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Some observations on *Denaea fournieri* (Chondrichthyes, Symmoriiformes) from the Lower Carboniferous of Belgium

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ABSTRACT:

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Preliminary observations are presented concerning endoskeletal morphology in the Lower Carboniferous symmoriiform shark *Denaea fournieri*, and some problems in the original description are highlighted. *D. fournieri* almost certainly possessed a tropibasic braincase and its cranial morphology agrees in most respects with that observed in other symmoriiforms, although it had an extremely narrow ethmoidal region and may have lacked supraorbital cartilages. Its pectoral fins were probably similar to those of other symmoriiforms, and the radial-bearing margin of its metapterygium most closely resembles that of falcatids and *Stethacanthulus*. Using *Cladoselache* as an outgroup, several apomorphic characters are identified in symmoriiform pectoral fins.

Key words: *Denaea*, Symmoriiformes, Chondrichthyes, Lower Carboniferous, Marbre Noir, Denée, Belgium.

INTRODUCTION

Denaea fournieri is a small (est. total length 50-60 mm) symmoriiform shark known from numerous incomplete but well preserved specimens of semi-articulated individuals from the Marbre Noir (Lower Viséan, Lower Carboniferous) of Denée, Belgium (FOURNIER & PRUVOST 1922). Historically, it represents the fourth symmoriiform taxon to have been described from articulated skeletal remains (see COPE 1893, 1894; TRAQUAIR 1898) and the first such find in mainland Europe. These fossils were described and a holotype was designated by FOURNIER & PRUVOST (1928), but since that time *D. fournieri* has been largely neglected. Unfortunately, the descriptions presented by PRUVOST (in FOURNIER & PRUVOST 1922) and FOURNIER & PRUVOST (1928) are somewhat basic and were undoubtedly limited by a lack of comparative data (since that time, numerous well preserved symmoriiform fossils have been described from Europe and North America). In the summer of 2007, the author was able to examine the material (still housed in the Collection Abbaye de Maredsous; specimen prefix CAM). A morphological revision of *Denaea fournieri* is now in progress and only a few preliminary observations will be made here. Although symmoriiforms share a common gestalt of conserved and derived characters (ZANGERL 1981, 1990) and are probably monophyletic, published family-level classifications of the group are almost certainly incorrect (MAISEY 2007, submitted). Thus, the systematic position of *Denaea fournieri* cannot be resolved satisfactorily until symmoriiform phylogeny has been thoroughly re-analyzed.

SYSTEMATIC PALEONTOLOGY

Order Symmoriiformes Zangerl, 1981

Genus *Denaea* Pruvost, 1922 (in Fournier & Pruvost 1922)

TYPE SPECIES: *Denaea fournieri* Pruvost, 1922 (in Fournier & Pruvost 1922)

HOLOTYPE: Collection Abbaye de Maredsous, CAM 201

REFERRED MATERIAL (all in CAM; list emended from Fournier & Pruvost 1928): 201 to 22g; 231, 232-235, 241-242.

Denaea fournieri Pruvost, 1922

The only published reconstruction of the head skeleton in *Denaea fournieri* is that of Fournier & Pruvost (1922, fig. 1; 1928, fig. 2; reproduced here as Text-fig. 1). Their depiction correctly shows a short and comparatively tall braincase with large, round orbits, jaws with a well developed postorbital articulation as well as an orbital articulation farther anteriorly, and very gracile jaw cartilages. In most cases the braincase is preserved in dorsal or ventral aspect (e.g., CAM 202-204, 208, 209, 211, 213, 217, 218, 224, 227) and only a single specimen provides a lateral view (CAM 219). The braincase of *D. fournieri* closely resembles that of "*Cobelodus*" (Maisey 2007) and appears to have been morphologically tropibasic (i.e., with the brain and cranial cavity separated from the basicranium by a deep interorbital septum). Although the head is preserved in lateral view in the holotype (CAM 201), little of its braincase is visible (Text-fig 2A). However, a thin sclerotic ring resembling that of *Falcatus* shows that the eye was large compared to the rest of the head. In dorsal and ventral views the anterior part of the cranium is extremely narrow from side to side (Fournier & Pruvost 1928, pl. 4, fig. 1). In their reconstruction, Fournier & Pruvost (1922, 1928) depicted *D. fournieri* with an elongated, slender suspensory hyomandibula, which is corroborated by its close proximity to the posterior margin of the palatoquadrate in CAM. The braincase is usually seen in dorsal or ventral view (Text-fig. 2D-F), but CAM 219 shows its lateral aspect (Text-fig. 2B). The gross morphology of the braincase is similar to that described by Maisey (2007) in an isolated three-dimensional symmoriiform braincase ("*Cobelodus*"; Text-fig. 2C, G, H). In most specimens of *D. fournieri* the basicranium is only preserved anteriorly as far as the orbital articulation, but it extends a considerable distance farther anteriorly in CAM 217, 224, and 227, suggesting that *D. fournieri* possesed a long snout as in *Falcatus* and *Damocles* (Lund 1985a, 1986). A continuous postorbital arcade is present, the

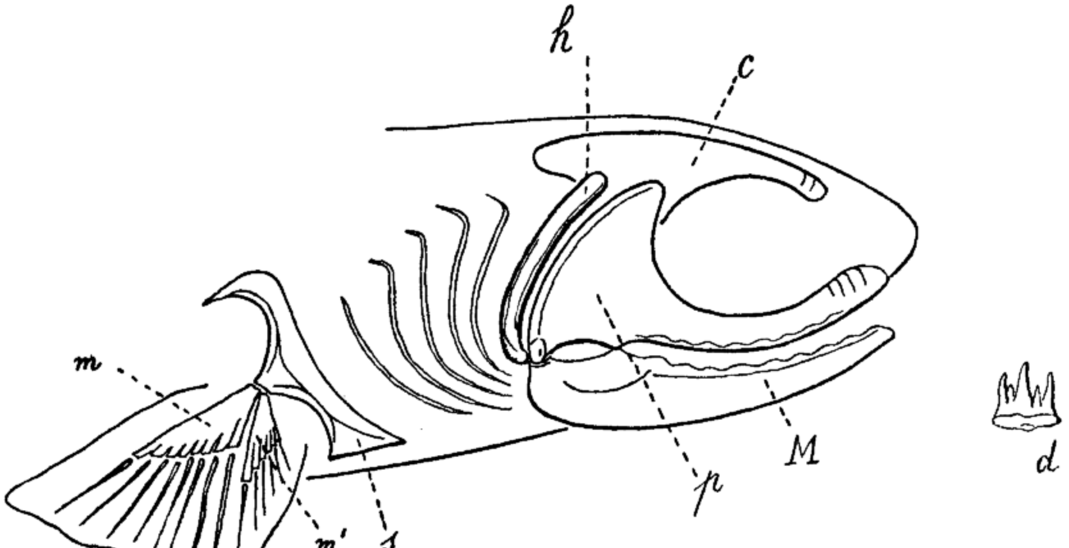

Fig. 1. Diagrammatic reconstruction of the head and pectoral fin in *Denaea fournieri* as provided by Fournier & Pruvost (1928). Abbreviations (emended translation): c, braincase; d, tooth (enlarged view); h, hyomandibula; M, Meckel's cartilage; m, pectoral metapterygium; m', supposed premetapterygial basal; p, palatoquadrate; s, scapulocoracoid. No scales, but illustration is approximately life-size, tooth approximately × 3

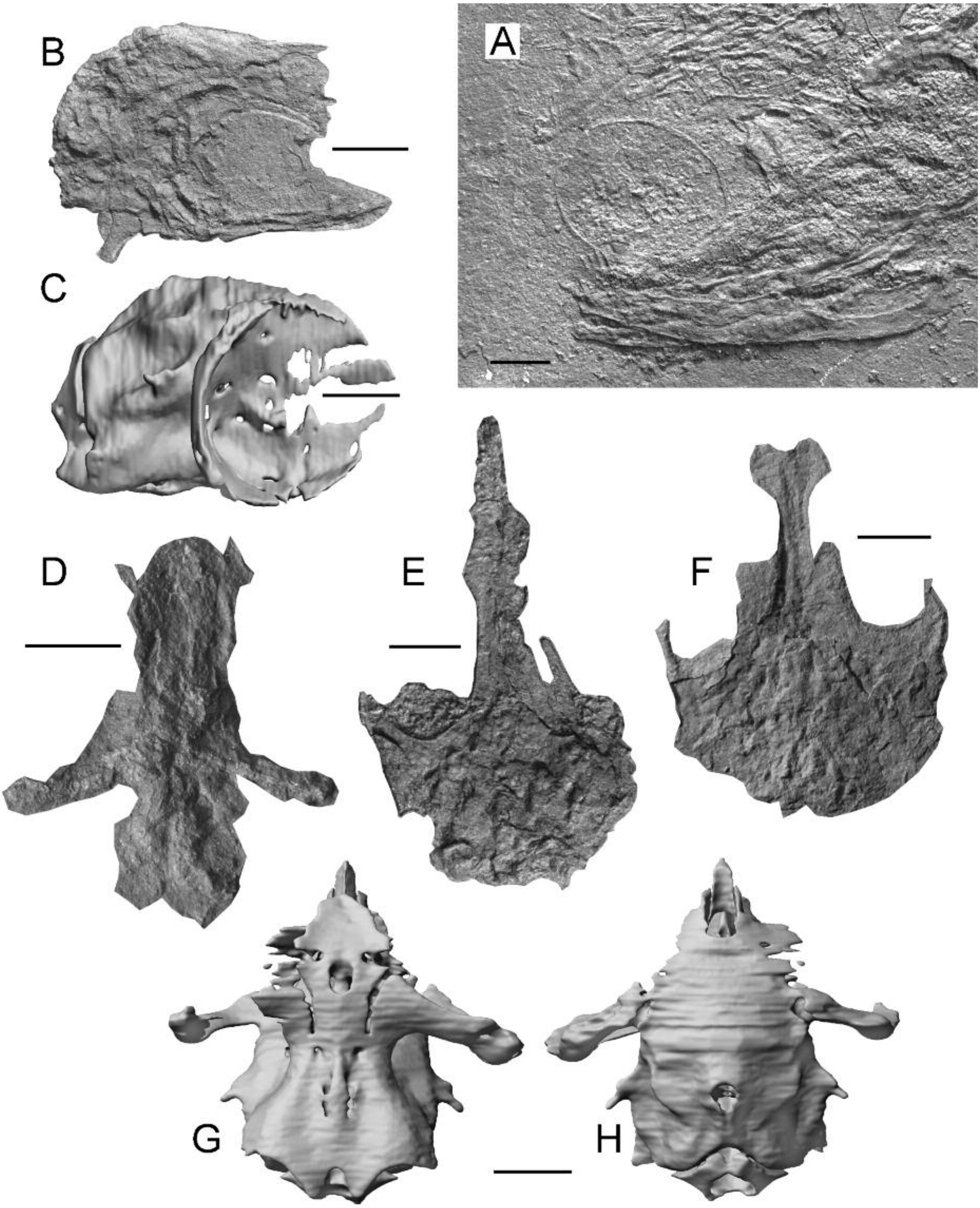

Fig. 2. Views of the braincase in *Denaea fournieri* compared with a three-dimensional Pennsylvanian symmoriiform braincase ("*Cobelodus*") A – lateral view of the head in the holotype CAM 201 (no braincase evident); B – CAM 219, lateral view of isolated braincase (right side, anterior to right); C – "*Cobelodus*" braincase in lateral view; D-F – *D. fournieri* braincases in dorsoventral views; D – CAM 208; E – CAM 224; F – CAM 202; G-H – "*Cobelodus*" braincase in (G) ventral and (H) dorsal views. Anterior to top in D-H. Scale bars = 10 mm. C, G, H after Maisey (2007)

ventral ramus of which is narrow anterioposteriorly and angled posterolaterally as in "*Cobelodus*" (MAISEY 2007). The dorsal part of the arcade is deepest at the site of the postorbital articulation and has a markedly concave anterior margin dorsally, forming a short supraorbital shelf which is confined to the back of the orbit (e.g., CAM 217; FOURNIER & PRUVOST 1928, pl. 4, fig. 1). The postorbital articulation is deep and elongated, apparently occupying much of the lateral commissure.

The tooth-bearing rami of the jaw cartilages are slender in *Denaea fournieri*, with distinct scalloped oral margins marking the location of the successional tooth families. FOURNIER & PRUVOST's (1922, 1928) reconstruction allowed for only eight or nine tooth families, but in several specimens there is evidence of 10-12 upper and lower tooth positions (e.g., CAM 203, 208, 218, 220, 224). Despite the fact that many specimens are disarticulated, Meckel's cartilages sometimes remain united symphyseally, suggesting the presence of a strong ligamentous connection (e.g., CAM 203, 212). These examples also indicate a very narrow gape, suggesting that the mandibular arcade did not broaden posteriorly as in many other sharks, and that the adductor musculature was not massive.

Comparison with other symmoriiforms suggests that the scapulocoracoid has been inverted in the reconstruction of the pectoral endoskeleton presented by FOURNIER & PRUVOST (1922, 1928). The scapulocoracoid in *Denaea fournieri* closely resembles those of several symmoriiforms from North America, including *Cobelodus aculeatus*, *Symmorium reniforme*, and *Stethacanthulus meccaensis*. The latter species was originally referred to *Denaea* (WILLIAMS 1985), but its teeth differ in some important respects from those of *D. fournieri* (discussed in MAISEY 2007, p. 80). In all those forms, the coracoid region is recurved posteriorly and the scapular process is trapezoidal with anterior and posterior projections separated by an almost straight upper margin. In other symmoriiforms (e.g, falcatids, *Akmonistion zangerli*, and specimens referred to *Stethacanthus*), the coracoid process is directed anteriorly but the scapular process is still usually trapezoidal (although it is slender and upcurved anteriorly in *Falcatus falcatus*). When the scapulocoracoid shown in Text-fig. 1 is inverted, the base of the scapular process is seen to have a distinct posterolateral angle (possibly a chondrichthyan synapomorphy; COATES & GESS 2007)

Another apparent anomaly in the original reconstruction is the arrangement of the pectoral fin cartilages (Text-fig. 1). In symmoriiforms generally, the scapulocoracoid articulates with a wedge-shaped metapterygium, which often has a distinctive scalloped or incised distal margin where it meets the fin radials. Several pre-metapterygial radials are also typically present, each articulated to a corresponding "basal" cartilage in front of the metapterygium. As depicted by FOURNIER & PRUVOST (1928), however, the fin of *Denaea fournieri* is dibasal and includes an inverted metapterygium-like element anteriorly, to which several pre-metapterygial radials were attached. Their interpretation can be traced to CAM 201, in which three "metapterygia" seem to be present, two of approximately equal size plus a slightly smaller element adjacent to one of the larger ones. All three elements have approximately eight indentations for radials. Based on the size difference alone, it is unlikely that the "extra" element represents the opposite surface of a single broken metapterygium. Nevertheless, the pectoral arrangement shown by FOURNIER & PRUVOST (1928) is certainly odd and therefore deserves critical examination.

In many symmoriiforms, the metapterygium bears a series of "axial" cartilages forming a metapterygial "whip". The most proximal element in the "whip" supports a series of radials, which are aligned in parallel with those of the metapterygium, and the radial-bearing surface of this segment may have a scalloped or incised margin like that of the metapterygium (e.g., "*Stethacanthus* species 2", *Falcatus falcatus*; LUND 1985b, 1986). Unfortunately none of the specimens of *Denaea fournieri* are sufficiently complete to determine whether such a "whip" was present, but the distal end of the metapterygium includes a short articular surface which may represent the attachment surface of a proximal "whip" segment. However, it is unlikely that the "extra" radial-bearing element of *D. fournieri* represents part of a pectoral "whip" because its radial-bearing surface cannot be aligned with that of the metapterygium. Another possibility is that the "extra" element belongs to the pelvic fin. The symmoriiform pelvic girdle often supports a series of radials, but it does not possess a scalloped margin and is elongated only in falcatids (it is more plate-like in the other forms). A pelvic metapterygium with radial-bearing projections has been described in female *F. falcatus*, but it supports only one or two radials (LUND 1985a, fig. 11B), and such an arrangement has not been identified in other symmoriiforms. It is nevertheless plausible that the "extra" metapterygial-like element in *D. fournieri* represents the pelvic metapterygium.

Several systematically useful characters are identified in the pectoral metapterygium of symmoriiforms, including: the number of radials supported by the cartilage, the degree to which the radial-bearing margin is scalloped or incised, its extent along the metapterygium, the width of the metapterygial shaft above the indentations, and the width of its attachment surface to the scapulocoracoid. Excluding the "whip" attachment surface, in *Denaea fournieri*, eight radials contacted the metapterygium, as in "*Stethacanthus* species 2" of LUND (1985b); seven are present in *Gutturensis nielsoni*, six are present in *Falcatus falcatus* and *Akmonistion zangerli* (there may have been even fewer in *Damocles serratus*), seven in *Stethacanthus* cf. S. *altonensis*, and seven to nine in *S. altonensis*, (LUND 1974, 1985a, 1985b, 1986; ZANGERL 1981; COATES & SEQUEIRA 2001). Metapterygial radials are more numerous in *Symmorium reniforme* (11), *Cobelodus aculeatus* (12), and *Stethacanthulus meccaensis* (14; ZANGERL 1981, 1990; WILLIAMS 1985). The radial-bearing margin of the metapterygium is imbricated but not scalloped in *Akmonistion zangerli* and in a specimen referred by LUND (1974) to *Stethacanthus altonensis*, but it is deeply incised in another specimen referred to that species by ZANGERL (1981) and WILLIAMS (1985). According to FOURNIER & PRUVOST (1928), in *D. fournieri*, the radial-bearing margin is scalloped but the proximal parts of the radial-bearing surfaces are in contact with each other. However, inspection of the specimens revealed that in places the margin is deeply incised and adjacent radial supports are widely spaced from each other, as in *F. falcatus*, *D. serratus*, and "*Stethacanthus* species 2". In *C. aculeatus*, *S. reniforme*, and *Stethacanthulus meccaensis*, incisions along the margin are deepest anteriorly but gradually become shallower farther posteriorly (dying out altogether in *S. meccaensis*), and the spaces between them taper proximally instead of maintaining an even width.

Although the phylogenetic value of these differences is questionable in the absence of a more comprehensive data matrix, comparison with *Cladoselache* (possibly the sister group of symmoriiforms; COATES & SEQUEIRA 2001; MAISEY 2007) suggests that the metapterygium was primitively short, supported from three to seven radials as well as a short segmented distal "axis" (also radial-bearing), and had a stepped or imbricated radial-bearing margin (see reconstructions of the pectoral fin in Bendix-Almgreen 1975). On that basis, the metapterygial pattern in *Akmonistion zangerli* and LUND's (1974) *Stethacanthus altonensis* may be viewed as conserved, while the patterns observed in other symmoriiforms may represent divergent specializations; e.g., the relatively high number of metapterygial radials in *Cobelodus aculeatus*, *Symmorium reniforme*, and *Stethacanthulus meccaensis*, the deeply incised radial-bearing margin in many symmoriiforms, and the widely separated radial supports in *Denaea fournieri*, *Falcatus falcatus*, "*Stethacanthus* species 2", *Damocles serratus* and *Stethacanthus* cf. *S. productus*. Within this last category, the presence of narrow incisures between at least some of the radial supports is shared by *D. fournieri* and *S. meccaensis*. Given the wide variation in pectoral metapterygial morphology seen in specimens referred to *Stethacanthus*, it is unlikely that these are all really congeneric.

The pectoral fin in *Cladoselache* and most symmoriiforms is plesodic (with radials supporting almost the entire fin). The tip of the fin is supported by the posteriormost metapterygial radials in *Cladoselache*, *Cobelodus aculeatus*, *Symmorium reniforme*, *Stethacanthulus meccaensis*, and in two specimens referred to *Stethacanthus altonensis* (ZANGERL 1981; LUND 1974), an arrangement that may be phylogenetically primitive. This is also the situation in modern plesodic lamniform sharks, although the condition there is almost certainly secondary. By contrast, in both *Akmonistion zangerli* and the specimen referred to *Stethacanthus* cf. *S. altonensis* (LUND 1985b), the tip of the fin is supported by the posteriormost pre-metapterygial radials, an unusual and possibly apomorphic condition within symmoriiforms. *Falcatus falcatus* and *Damocles serratus* are unusual in having comparatively short pectoral radials, suggesting that the fins were aplesodic (extending only into the fin base, as in the majority of modern sharks). It has not yet been established whether the pectorals in *Denaea fournieri* were plesodic, although isolated radials accompanying the pectoral girdles are usually long.

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