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100-million-year dynasty of giant suspension-feeding bony fishes in the Mesozoic seas

Matt Friedman¹, Kenshu Shimada^{2,3}, Larry D. Martin⁴, Michael J. Everhart³, Jeff Liston⁵, Anthony Maltese⁶, Michael Triebold⁶

¹Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, UK. ²Environmental Science Program and Department of Biological Sciences, DePaul University, 2325 North Clifton Avenue, Chicago, Illinois 60614, USA. ³Sternberg Museum of Natural History, Fort Hays State University, 3000 Sternberg Drive, Hays, Kansas 67601, USA. ⁴Natural History Museum and Biodiversity Research Center, University of Kansas, 1345 Jayhawk Boulevard, Lawrence, Kansas 66045, USA. ⁵Division of Ecology and Evolutionary Biology, Faculty of Biomedical and Life Sciences, University of Glasgow, University Avenue, Glasgow G12 8QQ, UK. ⁶Triebold Paleontology, Inc., and Rocky Mountain Dinosaur Resource Center, 201 South Fairview Street, Woodland Park, Colorado 80863, USA.

Large-bodied suspension feeders (planktivores), which include the most massive animals to have ever lived, are conspicuously absent from Mesozoic marine environments. The only clear representatives of this trophic guild in the Mesozoic are an enigmatic and apparently short-lived (ca. 20 Ma) radiation of bony fishes assigned to †Pachycormidae, a stem teleost clade. Here we report several new discoveries of these giant fishes from Asia, Europe and North America, which not only deliver the first

detailed anatomical information on this poorly understood group, but also extend its range deeper into the Jurassic and to the very end of the Cretaceous. Rather than a failed experiment in suspension feeding at large sizes, this successful radiation persisted in excess of 100 Ma, longer than any other vertebrate clade to occupy this functional role. The evolutionary diversification of modern large-bodied, suspension-feeding vertebrates took place only after the extinction of †pachycormids, consistent with the opportunistic re-filling of vacated ecospace.

The largest vertebrates—fossil or living—are marine suspension feeders. Modern groups adopting this ecological strategy include baleen whales and four independent lineages of cartilaginous fishes (sharks and rays) (Sanderson & Wasserug), all of which diversified in the Paleogene (66-23 Ma). In striking contrast to the array of giant suspension feeders found in modern marine environments, this trophic guild appears absent during most of the Mesozoic, an interval marked by the ecological ascendance of modern plankton clades (Falkowski et al. 2004). The only clear examples of large-bodied planktivores in the Mesozoic are a handful of bony fishes confined to a brief 20 Ma window during the Jurassic (Callovian-Tithonian; 165-145 Ma) and known almost exclusively from European deposits (Lambers, Liston MF3, MF4). These enigmatic taxa belong to the extinct family †Pachycormidae (dagger symbol indicates extinct groups), a stem-teleost clade otherwise composed of pelagic predators convergent upon tunas and billfishes (Lambers). Giant †pachycormids include the most massive bony fish of all time (8-9 m †*Leedsichthys*; Martill, Liston and Noe), but their short stratigraphic range had implied that they were an insignificant component of Mesozoic marine ecosystems and a minor—and ultimately unsuccessful—experiment in suspension feeding at large body sizes.

Here we report the earliest remains of suspension-feeding †pachycormids from the lower Middle Jurassic, as well as the latest specimens of Late Cretaceous age. These discoveries (i) clarify the poorly understood morphology of this radiation, (ii) establish a global distribution for this group, (iii) extend the stratigraphic range of this clade to approximately 100 million years, a duration longer than that of any other group of giant suspension feeders, (iv) fill a conspicuous ecological gap in Mesozoic marine faunas, and

(v) suggest that the origin of most modern groups of large-bodied marine planktivores in the early Cenozoic might represent ecological replacement following the extinction of suspension-feeding †pachycormids at or near the close of the Mesozoic.

New discoveries of suspension-feeding †pachycormids. Fossils reported here include a generically indeterminate cranium from the early Middle Jurassic (Bajocian; 172-168 Ma) Inferior Oolite of Dorset, UK (Fig. 1), the nearly complete skull of †*Rhinconichthys taylori* gen. et sp. nov. (taxonomic note 1) from the early Late Cretaceous (Cenomanian; 100-94 Ma) Lower Chalk of Kent, UK (Fig. 1; SOM) and a similar form from the Middle Yezo Group of Hokkaido, Japan, and multiple specimens of †*Bonnerichthys gladius* gen. nov. (taxonomic note 2) from mid-late Late Cretaceous (Coniacian-Maastrichtian; 89-66 Ma) deposits in the Interior Seaway and Coastal Plain of the USA (Fig. 2; Stewart, Parris et al.; SOM). Material of these new taxa was first collected and studied in the 19th Century, but has eluded proper identification until now. A cladistic analysis provides robust support for the monophyly of these giant edentulous fishes, corroborates their placement within †Pachycormidae, and reinforces the interpretation of †pachycormids as stem teleosts (SOM). Remarkably, this subset of †pachycormids is a unique example of suspension feeding at massive body sizes within the teleost total group, a clade which otherwise assumes a bewildering array of morphologies and whose living representatives are taxonomic dominants in marine vertebrate faunas (Nelson).

Morphology of suspension-feeding †pachycormids. The anatomy of this group, previously known only from Jurassic examples, is poorly understood. Material of †*Leedsichthys* is crushed, fragmented, and disarticulated (Liston MF3), while detailed structure is obscure in rare articulated remains of †*Asthenocormus* (Lambers) and †*Martillichthys* (Liston MF4). The specimens reported here yield considerable new morphological information about this poorly known clade, with †*Bonnerichthys* forming the basis of the following description (Fig. 2).

The snout is covered by a median rostrodermethmoid, a †pachycormid synapomorphy (Mainwaring, Lambers). Two lateral projections along the oral margin are unknown in other forms, but their position suggests that they might be co-ossified premaxillae. Two thickened ridges trace the lateral margins of the rostrodermethmoid,

and mark the position of the supraorbital canal, suggesting the rostrodermethmoid of †*Bonnerichthys* might also incorporate the nasals. The rectangular frontal bears a ridge on its visceral surface marking the course of the supraorbital sensory canal. The hook-shaped dermosphenotic lies lateral to the frontal, defines the dorsal margin of the orbit, and bears the anastomosis between the infraorbital and otic sensory canals. A triradiate canal-bearing ossification is identified as a dermopterotic. There is no indication of sutural contacts between the dermosphenotic, dermopterotic and frontal, or between the frontal and the rostrodermethmoid. The condition in †*Bonnerichthys* is derived relative to all other †pachycormids, where dermal bones of the skull roof are tightly linked.

As in many suspension-feeding fishes (Sanderson & Wasserug), the dentary of the lower jaw and the maxilla of the upper jaw are elongate and edentulous. Absence of dentition even extends to the prearticular, which lines the inner surface of the mandible, and the parasphenoid, which forms much of the roof of the oral chamber. The parasphenoid is pierced by foramina for the internal carotid artery, a derived feature of teleosts.

Members of the operculogular series recovered for †*Bonnerichthys* include the opercular, subopercular, and gular plate. The hyoid arch is represented by large, imperforate hyomandibulae with well-developed opercular processes and rod-shaped ceratohyals. Gill-arch remains include hypo- and infrapharyngobranchials with complex articular surfaces, plus long and deeply grooved cerato- and epibranchials. Enlarged gill rakers bearing long, needle-like teeth are found in †*Asthenocormus*, †*Leedsichthys* and †*Rhinconichthys*, but presence of these probable suspension-feeding structures has not yet been confirmed in †*Bonnerichthys*.

Typical of †pachycormids, the pectoral fins are scythe-shaped. The leading edge of the fin is fused, with an irregular margin that contrasts with the precisely patterned serrations in some species of †*Protosphyraena* (Woodward, Lambers, Stewart). Distally, the fin-rays bifurcate in the ‘Y’ pattern characteristic of †pachycormids (Mainwaring, Lambers). The pectoral endoskeleton of †*Bonnerichthys* agrees closely with those of †*Orthocormus* and †*Protosphyraena* (Woodward, Jessen). The second radial is ‘C’-shaped and makes two independent articulations with the primary shoulder girdle, and is trailed by a series of paddle-shaped radials (SOM).

The reconstructed skull of †*Bonnerichthys* specimen KUVV 60692 exceeds 1m from the tip of the snout to the rear of the pectoral girdle. Isometric scaling relative to articulated †*Asthenocormus* and †*Martillichthys* specimens suggests a total length of approximately 4 m. The largest known pectoral fins of †*Bonnerichthys* (KUVV 465) are over 20 percent larger than those of KUVV 60692 (0.86m vs. 1.06m), suggesting a length of 5 m. This is smaller than estimates for †*Leedsichthys* (Martill; Liston and Noe) but more than an order of magnitude larger than most living suspension-feeding teleosts (Nelson) and approaches the length of some modern planktivorous chondrichthyans (Sanderson & Wassersug, Nelson).

Macroevolutionary implications. The discovery of early Middle Jurassic and Late Cretaceous †pachycormids with anatomical features consistent with suspension feeding (Sanderson & Wasserug) substantially alters the picture of the evolution of this guild in the Mesozoic and afterwards. We now recognize that †pachycormids occupied this ecological role for most of the Mesozoic, closing a conspicuous gap in the history of large-bodied suspension feeding vertebrates (Fig 3). While marine reptiles diversified prolifically during the Mesozoic, attaining massive sizes and evolving specializations attributed to suction and ram feeding (Nicholls and Manabe), there is no clear evidence that they ever adopted planktivory. This, coupled with the apparent absence of large-bodied suspension feeders in the Mesozoic, has provoked speculation about anatomical constraints preventing these otherwise ecologically diverse marine amniote clades from exploiting suspension feeding (Colin & Janis). Our findings fill the apparent ecological void until the close of the Cretaceous, suggesting that marine reptiles might have been excluded from this trophic role by incumbent †pachycormids.

The first fossil occurrences of modern large-bodied suspension feeders are confined to the Cenozoic: manta rays and whale sharks in the late Paleocene (Cappetta et al.), basking sharks in the mid-Eocene (Cione & Reguero), and plankton-feeding whales near the Eocene-Oligocene boundary (Fitzgerald). The only example with a possible Mesozoic record is the megamouth shark *Megachasma*, but there is a 75 Ma gap between a few isolated Late Cretaceous teeth and the next oldest occurrence, which dates from the late Oligocene-early Miocene (Shimada). The radiation of large-bodied suspension-feeding chondrichthyans and whales in the Paleogene follows the disappearance of

†*Bonnerichthys* and many other large-bodied marine teleosts (Cavin; Friedman) during the end-Cretaceous extinction, suggesting that familiar modern groups might have diversified into the functional role vacated by giant †pachycormids.

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See supporting material on *Science Online*.

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Taxonomic note 1. Etymology: Generic name is a homophone of an unpublished name by G. Mantell (*Rhynchonichthys*) and evokes the living whale shark *Rhincodon*. Specific name honors H. W. Taylor, collector of the type.

Systematics: Osteichthyes Huxley, 1880; Actinopterygii Woodward, 1891; Teleostei Müller, 1846 (*sensu de Pinna* 1996); †Pachycormidae Woodward, 1895; †*Rhinconichthys taylori* gen. et sp. nov. Holotype: The Natural History Museum, London, BMNH 219, nearly complete three-dimensional skull lacking anterior skull roof and posterior portions of lower jaws. Diagnosis of genus and species: edentulous †pachycormid differing from other members of that group in having exceptionally elongated posterior processes of the dermopterotics, proximal head of hyomandibula rounded rather than laterally compressed.

Locality and age: Lower Chalk (Late Cretaceous: Cenomanian), Burham, Kent, UK.

Taxonomic note 2. Etymology: Generic name honors the Bonner family, Scott City, Kansas, which has made many important discoveries in the Niobrara Formation, including KUVF 60692. Systematics: Osteichthyes Huxley, 1880; Actinopterygii Woodward, 1891; Teleostei Müller, 1846 (*sensu de Pinna* 1996); †Pachycormidae Woodward, 1895; †*Bonnerichthys* nov. gen.; †*Bonnerichthys gladius* (Cope, 1874), comb. nov. Holotype: American Museum of Natural History, New York, AMNH FF 1849, incomplete pectoral fin. Diagnosis of genus and species: edentulous †pachycormid differing from other members of that group in having a median rostral with ventrolateral processes possibly representing fused premaxillae, basioccipital with a deep midline groove for the

dorsal aorta, dermal bones of skull unsutured, anterior margin of pectoral fins irregularly crenellated. Locality and age: type from Niobrara Formation (Late Cretaceous: Santonian), Kansas, USA.

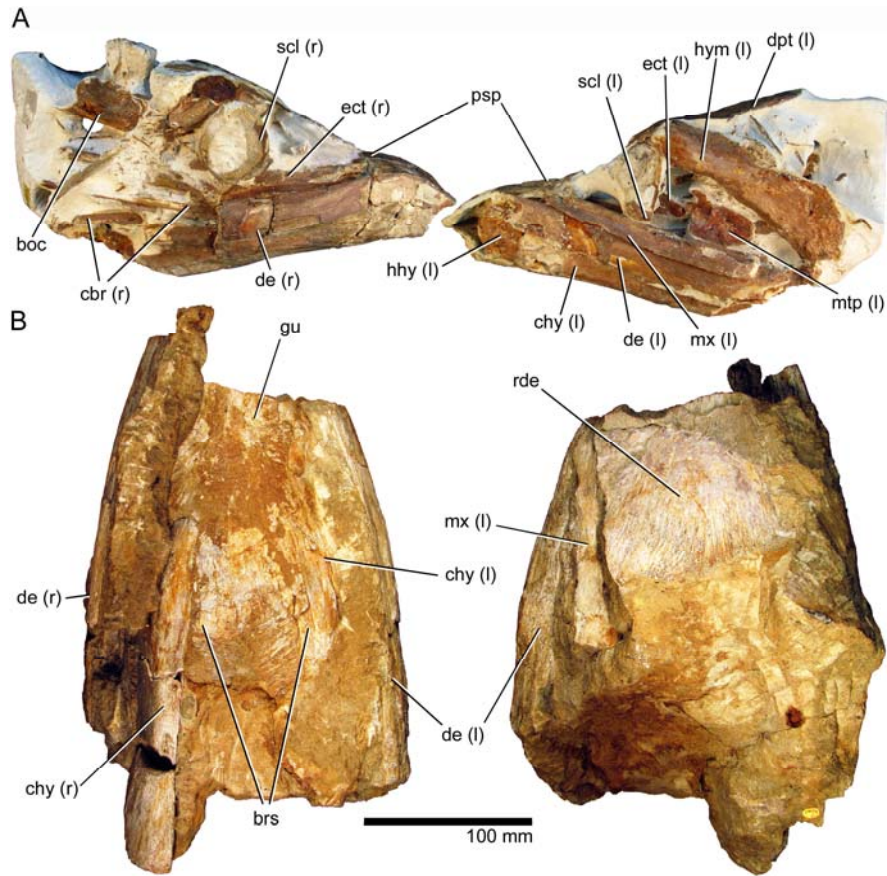


Fig. 1. Newly recognized material greatly expanding the stratigraphic range of giant suspension-feeding bony fishes during the Mesozoic. **(A)** †*Rhinconichthys taylori* gen. et sp. nov., BMNH 219, from the early Late Cretaceous (Cenomanian) Lower Chalk of Kent, UK, in right- and left-lateral views. **(B)** Indeterminate edentulous †pachycormid, BMNH P.41669, from the early Middle Jurassic (Bajocian) Inferior Oolite of Dorset, UK, in ventral and dorsal views. Abbreviations: boc, basioccipital; brs, branchiostegal rays; cbr, posterior certobranchials; chy, ceratohyal; de, dentary; dpt, dermopterotic; ect, ectopterygoid; gu, median gular; hhy, hypohyal; hym, hyomandibula; mx, maxilla; mtp, metapterygoid; psp, parasphenoid; rde, rostrodermethmoid; scl, sclerotic ring. Paired bones listed as right (r) or left (l).

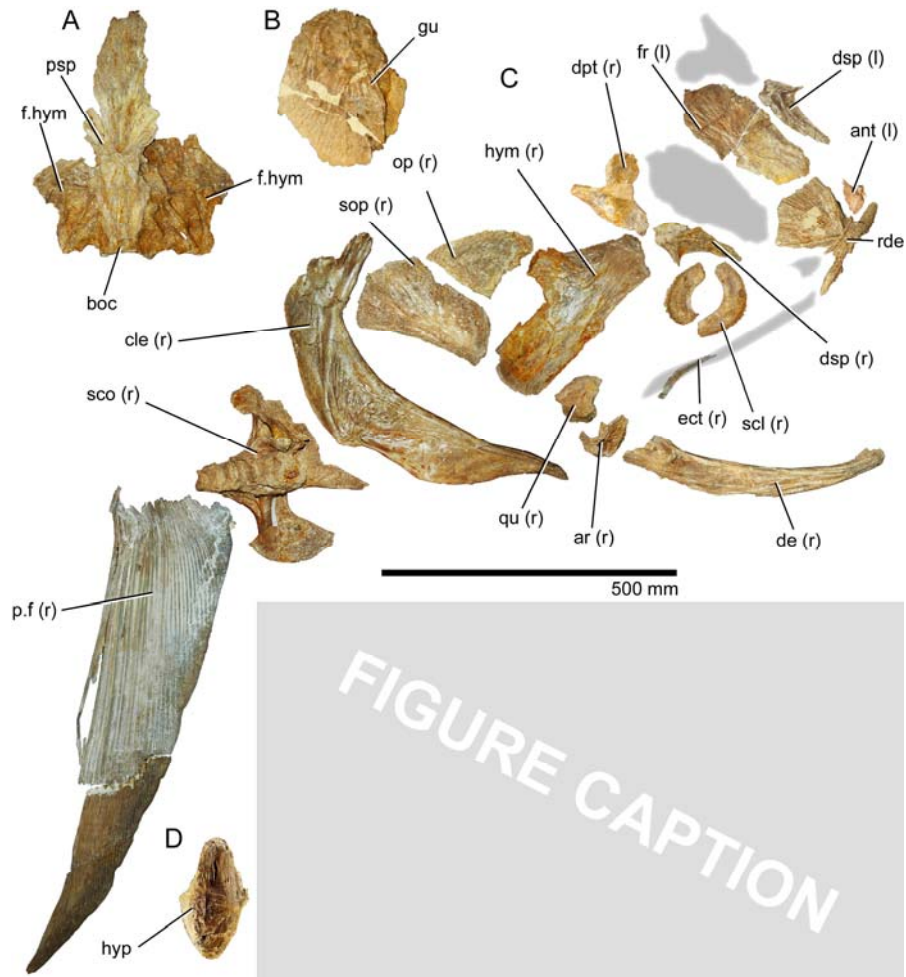


Fig. 2. †*Bonnerichthys gladius* gen. nov., a giant suspension-feeding bony fish from the Late Cretaceous of the USA. (A) Neurocranium and parasphenoid in ventral view. (B) Gular plate in ventral view. (C) Cranial and pectoral skeleton, shown in right-lateral view. Bones reconstructed from other specimens shown in grey. (D) Hypural plate in right lateral view. (A)-(C): specimen KUV 60692; (D): specimen FHS VP-17428. Abbreviations as in Fig. 1, plus: ant, antorbital; ar, articular; cle, cleithrum; dsp, dermosphenotic; f.hym, hyomandibular facet of neurocranium; fr, frontal; hyp, hypural plate; op, opercular; p.f, pectoral fin; qu, quadrate; sco, scapulocoracoid; sop, subopercular.

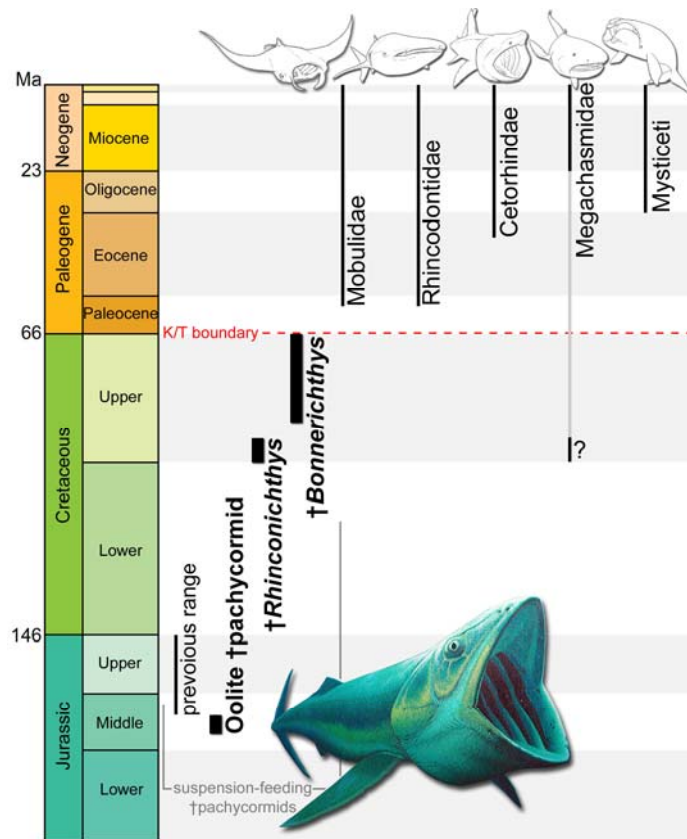


Fig. 3. New discoveries show that giant tpachycormid fishes were the dominant large-bodied, suspension-feeding vertebrates in Mesozoic marine environments, filling this ecological role in excess of 100 Ma. Previous occurrences of suspension-feeding tpachycormids were confined to a short interval in the Jurassic (shown as thin line), but newly recognized occurrences expand stratigraphic range of this group by a factor of 5 (shown as thick lines). Convincing records of other large-bodied planktivorous vertebrates only appear in the Paleogene, after the extinction of giant tpachycormids.