

## Eel-like swimming in the earliest ichthyosaurs

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ICHTHYOSAURS are extinct marine reptiles, probably belonging to the Diapsida<sup>1</sup>, that ranged from the Early Triassic to Late Cretaceous<sup>2,3</sup>. Post-Triassic ichthyosaurs achieved the highest level of aquatic adaptation among reptiles<sup>4</sup>, with a streamlined body, lunate tail and a dorsal fin, features exemplified today by thunniform (tuna-like) fishes. However, little is known of how such a body plan evolved from a terrestrial diapsid. Here we report the most complete specimen of the oldest known ichthyosaur, *Chensaurus*, representing a transition between the two body plans. The specimen, which has a partial skin impression, has a small caudal fin, a long and narrow body, and a high presacral vertebral count. These features all suggest an anguilliform swimming mode. Later ichthyosaurs retained the high vertebral count, but overcame the high swimming costs of this plesiomorphy, achieving a rigid thunniform bauplan by evolving discoidal vertebrae, and a deep fusiform body. *Chensaurus* therefore seems to be an evolutionary intermediate between the shorter-bodied terrestrial stock from which the group evolved, and advanced thunniform ichthyosaurs.

The specimen was collected in 1989 from the Lower Triassic (Spathian) of Anhui Province, China, about 50 km southwest of the type locality of *Chensaurus*<sup>5,6</sup>, which is also Spathian<sup>7</sup>. Based on overall similarities, the specimen is tentatively identified as *Chensaurus chaoxianensis* (Chen) 1985 (ref. 5). Its most remarkable feature is its slender trunk region (Fig. 1a), rare among ichthyosaurs. This slenderness is not a post-mortem artefact, because the gastralia are preserved *in situ*, the articulated series lying parallel to the vertebral column. Also noteworthy is that the body outline is partially preserved in the dorsal region. The outline of the caudal fin is the best preserved, located immediately dorsal to a change in orientation of the neural spines (Fig. 1a).

Sharks and ichthyosaurs are similar in that their vertebral columns continue into one of the caudal fin lobes: the upper and lower lobes, respectively<sup>8</sup>. Also, they both have high precaudal vertebral counts (usually 60–110), in contrast to scombrid fishes (about 40), and cetaceans (usually 40–60). Sharks evolved several body forms, some of which are also found in ichthyosaurs (Fig. 1). Because of these similarities, sharks provide the best analogue for ichthyosaurs in overall body shape and locomotion, although differing in details.

Vertebrates that swim by lateral undulations of the body may be described as anguilliform, sub-carangiform, carangiform, and thunniform, according to the proportion of the body utilized for the propulsion (highest in anguilliform and lowest in thunniform)<sup>9</sup>. These modes are also associated with body shape, ranging from the elongate and flexible anguilliform swimmers to the deep and more rigid-bodied thunniform ones, as noted among teleosts and sharks<sup>10</sup>. Sharks range from being anguilliform to thunniform<sup>8</sup>, though some authorities avoid these categories, preferring to use informal groups defined on shape<sup>11</sup>. The variation in body and tail shape among sharks is considerable, and we used two indices to quantify this: fineness ratio (precaudal length/body height) and tail *H/L* (tail height/length; Fig. 2a). These indices are positively correlated ( $r = 0.70$ ; Fig. 2a) and show a trend from the more anguilliform sharks, as exemplified by scyliorhinids, to the more thunniform ones, like lamnids (Fig. 2b). Two ichthyosaur genera were added to the data: *Stenopterygius* (Fig. 1d), a typical

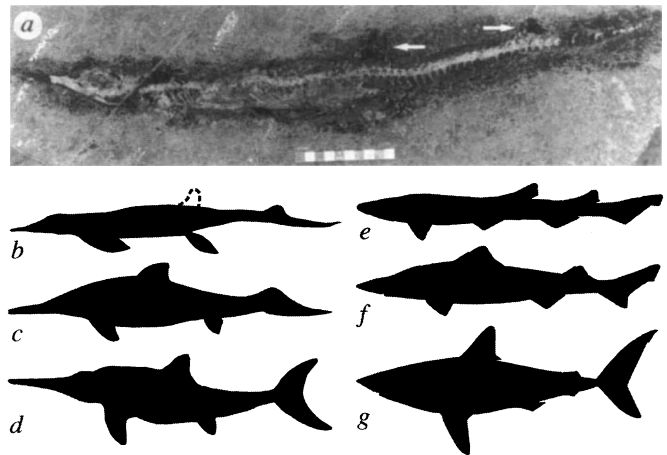


FIG. 1 Variation in body form among ichthyosaurs and sharks. a, The new specimen of *Chensaurus chaoxianensis*, Wuwei Cultural Relic Administrative Institute, Anhui Province, China (WCRAI 313). The fossil has been cleaved along the sagittal plane, and is disposed on two slabs. The left-hand arrow marks the position of a feature of uncertain identity (dorsal fin or hind fin), the right-hand arrow marks the anterior end of the caudal fin. The body outline is the narrow black zone lying close to the dorsal edge of the vertebral column. It is easiest to see in the region between the arrows. The dark zone lying ventral to the vertebral column is a recent artifact (a separator, used during mould making). A fault in the cervical region displaced the skull and the first several vertebrae relative to the body. Scale bar, 10 cm. b, reconstruction of WCRAI 313. Paired fins added from a smaller specimen, scaled to the appropriate size. The questionable feature is depicted by the broken line. Note the narrow body and small caudal fin. c, Reconstruction of *Mixosaurus cornalianus*, modified from ref. 23. The trunk is fusiform but the caudal fin is similar to that of *Chensaurus*. d, *Stenopterygius quadricissus*, Paleontologiska Museet, Uppsala Universitet (PMU R158). Body outline preserved as a carbonaceous film, showing deep fusiform body, lunate tail and dorsal fin. e, *Axybelus vincenti*, a scyliorhinid shark with a body outline resembling *Chensaurus*. f, *Centrophorus harrisoni*, a squalid shark similar in shape to *Mixosaurus*. g, *Lamna nasus*, a lamnid shark whose body plan is similar to *Stenopterygius*. e–g modified from ref. 24.

post-Triassic form, interpreted as being adapted for fast cruising<sup>8,12,13</sup>, and *Chensaurus* (Fig. 1b). *Stenopterygius* groups with the lamnid sharks, whereas *Chensaurus* lies at the extreme end of the scyliorhinid distribution, suggesting that it was anguilliform, and a forerunner of the advanced thunniform ichthyosaurs.

Anguilliform swimming requires body flexibility, which is enhanced by high vertebral counts. The presacral count of *C. chaoxianensis* is about 40, some 50 per cent higher than that of most limbed terrestrial amniotes, both living and extinct<sup>14,15</sup>. Most later ichthyosaurs have 40–50 presacrals<sup>16–18</sup>, except for long-bodied shastasaurids with approximately 65 (refs 19,20). The presacral count of *C. chaoxianensis* is therefore already within the range of typical ichthyosaurs. This suggests that a high presacral count appeared early in ichthyosaur evolution, as an adaptation for anguilliform swimming, and was retained in later forms.

The optimum efficiency of thunniform swimmers is achieved by a stiff body, limiting lateral propulsive movements to the caudal fin. Body stiffness is enhanced by restricting the degree of flexion between adjacent vertebrae. For ichthyosaurs, which have amphicoelous vertebrae, intervertebral flexion was probably largely a function of the thickness and compliance of the intervertebral discs. From simple geometry, the maximum angular displacement between adjacent vertebral centra decreases with increasing diameter, other dimensions remaining the same. *C. chaoxianensis*, and other Early Triassic ichthyosaurs, have cylindrical centra, but they became taller and wider in later forms, culminating in the

FIG. 2 The correlation between body shape and tail shape in sharks. *a*, 95% confidence ellipse fitted to data for 94 species, belonging to 14 families, ( $r = 0.70$ ,  $**P < 0.01$ ;  $r$  for the population estimated at  $0.58-0.80$ ,  $*P < 0.05$ ). Data were obtained by taking measurements from published figures<sup>24,25</sup>. The boundary between precaudal and caudal regions was determined according to a published method<sup>22</sup>. *b*, As *a*, but for ease of comparison only three shark families are depicted. It was not plausible to fit a 95% confidence ellipse to the lamnid data because of the small sample size. Note that the ichthyosaurs, *Chensaurus* and *Stenopterygius*, lie at the two extremes of the shark distributions.

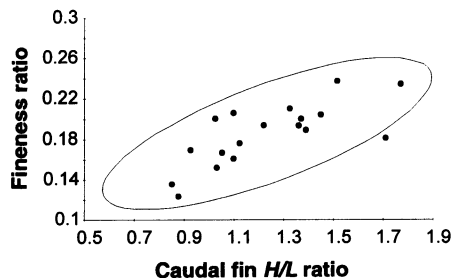
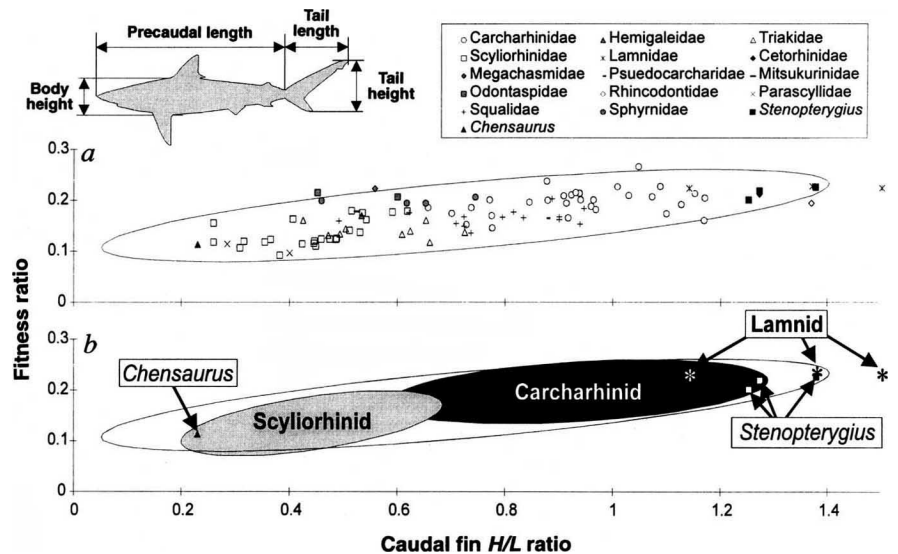


FIG. 3 The correlation between body shape and centrum shape in sharks. Data for 18 species belonging to 6 families were obtained from the literature<sup>22,24</sup>, ( $r = 0.74$ ,  $**P < 0.01$ ;  $r$  for the population estimated at  $0.41-0.91$ ,  $*P < 0.05$ ). Two species, *Prionace glauca* (blue shark) and *Eusphya blochii* (winghead shark), are unusual in precaudal count, hence were not included: blue shark has about 146 precaudals, almost 52 per cent more than average carcharhinid sharks, and winghead shark has about 50, nearly 47 per cent less than average hammerhead sharks. Measurements for ichthyosaurs (referred to in text) were taken for posterior dorsal vertebrae; those for sharks were for penultimate monospondylous vertebrae<sup>22</sup>.

discoidal centra typical of most ichthyosaurs. The depth of the centrum can be expressed by the ratio of centrum height to length (H/L). The ratio has values of 0.9 for *C. chaioxianensis*, 2.0 for *M. cornalianus* (Middle Triassic) and 2.5 for *S. quadricissus* (Lower Jurassic). Ichthyosaurs therefore seem to have overcome the problem of retaining their high presacral counts—the antithesis of rigidity—by evolving deep discoidal centra. Associated with this change was a deepening of the body. Riess<sup>21</sup> described *Mixosaurus* as an anguilliform swimmer, but his argument only establish that it was an axial swimmer, which accords with our hypothesis.

The only living animals with comparable centra are sharks, whose fossilized vertebrae are sometimes confused with those of

ichthyosaurs. Sharks, as noted, usually have precaudal counts similar to ichthyosaurs. Significantly, the deeper bodied sharks tend to have the deepest centra (Fig. 3), with the exception of those with unusual precaudal counts. Thus the centrum H/L ratio for scyllorhinid sharks average about 0.8, compared with 2.0 for lamnids<sup>22</sup>. This supports our contention that the evolution of a deep, fusiform body, typical of post-Triassic ichthyosaurs, was predicated upon the evolution of discoidal vertebrae. Anthracosaurs also have discoidal vertebrae, but their body plan is not comparable to that of ichthyosaurs: presence of both intercentra and pleurocentra resulted in about 80 joints in the presacral region, contributing flexibility to their presumed anguilliform locomotion. □

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