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. Nineteen genera of fishes have been found in the Middle and Late Devonian deposits of Michigan, of which thirteen are 'placoderms' represented by material ranging from articulated head 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 less common 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.

1 **An Examination of the Devonian Fishes of Michigan**

2 Jack Stack[1] and Lauren Sallan[1]

3 [1]Department of Earth and Environmental Science, University of Pennsylvania, 240 S. 33rd Street,

4 Philadelphia, PA, USA 19104-6316

6 Corresponding Authors:

7 Jack Stack[1]

8 stackj@sas.upenn.edu

10 Lauren Sallan[1]

11 lsallan@upenn.edu

12   *Abstract* —We surveyed the taxa, ecosystems, and localities of the Devonian fishes of Michigan

13   to provide a framework for renewed study, to learn about the diversity and number of these

14   fishes, and to investigate their connection to other North American faunas. Nineteen genera of

15   fishes have been found in the Middle and Late Devonian deposits of Michigan, of which

16   thirteen are 'placoderms' represented by material ranging from articulated head shields to

17   ichthyoliths. As expected from the marine nature of these deposits, 'placoderms' are

18   overwhelmingly arthrodire in nature, but two genera of ptyctodonts have been reported along

19   with less common petalichthyid material. The remaining fish fauna consists of fin-spines

20   attributed to 'acanthodians', two genera of potential crown chondrichthyans, an isolated dipnoan,

21   and onychodont teeth/jaw material. There was an apparent drop in fish diversity and fossil

22   abundance between Middle and Late Devonian sediments. This pattern may be attributed to a

23   paucity of Late Devonian sites, along with a relative lack of recent collection efforts at existing

24   outcrops. It may also be due to a shift towards open water pelagic environments at Late

25   Devonian localities, as opposed to the nearshore reef fauna preserved in the more numerous

26   Middle Devonian localities. The Middle Devonian vertebrate fauna in Michigan shows strong

27   connections with same-age assemblages from Ohio and New York. Finally, we document the

28   presence of partially articulated vertebrate remains associated with benthic invertebrates, an

29   uncommon occurrence in Devonian strata outside of North America. We anticipate this new

30   survey will guide future field work efforts in an undersampled yet highly accessible region that

31   preserves an abundance of fishes from a critical interval in marine vertebrate evolution.

INTRODUCTION

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37
38   The Devonian Period (419.2-358.9 Ma), the so-called "Age of Fishes," was marked by

39   major transitions in vertebrate biodiversity, including the takeover of ecosystems by jawed

40   fishes, the first appearance of tetrapods, and several group-specific and global extinctions

41   (Friedman and Sallan, 2012; Ogg et al., 2016). Despite the evolutionary importance of this

42   interval, Devonian vertebrates from the U.S. have been undersampled and understudied in the

43   last 50 years relative to specimens of the same age from the U.K., China, Australia and even

44   Antarctica (Long, 1995), with possible exceptions being select very Late Devonian faunas such

45   as the Cleveland Shale and Red Hill (Elliott et al., 2000; Carr and Jackson, 2008; Daeschler and

46   Cressler, 2011). Fishes are common in fossil-bearing Paleozoic strata throughout the

47   midwestern U.S., with many outcrops discovered over a century ago (Newberry, 1889;

48   Eastman, 1907; Eastman, 1908; Elliott et al., 2000). The Devonian-aged vertebrate fauna from

49   Michigan is abundant, but is poorly documented in the scientific literature relative to similar

50   strata in Ohio, Pennsylvania and elsewhere, despite heavy, ongoing collection efforts by

51   amateurs (Elliott et al., 2000). We undertook this survey of Devonian fishes from Michigan, the

52   first since 1970, as a result of new discoveries by J.S. (with the assistance of avocational

53   paleontologists).

54   During the Devonian, the Michigan Basin was located between, and connected to, the better

55   described Illinois (Hussakof, 1913; Cluff, 1980; Brusatte, 2007) and Appalachian Basins

56   (Newberry, 1873; Claypole, 1883; Carr and Jackson, 2008; Carr and Hlavin, 2010; Downs et al.,

57   2011; Daeschler and Cressler, 2011), yet it has been largely ignored by researchers for over a

58   century. Most of the handful of studies on Devonian vertebrates from Michigan are descriptions

59   of single taxa (e.g. Stevens, 1964; Miles, 1966; Schultze, 1982; Carr and Jackson, 2005). Only

60   one study from the last century attempted to survey Devonian fossil fishes from Michigan, but

61   was limited in scope to arthrodires (Case, 1931). Several decades later, an additional summary of

62   vertebrate fossils from the University of Michigan Museum of Paleontology was published by

63   Dorr and Eschman (1970), accompanied by a description of the Devonian ecosystems in

64   Michigan, including information on collecting sites, geologic history, and invertebrate faunae.

65   However, many of their identifications were incorrect, and some of their figured and described

66   specimens are currently missing from the UMMP collections.

67   Recent fieldwork in Michigan, undertaken mostly by amateur collectors, has revealed a

68   diverse and in many ways distinct Devonian vertebrate fauna containing taxa not reported by

69   Case (1931) and Dorr and Eschman (1970). New sites have produced an abundance of relatively

70   well-preserved vertebrate skeletal remains, including articulated material. Of the 201 Devonian

71   vertebrate specimens from Michigan that are catalogued in museums, 118 were collected by J.S.

72   after the previous survey. Here, we provide an updated and comprehensive summary of what is

73   known about the Devonian fish fauna from Michigan. We also compare the Devonian fish fauna

74   of Michigan to similarly aged marine faunas from New York and Ohio, placing it within the

75   larger regional context of the Devonian of North America.

76

77   **MATERIALS AND METHODS**
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79   We surveyed Michigan Devonian fish specimens in the collections of the University of

80   Michigan (UMMP), the Michigan History Museum (BV, JS, M, or a date), Michigan State

81   University Museum (VP), the Cleveland Museum of Natural History (CMNH), and the literature,

82   which contains records for other specimens from the Michigan State University Museum, the

83   Cleveland Museum of Natural History, and the Great Lakes Area Paleontological Museum

84   (GLAPM). We also performed surveys of known outcrops as described in text. Collections from

85   localities on public lands were approved by the State of Michigan, State Historic Preservation

86   Office Permit AE2016-10, and collections were deposited in the Michigan Historical Museum.

87   We compiled and organized information including type specimen, specimen counts, geologic

88   setting and localities (full list of localities available in supplemental files). A full list of examined

89   specimens is available as a supplement. Below, we describe the occurrence and distribution of

90   vertebrate remains by formation alongside information on associated invertebrate remains,

91   depositional environment, and the locations of vertebrate-bearing fossil sites. We also summarize

92   the characteristics of Devonian vertebrates resident in Michigan. We then synthesized temporal

93   patterns, ecology, and faunal similarities with other marine Devonian localities.

94
95   **MIDDLE DEVONIAN GEOLOGICAL DISTRIBUTION**
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98   Pre-Traverse Group
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100   The oldest vertebrate bearing Devonian localities in Michigan are from the Eifelian

101   (Middle Devonian; 393.3-387.7 Ma) (Swezey, 2002; Brett et al., 2011; Ogg et al., 2016; Fig.

102   1; Fig. 2). These occur in the Dundee Limestone formation, which has also produced

103   numerous invertebrate remains (Dorr and Eschman, 1970; Ehlers and Kesling, 1970). The fish

104   found in the Dundee Limestone include the onychodont *Onychodus sigmoides* Newberry, 1873

105   and *Onychodus* sp.*,* the stem-chondrichthyan 'acanthodian' *Machaeracanthus* sp. Newberry,

106   1873*,* the chondrichthyan *Acondylacanthus gracillimus* St. John and Worthen, 1875, the

107 presumptive arthrodire ?*Titanichthys* sp. Newberry, 1885, the ptyctodont *Ptyctodus* sp. Pander,

108 1858, and the petalichthyid ?*Macropetalichthys* sp. Norwood and Owen, 1846 (Dorr and

109 Eschman, 1970; Fig. 3). ?*Titanichthys* sp. (UMMP 26114), *A. gracillimus* (UMMP 26523)*,*

110 and *Machaeracanthus* sp. (UMMP 26111, UMMP 26112) and a jaw (UMMP 26113) from

111 *Onychodus* sp. are known from Sibley Quarry, Wyandotte, Wayne County (Dorr and

112 Eschman, 1970; Table 1). An isolated fin spine from *Machaeracanthus* sp. (UMMP 3521) and

113 an isolated tooth from O. *sigmoides* (UMMP 22006; Fig. 3A) are documented from a site in

114 London Township, Monroe County (Dorr and Eschman, 1970). One specimen of two

115 articulated armor plates (UMMP 14320; Fig. 3B) from ?*Macropetalichthys* sp. and another

116 specimen of *Ptyctodus* sp. (UMMP 14321) are documented from a locality near Trenton, in

117 Wayne County (Dorr and Eschman, 1970). It is important to note that the geological source of

118 the *Ptyctodus* specimen is uncertain and cannot be verified based on the matrix (Dorr and

119 Eschman, 1970). Despite this taxonomic diversity, vertebrate abundance and perhaps

120 preservation potential within the Dundee Limestone appears to be very poor (Ehlers and

121 Kesling, 1970).

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123           The Traverse Group

124   The Traverse Group encompasses all but two of the known vertebrate-bearing formations

125 from Michigan (Dorr and Eschman, 1970; Fig. 1). It was deposited in the Givetian (387-382.7

126 Ma), or the Erian (391.8-388 Ma) regional series (Swezey, 2002; Gradstein et al., 2004; Ogg et

127 al., 2016; Fig. 2). Six separate depositional environments or zones have been sampled from the

128 Traverse group, representing different water depths: a lagoonal zone, the zone of turbulence, the

129   stromatoporid-coral zone, the coral-brachiopod zone, the diverse fauna zone, and a bioherm

130   (Ehlers and Kesling, 1970). These zones were identified and described by Ehlers and Kesling

131   (1970), and are briefly summarized here for future reference. The stromatoporid-coral zone was

132   nearshore, shallow, and contained invertebrates such as brachiopods and crinoids (Ehlers and

133   Kesling, 1970). The coral-brachiopod zone represents deeper water coincident with the lowest

134   limit of stromatoporoids, with fossil material consisting mostly of brachiopods, corals, and

135   bryozoans (Ehlers and Kesling, 1970). Rocks from both of these zones are abundant in the

136   Traverse Group, and tend to be medium to fine grained limestones that can grade down into

137   calcareous shales (Ehlers and Kesling, 1970). The diverse fauna zone was reefal with abundant

138   vertebrates, brachiopods, trilobites, and crinoids with less common corals, bryozoans, and

139   mollusks (Ehlers and Kesling, 1970). The rocks from the diverse fauna zone tend to be thick

140   claystones or shale beds, with low calcareous content (Ehlers and Kesling, 1970). It is also

141   possible to find fish and invertebrate fossils in the lagoonal sediments, but these may have been

142   the result of marine incursions rather than distinct faunas (Stevens, 1964; Ehlers and Kesling,

143   1970). The rocks from the lagoonal zone are lithographic limestone (Ehlers and Kesling, 1970).

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146   Vertebrate Distribution in Early Erian (Givetian) Deposits
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149   *Bell Shale.*— One tooth plate (UMMP 14460) from *Ptyctodus* sp. has been reported

150   from the Bell Shale of Rogers City, Presque Isle County (Dorr and Eschman, 1970).

151   Invertebrate material suggests that the Bell Shale was deposited in the diverse fauna zone

152   (Pohl, 1930; Ehlers and Kesling, 1970).

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

154   include the arthrodires *Protitanicthys rockportensis* Case, 1931, ?*Holonema rugosum*

155   Claypole, 1883, *Holonema* sp. Newberry 1889, *Dunkleosteus* sp. Lehman, 1956, *Mylostoma*

156   sp. Newberry, 1883 and *Dinomylostoma* sp. Eastman, 1906, the ptyctodont *Ptyctodus* sp., the

157   'acanthodian' ?*Machaeracanthus* sp., and the chondrichthyan ?*Tamiobatis* sp. Eastman, 1897a

158   (Dorr and Eschman, 1970; personal observation; Fig. 4). There are also two specimens (7M,

159   VP. 522) of placoderms of unknown affinity that have been collected from the Rockport

160   Quarry Limestone. One of these specimens (7M) consists of armor fragments distinguishable

161   from other resident taxa by a lack of tubercles (Fig. 4B), but further material is required to

162   make an exact attribution. Also, a single specimen (UMMP 3898) was given an uncertain

163   designation as ?*Holonema rugosum* by Dorr and Eschman (1970).

164   The Rockport Quarry Limestone contains the most diverse Devonian vertebrate fauna in

165   Michigan (Dorr and Eschman, 1970; Sallan and Coates, 2010). The main vertebrate-bearing

166   outcrop is at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena

167   County (Dorr and Eschman, 1970). The degree of preservation is often good, with partially

168   articulated armor plates frequently observed in the field, but mining operations have damaged

169   many of the accessible fossils (personal observation). Fortunately, this locality is the most

170   productive Devonian vertebrate site in Michigan by far (personal observation), and better

171   specimens are likely to be recovered in the future. Despite the relatively high diversity and

172   abundance of fish material and collection efforts by amateurs, little material has been

173   accessioned in state museums. The UMMP contains only single specimens of

174   ?*Machaeracanthus* sp. (UMMP 13047), *Dunkleosteus* sp. (UMMP 16152; Fig. 4C),

175   *Mylostoma* sp. (UMMP 13612)*, Ptyctodus* sp. (UMMP 13045), and ?*Tamiobatis* sp. (UMMP

176   13147)*.* There are 59 specimens of *P. rockportensis* and 26 specimens of *Holonema* sp.

177   deposited in UMMP, MSU and the MHM, and many more recently recovered fossils of those

178   fishes reside in private collections (personal observation). The large numbers of

179   stromatoporoids and corals, alongside less common brachiopods, trilobites, and crinoids,

180   suggests that the vertebrate bearing rocks of the Rockport Quarry Limestone were deposited in

181   the stromatoporoid-coral zone (Ehlers and Kesling, 1970). In contrast to most Devonian sites,

182   articulated vertebrate remains are often preserved in conglomerates with invertebrate

183   specimens (personal observation). It is notable that the abundance and diversity of coincident

184   invertebrates is considerably lower than the underlying Bell Shale, most likely because of the

185   difference in depositional zone (Ehlers and Kesling, 1970).

186   *Genshaw Formation.*— A single specimen of an incomplete armor plate (UMMP 4169)

187   from the ptyctodont ?*Eczematolepis* sp. Miller, 1892 has been documented from the Genshaw

188   Formation near Posen, Presque Isle County (Dorr and Eschman, 1970). In addition, a specimen

189   of ?*H. rugosum* (UMMP 3899) has been reported from the Killians member of the Genshaw

190   Formation, at a locality referred to as French Road near Long Lake, near Rockport Quarry,

191   Alpena County (Dorr and Eschman, 1970). Invertebrates found in this formation are typical of

192   the diverse fauna zone (Ehlers and Kesling, 1970).

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194   Vertebrate Distribution in Middle Erian (Givetian) Deposits
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197   *Newton Creek Limestone.*— A single specimen of the lungfish (dipnoi) *Chirodipterus*

198   *onawayensis* (unnumbered) Schultze, 1982, along with two specimens of *Machaeracanthus* sp.

199   (UMMP 47691 and UMMP 47692) and two specimens of *Holonema farrowi* Stevens, 1964

200   (UMMP 46647, UMMP 46648) are documented from the Newton Creek Limestone (Stevens,

201   1964; Dorr and Eschman, 1970; Schultze, 1982). These fossils were collected from the north

202   edge of the Onaway Stone Quarry, Presque Isle County, where the Newton Creek Limestone is

203   referred to as the Koehler Limestone (Dorr and Eschman, 1970; Ehlers and Kesling, 1970).

204   While these fishes were recovered from the lagoonal zone (Stevens, 1964), some may have

205   been deposited during a deeper marine incursion (Ehlers and Kesling, 1970).

206   *Gravel Point Formation.*— This formation has produced single catalogued specimens of

207   *Gyracanthus* sp. Woodward, 1906 (UMMP 1329) ?*Onychodus* sp. (UMMP 14370) (Dorr and

208   Eschman, 1970), and a holonemiid (UMMP 3129) (Dorr and Eschman, 1970). These

209   specimens were found at South Point (Gravel Point), Little Traverse Bay, Charlevoix County

210   (Ehlers and Kesling, 1970). The invertebrate fossils from this formation are typical of the

211   diverse fauna zone (Pohl, 1930; Ehlers and Kesling, 1970).

212   *Alpena Limestone Formation.*— This formation was deposited contemporaneously with

213   the Gravel Point Formation (Ehlers and Kesling, 1970). Single specimens of *Dunkleosteus* sp.

214   (UMMP 16152) and *Ptyctodus* sp. (UMMP 16157), along with three specimens of ?*Mylostoma*

215   (BV3, BV6, and BV7) and a single specimen of some partially articulated pieces of armor from

216   the head shield of ?*Macropetalichthys* sp. (BV 4) comprise the catalogued vertebrate material

217   from the Alpena Limestone (Dorr and Eschman, 1970). The specimens of *Dunkleosteus* sp. and

218   *Ptyctodus* sp. are from a locality referred to as Alkali Quarry in Alpena, and the ?*Mylostoma* sp.

219   and ?*Macropetalichthys* sp. specimens are from the Besser Museum Fossil Park in Alpena

220   (personal observation; Dorr and Eschman, 1970). Amateur collectors have reported *P.*

221 *rockportensis* and other vertebrates from this formation, but none of these specimens are

222 deposited in museum collections. The invertebrate fossils from this formation are typical of the

223 coral-brachiopod zone. (Pohl, 1930; Ehlers and Kesling, 1970). Many of these are articulated

224 and occur in conglomerates with similarly partially articulated vertebrate specimens.

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226 Vertebrate Distribution in Late Erian (Givetian) Deposits
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229 *Four Mile Dam Formation.*— ?*Mylostoma* sp*., P. rockportensis*, ?*Macropetalichthys* sp.

230 and an unidentified 'acanthodian' and 'placoderm' have recently been collected by one of the

231 authors (JS) from the Four Mile Dam Formation (Fig. 5). At this time, ?*Mylostoma* sp. is

232 known from 39 specimens, while an unidentified 'placoderm' is known from one specimen (JS

233 4; Fig. 5C), an unidentified 'acanthodian' is known from two partial fin spines (JS 120, JS 121;

234 Fig. 5A), *P. rockportensis* is known from one specimen of an armor fragment (JS 101), and

235 ?*Macropetalichthys* sp. is known from a partial head shield (32M). The unidentified placoderm

236 (JS 4) is a specimen of an armor plate that does not resemble the other resident placoderms

237 (?*Mylostoma* sp., *P. rockportensis*, and ?*Macropetalichthys* sp., Fig. 5C). More material needs

238 to be collected before a concrete identification is made. Likewise, the two isolated acanthodian

239 fin spines are distinct from named acanthodians (*Gyracanthus*, *Machaeracanthus*, and

240 *Oracanthus*) and chondrichthyans (*Tamiobatis* and *Acondylacanthus*) reported from Michigan

241 (J.S. personal observation; Denison, 1979; Maisey 1982; Williams, 1998). The vertebrate fauna

242 from the Four Mile Dam Formation has high abundance but low diversity compared to the

243 Rockport Quarry Limestone (Dorr and Eschman, 1970). The main vertebrate-bearing outcrop

244 of this formation is the Specific Stone Products Quarry in Alpena, with the fossils recovered

245   from discarded piles of limestone from this quarry on the shores of Betsie Bay in Elberta,

246   Benzie County (J.S. personal observation).

247   Despite the fact that the Four Mile Dam Formation was only recently identified as a

248   vertebrate-bearing formation, fish material may be more abundant in these sediments than at

249   any other Devonian locality in Michigan. There have been 44 vertebrate specimens recovered

250   in a few years of limited yet deliberate collecting in rocks from this formation. However, this

251   represents more recent collection effort by university-affiliated researchers than has recently

252   been expended at other Michigan sites. Many of the Four Mile Dam ?*Mylostoma* sp. specimens

253   are well-preserved and partially articulated, including potential juveniles, suggesting that this

254   locality holds high potential for future research (personal observation). The degree of

255   preservation suggests rapid burial, perhaps by a mudflow initiated by a storm given the

256   environmental setting. This interpretation is supported by the fact that of the vertebrate

257   specimens from this formation are found in conglomerates with invertebrate specimens (Fig.

258   5D). This includes fully three-dimensional, articulated crinoid calyces, a rarity in the Devonian

259   record that requires quick deposition (Fig. 5D). These invertebrates are found in other outcrops

260   of the Four Mile Dam Formation, but fish fossils are absent from all but the site mentioned

261   above (Dorr and Eschman, 1970; Ehlers and Kesling, 1970), implying that vertebrate material

262   may not be preserved in this formation under more normal environmental conditions.

263   Invertebrate fossils found in this formation are typical of the diverse fauna zone (Ehlers and

264   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

268   and Eschman, 1970). The invertebrates from this formation suggest that the rocks were

269   deposited in the coral-brachiopod zone (Ehlers and Kesling, 1970).

270   *Potter Farm Formation.*—- One specimen of *Ptyctodus* sp. (UMMP 21718) is known from

271   the Potter Farm Formation, recovered from a locality referred to by Dorr and Eschman (1970) as

272   "Old Wamer's Brickyard", southwest of Alpena, Alpena County. However, Dorr and Eschman

273   (1970) noted that the exact geologic affinity of this specimen is uncertain (it may not have been

274   collected *in situ*). However, another specimen of *Ptyctodus* sp. (UMMP 21817) was collected

275   from an outcrop of the Potter Farm Formation at the "west edge of Alpena Cemetery", Alpena

276   (Dorr and Eschman, 1970). Amateur collectors have also reported specimens of *P. rockportensis*

277   from this formation, but these specimens are not deposited in museum collections and therefore

278   cannot be verified. The invertebrate fossils found from the Potter Farm Formation are typical of

279   the diverse fauna zone (Ehlers and Kesling, 1970). Many of these invertebrates are again

280   preserved in conglomerates with vertebrates, as in the Four Mile Dam Formation (Fig. 5D).

281   These invertebrate specimens are occasionally broken and preserved in a way that superficially

282   resembles dark, thin armor plates from vertebrates, and have been misidentified as such by

283   amateurs, so caution must be used when identifying specimens from this formation without

284   attention to histology.

285   *Thunder Bay Limestone.*— A tooth plate (UMMP 3023) from *Ptyctodus* sp. has been

286   reported from the Thunder Bay Limestone (Dorr and Eschman, 1970). This specimen was

287   collected from the bluffs on the northeast shore of Partridge Point, 6.4 kilometers south of

288   Alpena (Dorr and Eschman, 1970). The invertebrates from this formation are typical of the

289   diverse fauna zone (Pohl, 1930; Ehlers and Kesling, 1970).

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292   **LATE DEVONIAN GEOLOGICAL DISTRIBUTION**
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295   *Antrim Shale*.— The Antrim Shale was deposited in the Frasnian (382.7-372.2 Ma), or

296   Senecan (388-370 Ma) regional series and in the Famennian (372.2-358.9 Ma), or the

297   Chatauquan (370-359.2 Ma) regional series of the Late Devonian (Dorr and Eschman, 1970;

298   Ehlers and Kesling, 1970; Gutshick and Sandberg, 1991; Gradstein et al., 2004; Ogg et al., 2016;

299   Fig. 1; Fig. 2). Fish from the Antrim Shale that are accessioned in museum collections include *D.*

300   *lafargei* Carr and Jackson, 2005, ?*Trachosteus clarki* Newberry, 1889, *Dunkleosteus* sp*.,* and

301   *Aspidichthys clavatus* Newberry, 1873, all known only from single specimens (Dorr and

302   Eschman, 1970; Carr and Jackson, 2005). There are also reports of the presence of ptyctodonts,

303   cladodonts (Chondrichthyes), conodonts, and ray-finned fishes from the Antrim Shale (Ehlers

304   and Kesling, 1970; Elliott et al., 2000). It is not clear if these specimens are deposited in museum

305   collections, and therefore they were not examined in this study. ?*T. clarki* is known from an

306   isolated inferognathal (UMMP 18206) from a locality 1.6 kilometers north of Norwood,

307   Charleviox County (Dorr and Eschman, 1970). The armor plate (UMMP 3127) of *A. clavatus*

308   was collected from the shore of Grand Traverse Bay near Norwood (Dorr and Eschman, 1970).

309   *Dunkleosteus* is known from a suborbital plate (UMMP 15432) found in a concretion nodule

310   from Squaw Bay, 6.4 kilometers south of Alpena on U.S. 23 (Dorr and Eschman, 1970). *D.*

311   *lafargei* is known from an incomplete, disarticulated specimen (CMNH 50215) from Paxton

312   Quarry (Lafarge North America, Inc., Alpena Cement Plant, Great Lakes Region), Alpena (Carr

313   and Jackson, 2005).. Invertebrate fossils from this formation include brachiopods and

314   cephalopods (ammonoids), demonstrating relatively low invertebrate diversity compared to

315   Middle Devonian formations (Ehlers and Kesling, 1970; Gutshick and Sandberg, 1991; Hannibal

316   et al., 1992). This is likely reflective of the open water habitat the Antrim Shale was deposited in,

317   a contrast to the reefs and nearshore depositional environments of Michigan's Middle Devonian

318   localities (Gutshick and Sandberg, 1991). The Antrim Shale is a typical Late Devonian North

319   American black shale, containing large quantities of black mud rich in organic matter from

320   deposition on a poorly oxygenated ocean floor (Dorr and Eschman, 1970; Roen 1984).

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322
323   **THE ENVIRONMENT AND ASSEMBLAGES OF DEVONIAN MICHIGAN**
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326   During the Middle Devonian, Michigan was located underneath a shallow, tropical sea

327   (Briggs, 1959). Pinnacle reefs were situated in a ring around what is now the Lower Peninsula

328   (Dorr and Eschman, 1970). Most Middle Devonian localities are associated with these reef

329   formations due to abundant invertebrate life and bioherm construction, contributing to rock

330   formation (Ehlers and Kesling, 1970). Much of the center of the Lower Peninsula is covered

331   with a thick layer of glacial till, preventing detailed paleontological study (Lilienthal, 1978).

332   Sites situated along the northern edge of the Lower Peninsula give a fairly good window into

333   the structure of Michigan's Middle Devonian ecosystems (Ehlers and Kesling, 1970; Dorr and

334   Eschman, 1970). These sites present diverse invertebrate biotas including crinoids, trilobites,

335   cephalopods, gastropods, corals, bryozoans, brachiopods, and blastoids (Pohl, 1930; Ehlers

336   and Kesling, 1970). The vertebrate fauna includes numerous 'placoderms' (arthrodires,

337   petalichthyids, and ptyctodonts), chondrichthyans (ctenacanths), lungfish, onychodonts, and

338   'acanthodians' (Dorr and Eschman, 1970).

339   Vertebrate material, most of it at least partially articulated, from the Devonian of

340   Michigan is usually associated with numerous benthic shelled invertebrates, unlike most sites

341   of similar age outside of North America (Ehlers and Kesling, 1970; personal observation).

342   This type of assemblage is also found in similarly-aged Columbus and Delaware Limestones

343   of Ohio (Eastman, 1907; Westgate and Fischer, 1933; Wells, 1944; Denison, 1978; Martin,

344   2002). In several formations, fishes and invertebrates are found in association within the

345   same conglomerate or slab (Fig. 5D).

346   Michigan's faunas exhibited changes in the number, type, and diversity of fossils from the

347   Middle to Late Devonian. Most Late Devonian non-vertebrate fossils are cephalopods,

348   brachiopods, and assorted plant fossils, marking a significant change from the rich invertebrate

349   fauna from the Middle Devonian (Ehlers and Kesling, 1970; Hannibal et al., 1992). In addition,

350   the vertebrate assemblage in the Late Devonian is dominated by arthrodire and ptyctodont

351   'placoderms,' which is a much less diverse fish fauna than what was present in the Middle

352   Devonian (Dorr and Eschman, 1970; personal observation). As noted above, the Antrim Shale

353   was deposited in an open water pelagic habitat with little to no benthic community (Gutshick

354   and Sandberg, 1991). There was likewise a shift in rock types from primarily limestone in the

355   Middle Devonian to an alternating pattern of shale and limestone in the Late Devonian (Dorr

356   and Eschman, 1970). The Antrim Shale, the only vertebrate-bearing formation from the Late

357   Devonian in Michigan, is constructed in this manner (Dorr and Eschman, 1970; Gutshick and

358   Sandberg, 1991). This alteration suggests that sea levels shifted several times during this

359   interval, which would have contributed to the loss of older reef structures and upwelling of

360   anoxic waters for shale deposition (Roen, 1984; Sandberg et al., 2002). Similar black shale

361   deposition has been recorded from the Devonian of other areas of North America, such as New

362   York, Tennessee, Ohio, and Kentucky (Roen, 1984). In Michigan, coral reefs disappear at the

363   base of the Frasnian with the deposition of black shales (Ehlers and Kesling, 1970). This loss

364   precedes bioherm elimination in other regions of the world, where corals are virtually

365   eliminated by the climate-driven Frasnian-Famennian Kellwasser events (Kiessling et al., 2010).

366
367
368   **DEVONIAN FISHES OF MICHIGAN**
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370

371   Here we describe what is known about the occurrence and distribution of major

372   vertebrate clades and lineages from the Devonian of Michigan. Because of the aforementioned

373   absences in the record and new discoveries, much of the information comes from personal

374   observation as noted.

375
376   Arthrodires
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379   *Protitanichthys rockportensis.— Protitanichthys rockportensis* is one of the few endemic

380   species of fish from the Middle Devonian of Michigan (Case, 1931; Miles, 1966; Fig. 6).

381   However, *P. rockportensis* likely belongs to a particularly widespread group of arthrodires,

382   including *Dunkleosteus* as well as Chinese and Moroccan taxa (Zhu and Zhu, 2013). *P.*

383   *rockportensis* is known from 59 specimens housed in the MHM and UMMP that come from the

384   Rockport Quarry Limestone Formation at the abandoned Kelly Island Limestone Quarry at

385   Rockport State Park, Alpena County and one specimen (JS 101) that is known from the Four

386   Mile Dam Formation at the Betsie Bay Rockpiles in Elberta, Benzie County (Dorr and

387   Eschman, 1970, personal observation). Most specimens of *P. rockportensis* consist of

388   disarticulated and incomplete pieces of dermal bone from the head shield (Miles, 1966; Figure

389   6C). The poor quality and lack of articulation in these specimens is caused by breakage during

390   quarrying operations, scavenging, and high-energy water flow in the environment of deposition

391   (Ehlers and Kesling, 1970; personal observation). The majority of the specimens are from fish

392   that would have been about a meter in length in life, but a few rare individuals may have been

393   over two meters in total length, making them very large for coccosteids (Denison, 1978). Most

394   specimens appear to have been adults, but smaller juveniles and possibly senescent animals

395   have been identified (personal observation). A well-preserved specimen (4M) of the head shield

396   of a small placoderm that resembles *Bothriolepis* Eichwald, 1840 in size and ornamentation has

397   also been recovered from the Rockport Quarry Limestone at the abandoned Kelly Island

398   Limestone Quarry at Rockport State Park, Alpena County (Fig. 6D). There are also several

399   other small, far less complete specimens from that site bearing similar ornamentation (small,

400   dense tubercles). While these resemble *Bothriolepis*, they are most likely juvenile specimens of

401   *P. rockportensis*, as smaller (and presumably younger) *P. rockportensis* would have had

402   prominent sutures between the plates of their head shield, with their form distinct from larger

403   members of the same species. The relative age of these fishes can be estimated by the

404   distinction of the sutures between the armor plates of the head shield, with older animals

405   bearing less noticeable sutures that fused with age (R. Carr pers. comm. 2012). Better material

406   must be found in order to make a final determination as to these alternative attributions.

407   Because of the relatively high number of specimens, *P. rockportensis* has been described in

408   detail (Miles, 1966).

409   *Titanicthys*.— ?*Titanichthys* sp. is known from a single specimen (UMMP 26114) from the

410   Dundee Limestone of Sibley Quarry, Wyandotte (Dorr and Eschman, 1970). *Titanichthys* is

411   primarily known from open water settings in the Late Devonian, so it possible that this has been

412   misidentified (Janvier, 2003; Boyle and Ryan, 2017). Indeed, Dorr and Eschman (1970) stated

413   the exact affinity of this specimen was uncertain. Complicating matters further, the specimen is

414   currently missing from museum collections and has never been figured.

415   *Holonema.*— Two species of *Holonema* are found in Michigan: *H. farrowi* and ?*H. rugosum*

416   (Stevens, 1964; Dorr and Eschman, 1970). Most specimens consist of dorsal and/or ventral

417   shields with distinctive ornamentation of rows and ridges of tubercles, which are easily

418   identifiable even from fragmented remains (Dorr and Eschman, 1970; Fig. 4A). This fish is

419   most common in the Rockport Quarry Limestone at the abandoned Kelly Island Limestone

420   Quarry at Rockport State Park, Alpena County, with 26 specimens registered at UMMP and

421   MHM (Dorr and Eschman, 1970; personal observation). Two specimens of *H. farrowi* (UMMP

422   46647 and UMMP 46648) have been reported from the Newton Creek Limestone at Onaway

423   Stone Quarry, north edge of Onaway, Presque Isle County (Dorr and Eschman, 1970). One

424   specimen of ?*H. rugosum* (UMMP 3899) has been documented from the Genshaw Formation at

425   French Road, near Long Lake, Alpena County (Dorr and Eschman, 1970). A specimen that

426   Dorr and Eschman (1970) designated as a holonemiid was collected from the Gravel Point

427   Formation of South Point (Gravel Point; UMMP 3129). Finally, another specimen (UMMP

428   3130) that was designated as a holonemiid by Dorr and Eschman (1970) was collected from an

429   unknown formation in the quarry that is currently known as the Michigan Limestone and

430   Chemical Company quarry in Rogers City, Presque Isle County (Dorr and Eschman, 1970).

431   The flattened body shape and weak bite of *Holonema* indicates that it was a bottom feeder

432   (Miles, 1971; Denison, 1978).

433   *Dinomylostoma.*— *Dinomylostoma* sp. is known from eight specimens (UMMP 3046, UMMP

434   12974, UMMP 13042, UMMP 13056, UMMP 13148, UMMP 13041, and UMMP 16158) from

435   the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport

436   State Park, Alpena County (Dorr and Eschman, 1970). While the reported specimens of this

437   fish are currently missing from museum collections, one of these (the specimen number was not

438   specified) was figured in Dorr and Eschman (1970) and appears to have been accurately

439   identified.

440   *Mylostoma.*—*Mylostoma* sp. was previously known in Michigan from one specimen

441   (UMMP 13612) from the Rockport Quarry Limestone at the abandoned Kelly Island

442   Limestone Quarry at Rockport State Park, Alpena County (Dorr and Eschman, 1970). As with

443   many of the other specimens examined by Dorr and Eschman (1970), this specimen was not

444   figured, and cannot be located in the museum collections, even before the recent move of the

445   UMMP collections. In the last few years, J.S. has recovered 39 specimens of small to

446   medium-sized arthrodires that appear to be from *Mylostoma* sp. from the Four Mile Dam

447   Formation of the Betsie Bay Rockpiles, in Elberta, Benzie County, three specimens from the

448   Alpena Limestone Formation at the Besser Museum Fossil Park in Alpena (BV3, BV6, and

449   BV7), and one specimen from the Rockport Quarry Limestone at the abandoned Kelly Island

450   Limestone Quarry at Rockport State Park, Alpena County (15M). These are now deposited in

451   the MHM as per the permitting procedure for public lands in Michigan, awaiting transfer to

452   the UMMP. The above specimens resemble *Mylostoma* in having a thick, rounded median

453   dorsal plate and in lacking ornamentation on the surface of the armor plates (Denison, 1978;

454   Fig. 5(B)). These specimens are usually partially articulated, which is uncommon for

455   placoderm remains from Michigan, and remains of ventral and head shields are also known.

456   However, positive identification as *Mylostoma* sp. must await the recovery of gnathal plates

457   (Denison, 1978; personal observation). The size of most of these new specimens suggests that

458   they are most likely juveniles, an inference supported by the coincident collection of a

459   relatively large, poorly preserved specimen (2M) from Four Mile Dam with similar

460   morphology and lack of tubercles (personal observation). If this identification is correct,

461   *Mylostoma* sp. is currently represented by more specimens than any other fish from the

462   Devonian Michigan.

463   *Dunkleosteus.— Dunkleosteus* sp. is known from one specimen of a partial impression of a

464   suborbital plate (UMMP 15432) from the Antrim Shale of Squaw Bay, 6.4 kilometers south

465   of Alpena, one specimen of a supragnathal (UMMP 16152) from the Alpena Limestone of the

466   Alkali Quarry of Alpena, one specimen of an incomplete anterior ventrolateral plate (UMMP

467   16156; Fig. 4C) from the Rockport Quarry Limestone at the abandoned Kelly Island

468   Limestone Quarry at Rockport State Park, Alpena County and one specimen (VP.517) from

469   an undetermined site in Alpena (Dorr and Eschman, 1970). These specimens are generally

470   isolated plates, and are not usually articulated. Dorr and Eschman (1970) originally referred to

471   these specimens as *Dinichthys sp.* Newberry 1868, but this genus has since been synonymized

472   with *Dunkleosteus*, with the exception of a single species from the Famennian Huron Shale

473   Member of the Ohio Shale Formation (Carr and Hlavin, 2010). Although these specimens are

474   incomplete, the difference in age between the Michigan specimens and *Dinichthys herzeri*,

475   along with the resemblance they bear to more complete specimens of *Dunkleosteus* described

476   by Carr and Hlavin (2010), strongly indicates that they should be attributed to *Dunkleosteus*

477   *sp*.

478   *Aspidichthys clavatus.— A. clavatus* is known from a single specimen (UMMP 3127) from

479   the Antrim Shale of the shore of Grand Traverse Bay near Norwood, Charlevoix County (Dorr

480   and Eschman, 1970). As above, the reported specimen is missing from museum collections

481   and was not figured, so this identification may not be reliable.

482   *Diplognathus lafargei.— D. lafargei* is known from the Late Devonian of Michigan (Carr

483   and Jackson, 2005). Unfortunately, the recent flooding of Paxton Quarry means that the lens

484   that produced the holotype of *D. lafargei* is no longer accessible (R.L. Carr pers. comm.

485   2018). *D. lafargei* is currently known from an incomplete, disarticulated specimen (CMNH

486   50215) found in a talus slope in Paxton Quarry (Lafarge North America, Inc., Alpena Cement

487   Plant, Great Lakes Region), Alpena (Carr and Jackson, 2005). This specimen includes the

488   suborbital and anterior superognathal plates, along with the right inferognathal, posterior

489   supragnathal, and posterior ventrolateral (Carr and Jackson, 2005).

490   *Trachosteus clarki.*—?*T. clarki* is known from a single specimen (UMMP 18206) of a

491   infragnathal plate that was found from the Antrim Shale Formation 1.6 kilometers north of

492   Norwood, Charlevoix County (Dorr and Eschman, 1970; Fig. 7). This specimen was

493   designated as uncertain by Dorr and Eschman (1970), most likely because *T. clarki* is known

494   solely from a disarticulated and incomplete headshield from the Cleveland shale (Denison,

495   1978). UMMP 18206 resembles the infragnathal of *T. clarki* in having a low blade and sharp

496   teeth on the biting edge, but there is not enough information available on this fish for this

497   identification to be certain (Denison, 1978).

498

499   Petalichthyida

500

501   *Macropetalichthys.*—?*Macropetalichthys* sp. is known from a specimen of a spinal and

502   anterior ventrolateral plate (UMMP 14320) from the Middle Devonian of the Dundee

503   Limestone near Trenton (Fig. 3B), a partial headshield (32M; Fig. 8A) from the Four Mile

504   Dam Formation of the Betsie Bay Rockpiles, in Elberta, Benzie County, and from partially

505   articulated plates from the anterior portion of the headshield (BV 4; Fig. 8B) from the Alpena

506   Limestone formation at the Besser Museum Fossil Park in Alpena (Dorr and Eschman, 1970;

507   personal observation). UMMP 14320 was identified by Dorr and Eschman (1970) as

508   *Arctolepis* sp. Eastman, 1908 based on its elongated spinal plates ornamented with small

509   spines. However, this specimen (Fig. 3B; UMMP 14320) much more closely resembles

510   *Macropetalichthys* because the spinal plate is not as recurved as those in *Arctolepis*, the spines

511   on this spinal plate are more numerous and tightly spaced than those in *Arctolepis*, and because

512   its spines are present on the outer edge of the spinal plate (unlike *Arctolepis*, where the spines

513   are present on the interior edge of the spinal plate) (Denison, 1978; Janvier, 2003; personal

514   observation). Unfortunately, the specimen does not retain any of the diagnostic features of the

515   genus, so we can only tentatively reattribute it (Eastman, 1907; Denison, 1978). Whatever the

516   case, *Macropetalichthys* is already known from several localities in North America, including

517   the Delaware and Columbus limestone of Ohio, which were closely associated with Michigan

518   during the Middle Devonian (Eastman, 1907; Denison, 1978; Martin, 2002). *Arctolepis*,

519   however, is otherwise restricted to the Early Devonian of Spitsbergen (Denison, 1978). The

520   anatomical, temporal, and geographical evidence therefore indicates that UMMP 14320 is far

521   more likely to be from *Macropetalichthys* than *Arctolepis* (personal observation). The rounded

522   anterior portion of the indentation of the headshield in 32M strongly resembles the narrow,

523   rounded rostral plate in the headshield of *Macropetalichthys* in shape (Eastman, 1897b;

524   Denison, 1978; Fig. 8A). This specimen also resembles *Macropetalichthys* in bearing sparse,

525   irregularly arranged tubercles (Denison, 1978; Martin, 2002; Fig. 8A). Similarly, the shape of

526   the plates present in BV 4 also strongly resembles the anterior portion of the headshield of

527   *Macropetalichthys* (Eastman, 1897b; Denison, 1978; Martin, 2002; Fig. 8B). In particular, one

528   of the plates (labeled R in Fig. 8B) looks very similar to the rounded, blunt rostral plate seen in

529   *Macropetalichthys* (Denison, 1978). Despite the strong similarity in shape between these

530   specimens and *Macropetalichthys*, neither of these specimens are complete enough to make

531   their attribution to *Macropetalichthys* definitive.

532

533   Ptyctodontida
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536   *Ptyctodus.*— Specimens of *Ptyctodus* sp., consisting of isolated tooth plates, have been found

537   in the Dundee Limestone near Trenton, Wayne County (UMMP 14321), the Bell Shale of

538   Rogers City, Presque Isle County (UMMP 14460), the Thunder Bay Limestone of the bluffs on

539   the northeast shore of Partridge Point, 6.4 kilometers south of Alpena, Alpena County (UMMP

540   3023), the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at

541   Rockport State Park, Alpena County (UMMP 13045), the Alpena Limestone of Alkali Quarry,

542   Alpena (UMMP 16157), the Potter Farm Formation (uncertain) of "old Wamer's Brickyard"

543   southwest of Alpena (UMMP 21718), and the Potter Farm Formation of the west edge of

544   Alpena Cemetery, Alpena (UMMP 21817; Dorr and Eschman, 1970). Other single specimens

545 of *Ptyctodus* are recorded from an unknown formation in Afton Quarry, Cheboygan County

546 (VP.489) and the Traverse Group (unknown formation) of Emmet County (UMMP 14712)

547 (Dorr and Eschman, 1970). While many of these specimens have gone missing since 1970,

548 those figured (specimen numbers not specified) in Dorr and Eschman (1970) suggest their

549 attribution is accurate (personal observation). There are also reports of other ptyctodont

550 remains, including isolated gnathal plates and articulated specimens, from the Antrim Shale

551 (Elliott et al., 2000). However, it is not clear if the specimens this report is based upon are

552 deposited in museum collections, so they cannot currently be verified. The widespread

553 distribution of *Ptyctodus* fossils may be due to both the higher preservation potential of hard

554 tooth plates and/or association with abundant shelly invertebrates. Relatively poor taxonomic

555 knowledge of *Ptyctodus*, a wastebin taxon widely applied to various ptyctodont teeth, may also

556 be a contributing factor (Denison, 1978). In general, ptyctodont tooth plates are common, but

557 articulated remains are not (Denison, 1978; Trinajstic and Long, 2009). Therefore, tooth plates

558 form the basis for the majority of ptyctodontid taxa, including *Ptyctodus* (Denison, 1978;

559 Trinajstic and Long, 2009). Further taxonomic work on existing specimens, and on North

560 American ptyctodonts in general, is required to determine if the specimens from Michigan all

561 originate from the same genus.

562 *Eczematolepis*.— ?*Eczematolepis* sp. is known from a single partial armor plate from

563 (UMMP 4169) from the Genshaw formation, near Posen, Presque Isle County (Dorr and

564 Eschman, 1970; Fig. 9). UMMP 4169 was identified as *Bothriolepis* sp. by Dorr and Eschman

565 (1970), however we attribute this plate to ?*Eczematolepis* sp. because its ornamentation of

566 crowded, irregularly arranged, tubercles more closely resembles *Eczematolepis* (Denison,

567   1978; Martin, 2002; J.L. pers. comm.). Also, the shape of this plate does not resemble what is

568   seen in *Bothriolepis* (J.L. pers. comm). This specimen is not complete enough to make an exact

569   identification, so we designate it as uncertain. Besides this specimen, Dorr and Eschman

570   (1970) identified a large supragnathal plate (UMMP 14374; Fig. 10) from an unknown

571   formation in the Traverse Group of a locality in Alpena, Alpena County as *Eczematolepis* sp..

572   The locality this specimen was recovered from is referred to by Dorr and Eschman (1970) as

573   "Locality 650 of the Winchell Survey", but no other information is available on its geological

574   context. While this specimen appears to the supragnathal of a ptyctodont, *Eczematolepis* is

575   known only from head or body plates (Denison, 1978). Furthermore, there is uncertainty

576   surrounding whether or not *Eczematolepis* is a ptyctodont (Denison, 1978; J.L. pers comm.).

577   Therefore, although this specimen can be concretely identified as a ptyctodont, it cannot be

578   attributed to *Eczematolepis*. A general lack of taxonomic information for ptyctodonts from the

579   Eifelian of North America means that this specimen cannot be identified at a finer taxonomic

580   level at this point in time (Martin, 2002).

581
582   'Acanthodii'
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584
585   *Gyracanthus*.— *Gyracanthus* sp. is known from one specimen (UMMP 1329) from the

586   Gravel Point Formation of South Point (Gravel Point), Little Traverse Bay, Charlevoix

587   County (Dorr and Eschman, 1970). This specimen is currently missing from the UMMP and

588   was not figured by Dorr and Eschman (1970). This spine-based identification is therefore not

589   verifiable, particularly as Devonian specimens of this widespread Carboniferous genus are

590   dubious and in need of re-examination (Turner et al., 2005).

591   *Machaeracanthus.— Machaeracanthus* sp. is reported from one specimen (UMMP 3521)

592   from the Dundee Limestone of Monroe County, two specimens (UMMP 26111 and UMMP

593   26112) from the Dundee Limestone of Sibley Quarry, Wyandotte, Wayne County, one

594   specimen (UMMP 13047) of uncertain status from the Rockport Quarry Limestone at the

595   abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, and two

596   specimens (UMMP 47691 and UMMP 47692) from the Newton Creek Limestone at Onaway

597   Stone Quarry, Presque Isle County (Dorr and Eschman, 1970, personal observation; Fig. 11).

598   The specimen from the Rockport Quarry Limestone (UMMP 13047) was identified as *A.*

599   *gracillimus* by Dorr and Eschman (1970), but an examination of the specimen demonstrated

600   significant differences in the structure of this spine compared to what is known from *A.*

601   *gracillimus* (Maisey, 1983). This spine is long and thick with a smooth surface, and therefore

602   much more closely resembles the spines of *Machaeracanthus* (Denison, 1979; Maisey, 1983;

603   Fig. 11B). As shown by the specimen list (available in the supplemental files),

604   *Machaeracanthus* is relatively common in the Middle Devonian of Michigan and closely

605   associated areas (Eastman, 1907; Wells, 1944; Dorr and Eschman, 1970; Denison, 1978). In

606   contrast, *A. gracillimus* is known only from the Carboniferous of Iowa in North America,

607   after a major mass extinction event (Wellburn, 1901; Zangerl, 1981; Maisey, 1983; Itano et

608   al., 2003; Elliott et al., 2004; Brusatte, 2007; Sallan and Coates, 2010).

609   *Oracanthus.— Oracanthus* sp. is known from a fin spine (UMMP 23495) from the Norway

610   Point Formation of the Four Mile Dam, about 5.6 kilometers northwest of Alpena, Alpena

611   County (Dorr and Eschman, 1970). As above, this specimen was unfigured by Dorr and

612   Eschman (1970) and it is missing, so we cannot verify its identity.

613

614 Chondrichthyes
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617 *Acondylacanthus.*— A fin spine specimen of *A. gracillimus* (UMMP 26523) was collected

618 from the Dundee Limestone of Sibley Quarry, Wyandotte, Wayne County, (Dorr and Eschman,

619 1970). This specimen is now missing from the UMMP, so we cannot determine if this

620 identification is reliable or if it was misidentified in the same way as UMMP 13047. This

621 would be the earliest reported specimen of *Acondylacanthus* by far; other occurrences are

622 clustered in the Carboniferous of the U.S. and the U.K. (Wellburn, 1901; Maisey, 1983; Itano

623 et al., 2003; Elliott et al., 2004; Brusatte, 2007).

624 *Tamiobatis.*— ?*Tamiobatis* sp. is a small chondrichthyan reported from one specimen

625 (UMMP 13147) of a fin spine from the Rockport Quarry Limestone at the abandoned Kelly

626 Island Limestone Quarry at Rockport State Park, Alpena County (Dorr and Eschman, 1970;

627 Fig. 4D). Dorr and Eschman (1970) identified this spine as *Ctenacanthus* Agassiz 1835, but

628 comparisons of this specimen with more recent descriptive work disputes this attribution

629 (Maisey, 1982; Williams, 1998). This specimen more closely resembles a fin spine

630 impression from *Tambiobatis* from the Cleveland Shale (Williams, 1998). More complete

631 material from Michigan is needed to make a concrete diagnosis, so this assignment is

632 designated as uncertain.

633
634
635 Onychodontiformes
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639   *Onychodus.— Onychodus* is found in several parts of Michigan's geological column

640   (Dorr and Eschman, 1970), including the Dundee Limestone of London Township, Monroe

641   County (UMMP 22006; Fig. 3A), Sibley Quarry, Wyandotte, Wayne County (UMMP 26113) as

642   well as an uncertain specimen from the Gravel Point Formation of the shore of the Little

643   Traverse Bay, Charlevoix County (UMMP 14370) (Dorr and Eschman, 1970). UMMP 22006

644   was identified to the species level, *O. sigmoides* (Dorr and Eschman, 1970). In most cases, the

645   genus is represented solely by its large distinctive tooth whorls, with the exception of one lower

646   jaw (UMMP 26113; Dorr and Eschman, 1970).

647

648   Dipnoi
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651   *Chirodipterus onawayensis.— C. onawayensis* is the only lungfish known from the

652   Devonian of Michigan, and thus far is represented by a single specimen which was preserved

653   well enough to allow diagnosis as a new species (Schultze, 1982; Long, 1995). The holotype of

654   *C. onawayensis* represents the left side of the skull and jaws, and was collected from the

655   Onaway Stone Quarry, which is north of Onaway in Presque Isle County (Schultze, 1982; Fig.

656   12). This specimen was unnumbered at the GLAPM and appears to be missing (Schultze,

657   1982). It is similar to *Chirodipterus australis* Miles, 1977 from Gogo in Australia, and

658   possesses the powerful jaws typical of a durophagous Devonian lungfish (Schultze, 1982;

659   Long, 2011).

660
661
662   **DISCUSSION**
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665   Despite proximity to major research institutions and collections, the rich reef and

666   nearshore faunas of the Middle Devonian of North America have been neglected in recent

667   decades, particularly relative to similarly-aged localities in even more remote areas of

668   Antarctica, Australia, and Morocco (Gardiner, 1984; Derycke et al., 1995; Blieck and

669   Lelievre, 1995; Elliott et al., 2000; Janvier, 2003; Rücklin, 2010; Sallan and Coates, 2010;

670   Friedman and Sallan, 2012). There are significant gaps in the total Devonian record in

671   Michigan, with vertebrates in some intervals, particularly the Late Devonian, poorly

672   represented and deficient in number relative to similarly-aged horizons in Ohio (Dorr and

673   Eschman, 1970; Carr and Jackson, 2008). Complicating matters, a large proportion of

674   previously published and catalogued specimens could not be located in the paleontological

675   collections at the University of Michigan, leaving only brief and incomplete documentation

676   as proof of their existence (Dorr and Eschman, 1970). In addition, a large number of more

677   recently recovered specimens are resident in amateur collections - the result of a lack of

678   professional efforts in the state in recent decades - and cannot be used for scientific

679   purposes.

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

681   richer in diversity and sheer number of fish specimens than previously thought. This has

682   revealed several previously unreported but likely significant biogeographical and diversity

683   patterns, including a shift in environment and faunas between the Middle and Late Devonian

684   and greater connections to nearby basins. In addition, new localities have produced co-

685   occurring, well-preserved articulated vertebrate and invertebrate material, a rarity in the

686   Paleozoic record outside Michigan.

687   There is a definite shift in fish diversity, geologic range, and number between the Middle and

688   Late Devonian deposits of Michigan. Placoderms, acanthodians, dipnoans, onychodonts and

689   sharks are found in fair numbers in the primarily nearshore settings of the Middle Devonian

690   (Dorr and Eschman, 1970; Fig. 13A). This record includes 16 confirmed genera of fishes from

691   201 reported specimens sourced from 11 separate formations (Dorr and Eschman, 1970;

692   personal observation). In contrast, fish fossils from Late Devonian pelagic settings come from

693   just four confirmed genera, all arthrodiran or ptyctodont placoderms, in the Antrim Shale

694   formation (Dorr and Eschman, 1970, Carr and Jackson, 2005; Fig. 13B). Reports from Elliott

695   et al. (2000) indicates that there may be a greater diversity of vertebrates present in the Antrim

696   Shale than what is represented in museum collections (Dorr and Eschman, 1970; personal

697   observation). Even if these reports are confirmed it is still considerably less diverse and

698   abundant than what is observed in Middle Devonian deposits. A similar change is seen in the

699   invertebrate fauna; a thriving reef and nearshore fauna hosting a multitude of life, including

700   crinoids, trilobites, bryozoans, corals, blastoids, brachiopods, cephalopods, gastropods and

701   stromatoporoids in the Middle Devonian is succeeded by scattered fossils of brachiopods and

702   cephalopods further offshore in the Late Devonian (Dorr and Eschman, 1970; Ehlers and

703   Kesling, 1970; Hannibal et al., 1992; Carr pers. comm. 2014).

704   The contrast between the Middle and Late Devonian vertebrate and invertebrate faunas in

705   Michigan is due to differences in collection intensity, rock exposure, and environmental

706   representation. There are at least a dozen well-documented Middle Devonian localities from

707   Michigan that have been the focus of both professional and amateur collectors (Dorr and

708   Eschman, 1970; personal observation). These localities preserve a wide variety of habitats

709   (mostly near-shore, reef habitats) and have a large amount of exposed rock (especially in

710   limestone quarries) (Ehlers and Kesling, 1970; personal observation). In contrast, the Late

711   Devonian of Michigan is represented by four localities from a single, black shale heavy

712   formation that have comparatively little rock exposed (Ehlers and Kesling, 1970). Furthermore,

713   Ehlers and Kesling (1970) argued that an abundant vertebrate fauna is unlikely to be recovered

714   from the Antrim Shale because of the hardness of the concretions from this formation and the

715   rarity of vertebrate specimens within them. It is therefore unlikely that the small amount of

716   attention Late Devonian localities have received from amateur collectors is the driving factor

717   behind the observed drop in the diversity and abundance of vertebrates. It is notable that the

718   Antrim Shale was deposited in an open water pelagic habitat with little to no benthic community

719   (Gutshick and Sandberg, 1991). None of the localities from the Middle Devonian of Michigan

720   preserve this kind of habitat (Ehlers and Kesling, 1970). This difference in environment between

721   the Middle and Late Devonian deposits is most likely a major factor contributing to the observed

722   shift in the diversity of the vertebrate and invertebrate faunas.

723   Re-examination of Michigan's Devonian fossils sheds some light on biogeographic and

724   dispersal patterns for North American fishes of this age. A complete absence of endemic taxa

725   at the genus level within Michigan suggests that there were few barriers to dispersal with other

726   parts of the mid-continental region of the Old Red Sandstone Continent during the Middle

727   Devonian (Newberry, 1889; Dorr and Eschman, 1970; Denison, 1978; Markus, 1998; Palmer,

728   1999; Warren et al., 2000; Elliott et al., 2000; Thomson and Thomas, 2001; Sepkoski, 2002;

729   Johanson et al., 2007; Carr and Jackson, 2008; Carr and Hlavin, 2010). However, it is possible

730   that the aforementioned lack of taxonomic work and collection effort has resulted in the

731   incorrect attribution of distinct species from Michigan to taxa from the wider region.

732   Regardless, the types of fish found in the Devonian sediments of Michigan are fairly typical

733   for the eastern United States (Newberry, 1873; Cluff, 1980).

734   Michigan's fish fauna shares characteristics with several similarly-aged faunas from the

735   Middle Devonian of North America. Michigan's Middle Devonian vertebrate fauna is closest in

736   composition to the similarly aged Delaware and Columbus Formations of central Ohio, with

737   which it shares many taxa, including *Machaeracanthus*, *Gyracanthus*, *Holonema*,

738   *Macropetalichthys, Protitanichthys*, *Onychodus*, *Dunkleosteus*, *Ptyctodus*, and *Eczematolepis*

739   (Eastman, 1907; Westgate and Fischer, 1933; Wells, 1944; Dorr and Eschman, 1970; Denison,

740   1978; Martin, 2002). This suggests that the parts of Michigan and Ohio that these deposits

741   represent were closely connected during this period of time, yet the preservational mode was

742   quite different. Many of the described fish remains from the Delaware and Columbus limestones

743   are very small and worn, concentrated into bone beds where vertebrate remains are more

744   common than macroscopic invertebrate fossils (Westgate and Fisher, 1933; Wells, 1944). This is

745   very different than Michigan, where fish remains are generally large to medium size pieces of

746   armor or spines that are usually unworn (personal observation). However, Martin (2002)

747   describes the remains of more complete specimens of placoderms (petalichthyids and

748   ptyctodonts) and onychodonts from other, lesser known sections of the Delaware and Columbus

749   limestones, indicating that some beds are more similar to Michigan in preservation and

750   assemblage composition.

751   The Middle Devonian fish fauna of Michigan is also similar to the vertebrate fauna known

752   from the Onondaga Limestone of New York (Eifelian, Upper Ulsterian), which has a similar

753   environment to and is comparable in age to the Dundee Limestone (Brett and Ver Straeten, 1994;

754   Brett et al., 2011). Indeed, the Onondaga Limestone shares all but one of the taxa found in the

755   Dundee Limestone, including *Ptyctodus*, *Machaeracanthus*, *Onychodus*, *Eczematolepis*, and

756   *Macropetalichthys* (Eastman, 1907; Dorr and Eschman, 1970; Denison, 1978). A larger number

757   of vertebrate taxa have been reported from the Onondaga Limestone, although this might be an

758   artifact of the lesser number of outcrops of this age in Michigan and a lack of collecting effort at

759   said outcrops, rather than reflective of real differences in diversity (Eastman, 1907; Dorr and

760   Eschman, 1970; Denison, 1978).

761   The correlation between the vertebrate faunas of Michigan and New York continues into the

762   Givetian (Erian). The rocks of the Traverse Group in Michigan and the Hamilton Group of New

763   York are similar in age and share two vertebrate taxa, *Machaeracanthus* and *Dunkleosteus*

764   (Eastman, 1907; Dorr and Eschman, 1970; Denison, 1978; Brett and Ver Straeten, 1994). This is

765   despite an environmental shift that caused major changes in sedimentation, paleoecology, faunas,

766   and basin geometry that occurred in the transition between the Onondaga Limestone and the

767   Hamilton Group (Ver Straeten et al., 1994). This shift had a major effect on the invertebrate

768   fauna of the region, causing extinctions of some of the endemic Onondaga faunas (Ver Straeten

769   et al., 1994). While it is not clear what effect this shift had on the vertebrate fauna of New York,

770   it is evident that a close connection between the fish faunas of Michigan and New York

771   continued from the Eifelian (Ulsterian) into the Givetian (Erian).

772   The documented loss in the amount and diversity of fossil material in the Late Devonian of

773   Michigan makes detailed comparison with other Late Devonian faunas difficult. However, the

774   vertebrate genera found in the Late Devonian of Michigan, *D. lafargei*, ?*T. clarki*, ptyctodonts,

775   *A. clavatus*, and *Dunkleosteus,* are also found in open ocean sediments of the Late Devonian

776   Cleveland Shale (Newberry, 1889; Winston and Walker, 1956; Dorr and Eschman, 1970;

777   Denison, 1978; Carr and Jackson, 2008). The Cleveland Shale has been the focus of intense

778   collecting efforts for the past 150 years and has outcrops both within a major metropolitan area

779 and on the path of a major highway, while very little collecting has been conducted in the

780 relatively remote, low abundance, and difficult-to-sample Antrim Shale (Hlavin; 1976). In

781 contrast, the Cleveland Member of the Ohio Shale is a Konservat-Lagerstätten, and is

782 considered one of the most diverse vertebrate faunas from the Devonian (Carr and Jackson,

783 2008). Therefore, the gap in the diversity and number of fish specimens between the Late

784 Devonian of Michigan and the Late Devonian of Ohio is probably largely the result of the

785 differences in preservation between these sites, along with a lack of organized collection effort

786 in Michigan's Late Devonian sediments by both professionals and amateurs.

787 A notable occurrence, or non-occurrence, in the Middle Devonian fish fauna of Michigan is

788 a complete lack of antiarch placoderms (Dorr and Eschman, 1970). Additional benthic,

789 nearshore forms, such as gyracanthids and ptyctodonts, are also poorly represented relative to

790 other kinds of fishes (such as arthrodires) in Michigan's sediments. The relative absence of

791 benthic-associated fishes contrasts greatly with the large amount of benthic invertebrate

792 material at vertebrate-bearing localities, which indicates that preservation of the sea floor is

793 not the issue. It is possible that the rarity of antiarchs is purely the product of a lack of

794 collection effort outside of a handful of sites. However, it appears that antiarchs are also

795 uncommon in other Middle Devonian sites that are closely related to deposits of the same age

796 in Michigan (Eastman, 1907; Westgate and Fisher, 1933; Wells, 1944). This is despite the fact

797 that antiarchs have been recovered from nearshore marine and estuarine settings elsewhere,

798 such as the famous marine tetrapod assemblage, Andryevka-2 (Sallan and Coates, 2010;

799 Friedman and Sallan, 2012).

800 Another interesting aspect of the vertebrate record from the Middle Devonian of Michigan

801   is the occurrence of partially articulated vertebrate material preserved alongside invertebrate

802   remains not only in the same formations, but in the same rocks (Fig. 5D). This pattern is

803   consistent in several separate formations and sites. It is rare to find articulated fish remains,

804   rather than ichthyoliths like teeth, directly associated with complete invertebrate remains,

805   especially articulated crinoids, in the Middle Paleozoic (personal observation; Sallan et al.,

806   2011). This direct association can be used to concretely determine which invertebrate taxa

807   lived directly alongside vertebrates, potentially shedding light on the interactions and

808   associations between these groups.

809   Much more fieldwork is required to fully understand the Devonian vertebrate fauna from

810   Michigan. Recent efforts have revealed a surprising number of new occurrences of fishes in

811   geological formations where they were previously considered absent. *P. rockportensis* was

812   once thought to be restricted to the Rockport Quarry Limestone, but has now been

813   documented from the Four Mile Dam Formation and possibly the Alpena Limestone

814   Formation (Dorr and Eschman, 1970; personal observation). *Mylostoma* sp. was previously

815   only known from an isolated specimen (UMMP 13612) from the Rockport Quarry Limestone,

816   but it is now also known from large numbers of recently collected specimens from the Four

817   Mile Dam Formation and several specimens (BV3, BV6, and BV7) from the Alpena

818   Limestone Formation (Dorr and Eschman, 1970). Additionally, fish fossils had previously

819   never been documented from the Four Mile Dam Formation (personal observation; Dorr and

820   Eschman, 1970). These findings, which are a result of intensified collecting from a handful of

821   the vertebrate-bearing Middle Devonian localities in Michigan, show that these long-neglected

822   localities are still productive. Further collecting at sites that have been ignored for decades

823   will almost certainly lead to more discoveries. Renewed search efforts will create a less biased

824   understanding of the Late Devonian fish fauna of Michigan, allowing more accurate

825   comparisons to other Late Devonian faunas to be made and the ecology and biogeography of

826   Devonian marine fishes to be more completely known.

827

828   **CONCLUSIONS**
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831   Novel information about the ecology, diversity, and number of the fishes from the

832   Devonian of Michigan has been revealed by new surveys of old material and from new

833   specimens obtained through recent collecting efforts. These include many previously

834   unrecognized patterns, such as dramatic losses in vertebrate diversity between the Middle and

835   Late Devonian that are likely due to the differences in rock exposure and environmental

836   representation between these time periods. We have also documented strong connections with

837   other North American pelagic faunas, and the exceptional occurrence of partially-articulated

838   fishes preserved alongside benthic invertebrates. These discoveries show that there is still a lot of

839   work to be done in Michigan's vertebrate-bearing Devonian sediments, with implications for our

840   understanding of Devonian fish faunas as a whole.

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Figure Captions

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1097   Figure 1: Stratigraphy of the Devonian deposits of the northern part of the Lower Peninsula of

1098   Michigan. Figure modified from Elliott et al. (2000), Figure 3.

1099   Figure 2: Chart showing the correlation between international and North American Devonian

1100   stage names. Figure modified from Swezey (2002). U.S. Geological Survey.

1101   Figure 3: Vertebrate remains from the Dundee Limestone Formation. (A), a large tooth from *O.*

1102   *sigmoides*, from the Dundee Limestone of London Township, Monroe County, UMMP 22006.

1103   Scale bar equals 1 cm. (B), a spinal and anterior ventrolateral plate from ?*Macropetalichthys*

1104   sp. (previously identified as *Arctolepis* sp.), from the Dundee Limestone near Trenton, UMMP

1105   14320. Abbreviations: Sp, spinal; Spi, spines of the spinal plate; Avl, anterior ventrolateral.

1106   Scale bar equals 1 cm.

1107   Figure 4: Vertebrate remains from the Rockport Quarry Limestone Formation. (A), a partial

1108   skull roof from *Holonema* sp., from the Rockport Quarry Limestone at the abandoned Kelly

1109   Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 12991.

1110   Abbreviations: Nu, Nuchal; PNu, Paranuchal; C, Central Plate. Scale bar equals 2 cm. (B), The

1111   remains of an unidentified placoderm from the Rockport Quarry Limestone at the abandoned

1112   Kelly Island Limestone Quarry at Rockport State Park, Alpena County, 7M, Michigan History

1113   Museum. Scale bar equals 1 cm. (C), an incomplete right anterior ventrolateral from

1114   *Dunkleosteus* sp., from the from the Rockport Quarry Limestone of Rockport Quarry, Alpena

1115   County, UMMP 16156. Scale bar equals 2 cm. (D), a small spine from ?*Tamiobatis* sp.

1116   (previously identified as *Ctenacanthus* sp.) from the Rockport Quarry Limestone at the

1117   abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP

1118   13147. Scale bar equals 1 cm.

1119   Figure 5: Vertebrate remains from the Four Mile Dam Formation. (A), a broken spine from an

1120   unidentified acanthodian, from the Four Mile Dam Formation of the Betsie Bay Rockpiles,

1121   Elberta, Benzie County, JS 121, Michigan History Museum. Scale bar equals 0.5 cm. (B), a

1122   flattened specimen of a trunk shield from ?*Mylostoma* sp., from the Four Mile Dam Formation

1123   of the Betsie Bay Rockpiles, Elberta, Benzie County, 21M. Abbreviations: MD, Median

1124   dorsal; ADL, Anterior dorsolateral; Nu, Nuchal. Scale bar equals 1 cm. (C), a partial armor

1125   plate from an unidentified placoderm, from the Four Mile Dam Formation of the Betsie Bay

1126   Rockpiles, Elberta, Benzie County, JS 4, Michigan History Museum. Scale bar equals 1 cm.

1127   (D), a piece of limestone containing both crinoid heads and an armor plate from ?*Mylostoma*

1128   sp. from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County,

1129   9M, Michigan History Museum. This specimen is an example of the association between

1130   vertebrates and invertebrates in the Middle Devonian deposits of Michigan. The solid arrow

1131   indicates the armor plate and the dashed arrow indicates a crinoid head. Scale bar equals 1 cm.

1132   Figure 6: Specimens of *Protitanichthys rockportensis,* an arthrodire that is common in the

1133   Middle Devonian sediments of Michigan. (A), a photograph of an impression of the head of the

1134   holotype, from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone

1135   Quarry at Rockport State Park, Alpena County, UMMP 12980. Scale bar equals 2 cm. (B), a

1136   specimen drawing of UMMP 12980 (redrawn and modified from Case (1931: Figure 1).

1137   Dotted lines represent missing plate boundaries and dashed lines represent sensory grooves.

1138   (C), an incomplete nuchal and left paranuchal plate, from the Rockport Quarry Limestone at

1139   the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP

1140   2981. Scale bar equals 1 cm. (D), a partial headshield, most likely from a juvenile, from the

1141   Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State

1142   Park, Alpena County, 4M, Michigan History Museum. Scale bar equals 1 cm.

1143   Figure 7: An inferognathal from the Late Devonian arthrodire ?*Trachosteus clarki* from the

1144   Antrim Shale. Specimen recovered 1.6 km north of Norwood, MI. UMMP 18206. Scale bar

1145   equals 1 cm.

1146   Figure 8: Newly discovered specimens of ?*Macropetalichthys* sp. (A) a partially complete

1147   headshield from ?*Macropetalichthys* sp. Specimen found in the Four Mile Dam Formation of

1148   the Betsie Bay Rockpiles, Elberta, Benzie County. Abbreviations: Hd, Head Shield

1149   (incomplete), Un, Unidentified Armor Plate, R, Rostral Plate?. Scale bar equals 2 cm. 32M,

1150   Michigan History Museum. (B) crushed and partially articulated pieces of armor from the

1151   anterior portion of the headshield of ?*Macropetalichthys* sp.. Specimen found in the Alpena

1152   Limestone Formation at the Besser Museum Fossil Park, Alpena. BV 4, Michigan History

1153   Museum. Abbreviations: PrO, Preorbital; R, Rostral. Scale bar equals 1 cm.

1154   Figure 9: An incomplete armor plate from *Eczematolepis* sp. Specimen from the Genshaw

1155   Formation. Found near Posen, MI. UMMP 4169. Scale bar equals 1 cm.

1156   Figure 10: A supragnathal plate from an unknown ptyctodont from the Traverse Group.

1157   Specimen recovered from an unknown locality referred to as "Locality 650 of the Winchell

1158   Survey", in Alpena, Alpena County, MI. UMMP 14374. Scale bar equals 1 cm.

1159   Figure 11: Specimens of the acanthodian *Machaeracanthus* sp. (A), a large spine from

1160   *Machaeracanthus* sp., from the Dundee Limestone of London Township, Monroe County,

1161   UMMP 3521. Scale bar equals 1 cm. (B), a spine from ?*Machaeracanthus* sp. (originally

1162   identified as *A. gracillimus*), from the Rockport Quarry Limestone at the abandoned Kelly

1163   Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 13047. Scale bar

1164   equals 1 cm.

1165   Figure 12: The skull of *Chirodipterus onawayensis*. Specimen recovered from from the Newton

1166   Creek Limestone of Onaway Stone Quarry, north of Onaway, Presque Isle County. Specimen

1167   photo from Schultze (1982), Figure 2, modified and reprinted with permission of Taylor and

1168   Francis Ltd, http://www.tandfonline.com. This specimen is reported to be unnumbered at the

1169   Great Lakes Area Paleontological Museum, but is missing. Scale bar equals 1 cm.

1170   Figure 13: A representation of fish faunas from the Devonian of Michigan. Animals not to

1171   scale. Drawing by L.S. (A) The vertebrate fauna from the Middle Devonian of Michigan. (1)

1172   *Acondylacanthu*s (Chondrichthyes); (2), *Dinomylostoma* (Arthrodira; 'Placodermi'); (3),

1173   *Chirodipterus* (Dipnoi; Sarcopterygii); (4), *Dunkleosteus* (Arthrodira; 'Placodermi'); (5),

1174   *Onychodus* (Onychodontida; Sarcopterygii); (6), *Mylostoma* (Arthrodira; 'Placodermi'); (7),

1175   *Protitianichthys* (Arthrodira; 'Placodermi'); (8), *Oracanthus* (Acanthodida; 'Acanthodii'); (9),

1176   *Machaeracanthus* (Ischnacanthida; 'Acanthodii'); (10), *Gyracanthus* (Gyracanthida;

1177   'Acanthodii'); (11), *Eczematolepis* (Ptyctodontida; 'Placodermi'); (12), *Holonema*

1178   (Arthrodira; 'Placodermi'). (B) The vertebrate fauna from the Late Devonian of Michigan.

1179   (13) *Aspidichthys* (Arthrodira; 'Placodermi'); (14), *Trachosteus* (Arthrodira: 'Placodermi');

1180   (15), *Diplognathus* (Arthrodira; 'Placodermi'); (16), Ptyctodontida indet. ('Placodermi').

1181

Figure 1

Stratigraphy of the Devonian deposits of the northern part of the Lower Peninsula of Michigan.

Figure modified from Elliott et al. (2000), Figure 3.

Figure 2

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

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

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

Figure 3

Vertebrate remains from the Dundee Limestone Formation.

(A), a large tooth from *O. sigmoides*,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*sp. (previously identified as *Arctolepis* sp.),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.
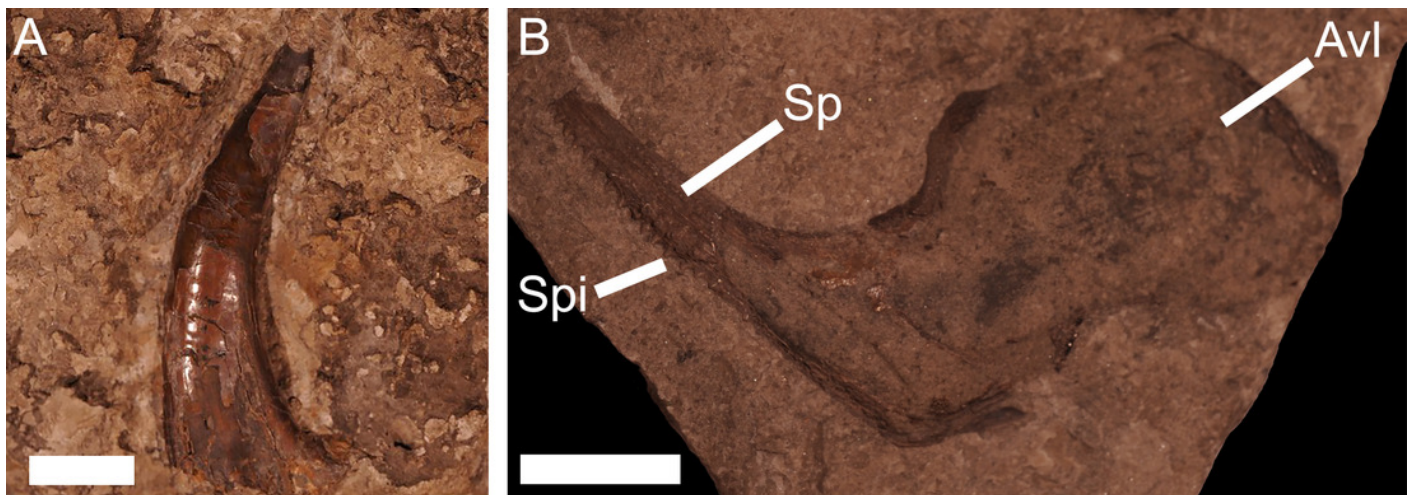
Figure 4

Vertebrate remains from the Rockport Quarry Limestone Formation.

(A), a partial skull roof from *Holonema* sp., from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 12991. Abbreviations: Nu, Nuchal; PNu, Paranuchal; C, 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, 7M, Michigan History Museum. Scale bar equals 1 cm. (C), an incomplete right anterior ventrolateral from *Dunkleosteus* sp.,from the Rockport Quarry Limestone of Rockport Quarry, Alpena County, UMMP 16156. Scale bar equals 2 cm. (D), a small spine from ?*Tamiobatis*sp. (previously identified as *Ctenacanthus* sp.)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

Vertebrate remains from the Four Mile Dam Formation.

(A), a broken spine froman 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, JS 4, Michigan History Museum. Scale bar equals 1 cm. (D), a piece of limestone containing both crinoid heads and an armor plate from ?*Mylostoma* sp.from the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County, 9M, 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 armor plate and the dashed arrow indicates a crinoid calyx. Scale bar equals 1 cm.
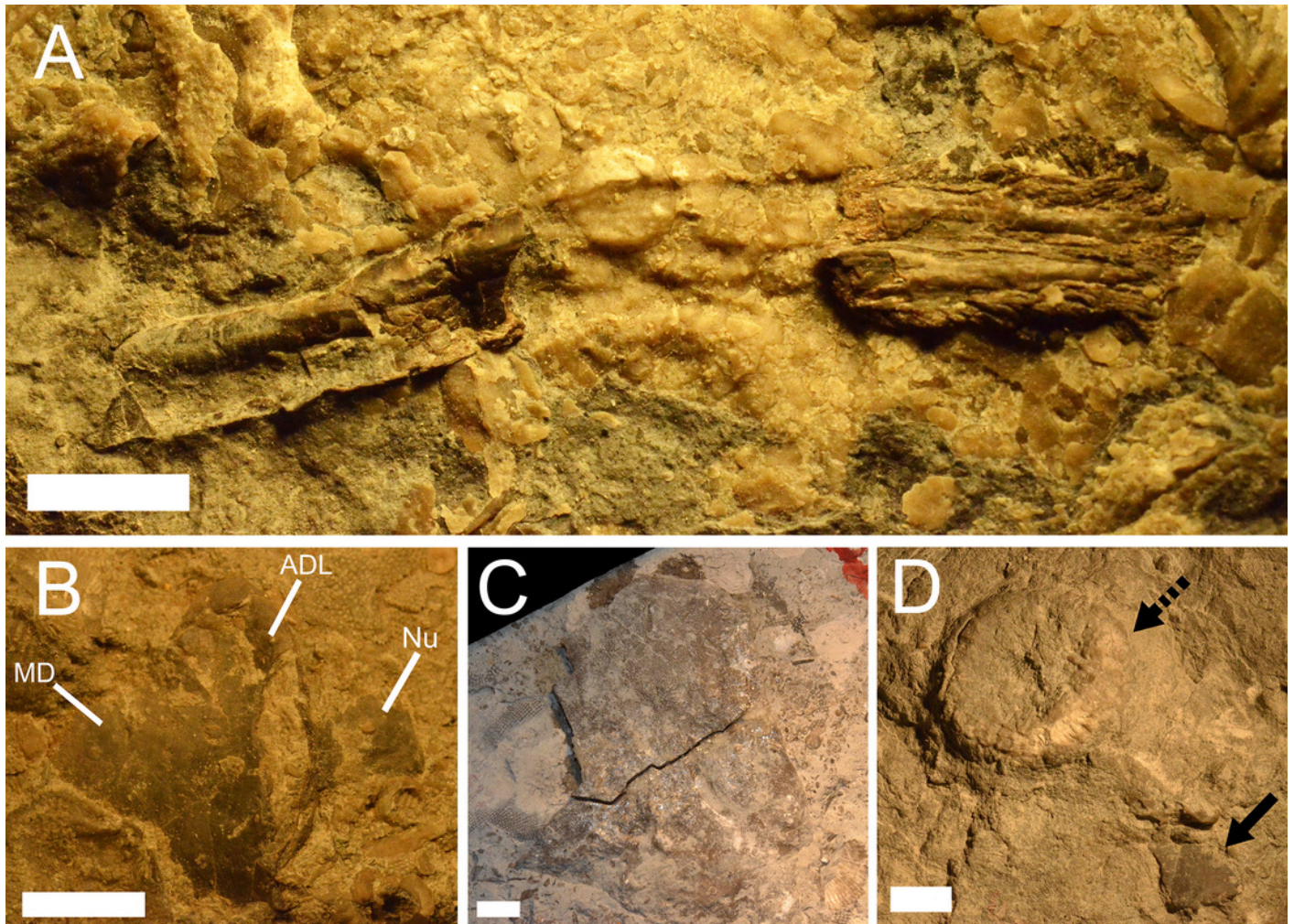
Figure 6

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

(A), a photograph of an impression of the head of the holotype, from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 12980. Scale bar equals 2 cm. (B), a specimen drawing of UMMP 12980 (redrawn and modified from Case (1931: Figure 1). Dotted lines represent missing plate boundaries and dashed lines represent sensory grooves. (C), an incomplete nuchal and left paranuchal plate, from the Rockport Quarry Limestone at the abandoned Kelly Island Limestone Quarry at Rockport State Park, Alpena County, UMMP 2981.Scale bar equals 1 cm. (D), a partial headshield, most likely from 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.
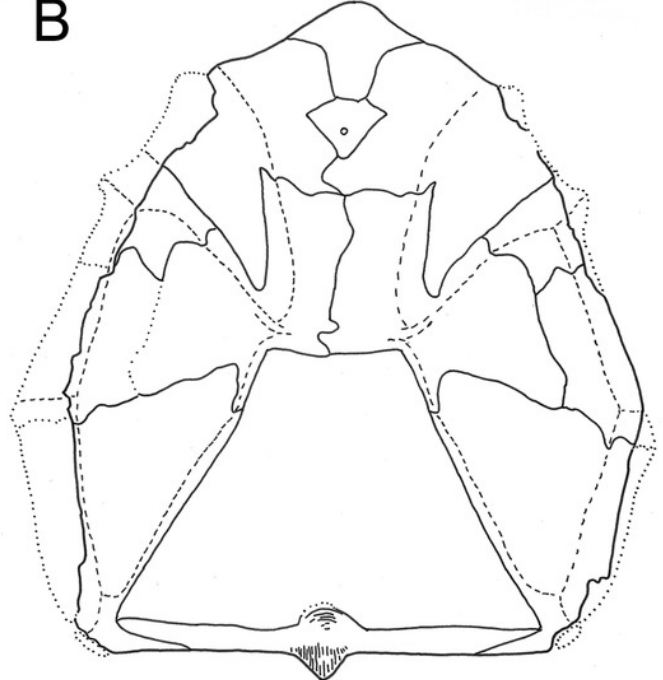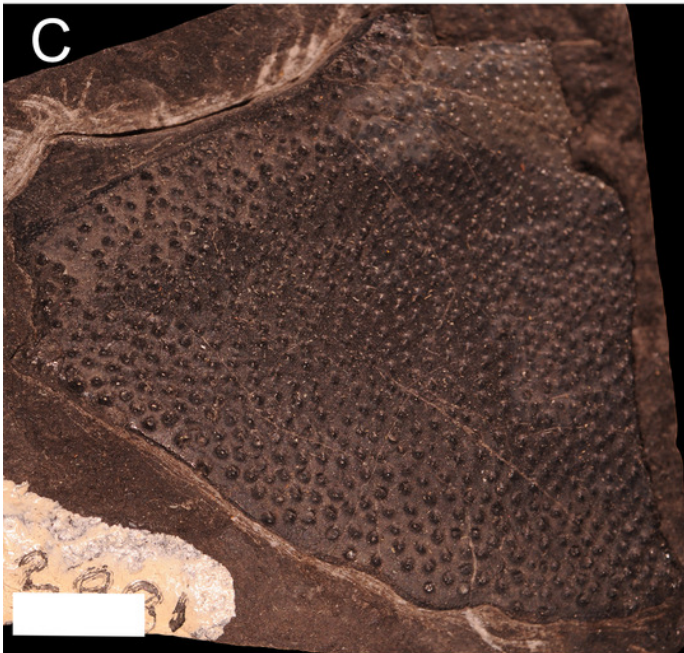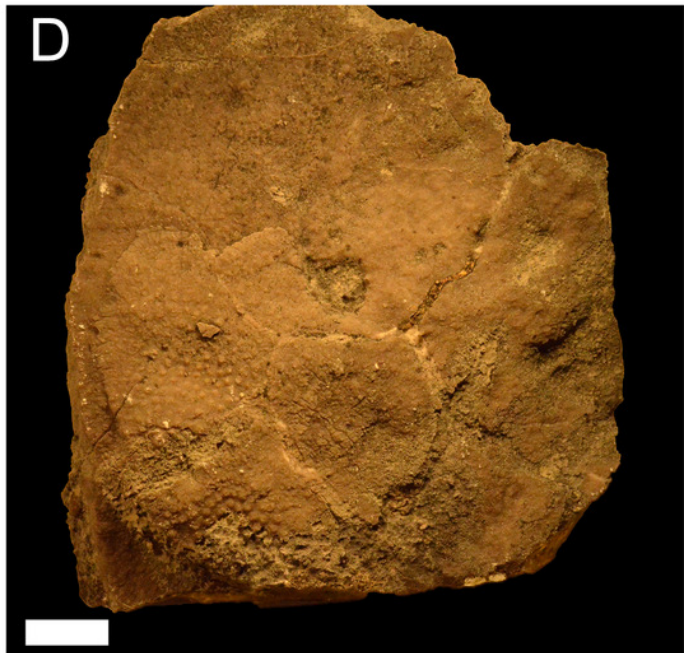
Figure 7

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

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

Figure 8

Newly discovered specimens of ?*Macropetalichthys* sp.

(A) a partially complete headshield from ?*Macropetalichthys*sp. Specimen found in the Four Mile Dam Formation of the Betsie Bay Rockpiles, Elberta, Benzie County. Abbreviations: Hd, Head Shield (incomplete), Un, Unidentified Armor Plate, R, Rostral Plate?. Scale bar equals 2 cm. 32M, Michigan History Museum. (B) crushed and partially articulated pieces of armor from the anterior portion of the headshield of ?*Macropetalichthys* sp.. Specimen found in the Alpena Limestone Formation at the Besser Museum Fossil Park, Alpena. BV 4, Michigan History Museum. Abbreviations: PrO, Preorbital; R, Rostral. Scale bar equals 1 cm.
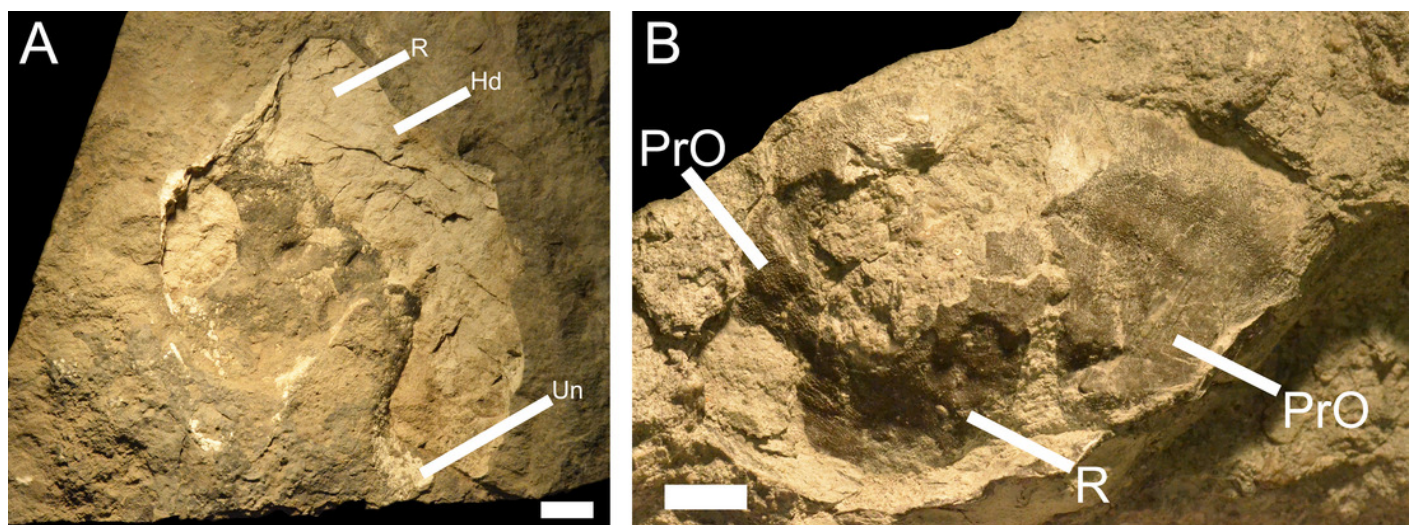
Figure 9

An incomplete armor plate from *Eczematolepis* sp.

Specimen from the Genshaw Formation. Found near Posen, MI. UMMP 4169. Scale bar equals 1 cm.

Figure 10

A supragnathal plate from an unknown ptyctodont from the Traverse Group.

Specimen recovered from an unknown locality referred to as "Locality 650 of the Winchell Survey", 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.(originally identified as *A.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.
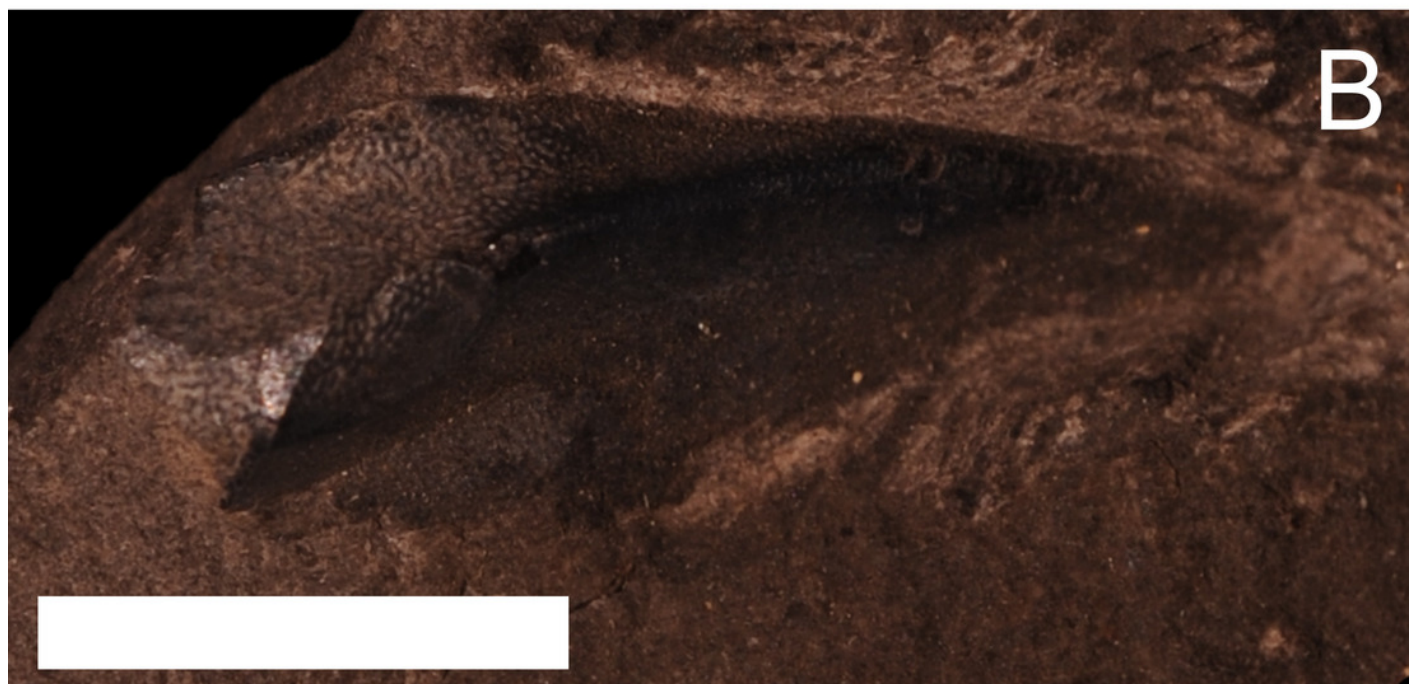
Figure 12

The skull of *Chirodipterus onawayensis*.

Specimen recovered from from the Newton Creek Limestone of Onaway Stone Quarry, north of Onaway, Presque Isle County. Specimen photo from Schultze (1982), Figure 2, modified and reprinted with permission of Taylor and Francis Ltd, http://www.tandfonline.com. This specimen is reported to be unnumbered at the Great Lakes Area Paleontological Museum, but is missing. 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.
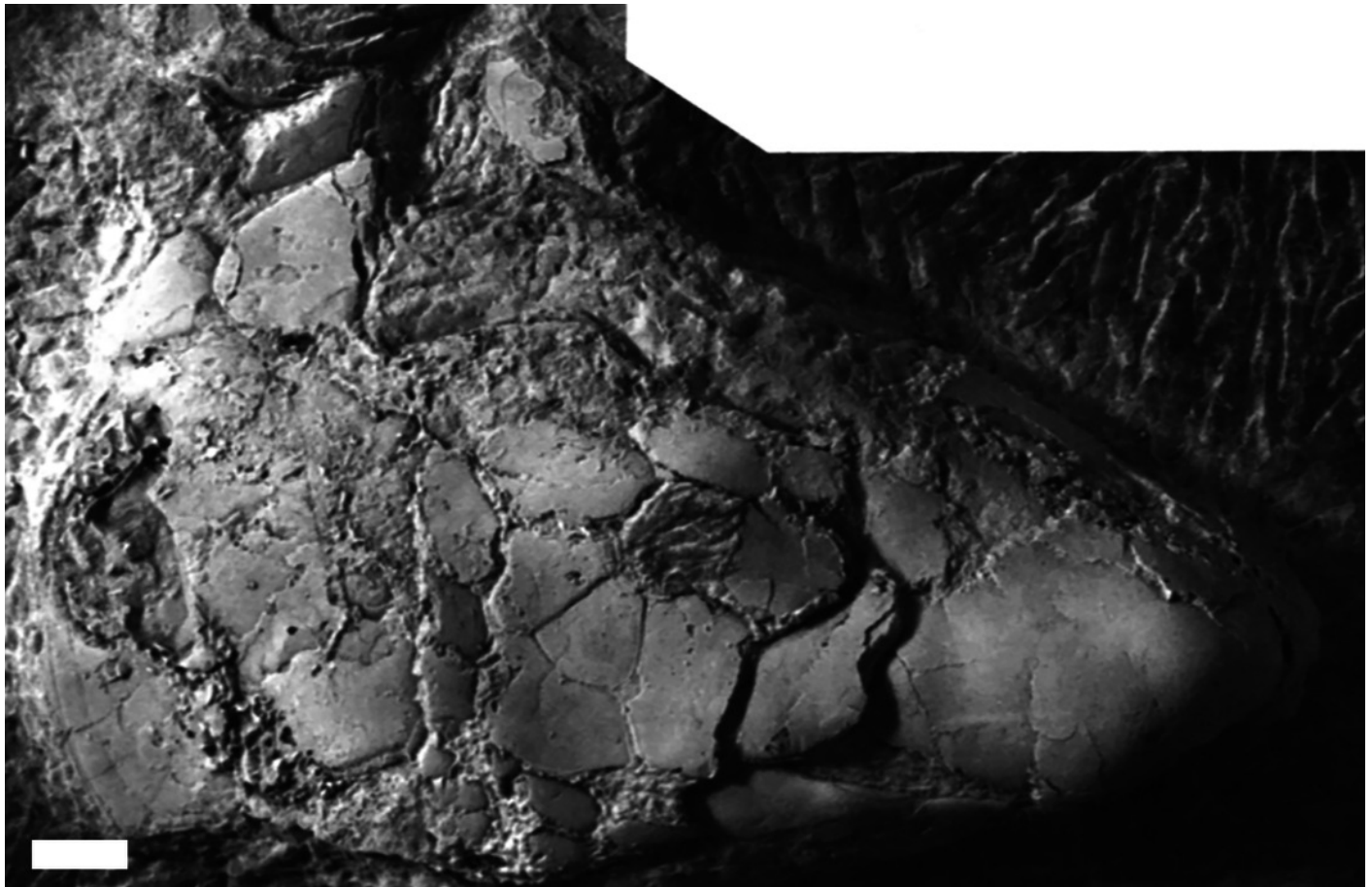
Figure 13

A representation of the Devonian vertebrate fauna known from Michigan.

Animals not to scale. Drawing by L.S. (A) The vertebrate fauna from the Middle Devonian of Michigan. (1) *Acondylacanthu*s (Chondrichthyes); (2), *Dinomylostoma* (Arthrodira; 'Placodermi'); (3), *Chirodipterus* (Dipnoi; Sarcopterygii); (4), *Dunkleosteus* (Arthrodira; 'Placodermi'); (5), *Onychodus* (Onychodontida; Sarcopterygii); (6), *Mylostoma* (Arthrodira; 'Placodermi'); (7), *Protitianichthys* (Arthrodira; 'Placodermi'); (8), *Oracanthus* (Acanthodida; 'Acanthodii'); (9), *Machaeracanthus* (Ischnacanthida; 'Acanthodii'); (10), *Gyracanthus* (Gyracanthida; 'Acanthodii'); (11), *Eczematolepis* (Ptyctodontida; 'Placodermi'); (12), *Holonema* (Arthrodira; 'Placodermi'). (B) The vertebrate fauna from the Late Devonian of Michigan. (13) *Aspidichthys* (Arthrodira; 'Placodermi'); (14), *Trachosteus* (Arthrodira: 'Placodermi'); (15), *Diplognathus* (Arthrodira; 'Placodermi'); (16), Ptyctodontida indet. ('Placodermi').