

A preliminary note of egg-case oviparity in a Devonian placoderm fish

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ABSTRACT:

Carr, R.K. and Jackson, G. 2018. A preliminary note of egg-case oviparity in a Devonian placoderm fish. *Acta Geologica Polonica*, **68** (3), 381–389. Warszawa.

Six enigmatic fossils from the Famennian (Devonian) Cleveland Shale in Ohio, U.S.A., are interpreted here as arthrodiran (Placodermi) egg cases. Recognition as egg cases is confirmed based on the observation of layered collagen fibers. The presence of a tuberculated bone fragment preserved within one case confirms a vertebrate source. The nature of the tubercles and the unique morphology of the egg cases supports the interpretation of an arthrodiran source. Reports of Devonian egg cases are limited to either assumed chondrichthyan producers or a putative ‘egg sac’ with a morphology atypical for any vertebrate. The Cleveland Shale egg cases thus represent the first record for a non-chondrichthyan producer. Among placoderms, behaviors of a pelagic life style with obligate nesting sites, reef fishes with live birth, and estuarine and fluvial nurseries, along with egg-case oviparity testifies to the diversity of reproductive strategies. As with modern fishes these strategies may be ecologically driven and the derived and variable reproductive biology of extant chondrichthyans is actually a primitive condition among gnathostomes. One consequence of the diversity of reproductive strategies (dependent on the topology of relationships) is the independent origin of internal fertilization within placoderms, possibly suggesting external fertilization as the primitive gnathostome reproductive mode.

Key words: Devonian; Famennian; Cleveland Shale; Ohio; U.S.A.; Placodermi; Arthrodira; Oviparity; Egg Case.

INTRODUCTION

Vertebrate reproductive biology, specifically internal fertilization, has rarely been documented by fossils (Grogan and Lund 2004; Long *et al.* 2008 Cloutier 2010; Trinajstić *et al.* 2015). However, new discoveries among early gnathostomes (jawed vertebrates) have elucidated the origin of various reproductive strategies. The presence in the extinct Class Placodermi McCoy, 1848, of claspers (an intromittent organ) recognized in the Arthrodira Woodward, 1891, Ptyctodontida Gross, 1932, and Antiarchi Cope, 1885 (Ahlberg *et al.* 2009; Trinajstić *et al.* 2014; Long *et al.*

2015), the presence of *in situ* embryos in Arthrodira and Ptyctodontida (Long *et al.* 2009; Trinajstić *et al.* 2015), and one ptyctodontid embryo with a preserved umbilicus and yolk sac (Long *et al.* 2008) suggest that yolk-sac viviparity is a primitive condition among gnathostomes (refer to Musick and Ellis 2005, for the plesiomorphy of yolk-sac viviparity within chondrichthyans). Previously undetermined sources of Devonian ‘egg cases’ (Crookall 1928a; Chaloner *et al.* 1980) have limited the value of this evidence for the antiquity of egg-case oviparity. Here we document the first confirmed arthrodiran (Placodermi) egg-case based on the presence of embryonic dermal

bone. The morphology of the new egg cases and their uniqueness relative to extant chondrichthyan examples suggests an independent origin and the equal antiquity of chondrichthyan and placoderm egg-case oviparity. The presence of egg-cases and internalized embryos within a single order of placoderms (Arthrodira) indicates, as in modern chondrichthyans that the mode of reproductive biology may be an ecologically driven strategy (Wourms 1977; Dodd 1983; Wourms and Lombardi 1992). Both egg-case oviparity and viviparity represent early and successful strategies following the origin of internal fertilization.

MATERIALS AND METHODS

Table 1 lists the Cleveland Museum of Natural History specimens analyzed. This material was recovered from the Cleveland Shale Member of the Ohio Shale Formation (Upper Famennian, northern Ohio; *aculeatus* to *costatus-ultimus* Conodont Zones (Spalletta *et al.* 2017) with the top of the Cleveland Member not clearly defined. The black-shale facies of the Cleveland Shale represent distal sediments within the Appalachian Basin associated with an anoxic depositional environment (Carr 2010). The toxic and unstable nature of the sediments suggest that the fishes were restricted to life within the water column. The fauna associated with the Cleveland Shale represents the most speciose Famennian vertebrate fauna known (66 species; Carr 2010).

Scanning electron micrographs (SEM) were produced using a Cambridge Stereoscan S-240 SEM fitted with an Orion Digital Image Capture System. Fossil specimens were whitened with ammonium chloride sublimate for high contrast photography.

Institutional abbreviation: CMNH, Cleveland Museum of Natural History, Cleveland, Ohio.

RESULTS

Table 1 documents the dimensions (length and width) for the six egg-case specimens. The average width/length ratio for five of the six specimens is *ca.* 0.63. They share a similar morphology (Text-fig. 1), each with a surface ornament of rows of raised ribs (Text-figs 1, 2) and frilled edges (Text-figs 1, 3). The ultrastructure of the case consists of obliquely arranged layers of collagen fibers (Text-fig. 4A). Within a single specimen, dermal bone has been ex-

| CMNH# | Length (cm) | Width (cm) |
|-------|-------------|------------|
| 5309 | 25.4 | incomplete |
| 5978 | 24.1 | 17.8 |
| 8134 | 20.3 | 14.0 |
| 8135 | 22.9 | 12.7 |
| 8136 | 24.8 | 15.2 |
| 9461 | 22.9 | 12.7 |

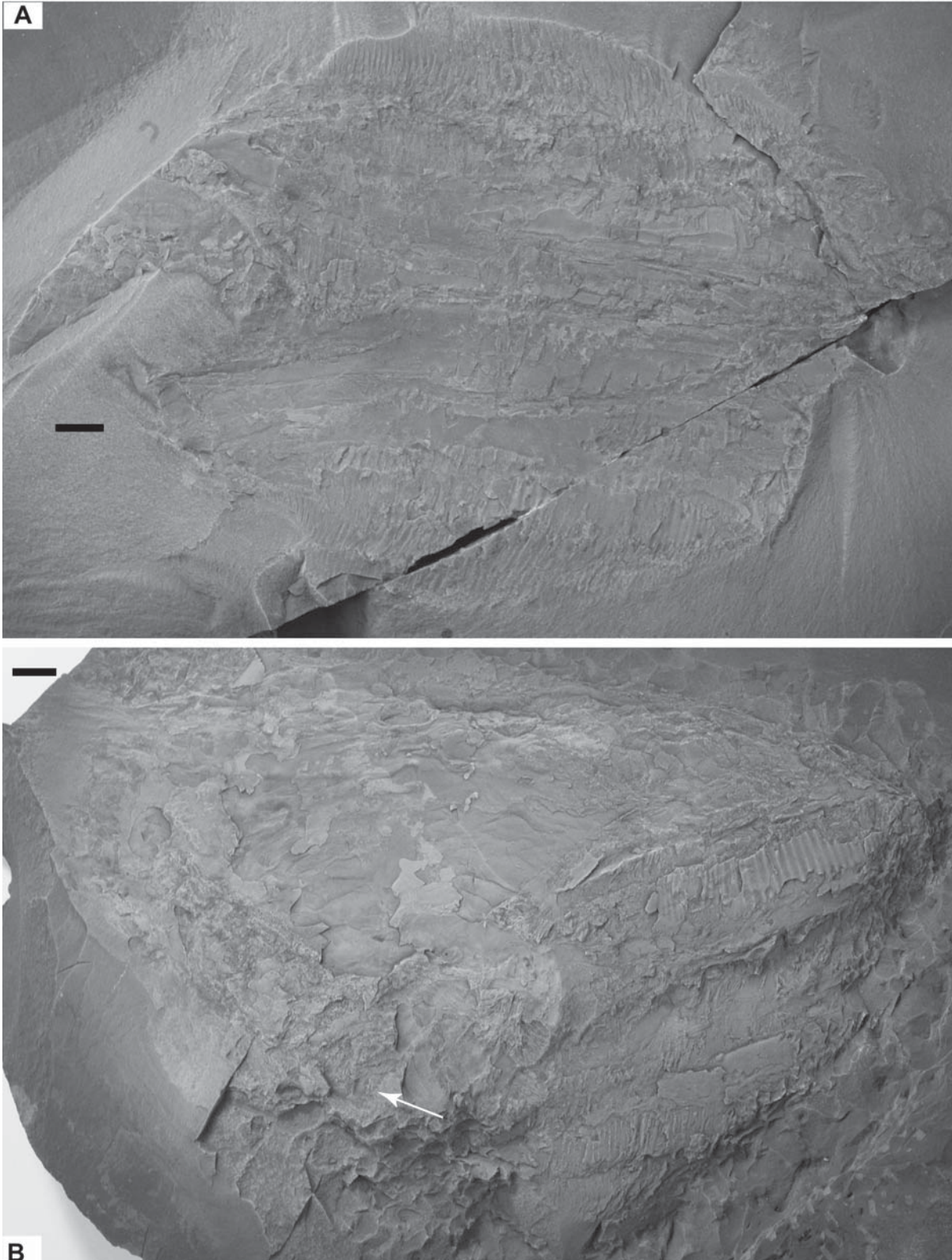
Table 1. Dimensions for the six known egg cases. CMNH#, Cleveland Museum of Natural History specimen number

posed beneath the egg-case covering and appears to represent content within the egg case rather than an object lying beneath (Text-fig. 1B). Its outline is unclear but possesses a surface ornament of tubercles (Text-fig. 4B).

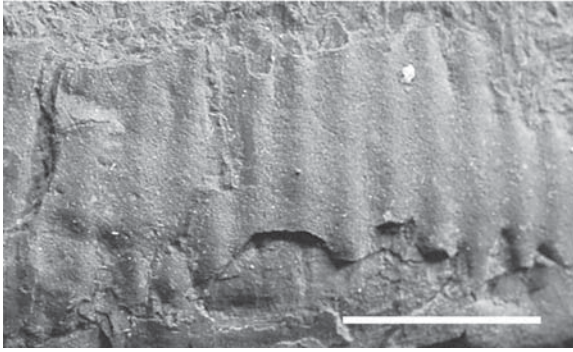
DISCUSSION

Among extant fishes, internal fertilization is ubiquitous among chondrichthyans (Wourms 1977) and restricted to a small minority among osteichthyans (Wourms and Lombardi 1992). For the chondrichthyans, modes of reproduction include oviparity (egg cases) and various forms of viviparity. The extant holocephalans are limited to the former while the elasmobranchs possess both modes with viviparity more common (Wourms and Lombardi 1992; Fischer *et al.* 2014). Oviparity has been considered the plesiomorphic condition based on its basal distribution among extant fishes (Wourms 1977; Fischer *et al.* 2014). However, the documentation of viviparity in Carboniferous holocephalans (Lund 1980; Grogan and Lund 2004, 2011) suggests that viviparity may be the chondrichthyan plesiomorphic condition (Grogan and Lund 2004; Musick and Ellis 2005).

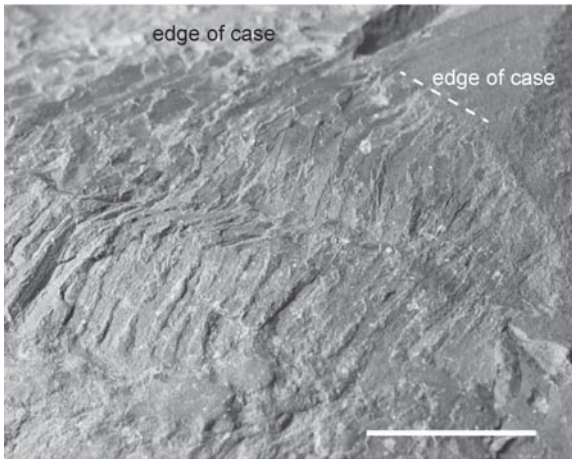
Fischer *et al.* (2014) described nine egg capsule morphotypes with four genera having a fossil record extending back to the Paleozoic (*Fayolia* Renault and Zeiller, 1884, Late Devonian–Middle Triassic; *Vetacapsula* Mackie, 1867, and *Crookallia* Chabakov, 1949, Pennsylvanian; and *Palaeoxyris* Brongniart, 1828, Middle Mississippian–Late Cretaceous). Of the nine morphotypes, only *Fayolia* is known from the Devonian (Fischer *et al.* 2014). The examples Crookall (1928b) referred to *Vetacapsula* Mackie, 1867, and *Palaeoxyris* Brongniart, 1828, remain as unconfirmed egg cases, i.e., form-genera considered as chondrichthyan egg cases based on general similarities to extant egg cases (Zidek 1976; McGhee and Richardson 1982). Their temporal distribution does not extend to the Devonian (Zidek 1976; Fischer



Text-fig. 1. Arthrodire (Placodermi) egg cases. Each egg case is preserved in part and counter-part with only one-half of each specimen shown. A – CMNH 8135; B – CMNH 5978, arrow indicates region of partially exposed bone (see Text-fig. 4B for a close-up). Both specimens whitened with ammonium chloride sublimate. Scale bar = 1 cm



Text-fig. 2. CMNH 5978 – close up of a row of raised ribs. Whitened with ammonium chloride sublimate. Scale bar = 1 cm



Text-fig. 3. CMNH 5978 – close up of the egg case edge. Whitened with ammonium chloride sublimate. Scale bar = 1 cm

et al. 2014). If verified as egg cases, their distribution in the Carboniferous (both genera) and into the Mesozoic (*Palaeoxyris*) would indicate a chondrichthyan source. *Crookallia* is also restricted to the Carboniferous (Fischer *et al.* 2014).

There are three reports of Devonian egg cases and one report of an egg sac. *Fayolia* (*Spiraxis* of Stainier, 1894, and Newberry, 1885; synonymized with *Fayolia* in Crookall's 1928 revision of the genus) is known from the Famennian of Belgium (Stainier 1894) and the Frasnian of the U.S.A. (Newberry 1885). An unnamed egg case is described by Chaloner *et al.* (1980) from the Middle or Upper Devonian of South Africa. Finally, Ritchie (2005, p. 235) reported an apparent "egg sac" from the Late Givetian to Early Frasnian of Australia. *Fayolia*, although it is known from the Devonian, has a temporal distribution from the Late Devonian to the Middle Triassic (Fischer *et al.* 2014) that preclude placoderms as its producer.

Fischer and Kogan (2008) note a likely assignment to xenacanthid sharks.

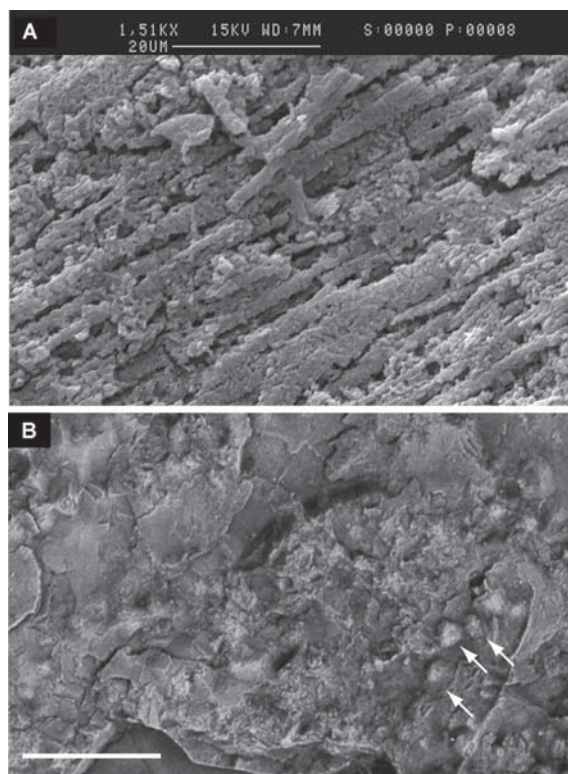
Chaloner *et al.* (1980) noted a similarity to chimaeroid egg cases for their South African specimen (morphologically indistinguishable from that of extant chimaerids, e.g., *Callorhinchus* La Cépède, 1798, shaped like a spindle with thin lateral longitudinal flanges that are marked by radiating ridges). However, they considered a possible placoderm producer for the egg case based on an unsupported parsimony argument and the need for an extended ghost lineage for the Chimaeroidei (extending their known range from the Jurassic to the Devonian). Their underlying phylogeny was based on a currently unsubstantiated monophyletic Elasmobranchiomorpha Jarvik, 1955 (placoderms and chondrichthyans as sister groups). Fischer *et al.* (2014) noted the resemblance between the South African specimen and chimaerids; however, they also consider the potential producer to be an arthrodire due to the total absence of holocephalian fossils within the adjoining sediments (an application of negative evidence). Earlier, Fischer and Kogan (2008) noted the often lack of direct evidence for establishing a link between an egg case and its producer (either identifiable egg-case contents or an internalized case within the body of the producer). This is the case here for the South African specimen. Additionally, recent finds have extended the fossil record for holocephalans to the Middle Devonian (Darras *et al.* 2008).

The remaining Devonian occurrence is the single "egg sac" reported by Ritchie (2005, p. 235) from the Merriganowry Shale. This specimen consists of a natural mold that "contains perhaps 200 tightly packed, uniform, oval bodies, each 3–4 mm long and oriented parallel to or slightly oblique to the long axis of the whole mass." Due to the tight packing, Ritchie hypothesized that the bodies were encased in a membrane or sac. Although he noted the preservation of a single species of a phyllolepid placoderm (*Cowralepis mclachlani*), "possible thelodont scales (in coprolites), and rare eurypterid fragments," Ritchie limited his interpretation to the possibility that the fossil represents unhatched fish eggs. This locality is unique for several reasons: (1) it is limited to a single fish species; (2) there are a large number of specimens (several hundred at the time of publication and more since); (3) the large number of fully articulated specimens with tails; and (4) the full range of age classes. Despite the vast amount of material there is no direct evidence of the reproductive mode for *Cowralepis*. Although negative evidence, this is the one locality where you might expect to find a direct

association between a producer and its reproductive mode. Since the described “egg sac” is atypical for fishes, an equally plausible hypothesis might relate the “egg sac” to arthropods (e.g., eurypterids) or other invertebrates (e.g., molluscs) within the fauna.

Among the placoderms, internal fertilization was originally inferred for the Order Ptyctodontida Gross, 1932, based on the presence of claspers (e.g., Miles 1967). The early debate concerning these structures centered on the question of homology of the ptyctodont clasper (given the limited distribution among placoderms known at the time) with the condition found in chondrichthyans. Young (1986) summarized the historical debate. However, since that time the limited distribution of claspers among placoderms has expanded to include antiarchs (Long *et al.* 2015), several arthrodires, and additional ptyctodonts (Trinajstić *et al.* 2015). The discovery of *in situ* embryos in arthrodires (Long *et al.* 2009) and an embryo with an umbilicus and yolk sac in ptyctodonts (Long *et al.* 2008) provides evidence for the occurrence of viviparity in placoderms. However, the recent discovery of placoderm egg cases (Text-fig. 1) is a testament to the equivalent antiquity for this mode of reproduction.

The six placoderm egg cases (Table 1) recovered from the Cleveland Shale Member of the Ohio Shale Formation share a similar morphology (frilled edges and rows of raised ridges) that is distinct from known chondrichthyan egg cases. The ultrastructure of the cases is similar to that in extant elasmobranchs consisting of obliquely arranged layers of collagen fibers (Text-fig. 4A). The presence of a structurally-reinforced ribbed ornament and multiple collagen layers distinguish this example of egg-case oviparity from retained egg-capsule oviparity (Lombardi and Files 1993; Wourms 1994) with the latter possessing reduced thickness and complexity. The dermal bone found within a single egg-case specimen possesses a surface ornament of tubercles (Text-fig. 4B). The position of the fragment suggests it is contained within the egg case and not merely an associated fragment from another source. It should be noted that the smallest juveniles of the antiarch *Asterolepis ornata* (Upeniec 2001) lack tubercles and possess dermal bone with an open weave or reticulate pattern. A similar pattern is seen in most of the embryonic bones in the arthrodire *Incisoscutum ritchei* (Long *et al.* 2009); however, Johanson and Trinajstić (2014) note the limited development of tubercles on an embryonic median dorsal plate (Johanson and Trinajstić 2014, fig. 2D). The outline of the bone is unclear so the exact source (specific dermal plate) cannot be de-



Text-fig. 4. A – CMNH 8136, SEM of collagenous fibers taken from a row of raised ribs. Individual fibers are covered, in part, by preserved bacteria. Scale bar = 20 μ m. B – CMNH 5978, preservation of partially exposed embryonic bone (Text-fig. 1B, location within the egg case indicated by an arrow). The bone lies beneath the superficial layers of the egg case and above the layer representing the opposite side of the egg case. Arrows indicate individual dermal tubercles. Figure B whitened with ammonium chloride sublimate. Scale bar = 0.25 cm

termined. Tuberculation near the ossification center of a dermal plate is a feature seen in several of the arthrodire taxa in the Cleveland Shale fauna.

An assignment of the egg-case to arthrodires is based on the known presence of tubercles in Cleveland Shale arthrodires and the lack of tubercles in any of the chondrichthyans in the fauna. *Ctenacanthus* possesses pectinated ridges on its spines, *Stethacanthus* and *Cladoselache* have no ornament on their spines, and tuberculated spines are not associated with other Cleveland Shale chondrichthyans known only from isolated teeth or body parts (Zangerl 2004; John Maisey, personal communication 2017). An alternative source for tuberculated bone includes the acanthodians. Acanthodians remains are not known from the Cleveland Shale. The report of a single spine, attributed to the acanthodian *Hoplonchus parvulus* (Newberry, 1875) by Denison (1979) actually

represents the cephalic spine of an unnamed shark (Michael Williams, personal communication 2003). Additionally, the pattern of tuberculation seen in the egg-case (Text-fig. 4B) does not match known acanthodian spines from the Devonian (Denison 1979).

In extant chondrichthyans, egg cases of similar size are known from whale sharks, holocephalans, and skates. Considering the whale shark as an analogue (an egg case of 30 cm by 17 cm in *Rhincodon typus* Smith, 1828; Baughman 1955; Joung *et al.* 1996), the dimensions of the Cleveland Shale egg cases have lengths that range from 68% to 85% and widths ranging from 85% to 119% of that in *R. typus*. Within the Cleveland Shale fauna, several taxa reach a size (total length) comparable to a mature whale shark (approximately 8 m, Norman and Stevens 2007), for example, *Dunkleosteus* Lehman, 1956 (Carr 2010) and *Titanichthys* Newberry, 1885. *Dunkleosteus* (Carr 2010) and likely *Titanichthys* are pelagic fishes ranging throughout the epicontinental sea of the Appalachian Basin. The range of *Dunkleosteus* further includes California (Dunkle and Lane 1971), Texas (Dunkle and Wilson 1952), and Morocco (Lehman 1956) with an indeterminate dunkleosteid reported from Bolivia (Díaz-Martínez *et al.* 1996). Within the distal parts of the Appalachian Basin the benthos is inhospitable (anoxic and H₂S-rich sediments; Carr 2010). The Cleveland Shale egg cases lack tendrils that would allow their attachment to floating substrates within the basin, thus implying that at least one of the large pelagic species relied on shallow-water nesting sites (analogous to extant holocephalans depositing their egg cases “on or near the bottom”; Wourms 1977, p. 392).

Both oviparity and viviparity possess a fossil record (Chaloner *et al.* 1980; Lund 1980; Grogan and Lund 2004, 2011; Musick and Ellis 2005; Long *et al.* 2008, 2009; Ahlberg *et al.* 2009; Cloutier 2010; Fischer *et al.* 2014; Trinajstić *et al.* 2015). Resolving whether oviparity or viviparity is the plesiomorphic mode of reproduction requires an analysis of the fossil record for the Devonian Period and consideration of potential sister groups to chondrichthyans and osteichthyans, either the Class Placodermi (Schaeffer and Williams 1977; Goujet and Young 2004; Young 2008, 2010; King *et al.* 2017) or subgroups if the placoderms are paraphyletic (Brazeau 2009; Davis *et al.* 2012; Long *et al.* 2015).

Summary statements about the antiquity of internal fertilization are dependent both on the evidence for an intromittent organ (or internalized embryos) and a parsimony argument based on its distribution among basal gnathostomes. In paraphyletic-hypothese

for placoderms, the sister group to all other gnathostomes (the antiarchs) have been shown to possess both pelvic fins and claspers within the group (Long *et al.* 2015). It is on this basis that Long *et al.* (2015, p. 196) proposed that external fertilization in extant fishes, although “implausible,” was derived from internal fertilization (a loss of the plesiomorphic condition of internal fertilization in stem gnathostomes).

The latest monophyletic-hypothesis for placoderms (King *et al.* 2017) also suggests that pelvic fins are a gnathostome plesiomorphic character; however, the basal placoderm groups (rhenanids of King *et al.* 2017; or acanthothoracids and rhenanids of Goujet and Young 2004) have not been shown to possess claspers (missing data or absent). Although the absence of claspers represents negative evidence, it does leave open the alternative hypothesis that the origin of an intromittent organ is a possible derived character within the gnathostomes.

The distribution of character states in the monophyletic-hypothesis eliminates the “implausible” by suggesting that the primitive gnathostome condition was external fertilization and that internal fertilization (associated with the development of an intromittent organ) was independently derived within the placoderm clade and a second time well-within the crown gnathostomes (Long *et al.* 2015, fig. 4). This is supported by four observations. First is the lack of data to extend the distribution of claspers to the base of the placoderm clade (rhenanids or acanthothoracids and rhenanids). Second is the unique structure and separation of an intromittent organ from the pelvic girdle in placoderms (Trinajstić *et al.* 2015; Trinajstić *et al.* 2014; Long *et al.* 2015) in contrast to the condition in chondrichthyans. Third is the proposal that the placoderm clasper may represent a developmental competence-stripe for a paired appendage found posterior to the paired pelvic appendage unlike the condition in other gnathostomes (Trinajstić *et al.* 2015; Trinajstić *et al.* 2014; Sansom *et al.* 2013 record the presence of paired anal fins in the agnathan *Euphanerops*, but note a lack of homology with the gnathostome paired pelvic fin or single anal fin). Finally, the fourth observation is that the only other documented occurrence of claspers is found well-embedded within the crown gnathostomes and consists of an endoskeletal modification of the pelvic girdle/fin in contrast to the placoderm condition (Trinajstić *et al.* 2014, 2015; Long *et al.* 2015).

The complex behaviors of a pelagic life style with obligate nesting sites (Carr 2010), reef fishes with live birth (Long *et al.* 2008), estuarine nurseries (Gess and Trinajstić 2017), and fluvial nurseries

(Olive *et al.* 2016; paleoenvironmental interpretation by Denayer *et al.* 2015) testify to the diversity of reproductive behaviors in such a small sample of placoderms. This implies that a broader search among placoderms and other Paleozoic fishes has a great potential for aiding our understanding of gnathostome reproductive biology. The presence of both yolk-sac viviparity and egg-case oviparity in basal gnathostomes (Placodermi) suggests that the derived and variable reproductive biology of extant chondrichthyans is actually a primitive condition among gnathostomes with both approaches representing early and successful strategies.

Acknowledgments

It was Gary Jackson who brought to my attention these interesting fossils, which had been sitting in the collections at the CMNH for decades. That began our joint work on this project. It is with sadness that Gary will not see the culmination of our work. Gary and I worked on a second project published in this volume, but with his passing, and in his honor, a new species was erected in his name (*H. jacksoni*). I thank J. Long for discussions on an early draft of the manuscript and his current review, also K. Trinajstić for her review, M. Ryan for access to the Cleveland Museum of Natural History collections, and R. Feldman for access to photographic whitening equipment. I also thank I. Miller and the Neuroscience Program, Ohio University, for SEM microscopy assistance. Supported, in part, by an Ohio University Research Challenge grant.

REFERENCES

- Ahlberg, P., Trinajstić, K., Johanson, Z. and Long, J. 2009. Pelvic claspers confirm chondrichthyan-like internal fertilization in arthrodires. *Nature*, **460**, 888–889.
- Baughman, J.L. 1955. The oviparity of the whale shark, *Rhincodon typus*, with records of this and other fishes in Texas waters. *Copeia*, **1955**, 54–55.
- Brazeau, M.D. 2009. The braincase and jaws of a Devonian ‘acanthodian’ and modern gnathostome origins. *Nature*, **457**, 305–308.
- Brongniart, A. 1828. Essai d’une Flore du gres bigarré. *Annales des sciences naturelles*, **15**, 435–460.
- Carr, R.K. 2010. Paleocology of *Dunkleosteus terrelli* (Placodermi: Arthrodira). *Kirtlandia*, **57**, 36–45.
- Chabakov, A.W. 1949. About two new problematic fossil *Crookallia* from the Carboniferous of Donetz Basin and *Palaeoxyris* from the Jurassic of Crimea. *Annual of the All-Union Paleontological Society*, **13**, 83–87. [In Russian]
- Chaloner, W.G., Forey, P.L., Gardiner, B.G., Hill, A.J. and Young, V.T. 1980. Devonian fish and plants from the Bokkeveld Series of South Africa. *Annals of the South African Museum*, **81**, 127–156.
- Cloutier, R. 2010. The fossil record of fish ontogenies: insights into developmental patterns and processes. *Seminars in Cell & Developmental Biology*, **21**, 400–413.
- Cope, E.D. 1885. The position of *Pterichthys* in the system. *American Naturalist*, **19**, 289–291.
- Crookall, R. 1928a. The genus *Fayolia*. *The Naturalist*, **862**, 325–332, 361–367.
- Crookall, R. 1928b. Paleozoic species of *Vetacapsula* and *Palaeoxyris*. *Memoir of the Geological Survey of Great Britain, Summary of Progress for 1927*, **2**, 87–107.
- Darras, L., Derycke, C., Blicek, A. and Vachard, D. 2008. The oldest holocephalan (Chondrichthyes) from the Middle Devonian of the Boulonnais (Pas-de-Calais, France). *Comptes Rendus Palevol*, **7**, 297–304.
- Davis, S.P., Finarelli, J.A. and Coates, M.I. 2012. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature*, **486**, 247–250.
- Denayer, J., Prestianni, C., Gueriau, P., Olive, S. and Clément, G. 2015. Stratigraphy and depositional environments of the Late Famennian (Late Devonian) of Southern Belgium and characterization of the Strud locality. *Geological Magazine*, **153**, 112–127.
- Denison, R. 1979. *Acanthodii*. In: Schultze, H.-P. (Ed.), *Handbook of Paleichthyology* 5, pp. 1–62. Gustav Fischer Verlag; Stuttgart.
- Díaz-Martínez, E., Suárez-Riglos, M., Lelièvre, H. and Janvier, P. 1996. Première découverte d’un Arthrodire (Placodermi, Vertebrata) dans le Dévonien d’Amérique du Sud. *Comptes rendus de l’Académie des sciences*, **349**, 349–356.
- Dodd, J.M. 1983. Reproduction in cartilaginous fishes (Chondrichthyes). In: Hoar, W.S., Randall, D.J. and Donaldson, E.M. (Eds), *Fish Physiology*, Vol. IX: Reproduction, Part A: Endocrine Tissues and Hormones, pp. 31–95. Academic Press; New York.
- Dunkle, D.H. and Lane, N.G. 1971. Devonian fishes from California. *Kirtlandia*, **15**, 1–5.
- Dunkle, D.H. and Wilson, J.A. 1952. Remains of Devonian fishes from Texas. *Journal of the Washington Academy of Science*, **42**, 213–215.
- Fischer, J. and Kogan, I. 2008. Elasmobranch egg capsules *Palaeoxyris*, *Fayolia* and *Vetacapsula* as subject of palaeontological research – an annotated bibliography. *Freiberger Forschungshefte C*, **528**, 75–91.
- Fischer, J., Licht, M., Kriwet, J., Schneider, J.W., Buchwitz, M. and Bartsch, P. 2014. Egg capsule morphology provides new information about the interrelationships of chondrichthyan fishes. *Journal of Systematic Palaeontology*, **12**, 389–399.
- Gess, R.W. and Trinajstić, K.M. 2017. New morphological information on, and species of placoderm fish *Africanaspis*

- (Arthrodira, Placodermi) from the Late Devonian of South Africa. *PLoS ONE* **12**, e0173169. <https://doi.org/10.1371/journal.pone.0173169>.
- Goujet, D. and Young, G.C. 2004. Placoderm anatomy and phylogeny: new insights. In: Arratia, G., Wilson, M.V.H. and Cloutier, R. (Eds), Recent Advances in the Origin and Early Radiation of Vertebrates, pp. 109–126. Verlag Dr Friedrich Pfeil; München.
- Grogan, E.D. and Lund, R. 2004. The origin and relationships of early Chondrichthyes. In: Carrier, J.C., Musick, J.A. and Heithaus, M.R. (Eds), Biology of Sharks and Their Relatives, pp. 3–31. CRC Press; Boca Raton, Florida.
- Grogan, E.D. and Lund, R. 2011. Superfoetative viviparity in a Carboniferous chondrichthyan and reproduction in early gnathostomes. *Zoological Journal of the Linnean Society*, **161**, 587–594.
- Gross, W. 1932. Die Arthrodira Wildungens. *Geologische und Paläontologische Abhandlungen (Neue folge)*, **19**, 1–61.
- Jarvik, E. 1955. The oldest tetrapods and their forerunners. *Scientific Monthly*, **80**, 141–154.
- Johanson, Z. and Trinajstić, K. 2014. Fossilized ontogenies: the contribution of placoderm ontogeny to our understanding of the evolution of early gnathostomes. *Palaeontology*, **57**, 505–516.
- Joung, S.-J., Chen, C.-T., Clark, E., Uchida, S. and Huang, W.Y.P. 1996. The whale shark, *Rhincodon typus*, is a live-bearer: 300 embryos found in one ‘megamamma’ supreme. *Environmental Biology of Fishes*, **46**, 219–223.
- King, B., Qiao, T., Lee, M.S.Y., Zhu, M. and Long, J.A. 2017. Bayesian morphological clock methods resurrect placoderm monophyly and reveal rapid early evolution in jawed vertebrates. *Systematic Biology*, **66**, 499–516.
- La Cépède, J.-B.P. 1798. Histoire Naturelle des Poissons. Tome Premier, 532 p. Chez Plassan, Imprimeur Libraire; Paris.
- Lehman, J.P. 1956. Les arthrodiras du Dévonien supérieur du Tafilalet (sud marocain). *Notes et Mémoires du Service Géologique du Maroc*, **129**, 4–70.
- Lombardi, J. and Files, T. 1993. Egg capsule structure and permeability in the viviparous shark, *Mustelus canis*. *Journal of Experimental Biology*, **267**, 76–85.
- Long, J.A., Mark-Kurik, E., Johanson, Z., Lee, M.S.Y., Young, G.C., Min, Z., Ahlberg, P.E., Newman, M., Jones, R., Blauwien, J., den, Choo, B. and Trinajstić, K. 2015. Copulation in antiarch placoderms and the origin of gnathostome internal fertilization. *Nature*, **517**, 196–199.
- Long, J., Trinajstić, K. and Johanson, Z. 2009. Devonian arthrodira embryos and the origin of internal fertilization in vertebrates. *Nature*, **457**, 1124–1127.
- Long, J., Trinajstić, K., Young, G.C. and Senden, T. 2008. Live birth in the Devonian period. *Nature*, **453**, 650–652.
- Lund, R. 1980. Viviparity and interuterine feeding in a new holcephalan fish from the Lower Carboniferous of Montana. *Science*, **209**, 697–699.
- Mackie, S.J. 1867. Undescribed Vegetable Fossil. *The Geological and Natural History Repertory*, **1** (1865–67), 79–80.
- McCoy, F. 1848. On some new fossil fish of the Carboniferous period. *Annals and Magazine Natural History*, **2**, 1–10, 115–134.
- McGhee, G.R., Jr. and Richardson, E.S., Jr. 1982. First occurrence of the problematic fossil *Vetacapsula* in North America. *Journal of Paleontology*, **56**, 1295–1296.
- Miles, R.S. 1967. Observations on the ptyctodont fish, *Rhamphodopsis* Watson. *Zoological Journal of the Linnean Society*, **47**, 99–120.
- Musick, J.A. and Ellis, J.K. 2005. Reproductive evolution of chondrichthyans. In: Hamlett, W.C. (Ed.), Reproductive Biology and Phylogeny of Chondrichthyes, pp. 45–79. Science Publishers; Enfield.
- Newberry, J.S. 1875. Description of fossil fishes. In: Report of the Geological Survey of Ohio; Volume II, Geology and Palaeontology; Part II, Palaeontology, pp. 1–64. Nevins & Myers, State Printers; Columbus, Ohio.
- Newberry, J.S. 1885. Descriptions of some gigantic placoderm fishes recently discovered in the Devonian of Ohio. *Transactions of the New York Academy of Sciences*, **5**, 25–28.
- Norman, B.M. and Stevens, J.D. 2007. Size and maturity status of the whale shark (*Rhincodon typus*) at Ningaloo Reef in Western Australia. *Fisheries Research*, **84**, 81–86.
- Olive, S., Clément, G., Daeschler, E.B. and Dupret, V. 2016. Placoderm assemblage from the tetrapod-bearing locality of Strud (Belgium, Upper Famennian) provides evidence for a fish nursery. *PLoS ONE*, **11**, e0161540. doi:10.1371/journal.pone.0161540.
- Renault, B. and Zeiller, R. 1884. Sur un nouveau genre de fossils végétaux. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences*, **98**, 1391–1394.
- Ritchie, A. 2005. *Cowralepis*, a new genus of phyllolepid fish (Pisces, Placodermi) from the Late Middle Devonian of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales*, **126**, 215–259.
- Sansom, R.S., Gabbott, S.E. and Purnell, M.A. 2013. Unusual anal fin in a Devonian jawless vertebrate reveals complex origins of paired appendages. *Biology Letters*, **9**, 20130002. <http://dx.doi.org/10.1098/rsbl.2013.0002>.
- Schaeffer, B. and Williams, M. 1977. Relationships of fossil and living elasmobranchs. *American Zoologist*, **17**, 293–302.
- Smith, A. 1828. Descriptions of new, or imperfectly known objects of the animal kingdom, found in the south of Africa. *South African Commercial Advertiser* (Nov. 5), **3**, 2.
- Spalletta, C., Perri, M.C., Over, D.J. and Corradini, C. 2017. Famennian (Upper Devonian) conodont zonation: revised global standard. *Bulletin of Geosciences* **92**, 31–57.
- Stainier, X. 1894. Un *Spiraxix* nouveau du Devonien Belge. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie*, **8**, 23–28.
- Trinajstić, K., Boisvert, C., Long, J., Maksomenko, A. and

- Johanson, Z. 2015. Pelvic and reproductive structures in placoderms (stem gnathostomes). *Biological Reviews*, **90**, 467–501.
- Trinajstić, K., Johanson, Z., Mark-Kurik, E., Zhu, M., Lee, M., Young, G., Boisvert, C. and Long, J. 2014. The diversity of copulatory structures and reproductive strategies in stem gnathostomes. *Journal of Vertebrate Paleontology, Program and Abstracts*, **2014**, 241.
- Upeniec, I. 2001. The unique fossil assemblage from the Lode Quarry (Upper Devonian, Latvia). *Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaften Reihe*, **4**, 101–119.
- Woodward, A.S. 1891. Catalogue of the fossil fishes in the British Museum (Natural History), Part II, 567 p. Taylor & Francis; London.
- Wourms, J.P. 1977. Reproduction and development in chondrichthyan fishes. *American Zoologist*, **17**, 379–410.
- Wourms, J.P. 1994. Chondrichthyan egg cases: comparative ultrastructure and morphogenesis. *Journal of Morphology*, **220**, 411–412.
- Wourms, J.P. and Lombardi, J. 1992. Reflections on the evolution of piscine viviparity. *American Zoologist*, **32**, 276–293.
- Young, G.C. 1986. The relationships of placoderms. *Journal of Vertebrate Paleontology*, **4**, 379–395.
- Young, G.C. 2008. The relationships of antiarchs (Devonian placoderm fishes) – evidence supporting placoderm monophyly. *Journal of Vertebrate Paleontology*, **28**, 626–636.
- Young, G.C. 2010. Placoderms (armored fish): dominant vertebrates of the Devonian Period. *Annual Review of Earth Planetary Sciences*, **38**, 523–550.
- Zangerl, R. 2004. Chondrichthyes I. In: Schultze, H.-P. (Ed.), *Handbook of Paleichthyology* 3A, pp. 1–115. Verlag Dr. Friedrich Pfeil; München.
- Zidek, J. 1976. A new shark egg capsule from the Pennsylvanian of Oklahoma, and remarks on the chondrichthyan egg capsules in general. *Journal of Paleontology*, **50**, 907–915.

Manuscript submitted: 16th October 2017

Revised version accepted: 26th June 2018