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DIPLOGNATHUS LAFARGEI SP. NOV. FROM THE ANTRIM SHALE (UPPER DEVONIAN) OF THE MICHIGAN BASIN, MICHIGAN, USA

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ABSTRACT - Devonian fishes of the Michigan Basin are poorly documented; however, recent fieldwork has demonstrated a relatively rich vertebrate fauna in both the Middle and Upper Devonian sediments. The current study presents the first of this material, with description of a new species of *Diplognathus* Newberry, *Diplognathus lafargei* n. sp., from the Antrim Shale (Upper Devonian). Based on a single specimen, *Diplognathus lafargei* possesses a number of derived features that help to determine its phylogenetic assignment. Fused occlusal and non-occlusal regions of the inferognathal indicate a eubrachythoracid arthrodiran level of organization. Within this clade, the form of the suborbital (elongated anterior process beneath the orbit and a reduced posterior portion) and posterior ventrolateral (elongated) plates indicates assignment to the aspinothoracid arthrodires. Assignment to *Diplognathus* is based on the large portion of the inferognathal occupied by the occlusal region (about 58.1%) and the possession of well-spaced and relatively large denticles (teeth) on the gnathal plates. Characterizing the new species, *Diplognathus lafargei*, is the depth of the inferognathal relative to the type species, *Diplognathus mirabilis*; the proportions of the occlusal surface for the superognathals, with the posterior superognathal much longer than the anterior superognathal (opposite to that in *Diplognathus mirabilis*); and the form of the posterior ventrolateral plate. *Diplognathus* is assigned to the Aspinothoracidi (Arthrodira) *incertae sedis*.

Key words: Placodermi, Arthrodira, Aspinothoracidi, Devonian, Michigan Basin.

RESUMO – Os peixes devonianos da Bacia de Michigan são pobremente documentados. Todavia, recente trabalho de campo nessa bacia demonstrou a ocorrência de uma fauna relativamente rica nos sedimentos devonianos médios e superiores. Este estudo apresenta parte desses materiais, com a descrição de uma nova espécie de *Diplognathus* Newsberry, *Diplognathus lafargei* n. sp., do Antrim Shale (Devoniano Superior), bacia de Michigan, USA. Baseado em um único espécimen, *Diplognathus lafargei* n. sp. possui um número de características derivadas que auxiliam a determinar o seu posicionamento filogenético. A presença de regiões oclusais e não-oclusais fusionadas do inferognatal indica um nível de organização de artrodira eubraquitoracida. Dentro deste grande clado, a forma das placas suborbital e ventrolateral posterior indica afinidade com arthodiros aspinothoracídeos. A identificação com *Diplognathu*s baseia-se na grande porção do inferognatal ocupada pela região oclusal (cerca de 58.1%) e por possuir dentículos relativamente grandes e bem espaçados nas placas gnatais. *Diplognathus lafargei* n. sp. é caracterizado pela altura do inferognatal em relação a espécie-tipo, *D. mirabilis*; as proporções da face oclusal dos superognatais, com o superognatal posterior bem mais longo que o anterior (ao contrário do que ocorre em *D. mirabilis*); e pela forma da placa ventro-lateral posterior. *Diplognathus* é classificado em Aspinothoracidi (Arthrodira) *incertae sedis*.

Palavras-chave: Placodermi, Arthrodira, Aspinothoracidi, Devoniano, bacia de Michigan.

INTRODUCTION

Our understanding of Devonian fishes from the Michigan Basin is limited, with most of the research on Devonian vertebrate paleontology in the mid-continent of America centered on the Appalachian Basin, including both the Catskill Delta and its distal sediments (Elliot *et al*., 2000). The Devonian sediments of the Michigan and Appalachian Basins are laterally equivalent, but the basins are separated by the Cincinnati-Findlay-Algonquin Arch (Elliot *et al*., 2000:figs. 2-3). The potential of the arch as a biological isolating mechanism is still debated (Gutschick & Sandberg, 1991), although lithological similarities between the basins for Middle and Upper Devonian sediments may suggest similar habitats and thus similar faunas. A first step in a comparison of the basins is to review the Michigan Basin vertebrate fauna. Case (1931) provides the largest single description of fishes from the basin while other limited work primarily adds individual taxa to the faunal list (e.g., Schultze, 1982; Stevens, 1964). Invertebrate research within the Michigan Basin Middle Devonian ignored vertebrate remains. However, Ehlers & Kesling (1970) did note the presence of fish remains in the Upper Devonian Antrim Shale, but stated that their rarity and the difficulty to extract them from large spherical concretions prohibited any meaningful collection.

Recent fieldwork within the basin has demonstrated a relatively rich vertebrate fauna in both the Middle and Upper Devonian sediments. This paper presents the first study on this material.

MATERIALS AND METHODS

The holotype and only specimen was prepared using sodium bicarbonate air abrasion. Photographs are whitened with ammonium chloride except in cases where surface contours are too small to reveal the shape of individual plates. In this case, natural light and color of the bone was used to distinguish the plate. The suffix "id" when used to form taxonomic adjectives does not refer to the familial level in Linnean classification, but is used as a convenience for discussing informal taxonomic units. The anatomical abbreviations used in the text and figures follow Dennis-Bryan (1987) and Carr (1991).

Institutional abbreviations. CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; **AMNH**, American Museum of Natural History, New York.

Anatomical abbreviations. a.Au, depression for autopalatine; **ASG**, anterior superognathal; **cr.po**, postocular crista; **cr.sau**, subautopalatine crista; **cr.so**, subocular crista; **frag.surf**, fragmented surface of ASG suggesting missing medial extension; **IG**, inferognathal; **ioc.pt**, postorbital branch of the infraorbital canal groove; **ioc.sb**, suborbital branch of the infraorbital canal groove; **PSG**, posterior superognathal; **PVL**, posterior ventrolateral plate; **SO**, suborbital plate; **sorc**, supraoral sensory canal groove.

SYSTEMATIC PALEONTOLOGY

PLACODERMI McCoy, 1848
ARTHRODIRA Woodward, 1891
BRACHYTHORACI Gross, 1932
EUBRACHYTHORACIDI Miles, 1971
ASPINOTHORACIDI (*sensu* Miles & Dennis, 1979)
Diplognathus Newberry,1878

Type Species. *Diplognathus mirabilis*.

Holotype. AMNH 12, a right inferognathal.

Remarks on known material. Another specimen (pertinent to this discussion) described by Dunkle & Bungart (1943), CMNH 7255 (Figure 1A), consists of right and left inferognathals, left posterior superognathal and suborbital plates, and mentomandibular ossifications of Meckel's cartilage, along with other unidentified elements.

Diagnosis. An aspinothoracid arthrodire that possesses an obtuse orbital margin on the suborbital plate suggesting a relatively large orbit. The gnathal plates are characterized by large well-spaced denticles (teeth) that may be recurved and an elongate occlusal region relative to the non-occlusal portion of the inferognathal.

Diplognathus lafargei sp. nov.
(Figures 1B, 2-5)

Holotype. CMNH 50215, an incomplete disarticulated specimen (Figure 2). No additional material is known. Recognized elements include paired suborbital and anterior superognathal plates, right inferognathal, and single posterior superognathal and posterior ventrolateral plates.

Locality and Horizon. The type specimen was found on a talus slope in the Paxton Quarry (Lafarge North America, Inc., Alpena Cement Plant, Great Lakes Region), Alpena, MI. The only horizon source for the fossil, based on its position on the slope, is the upper Paxton Member (Frasnian) or lower Lachine Member (Famennian, only approximately one meter of the Lachine is exposed in this portion of the quarry). The exposed section is equivalent to the *Palmatolepis gigas* to *P. triangularis* conodont zones (Gutshick & Sandberg, 1991:fig. 2). However, Gutshick & Sandberg (1991: fig.5) only recovered in the Paxton Quarry *P. gigas* from the middle Paxton Member (1.3-2.8 m below the Paxton-Lachine contact) and *P. crepida* from the Lachine Member (12.5-13.5 m above the contact). The upper 1.3 meters of the Paxton Member and the lower Lachine Member (the 1 m potential source for *Diplognathus lafargei* and the lower 11-12 m of the Lachine Member in general) remain unzoned.

Etymology. Named after Lafarge North America, Inc., Alpena, MI, who provided access to their quarries, where the holotype was found.

Diagnosis. As in the genus. Distinguished from the only other known species (*Diplognathus mirabilis*) by differences in the gnathal elements and a relatively larger orbit. The inferognathal is characterized by a relatively equal depth along its length with a steep and short adsymphyseal region. The posterior superognathal occupies the majority of the occlusal region with a short anterior superognathal. The autopalatine groove on the suborbital plate is equally elongate resulting in a relatively long anterior process or "handle" portion of the suborbital plate.

DESCRIPTION

A taxonomic assignment is difficult when there is a paucity of material for comparison, as is the case here with a single incomplete specimen. Sufficient anatomical information (described below) is present to establish the new specimen's

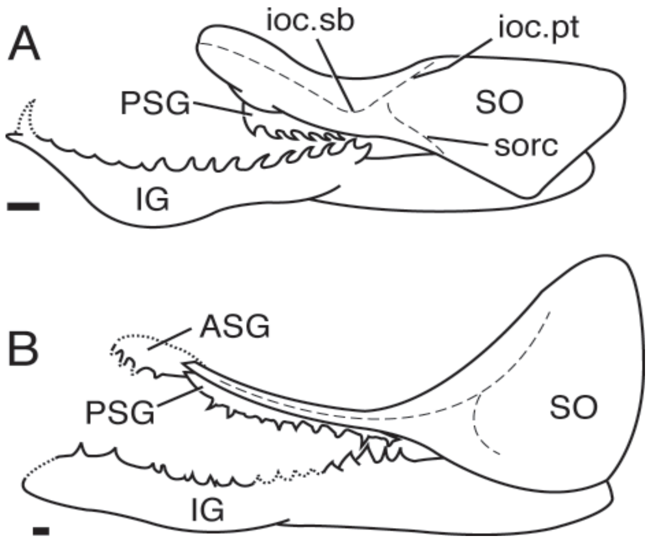

Figure 1. A, *Diplognathus mirabilis,* CMNH 7255, reconstruction modified from Dunkle & Bungart (1943); **B**, *Diplognathus lafargei* sp. nov., CMNH 50215, reconstruction using PSG, left ASG, and mirror image of right SO plate. Dashed lines correspond to lateral line canals (hypothetical in *D. lafargei*); dotted lines correspond toreconstructed parts of gnathal plates. Not drawn to scale with scale bar in A= 10 mm, and in B= 1 mm.

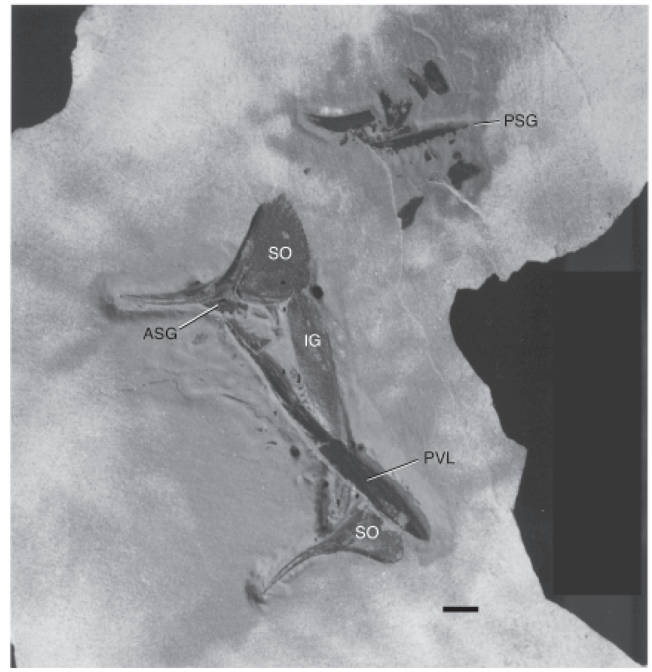

Figure 2. *Diplognathus lafargei* sp. nov., CMNH 50215. View of the disarticulated plates. Scale bar = 5 mm.

affinity to aspinothoracid arthrodires. This includes the presence of two superognathals (eubrachythoracid-level characteristic) and an aspinothoracid-form for the suborbital and posterior ventrolateral plates. The suborbital plate is consistent with other aspinothoracid arthrodires in the presence of an elongated anterior dermal process extending beneath the orbit and a reduced posterior expanded or "blade" portion. The elongation of the posterior ventrolateral plate is consistent with the pattern seen in a number of selenosteid Aspinothoracidi. Anatomical evidence for the assignment to *Diplognathus* is limited to similarities of the gnathal plates.

Gnathal Plates

General features. The gnathal plates in arthrodires consist of two upper plates (anterior and posterior superognathals) and inferognathal. In the holotype for *Diplognathus lafargei*, both anterior superognathals, one posterior superognathal, and one inferognathal are preserved.

Inferognathal. A right inferognathal is present in internal view revealing the posterior nonocclusal region (Figure 3A). Preparation of the anterior portion from the opposite side has exposed the anterior occlusal and adsymphyseal regions (Figure 3B). The inferognathal is *about* 37.9 mm long with the occlusal region representing *about* 58.1% of the total length. Twelve large denticles (or teeth *sensu* Smith & Johanson, 2003) are present in the exposed portion of the occlusal region along with three small or accessory denticles (based on combined internal and external views from both sides of the specimen). The posterior five denticles are evenly spaced at *about* 1 mm with the anterior denticles unevenly spaced (gaps up to *about* 2.5 mm). Using the spacing for posterior denticles, it is possible that four denticles are present in the unexposed region (a total of 16 primary denticles). *Diplognathus mirabilis* (CMNH 7255, Figure 1A) possesses 15 denticles (16 are visible in Newberry, 1889, pl. XI, 4. This potentially represents an age difference with denticles or teeth added posteriorly, Smith & Johanson, 2003). The denticles in *Diplognathus lafargei* are vertical, unlike the posterior denticles in *Diplognathus mirabilis*, CMNH 7255, which are posteriorly recurved. This does not seem to be the case in the specimens figured by Newberry (1889, pls. XI and XII; thus the recurved form of denticles in CMNH 7255 may represent individual variation). The depth of the inferognathal in *Diplognathus lafargei* is relatively consistent throughout its length (about 4.3 mm on average). The beginning of the adsymphyseal region (at the first denticle) is equally deep, but appears to rapidly decline in depth. This pattern is unlike that seen in *Diplognathus mirabilis* where there are distinct differences in the depth of the inferognathal (Figure 1A; Dunkle & Bungart, 1943:fig. 1A), which narrows in depth to the first denticle. The adsymphyseal pattern in *Diplognathus lafargei*, although incomplete, is more reminiscent of the condition seen in *Gymnotrachelus* (Carr, 1994:fig. 8A) or *Stenosteus* (Carr, 1996: fig.8A, B), although there is no evidence of adsymphyseal denticles in *Diplognathus lafargei* (the medial surface of the symphysis is not exposed).

Posterior superognathal. The body of the posterior superognathal (PSG, Figures 1B, 2, 4A) is about 10.7 times longer than deep if excluding the denticles (approximately 6.4 times if the large denticles are included in the measured depth). There are nine denticles (teeth) present although there is potential room for more (it is not clear if one or more denticles are broken or whether nine is the limit). Each denticle is

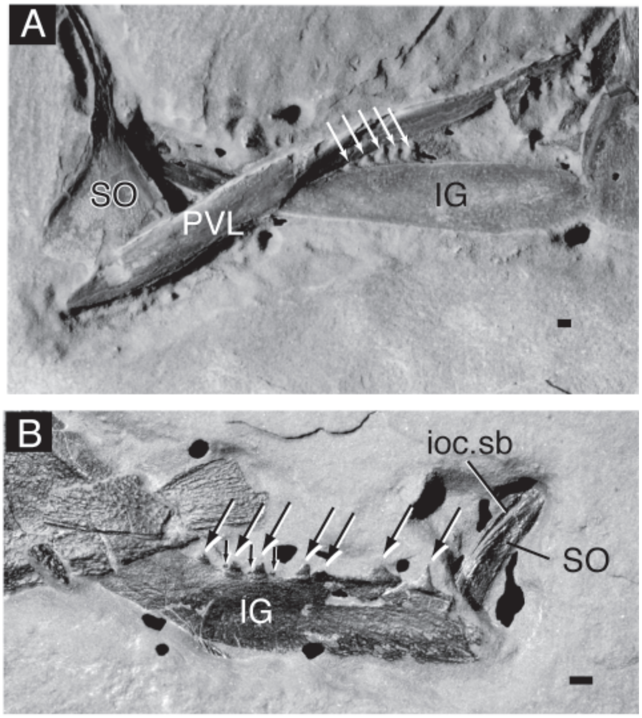

Figure 3. *Diplognathus lafargei* sp. nov., CMNH 50215. **A**, inferognathal in internal view with the posterior ventrolateral plate; **B**, anterior portion of inferognathal in external view showing anterior occlusal and adsymphyseal regions. Large arrows indicate individual denticles and small arrows indicate smaller or accessory denticles. Only a small portion of the anterior process of the SO plate in external view (from the opposite side) is exposed. Scale bars = 1 mm.

relatively large (about 40% of the total depth). In *D. mirabilis*, CMNH 7255, Dunkle & Bungart (1943:fig. 1; reproduced in Figure 1A) illustrate only six denticles that are posteriorly recurved as are the occluding denticles of the inferognathal.

Anterior superognathal. A left anterior superognathal (Figure 4B) is present in medial view and partially obscured by the right suborbital plate. Four denticles (teeth) are present along its ventral occlusal margin. A fragmented right anterior superognathal plate (Figure 4C) possesses three denticles (the third was dislodged and lost in preparation, only its base remains). The anterodorsal surface of the right element is fragmented suggesting the presence of a medial extension. The exact form of the anterior superognathal is not clear. The possible presence of a medial extension on the right element suggests that there may be a vertical lateral face with the denticles (teeth) along its ventral margin (similar in general form to *Dunkleosteus*). In contrast, the left element may be secondarily deformed, but is reminiscent of the anterior superognathal in *Gymnotrachelus* (Carr, 1994:fig. 8E) where the element is flattened with a broad contact with the overlying ethmoid and ventrally pointed denticles along its anterior and lateral edges.

When comparing the occlusal region of the inferognathal to the upper tooth plates it is estimated that the anterior superognathal should be approximately 5.5 mm in length (21.5 mm occlusal length of IG - 16 mm PSG = 5.5 mm estimated length of ASG). The left anterior superognathal has a visible total length of about 6 mm with an occlusal length of about 3.4 mm.

Based on the presence and proportions of anterior and posterior superognathal elements in *D. lafargei* it could be argued that the isolated posterior superognathal of *D. mirabilis* (Dunkle & Bungart,1943) was misinterpreted and actually represents an anterior superognathal based on its short length in relation to the inferognathal (the case in *Diplognathus lafargei*). Arguing against this interpretation is the length of the anterior portion of the suborbital plate ("handle") where the autopalatine is located. Relative to the occlusal length of the inferognathal, this portion of the suborbital plate is *about* 10% shorter in *Diplognathus mirabilis* than in *D. lafargei*. To assume that the gnathal plate in CMNH 7255 is an anterior superognathal requires the reconstruction of a posterior superognathal that would be *about* 143% the length of the potential autopalatine groove. We consider this an untenable argument and concur with Dunkle & Bungart's original interpretation in *Diplognathus mirabilis*. The difference in the proportions of the superognathals and suborbital "handle" supports the establishment of a distinct species.

Cheek Plates

General features. The cheek plates of arthrodires consist of suborbital, postsuborbital, and submarginal plates. Only the former is preserved in the holotype of *Diplognathus lafargei*.

Suborbital plate. Both suborbital plates are present in internal view (Figures 2, 5). The left suborbital plate appears to be smaller, but this is a preservational artifact. Attempts to expose the external surface demonstrate that the expanded posterior "blade" portion is paper-thin and at present too delicate to expose. The individual plate consists of a narrow anterior process or "handle" and expanded posterior regions. The anterior external portion of the left suborbital plate shows a sensory line groove (ioc.sb, Figure 3B) extending onto this portion of the plate (exposed for only a short distance). The groove is located close to the ventral edge of the plate in this region.

Internally, an autopalatine groove (a.Au, Figure 5B) is present along the anterior portion and is bounded dorsally by a narrow orbital shelf (Figure 5B; R2 of Heintz, 1932:figs. 21-22) and ventrally by a subautopalatine crista (cr.sau, Figure 5B). The orbital shelf extends more medially. A pair of thickened ridges extends from the anterior region onto the expanded posterior portion of the suborbital plate; one extending posteroventrally (R3 of Heintz, 1932:fig. 22) and the other anterodorsal as the postocular crista (Figure 5A; R1 of Heinstz, 1932:fig. 22). The angle formed in the orbital margin by the anterior and posterior regions is *about* 120°. In *Diplognathus mirabilis* this angle is equivalent, but is *about* 105° when using Dunkle & Bungart's (1943) reconstructed posterior margin of the orbit. This smaller angle, given Dunkle & Bungart's reconstruction, possibly indicates that this species has a relatively smaller orbit than in *Diplognathus lafargei*.

The anterior portion ("handle") of the suborbital plate represents *about* 48.1% of the total plate length. Internally, the attached autopalatine represents the site of contact between the posterior superognathal and palatoquadrate. The relatively long occlusal region in this organism is dominated by the posterior superognathal among the upper gnathal elements, which accounts for the relatively long "handle" region.

Thoracic Plates

Posterior ventrolateral plate. The thoracic plates of arthrodires consist of a ring of enclosing dermal bones (Goujet, 1984). One plate in *Diplognathus lafargei* is interpreted as a posterior ventrolateral plate lying across the inferognathal (Figure 3A). An initial interpretation, based on its association with the right inferognathal and its length, was that it was the opposite inferognathal at an oblique angle within the shale. Although not possible to free the element with subsequent preparation, it is clear that it lacks any gnathal characteristics (denticles, depth, and general shape other than being elongate). After a comparison with other Cleveland Shale taxa, this plate is interpreted as a posterior ventrolateral plate similar to that seen in *Stenosteus angustopectus* (Carr, 1996:figs. 15, 16B-C). In *S. angustopectus*, the posterior ventrolateral plate is narrow and *about* 8 times longer than wide. The plate in *Diplognathus lafargei* is *about* 10 times longer than wide (maximum length/maximum width) with an average width of *about* 2.7 mm. The greatest width is seen anteriorly while the plate tapers posteriorly.

Miscellaneous Plates.

A few unidentifiable plate fragments (Figures 2, 3B, 4A) provide no diagnostic information.

DISCUSSION

Dunkle & Bungart (1943) summarize the history of the phylogenetic assignments of *Diplognathus* to that time. Of interest to this study is Newberry's (1889) assignment to the Dinichthyidae based on a similarity of the inferognathal to that seen in *Dinichthys*, *Titanichthys*, and *Trachosteus*. This assignment was based on the common possession of a spatulate posterior portion of the inferognathal; however, this feature is a plesiomorphic character of the pachyosteomorph arthrodires (character #63, Carr, 1991:379-380 for discussion). Newberry (1889) also noted a similarity between *Trachosteus* and *Diplognathus*, but concluded that due to a lack of knowledge of the former, *Diplognathus* could not be clearly associated with any of the fishes known at that time. Although later authors (e.g., Eastman, 1907) suggested putative relationships, Dunkle & Bungart (1943) concluded that they could find no evidence to support a close relationship between *Diplognathus* and any other member of the Cleveland Shale fauna.

Obruchev (1967) questionably unites *Diplognathus* and *Hadrosteus* within the Hadrosteidae Gross, 1932, (pachyosteomorph arthrodires) based on the pattern of

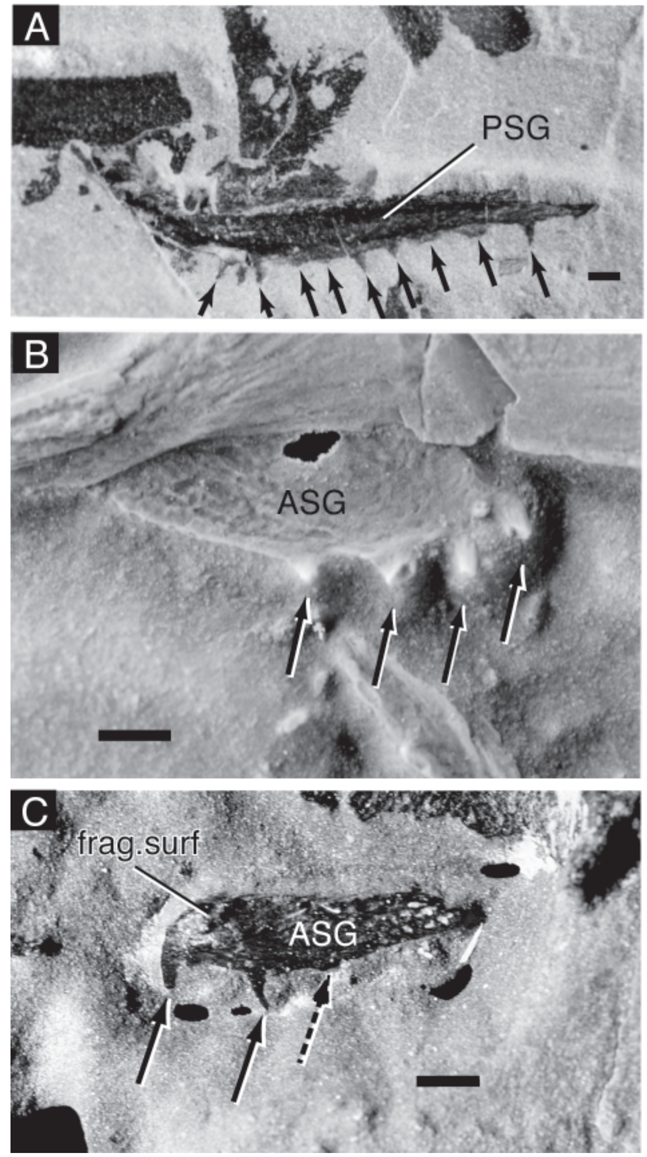

Figure 4. *Diplognathus lafargei* sp. nov., CMNH 50215. **A**, posterior superognathal; **B**, left anterior superognathal in medial view; **C**, Right anterior superognathal in medial view. Arrows indicate individual denticles. Dashed arrow indicates base of noted denticle lost in preparation. Scale bars = 1 mm.

denticles (teeth) on the inferognathal, while Denison (1978) considers *Diplognathus* as Arthrodira *incertae sedis*, although presumably a member of the pachyosteomorph arthrodires.

The limited diagnostic features of *Diplognathus* raise a question concerning its relationship to *Trachosteus* or *Hadrosteus*. Newberry (1889) first suggested a possible relationship between *Diplognathus* and *Trachosteus* based on the form of the inferognathal, a pleisiomorphic feature of little phylogenic value. He did not compare the distinct and evenly spaced denticles (teeth) of the inferognathal. *Trachosteus*, like *Diplognathus*, possesses relatively large orbits (again not clearly a diagnostic feature; character #28, Carr, 1991:384). The lack of knowledge for the anterior portion of the inferognathal in *Trachosteus* further clouds the issue and prevents assessment of any clear relationship.

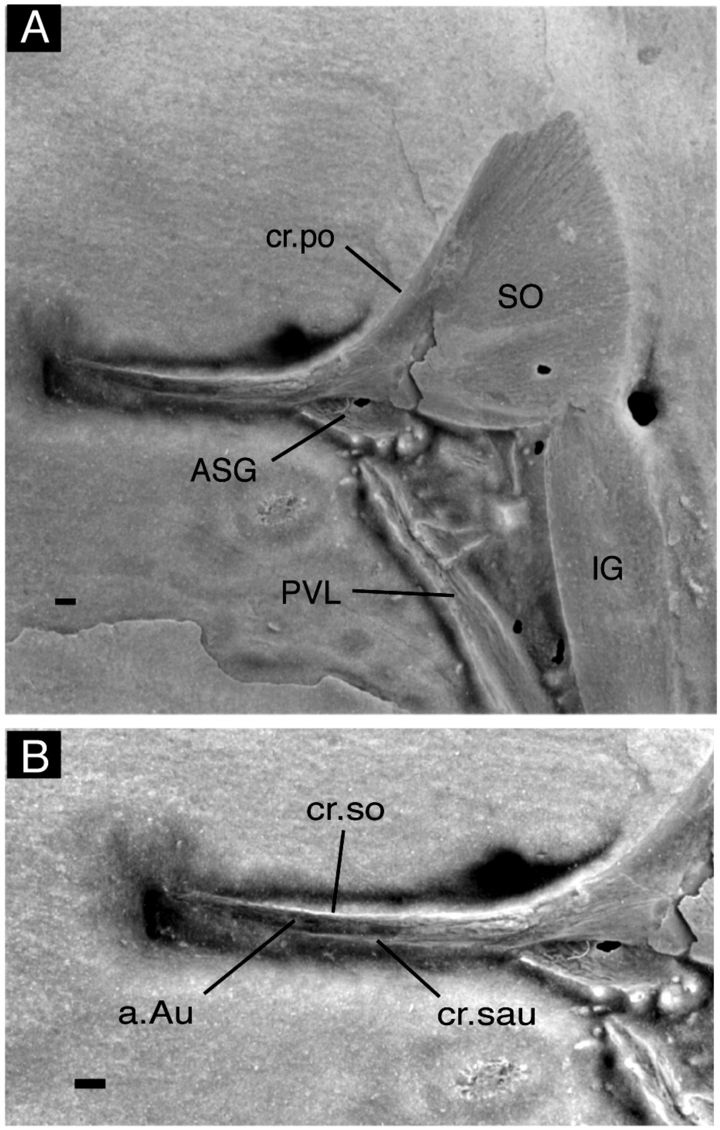

Figure 5. *Diplognathus lafargei* sp. nov., CMNH 50215. **A**, right suborbital plate in internal view; **B**, close-up internal view of right suborbital plate's anterior process. Scale bars = 1 mm.

In the case of *Hadrosteus*, it shares with *Diplognathus* the enlarged proportion of the occlusal region (compare Carr, 1995:figs. 12F and G) and the presence of distinct denticles (teeth). Unlike *Diplognathus*, the anterior portion of the inferognathal in *Hadrosteus* possesses a shearing edge with wear surfaces for distinct enlarged cusps on the superognathals. There is no data available for *Diplognathus* to compare elements of the dermal head (lacking in *Diplognathus*) and ventral thoracic plates (lacking in *Hadrosteus*). *Diplognathus* shares with *Hadrosteus* the general form of the suborbital plate (Gross, 1932:fig. 11). This limited similarity is shared with a number of aspinothoracid taxa and therefore of little systematic value in the current study. The form of the superognathals would preclude a close relationship between these two genera.

The small number of characters available to evaluate the phylogenetic position of *Diplognathus mirabilis* and *Diplognathus lafargei* limits our ability to fully resolve relationships. Both species possess features suggesting their assignment to arthrodires (possession of two upper gnathal plates) while the presence of an ossified blade and occlusal region in the inferognathal indicates a brachythoracid-level of organization (although the presence of this feature is variably present among basal brachythoracids, Young *et al.*, 2001; Carr, 1991). Suggesting an assignment within the aspinothoracid arthrodires (*sensu* Miles & Dennis, 1979) is the form of the suborbital plate with its elongated suborbital dermal process and reduced posterior expanded or "blade" portion and the interpretation of the posterior ventrolateral plate in *Diplognathus lafargei* (the degree of elongation in this plate is only seen in *Stenosteus angustopectus*, although an elongation is present in other selenosteids).

Assignment of the new species to *Diplognathus* is based on three gnathal characteristics; the size and spacing of the denticles (teeth), the relatively large portion of the inferognathal occupied by the occlusal region, and the low form of the posterior superognathal (with equal sized denticles). The shape of the adsymphyseal region of the inferognathal in the new species shows similarity with some selenosteid arthrodiress (e.g., *Pachyosteus*, Denison, 1978:fig. 67J; *Gymnotrachelus*, Carr, 1994:fig. 8C; and *Stenosteus angustopectus*, Carr, 1996:fig. 8A, B), but not uniquely to any one genus. The shape of the posterior ventrolateral is shared with *Stenosteus angustopectus* (Carr, 1996:figs. 15, 16B, C); however, a parsimony argument may suggest that elongation of the ventral plates is independently derived or a general feature among selenosteids.

At present, the only diagnostic features of the genus *Diplognathus* are represented by gnathal characters with species-level differences based on the shape of the inferognathal and suborbital plates and the differences in the interpreted proportions of the occlusal surface occupied by the posterior and anterior superognathals (a long PSG and short ASG in *D. lafargei* and the opposite in *D. mirabilis*, Figure 1). Finally, the two species of *Diplognathus* are from contemporaneous geographically adjacent regions (Elliot *et al.*, 2000) that, based on lithology, shared similar environments (distal basin habitats).

An alternative hypothesis to the designation of a new species within *Diplognathus* is that the new specimen represents a juvenile *Diplognathus mirabilis*. This would account for the apparent larger orbit in the smaller specimen (*D. lafargei*). The diagnostic gnathal characters that support assignment of a new species also rule out an ontogenetic sequence. Smith & Johanson (2003; see also Ørvig, 1980) note the acquisition of additional teeth (denticles, as used here) on the inferognathal with age. The possession of an equal number of inferognathal denticles in *Diplognathus lafargei* and the greater than five-fold larger inferognathal in *Diplognathus mirabilis* is not consistent with the ontogenetic pattern in other arthrodires (based on a comparison of *Diplognathus lafargei* with *D. mirabilis*, Newberry, 1889:pl.11, 1, 4; the CMNH 7255 IG with 15 denticles is greater than ten-times larger). Although allometric growth may be expected in the development of the superognathals, no case is recognized among arthrodires where a posterior superognathal is greater than twice the size of an anterior superognathal in a juvenile and is reversed in the adult (ASG > twice the size of the PSG). These inconsistencies further support the assignment of a new taxon (rather than a juvenile specimen of *Diplognathus mirabilis*).

Further evaluation of the congeneric assignment of these two species (*Diplognathus lafargei* and *D. mirabilis*) and their relationships to other Upper Devonian pachyosteomorph arthrodires must await additional fossil material for these problematic forms. Dunkle & Bungart's (1943, CMNH 7255) specimen was only partially prepared due to the limited preparation methods of the time. This specimen may be amenable to acid preparation and thus would add greatly to our knowledge. For the remaining taxa (*Hadrosteus*, *Diplognathus lafargei*, and *Trachosteus*) our only recourse is a redoubled effort to collect and/or prepare new material. Despite the limited material available, it is important to document the diversity of forms during this critical time in gnathostome evolution.

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