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The oldest articulated chondrichthyan from the Early Devonian period

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Chondrichthyans (including living sharks, skates, rays and chimaeras) have a fossil record of scales and dermal denticles perhaps dating back to the Late Ordovician period, about 455 million years ago^{1,2}. Their fossil tooth record extends to the earliest Devonian period, almost 418 million years ago³, whereas the oldest known articulated shark remains date from the Early Devonian period⁴, about 394 million years ago⁵. Here we report the discovery of an articulated shark that is almost 409 million years old⁵ from the Early Devonian (early Emsian) period of New Brunswick, Canada. The specimen, identified as *Doliodus problematicus* (Woodward)⁶, sheds light on the earliest chondrichthyans and their interrelationships with basal jawed

vertebrates. This species has been truly problematic⁷. Previously known only from isolated teeth^{2,6,8}, it has been identified as an acanthodian and a chondrichthyan. This specimen is the oldest shark showing the tooth families *in situ*, and preserves one of the oldest chondrichthyan braincases. More notably, it shows the presence of paired pectoral fin-spines, previously unknown in cartilaginous fishes.

Isolated and articulated Early to Middle Devonian shark specimens are rare^{1,9}. Until now, the oldest partial articulated shark, consisting of the braincase articulated with parts of the visceral skeleton, was *Pucapampella* from the Early Devonian of South Africa⁴. Significant Middle Devonian partially articulated specimens include *Pucapampella* from Bolivia^{10,11}, *Antarctilamna prisca* from Antarctica and Australia^{7,12}, and *Gladbachus adentatus* from Germany¹³.

Specimen NBMG (New Brunswick Museum, Geology) 10127/1a,b-4 consists of the anterior part of *D. problematicus*, forward of the mid-trunk region (Fig. 1). It is preserved dorsoventrally, oriented dorsal side up with exo- and endoskeletal elements preserved, including characteristic prismatic calcified cartilage, teeth, scales and large fin-spines. The specimen is cleaved in five parts, providing a series of transverse sections through the head and branchial region. The preserved length is 23 cm, suggesting a body length of perhaps 50–75 cm on the basis of shark comparative anatomy.

Prismatic calcified cartilage, considered to be a chondrichthyan synapomorphy^{1,14}, compose the neurocranium and splanchnocranium. The articulated jaws confirm that *D. problematicus* possessed tooth families and provide early evidence in chondrichthyans of the relationship of teeth to the dental lamina^{1,15}. Most teeth are partially buried; however, tooth families that are visible have teeth stacked in a row, with newer teeth sitting in a space representing the position of the dental lamina groove. Tooth bases abut a prominent dark-brown concave surface, interpreted as preserved basal connective tissue. The dentition shows weak dignathic and disjunct monognathic heterodonty, suggesting revision of earlier opinions about the evolution of shark teeth¹⁶. Functional upper and lower teeth, offset anteriorly, oppose one another with sharp lateral edges of principal cusps connecting in a scissors movement. The functional teeth show the asymmetry and range of variation previously recognized^{2,6,8}, and verify the position and number of tooth types in the jaw. Teeth are not seen in the symphyseal and parasymphyseal portions of the lower jaw.

The right side of the lower jaw shows about 15 tooth families; the left side has only 11 tooth families preserved, with bases of at least three anterior rows present in the cartilage. Tooth families expose up to three teeth each. Near the posterior jaw articulation, flat basal pads might represent the most posterior teeth. Lower tooth families are seen in cross-section, showing the apparently highly vascularized lower edge and new tooth germs. The last three to four posterior tooth families do not show dental membranes and thus are more like modified dermal scales. In a few teeth, two large divergent lateral outer cusps with two to four intermediate small cusps can be seen in cross-section. These and a thin section of a *D. problematicus* tooth from the National Museums of Scotland (RSM1897.51.46) show that the cusps are formed of orthodontine². Bases are rounded and cap-like with a row of five to six large foramina in the slightly concave foot. Cross-sections show osteodontine with a basal lamellar tissue, which directly abuts the dental membrane. The difference between the structure of the smaller posterior teeth (equivalent to type specimen BMNH (British Museum, Natural History) P.6540) and that of branchial denticles is still strong, contrary to one hypothesis on the origin of teeth¹⁷.

Woodward⁶ diagnosed the taxon “*Diplodus*” *problematicus* on an isolated tooth (BMNH P.6540), concluding that the diplodont (xenacanth) tooth type was present by Early Devonian. Traquair⁸

reassigned holotype and topotype specimens to *Doliodus*, with no doubt of its selachian nature, noting the succession of teeth. Since the early work and until recently^{2,7}, however, the teeth have been erroneously assigned to the Acanthodii¹⁸. *D. problematicus* teeth are now reassigned to Chondrichthyes, with a structure similar to that of some xenacanthiforms, and included in the Omalodontida Turner 1997, known from shark teeth with a labially extended base².

Until now, *Pucapampella* from the Late Emsian of South Africa⁴ and Emsian?/Late Eifelian/Givetian of Bolivia¹⁰ showed the oldest chondrichthyan cranium. The large braincase of *Doliodus*, in part and counterpart, is preserved from the precerebral fontanelle to just in front of the occipital region with the basal surface abutting the palatoquadrate (Fig. 2a, b). The precerebral fontanelle is prominent and large, similar to that of *Tamiobatis*⁹ and *Gladbachus*¹³. We considered its presence as a putative elasmobranch synapomorphy¹⁰ (neoselachian synapomorphy sensu Coates and Sequeira¹⁹); non-chondrichthyan taxa and holocephalans do not have a precerebral fontanelle^{10,19}. The neurocranium of *Doliodus* is the oldest to possess this fontanelle. The *Doliodus* neurocranium has a moderately long otico-occipital region and shows similar proportions to *Tamiobatis* and *Xenacanthus*⁹. Postorbital processes are wider than in *Pucapampella*, although narrower than the total width of the otico-occipital unit, a purported plesiomorphic condition

within chondrichthyans¹⁹. Poorly developed lateral otic processes are present, a character considered to be a chondrichthyan synapomorphy¹⁰. Evidence of a ventral otic fissure cannot be observed as preserved. Comparison of this feature to *Pucapampella*^{4,10} is not possible. Posteriorly, an elongate median endolymphatic fossa is present; this character sets *Doliodus* as a chondrichthyan above *Pucapampella*¹⁰.

The mandibular, hyoid and branchial arches are preserved almost in life-position (Fig. 1), but the latter two are slightly displaced posteriorly. The right side is more difficult to interpret because of the overpositioning and lateral compression of the meckelian cartilage, basihyal, palatoquadrate, ceratohyal and anterior three ceratobranchials. The inverted U-shaped median basihyal is wide and constricted at the symphysis. The basihyal and basibranchials are separated by a gap. Two basibranchials are preserved; the posterior one being the largest. Four (perhaps five) pairs of elongated, slightly sigmoid ceratobranchials form the main part of the branchial apparatus. The visceral skeleton of *Doliodus* shows gross similarity to that of *Gladbachus*¹³, with the exception of the shape of the basibranchials and ceratobranchial IV.

Morphology of both pectoral fins is well preserved (Figs 1 and 3). Uniquely for chondrichthyans, fin-spines form the anterior margin of the pectoral fins in *D. problematicus*. Notably, the fin-spine of the articulated shark *Antarctilamna prisca* (CPC (Commonwealth

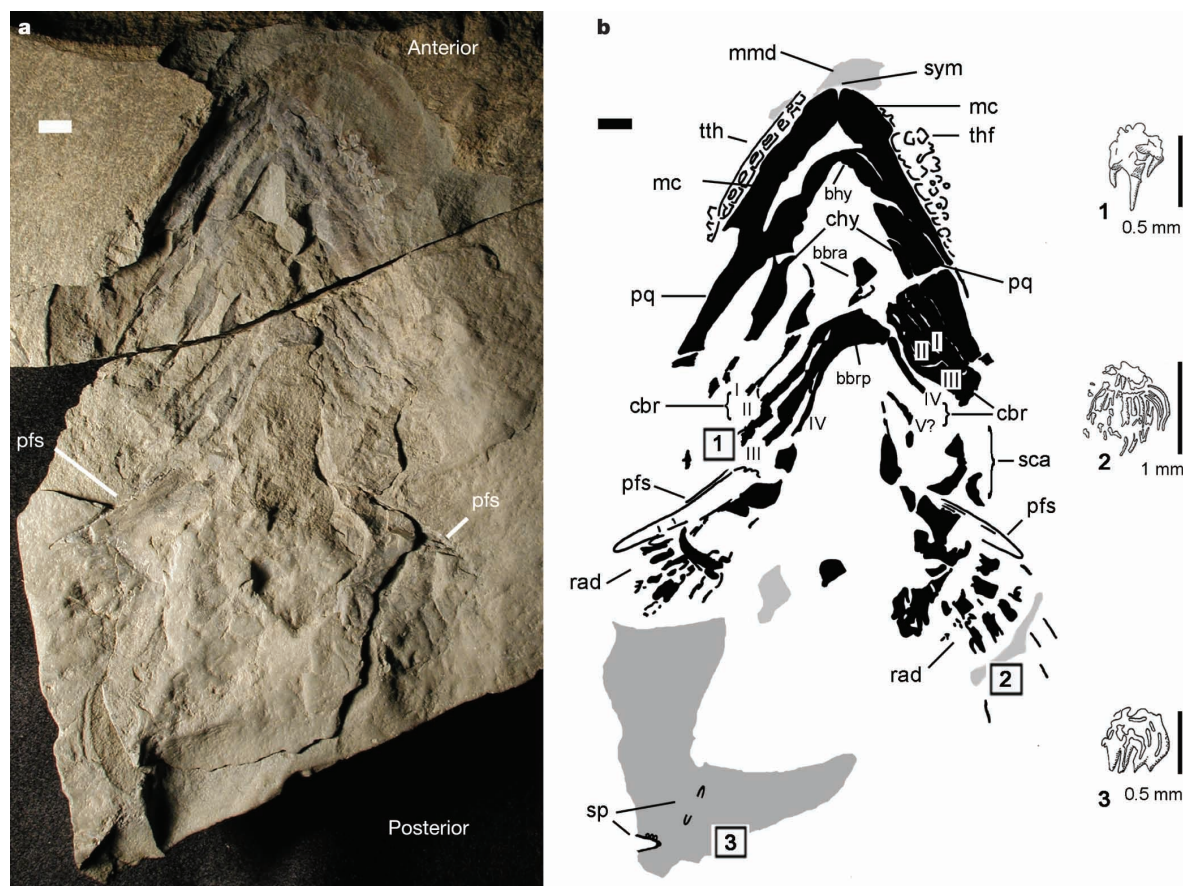


Figure 1 Partial articulated shark, *Doliodus problematicus* (NBMG 10127/1b,2,3). **a**, Specimen lying dorsal side up with the head at top and extending posteriorly to behind the pectoral fins. pfs, pectoral fin-spines. **b**, Map showing cartilage elements (black infill) and large areas of denticles (grey). mmd, location of mucous membrane denticles on counterpart; sym, symphysis; tth, area with *in situ* teeth; thf, *in situ* tooth family; mc, Meckel's cartilage; pq, palatoquadrate; bhy, basihyal; chy, ceratohyal;

bbra, anterior basibranchial; bbrp, posterior basibranchial; cbr, ceratobranchials (I–V?); sca, scapulocoracoid; pfs, pectoral fin-spines; rad, radials; sp, partial spines; denticle enlargements as preserved from branchial region (1), from pectoral fin (2) and from trunk region (3). Scale bar, 1 cm. Scales are separate for denticle enlargements.

Palaeontological Collection) 21187), which has been interpreted¹² as a dorsal spine, is suggestive of a pectoral fin-spine, being in the same position as the pectoral fin-spines described here. Until now, only dorsal fin-spines were known in basal chondrichthyans^{1,9}. Paired, dermal pectoral fin-spines were previously known only in placoderms, acanthodians and the basal osteichthyan *Psarolepis*²⁰. Their presence in *Doliodus* and perhaps *Antarctilamna* and the above-mentioned groups, suggests that it represents a gnathostome synapomorphy lost independently in Osteichthyes other than *Psarolepis*²¹, Placodermi and Chondrichthyes. The presence of large fin-spines associated with all fins except the caudal fin, or more specifically the presence of paired fin-spines, had been considered an acanthodian synapomorphy¹. This character can no longer be considered an acanthodian synapomorphy and the tenuous monophyly of acanthodians is now supported by a single scale histology synapomorphy¹.

The fin is aplesodic with radials extending half way to the margin (Figs 1 and 3). At least six (possibly seven) radials articulate on the lateral edge of a large basipterygial element (meso- or metapterygium); this feature is considered to be another chondrichthyan synapomorphy²². The area of dermal scales extends well lateral of the fin-spine distal tips, suggesting a large rounded pectoral fin. Left of the midline, near the posterior of the specimen, are small fin-spines that are furnished with hook-like denticles. These might be paired pelvic or intermediate spines, or parts of a collapsed dorsal fin-spine. Disarticulated fin-spines from the Campbellton Formation are identified as probable chondrichthyan and acanthodian^{6,8,23}. Pectoral fin-spines on NBMG 10127 are closest in size and ornament to those that were originally named "*Ctenacanthus*" *latispinosus*²³ and subsequently reassigned to *Climatius*⁶, a climatiid acanthodian¹⁸. Isolated *Climatius latispinosus* spines, NBMG 9986 and 10017, are preserved with *Doliodus* teeth and scales, and spine NMC (Canadian Museum of Nature) 12002 includes a nearby patch

of prismatic cartilage and branchial denticles. Further work is required to determine whether *D. problematicus* and *C. latispinosus* are synonymous.

Doliodus has rounded to polygonal, polyodontode mucous membrane denticles lining the inner upper palate and jaw edges (Fig. 2c) and rounded head denticles, multicuspid branchial denticles and ctenacanth-type complex trunk scales similar to those of *Antarctilamna* (Fig. 1), and thus is relatively advanced as compared with known purported Ordovician to Silurian sharks with simple placoid scales^{1,9}. Behind the branchial region shagreen extends posteriorly, with scattered denticles and dorsal scales infilling the central body area. Trunk scale morphology is most like scales described from the (Pragian) Jauf Formation in Saudi Arabia²⁴.

The Campbellton Formation²⁵, with its rich flora^{26,27} and terrestrial invertebrates²⁸, yields vertebrates in the lower "Atholville beds"²⁹. Miospores immediately below the articulated shark bed identify the *Emphanisporites annulatus*–*Camazonotriteles sextantii* Assemblage Zone²⁶, corresponding to early, to early late Emsian (*dehiscens* to *serotinus* Conodont Zones) age. *Doliodus* teeth^{6,8} come from older beds at the base of the formation, perhaps near the 409-Myr-old Pragian/Emsian boundary⁵. The depositional environment has been considered fluvial²⁵; however, fossil assemblages^{26–28} suggest lagoonal and estuarine environments. Rare prasinophytes (tasmanids)²⁶ indicate a marine connection.

Discoveries of Early and Middle Devonian chondrichthyans from Gondwanan or neighbouring terranes have led to suggestions of a

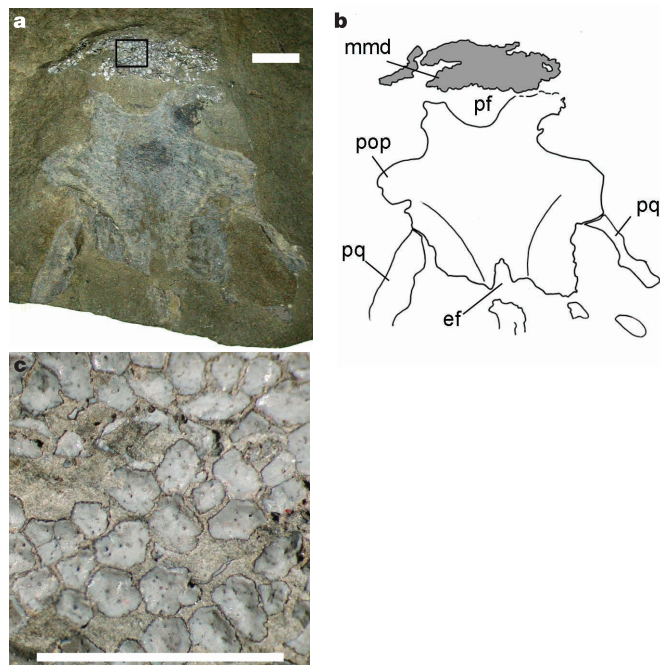


Figure 2 Neurocranium of *Doliodus problematicus* (NBMG 10127/4). **a**, Neurocranium and patch of mucous membrane denticles with enlarged area outlined. **b**, Map of neurocranium. pf, precerebral fontanelle; pop, postorbital process; ef, endolymphatic fossa; pq, palatoquadrate; mmd, mucous membrane denticles. Scale bar, 1 cm. **c**, Enlargement of mucous membrane denticles lining the inside of the mouth forward of the neurocranium. Scale bar, 0.5 cm.

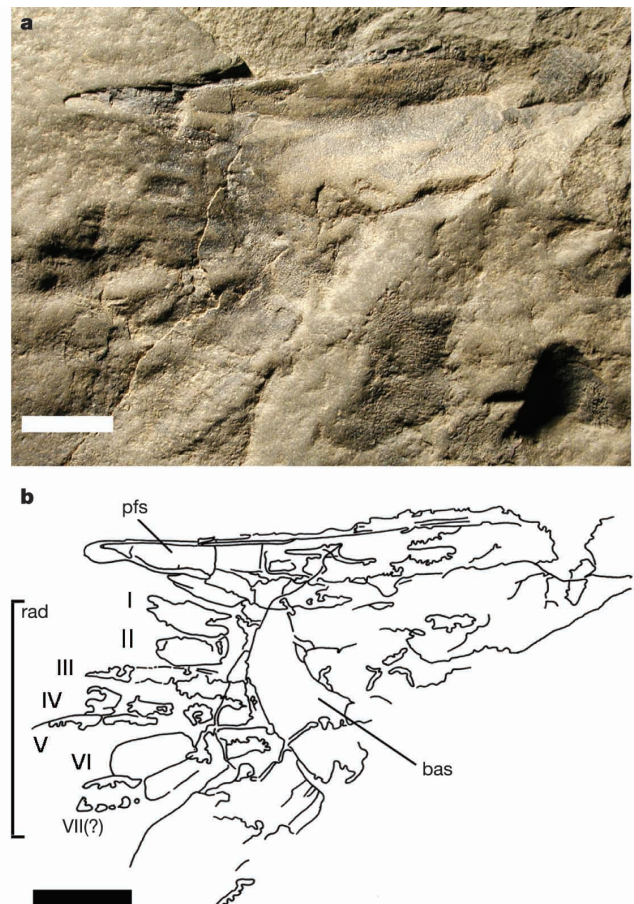


Figure 3 Left pectoral fin of *Doliodus problematicus* (NBMG 10127/3). **a**, Left pectoral fin. **b**, Map of left pectoral fin. pfs, pectoral fin-spine; rad, radials I–VII(?); bas, basipterygial element (meso- or metapterygium). Scale bar, 1 cm.

Gondwanan origin for sharks, although *D. problematicus* teeth presented a contradiction⁷. This specimen clearly places *D. problematicus* in Laurentia by the Early Devonian. Northern Gondwana and Laurentia were possibly close³⁰, across a shallow shelf connecting north Gondwanan shoreline locales. □

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Temperature excludes N₂-fixing heterocystous cyanobacteria in the tropical oceans

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Whereas the non-heterocystous cyanobacteria *Trichodesmium* spp. are the dominant N₂-fixing organisms in the tropical oceans¹, heterocystous species dominate N₂ fixation in freshwater lakes and brackish environments such as the Baltic Sea². So far no satisfactory explanation for the absence of heterocystous cyanobacteria in the pelagic of the tropical oceans has been given, even though heterocysts would seem to represent an ideal strategy for protecting nitrogenase from being inactivated by O₂, thereby enabling cyanobacteria to fix N₂ and to perform photosynthesis simultaneously. *Trichodesmium* is capable of N₂ fixation, apparently without needing to differentiate heterocysts³. Here we show that differences in the temperature dependence of O₂ flux, respiration and N₂ fixation activity explain how *Trichodesmium* performs better than heterocystous species at higher temperatures. Our results also explain why *Trichodesmium* is not successful in temperate or cold seas. The absence of heterocystous cyanobacteria in the pelagic zone of temperate and cold seas, however, requires another explanation.

As primary production in vast areas of the oceans is predominantly controlled by the availability of nitrogen, biological N₂ fixation could overcome this limitation¹. But N₂ fixation in the marine pelagic environment seems to be mainly restricted to (sub) tropical regions. The organisms responsible for most of the N₂ fixation in the tropical oceans are *Trichodesmium* spp., filamentous non-heterocystous cyanobacteria that can form massive surface blooms^{4,5}. Although free-living heterocystous cyanobacteria are reported to be present in the marine pelagic environment, their numbers are low and presumably they show very low growth rates⁶. This is notable because heterocystous cyanobacteria are considered to be better adapted to diazotrophic growth than are non-heterocystous species^{1,7}, as heterocysts (differentiated cells enveloped by a glycolipid layer in which N₂ fixation takes place) are assumed to be effective in protecting the N₂-fixing enzyme nitrogenase from inactivation by O₂ (refs 8, 9).

The absence of heterocystous cyanobacteria in the marine pelagic environment contrasts strongly with their presence in freshwater lakes and brackish environments, where they can form dense blooms. Although heterocystous cyanobacteria can thrive in marine tropical systems, they are found mostly as epiphytes, in symbiosis with the planktonic diatom *Rhizosolenia* or in microbial mats¹⁰. But these specific environments are regularly oversaturated with O₂ during the daytime, and therefore provide conditions that are different from those experienced by free-living organisms in pelagic systems. The expected higher O₂ fluxes require a better protection of nitrogenase.

This leaves us with two main questions regarding the global distribution of N₂ fixation. First, why are free-living heterocystous cyanobacteria not the dominant N₂-fixing organisms in the tropical oceans? Second, why are *Trichodesmium* spp. not able to thrive in marine, brackish or even freshwater environments in temperate and polar regions? Here, we propose that a glycolipid cell envelope, which acts as an effective diffusion barrier for O₂ in heterocysts, does not provide an advantage in sea water at increased temperatures, and thus heterocystous cyanobacteria are out-competed by *Trichodesmium* spp. Our results also explain why *Trichodesmium*