970). The specimens of *Dunkleosteus* and *Ptyctodus* are from a locality referred to as Alkali Quarry in Alpena, and the ?*Mylostoma* specimens are from the Besser Museum Fossil Park in Alpena (personal observation; Dorr and Eschman,

1970). Amateur collectors have reported the arthrodire *Protitanichthys* and other vertebrates from this formation, but none of these specimens are deposited in museum collections. The invertebrate fossils from this formation are typical of the coral-brachiopod zone. (Pohl, 1930; Ehlers and Kesling, 1970). Many of these are articulated and occur in conglomerates with similarly partially-articulated vertebrate specimens.

Vertebrate Distribution in Late Erian (Givetian) Deposits

Four Mile Dam Formation.— ?*Mylostoma* sp., *Protitanichthys rockportensis*, and an unidentified acanthodian and placoderm have recently been collected by one of the authors (JS) from the Four Mile Dam Formation (Fig. 6). At this time, ?*Mylostoma* sp. is known from 59 specimens, while an unidentified ?placoderm is known from one specimen (4M; Fig. 6(C)), an unidentified acanthodian is known from two partial fin spines (JS 120, JS 121; Fig. 6(A)), and *P. rockportensis* is known from one specimen of a partial headshield (32M; Fig. 7(C)) and an armor fragment (JS 101). The unidentified placoderm is a specimen of an armor plate that does not resemble the other resident placoderms (?*Mylostoma* sp. and *P. rockportensis*) (Fig. 6(C)). More material needs to be collected before a concrete identification is made. Likewise, the two isolated acanthodian fin spines are distinct from named acanthodians (*Gyracanthus*, *Machaeracanthus*, and *Oracanthus*) and chondrichthyans (?*Tamiobatis* and *Acondylacanthus*; Denison, 1979) reported from Michigan (J.S. personal observation). The vertebrate fauna from the Four Mile Dam Formation has high abundance but low diversity compared to the Rockport Quarry Limestone (Dorr and Eschman, 1970). The main vertebrate-bearing outcrop of this formation is the Specific Stone Products Quarry in Alpena, with the fossils recovered from

246 discarded piles of limestone on the shores of Betsie Bay in Elberta, Benzie County (J.S.
247 personal observation).
248 Despite the fact that Four Mile Dam was only recently identified as a vertebrate-bearing
249 locality, fish material may be more abundant in these sediments than at any other Devonian
250 locality in Michigan. Over 50 vertebrate specimens have been recovered in a few years of
251 limited yet deliberate collecting. However, this represents more recent collection effort by
252 university-affiliated researchers than has recently been expended at other Michigan sites. Many
253 of the Four Mile Dam ?*Mylostoma* sp. specimens are well-preserved and partially articulated,
254 including potential juveniles, suggesting that this locality holds high potential for future
255 research (personal observation). The degree of preservation suggests rapid burial, perhaps by a
256 mudflow initiated by a storm given the environmental setting. Adding to this interpretation,
257 many of the benthic invertebrates are found conglomerates with vertebrate specimens, as
258 previously in the Alpena limestone (Fig. 6(B)). This includes fully three-dimensional,
259 articulated crinoid calyces, a rarity in the Devonian record that requires quick deposition (Fig.
260 6(D)). These invertebrates are found in other outcrops of the Four Mile Dam Formation, but
261 fish fossils are absent from all but the site mentioned above (Dorr and Eschman, 1970; Ehlers
262 and Kesling, 1970), implying that vertebrate material may not be preserved in this formation
263 under more normal environmental conditions. Invertebrate fossils found in this formation are
264 typical of the diverse fauna zone (Ehlers and Kesling, 1970).
265 *Norway Point Formation*.— A single spine (UMMP 23495), attributed to the acanthodian
266 *Oracanthus* sp. Agassiz, 1843, has been reported from the Norway Point formation at the Four
267 Mile Dam, 6 kilometers northwest of Alpena, Alpena County (Ehlers and Kesling, 1970, Dorr

and Eschman, 1970). The invertebrates from this formation suggest that the rocks were deposited in the coral-brachiopod zone (Ehlers and Kesling, 1970).

Potter Farm Formation.—- One specimen of *Ptyctodus* sp. (UMMP 21718) is known from the Potter Farm Formation, recovered from a locality referred to by Dorr and Eschman (1970) as "Old Wamer's Brickyard", in Alpena County. However, Dorr and Eschman (1970) noted that the exact geologic affinity of this specimen is uncertain (it may not have been collected *in situ*). However, another specimen of *Ptyctodus* sp. (UMMP 21817) was definitely collected from an outcrop of the Potter Farm Formation at Alpena Cemetery (Dorr and Eschman, 1970). The invertebrate fossils found from the Potter Farm Formation are typical of the diverse fauna zone (Ehlers and Kesling, 1970). Many of these invertebrates are again preserved in conglomerates with vertebrates, as in the Four Mile Dam Formation (Fig. 6(D)). These invertebrate specimens are occasionally broken and preserved in a way that superficially resembles dark, thin armor plates from vertebrates, and have been misidentified as such by amateurs, so caution must be used when identifying specimens from this formation without attention to histology.

Thunder Bay Limestone.— A tooth plate (UMMP 3023) from *Ptyctodus* sp. has been reported from the Thunder Bay Limestone (Dorr and Eschman, 1970). This specimen was collected from the bluffs on the northeast shore of Partridge Point, 6.4 kilometers south of Alpena (Dorr and Eschman, 1970). The invertebrates from this formation are typical of the diverse fauna zone (Pohl, 1930; Ehlers and Kesling, 1970).

LATE DEVONIAN GEOLOGICAL DISTRIBUTION

Antrim Shale.— The Antrim Shale was deposited in the Frasnian (Senecan) and Famennian (Chautauquan) Stages of the Late Devonian (Dorr and Eschman, 1970; Ehlers and Kesling, 1970; Gutshick and Sandberg, 1991; Fig. 1). Fish from the Antrim Shale include *Diplognathus larfargei* Carr and Jackson, 2005, ?*Trachosteus clarkii* Newberry, 1889, *Dunkleosteus sp.,* and *Aspidichthys sp.* Newberry, 1873, all known only from single specimens (Dorr and Eschman, 1970; Carr and Jackson, 2005). There are also unverified reports of ptyctodont remains from the Antrim Shale. ?*Trachosteus clarkii* is known from an isolated inferognathal (UMMP 18206) from a locality 1.6 kilometers north of Norwood, Charleviox County (Dorr and Eschman, 1970). The armor plate (UMMP 3127) of *Aspidichthys* was collected from the shore of Grand Traverse Bay near Norwood (Dorr and Eschman, 1970). *Dunkleosteus* is known from a suborbital plate (UMMP 15432) found in a concretion nodule from Squaw Bay, 6.4 kilometers south of Alpena on U.S. 23 (Dorr and Eschman, 1970). *Diplognathus* is known from an isolated jaw (CMNH 50215) from Paxton Quarry (Lafarge North America, Inc., Alpena Cement Plant, Great Lakes Region), Alpena (Carr and Jackson, 2005). Invertebrate fossils from this formation include brachiopods and cephalopods (ammonoids), demonstrating relatively low invertebrate diversity compared to Middle Devonian formations (Ehlers and Kesling, 1970; Gutshick and Sandberg, 1991; Hannibal et al. 1992). This is likely reflective of the Antrim Shale's open water habitat, a contrast to the reefs and nearshore environments of Middle Devonian Michigan localities (Gutshick and Sandberg, 1991). The Antrim Shale is a typical Late Devonian North American black shale, containing large quantities of black mud rich in organic matter from deposition on a poorly oxygenated ocean floor (Dorr and Eschman, 1970; Roen 1984).

THE ENVIRONMENT AND ASSEMBLAGES OF DEVONIAN MICHIGAN

317

318 During the Middle Devonian, Michigan was located underneath a shallow, tropical sea
319 (Briggs, 1959). Pinnacle reefs were situated in a ring around what is now the Lower Peninsula
320 (Dorr and Eschman, 1970). Most Middle Devonian localities are associated with these reef
321 formations due to abundant invertebrate life and bioherm construction, contributing to rock
322 formation (Ehlers and Kesling, 1970). Much of the center of the Lower Peninsula is covered
323 with a thick layer of glacial till, preventing detailed paleontological study (Lilienthal, 1978).
324 Sites situated along the northern edge of the Lower Peninsula give a fairly good window into
325 the structure of Middle Devonian Michigan ecosystems (Ehlers and Kesling, 1970; Dorr and
326 Eschman, 1970). These sites present diverse invertebrate biotas including crinoids, trilobites,
327 cephalopods, gastropods, corals, bryozoans, brachiopods, and blastoids (Pohl, 1930; Ehlers
328 and Kesling, 1970). The vertebrate fauna includes numerous placoderms (arthrodires,
329 petalichthyids, ptyctodonts, and antiarchs), chondrichthyans (ctenacanths), lungfish,
330 onychodonts, and acanthodians (Dorr and Eschman, 1970).
331 Vertebrate material, most at least partially articulated, from the Devonian of Michigan
332 is usually associated with numerous benthic shelled invertebrates, unlike most sites of similar
333 age outside of North America (Ehlers and Kesling, 1970; personal observation). This type of
334 assemblage is also found in similarly-aged Columbus and Delaware Limestones of Ohio
335 (Eastman, 1907; Westgate and Fischer, 1933; Wells, 1944; Denison, 1978; unpublished data,
336 R.L. Martin). These invertebrates would have provided a food source for some of the
337 coincident fish (Long, 2011; Syverson and Baumiller, 2014). In several formations, fishes
338 and invertebrates are found in association within the same conglomerate or slab (Fig. 6(D)).

Michigan's faunas exhibited changes in the number, type, and diversity of fossils from the Middle to Late Devonian. Most Late Devonian non-vertebrate fossils are cephalopods, brachiopods, and assorted plant fossils, marking a significant change from the rich invertebrate fauna from the Middle Devonian (Ehlers and Kesling, 1970; Hannibal et al. 1992). In addition, the vertebrate assemblage is dominated by arthrodire and ptyctodont placoderms, which is a much less diverse fish fauna than in the Middle Devonian (Dorr and Eschman, 1970; personal observation). As noted above, the Antrim Shale was deposited in an open water pelagic habitat with little to no benthic community (Gutshick and Sandberg, 1991). There was likewise a shift in rock types from primarily limestone in the Middle Devonian to an alternating pattern of shale and limestone in the Late Devonian (Dorr and Eschman, 1970). The Antrim Shale, the only vertebrate-bearing formation from the Late Devonian in Michigan, is constructed in this manner (Dorr and Eschman, 1970; Gutshick and Sandberg, 1991). This alteration suggests that sea levels shifted several times during this interval, which would have contributed to the loss of older reef structures and upwelling of anoxic waters for shale deposition (Roen, 1984; Sandberg et al. 2002). Similar black shale deposition has been recorded from the Devonian of other areas of North America, such as New York, Tennessee, Ohio, and Kentucky (Roen, 1984). In Michigan, coral reefs disappear at the base of the Frasnian with the deposition of black shales (Ehlers and Kesling, 1970). This loss precedes bioherm elimination in other regions of the world, where corals are virtually eliminated by the climate-driven Frasnian-Famennian Kellwasser events (Kiessling et al. 2010).

DEVONIAN FISHES OF MICHIGAN

Here we describe what is known about the occurrence and distribution of major vertebrate clades and lineages from the Devonian of Michigan. Because of the aforementioned absences in the record and new discoveries, much of the information comes from personal observation as noted.

Arthrodires

Protitanichthys rockportensis.— *Protitanichthys rockportensis* is one of the few endemic species of fish from the Middle Devonian of Michigan (Case, 1931; Miles, 1966; Fig. 7). 62 specimens housed in the MHM and UMMP come from the Rockport Quarry Limestone Formation at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County and two specimens (32M, JS 101) are known from the Four Mile Dam Formation at the Betsie Bay Rockpiles in Elberta, Benzie County (Dorr and Eschman, 1970, personal observation). Most specimens of *P. rockportensis* consist of disarticulated and damaged dermal bone from the head shield (Miles, 1966). The poor quality and lack of articulation is caused by breakage during quarrying operations, scavenging, and high-energy water flow in the environment of deposition (Ehlers and Kesling, 1970; personal observation). The majority of the specimens of this fish were only about a meter in length, but a few rare individuals were over two meters in total length, making them very large for coccosteids (Denison, 1978). Most specimens appear to have been adults, but smaller juveniles and possibly senescent animals have been identified (personal observation). The relative age of the animal can be estimated by the distinction of the sutures between the armor plates of the cephalic shield, with older animals

bearing less noticeable sutures that fused with age (R. Carr pers. comm. 2012). Because of the relatively high number of specimens, *P. rockportensis* has been described in detail (Miles, 1966).

Titanicthys.— ?*Titanichthys* sp. is known from a single specimen in Michigan (UMMP 26114), from the Dundee Limestone of Sibley Quarry, Wyandotte (Dorr and Eschman, 1970). *Titanichthys* is primarily known from open water settings in the Late Devonian, so it possible that this has been misidentified or transported (Janvier, 2003; Boyle et al. 2011). Indeed, Dorr and Eschman (1970) stated the exact affinity was uncertain. Complicating matters further, specimen is currently missing from museum collections and has never been figured.

Holonema.— Two species of *Holonema* are found in Michigan: *H. farrowi* and ?*H. rugosum* (Dorr and Eschman, 1970; Stevens, 1964). Most specimens consist of dorsal and/or ventral shields with distinctive ornamentation of rows and ridges of tubercles, which are easily identifiable even from fragmented remains (Dorr and Eschman, 1970; Fig. 4(A)). This fish is most common in the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, with 32 specimens registered at UMMP and MHM (Dorr and Eschman, 1970; personal observation). Two specimens of ?*H. rugosum* (UMMP 46647 and UMMP 46648), two specimens of *H. farrowi* (UMMP 46648 and UMMP 46647), and another specimen that is not complete enough to identify to the species level (UMMP 3130) have been reported from the Newton Creek Limestone at Onaway Stone Quarry (Crawford's Quarry), north edge of Onaway, Presque Isle County. UMMP 3130 was originally designated as *Gyracanthus* by Dorr and Eschman (1970), but we identify it as a fragment of armor from *Holonema* from ornamentation. One specimen of ?*H. rugosum* (UMMP 3899) has

been documented from the Genshaw Formation at French Road, near Long Lake, Alpena County (Dorr and Eschman, 1970). A specimen that Dorr and Eschman (1970) designated as a holonemiid was collected from the Gravel Point Formation of South Point (Gravel Point; UMMP 3129). *Holonema* was up to a meter long and was most likely a bottom feeder (Denison, 1978), because of its somewhat flattened body shape and weak bite (Miles, 1971).

Dinomylostoma.— Dinomylostoma sp. is known from seven specimens (UMMP 3046, UMMP 12974, UMMP 13042, UMMP 13056, UMMP 13148, and UMMP 16158) from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County (Dorr and Eschman, 1970). While the reported specimens of this fish are currently missing from museum collections, one of these was figured in Dorr and Eschman (1970) and appears to have been accurately identified.

Mylostoma.—Mylostoma sp. was previously known in Michigan from one specimen (UMMP 13612) that was found at the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County (Dorr and Eschman, 1970). As with many of the other specimens examined by Dorr and Eschman (1970), this specimen was not figured, and cannot be located in the museum collections, even before the recent move of the UMMP collections. In the last few years, one of us has recovered 52 specimens of small arthrodires that appear to be *Mylostoma* from the Four Mile Dam Formation of the Betsie Bay Rockpiles, in Elberta, Benzie County, four specimens from the Besser Museum Fossil Park in Alpena (BV3, BV4, BV6, and BV7), and one specimen from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County (15M). These are now deposited in the MHM as per the permitting procedure for public lands

in Michigan, awaiting transfer to the UMMP. The above specimens resemble *Mylostoma* in having a thick, rounded median dorsal plate and in lacking ornamentation on the surface of the armor plates (Denison, 1978; Fig. 6(B)). These specimens are usually partially articulated, which is uncommon for placoderm remains from Michigan, and remains of ventral and cephalic shields are also known. However, positively identification as *Mylostoma* must await the recovery of gnathal plates (Denison, 1978; personal observation). The size of most of these new specimens suggests that they are most likely juveniles, an inference supported by the coincident collection of relatively large, poorly preserved specimen (2M) from Four Mile Dam with similar morphology and lack of tubercules (personal observation). If this identification is correct, *Mylostoma* is currently represented by more specimens than any other fish from the Devonian Michigan.

Dunkleosteus.— *Dunkleosteus* sp. is known from one specimen of a partial impression of a suborbital plate (UMMP 15432) from the Antrim Shale of Squaw Bay, south of Alpena, one specimen of a superognathal (UMMP 16152) from the Alpena Limestone of the Alkali Quarry of Alpena, one specimen of an incomplete anterior ventrolateral plate (UMMP 16156; Fig. 4(C)) from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County and one specimen (VP. 517) from an undetermined site in Alpena (Dorr and Eschman, 1970). These specimens are generally isolated plates, and are not usually articulated. Dorr and Eschman (1970) originally referred to these specimens as *Dinichthys sp.* Miller 1841, but this genus has since been synonymized with *Dunkleosteus*, with the exception of a single species from the Famennian Huron Shale Member of the Ohio Shale Formation (Carr and Hlavin, 2010). Although these specimens are

incomplete, the difference in age between the Michigan specimens and the remaining species of *Dinichthys*, along with the resemblance they bear to more complete specimens of *Dunkleosteus* described by Carr and Hlavin (2010), strongly indicates that they should be attributed to *Dunkleosteus sp*.

Aspidichthys.— Aspidichthys sp. is known from a single specimen (UMMP 3127) from the Antrim Shale of the shore of Grand Traverse Bay near Norwood, Charlevoix County (Dorr and Eschman, 1970). As above, the reported specimen is missing from museum collections and was not figured, so this identification may not be reliable.

Diplognathus lafargei.— D. lafargei is known from the Late Devonian of Michigan (Carr and Jackson, 2005). It is the most recently described fish taxon from Michigan and is hopefully the first of many new taxa to be described from a relatively recently discovered lens at the Antrim Shale (Late Devonian; Carr and Jackson, 2005). *D. lafargei* is currently known from a disarticulated and incomplete jaw plate specimen (CMNH 50215) found in a talus slope in Paxton Quarry (Lafarge North America, Inc., Alpena Cement Plant, Great Lakes Region), Alpena (Carr and Jackson, 2005).

Trachosteus clarkii.—?T. clarkii is known from a single specimen (UMMP 18206) of a infragnathal plate that was found from the Antrim Shale Formation 1.6 kilometers north of Norwood, Charlevoix County (Dorr and Eschman, 1970; Fig. 8). The jaw of ?*T. clarkii* was ornamented with small tubercles and contained short peg-like teeth (Dorr and Eschman, 1970; Fig. 8). It was a small fish with large eyes and a shallow head (Denison, 1978; Carroll, 1988).

Petalichthyida

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476 *Macropetalichthys*.—?*Macropetalichthys* sp. is known from a single specimen (UMMP
477 14320) of a spinal and anterior ventrolateral plate from the Middle Devonian of the Dundee
478 Limestone near Trenton (Dorr and Eschman, 1970; personal observation; Fig. 2(B)). This
479 specimen was identified by Dorr and Eschman (1970) as *Arctolepis* Eastman, 1908 based on
480 its elongated spinal plates ornamented with small spines. However, the specimen (Fig. 2(B))
481 much more closely resembles ?*Macropetalichthys*, in which the spinals are not as recurved as
482 those in *Arctolepis,* and the spines more numerous and tightly spaced, and small spines are
483 also present outside of the spinal plate itself (Denison, 1978; Janvier, 2003; personal
484 observation). Unfortunately, the specimen does not retain any of the diagnostic features of the
485 genus, so we can only tentatively reattribute it (Eastman, 1907; Denison, 1978). Whatever the
486 case, ?*Macropetalichthys* is already known from several localities in North America, including
487 the Delaware and Columbus limestone of Ohio, which were closely associated with Michigan
488 during the Middle Devonian (Eastman, 1907; Denison, 1978; unpublished data, R. L. Martin).
489 *Arctolepis*, however, is otherwise restricted to the Early Devonian of Spitsbergen (Denison,
490 1978). The anatomical, temporal, and geographical evidence therefore indicates that UMMP
491 14320 is from a petalichthyid (personal observation).

492
493
494 Antiarchi
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497 *Bothriolepis*.— In Michigan, *Bothriolepis* sp. is represented by a single well-preserved
498 lateral plate (UMMP 4169) from the Genshaw formation, near Posen, Presque Isle County
499 (Dorr and Eschman, 1970; Fig. 9). It is possible that this individual was not resident in
500 Michigan, but traveled from an established population in a nearby region (personal

observation). There is also a well-preserved specimen (4M) of the cephalic shield of a small placoderm that resembles *Bothriolepis* in size and ornamentation from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County (Fig. 7(D)). While several other small, far less complete specimens from that site bear similar ornamentation (small, dense tubercles), these are most likely juvenile specimens of much more common *P. rockportensis*, as smaller (and presumably younger) *P. rockportensis* also have similar ornamentation and prominent sutures between the plates of their cephalic shield, with their form distinct from larger members of the same species. Better material must be found in order to make a final determination as to these alternative attributions.

Ptyctodontida

Ptyctodus.— Specimens of *Ptyctodus* sp., consisting of isolated tooth plates, have been found in the Dundee Limestone near Trenton, Wayne County (UMMP 14321), the Bell Shale of Rogers City (UMMP 14460), Presque Isle County, the Thunder Bay Limestone of Partridge Point (UMMP 3023), the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County (UMMP 13045), the Alpena Limestone of Alkali Quarry (UMMP 16157), Alpena, the Potter Farm Formation? of old Wamer's Brickyard southwest of Alpena (UMMP 21718), and the Potter Farm Formation of the west edge of Alpena Cemetery (UMMP 21817) of Alpena (Dorr and Eschman, 1970). All of these localities are located in Alpena County (Dorr and Eschman, 1970). Other single specimens of *Ptyctodus* are recorded from an unknown formation of Afton Quarry from Cheboygan County (VP.489) and the Traverse Group (unknown formation) of Emmet County (UMMP 14712) (Dorr and

Eschman, 1970). While many of these specimens have gone missing since 1970, those figured in Dorr and Eschman (1970) suggest their attribution is accurate (personal observation). The widespread distribution of *Ptyctodus* fossils may be due to both the higher preservation potential of hard tooth plates and/or association with abundant shelly invertebrates. Relatively poor taxonomic knowledge of *Ptyctodus*, a wastebin taxon widely applied to various ptyctodont teeth, may also be a contributing factor. Further taxonomic work on existing specimens is required to determine if these specimens all originate from the same genus.

Eczematolepis.— *Eczematolepis* sp. Miller, 1892 is known from a single gnathal plate (UMMP 14374; Fig. 10) recovered from an unknown formation in the Traverse Group of a locality in Alpena, Alpena County (Dorr and Eschman, 1970). This locality referred to by Dorr and Eschman (1970) as "Locality 650 of the Winchell Survey", but no other information is available on the geological context of this specimen. It is difficult to evaluate whether or not this attribution is reliable because *Eczematolepis* is known only from isolated plates, and is most likely a wastebasket taxon (Denison, 1978; unpublished data, R.L. Martin). This attribution is supported by the fact that it is known from Middle Devonian deposits in the Columbus Formation of Ohio and the Onondaga Limestone of New York, but these identifications are considered to be unreliable by (Eastman, 1907; Westgate and Fischer, 1933; Wells, 1944; Denison, 1978; unpublished data, R.L. Martin). Due to the lack of taxonomic information available for this genus (and in general for ptyctodonts from the Eifelian of North America), the attribution of UMMP 14374 to *Eczematolepis* should also be considered dubious.

Acanthodii

Gyracanthus.— *Gyracanthus* sp. has been identified known from one specimen (UMMP 1329) from the Gravel Point Formation of South Point (Gravel Point), Little Traverse Bay, Charlevoix County(Dorr and Eschman, 1970). This specimen is currently missing from the UMMP and was not figured. This spine-based identification is therefore not verifiable, particularly as Devonian specimens of this widespread Carboniferous genus are dubious and in need of re-examination (Turner et al., 2005).

Machaeracanthus.— *Machaeracanthus* sp. is reported from one specimen (UMMP 3521) from the Dundee Limestone of Monroe County, two specimens (UMMP 2611 and UMMP 26112) from the Dundee Limestone of Sibley Quarry, Wyandotte, Wayne County, one specimen (UMMP 13047) of uncertain status from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, and two specimens (UMMP 4761 and UMMP 47692) from the Newton Creek Limestone at Onaway Stone Quarry, Presque Isle County (Dorr and Eschman, 1970, personal observation; Fig. 11). The isolated specimen from the Rockport Quarry Limestone (UMMP 13047) was originally identified as *Acondylacanthus* by Dorr and Eschman (1970), but an examination of the specimen showed significant differences in spine structure (Maisey, 1983). It is long and thick with a smooth surface, and so much more closely resembles the spines of *Machaeracanthus* (Denison, 1979; Maisey, 1983; Fig. 11(B)). As shown by the specimen list, *Machaeracanthus* is relatively common in the Middle Devonian of Michigan and closely associated areas (Eastman, 1907; Wells, 1944; Dorr and Eschman, 1970; Denison, 1978). In

571 contrast, *Acondylacanthus* is known only from the Carboniferous of Iowa in North America,
572 after a major mass extinction event (Wellburn, 1901; Zangerl, 1981; Maisey, 1983; Itano et
573 al., 2003; Elliot et al., 2004; Brusatte, 2007; Sallan and Coates, 2010).

574 *Oracanthus*.— *Oracanthus* sp. is known from a fin spine (UMMP 23495) from the Middle
575 Devonian of the Norway Point Formation (Newberry, 1891; Dorr and Eschman, 1970). This
576 specimen was found at the Four Mile Dam, about 5.6 kilometers northwest of Alpena, Alpena
577 County (Dorr and Eschman, 1970). As above, the current location of this unfigured specimen is
578 unknown, so we cannot verify its identity.

579

580 Chondrichthyes
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583 *Acondylacanthus*.— Another fin spine specimen of *A. gracillimus* (UMMP 26523) was
584 previously reported from the Dundee Limestone of Sibley Quarry, Wyandotte, Wayne County,
585 (Dorr and Eschman, 1970). This specimen is now missing from the collections at the
586 University of Michigan, so we cannot determine if it also represents *Machaeracanthus*. This
587 would be the earliest reported specimen of *Acondylacanthus* by far; other occurrences are
588 clustered in the Carboniferous of the U.S. and the U.K. (Wellburn, 1901; Maisey, 1983; Itano
589 et al., 2003; Elliot et al., 2004; Brusatte, 2007).

590 *Tamiobatis*.— ?*Tamiobatis* sp. is a small shark reported from one specimen (UMMP
591 13147) of a fin spine from the Rockport Quarry Limestone at the abandoned Kelly Island
592 Limestone Quarry at Rockport State Park, Alpena County (Dorr and Eschman, 1970; Fig.
593 4(D)). Dorr and Eschman (1970) identified this spine as *Ctenacanthus*, but comparisons of

this specimen with more recent descriptive work disputes this attribution (Maisey, 1982; Williams, 1998). This specimen closely resembles a fin spine impression from ?*Tambiobatis* from the Cleveland Shale (Williams, 1998). More complete material from Michigan is needed to make a concrete diagnosis, so this assignment is designated as uncertain.

Onychodontiformes

Onychodus.— *Onychodus* is found in several parts of Michigan's geological column (Dorr and Eschman, 1970), including the Dundee Limestone of London Township, Monroe County (UMMP 22006; Fig. 2(A)), Sibley Quarry, Wyandotte, Wayne County (UMMP 26113) as well as an uncertain specimen from the Gravel Point Formation of the shore of the Little Traverse Bay, Charlevoix County (UMMP 14370) (Dorr and Eschman, 1970). The single specimen from the Dundee Limestone of Monroe County was identified to the species level, *O. sigmoides* (Dorr and Eschman, 1970). In most cases, the genus is represented solely by its large distinctive tooth whorls, with the exception of one lower jaw (UMMP 26113; Dorr and Eschman, 1970).

Dipnoi

Chirodipterus onawayensis.— *C. onawayensis* is the only lungfish known from the Devonian of Michigan, and thus far is represented by a single specimen which was preserved well enough to allow diagnosis as a new species (Schultze, 1982; Long 1995). The holotype is the left side of the skull and jaws from the Onaway Stone Quarry, which is north of Onaway in Presque Isle County (Schultze, 1982; Fig. 12). This specimen is unnumbered but resident at the

Great Lakes Area Paleontological Museum. It is similar to *Chirodipterus australis* Miles, 1977 from Gogo in Australia, and possesses the powerful jaws typical of a durophagous Devonian lungfish (Schultze, 1982; Long, 2011).

DISCUSSION

Despite proximity to major research institutions and collections, the rich reef and nearshore faunas of the Middle Devonian of North America have been neglected in recent decades, particularly relative to similarly-aged localities in even more remote areas of Antarctica, Australia, and Morocco (Gardiner, 1984; Derycke et al. 1995; Blieck and Lelievre, 1995; Janvier, 2003; Rucklin, 2010; Sallan and Coates, 2010; Friedman and Sallan, 2012). There are significant gaps in the total Devonian record in Michigan, with vertebrates in some intervals, particularly the Late Devonian, poorly represented and deficient in number relative to similarly-aged horizons in Ohio (Dorr and Eschman, 1970; Carr and Jackson, 2008). Complicating matters, a large proportion of previously published and catalogued specimens could not be located in the paleontological collections at the University of Michigan, leaving only brief and incomplete documentation as proof of their existence (Dorr and Eschman, 1970). In addition, a large number of more recently recovered specimens are resident in amateur collections - the result of a lack of professional efforts in the state in recent decades - and cannot be used for scientific purposes.

Never-the-less, examination of available new and old material shows that Michigan is much

richer in diversity and sheer number of fish specimens than previously thought. This has revealed several previously unreported but likely significant biogeographical and diversity patterns, including a shift in environment and faunas between the Middle and Late Devonian and greater connections to nearby basins, and a near complete lack of antiarchs in Michigan even when nearshore outcrops are available. In addition, new localities have produced co-occurring, well-preserved articulated vertebrate and invertebrate material, a rarity in the Paleozoic record outside Michigan.

There is a definite shift in fish diversity, geologic range, and number between the Middle and Late Devonian deposits of Michigan. Placoderms, acanthodians, dipnoans, onychodonts and sharks are found in fair numbers in the primarily nearshore settings of the Middle Devonian (Dorr and Eschman, 1970; Fig. 13). This record includes 19 genera of fishes from 187 reported specimens sourced from 11 separate formations (Dorr and Eschman, 1970; personal observation). In contrast, fish fossils from Late Devonian pelagic settings come from just four confirmed (possibly five, if reports of ptyctodonts from the Antrim Shale are confirmed) genera, all arthrodiran or ptyctodont placoderms, in the Antrim Shale formation (Dorr and Eschman, 1970, Carr and Jackson, 2005; Fig. 13). A similar change is seen in the invertebrate fauna; a thriving reef and nearshore fauna hosting a multitude of life, including crinoids, trilobites, bryozoans, corals, blastoids, brachiopods, cephalopods, gastropods and stromatoporoids in the Middle Devonian is succeeded by scattered fossils of brachiopods, cephalopods, and assorted plant material further offshore in the Late Devonian (Dorr and Eschman, 1970; Ehlers and Kesling, 1970; Hannibal et al., 1992; Carr pers. comm. 2014).

666 The contrast between the Middle and Late Devonian vertebrate and invertebrate faunas in
667 Michigan is due to differences in collection intensity, rock exposure, and environmental
668 representation. There are at least a dozen well-documented Middle Devonian localities from
669 Michigan that have been the focus of both professional and amateur collectors (Dorr and
670 Eschman, 1970; personal observation). These localities preserve a wide variety of habitats
671 (mostly near-shore, reef habitats) and have a large amount of exposed rock (especially in
672 limestone quarries) (Ehlers and Kesling, 1970; personal observation). In contrast, the Late
673 Devonian of Michigan is represented by a few localities from a single, black shale heavy
674 formation that have comparatively little rock exposed (Ehlers and Kesling, 1970). Late Devonian
675 localities have received little attention from amateur collectors, suggesting that the differences
676 between Middle and Late Devonian diversity is due partly to sampling bias. However, it is
677 notable that the Antrim Shale was deposited in an open water pelagic habitat with little to no
678 benthic community (Gutshick and Sandberg, 1991). This difference in environment between the
679 Middle and Late Devonian deposits is most likely a major factor contributing to the observed
680 shift in the diversity of the vertebrate and invertebrate faunas. None of the localities from the
681 Middle Devonian of Michigan preserve this kind of habitat (Ehlers and Kesling, 1970).
682 Reexamination of Michigan's Devonian fossils sheds some light on biogeographic and
683 dispersal patterns for North American fishes of this age. There were likely few barriers to
684 dispersal between Michigan and the Illinois and Appalachian Basins, as there is a complete
685 absence of endemic taxa at the genus level within Michigan (Newberry, 1889; Dorr and
686 Eschman, 1970; Denison, 1978; Markus, 1998; Palmer and Cox, 1999; Warren et al., 2000;
687 Thomson and Thomas, 2001; Sepkoski, 2002; Johanson et al., 2007; Carr and Jackson, 2008;
688 Carr and Hlavin, 2010). However, it is possible that the aforementioned lack of taxonomic

689 work and collection effort has resulted in the incorrect attribution of distinct species from
690 Michigan to taxa from the wider region. Regardless, the types of fish found in the Devonian
691 sediments of Michigan are fairly typical for the eastern United States (Newberry, 1873; Cluff,
692 1980).

693 Michigan's fish fauna shares characteristics with several similarly-aged faunas from the
694 Middle Devonian of North America. Michigan's Middle Devonian vertebrate fauna is most
695 similar to the Delaware and Columbus Formations of central Ohio, with which it shares many
696 taxa, including *Machaeracanthus*, *Gyracanthus*, *Holonema*, *Macropetalichthys, Protitanichthys*,
697 *Onychodus*, *Dunkleosteus*, *Ptyctodus*, and *Eczematolepis* (Eastman, 1907; Westgate and Fischer,
698 1933; Wells, 1944; Dorr and Eschman, 1970; Denison, 1978). This suggests that the parts of
699 Michigan and Ohio that these deposits represent were closely connected during this period of
700 time, yet the preservational mode was quite different. Many of the described fish remains from
701 the Delaware and Columbus limestones are very small and worn, concentrated into bone beds
702 where vertebrate remains are more common than macroscopic invertebrate fossils (Westgate and
703 Fisher, 1933; Wells, 1944). This is very different than Michigan, where fish remains are
704 generally large to medium size pieces of armor or spines that are usually unworn (personal
705 observation). However, an unpublished PhD thesis by Martin (2002) describes the remains of
706 more complete specimens of placoderms (petalichthyids and ptyctodonts) and onychodonts from
707 other, lesser known sections of the Delaware and Columbus limestones, indicating that some
708 beds are more similar to Michigan in preservation and assemblage composition.

709 The Middle Devonian fish fauna of Michigan is also similar to the vertebrate fauna known
710 from the Onondaga Limestone of New York (Eifelian, Upper Ulsterian), which has a similar
711 environment to and is correlated with the Dundee Limestone (Brett and Ver Straeten, 1994; Brett

et al., 2011). Indeed, the Onondaga Limestone shares all but one of the taxa found in the Dundee Limestone, including *Ptyctodus*, *Machaeracanthus*, *Onychodus*, *Macropetalichthys*, and *Eczematolepis* (Eastman, 1907; Dorr and Eschman, 1970; Denison, 1978). A larger number of vertebrate taxa have been reported from the Onondaga Limestone, although this might be an artifact of the lesser number of outcrops of this age in Michigan and a lack of collecting effort, rather than reflective of real differences in diversity (Eastman, 1907; Dorr and Eschman, 1970; Denison, 1978).

The correlation between the vertebrate faunas of Michigan and New York continues into the Givetian (Erian). The rocks of the Traverse Group in Michigan and the Hamilton Group of New York are similar in age and share two taxa of vertebrates, *Machaeracanthus* and *Dunkleosteus* (Eastman, 1907; Denison, 1978; Dorr and Eschman, 1970; Brett and Ver Straeten, 1994). This is despite an environmental shift that caused major changes in sedimentation, paleoecology, faunas, and basin geometry that occurred in the transition between the Onondaga Limestone and the Hamilton Group (Ver Straeten et al., 1994). This shift had a major effect on invertebrates, causing extinctions of some of the endemic Onondaga faunas (Ver Straeten et al., 1994). While it is not clear what effect this shift had on the vertebrate fauna, it is evident that a close connection between the fish faunas of Michigan and New York continued from the Eifelian (Ulsterian) into the Givetian (Erian).

The documented loss in the amount and diversity of fossil material in the Late Devonian Michigan makes detailed comparison with other Late Devonian faunas difficult. However, every genus found in the Late Devonian of Michigan, *Diplognathus*, ?*Trachosteus*, ptyctodonts, *Aspidichthys*, and *Dunkleosteus,* is also found in open ocean sediments of the Late Devonian Cleveland Shale (Newberry, 1889; Winston and Walker, 1956; Dorr and

735 Eschman, 1970; Denison, 1978; Carr and Jackson, 2008). The Cleveland Shale has been the
736 focus of intense collecting efforts for the past 150 years and has outcrops both within a major
737 metropolitan area and on the path of a major highway, while very little collecting has been
738 conducted in the relatively remote Antrim Shale (unpublished data, W.J. Hlavin). This may
739 explain the difference in recorded diversity between these faunas, but there is also a
740 taphonomic difference in that Antrim Shale specimens are not protected by large nodules and
741 thus less likely to be complete and identifiable. Furthermore, the Cleveland Member of the
742 Ohio Shale is a Konservat-Lagerstätten, and is considered one of the most diverse vertebrate
743 faunas from the Devonian (Carr and Jackson, 2008). Therefore, the gap in the diversity and
744 number of fish specimens between the Late Devonian of Michigan and the Late Devonian of
745 Ohio is probably largely the result of the differences in preservation between these sites, along
746 with a lack of organized collection effort in Michigan's Late Devonian sediments by both
747 professionals and amateurs.

748 As documented above, a notable occurrence, or non-occurrence, in the Middle Devonian
749 fish fauna of Michigan is an almost complete lack of antiarch placoderms (Dorr and Eschman,
750 1970). Other benthic, nearshore forms, such as gyracanthids and ptyctodonts, are also poorly
751 represented relative to other kinds of fishes (such as arthrodires) in Michigan's sediments. The
752 relative absence of benthic-associated fishes contrasts greatly with the large amount of benthic
753 invertebrate material at vertebrate-bearing localities, which indicates that preservation of the
754 sea floor is not the issue. It is possible that the rarity of antiarchs is purely the product of a lack
755 of collection effort outside of a handful of sites. However, it appears that antiarchs are also
756 uncommon in other Middle Devonian sites that are closely related to deposits of the same age

757 in Michigan (Eastman, 1907; Westgate and Fisher, 1933; Wells, 1944). This is despite the fact
758 that antiarchs have been recovered from nearshore marine and estaurine settings elsewhere,
759 such as the famous marine tetrapod assemblage, Andryevka-2 (Sallan and Coates, 2010;
760 Friedman and Sallan, 2012).

761 Another interesting aspect of the vertebrate record from the Middle Devonian of Michigan
762 is the occurrence of partially articulated vertebrate material often preserved alongside
763 invertebrate remains not only in the same formations, but in the same rocks (Fig. 6(D)). This
764 pattern is consistent in several separate formations and sites. It is rare to find articulated fish
765 remains, rather than ichthyoliths like teeth, directly associated with complete invertebrate
766 remains, especially articulated crinoids, in the Middle Paleozoic (personal observation; Sallan
767 et al. 2011). This direct association can be used to concretely determine which invertebrate
768 taxa lived directly alongside vertebrates, potentially shedding light on the interactions and
769 associations between these groups.

770 Much more fieldwork is required to fully understand the Devonian vertebrate fauna from
771 Michigan. Recent efforts have revealed a surprising number of new occurrences of fishes in
772 geological formations where they were previously considered absent. *Protitanichthys* was
773 once thought to be restricted to the Rockport Quarry Limestone, but has now been
774 documented from two new formations (the Four Mile Dam Formation and possibly the Alpena
775 Limestone Formation; personal observation; Dorr and Eschman, 1970). *Mylostoma* was
776 previously only known from an isolated specimen (UMMP 13612) from the Rockport Quarry
777 Limestone, but it is now also known from large numbers of recently collected specimens from
778 the Four Mile Dam Formation and several specimens (BV3, BV7, BV6, and BV4) from the

Alpena Limestone Formation (Dorr and Eschman, 1970). Additionally, fish fossils had previously never been documented from the Four Mile Dam Formation (personal observation; Dorr and Eschman, 1970). These findings, which are a result of intensified collecting from a handful of the vertebrate-bearing Middle Devonian localities in Michigan, show that these long-neglected localities are still productive. Further collecting at sites that have been ignored for decades will almost certainly lead to more discoveries. Renewed search efforts will create a less biased understanding of the Late Devonian fish fauna of Michigan, allowing more accurate comparisons to other Late Devonian faunas to be made and the ecology and biogeography of Devonian marine fishes to be more completely known.

CONCLUSIONS

Novel information about the ecology, diversity, and number of the fishes from the Devonian of Michigan has been revealed by new surveys of old material and from new specimens obtained through recent collecting efforts. These include many previously unrecognized patterns, such as dramatic losses in diversity between the Middle and Late Devonian likely due to the differences in collection intensity, rock exposure, and environmental representation between these time periods. We have also documented strong connections with other North American pelagic faunas, and the exceptional occurrence of partially-articulated fishes preserved alongside benthic invertebrates. These interesting new discoveries show that there is still much work to be done in Michigan vertebrate-bearing sediments, with implications for our understanding of Devonian fish faunas as a whole.

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Figure Captions

Figure 1: Chart showing the correlation between international and North American Devonian stage names. Figure modified from Swezey (2002). Credit, U.S. Geological Survey.

Figure 2: Vertebrate remains from the Dundee Limestone Formation. A, A large tooth from *Onychodus*, from the Dundee Limestone of London Township, Monroe County, UMMP 22006. Scale bar equals 1 cm. B, A spinal and anterior ventrolateral plate from ?*Macropetalichthys* (formerly *Arctolepis*), from the Dundee Limestone near Trenton, UMMP 14320. Abbreviations: Sp, spinal; Spi, spines of the spinal plate; Avl, anterior ventrolateral. Scale bar equals 1 cm.

Figure 3: Stratigraphy and correlations of the Traverse Group in the northern part of the lower peninsula of Michigan. A, east part of outcrop area and B, west side of outcrop area. Figure modified from Pojeta and Renjie (1986), Figure 12. Credit, U.S. Geological Survey.

Figure 4: Vertebrate remains from the Rockport Quarry Limestone Formation. A, A partial skull roof from *Holonema*, from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 12991. Abbreviations: Nu, Nuchal; Pn, Paranuchal; Cn, Central Plate. Scale bar equals 2 cm. B, The remains of an unidentified placoderm from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, 14M, Michigan History Museum. Scale bar equals 1 cm. C, An incomplete right anterior ventrolateral from *Dunkleosteus,* from the from the Rockport Quarry Limestone of Rockport Quarry, Alpena County, UMMP 16156. Scale bar equals 2 cm. C, a small spine from ?*Tamiobatis* (previously identified as *Ctenacanthus*) from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 13147. Scale bar equals 1 cm.

Figure 5: Partially articulated armor from ?*Mylostoma*, found in rocks originally from the Alpena Limestone Formation at the Besser Museum Fossil Park, Alpena. BV 4, Michigan History Museum. Scale bar equals 1 cm.

Figure 6: Vertebrate remains from the Four Mile Dam Formation. A, a broken spine from an unidentified acanthodian, from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, JS 121, Michigan History Museum. Scale bar equals 0.5 cm. B, a flattened specimen of a trunk shield from ?*Mylostoma* sp., from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, 21M. Abbreviations: Md, Median dorsal; Adl, Anterior dorsolateral; Nu, Nuchal. Scale bar equals 1 cm. C, a partial armor plate from an unidentified placoderm, from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, 4M, Michigan History Museum. Scale bar equals 1 cm. D, a piece of limestone containing both crinoid heads and an armor plate from ?*Mylostoma* sp. found in the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, JS 6, Michigan History Museum. This specimen is an example of the association between vertebrates and invertebrates in the Middle Devonian deposits of Michigan. The solid arrow indicates the piece of armor and the dashed arrow indicates a crinoid head, Scale bar equals 1 cm.

Figure 7: Specimens of *Protitanichthys rockportensis,* an arthrodire that is common in the Midddle Devonian sediments of Michigan. A, a photograph a cephalic shield from *Protitanichthys rockportensis*, from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 12980. B, a specimen drawing of UMMP 12980 (modified from Case (1931), Figure 1). Dotted lines represent missing plate boundaries and dashed lines represent sensory grooves, Scale bar equals

2 cm. C, a partial cephalic shield from *Protitanichthys rockportensis*, from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, 32M. Abbreviations: Ce, Cephalic Shield (Incomplete); Un, Unidentified Armor Plate. Scale bar equals 2 cm. D, a partial headshield from ?*Protitanichthys rockportensis* (most likely a juvenile), from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, 4M, Michigan History Museum. Scale bar equals 1 cm.

Figure 8: An inferognathal from the Late Devonian arthrodire ?*Trachosteus clarkii* from the Antrim Shale. Specimen recovered 1.6 km north of Norwood, MI. UMMP 18206. Scale bar equals 1 cm.

Figure 9: An anterior ventrolateral plate from *Bothriolepis* sp., from the Genshaw Formation Specimen recovered near Posen, MI. UMMP 4169. Scale bar equals 1 cm.

Figure 10: A gnathal plate of *Eczematolepis* sp., from the Traverse Group. Specimen recovered from an unknown locality in Alpena, Alpena County, MI. UMMP 14374. Scale bar equals 1 cm.

Figure 11. Specimens of the acanthodian *Machaeracanthus* sp. A, a large spine from *Machaeracanthus* sp., from the Dundee Limestone of London Township, Monroe County, UMMP 3521. Scale bar equals 1 cm. B, a spine from ?*Machaeracanthus* sp. (previously identified as *Acondylacanthus gracillimus*), from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 13047. Scale bar equals 1 cm.

Figure 12: The skull of *Chirodipterus onawayensis* from the Newton Creek Limestone of Onaway Stone Quarry. Specimen recovered from north of Onaway, Presque Isle County, MI. Specimen photo modified from Schultze (1982), Figure 2. This specimen is unnumbered at

the Great Lakes Area Paleontological Museum. Scale bar equals 1 cm.

Figure 13: A representation of fish faunas from the Middle Devonian and the Late Devonian of Michigan. Animals not to scale. A) *Acondylacanthus* (Chondrichthyes); B) *Dinomylostoma* (Arthrodira; 'Placodermi'); C) *Chirodipterus* (Dipnoi; Sarcopterygii); D) *Dunkleosteus* (Arthrodira; 'Placodermi'); E) *Onychodus* (Onychodontida; Sarcopterygii); F) *Mylostoma* (Arthrodira; 'Placodermi'); G) *Protitianichthys* (Arthrodira; 'Placodermi'); H) *Oracanthus* (Acanthodida; Acanthodii); I) *Machaeracanthus* (Ischnacanthida; 'Acanthodii'); J) *Bothriolepis* (Antiarchi; 'Placodermi'); K) *Gyracanthus* (Gyracanthida; 'Acanthodii'); L) *Eczematolepis* (Ptyctodontida; 'Placodermi'); M) *Holonema* (Arthrodira; 'Placodermi'); N) *Aspidichthys* (Arthrodira; 'Placodermi'); O) *Trachosteus* (Arthrodira: 'Placodermi'); P) *Diplognathus* (Arthrodira; 'Placodermi'); Q) Ptyctodontida indet. ('Placodermi').

Table Captions

Table 1: Vertebrate bearing localities from Dundee Limestone and Rogers City Limestone.

Table 2: Vertebrate bearing localities from the Bell Shale, Rockport Quarry Limestone, Genshaw Formation, Newton Creek Limestone, Gravel Point Formation, and Alpena Limestone.

Table 3: Vertebrate bearing localities from the Alpena Limestone, Four Mile Dam Formation, Norway Point Formation, and Potter Farm Formation.

Table 4: Vertebrate bearing localities from the Potter Farm Formation, the Thunder Bay Limestone, and the Antrim shale.

Table 1(on next page)

Table 1: Vertebrate bearing localities from Dundee Limestone and Rogers City Limestone.

1
2

Locality	Sibley Quarry	Trenton	Monroe County
Vertebrates	?*Titanichthys*, *Onychodus sigmoides,* and *Acondylacanthus gracillimus*	?*Macropetalichthys* and *Ptyctodus*	*Onychodus* and *Machaeracanthus*
International Stage	Eifelian	Eifelian	Eifelian
Regional Stage	Ulsterian	Ulsterian	Ulsterian
Formation	Dundee Limestone	Dundee Limestone	Dundee Limestone
County	Wayne	Wayne	Monroe
City	Trenton	Trenton	Unknown
Location	Sibley Quarry near Fort Street and Sibley Road, Wyandotte, Wayne County	Near Trenton	Unknown

Table 2(on next page)

Table 2: Vertebrate bearing localities from the Bell Shale, Rockport Quarry Limestone, Genshaw Formation, Newton Creek Limestone, Gravel Point Formation, and Alpena Limestone.

1
2

Locality	Rogers City	Rockport Quarry	Posen	Onaway Stone Quarry	South Point	Besser Museum Fossil Park
Vertebrates	*Ptyctodus*	*Protitanichthys*, ?*Mylostoma*, ?*Holonema rugosum*, *Dinomylostoma*, *Dunkleosteus,* *Mylostoma*, *Ptyctodus*, ?*Tamiobatis*, and ?*Machaeracanthus*	*Bothriolepis*	*Holonema farrowi*, *Holonema*, ?*Holonema rugosum*, *Machaeracanthus*, and *Chirodipterus onawayensis*	?*Onychodus*, *Gyracanthus*, and an unidentified holonemiid	?*Mylostoma*
International Stage	Givetian	Givetian	Givetian	Givetian	Givetian	Givetian
Regional Stage	Early Erian	Early Erian	Early Erian	Middle Erian	Middle Erian	Middle Erian
Formation	Bell Shale	Rockport Quarry Limestone.	Genshaw Formation	Newton Creek Limestone	Gravel Point (South Point)	Alpena Limestone
County	Presque Isle	Alpena	Presque Isle	Presque Isle	Charlevoix	Alpena
City	Rogers City	Alpena	Posen	Onaway	South Point	Alpena
Location	Unknown	NE Michigan. Abandoned strip mine in Rockport State Park 15 miles north of Alpena.	Near Posen.	Onaway Stone Quarry, north edge of Onaway, Presque Isle County.	Exposures along Lake Michigan shore at South Point, little Traverse Bay.	Fossil park maintained by the Besser Museum in Alpena, Michigan.

3

Table 3(on next page)

Table 3: Vertebrate bearing localities from the Alpena Limestone, Four Mile Dam Formation, Norway Point Formation, and Potter Farm Formation.

Locality	Alkali Quarry	Betsie Bay Rockpiles	Four Mile Dam	Old Wamer's Brickyard	Alpena Cementary
Vertebrates	Ptyctodus	?*Mylostoma* , *Protitanichthys rockportensis*, an unidentified acanthodian, and an unidentified placoderm	*Oracanthus*	*Ptyctodus*	*Ptyctodus*
International Stage	Givetian	Givetian	Givetian	Givetian	Givetian
Regional Stage	Middle Erian	Late Erian	Late Erian	Late Erian	Late Erian
Formation	Alpena Limestone	Four Mile Dam	Norway Point	Potter Farm?	Potter Farm
County	Alpena	Benzie	Alpena	Alpena	Alpena
City	Alpena	Elberta	Unknown	Alpena	Alpena
Location	Alkali Quarry, loose block.	NW Michigan: Southern Shore of Betsie Lake near the Bay: Village of Elberta: adjacent to Waterfront Park: Village of Elberta: Bruce Tobin property. Rocks at the site are originally from the Specification Stone Products Quarry in Alpena, MI. Address: 1009 Long Lake Rd, Alpena, MI 49707.	Four Mile Dam about 3.5 miles northwest of Alpena.	Southwest of Alpena	West edge of Alpena Cemetery, Evergreen Cemetery.

Table 4(on next page)

Table 4: Vertebrate bearing localities from the Potter Farm Formation, the Thunder Bay Limestone, and the Antrim shale.

1

Locality	Partridge Point	Norwood	Squaw Bay	Grand Traverse Bay	Paxton Quarry
Vertebrates	*Ptyctodus*	?*Trachosteus clarkii*	*Dunkleosteus*	*Aspidicthys*	*Diplognathus larfargei*
International Stage	Givetian	Frasnian/Famennian	Frasnian/Famen-nian	Frasnian/Famennian	Frasnian/Famenni-an
Regional Stage	Late Erian	Senecan/Chautauqu-an	Senecan/Chaut-auquan	Senecan/Chautauqu-an	Senecan/Chautauq-uan
Formation	Thunder Bay Limestone	Antrim Shale	Antrim Shale	Antrim Shale	Antrim Shale
County	Alpena	Charlevoix	Alpena	Charlevoix	Alpena
City	Unknown	Norwood	Alpena	Norwood	Alpena
Location	Partridge Point	1 mile north of Norwood. Exact location unknown.	Squaw Bay, 4 miles south of Alpena on U.S 23.	Shore of Grand Traverse Bay near Norwood. Exact location unknown.	Paxton Quarry (Lafarge North America, Inc., Alpena Cement Plant, Great Lakes Region), Alpena.

2

Figure 1

Chart showing the correlation between international and North American Devonian stage names.

Figure modified from Swezey (2002). Credit, U.S. Geological Survey.

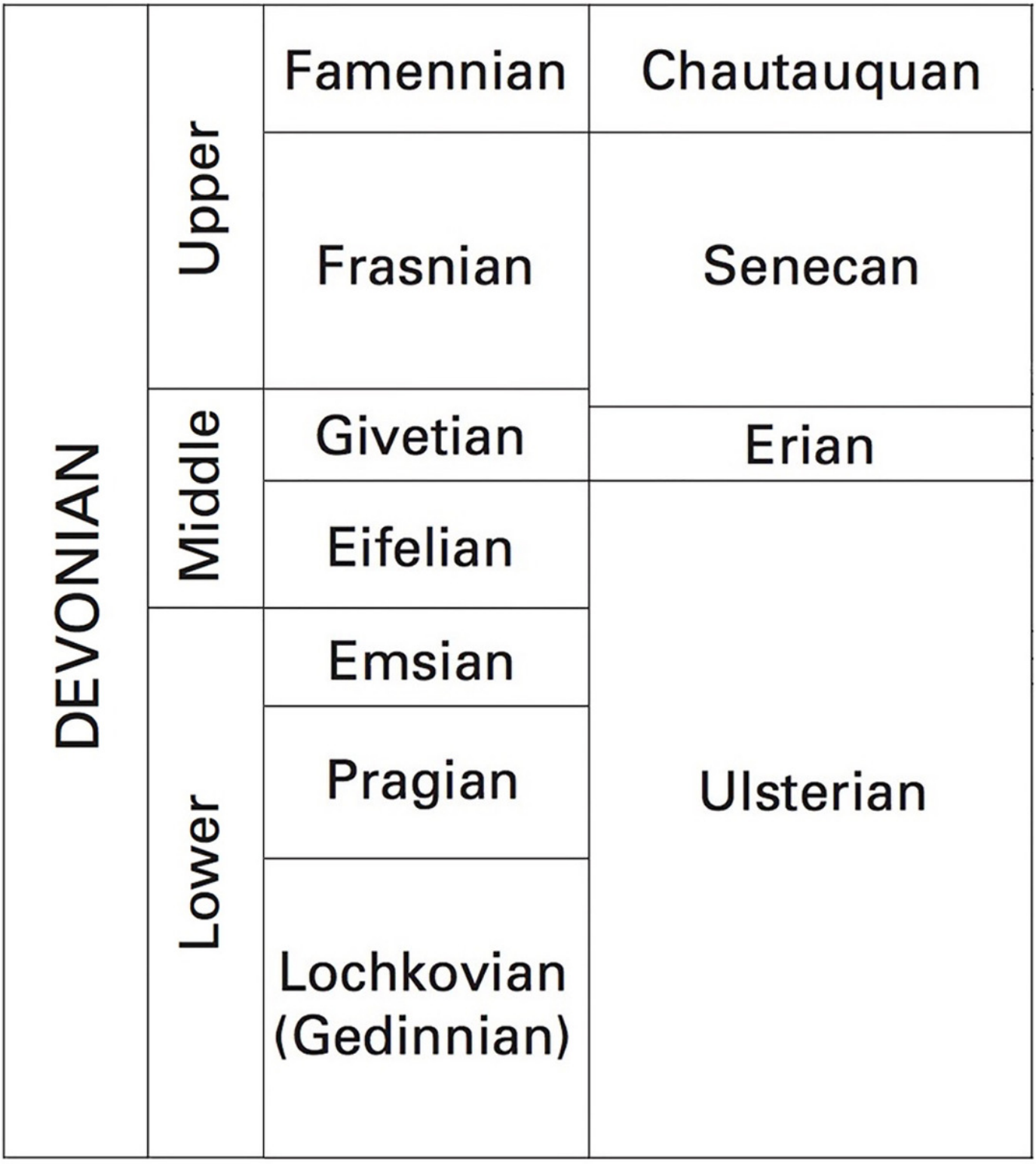

DEVONIAN
Upper
Middle
Lower
Famennian
Chautauquan
Frasnian
Senecan
Givetian
Erian
Eifelian
Emsian
Pragian
Ulsterian
Lochkovian
(Gedinnian)

Figure 2

Vertebrate remains from the Dundee Limestone Formation.

A, A large tooth from *Onychodus*, from the Dundee Limestone of London Township, Monroe County, UMMP 22006. Scale bar equals 1 cm. B, A spinal and anterior ventrolateral plate from ?*Macropetalichthys* (formerly *Arctolepis*), from the Dundee Limestone near Trenton, UMMP 14320. Abbreviations: Sp, spinal; Spi, spines of the spinal plate; Avl, anterior ventrolateral. Scale bar equals 1 cm.

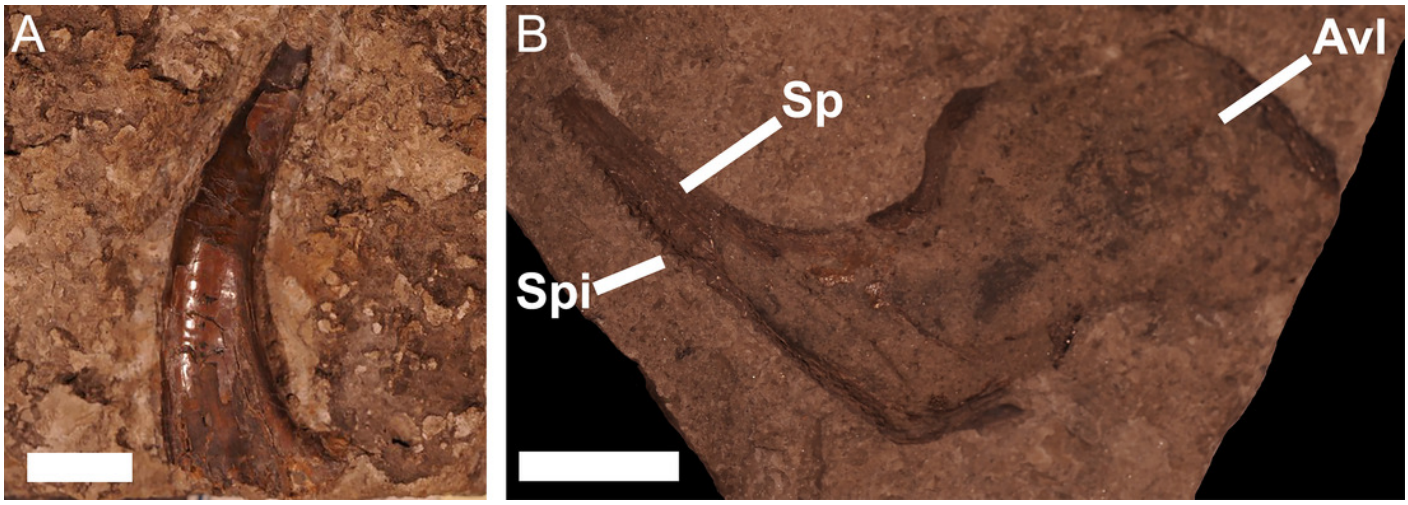


Figure 3

Stratigraphy and correlations of the Traverse Group in the northern part of the lower peninsula of Michigan.

A, east part of outcrop area and B, west side of outcrop area. Figure modified from Pojeta and Renjie (1986), Figure 12. Credit, U.S. Geological Survey.

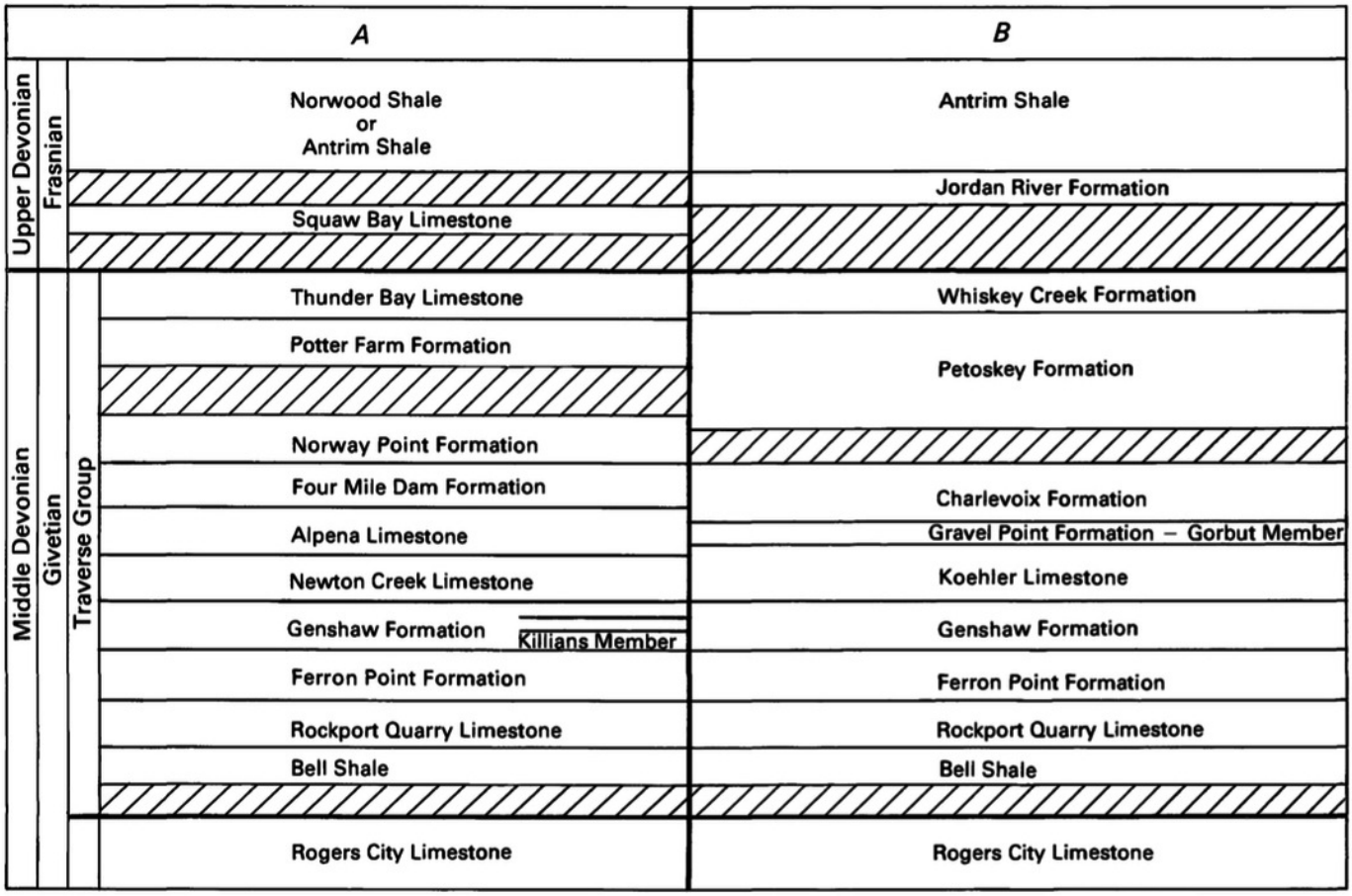


Figure 4

Vertebrate remains from the Rockport Quarry Limestone Formation.

A, A partial skull roof from *Holonema*, from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 12991. Abbreviations: Nu, Nuchal; Pn, Paranuchal; Cn, Central Plate. Scale bar equals 2 cm. B, The remains of an unidentified placoderm from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, 14M, Michigan History Museum. Scale bar equals 1 cm. C, An incomplete right anterior ventrolateral from *Dunkleosteus,* from the from the Rockport Quarry Limestone of Rockport Quarry, Alpena County, UMMP 16156. Scale bar equals 2 cm. C, a small spine from ?*Tamiobatis* (previously identified as *Ctenacanthus*) from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 13147. Scale bar equals 1 cm.

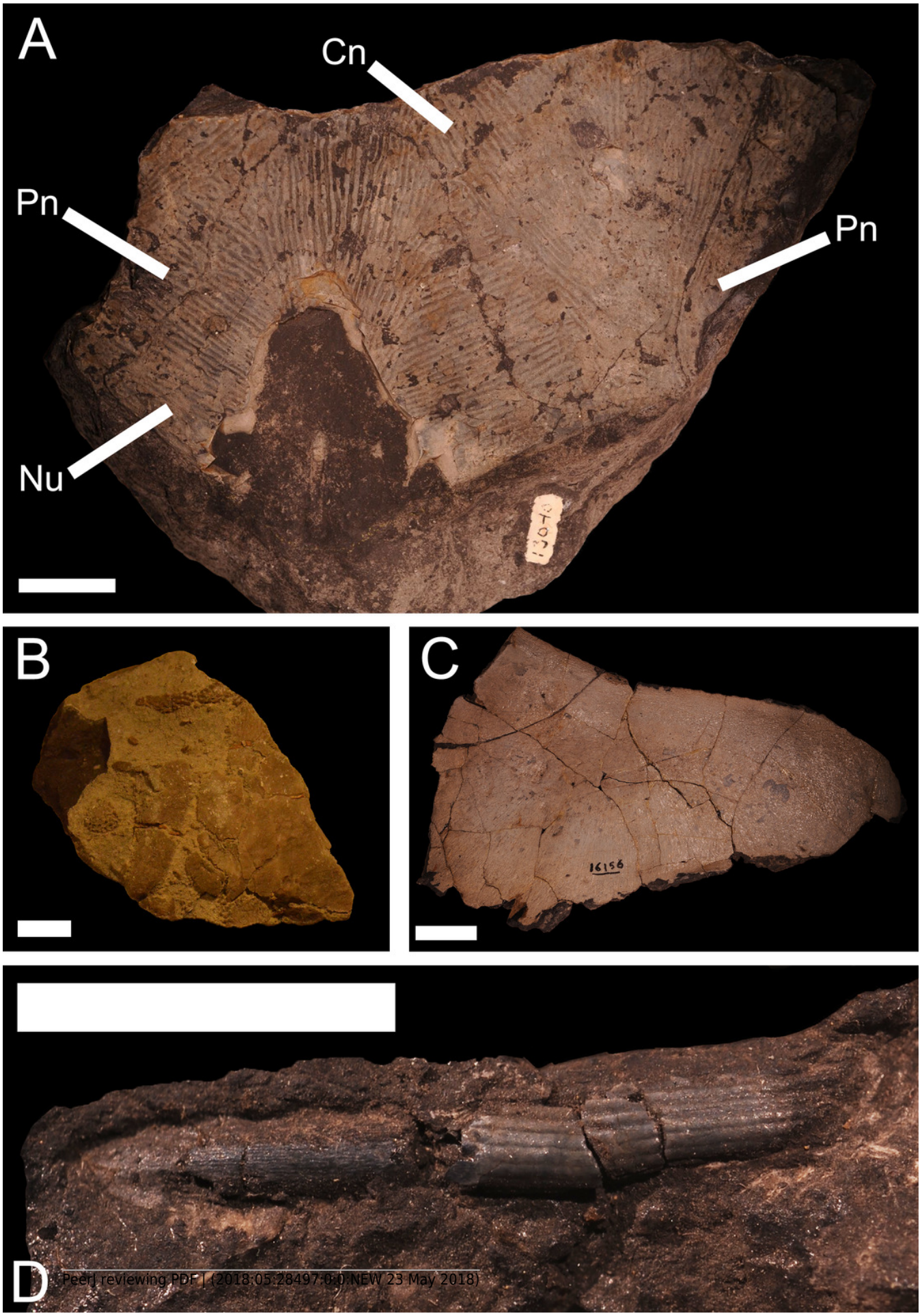

A
Cn
Pn
Pn
Nu
B
C
16156
D

Figure 5

Partially articulated armor from ?*Mylostoma*, found in rocks originally from the Alpena Limestone Formation at the Besser Museum Fossil Park, Alpena.

BV 4, Michigan History Museum. Scale bar equals 1 cm.

Figure 6

Vertebrate remains from the Four Mile Dam Formation.

A, a broken spine from an unidentified acanthodian, from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, JS 121, Michigan History Museum. Scale bar equals 0.5 cm. B, a flattened specimen of a trunk shield from ?*Mylostoma* sp., from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, 21M. Abbreviations: Md, Median dorsal; Adl, Anterior dorsolateral; Nu, Nuchal. Scale bar equals 1 cm. C, a partial armor plate from an unidentified placoderm, from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, 4M, Michigan History Museum. Scale bar equals 1 cm. D, a piece of limestone containing both crinoid heads and an armor plate from ?*Mylostoma* sp. found in the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, JS 6, Michigan History Museum. This specimen is an example of the association between vertebrates and invertebrates in the Middle Devonian deposits of Michigan. The solid arrow indicates the piece of armor and the dashed arrow indicates a crinoid head, Scale bar equals 1 cm.

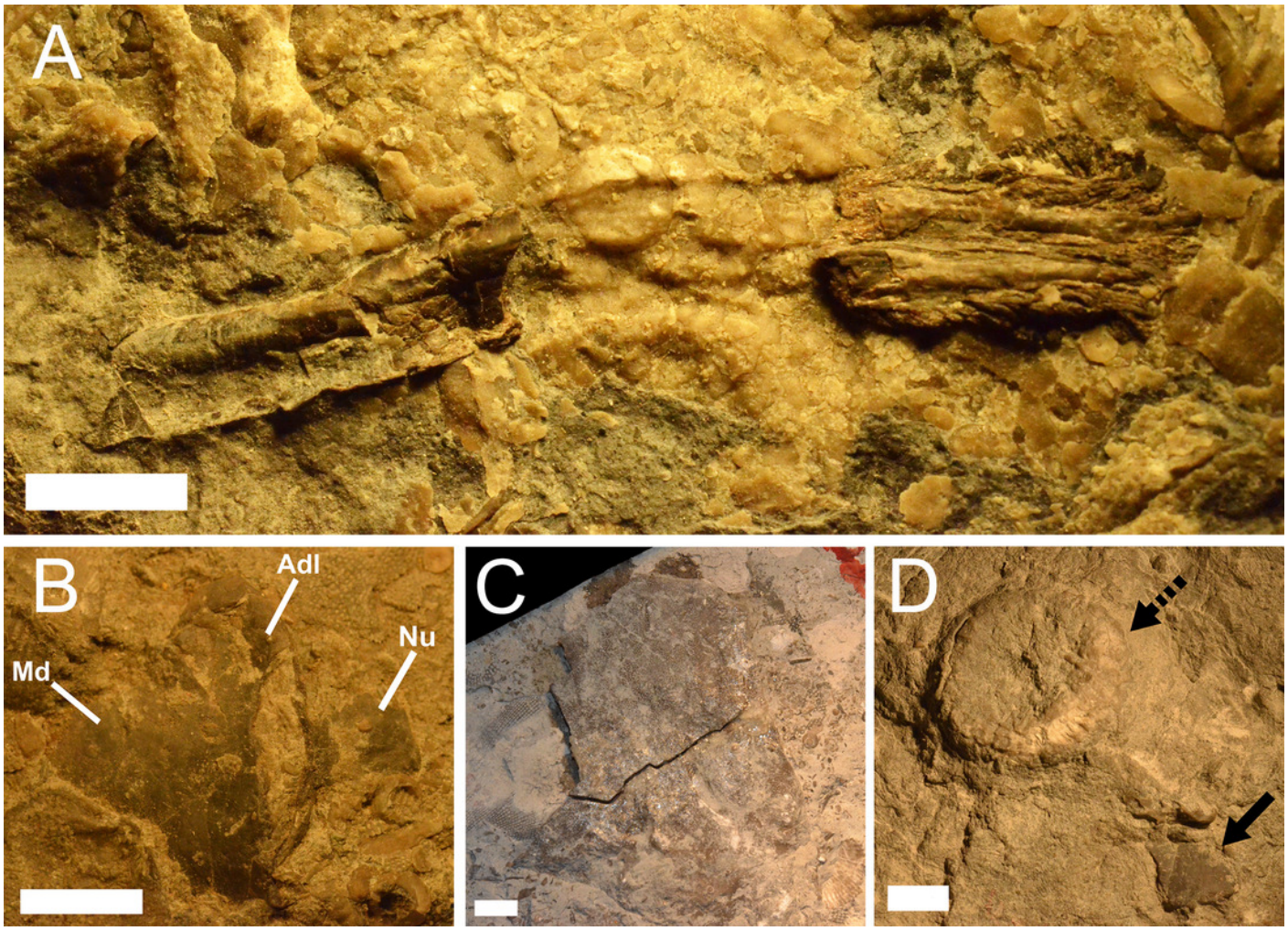

A
B
Adl
Nu
Md
C
D

Figure 7

Specimens of *Protitanichthys rockportensis,* an arthrodire that is common in the Midddle Devonian sediments of Michigan.

A, a photograph a cephalic shield from *Protitanichthys rockportensis*, from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 12980. B, a specimen drawing of UMMP 12980 (modified from Case (1931), Figure 1). Dotted lines represent missing plate boundaries and dashed lines represent sensory grooves, scale bar equals 2 cm. C, a partial cephalic shield from *Protitanichthys rockportensis*, from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, 32M. Abbreviations: Ce, Cephalic Shield (Incomplete); Un, Unidentified Armor Plate. Scale bar equals 2 cm. D, a partial headshield from ?*Protitanichthys rockportensis* (most likely a juvenile), from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, 4M, Michigan History Museum. Scale bar equals 1 cm.

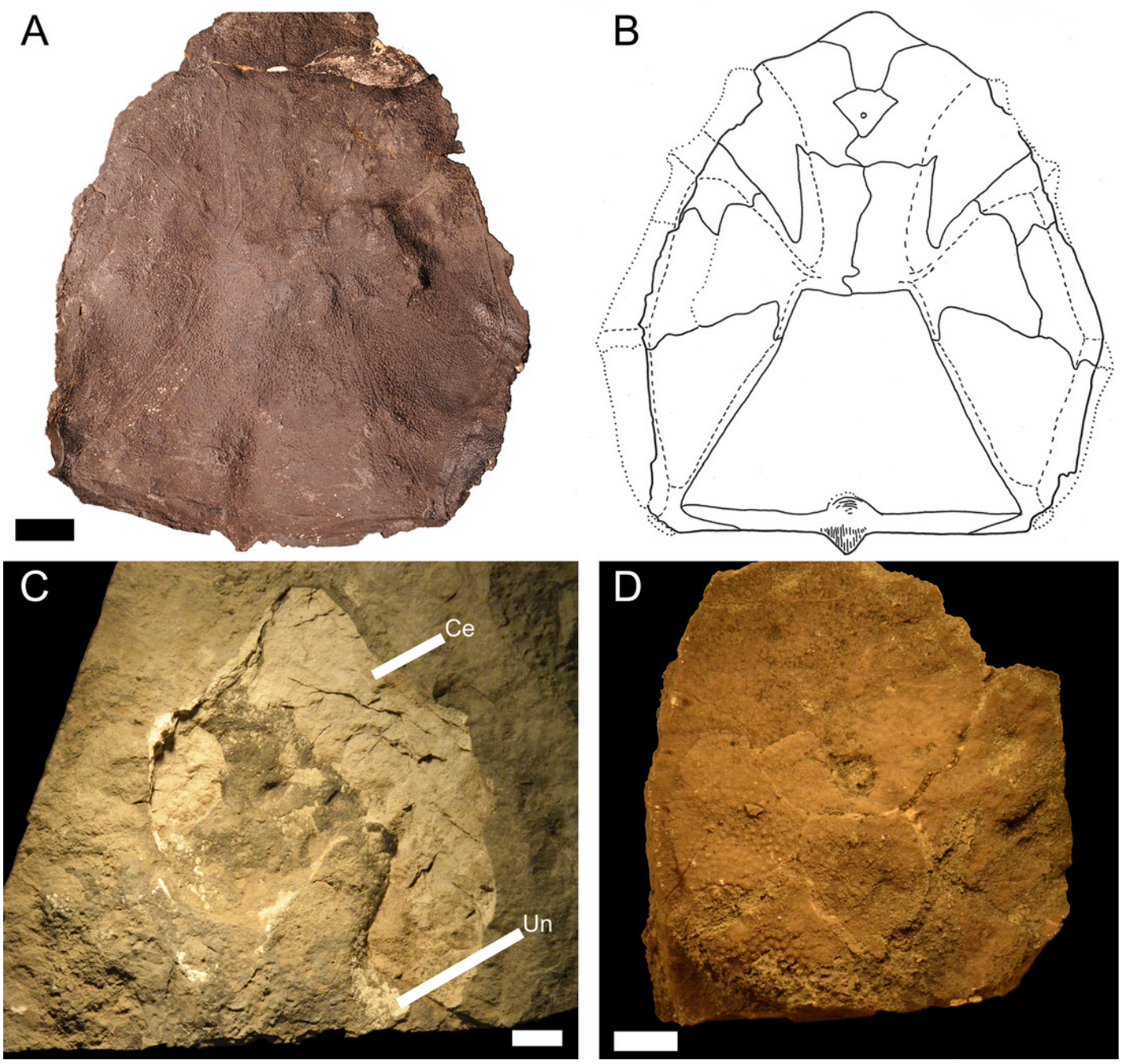

A
B
C
Ce
Un
D

Figure 8

An inferognathal from the Late Devonian arthrodire ?*Trachosteus clarkii* from the Antrim Shale.

Specimen recovered 1.6 km north of Norwood, MI. UMMP 18206. Scale bar equals 1 cm.

Figure 9

An anterior ventrolateral plate from *Bothriolepis* sp., from the Genshaw Formation.

Specimen recovered near Posen, MI. UMMP 4169. Scale bar equals 1 cm.

Figure 10

A gnathal plate of *Eczematolepis* sp., from the Traverse Group.

Specimen recovered from an unknown locality in Alpena, Alpena County, MI. UMMP 14374.

Scale bar equals 1 cm.

Figure 11

Specimens of the acanthodian *Machaeracanthus* sp.

A, a large spine from *Machaeracanthus* sp., from the Dundee Limestone of London Township, Monroe County, UMMP 3521. Scale bar equals 1 cm. B, a spine from ?*Machaeracanthus* sp. (previously identified as *Acondylacanthus gracillimus*), from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 13047. Scale bar equals 1 cm.

Figure 12

The skull of *Chirodipterus onawayensis* from the Newton Creek Limestone of Onaway Stone Quarry.

Specimen recovered from north of Onaway, Presque Isle County, MI. Specimen photo modified from Schultze (1982), Figure 2. This specimen is unnumbered at the Great Lakes Area Paleontological Museum. Scale bar equals 1 cm.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

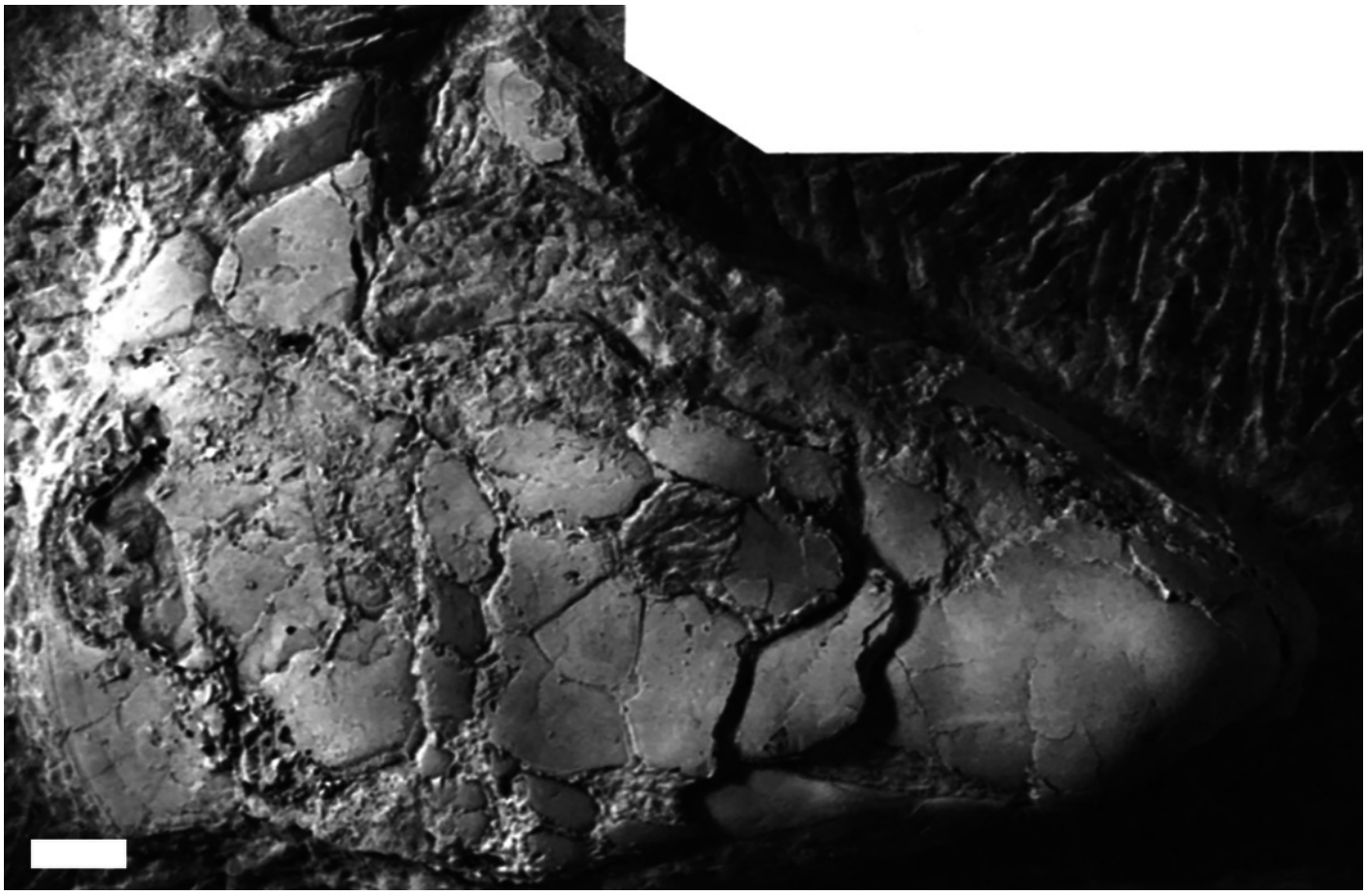
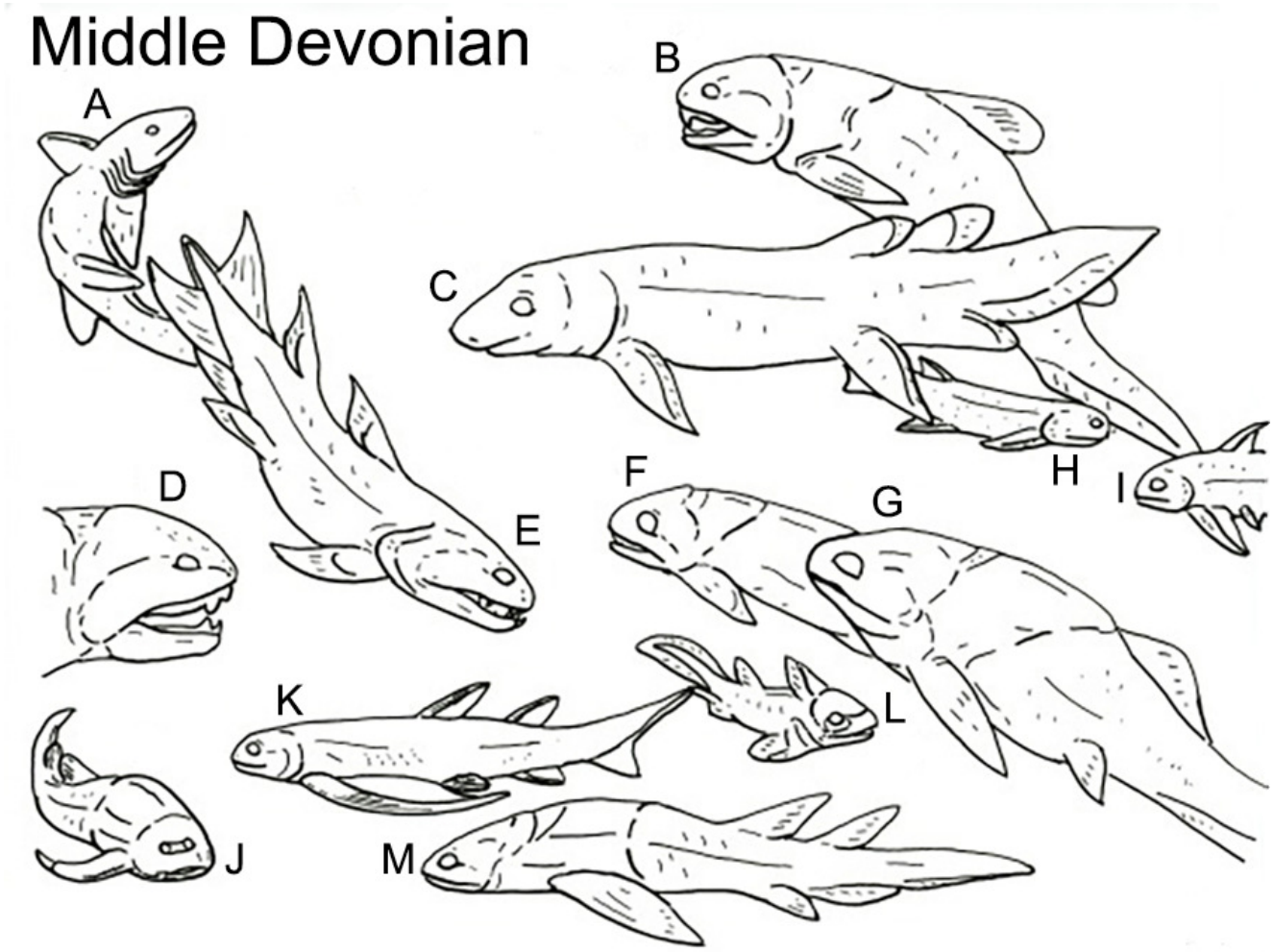
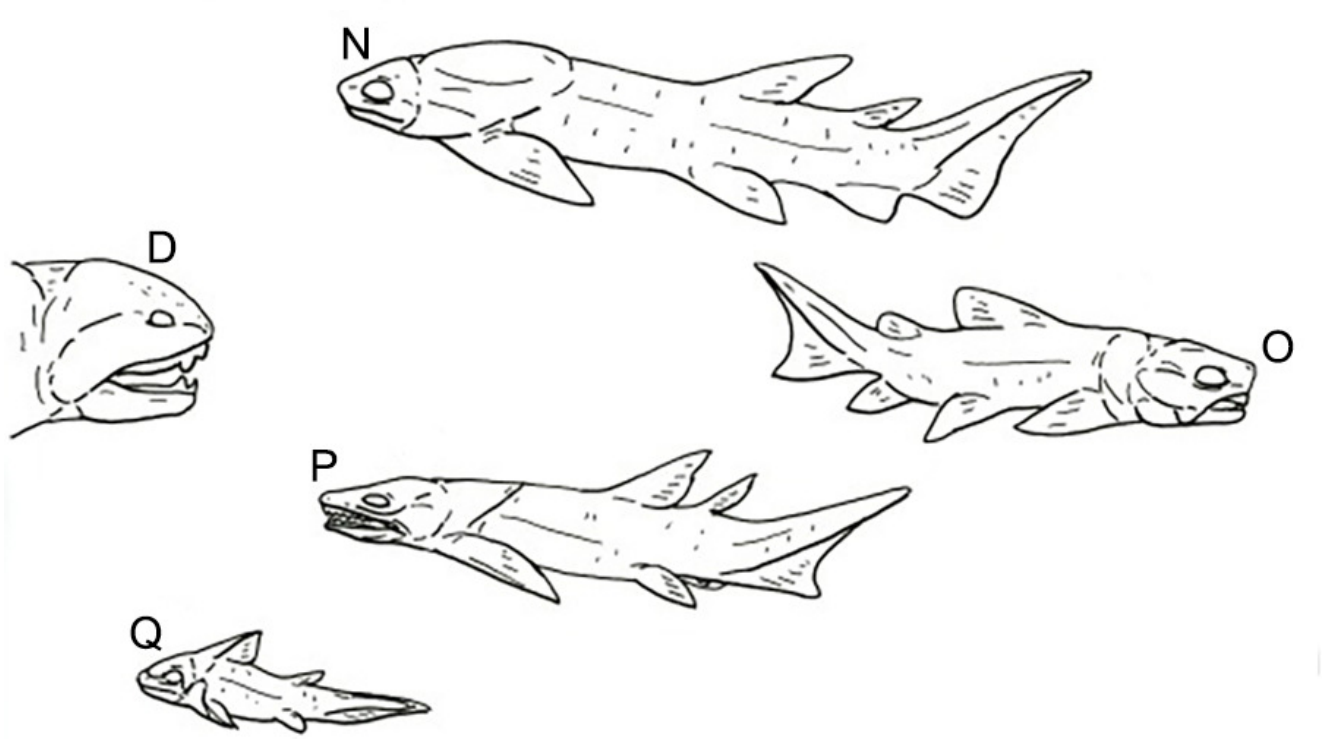


Figure 13

A representation of fish faunas from the Middle Devonian and the Late Devonian of Michigan.

Animals not to scale. A) *Acondylacanthu*s (Chondrichthyes); B) *Dinomylostoma* (Arthrodira; 'Placodermi'); C) *Chirodipterus* (Dipnoi; Sarcopterygii); D) *Dunkleosteus* (Arthrodira; 'Placodermi'); E) *Onychodus* (Onychodontida; Sarcopterygii); F) *Mylostoma* (Arthrodira; 'Placodermi'); G) *Protitianichthys* (Arthrodira; 'Placodermi'); H) *Oracanthus* (Acanthodida; Acanthodii); I) *Machaeracanthus* (Ischnacanthida; 'Acanthodii'); J) *Bothriolepis* (Antiarchi; 'Placodermi'); K) *Gyracanthus* (Gyracanthida; 'Acanthodii'); L) *Eczematolepis* (Ptyctodontida; 'Placodermi'); M) *Holonema* (Arthrodira; 'Placodermi'); N) *Aspidichthys* (Arthrodira; 'Placodermi'); O) *Trachosteus* (Arthrodira: 'Placodermi'); P) *Diplognathus* (Arthrodira; 'Placodermi'); Q) Ptyctodontida indet. ('Placodermi').


Middle Devonian
A
B
C
D
E
F
G
H
I
J
K
L
M


Late Devonian
N
D
O
P
Q