

# An exceptional Devonian fish from Australia sheds light on tetrapod origins

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The transition from fishes to tetrapods was one of the most dramatic events in the evolution of vertebrates, but many pivotal fossils are incomplete, resulting in gaps in the data that are used for phylogenetic reconstruction. Here we present new observations from the most complete, acid-prepared Devonian tetrapodomorph fish yet discovered, *Gogonasmus*<sup>1,2</sup>, which was previously placed just crownward of *Kenichthys* and rhizodontids<sup>3,4</sup>, the most primitive taxa on the tetrapod lineage. Unexpectedly, *Gogonasmus* shows a mosaic of plesiomorphic and derived tetrapod-like features. Whereas the braincase and dermal cranial skeleton exhibit generalized morphologies with respect to *Eusthenopteron*<sup>5</sup> or *Panderichthys*<sup>6</sup>, taxa that are traditionally considered to be phylogenetically close to tetrapods<sup>7,8</sup>, the presence of a deeply invaginated, wide spiracle, advanced internal spiracular architecture and near-horizontal hyomandibula are specialized features that are absent from *Eusthenopteron*<sup>9</sup>. Furthermore, the pectoral fin skeleton of *Gogonasmus* shares several features with that of *Tiktaalik*, the most tetrapod-like fish<sup>10</sup>. A new phylogenetic analysis places *Gogonasmus* crownward of *Eusthenopteron* as the sister taxon to the Elpistegalia. Aspects of the basic tetrapod limb skeleton and middle ear architecture can now be traced further back within the tetrapodomorph radiation.

Recently, the discovery of transitional fossil forms of advanced tetrapod-like fishes<sup>6,10–12</sup> and primitive tetrapods<sup>13–15</sup> from the Devonian period have provided important insights into the evolution of the first land vertebrates<sup>16</sup>. For almost a century, the anatomy of *Eusthenopteron*, which is considered to be a fairly derived tetrapodomorph fish<sup>5,7–9</sup>, has served as a basis for comparison with early tetrapods.

Many complete specimens of *Eusthenopteron* have been studied, and it has been universally positioned by many workers<sup>3–9,11</sup> as an intermediate form between the generalized cosmine-covered tetrapodomorph fishes (such as *Osteolepis*) and the more advanced tetrapod-like elpistogalians<sup>6,10,11</sup>. *Kenichthys*<sup>4</sup>, the most generalized sarcopterygian fish directly on the tetrapodomorph lineage, is known only from isolated skulls and cranial dermal bones, so we lack knowledge of its paired fins, endoskeletal girdles, gill arches, and overall body form to contribute to the understanding of early character development in the lineage. New anatomical data on basal tetrapodomorph fishes is therefore vital to clarify the incipient stages that led to the origin of the tetrapod body plan.

The new specimen described here (NMV P221807, Museum Victoria, Melbourne) was discovered in 2005 in a limestone concretion of the Lower Frasnian Gogo Formation of Western Australia (dated as ~384–380 million years old). The Gogo fish fauna (more than 44 taxa) is widely acknowledged<sup>17–19</sup> for its perfect three-dimensional preservation, and *Gogonasmus* is its only known tetrapodomorph. Previous specimens<sup>1,2</sup> lacked the detailed preservation of

the spiracular region, complete visceral skeleton, body and fins seen in this exceptional new example, study of which has been enhanced by high resolution X-ray tomography after acid preparation. The conspicuously large spiracular opening (Fig. 1a–c) is proportionally similar to those recently reconstructed for *Panderichthys*<sup>9</sup> and *Tiktaalik*<sup>11</sup>. The pectoral fin endoskeleton of *Gogonasmus* is described here for the first time (Fig. 2), the new specimen being the only known Devonian fish that shows a complete acid-prepared pectoral limb. There are some surprising similarities to the recently described pectoral fin in the advanced elpistostegalian *Tiktaalik*<sup>10</sup>. As such features could indicate homoplasy between *Gogonasmus* and early tetrapods, we present a revised character analysis to determine whether the new anatomical information supports a more crownward position for *Gogonasmus* in the stem-tetrapod phylogeny.

The articulated cranium of *Gogonasmus* (Fig. 1a, b) shows the natural gaps between the boundary of the skull-roof and the cheek unit. The most conspicuous feature is the ventrally down-turned cosmine-covered lamina of the tabular bone, which forms a posterior externally open wall to the spiracular opening (Fig. 1d, e). **The spiracle is a very small slit-like opening in *Eusthenopteron*<sup>5</sup>, progressively larger in elpistostegalians, and forms a wide otic notch in early tetrapods<sup>9</sup>.**

No previously described tetrapodomorph fish shows such a large spiracular opening, or a downward facing dermal lamina forming a posterior wall to the spiracular chamber, so the condition in *Gogonasmus* is highly unusual. This indicates that spiracular breathing might have evolved independently in some stem tetrapodomorphs. The shape of the spiracular chamber has been restored from the perfectly preserved palatoquadrate with the distinct ridge on the entopterygoid delineating the ventral boundary of the spiracular region (the posterior wall of the eustachian tube) as in *Eusthenopteron* (see Supplementary Information for details). *Panderichthys* lacks such a ridge on the entopterygoid, but still has a horizontally oriented spiracular chamber<sup>9</sup>. The shallower angle of the spiracular chamber margin in *Gogonasmus* (Fig. 1g) is a perfect intermediate morphology between the deeper spiracular chamber of *Eusthenopteron* (Fig. 1h) and the almost horizontal chamber of *Panderichthys*<sup>9</sup> (Fig. 1f). However, in having the entopterygoid located lateral to the ventral opening of the spiracular tract, the condition in *Panderichthys* is more derived than either *Eusthenopteron* or *Gogonasmus*.

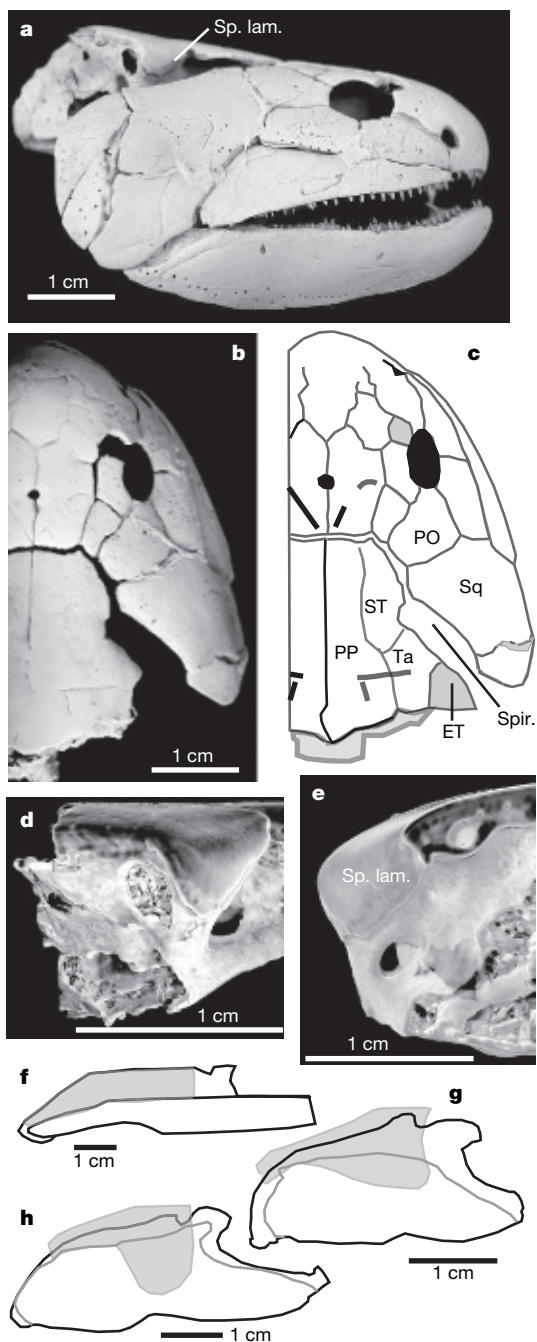
Both hyomandibulae are well preserved, with similar morphology to the previously described *Gogonasmus* specimens<sup>2</sup>. Compared to the relatively long and slender hyomandibula of *Eusthenopteron*, that of *Gogonasmus* has similar relative proportions (proximal:distal section ratio) but with a slightly thicker, more robust proximal shaft. The more horizontal angle of the *Gogonasmus* hyomandibula compared to that of *Eusthenopteron* is confirmed by the new specimen, except that the opercular process does not meet the skull roof bones, instead attaching at its ventral end to an elevated, dorsolaterally facing

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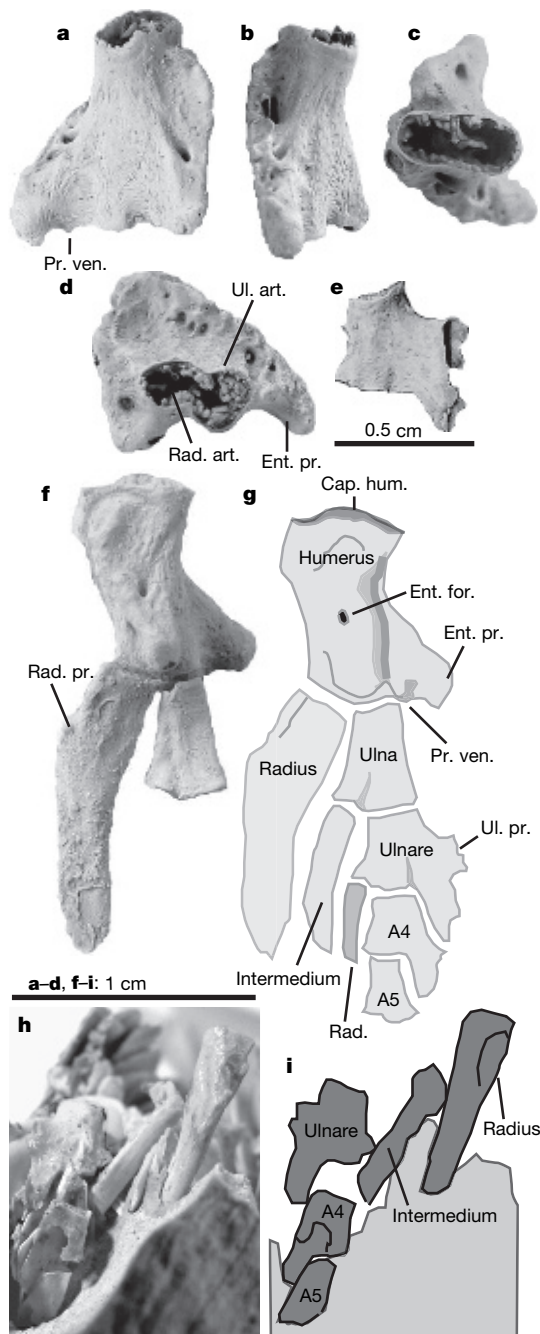
opercular bone. The dorsal position of the hyomandibula conforms more closely to that in elpistostegalians than to those in tristichopterids and more generalized tetrapodomorphs.

The pectoral fin skeleton of *Gogonasus* (Fig. 2) shows not only the three-dimensional form of the endoskeletal elements, but also preserves spacing between elements as filled by cartilage in life. The humerus (Fig. 2a–d, f, g) has a relatively flat cross-section and broad, strap-like caput humeri. An unusual short ventral process between

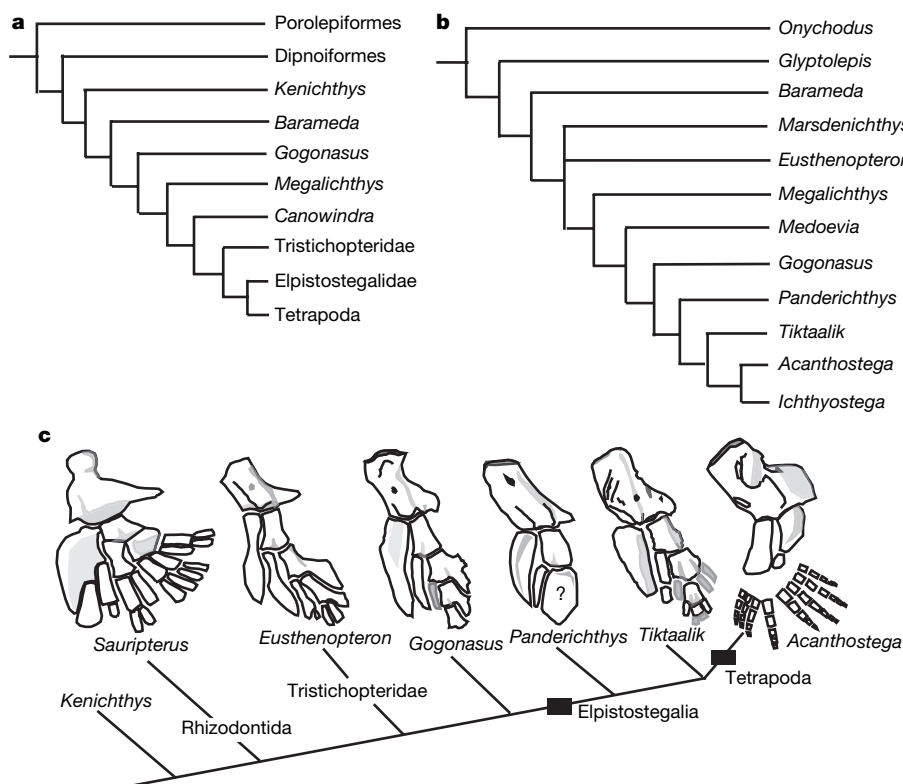
the metapodial facets and the entepicondyle is also present in *Tiktaalik*<sup>10</sup>. The entepicondyle (Fig. 2a, c, d, f) is significantly smaller, relative to the length of the humerus shaft, than those of rhizodontids and tristichopterids (Fig. 3c), and the two subrectangular facets of the ulna and radius are offset at an angle similar to that of *Tiktaalik*, in having a forward-reaching radial joint (Fig. 2f). The radius (Fig. 2f–i) is an elongate, tapering bone, unlike the significantly broader or distally flared hour-glass elements seen in tristichopterids and



**Figure 1 | Cranial features of *Gogonasus andrewsae*, NMV P221807.** **a**, Skull in lateral view. **b**, **c**, skull in dorsal view. **d**, **e**, X-ray micro-tomograms showing the spiracular region in lateral (**d**) and anterior (**e**) views. **f–h**, Restorations of palatoquadrates showing the spiracular chamber (shaded) for *Panderichthys* (**f**), *Gogonasus* (**g**) and *Eusthenopteron* (**h**); panels **f** and **h** are based on ref. 9. ET, extratemporal bone; PO, postorbital; PP, postparietal; Spir, spiracular opening; Sp. lam., down-turned lamina of tabular for spiracular chamber; Sq, squamosal; ST, supratemporal; Ta, tabular. All bones whitened with ammonium chloride.



**Figure 2 | Pectoral fin skeleton of *Gogonasus andrewsae*, NMV P221807.** **a–d**, Right humerus in dorsal (**a**), mesial (**b**), proximal (**c**) and distal (**d**) views. **e**, Right ulnare in ventral view. **f**, Left humerus, ulna and radius articulated in dorsal view. **g**, Reconstructed left pectoral fin in dorsolateral view. **h**, Left pectoral distal elements. **i**, Key to **h**. A4, A5, distal mesomeres of the pectoral fin; Cap. hum., caput humeri; Ent. for., entepicondylar foramen; Ent. pr., entepicondyle; Pr. ven., ventral process on entepicondyle; Rad., presumed radial element; Rad. art., radial articulation; Rad. pr., radial process; Ul. pr., postaxial process of ulnare. All (except **g**) whitened with ammonium chloride. Scale bar, 1 cm for **a–d**, **f–i**; 0.5 cm for **e**.



**Figure 3 | Phylogenetic position of *Gogonasmus*.** **a**, Previous phylogenetic position of *Gogonasmus* (based on refs 4, 7). **b**, New position of *Gogonasmus* based on our PAUP analysis of 103 characters (see Supplementary Information for protocols). **c**, Position of *Gogonasmus* relative to other

tetrapodomorph fishes, showing pectoral fin endoskeleton comparisons (diagrams after ref. 10). We note that new information on the correct pectoral fin arrangement of *Panderichthys* is forthcoming (P. E. Ahlberg, personal communication).

rhizodontids (Fig. 3c). It also has a well defined radial process (Fig. 2f). The elongate ulna (Fig. 2f, g) has two distal articulations, one large one for the ulnare and a small one for a thin, tapering intermedium. The ulnare (Fig. 2g–i) shows a well developed postaxial process, as in *Eusthenopteron*, except that in *Gogonasmus* the process does not extend very far distally as a flared lamina. The ulnare articulates distally with a broad, flat mesomere (A4) and a smaller anterior facet indicates that smaller radial elements were also present. The A4 element has a single distal, broad A5 element articulating with it (Fig. 2g–i), in contrast to the slender paired elements seen in *Eusthenopteron* and the rhizodontids. This condition approaches that of *Tiktaalik*, which has one large element and three narrow elements in this position. Such features can be interpreted as either generalized (plesiomorphic) for *Gogonasmus* and elpistostegalians, or shared apomorphies that unite them, and as such would exclude the rhizodontids and tristichopterids from the higher clade.

Our new cladistic analysis (Fig. 3b) places *Gogonasmus* crownwards of tristichopterids as a sister taxon to elpistostegalians, based mainly on its spiracular morphology and pectoral fin skeleton (Fig. 3c). Supporting this is the fact that elpistostegalian fishes still retain primitive rhombic scales, as seen in many basal sarcopterygian fishes. The rounded scales of tristichopterids and rhizodontids<sup>20</sup> characteristically possess a median boss on their inner surface, consistent with the suggestion that these groups were divergent from the lineage containing *Gogonasmus* and elpistostegalians, although the current analysis lacks evidence to unite them in a separate clade.

*Gogonasmus* is a marine tetrapodomorph fish with cosmine-covered rhombic scales and dermal bones, in this respect resembling *Kenichthys* from China, the earliest member of the tetrapodomorph clade in which an incipient internal nostril or choana has been identified<sup>4</sup>. Thus, this key tetrapod innovation evolved as early as the Emsian (late Early Devonian), and the new data from *Gogonasmus* indicate that the basic tetrapod pectoral fin pattern, and the broad

spiracular opening as a precursor to tetrapod middle ear architecture, might also have originated further back than previously thought within the tetrapodomorph radiation.

Our new phylogeny replaces the tristichopterid *Eusthenopteron* as the typical fish model for the fish–tetrapod transition. It also raises the question of what environment the immediate stem group of the elpistostegalians inhabited. The marine environment inhabited by *Gogonasmus* is in accord with the marginal marine environments of some elpistostegalians (*Panderichthys*, *Elpistostegia*, *Tiktaalik*) and the tetrapod *Tulerpeton*. Such observations support a model in which the first tetrapods, like their immediate piscine sister taxa, were capable of marine dispersal, thus explaining the widespread global distribution achieved shortly after their first appearance in the late Frasnian.

Finally, we note that strata of similar age to those producing *Gogonasmus*, *Panderichthys* and *Tiktaalik*, or slightly younger, have yielded tetrapod jaws in Australia and China<sup>21,22</sup>, and also trackways attributed to two different unknown tetrapods on the Gondwana supercontinent<sup>23</sup>. This indicates that the initial radiation of tetrapods from elpistostegalian fishes, with evidence currently confined to the northern hemisphere landmass of Euramerica, was probably an extremely rapid global event. Migration of some Middle–Late Devonian fishes from a Gondwana place of origin to Euramerica has been well documented<sup>24</sup>. With *Gogonasmus* now positioned phylogenetically close to elpistostegalian fishes, we suggest that the current lack of fossil evidence for elpistostegalian fishes in Gondwana could be due to poor sampling. We are now exploring areas in Australia with undescribed Devonian sarcopterygian fish remains to test this hypothesis.

## METHODS

**Preparation.** The acid immersion procedure (in 10% acetic acid for 2 days, washed in running water for a day, air-dried, all exposed bones then hardened

with Mowital B30 consolidant dissolved in pure ethanol) was repeated over 4 months to fully extract the anterior two-thirds of the specimen, with the tail section embedded in an acrylic resin slab to retain articulation.

**Phylogenetic analysis.** The matrix includes 103 morphological characters in 12 taxa, of which 9 were based on fairly complete specimens with few missing codings. All characters were treated as unordered, and were weighted equally. Character data entry and formatting was performed in MacClade (version 4.05). Our new analysis is based on the data matrix for the recently described, and now best known, elpistogalian, *Tiktaalik*<sup>10,11</sup>, with some new characters added and some recoded (see Supplementary Information for details and the data matrix). We use the recently described basal sarcopterygian *Onychodus* from Gogo<sup>19</sup> together with *Glyptolepis* for our outgroups. For rhizodontids, new material of the Australian form *Barameda*<sup>20</sup> provided more complete data on the primitive fin skeleton (poorly known in *Gooloogongia*, as used in previous analyses<sup>4</sup>). The character analysis was performed using PAUP 4.1. The Supplementary Information provides more details on the phylogenetic analysis and the X-ray micro-tomography used to study the specimen.

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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