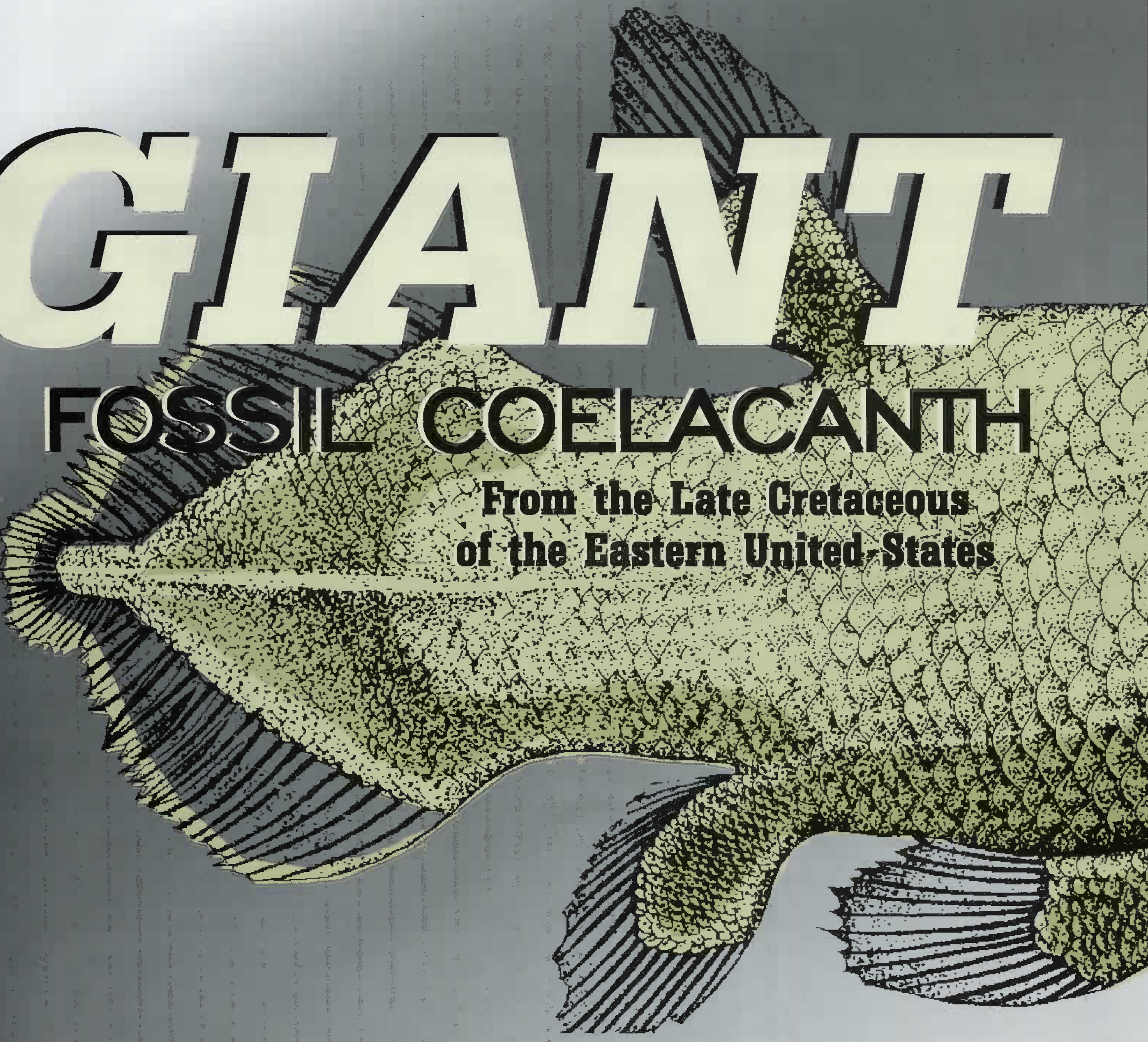
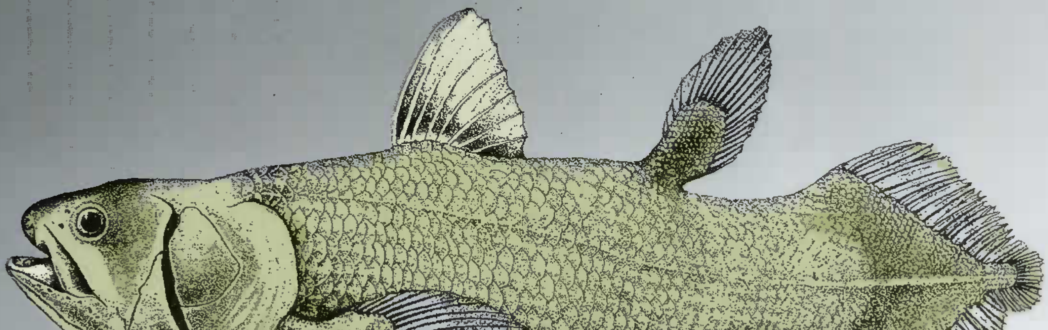
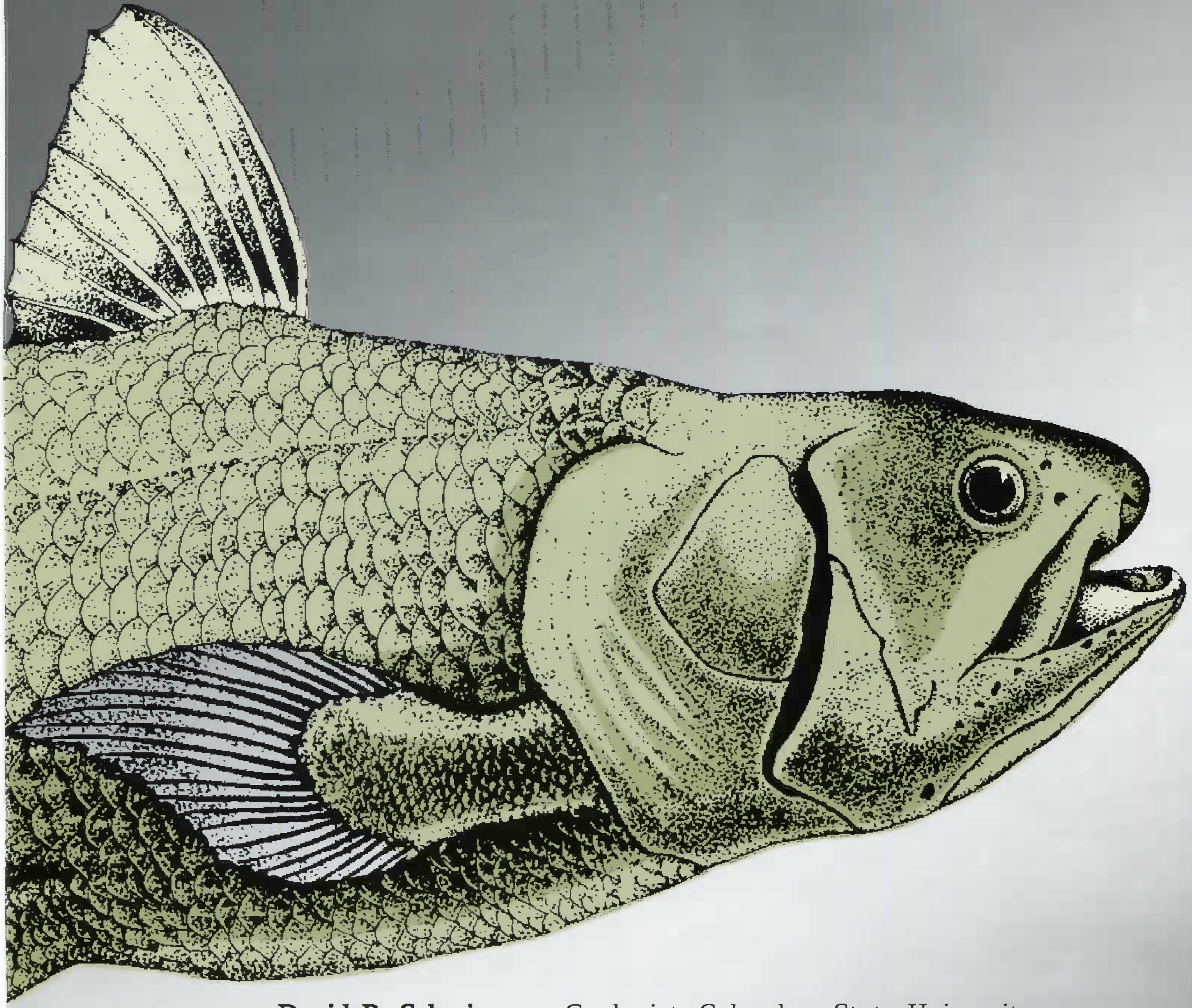
GIANT

FOSSIL COELACANTH

From the Late Cretaceous of the Eastern United States







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Introduction

In Autumn, 1987, a sizeable mass of fossil bone was discovered by amateur collectors in the bed of a small creek in eastern Alabama. The bone-bearing rock, some 300 kg in weight, was collected by a party led by G. Dent Williams and transferred to the paleontology laboratory at Columbus State University. Williams prepared most of the material using air percussion tools, and I further cleared some bones with acetic acid.

A mandible (lower jaw bone) of 502 mm length was the first bone prepared from the material. It strangely lacked evidence of both teeth and tooth sockets, and it was covered medially with coarse denticulation resembling #40 grit sandpaper. The jawbone conformed with no recognizable North American Late Cretaceous fish or four-legged animal, and, given the large size of the mandible, my initial search for an identification ranged from ankylosaurid dinosaurs, to mosasaurs, to the larger contemporary fish, such as Xiphactinus. Nothing known in the Late Cretaceous of North America matched the mandible nor any other bone which was subsequently prepared from this matrix.

J.D. Stewart of the L.A. County Museum was concurrently studying fossils of small marine coelacanths from the Late Cretaceous of western Kansas, USA (which were also a new discovery at the time: see Stewart et al., 1991). He recognized that the Alabama specimen consisted of the partial head skeleton, gill arches and pectoral girdle of a huge fossil coelacanth fish. This discovery was extraordinarily surprising to all concerned, since the fossil occurred in rock much younger (more than 130 million years) than any reported North American coelacanth fossil (aside from the Kansas specimens Stewart was then studying). Equally surprising, the bones appear to come from a fish we estimated at 4.0 m length, which is nearly an order of magnitude greater than the largest of the older North American coelacanths.

Four additional giant coelacanth specimens were collected in the field within three years of the first discovery, all from the southeastern United States. And, simultaneously, three additional specimens were discovered to have been previously placed in existing museum collections in the USA, all misidentified as other fish remains. One of these museum collections contained ten well-preserved bones, including a complete gular (ventral jaw plate), operculum (gill cover) and coronoid (middle jaw bone), which complemented the relatively poor preservation of the same bones in the original specimen.

The initial oral report of the existence of these North American giant coelacanths was made in at Society of Vertebrate Paleontology (Schwimmer, et al. 1990), followed by a formal systematic description in Schwimmer, et al., 1994, in which the new fish was given the genus and species name Megalocoelacanthus dobiei. The specimen from the eastern Alabama stream, described above, is designated as the holotype (name-bearing specimen) and consists of at least 28 associated bones with others still awaiting preparation. These bones are presently housed at Columbus State University, but they will eventually be placed in permanent depository at the American Museum of Natural History. The set of 10 associated bones mentioned above, collected from Late Cretaceous chalk in western Alabama, is designated as the paratype (associated name-bearing material) and is permanently housed at the Auburn University Museum of Paleontology.

The Later Fossil Record of Coelacanths

To put this discovery in perspective, it is useful to review the larger fossil record of coelacanths as perceived before this discovery, focusing on their late fossil record and near-recent history. Coelacanth fossils are fairly common and nearly globally distributed in rocks ranging from the Middle Devonian (ca. 375 Myr: i.e. million years ago), through the Triassic age (ca. 230 Myr.). All of these very early coelacanths were relatively small fish of less than 30 cm, and they include both marine and freshwater forms. Freshwater coelacanths are especially abundant in Triassic deposits of eastern United States (Schaeffer, 1952). The youngest prior fossil record of a North American coelacanth is Diplurus newarki, from freshwater deposits of earliest Jurassic age (ca. 205 Myr.: Schaeffer, 1941, 1952).

Forey (1981) and Maisey (1991) recognized two subfamilies within the Mesozoic coelacanths, which Maisey termed the Diplurinae and Coelacanthinae. The first contains the North American Triassic non-marine genera Chinlea and Diplurus, along with the Early Cretaceous Gondwanan (Southern Hemisphere) genera Mawsonia and Axelrodicthys. These latter two taxa, which are best known from eastern Brazil (Wenz, 1980; Maisey, 1986), may have inhabited non-marine or brackish water environments. Mawsonia is also known in northern Africa (Tabaste, 1963) and contains two giant species, reportedly reaching lengths estimated to reach 3.5 m (Wenz, 1981, Maisey, 1986).

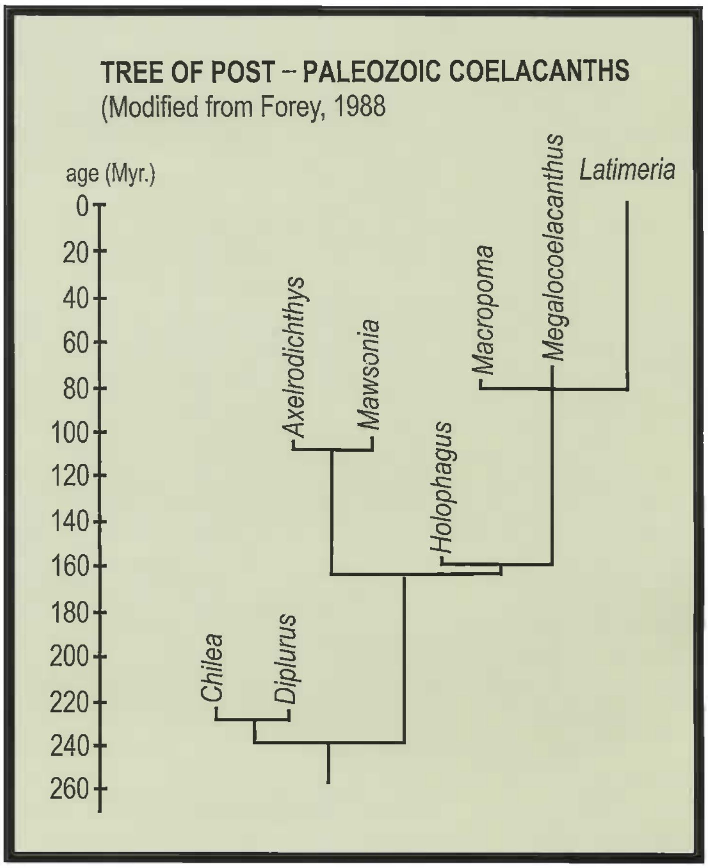

Fig. 1. Ages and relationships of representative Mesozoic coelacanth genera, including Megalocoelacanthus. For clarity, the closely-related genera Holophagus/Undina and Macropoma/Macropomoides are each represented by single branches.

The Coelacanthinae subfamily contains Holophagus (also called Undina), from the Jurassic of Europe, Macropoma (a.k.a. Macropomoides), from the Late Cretaceous of Europe and Lebanon, and the famous living genus, Latimeria. All of these fish are apparently fully marine, with the fossil species collected from continental shelf strata and, of course, the modern coelacanth, Latimeria known only from modern deep-water marine habitats.

During later Mesozoic time (Late Jurassic and Cretaceous), coelacanth diversity declined greatly (Figure 1), and by the later Early Cretaceous (ca. 115 Myr.) only

Fig. 2. The holotype specimen of Megalocoelacanthus in partial stage of preparation. This portion of matrix contains the right pterygoquadrate (cheek region) and dorsal fin spine (at bottom). Scale bar has 1 cm units.

three coelacanth genera survived: Mawsonia, Axelrodichthys (of the Diplurinae) and Macropoma (of the Coelacanthinae), with perhaps ten valid species among them (Forey and Cloutier, 1988; Cloutier, 1991). Mawsonia was the last of the Diplurinae and apparently went extinct in the mid-Cretaceous (ca. 97 Myr.). The last fossil coelacanth formerly known anywhere was Macropoma from the English Upper Chalk (Jukes-Browne, 1904), which is a marine deposit of the early Campanian Epoch of the Late Cretaceous (ca. 80 Myr.).

Coelacanths obviously did not go extinct during the Late Cretaceous despite the lack of younger fossils, since we have the living species Latimeria chalumnae. Species of Macropoma in the Cretaceous were generally similar to Latimeria, except for their smaller size (most less than 40 cm, whereas Latimeria reaches ~1.5 m), their calcified swim bladders, and their absence of a rostral organ. Nevertheless, the modern appearance of Latimeria follows an 80-Myr. gap in the fossil record of the Coelacanthinae, and with no previously-known fossil ancestor of comparable giant size.

A small bone fragment from the Paleocene of Denmark (Orvig, 1986) was the only plausible post-Cretaceous coelacanth fossil reported; however, its identification as a coelacanth fossil was based on histological comparison with other coelacanth bone, which is a diagnostic tool of undetermined reliability. Some further, and perhaps apocryphal reports, cite the finding of giant cosmoid fish scales, alleged to be of coelacanth origin, in younger settings. Ley (1957) reported

TABLE 2. Comparison of Skeletal Characteristics of Jurassic, Cretaceous, and Holocene Coelacanth Genera

	Pterygoid*	Operculum shape	Basisphenoid+	Dentition	Size~	Habitat	Coronoid shape
Megalocoelacanthus	Flanged	Quadrilateral	Very high	Absent	Giant	Marine	Subround
Latimeria	Flanged	Quadrilateral	High	Present	Large	Marine	Subquadrangular
Macropoma	Flanged	Quadrilateral	High	Present	Medium	Marine	Subtriangular
Holophagus	Partial	Quadrilateral	High	Present	Medium	Marine	Subtriangular
Mawsonia	Straight	Triangular	Low	Absent	Giant	Nonmarine?	Subtriangular
Axelrodichthys	Straight	Triangular	Low	Absent	Medium	Nonmarine?	Subtriangular
Diplurus	Straight	Quadrilateral	Low	tIntermediate	Small	Nonmarine	Subtriangular

*Ventral margin - straight, partial, or fully flanged.
+ Relative dorsoventral height.
~Small: <25 cm; 25 - 100 cm; large: 100 - 250 cm; >250 cm.

Fig. 3. Table comparing diagnostic characteristics of Megalocoealacanthus with other Mesozoic coelacanths and living Latimeria. Reproduced from Schwimmer, et al, 1994.

Fig. 4. Representative bones of M. dobiei from the right side of the skull and mandibles (lateral views): clockwise from upper right: pterygoquadrate with attached metapterygoid (i.e. cheek region), mandible (note sensory pits on lower right margin), gular plate, pectoral assembly with partial clavicle and cleithrum, and operculum with ablated posterior margin. Pterygoquadrate and pectoral are from the holotype, other bones from the paratype.

seeing such scales collected from a living fish in the Gulf of Mexico, and Ward (1992) described them in an unspecified Late Cretaceous stratum in Vancouver, British Columbia, Canada. Both references are in popular books and neither includes figures nor specimen data. However, both reports become more plausible following the discovery of Megalocoelacanthus, which is of the correct age for the British Columbia scales and occurs in strata of the ancient Gulf of Mexico.

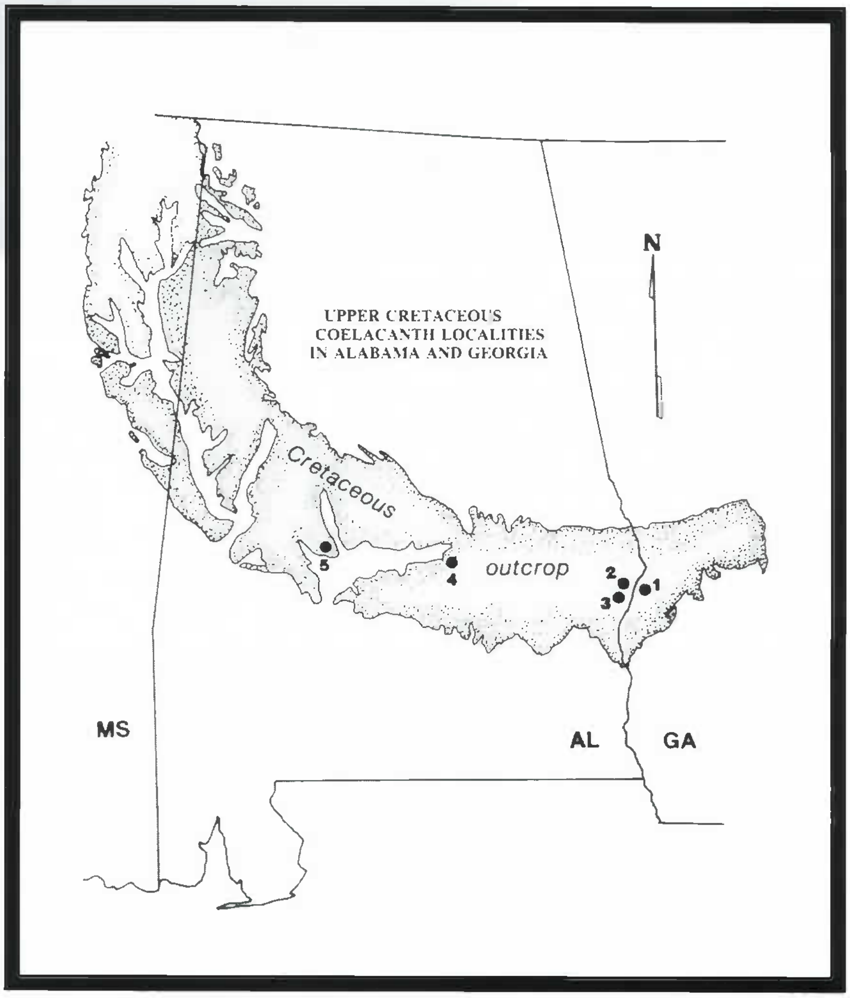

Fig. 6. Late Cretaceous fossil localities in Alabama and Georgia with fossils of Megalocoelacanthus dobiei.

Morphology of *Megalocoelacanthus dobiei*

We have now found excellent remains of the cranium, mandibles, pectoral girdles, and visceral skeletons of the new coelacanth taxon, but thus far have not identified skull roofing bones nor any bones posterior to the pectoral girdle, except for a single dorsal spine. Making taxonomic analysis more difficult, we have no knowledge of the scales, and poor knowledge of the sensory system of Megalocoelacanthus. The characters commonly used to discriminate higher groups of fossil coelacanths (e.g. position of the jugal canal in the squamosal, presence of anterior dorsal laminae on the parasphenoid) are not determinable from the known remains of Megalocoelacanthus dobiei. Fortunately, the new species shares so many gross similarities with living Latimeria chalumnae and the English Cretaceous Macropoma mantelli, that it is evidently a member of the same subfamily, and description of the species can be made by comparison and contrast with these species.

J.D. Stewart and I compared the prepared bones of Megalocoelacanthus with a freshly skeletonized modern Latimeria (AMNH 56150), as well as with several acid-prepared fossil Axelrodichthys at the American Museum of Natural History in New York. I also made similar comparisons between the bones of Megalocoelacanthus and specimens of Mawsonia in the collections of the Institute d'Histoire naturelle in Paris. From these comparisons it was evident that the giant North American coelacanth was not at all close to the giant Brazilian coelacanth Mawsonia, and the great size of both was a case of convergent evolution.

Shared-derived characters that unite Megalocoelacanthus, Macropoma and Latimeria, as well as unique characters of Megalocoelacanthus, are determinable from Figure 2, reprinted from the report of the new species. (Schwimmer, et al., 1994) In essence, we noted that all of these coelacanthinae feature a wide pterygoid (cheek region) with a ventral flange, a long quadrate (upper jaw hinge), a triangular (rather than rounded, fan-shaped) operculum, a dorso-ventrally deep basisphenoid (skull base), and a relatively large, rounded coronoid bone. Megalocoelacanthus is distinguished from both Latimeria and Macropoma by its total lack of true oral teeth, the presence of coarse denticles covering most inner mouth surfaces, and the giant size (discussed below). In summary, from the remains preserved and prepared to date, we believe Megalocoelacanthus resembled a double-sized Latimeria, with a slightly higher skull, and lacking teeth.

The great size of Megalocoelacanthus is extrapolated from measured dimensions of the holotype left mandible (502 mm length) and right palate (395 mm dorsoventrally by 330 mm anteroposteriorly), and the paratype right gular (481 mm length). These were compared with the corresponding bones in a mature Latimeria (AMNH 56150) and several large Mawsonia (AMNH 12217, 12216). Allowing for some allometry and individual variability, an overall length of 3.8 to 4.0 m is estimated for the holotype Megalocoelacanthus specimen, which is approximately 0.3 to 0.5 m longer than any other reported fossil coelacanth. Modern Latimeria chalumnae is also a big fish, with lengths measured up to 180 cm (Bruton and Coutouvidis, 1991). This large size in Latimeria is three times that of the largest known specimen of Macropoma, previously considered its closest relative (Forey, 1984, 1988). Although size is not always significant, the fact that giant Megalocoelacanthus is most similar to relatively big Latimeria, as well as being the youngest fossil coelacanth, suggests that it is the direct ancestor of the living coelacanth.

Fig. 5. Representative paired bones of Megalocoelacanthus dobiei. Shown (right to left) are mandibles, a zygal plate (the anteriormost arch of the notochord region), ceratohyals and branchials (both gill arches). Bones here come from both holotype and paratype assemblages.

Age of Megalocoelacanthus dobiei

The seven known specimens of Megalocoelacanthus dobiei come from rocks dating from the late Santonian (ca. 85 Myr.) to the early Maastrichtian (ca. 73 Myr.) stages of the Late Cretaceous. The fragmentary coronoid bone from Megalocoelacanthus cataloged as AMNH 6643, was collected by Gerard R. Case from stream lag deposit at Big Brook, New Jersey. This is the sole fossil of Megalocoelacanthus which comes from outside the southeastern USA. The oldest date possible for this fossil occurrence is about 75 Myr., whereas the youngest

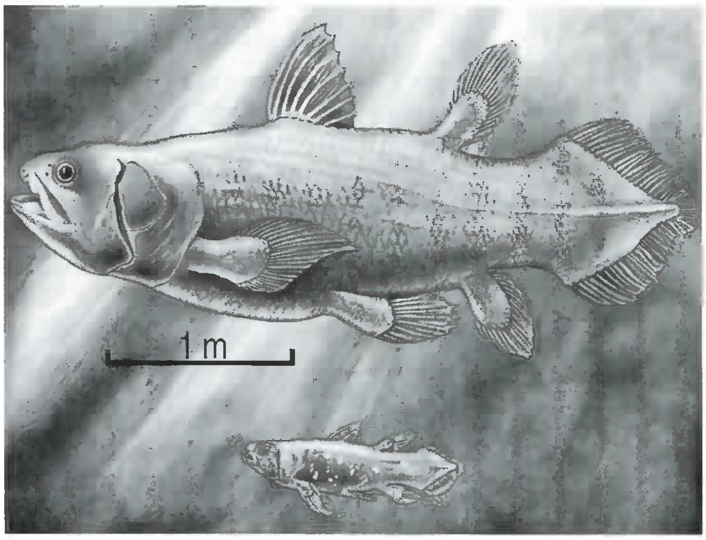

Fig. 7. A Reconstruction of Megalocoelacanthus dobiei based on the known bones and the inferred similarities to Latimeria. Artwork by Wendy Griswold-Smith, copyright 1994, all rights reserved.

date is about 70 Myr. Although the precise age is indeterminable, even the oldest date is 5 million years later than any other known coelacanth fossil in the world.

Habitat implications

All known Late Cretaceous coelacanths come from marine Continental Shelf deposits. There can be little doubt that coelacanths were predominantly, if not exclusively marine by the Late Cretaceous; but, whether they also inhabited deep-water marine environments at that time, as does Latimeria, is unknown. The sizeable number of individuals of Megalocoelacanthus dobiei in my collections suggests that these large fish were abundant in the southeastern American Late Cretaceous nearshore marine biota. Nothing in the preserved remains allows interpretation of their ecological role in the regional food webs, except that the giant size implies that they must have been a significant factor. The absence of oral teeth and presence of lingual denticulation suggests that they were entirely suction feeders, presumably living on small fish.

Conclusion

The surprising discovery of this new, late North American coelacanth taxon reduces the time gap between the last fossils of coelacanth fish and the living Latimeria chalumnae, by about 5 million years. It also reinforces the impression that Late Cretaceous coelacanths were entirely marine, shelf-dwelling inhabitants of primarily the Northern Hemisphere. This information detracts nothing from the surprise of the re-appearance of modern Latimeria in deep waters of the Southern Hemisphere, since over 70 million years and half a world still separate the last fossils and the living fish.

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