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Pectoral morphology in *Doliodus*: bridging the 'acanthodian'-chondrichthyan divide

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ABSTRACT

Doliodus problematicus (NBMG 10127), from the Lower Devonian of New Brunswick, Canada (approx. 397–400 Mya) is the earliest sharklike jawed vertebrate (gnathostome) in which the pectoral girdle and fins are well preserved. Its pectoral endoskeleton included sharklike expanded paired coracoids, but *Doliodus* also possessed an "acanthodian-like" array of dermal spines, described here for the first time. *Doliodus* provides the strongest anatomical evidence to date that chondrichthyans arose from "acanthodian" fishes by exhibiting an anatomical mosaic of "acanthodian" and sharklike features.

INTRODUCTION

The pectoral complex is a critical anatomical region both for osteichthyan and chondrichthyan systematics, yet it is almost completely unknown in the earliest chondrichthyans, constraining our ability to infer relationships in this clade (which is coeval with comparatively better-known bony fishes). Major vertebrate evolutionary transitions, such as "fin to limb" and "dinosaur to bird," are substantiated by numerous fossil discoveries. By contrast, the much earlier rise of sharklike fishes (chondrichthyans) within jawed vertebrates (gnathostomes) is poorly documented. Although this "fish to fish" transition involved less profound anatomical

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reorganization than the evolution of tetrapods or birds, it is no less important for informing the evolutionary origins of modern lower vertebrate diversity.

Interest in chondrichthyan origins has been revitalized by discovery of a remarkable fossil skeleton of a sharklike fish from the early Devonian of eastern Canada, referred to *Doliodus problematicus* (Miller et al., 2003; NBMG 10127; fig. 1). Prior to this discovery, *Doliodus* was known only from isolated sharklike teeth and had been classified either as a chondrichthyan (Woodward, 1892; Traquair, 1893) or an acanthodian (Denison, 1979). NBMG 10127 exhibits a previously unrecognized combination of morphological features, including a sharklike dentition and endoskeleton along with paired, "acanthodian-like" pectoral fin spines (see Discussion).

There is emerging consensus that "acanthodian" fishes represent a paraphyletic assemblage of gnathostomes, and that some (or even all) "acanthodians" populate the chondrichthyan stem (Brazeau, 2009; Zhu et al., 2013; Dupret et al., 2014). There is also agreement that some "acanthodian" taxa (e.g., *Lupopsyrus*, *Obtusacanthus*, *Kathemacanthus*, *Brochoadmones*, *Vernicomacanthus*, and perhaps *Gyracanthides*) are phylogenetically closer to "conventionally defined" chondrichthyans (sensu Zhu et al., 2013) than other "acanthodians" (Brazeau, 2009; Zhu et al., 2013; Burrow et al., 2015).

The morphology of the cranium, jaws, and dentition in *Doliodus* have been investigated by means of computerized tomography and scan reconstitution (segmentation analysis [Maisey et al., 2009; 2014]). Until now, however, its intriguing pectoral region was known only from the preliminary findings presented by Miller et al. (2003). In order to elucidate its pectoral structure, the main *Doliodus* slab (NBMG 10127/3) was scanned at the Muséum National d'Histoire Naturelle in Paris. Segmentation analysis revealed separate pairs of "acanthodian-like" dermal spines, completely enclosed by matrix and clearly associated with the ventral part of the pectoral endoskeleton (fig. 2), the first time such structures have been recognized in a sharklike chondrichthyan, plus fragments of a possible dorsal and pelvic fin spine.

Materials and Methods

Incomplete, articulated fossil of a sharklike fish, New Brunswick Museum NBMG 10127, Lower Devonian, Emsian, "Atholville" beds (Dineley and Williams, 1968), Campbellton Formation, New Brunswick, Canada, collected in 1996 (Miller et al., 2003). For a description of the braincase, jaws, and jaw suspension, see Maisey et al. (2009); for the dentition, see Maisey et al. (2014) . The specimen is preserved in several pieces of matrix, the largest of which (NBMG 10127/3, investigated here) includes the pectoral region.

This piece was subjected to X-ray computed tomographic (CT) imaging on the AST-RX platform of the Muséum National d'Histoire Naturelle, using a GE Sensing and Inspection Technologies Phoenix|x-ray v|tome|x L240-180 CT scanner. We used the microfocus RX source at 240 kV/320 W, detector 400 × 400 mm, with a matrix of 2024 pixels (pixel size: 200 × 200 microns). Scan parameters were as follows: voltage = 135 kV; current = 300 μA; exposure: 333 ms; isotropic voxel size of 0.1095 mm. Data were reconstructed using datos|x reconstruction software (Phoenix|x-ray, release 2.0), then exported into a 16-bit TIFF image stack of 1010

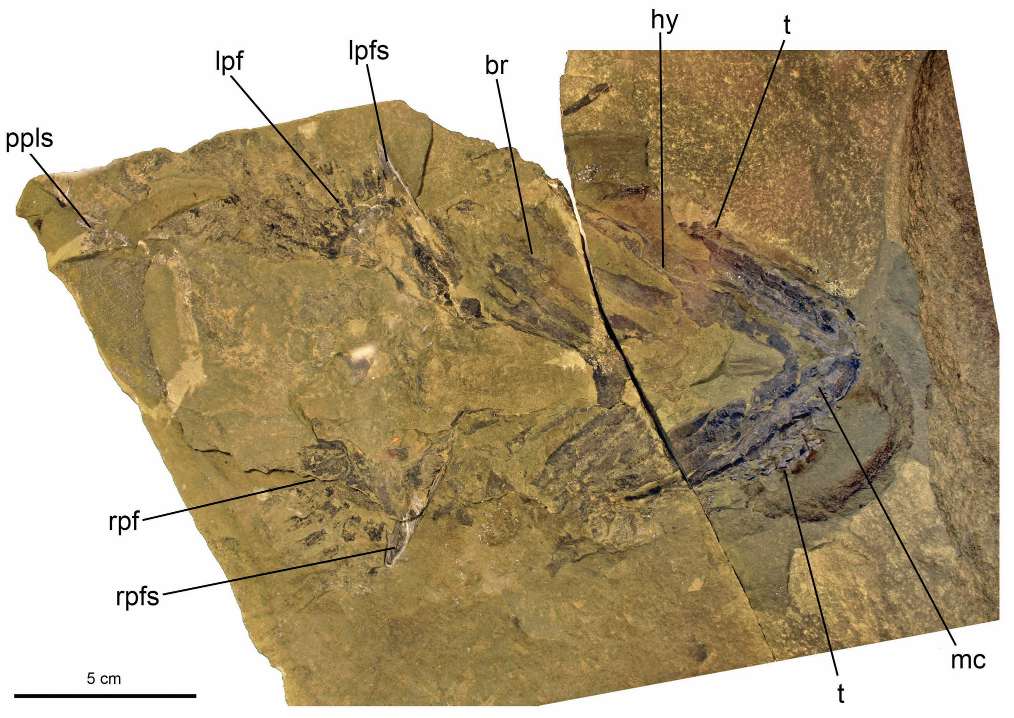


FIGURE 1. General view of the *Doliodus* specimen NBMG 10127, showing the ventral part of the individual viewed in dorsal aspect, with major features identified. Abbreviations as designated in the main body of the text. Scale bar = 5 cm.

virtual slices in transverse view. Materialise Mimics Innovation Suite software version 18 was utilized for the 3D reconstructions.

Abbreviations

Abbreviations used in the figures are as follows: **ads**, admedian spine; **ap**, apex of spine ornament; **ax**, possible cartilages of "metapterygial" axis; **bas**, basal cartilage of pectoral fin; **br**, branchial arches; **cor**, coracoid region; **cor pr**, coracoid process of pectoral endoskeleton; **cor r**, coracoid recess; **cor sh**, coracoid shelf; **dfs**, base of dorsal fin spine; **dr**, fragments of possible distal radials; **fspc**, fin spine posterior closure; **fw**, fin web; **hy**, hyoid arch; **lpf**, left pectoral fin; **lpfc**, level of fin spine posterior closure; **lpfs**, left pectoral fin spine; **ls**, lorical spine; **lum**, lumen of pectoral fin spine; **mc**, meckelian cartilage of lower jaw; **me**, median element of shoulder girdle; **pfs**, pectoral fin spine; **pin**, pinnal plate; **plfs**, base of pelvic fin spine; **ppls**, prepelvic spines; **pps**, prepectoral spine; **pr**, proximal radials of pectoral fin; **rpf**, right pectoral fin; **rpfs**, right pectoral fin spine; **scap**, scapular process; **sp b**, base of pectoral fin spine; **t**, teeth.

RESULTS

As preserved, the jaws and branchial arches in the articulated specimen are almost as wide as the pectoral fins (fig. 1). While it is possible that the apparent width of the branchial

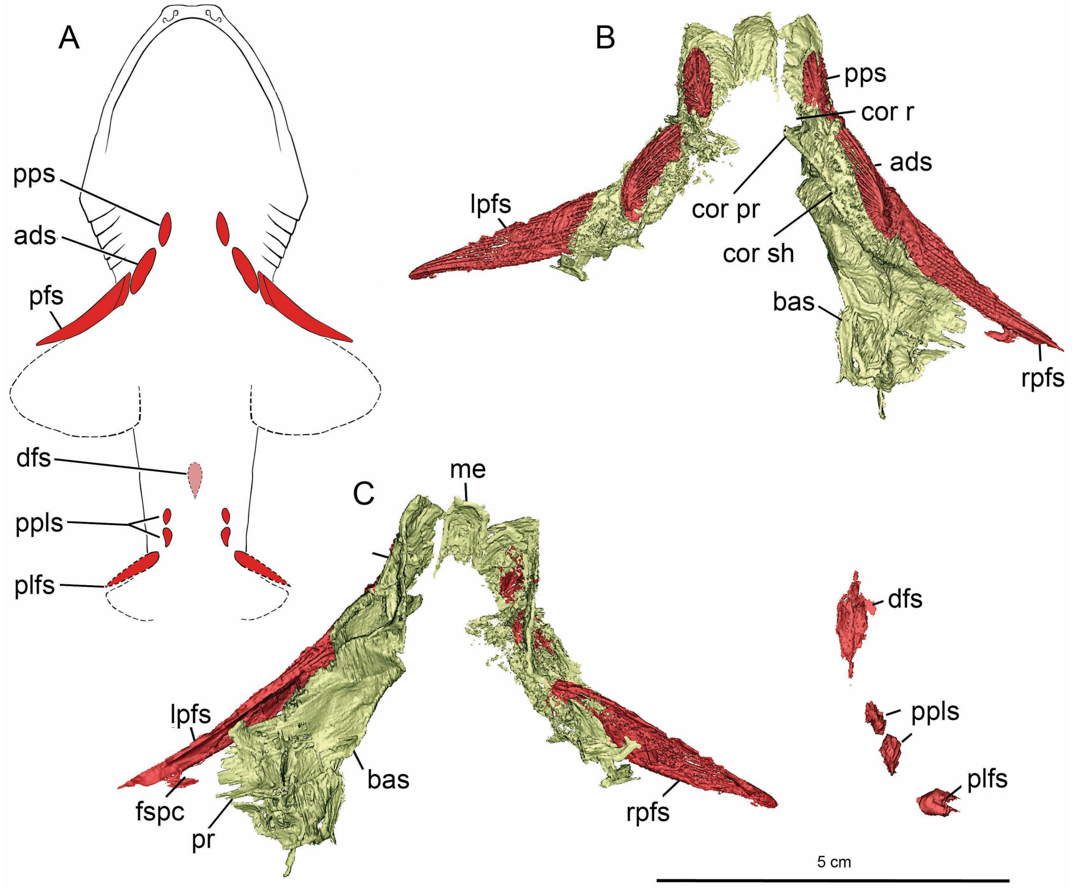


FIGURE 2. The main dermal and cartilaginous components of the pectoral region in *Doliodus* (NBMG 10127/3): **A,** schematic ventral view of *Doliodus* showing general arrangement of dermal spines; **B,** pectoral endoskeleton and dermal spines rendered from scan, viewed from below (also showing postpectoral spines of left side); **C,** the same viewed from above (postpectoral spines not shown). Anterior to top. Scale bar for B and C = 5 cm.

arches has been exaggerated by flattening during burial, the pectoral fins in other dorsoventrally compressed Paleozoic chondrichthyan fossils (e.g., *Cladoselache*, Symmoriiformes) project much farther laterally (as in many modern sharks), suggesting that the pectoral fins in *Doliodus* arose somewhat closer to the ventral midline. Additionally, the fins in *Doliodus* are located posterolateral to the coracoid region (as in many modern sharks), rather than lateral to it (e.g., as in *Cladoselache*).

Pectoral Endoskeleton

The appendicular skeleton of the pectoral fin in *Doliodus* is well developed, with a large basal plate forming the main attachment of the fin to the scapulocoracoid (Miller et al., 2003) (figs. 2–4). This plate extends inside the fin spine lumen and also spans the entire fin base,

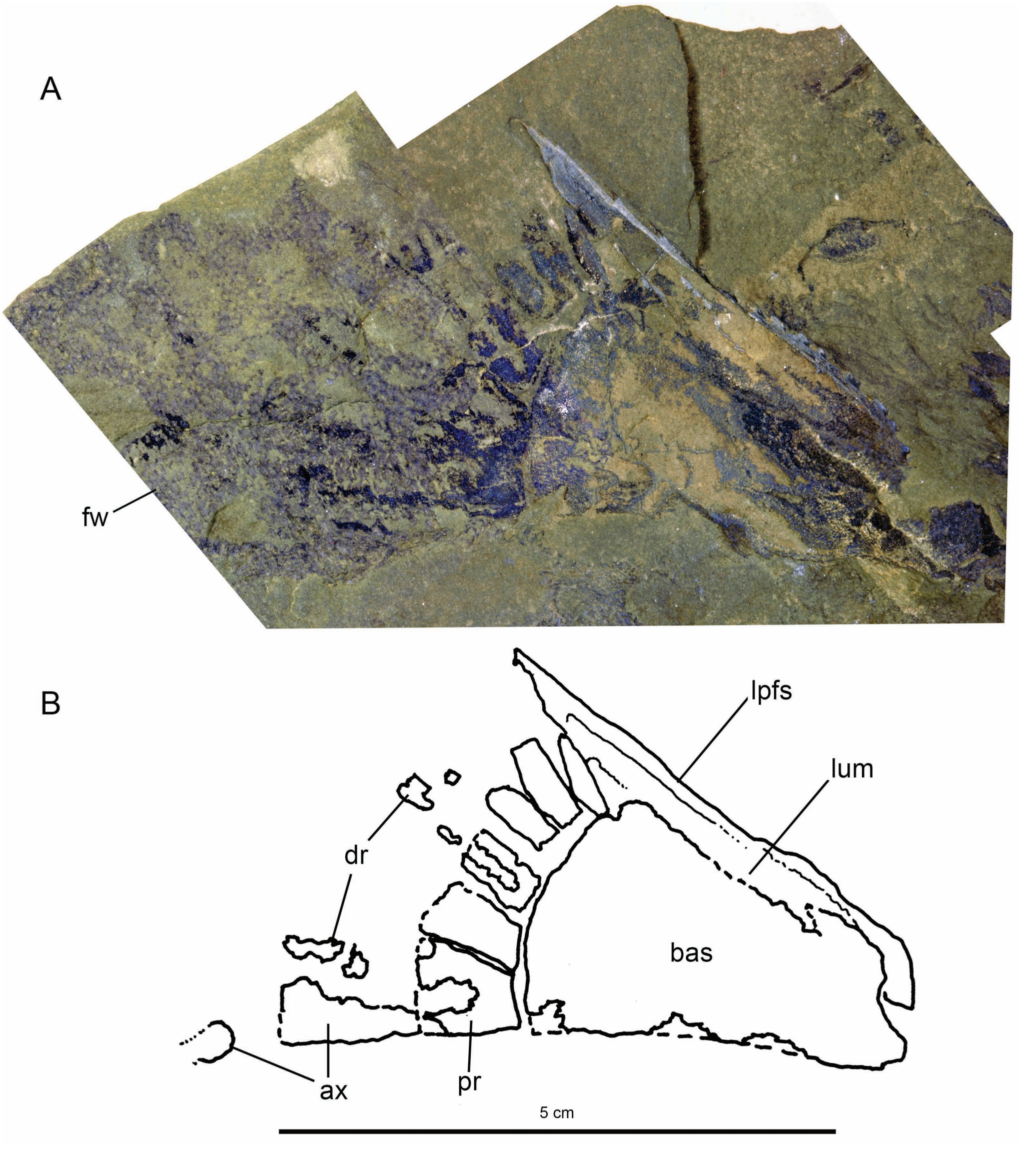


FIGURE 3. Left pectoral fin of NBMG 10127/3 as preserved, in dorsal view: **A,** photograph of the fin, digitally enhanced to emphasize areas of calcified cartilage and denticle-covered fin web; **B,** annotated outline of principal features. Abbreviations as designated in the main body of the text. Anterior is to right. Scale bar = 5 cm.

although it was not possible to determine whether the plate is subdivided into separate pterygial elements like those of many modern chondrichthyans. *Doliodus* therefore differs from many other Paleozoic chondrichthyans (e.g., *Cladoselache*, Symmoriiformes, Eugeneodontiformes), in which a variable number of radials (either jointed or unjointed) meet the scapulocoracoid anterior to a large basal cartilage (Zangerl, 1981).

Several proximal radials meet the distal border of the basal plate (figs. 3, 4), although the upper and lower surfaces of many radials either are not preserved or were not mineralized

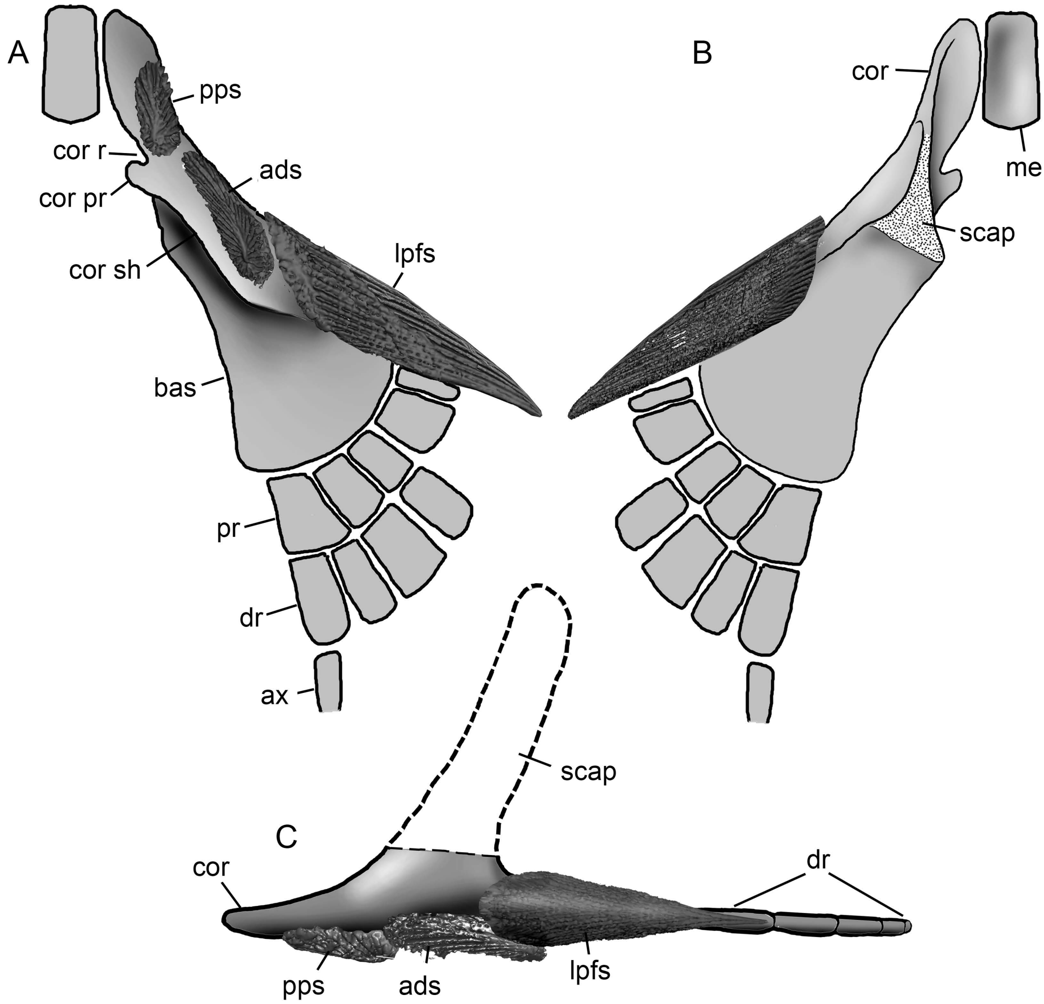


FIGURE 4. Schematic reconstruction of the pectoral endoskeleton and dermal skeleton of the left side in *Doliodus*, based on the results of scan reconstitution using segmentation analysis of NBMG 10127/3. **A,** ventral view; **B,** dorsal view; **C,** lateral view. Anterior to top in A and B, to left in C. No scale. Note: parts of the pectoral fin spine shown here have been reconstructed for clarity.

originally, so mostly their anterior and posterior margins are preserved. The anteriormost radials are slender, whereas those farther posteriorly are wider. The first proximal radial (located directly behind the fin spine) is triangular and slightly shorter than the second, although all the proximal radials are of approximately equal length. A few traces of cartilage in the fin web suggest the presence of additional, poorly mineralized distal radials and possibly a post-metapterygial series. The fin web was apparently separated from the fin spine at the level of the proximal radials, and was extensively covered by dermal denticles that extend far beyond the distal ends of endoskeletal mineralization, suggesting that the fins were aplesodic (as in modern chimaeroids and many sharks) i.e., with radials not extending to the fin margins.

The scapular region of the pectoral girdle is not preserved, but the ventral (coracoid) part of the girdle is almost complete. An anteriorly directed area of cartilage extending anteriorly (identified as the procoracoid region by Miller et al., 2003) is continuous with the rest of the girdle and corresponds to the coracoid process in modern chondrichthyans. The ventral surface of this part of the girdle supports a dermal spine (identified here as a prepectoral spine; see Pectoral Dermal Skeleton). Separate, paired procoracoids are not present. However, between the paired coracoid processes there is a large and apparently unornamented, subrectangular median element, overlain by dermal denticles that resemble those covering the trunk farther posteriorly. This structure was therefore presumably located entirely within mesenchymal tissue. It may represent part of the pectoral endoskeleton, like the median sternal cartilage (omosternum) in the broadnose sevengill shark, *Notorynchus cepedianus*. It could also be interpreted as the perichondral component of a lorical plate (a median, usually ornamented element, sometimes found in "acanthodians"). Although the lorical plate of "acanthodians" is generally considered to be part of the dermal skeleton, it has been suggested that the base of this plate in *Climatius* may include perichondral bone (Burrow et al., 2015).

Behind this median element, the ventral margin of the coracoid bears an anteriorly recurved, ventromedially directed process, which is located just behind a rounded coracoid recess (fig. 4). The latter resembles the scapulocoracoid notch in iniopterygians, although it differs in not forming an articulation with the posterior basibranchial plate in *Doliodus* (c.f., Zangerl, 1981: fig. 30; Pradel et al., 2009). Behind the ventromedial process, a continuous shelf of cartilage extends from the coracoid cartilage and supports an admedian spine (see next section). This cartilaginous shelf is located below the level of the pectoral basal cartilage, apparently merging with the latter lateral to the admedian spine. This arrangement suggests that there was little fin mobility, although the structure of the joint between the girdle and fin could not be resolved clearly from the scan.

Pectoral Dermal Skeleton

Each pectoral fin in *Doliodus* is preceded by a stout fin spine, angled posterolaterally at 40°–45° from the body axis (Miller et al., 2003). The fin spines are considerably shorter than the pectoral fin span, even though the spine tips are broken and originally would have extended slightly farther laterally (fig. 5 A, B, E, F). The fin spines are ornamented by ridges, each bearing a series of closely spaced pectinations. The ridges extend diagonally along the spine length, with new ridges inserted at intervals along the anterior midline and passing to the spine base in a chevron arrangement. The ornamented field terminates just above the base of the fin spine, leaving only a short region of attachment (fig. 5 B, E). Numerous isolated spines with similar ornament have been collected from the same locality, and were customarily identified as *Climatius latispinosus* (a generic assignment based on superficial similarities to spine ornamentation in the type species, *C. reticulatus*).

The fin spines reach the scapulocoracoids proximally, but do not extend deep inside the body and are not associated with any opening in the coracoid (e.g., unlike in *Acanthodes* [Miles,

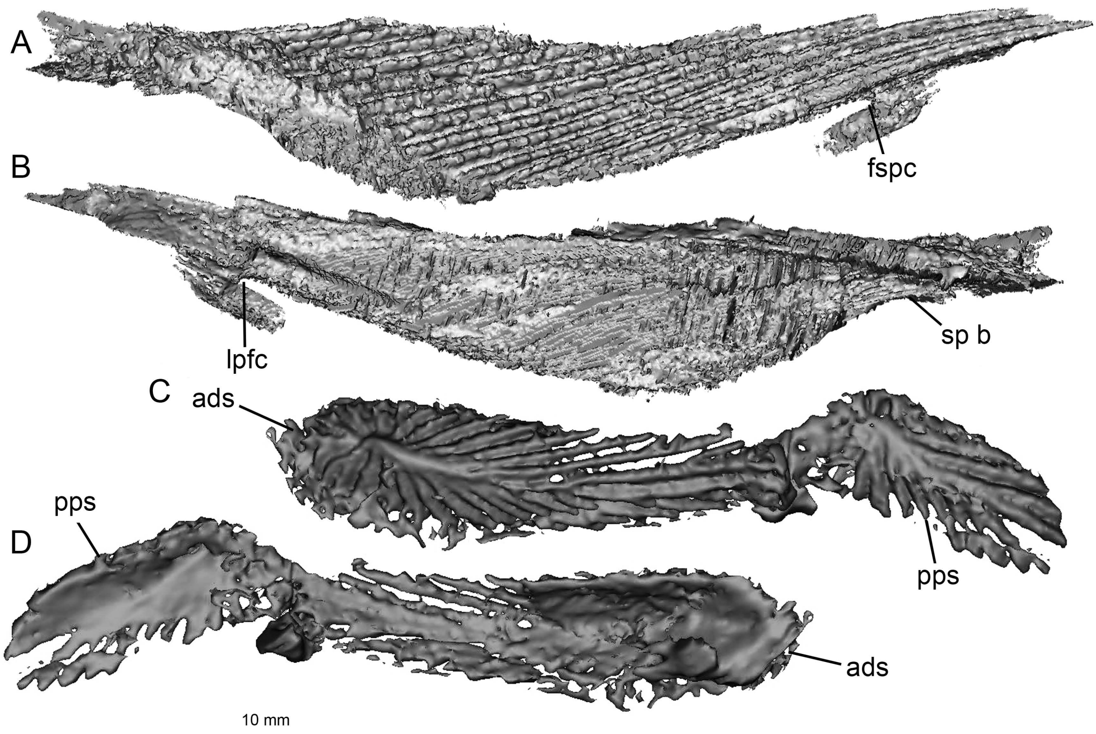
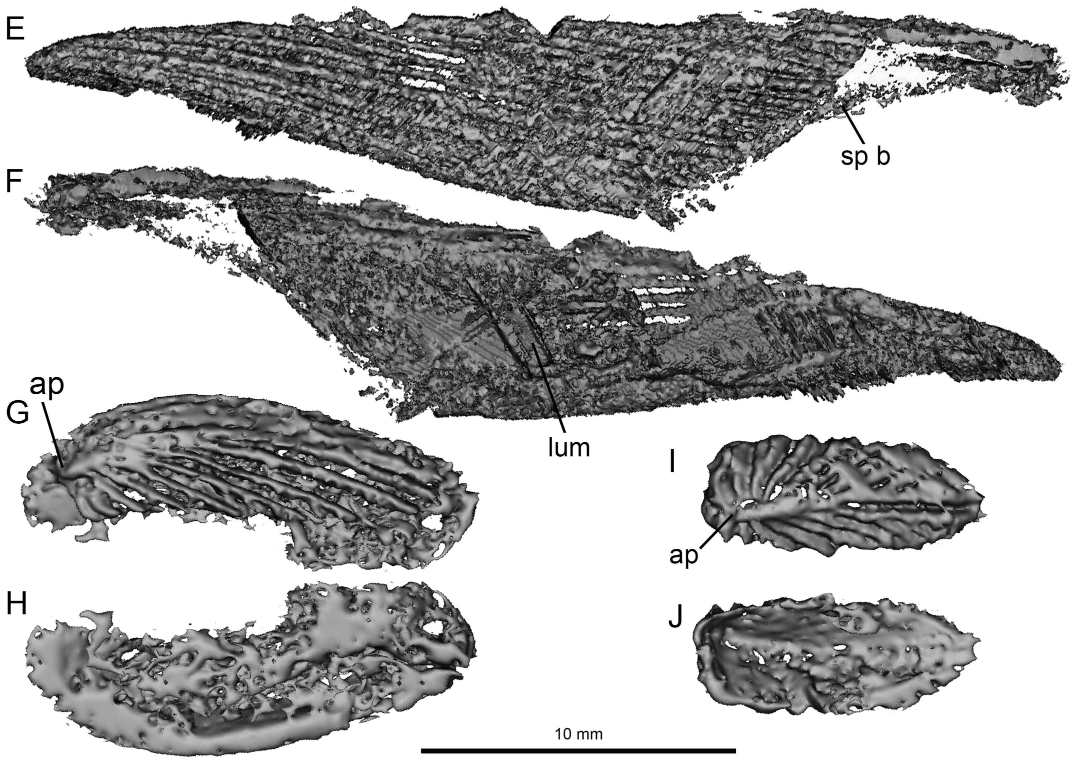


FIGURE 5. Dermal elements of the pectoral girdle in *Doliodus* reconstituted by scan segmentation analysis of NBMG 10127/3. **A, C,** external surfaces; **B, D,** internal surfaces. **A, B,** left fin spine; **C, D,** left prepectoral and

1973]). The odd, hooklike feature seen on the left fin spine (fig. 5A, B) is all that remains of the fin spine posterior wall. This region of the spine is unornamented and is slightly concave in transverse section. The "hook" is the archlike distal border of a large posterior opening (fig. 5A: fspc). Since only the tips of the fin spines are missing in the articulated specimen, the posterior region of each pectoral fin spine was probably open for most of its length.

The newly discovered paired dermal elements (fig. 5C, D, G–J) are low spines associated with the coracoid process that could not have projected very far from the body surface. Their external surface is ornamented with pectinated ridges that, instead of displaying a chevron arrangement like the fin spines, radiate from an apical growth center, located near the posterior end of each element (fig. 5G, I: ap). The internal surface of these spines is concave, forming a wide, open basal cavity.

The spines correspond topographically to elements found in many "acanthodians" and are identified using terminology after Burrow et al. (2015). The anteriormost paired spines (identified here as prepectorals) are located directly beneath the coracoid process. Each spine is approximately twice as long as wide and is widely separated from its antimere. The paired spines farther posteriorly (identified here as admedian spines, although they could represent a second pair of prepectoral spines) are more elongated than the preceding prepectorals, and diverge posteriorly toward the base of each fin spine. These spines are located medial to the pectoral fin spine and are separated by a space from the prepelvic spines farther posteriorly (fig. 2B).



admedian spines. **E, G, I,** external surfaces; **F, H, J,** internal surfaces. **E, F,** right fin spine; **G, H,** right admedian spine; **I, J,** right prepectoral spine. Scale bars = 1 cm.

Spines behind the Pectoral Region

Several spines are preserved in varying states of completeness behind the pectoral region in NBMG 10127/3. Two of them correspond topographically and morphologically to the prepelvic spines in "acanthodians" (fig. 6). The most complete examples are located to the left of the ventral midline, but those on the right are represented by tiny fragments that are still buried in matrix. The base of each prepelvic spine is open, with a wide central cavity, like the prepectoral and admedian spines. The external surface of each prepelvic spine is ornamented by ridges that radiate from a posteriorly located apex and are slightly extended anteriorly. These spines are still surrounded by in situ dermal denticles of the trunk region.

Two somewhat larger but incomplete spine fragments are also present, one in front and the other behind the prepelvic spines (fig. 2B: dfs, plfs). The fragment in front is the largest, but is not exposed and was discovered only by inspection of the scan. It exhibits traces of poorly preserved ornament (apparently pectinated, like the pectoral fin spine ornament), facing in the opposite direction to the prepelvic spines behind it (i.e., its ornament is directed dorsally rather than ventrally). On its other side is a deep concavity, probably representing part of the spine central cavity. We provisionally interpret this fragment as the base of a dorsal fin spine, although it is very incomplete and was presumably damaged prior to burial in sediment.

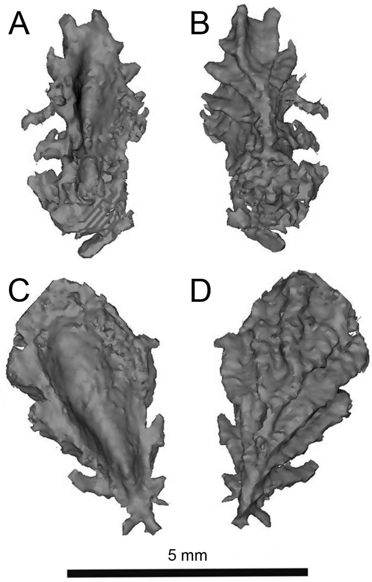


FIGURE 6. Detail of left prepelvic spines, showing ornamented and internal surfaces with open base. **A, B,** anterior prepelvic spine; **C, D,** posterior prepelvic spine. Anterior to top. Scale bar = 5 mm.

Another large spine fragment is located behind the prepelvic spines. It is also hollow, with part of the spine wall surrounding a central cavity. No ornament could be discerned, but the central cavity is elongated posterolaterally, suggesting that the fragment represents the base of a (paired) pelvic fin spine.

DISCUSSION

According to these findings, *Doliodus* not only possessed paired pectoral fin spines (Miller et al., 2003), but was also endowed with paired prepectoral (and admedian?) spines, at least two pairs of prepelvic spines, and possibly dorsal and pelvic fin spines. It is still unknown whether an anal fin spine was also present, but the dermal skeleton in *Doliodus* clearly included many other spine elements classically associated with "acanthodian" fishes. *Doliodus* also possessed an impressive suite of "sharklike" features, including: a braincase and jaws similar to that of many Paleozoic sharks (Maisey et al., 2009); a sharklike dentition, comprising successional replacement teeth in apparently fixed positions in the mouth ("tooth families"); teeth displaying both monognathic and dignathic heterodonty (Maisey et al., 2014); a pectoral girdle with an expanded coracoid region; a pectoral fin with large basals and elongated radials, implying an extensive appendicular skeleto-muscular system (also present in *Kathemacanthus* [Gagnier and Wilson, 1996]); and a regionally differentiated, micromeric dermal squamation that includes chondrichthyanlike polyodontode mucous membrane denticles, multicuspid branchial denticles, and ctenacanthlike head and trunk denticles (Miller et al., 2003). The "chondrichthyan" features of *Doliodus* are therefore widespread throughout its head and pectoral region, whereas its "acanthodian" features are confined to the postcranial dermal skeleton.

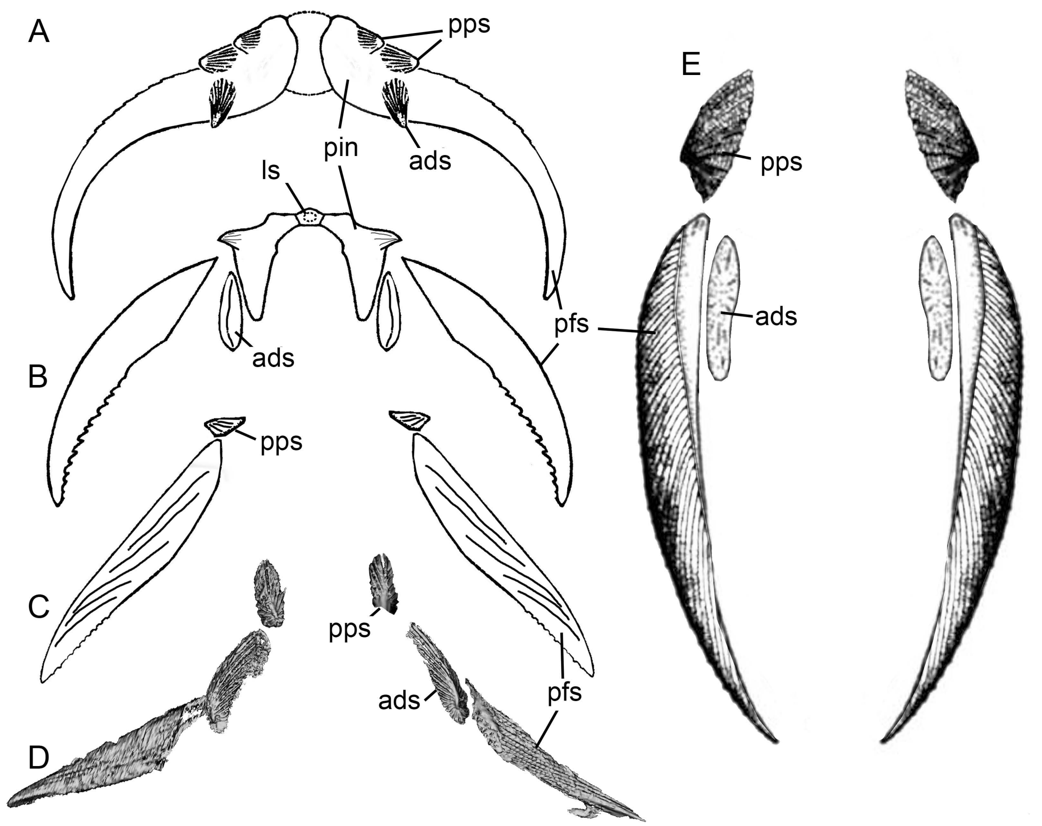


FIGURE 7. Comparison of the pectoral spines in *Doliodus* and selected "acanthodians," all in ventral view. **A,** *Erriwacanthus falcatus*; **B,** *Vernicomacanthus uncinatus*; **C,** *Lupopsyrus pygmaeus*; **D,** *Doliodus problematicus*; **E,** *Gyracanthides murrayi*. Not to scale. **A–C** redrawn after Denison (1979), **D** redrawn after Warren et al. (2000).

The pectoral fin in *Doliodus* has only a narrow attachment to the pectoral girdle, providing circumstantial corroboration of the hypothesis that pectoral fins with a large basal cartilage represent a primitive condition for "conventionally defined chondrichthyans" (Coates, 2003). The morphology of the pectoral endoskeleton is poorly known in most "acanthodians"; nevertheless, *Doliodus* clearly differs from forms such as *Acanthodes* and *Ischnacanthus* that have several small elements (usually identified as radials [Miles, 1973]) articulating with the scapulocoracoid without evidence of a large basal plate.

The spines associated with the pectoral girdle in *Doliodus* do not form a continuous "macromeric shoulder girdle" (Zhu et al., 2013: char. 104), but are nevertheless clearly associated with the ventral region of the girdle (Zhu et al., 2013: char. 105) and could therefore be characterized as a "discontinuous macromeric shoulder girdle." A brief visual comparison is appended here of pectoral spine arrangement in *Doliodus* and selected "acanthodian" taxa (fig. 7). Prepectoral and admedian spines are absent in acanthodiids, but occur in many other "acanthodians" (sometimes with multiple pairs of prepectoral spines). In some taxa, the pre-

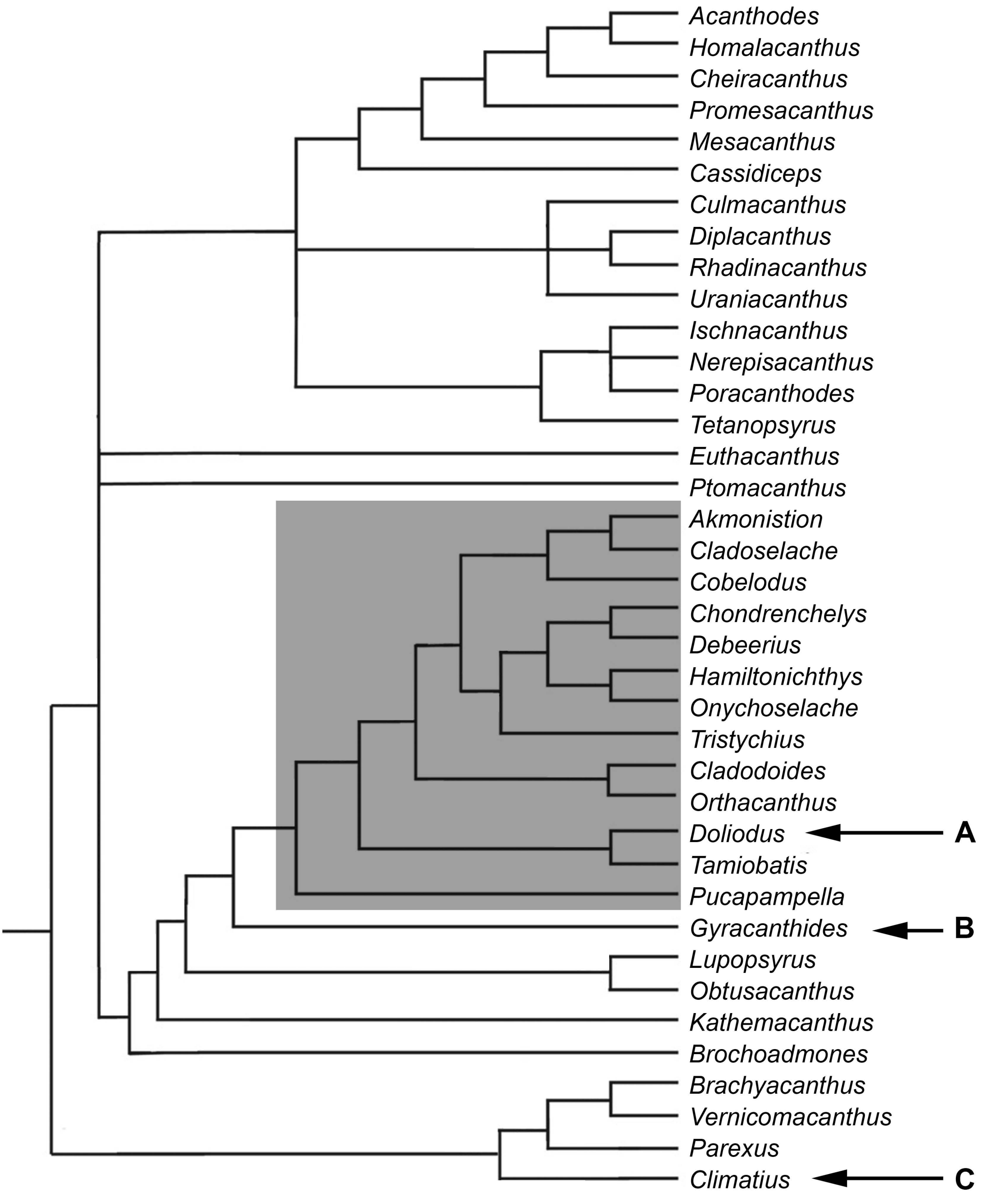


FIGURE 8. Three plausible alternative phylogenetic positions of *Doliodus* within the chondrichthyan total group (comprising "acanthodians" and "conventionally defined chondrichthyans" [shaded]). **A,** within "conventional" chondrichthyans; **B, C,** outside "conventional" chondrichthyans; **B,** close to *Gyracanthides* (and/or *Lupopsyrus*?), based on similar pectoral spine arrangement; **C,** close to *Climatius* (based on similarities in spine structure and ornament). Tree after Burrow et al. (2016).

pectoral and admedian spines are incorporated into compound, paired pinnal plates (e.g., *Erriwacanthus falcatus*; fig. 7A). In others, the admedian spines may be separate, with only the prepectoral spine/s attached to the pinnal plate (e.g., *Vernicomacanthus uncinatus*: fig. 7B). In *Lupopsyrus pygmaeus* (fig. 7C), a small prepectoral spine is associated with the procoracoid cartilage, but admedian spines and loricals are absent (Hanke and Davis, 2012). In *Gyracanthides murrayi*, a pair of comparatively large prepectoral spines is located anterior to the coracoids (fig. 7D), and a second pair of spines (topographically corresponding to admedian spines in other "acanthodians," but lacking ornament) is located ventral to the scapulocoracoids and medial to the base of the pectoral fin spines (Warren et al., 2000). A median lorical plate is absent in *Gyracanthides*. The median element anterior to the coracoids in *Doliodus* lacks dermal ornament typically found on "acanthodian" lorical plates, and compound pinnal plates are absent (fig. 7E).

Although *Doliodus* possessed an "acanthodian-like" dermal spine complex, few "acanthodians" exhibit the same character combination (with "free" prepectoral and admedian spines, but lacking compound pinnals and ornamented loricals). *Gyracanthides* is one of very few "acanthodian" taxa to display a similar arrangement (moreover, it has been resolved phylogenetically in a position close to the base of "conventionally defined chondrichthyans" [Burrow et al., 2016]), although its presumed admedian spines lack ornament. Additionally, the pectoral fin spines in *Doliodus* and *Gyracanthides* are ornamented with ridges arranged in chevrons, whereas paired spines associated with the endoskeletal girdle are ornamented with fanlike or radiating ridges and rows of tubercles (as are the prepelvic spines in *Doliodus*; fig. 6). Although the distinctive ornamentation pattern in *Gyracanthides* (considered diagnostic for the family Gyracanthidae [Denison, 1979; Warren et al., 2000]) is not shared with *Doliodus*, the conjunction of chevron and radiating spine ornament in these taxa is interesting; these two patterns have been characterized elsewhere as "either-or" character states among "acanthodians," without specifying which spines actually display the feature (e.g., Giles et al., 2015: char. 225), so the conjunction of fanlike and radiating spine ornament patterns is an unusual and potentially apomorphic arrangement.

CONCLUSIONS

In several recently published phylogenetic hypotheses, *Doliodus* has been resolved in a relatively basal position within "conventionally defined" chondrichthyans. The conjunction in *Doliodus* of a sharklike cranial morphology, dentition and pectoral endoskeleton, with a decidedly "acanthodian-like" array of dermal spines, strongly corroborates the hypothesis that some (or even all) "acanthodians" populate the chondrichthyan stem. However, the observations presented here are also congruent with a phylogenetically lower position on the chondrichthyan stem for *Doliodus* than was previously supposed, possibly even outside the "conventionally defined chondrichthyans" (fig. 8). In particular, *Doliodus* resembles some "acanthodians" in which the dermal pectoral skeleton consisted of isolated spines rather than compound, macromeric dermal plates, with both chevron and radiating spine-ornament patterns (e.g., gyracanthids). Furthermore, the internal structure and ornamentation of dermal spines in *Doliodus* are remarkably like those of *Climatius* (the taxon to which they were originally referred [Whiteaves, 1881]). The phylogenetic position of *Doliodus* within the chondrichthyan total group is therefore considered ambiguous; it could fall within "conventionally defined chondrichthyans," or within "acanthodians," or between both of them.

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