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A large onychodontiform (Osteichthyes: Sarcopterygii) apex predator from the Eifelian-aged Dundee Formation of Ontario, Canada.

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Abstract

The Devonian marine strata of southwestern Ontario, Canada have been well documented geologically, but their vertebrate fossils are poorly studied. Here we report a new onychodontiform (Osteichthyes, Sarcopterygii) *Onychodus eriensis* n. sp. from the Dundee Formation (Eifelian-Givetian boundary, 390-387 Ma) of southwestern Ontario represented by two well-preserved onychodontiform lower jaws. The most complete specimen consists of a large (28cm), well preserved right jaw with most of the dentition present. The dentary has 50 teeth, not including the parasymphysial tusk whorl, which is poorly preserved but consists of at least three tusks. The anteriormost teeth of the dentary are also not complete, but the second dentary tooth is notably procurved. The posterior teeth are conical and approximately equal in size for much of the length of the tooth row. *Onychodus eriensis* n. sp. differs from the closely related contemporary species *Onychodus sigmoides* and all other onychodonts, in that it has a strong dorsal curvature of the anterior dentary ramus, and marked anterior expansion of the dentary. An expanded phylogenetic analysis of Devonian onychodontiforms suggests that *O. eriensis* is closely related to *Onychodus jandemarraii*. The new material indicates that Onychodontiformes is more diverse than previously recognized, and that further analysis of vertebrate remains from southwestern Ontario will lead to additional insights into the diversity of Devonian sarcopterygians.

Keywords: Sarcopterygii; Onychodontiformes; Body size; Middle Devonian, Eifelian

Introduction

Sarcopterygii are a clade of osteichthyans that include lobe-finned fish and all tetrapods. Transitional tetrapodomorph sarcopterygians such as *Tiktaalik* and *Panderichthys* have been extensively studied for anatomical changes occurring through the “fin to limb” transition (Shubin *et al.* 2004; Ahlberg and Clack 2006; Shubin *et al.* 2006; Daeschler *et al.* 2006; Boisvert *et al.* 2008; Clack 2009). Extant sarcopterygian fish are represented by coelacanths (Actinistia) and lungfish (Dipnoi); however, fossils show that sarcopterygians had a much greater diversity (Johanson, 2004), particularly during their early radiation in the Devonian (419-358 Ma). Several (extinct) lobe-finned lineages, including Onychodontiformes, evolved relatively large sizes (up to several meters in length) and diverse feeding strategies (Andrews *et al.* 2006).

Onychodontiformes is a monophyletic group of sarcopterygian fish that are abundant in Middle to Late Devonian (Lu and Zhu 2010). Onychodontiforms are defined by their highly kinetic skulls and the presence of proportionally large parasymphysial tusk whorls on the anterior end of the dentary (Andrews *et al.* 2006). The exact phylogenetic position of the Onychodontiforms is debated, though most authors consider them as early diverging sarcopterygians (Cloutier and Ahlberg 1996; Long 2001; Lu *et al.* 2016).

The most recent phylogenetic analysis by Lu *et al.* (2016), recovers Onychodontiformes as the sister group to Dipnomorpha and Tetrapodomorpha, however previous analyses have recovered a sister group relationship to Actinistia (Long *et al.* 2008; Friedman and Brazeau 2010; Brazeau and Friedman 2014, Lu *et al.* 2016).

Furthermore, the first phylogenetic analysis for the interrelationships within the clade Onychodontiformes was presented by Lu & Zhu (2010). The clade Onychodontiformes includes *Onychodus* (Newberry 1857), *Strunius* (Jessen 1966), *Grossius* (Schultze 1973), *Luckeus* (Young and Schultze 2005), *Qingmenodus* (Lu and Zhu 2010), and *Bukkanodus* (Johanson *et al.* 2007). *Onychodus* is regarded as a large apex predator, ranging from 1-3 meters in length (Andrews *et al.* 2006; Sallan and Galimberti 2015), and is best known for its large recurved sigmoidal-shaped tooth whorls. Specimens assigned to *Onychodus* have a global distribution with known occurrences from geographically widespread deposits in North America, Europe, the Middle East and Australia (Woodward 1888; Hairapetian *et al.* 2000; Andrews *et al.* 2006). Although several species of *Onychodus* have been described from the Middle Devonian, most are based on fragmentary material and as such we follow the conservative opinion of Andrews *et al.* (2006), which consider them in need of revision and at present not properly defined species.

The type species of *Onychodus*, *O. sigmoides* (Newberry 1857), is only known from isolated teeth (parasymphysial tusks), jaw fragments, and cranial elements from various Middle Devonian localities in North America (Andrews *et al.* 2006). To date, this is the only onychodontiform taxon from North America. Here we describe a new large onychodontiform fish based on well-preserved lower jaw material from the Eifelian-aged Dundee Formation of Pelee Island, Ontario, Canada. The new taxon, *Onychodus eriensis* n. sp. is assessed in the context of a revised phylogeny of Onychodontiformes (Lu and Zhu 2010). The new material demonstrates the potential for further well-preserved sarcopterygian material from the poorly studied Devonian vertebrate faunas of southern Ontario.

Institutional abbreviations

ROM, Royal Ontario Museum; PIHC, Pelee Island Heritage Centre; FMNH, Field Museum of Natural History; CMN, Canadian Museum of Nature.

Materials and Methods

Specimens examined in this study include four onychodontiform jaw fragments: one onychodontid specimen from the Pelee Island Heritage Museum (uncatalogued) (ROM 72893 cast), and three onychodontiform specimens from the Royal Ontario Museum (ROM 00198, ROM 00190, ROM 00199). A parasymphysial tusk whorl of *Onychodus sigmoides* from the Columbus limestone of Ohio was also examined at the Canadian Museum of Nature (CMN 3566) as well as two jaw fragments (FMNH UF 534 and FMNH UF 328) and a tooth (FMNH UF 325) from the Onondaga Formation of New York. Additional specimens examined from Pelee Island include an onychodontiform parasymphysial tusk (ROM 66177). The historically collected (donated in the 1920's by private collectors) lower jaws (ROM 00198, PIHC specimen (ROM cast 72893)), were mechanically prepared at the ROM in 2014.

All specimens were photographed with a Nikon D700 Camera using an AF-S NIKKOR 24-85mm lens, and were prepared with ammonium chloride immediately prior to photography. Digital photographs were processed using Adobe Photoshop CS3 and CS4. Microscopic images of specimen ROM 00198 were taken using a Nikon DS-Fi1

camera mounted to a Nikon AZ-100 microscope. Images were processed using Nikon NIS-Elements (Basic Research) imaging software.

The phylogenetic position of *Onychodus eriensis* n. sp. was assessed using a modified version of the data matrix from Lu & Zhu (2010). Two new morphological characters were added to the matrix: 1) the presence-absence of procurved teeth on the anteriormost end of the dentary, and 2) the presence-absence of tuberculated dermal bone ornamentation on the dentary. In addition to *O. eriensis*, *Onychodus sigmoides* was added to the matrix and coded based on the illustrations of the type series and original description by Newberry (1857, 1873). The final data matrix consisted of 41 characters and 10 taxa including *Psarolepis*, *Styloichthys*, *Diplocercides*, *Strunius*, *Bukkanodus*, *Qingmenodus*, *Grossius*, *Onychodus jandamarrai*, *Onychodus sigmoides* and *O. eriensis* (see Appendix 1). The data matrix was assembled using the program MacClade 4.08. We ran a modified version of their matrix under the same parameters (see methodology in Lu & Zhu, 2010) using the exhaustive search option in PAUP 4.0b10 (Swofford, 2003). All characters were unordered and equally weighted. *Psarolepis* was designated as the outgroup taxon. In order to assess the robustness of the results, a bootstrap analysis was performed with 10 000 bootstrap replicates.

Geological setting

Specimens examined in this study are the first fossil vertebrates from the Middle Devonian Dundee Formation of Pelee Island, Ontario, Canada (Fig. 1AB), to be formally described. ROM 00198, ROM 66177 and the specimen from the Pelee Island Heritage Centre (ROM 72893 cast) were collected from shoreline exposures near Mill Point on

Pelee Island (Fig. 2A and Fig. 3AB), although the precise localities of ROM 00198 and the Pelee Island Heritage Centre specimen are unknown. The regional stratigraphy has been well documented by the Ontario Geologic Survey of Canada (Fig. 1C), having been recorded from drill cores, while age constraints are provided by detailed conodont biostratigraphy (robustus, patulus, costatus, australis, and kockelianus zones) (Uyeno *et al.*, 1982; Armstrong and Carter, 2006). The Dundee Formation is widely exposed on Pelee Island (Fig. 1), and extends southward into areas of Michigan, USA, based on subsurface records (Armstrong and Dodge 2007).

The Dundee Formation consists of a mostly uniform fossiliferous micritic limestone; however, six distinctive lithofacies have been identified: 1) bioturbated dolomitic sandy wackestone, 2) cherty bioclastic, 3) cherty mudstone, 4) crinoid-brachiopod grainstone to wackestone firm-ground, 5) argillaceous bioturbated brachiopod mudstone to wackestone, and 6) a muddy bioturbated wacke-packstone facies (Birchard and Risk 1990). Outcrop on Pelee Island consists of a light brown, medium to coarse grained bioclastic limestone facies (Armstrong and Dodge 2007). Invertebrate fossils are abundant, mostly consisting of broken/disarticulated bryozoan colonies, crinoids and a variety of rugose horn corals (Birchard and Risk 1990). This facies is interpreted as a normal-marine open-shelf at (or below) storm wave base (Birchard and Risk 1990). Specimen ROM 66177 was collected by the ROM staff in 2013 from Pelee Island (Fig. 3B). Specimens ROM 00198 and the specimen from the Pelee Island Heritage Museum (ROM 72893 cast) were historically collected and acquired by the museums in the early 1900's (exact dates unknown) (Fig. 2A and Fig. 3A).

Systematic paleontology

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

Onychodontiformes Andrews, 1973

Onychodontidae Woodward, 1891

Onychodus Newberry, 1857

Onychodus eriensis n. sp.

Etymology: The specific epithet refers to Lake Erie.

Holotype: ROM 00198 (Fig. 2A), a nearly complete right jaw (submandibular, infradentaries 2-3-4, gular, and tooth whorls not preserved), is 28 cm long and consists of a right dentary with 50 teeth, infradentaries 1, and the symphyseal plate as well as the remnants of at least 2 small sigmoidal tusks at the anteriormost end.

Locality and Horizon: Dundee Formation, Middle Devonian (Eifelian), Pelee Island, Ontario, Canada.

Diagnosis: Large onychodontiform diagnosed by the following autapomorphies: highly curved lower jaw; jaw curves anteriorly from middle of dentary to mandibular ramus; anterior surface of dentary ramus flat; 50 teeth (27 of which are present and well preserved) which decrease in size both anteriorly and posteriorly; 5 anteriormost teeth procurved; 1 row of small pointed denticles on interior surface of dentary; dermal bone ornamented with large tubercles. *Onychodus eriensis* n. sp. differs from *O. sigmoides* by its highly curved and expanded anterior dentary and the flattened anterior surface of the mandibular rami (rounded in *O. sigmoides*). The pointed teeth of *O. eriensis* are distinct

from the barbed teeth in *O. jaekeli*. *O. eriensis* also possesses a unique highly elongated dentary that tapers posteriorly. The large size of *O. eriensis* distinguishes it from smaller species such as *O. jandamarrai*, *O. jaekeli*, *O. yassensis*, and *O. obliquidentatus*. Note that *O. arcticus* Woodward (1889), *O. anglicus* Woodward (1888), *O. hopkinsi* Newberry (1889), and *O. ortonii* Newberry (1889) are based on fragmentary materials which are insufficient for proper diagnosis (Andrews *et al.* 2006).

Comments: ROM 00198 was historically collected on Pelee Island, Ontario and accessioned to the Royal Ontario Museum (ROM) Vertebrate Paleontology collections. Analysis of the matrix surrounding ROM 00198 corresponds to the lithofacies of the Dundee formation exposed at the Mill point locality, Pelee Island (Birchard and Risk 1990).

Description

Mandible Size and Preservation

ROM 00198 consists of a well preserved, articulated right jaw preserved in lateral view (Fig. 2) with an overall mandibular length of 28 cm (30 cm when accounting for the recurve) and a maximum depth of 3.8 cm (Table 1). The specimen includes the first infradentary, dentary, as well as associated teeth and parasymphysial dentition (Fig. 2BD). Accounting for missing anatomical features (infradentary 4, infradentaries 2 and 3, submandibular, parasymphysial median plate, and parasymphysial whorl), we estimate that the total length of the lower jaw at approximately 35 cm. ROM 00198 is heavily weathered, removing most of the original dentary and leaving a negative impression of the bone, but with

isolated pieces of bone present throughout that are most completely represented on the dorsal tooth bearing surface of the dentary. No coronoid elements are preserved. The anterior end of the dentary preserves much of the original bone including large chunks of the anterior face. Conversely, the lateral face of the dentary is highly worn. This weathering has exposed internal features of the mesial and internal face of the jaw such as the parasymphysial plate.

Dentary

The dentary is slender, elongate and strongly curved anteriorly with flat surfaces on the anterior and dorsal sides of the mandibular ramus (Fig 2D). Similar to specimens of *Onychodus* (Fig. 5), the anterior end of the dentary has been modified to accommodate a large parasymphysial tusk whorl, an independent tusk bearing structure that associates with the anteriormost end of the jaw (Andrews *et al.* 2006). The anteriormost end of the dentary also shows no defined contact area for its antimere, suggesting a weak dentary symphysis (Andrews *et al.* 2006). The dentary is deep anteriorly and is not strongly constricted dorsoventrally posterior to the tooth whorl. In this respect, it is more similar to *O. jandamarrai* but differs from the type series of *O. sigmoides* (Fig. 5A-C). The anteriormost end the dentary is worn away exposing the symphysial plate. On the symphysial plate there are preserved linear structures that possibly represent pores for nerves or blood vessels (Fig. 2D). The dorsal margin of the anteriormost end of the dentary is planar where the parasymphysial whorl and associated parasymphysial tusks were positioned. Conversely the dentary tapers to a small point at its posterior

end. Numerous grooves are present on the ventral surface of the dentary which may be partially exaggerated from weathering of the area. These grooves form a step-like pattern towards the posterior end of the dentary and may represent the attachment sites for infradentaries 2, 3, and 4. Intense weathering to the middle of the dentary has exposed a mesial dentary ridge that runs along the middle of the jaw from the anteriormost end to the last visible tooth position (Fig. 2B). Bone fragments of the dentary are highly ornamented with small opaque tubercles in linear rows. The tubercles have a clear and glassy appearance, likely due to an enameled layer. Tubercles are found in linear rows that are oriented in random directions (Fig. 2C). The largest tubercles are located on the anteriormost end of the dentary. The tooth bearing ramus is dorsally curved in lateral view. The curvature begins in the middle of the tooth row, and is more pronounced than in other onychodontiform specimens of similar size from the Devonian North America (e.g. Fig. 5A-F) and Australia (Andrews *et al.* 2006).

Infradentaries and Articular

Infradentary 1 is present; however, infradentaries 2, 3, and 4 are not preserved. The majority of infradentary 1 is not preserved and in its place is a negative impression outlined with positive ridges of the original bone. Infradentary 1 occupies the anteriormost position and is present ventrally to the dentary ramus (Fig. 2B). It is small and elongate, measuring 2.3 cm; however, it may be incomplete. Infradentary 1 is located just below the flat anterior surface of the dentary, which is lower than in *O. jandamarrai*. A negative impression shows

evidence of the lateral line canal system penetrating infradentary 1; however, this feature is extremely weathered. Although Infradentaries 2 and 3 are not preserved, grooves along the dentary suggest that they were likely elongated and expanded posteriorly. The possible articular is a highly weathered, and only the posterior portion of the original bone is preserved (approximately 4.2 cm; Fig. 2B). The element is located in the most posterior position to the dentary, and is elongated and widens posteriorly into a dorsally oriented position.

Dentition

ROM 00198 has 50 tooth positions preserved, 27 of which allow for detailed descriptions of their shape. In addition, there is a small row of sharply pointed denticles on the interior surface of the dentary behind the main row of teeth (Fig. 2C). A second row of teeth is likely however, they are not preserved. The teeth remain conical and straight for the majority of the length of the jaw; however, the five anteriormost teeth are procurved (Fig. 2D). Two of the procurved teeth consist of one full tooth and a subsequent tooth root, while the anteriormost three teeth are heavily weathered and are displaced to the flat ridge on the symphyseal end of the dentary. These procurved teeth can be distinguished from the parasymphyseal tusks by their short and stout morphology that is more noticeably procurved than the sigmoidal tusks. In addition, the procurved teeth that are present possess a visible tooth base and are all of similar size (Table 1). The largest teeth are located in the middle of the dentary, decreasing in size both anteriorly and posteriorly. The teeth are tall and slender, and are large relative to

the depth of dentary, as in the type series of *O. sigmoides* (Fig. 5A-C), but unlike *O. jandamarrai* and some specimens referred to *Onychodus* from the Devonian of Ohio and New York (e.g., Fig. 5E). The teeth appear to be curved lingually, which is consistent with other species of *Onychodus* (e.g. WAM 92.8.2). Repeated tooth absence in the mandible likely demonstrates a continued tooth replacement. This presumed tooth replacement also occurs in *O. jandamarrai*; however, Andrews *et al.* (2006) describe this regular tooth absence as taphonomic.

Parasymphysial Anatomy

Two poorly preserved teeth of the parasymphysial whorl are visible near the flat ridge of the anteriormost portion of the dentary (Fig. 2D). This surface normally accommodates the whorl which typically extends beyond the length of the dentary. The small size of the parasymphysial tusks, and their position below the normal location of the whorl in close association with the dentary, suggests that they represent replacement teeth that were not fully grown or attached to the whorl (Andrews *et al.* 2006). Both teeth are thin and gracile, further distinguishing them from the nearby teeth of the dentary. The anterior tooth is the larger of the two parasymphysial tusks and shows a sigmoidal recurve. The posterior tooth mainly preserves the crown portion and shares a sharp pointed morphology with *O. sigmoides* and *O. jandamarrai*.

Onychodus cf. O. eriensis

Material: Pelee Island Heritage Museum (PIHC uncatalogued; ROM 72893 cast of original), a fragmentary lower jaw including the posterior portion of the dentary preserved with associated teeth (Fig. 3A); ROM 66177, a parasymphysial tusk (Fig. 3B).
Locality and Horizon: Dundee Formation, Middle Devonian (Eifelian), Mill Point, Pelee Island, Ontario, Canada.

Remarks: The PIHC specimen (ROM 72893) is conferred to this species on the basis of its posterior tapering dentary and similar straight conical tooth morphology. Based on the thin posterior end of the dentary the specimen may represent a slightly smaller individual of *O. eriensis*, however, there is not enough diagnostic morphology preserved to definitively assign it to this species. ROM 66177 is assigned to *Onychodus c.f. eriensis* due to its similar size and sigmoidal curvature.

Description

The PIHC specimen consists of the posterior portion of the dentary with associated teeth (Fig. 3A). The entire length of the specimen is 14.4 cm, and it has 17 teeth preserved including 16 nearly complete teeth and one tooth root. The dentary bone is mostly worn away, with only the most posterior portion still preserved in addition to a thin strip of bone just below the visible teeth. The negative impression of the bone suggests that the dentary tapers posteriorly to a point, as in ROM 00198. The impression of the dentary also shows an indentation towards the middle of the bone that is likely the position of the mesial dentary ridge.

The conical teeth are tall and sharply pointed, and measure less than 1 cm in

length. In all respects, including size, they resemble the corresponding teeth in ROM 00198. The teeth have been severely weathered, with most of them having lost their enamel, and in some cases the pulp cavity is exposed. In addition, an isolated parasymphysial tusk found from the same locality (ROM 66177) likely belongs to *O. eriensis* and aids in characterizing the dentition. ROM 66177 is sigmoidally recurved, pointed, and has visible impressions of ribbed enamel (Fig. 3C).

Phylogenetic Results

The phylogenetic analysis recovered three most parsimonious trees (MPT) of 48 steps [Consistency index (CI)=0.875; Homoplasy index (HI) = 0.125; Retention index (RI)=0.833; Rescaled Consistency Index (RC) = 0.729]. In the strict consensus tree, *Onychodus eriensis* n. sp. is recovered as the sister taxon to *Onychodus jandamarrai*, and form a clade with *Grossius* and *Onychodus sigmoides* to the exclusion of all other Onychodontiformes. *Bukkanodus* is still considered a basal member of Onychodontiformes and *Diplocercides* (a coelacanth) is resolved at the sister group of Onychodontiformes. The position of *Grossius* within the least inclusive clade containing *O. jandamarrai* and *O. sigmoides* in two of the three MPTs suggests that the genus *Onychodus* may be paraphyletic however further research is needed to clarify this point (Fig. 4).

All ambiguous character states were resolved using DELTRAN, as in the original Lu and Zhu 2010 analysis. The apomorphies and character states (the character state is (1) unless indicated). The least inclusive clade containing *O. jandamarrai* and *O. sigmoides* is supported by the following synapomorphies; the presence of a ventrally

curved maxilla (21) and middle pit-line: on or not on the same lineation as the tabular pit-line (28). The sister group relationship between *Onychodus eriensis* and *Onychodus jandamarrai* is supported by characters 40) Large enameled tuberculate ornamentation on the tooth bearing surface of dentary and 41) Procured teeth on the anteriormost end of the dentary. Bootstrap Analysis and Bremer Decay show relatively low support values for the monophyly and interrelationships of Onychodontiformes (Fig. 4).

Discussion

Onychodus, the best known onychodontiform, is known from both geographically and stratigraphically widespread localities in North America, Europe, the Middle East, and Australia that span the late Early to early Late Devonian (Woodward 1888; Hairapetian *et al.* 2000; Andrews *et al.* 2006). The earliest occurrence of *Onychodus*, *O. sigmoides*, is from the lower Devonian strata of the Columbus (Newberry 1873; Martin 2002) and Onondaga formations (Fig. 5D-F) of Ohio and New York respectively. The now lost type specimens of *O. sigmoides* (Fig. 5A-C) (Newberry 1857; Plate 26 and 27), were collected from the Eifelian-aged (Middle Devonian) Delaware Limestone of Ohio (Newberry 1857; Andrews 2006). The Dundee limestone in Ontario is the chronostratigraphic equivalent of Delaware limestone in Ohio, suggesting that *O. eriensis* may have been contemporaneous with the closely related *O. sigmoides*. The latest putative occurrence of the genus *Onychodus* is from the late Devonian Frasnian aged Gogo Formation in Australia, and is represented by the well known species *O. jandamarrai* (Andrews *et al.* 2006).

Our survey of *Onychodus sigmoides*, based on the descriptions by Newberry

(1857) and specimens from the ROM and FMNH (e.g., Fig. 5EF) revealed considerable morphological variation possibly indicating the presence of multiple species or ontogiomorphs of a single species. Two morphotypes can be easily distinguished on dentary morphology. This includes a smaller, more gracile morph (Fig. 5AE) with a relatively straight dentary that constricts anteriorly before expanding at the symphysis, and a robust form (Fig. 5BF) with deep anterior dentary, less pronounced dorsoventral symphyseal expansion. This smaller, more gracile morph is seen to have taller and elongate teeth that are similar in morphology to *Onychodus eriensis*. *O. eriensis* shows a mosaic of characters that occur in these forms including the stronger expanded highly curved dentary of the large morph and the slender dentary morphology of the smaller morph. It should be noted that the gracile morph is characterized by the type series *O. sigmoides* (1873), whereas the larger, more robust form is more similar to the later occurring *O. jandamarrai*, and that the robust form may represent a distinct taxon. Finally, the larger *Onychodus* specimens from the Onondaga Formation are typically found in deeper water facies than other species which may represent a different niche occupancy for this morph (Martin 2002). These morphological observations, suggest that the genus *Onychodus* requires further revision.

Body Size and Shape of Onychodus eriensis

The flexible skulls of onychodontiform fish have many loosely connected and overlapping cranial elements that explains the frequency of fragmentary, disarticulated remains in their fossil record (Andrews *et al.* 2006). The relatively complete specimens of *Onychodus jandamarrai* (e.g., WAM 92.8.2) from the

Gogo Formation of Australia have shed light on the anatomy and structure of Onychodontiformes (Andrews *et al.* 2006). Given the fragmentary nature of *Onychodus* specimens worldwide, only recently have detailed interpretations of the overall body morphology been described. An elongated body was proposed by Long (1991). Andrews *et al.* (2006) agree that the body of *Onychodus* was elongated and further described postcranial features such as the pelvic and caudal fins based on a virtually complete specimen WAM 86.9.694 from the Gogo Formation. Based on WAM 86.9.694, Andrews *et al.* (2006) also suggest *Onychodus* swam in the subcarangiform mode. Some juvenile specimens presented by Andrews *et al.* (2006) suggest an overall oval cross-section for the body.

The largest known Palaeozoic sarcopterygians were Carboniferous rhizodonts that reached over 3 m in length, with the largest species *Rhizodus hibberti* reaching up to 7 m (Johanson 1998; Sallan and Galimberti 2015). However recent evidence suggests that Devonian non-tetrapodomorph sarcopterygians, including onychodontiforms, also approached these huge sizes (Andrews *et al.* 2006; Young *et al.* 2013; Sallan and Galimberti 2015).

Although specimens of *Onychodus jandamarrai* only show an estimated length of 95 cm, considerably larger specimens from North America suggest that *Onychodus* could obtain much larger body sizes (Sallan and Galimberti 2015). Young *et al.* (2013), citing a personal communication from J. Long, suggest that an unidentified species of *Onychodus* could likely exceed 4 meters in body length based on an undescribed maxilla approximately 30 cm in length from the

Delaware Limestone, USA. Informal size estimates based on described specimens of *O. sigmoides* suggest that the taxon could obtain at least 3 m in length (Andrews *et al.* 2006). The mandibular length of *O. sigmoides* was described by Newberry (1873) as being around “a foot-long”. Even larger jaws of *Onychodus* exist in museum collections that remain undescribed (A. Mann personal observation). The reconstructed mandibular length of *O. eriensis* matches the lengths of most described large mandibles of *O. sigmoides*, suggesting that *O. eriensis* also achieved a similar large size. However, the exact sizes of these taxa remain obscure and will only be clarified with further descriptions of new and more complete specimens.

Large sarcopterygians such as *O. eriensis* were obligate carnivores needing significant amounts of prey to sustain their body sizes. The host strata for *Onychodus* fossils suggest that they inhabited reef and shelf ecosystems, and would have likely been one of the largest carnivores; it is possible that *O. eriensis* occupied a similar top predator niche. The large size of early sarcopterygians like *Onychodus* has important implications for the evolution and diversity of the group as a whole. The size range present in Onychodontiformes, ranging from the small (approx. 20 cm body length) *Bukkanodus jesseni* to the large *Onychodus sigmoides* (>150 cm), is evidence that early Sarcopterygii diversified into a variety of niches early in the group’s evolutionary history (Sallan and Galimberti 2015).

Conclusion

Onychodus eriensis, the first new onychodontiform taxa described on the basis of material from North America since Newberry (1873). The phylogenetic results suggest that *O. eriensis* is the sister taxon of *Onychodus jandamarrai*, however the taxon differs from other species of *Onychodus* by a strongly curved anterior end of the dentary, 50 tooth positions, and expanded flat anterior dentary ramus. *O. eriensis* and *O. sigmoides* are known from overlapping Eifelian-aged strata, in the Dundee and Delaware Formations respectively, however we note that the *Onychodus* material from these sites is in need of revision and the available material may represent a variety of sarcopterygian taxa.

Onychodus eriensis is the largest known sarcopterygian fish from the Palaeozoic of Ontario. Its large size indicates that it was an apex predator in the ecosystem it inhabited, although the body shape of *O. eriensis* remain unknown. The discovery of *O. eriensis* adds to the diversity of Devonian Sarcopterygii and may provide important information on the evolution of large size within the group's early radiation.

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Figure Captions

Figure 1. A) Map of Pelee Island showing significant areas of outcrop. B) Map showing the position of Pelee Island within Lake Erie. C) Idealized stratigraphy of the Devonian of southwestern Ontario; the Dundee Formation is marked by a star with significant specimens found at mill point listed beside (modified from Uyeno (1982) and Armstrong & Dodge (2007)). [planned for column width]

Figure 2. A) A photograph of the holotype of *Onychodus eriensis* n. sp., ROM 00198. B) Labeled diagram of the lower jaw bones C) Anterior end of dentary showing detailed

anatomical structures including symphyseal dentition, procurved teeth, and ornamentation. D) High resolution microscope image of the anterior end of the dentary showing a small row of heavily weathered, pointed denticles, located on the interior surface of the dentary. [planned for page width]

Figure 3. A) A second highly weathered specimen of *Onychodus* cf. *O. eriensis* n. sp. B) A parasymphysial tusk of *Onychodus* cf. *O. eriensis* n. sp. (ROM 66177) collected from Mill Point on Pelee Island, Ontario, C) High resolution microscope image of specimen ROM 66177 showing ribbed impressions. [planned for page width]

Figure 4. Phylogenetic results showing nodes numbered in circles 1-8, bremer support values on top, with bootstrap values on the bottom in italics (only values above 50 reported). At node 8, *Onychodus eriensis* n. sp. is reconstructed as sister to *O. jandamarrai*. [planned for column width]

Figure 5. A-C) The type series of *Onychodus sigmoides* figured in Newberry (1873). D-F) Field Museum specimens of *Onychodus* from the Onondaga Formation of New York, including E) A gracile morph FMNH UF 534 and F) A robust morph FMNH UF 328. [planned for page width]

Table 1. Measurements of *Onychodus eriensis* n. sp. specimens (Teeth counted from anterior to posterior, T1=first tooth in series). Measurements are reported in mm.

Measurement Index	ROM 00198	PIHC specimen (ROM 72892 cast)
Total jaw length	280	144
Dentary length	255	144
Dentary height at mid-tooth row	38	06
Infradentary 1-length	23	10
Exposed symphyseal plate length	12	09

T1, height	05	05
T2, height	05	09
T3, height	07	02
T4, height	09	08
T5, height	12	10
T6, height	10	17
T7, height	11	15
T8, height	10	98
T9, height	10	91
T10, height	10	n/a
T11, height	11	n/a
T12, height	12	n/a
T13, height	15	n/a
T14, height	13	n/a
T15, height	13	n/a
T16, height	11	n/a
T17, height	10	n/a
T18, height	10	n/a
T19, height	10	n/a
T20, height	08	n/s
T21, height	07	n/a
T22, height	06	n/a
T23, height	07	n/s
T24, height	06	n/a

T25, height	04	n/a
T26, height	03	n/a

Draft

Figure 1. A) Map of Pelee Island showing significant areas of outcrop. B) Map showing the position of Pelee Island within Lake Erie. C) Idealized stratigraphy of the Devonian of southwestern Ontario; the Dundee Formation is marked by a star with significant specimens found at mill point listed beside (modified from Uyeno (1982) and Armstrong & Dodge (2007)). [planned for column width]

90x154mm (300 x 300 DPI)

Figure 2. A) A photograph of the holotype of *Onychodus eriensis* n. sp., ROM 00198. B) Labeled diagram of the lower jaw bones C) Anterior end of dentary showing detailed anatomical structures including symphyseal dentition, procurved teeth, and ornamentation. D) High resolution microscope image of the anterior end of the dentary showing a small row of heavily weathered, pointed denticles, located on the interior surface of the dentary. [planned for page width]

190x222mm (300 x 300 DPI)

Figure 3. A) A second highly weathered specimen of *Onychodus* cf. *eriensis* n. sp. B) A parasymphysial tusk of *Onychodus* cf. *eriensis* n. sp. (ROM 66177) collected from Mill Point on Pelee Island, Ontario, C) High resolution microscope image of specimen ROM 66177 showing ribbed impressions. [planned for page width]

181x143mm (300 x 300 DPI)

Figure 4. Phylogenetic results showing nodes numbered in circles 1-8, bremer support values on top, with bootstrap values on the bottom in italics (only values above 50 reported). At node 8, *Onychodus eriensis* n. sp. is reconstructed as sister to *O. jandamarrai*. [planned for column width]

183x234mm (300 x 300 DPI)

Figure 5. A-C) The type series of *Onychodus sigmoides* figured in Newberry (1873). D-F) Field Museum specimens of *Onychodus* from the Onondaga Formation of New York, including E) A gracile morph FMNH UF 534 and F) A robust morph FMNH UF 328. [planned for page width]

181x232mm (300 x 300 DPI)

APPENDIX 1

Fig.A1. Data matrix used in the phylogenetic analysis of *Sarcovenator eriensis* n. gen. et. sp. Character numbers refer to those in Lu and Zhu (2009), plus two additional characters from this analysis.

Character	000000000011111111112222222222333333333344
Number	12345678901234567890123456789012345678901
<i>Psarolepis</i>	101100001?010001100000000000000101011011??
<i>Styloichthys</i>	000100001?101101000101001?00101001?0011??
<i>Diplocercides</i>	01???00110?01110110??11-011?11000100100??
<i>O.sigmoides</i>	?????????????????1?11?????????????1?00
<i>O.jandamarrai</i>	01001112010101?00110111101101011010010011
<i>Strunius</i>	010??10100?????001100111?11110010100100??
<i>Qingmenodus</i>	??????120???011????00?11??11?0?1????????
<i>Grossius</i>	?????11201?????????0?111??10?0??01?0??0??
<i>Bukkanodus</i>	???01?011?????????1???11??01?0?1????100??
<i>Sarcovenator eriensis</i>	?????????????????0?????????10?????11?????1??11
end.	