Giant fossil coelacanths of the Late Cretaceous in the eastern United States

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ABSTRACT

Remains of giant fossil coelacanth fish are relatively common in Upper Cretaceous strata (late Santonian to early Campanian age) in Alabama and Georgia. These are penecontemporaneous with the youngest reported fossil coelacanths from any global location and ~135 m.y. younger than the last coelacanth fish reported from North America. A coelacanth coronoid fragment from New Jersey, apparently from the same taxon, is of latest Campanian or Maastrichtian age and is the youngest known definite coelacanth fossil. The species reconstructs to 3.5 m, which is as large as any known coelacanth. The name *Megalocoelacanthus dobiei* is proposed for this new coelacanth, which is also the last known member of the clade that includes the extant *Latimeria*.

INTRODUCTION

In autumn 1987, a large fossil bone mass was discovered in the bed of the North Fork of Cowikee Creek, northern Barbour County, Alabama (Fig. 1); the mass was spread over ~3 m^2 of silty sandstone of the Upper Cretaceous Blufftown Formation. The bone came from a single giant coelacanth fish that lived ~135 m.y. later than any other coelacanth reported from North America. The species represented is new; subsequent to the first discovery, six additional specimens have been found in Alabama, western Georgia, and New Jersey, either collected in the field or identified in existing collections. The size of the new coelacanth is extraordinary, and the maximum length is estimated as 3.5 m. The size, combined with the apparent wide distribution and abundance, suggests that these coelacanths were important, previously unrecognized elements of the Late Cretaceous nearshore biota.

LATER FOSSIL RECORD OF COELACANTHS

Coelacanth fishes are notable "living fossils" because a single species, *Latimeria chalumnae,* has survived to the Holocene following an apparent 80 m.y. hiatus in the fossil record of the Coelacanthiformes (Forey, 1988). *Latimeria* is fished and observed only in bathyal waters of the southern Indian Ocean in the vicinity of the Comores Islands (Thompson, 1991), whereas the last reported fossil coelacanth remains come from shelfal marine chalks of the European Upper Cretaceous.

Coelacanth fossils appear commonly and nearly globally in Devonian through Triassic strata, and represent taxa of moderate diversity and abundance in both marine and freshwater environments. During Jurassic and Cretaceous time, coelacanth diversity declined, their geographic range narrowed, and they almost disappeared from the nonmarine realm. The fossil record of coelacanths as known appeared to end with the western European genus *Macropoma* in early Campanian time (Jukes-Browne, 1904). The fossil record in North America was assumed to show a much longer hiatus, the last coelacanth fossils coming from freshwater Newark basin deposits of latest Triassic or earliest Jurassic age (Schaeffer, 1941, 1952).

Coelacanths clearly did not become extinct during the Late Cretaceous, given the extant species, but the 80 m.y. gap in their fossil record is anomalous. A small bone fragment from the Paleocene of Denmark (Ørvig, 1986) is the only plausible post-Cretaceous coelacanth fossil reported; however, its identification is based solely on histological comparison with known coelacanth bone, which is of undetermined specificity.

The new species reported here extends the North American fossil record of coelacanths by 135 m.y., on the basis of six fossils from late Santonian and early Campanian deposits in Alabama and western Georgia. An additional fossil from the same or a similar coelacanth comes from younger Cretaceous marine strata (latest Campanian to middle Maastrichtian age: <75 Ma) from New Jersey, and is the world's youngest definite fossil coelacanth record.

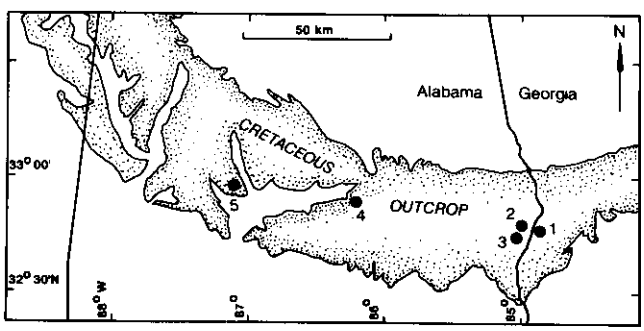

Figure 1. Upper Cretaceous coelacanth localities in Alabama and Georgia. Localities 1–3 in Blufftown Formation (early to mid-Campanian): 1—Hannahatchee Creek, Stewart County, Georgia; 2—High Log Creek, Russell County, Alabama; 3—North Fork Cowikee Creek, Barbour County, Alabama. Locality 4 is in Tombigbee Member, Eutaw Formation (mid- to late Santonian), Catoma Creek, Montgomery County, Alabama. Locality 5 is in Mooreville Formation (early Campanian), Harrell Station, Dallas County, Alabama.

SYSTEMATICS

Order Actinistia, Family Coelacanthidae

Megalocoelacanthus gen. nov.

Diagnosis. Very large marine coelacanth fish, lengths estimated to reach 3.5 m. Body form and postbranchial skeleton unknown.

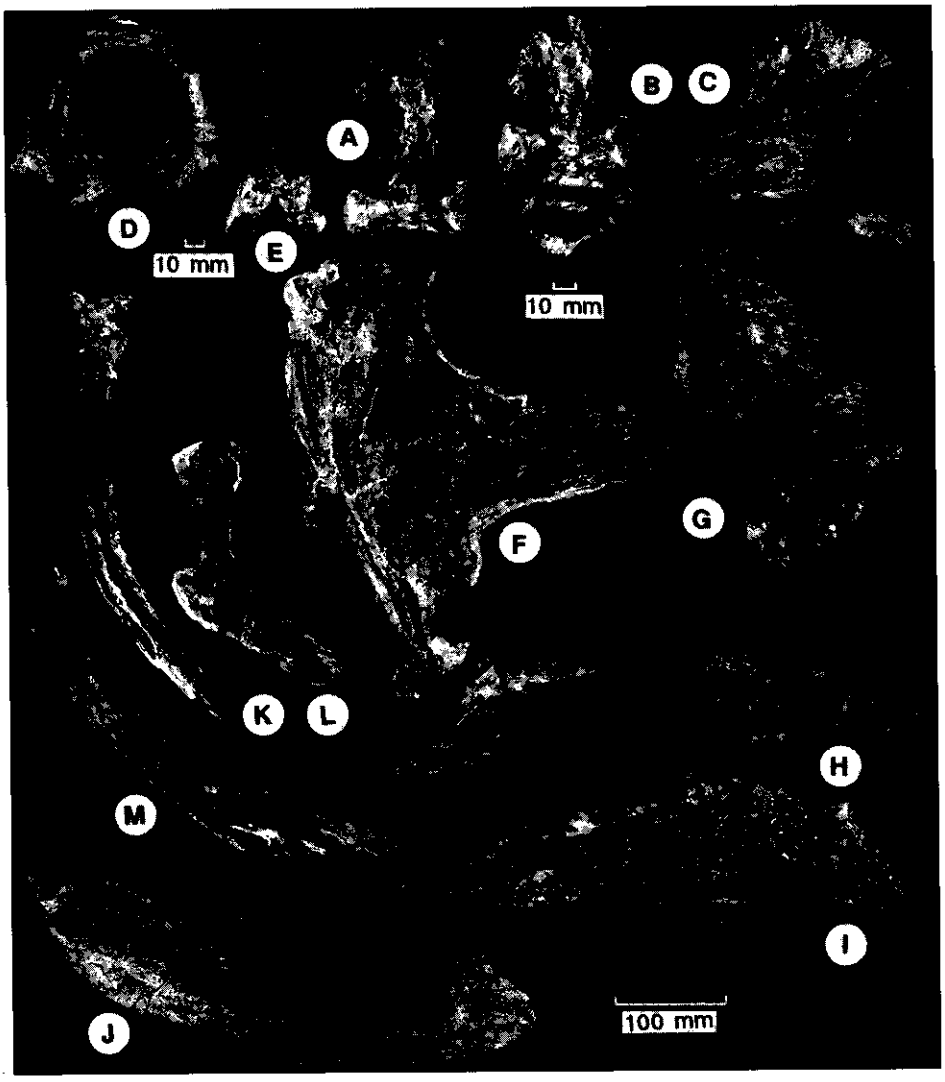

Figure 2. ***Megalocoelacanthus dobiei,*** **new species, holotype and paratype specimens. A–C, partial basisphenoid: A—posteroventral, B—posterior, and C—lateral views, size indicated by upper right scale bar. Upper left scale bar for D–E: D—zygal plate, posterior view, E—dorsal fin spine, anterior view. Sizes of F–M indicated by lower scale bar: F—right pterygoquadrate with attached metapterygoid, lateral view; G—left operculum, lateral view; H, I—left mandible, medial and external views; J—right gular, ventral view; K—branchial, position indeterminate; L—left ceratohyal, ventral view; M—right cleithrum-clavicle, lateral view. All materials shown from holotype CCK-88-2-1, except G, and J, which are from paratype AUMP 3834.**

Neurocranium known from partial basisphenoid, which is very deep dorsoventrally. Palate with distinct flange extending from the ventral pterygoid margin immediately anterior to the quadrate; quadrate narrow and elongate in labial view. Mandibles relatively elongate posterior to the articular; articular fused to the angular. Lingual surfaces of the angular, pterygoquadrate, and coronoid covered with small denticles. No marginal teeth are present in the mandible. Coronoid large, with subcircular dorsal margin. External surfaces of angular bear eight large sensory pits and very faint longitudinal grooves on posterior. Gular and operculum lack external ornamentation; other dermal bones not identified certainly, but no additional bone surfaces show ornamentation. Operculum subrhomboidal, with sharply angled anteroventral margin. Gulars diverge strongly along posterior midline.

Megalocoelacanthus dobiei sp. nov.

Etymology. Named for James L. Dobie of Auburn University.

Type Series. (See Figs. 2, A–J and 3, A–C; see Table 1 for collections and abbreviations). Holotype: CCK 88-2-1, 19 associated identified bones and unidentified bone fragments; paratypes: AUMP 3834, ten associated bones; referred material: FMNH P27524, left pterygoquadrate; CCK 93-6-1, and AUMP 3944, distal quadrate fragments; CCK 93-13-1, right angular fragment; AMNH 6643, left coronoid fragment.

Diagnosis. The only known species; diagnosis as above.

Age. The type series is early Campanian age. Referred specimens are late Santonian to mid-Maastrichtian age (see Table 1). The holotype matrix contains *Calculites ovalis* and *C. obscurus* (W. G. Siesser, 1990, written commun.), delimiting occurrence within nannofossil zones 17–19 (Sissingh, 1977). The matrix from paratype AUMP 3834 contains *Calculites ovalis* and *Aspidolithus parcus,* which delimit nannofossil zones 18–19 (W. G. Siesser, 1991, written commun.). AUMP 3944, from the subjacent Tombigbee Sand Member of the Eutaw Formation, is associated with late Santonian invertebrates and selachian fossils (G. R. Case, 1992, personal commun.), but the rock unit ranges into the early Campanian (Smith, 1989): thus, AUMP 3944 occurs within zones 16–17.

AMNH 6643 (Fig. 3, D–F) was collected by Gerard R. Case (AMNH collections data) from stream lags at Big Brook, New Jersey, which incorporate materials from the Marshalltown through Navesink Formations (Petters, 1976; Gallagher et al., 1986). The range of ages for this specimen is latest Campanian through middle Maastrichtian.

DISCUSSION

Coelacanths, especially post-Triassic coelacanths, show a low rate of acquisition of new characters through time (Shaeffer, 1952; Forey, 1984; Cloutier, 1991). The taxonomy of such slowly evolving organisms must give considerable weight to subtle changes in morphology. Ideally, analysis of the taxonomic relations of this coelacanth fish would employ a suite of morphologies that have been evaluated in previous coelacanth systematic studies (e.g., Schaeffer, 1952; Bjerring, 1977; Maisey, 1986; Cloutier, 1991) to determine how many shared and novel characters are present. However, the coelacanth material here does not lend itself to such comparisons, largely due to the state and nature of the preservation, which in part reflects the very large size of the fish.

We have found excellent remains of the cranium, mandibles, pectoral girdles, and branchial skeletons, but thus far have not identified skull roofing bones. Furthermore, we have no knowledge of the squamation, and poor knowledge of the sensory system. In consequence, many characters used in recent analyses of coelacanth phylogeny (as above) are not useful for the materials at hand. Morphologies evident in the new coelacanth specimens in study, compared with the same characters in established genera of Cretaceous coelacanths and *Latimeria* (the latter based on examination of pre-

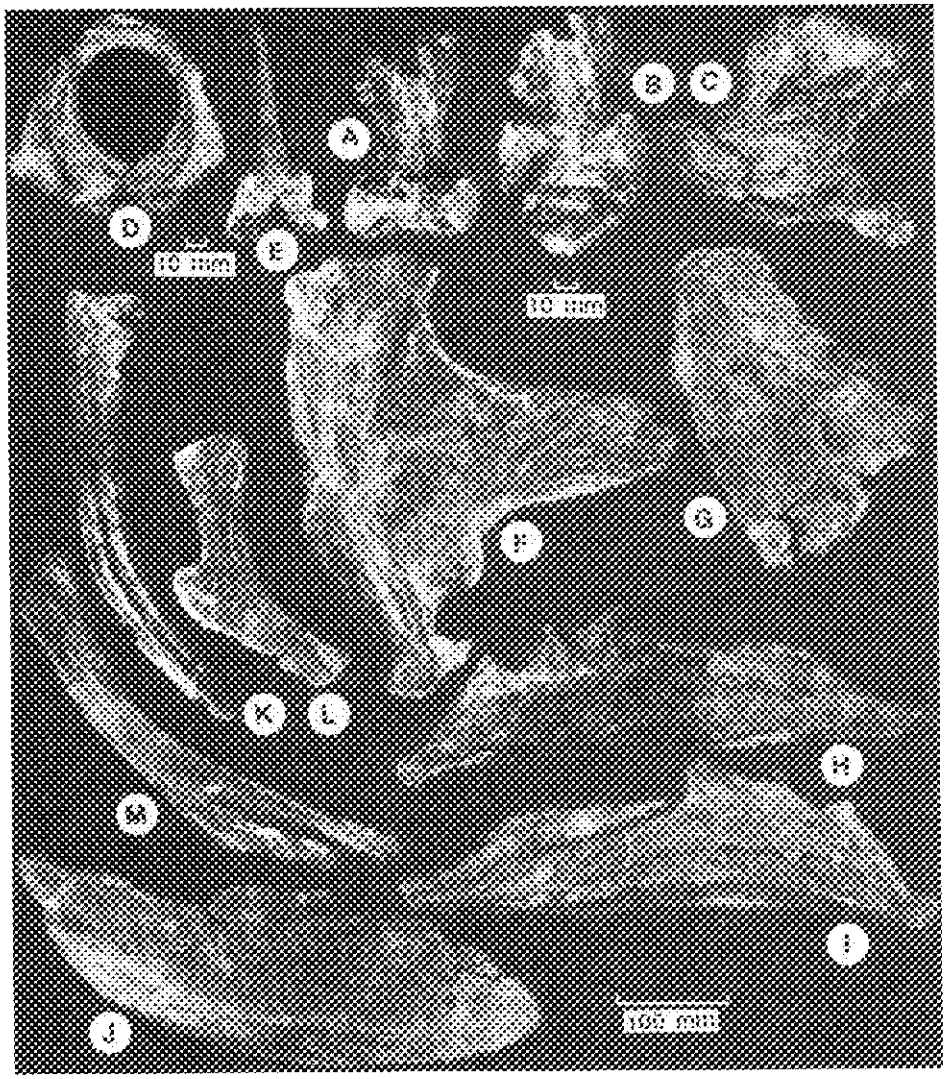

Figure 2. Megalocoelacanthus dobiei, new species, holotype and paratype specimens. A–C, partial basisphenoid: A—posteroventral, B—posterior, and C—lateral views, size indicated by upper right scale bar. Upper left scale bar for D–E: D—zygal plate, posterior view. E—dorsal fin spine, anterior view. Sizes of F–M indicated by lower scale bar: F—right pterygoquadrate with attached metapterygoid, lateral view; G—left operculum, lateral view; H, I—left mandible, medial and external views; J—right gular, ventral view; K—branchial, position indeterminate; L—left ceratohyal, ventral view; M—right cleithrum-clavicle, lateral view. All materials shown from holotype CCK-88-2-1, except G, and J, which are from paratype AUMP 3834

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pared material, including AMNH 56150, are presented in Table 2.

Mathematical analysis of Table 2 would be trivial, given the few characters available for comparison, but it is apparent that sufficient synapomorphies (e.g., ventral pterygoid flange, giant size, subcircular coronoid, absence of marginal dentition) are present to separate *Megalocoelacanthus* from all other genera; the data also indicate that *Latimeria* and *Macropoma* are closest morphologically to *Megalocoelacanthus*.

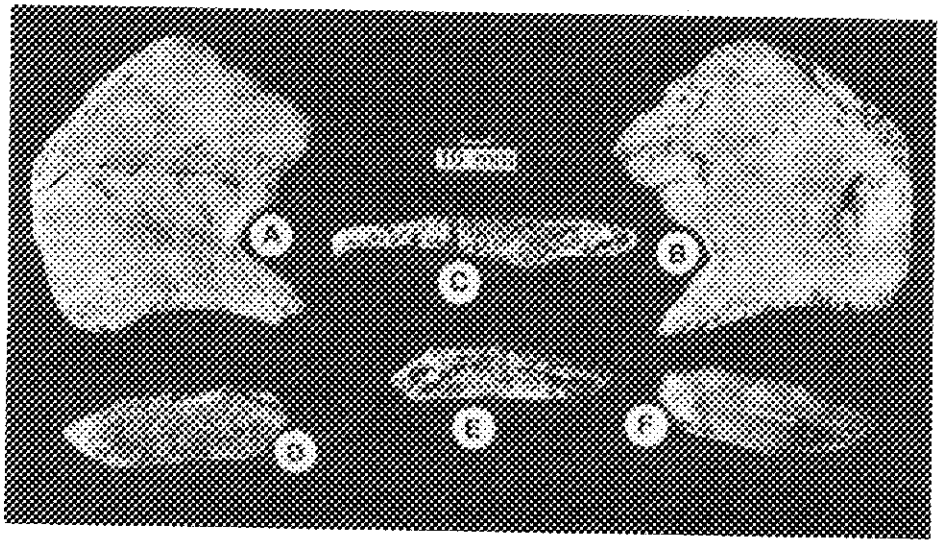

Figure 3. Coronoids of *Megalocoelacanthus*. Top row: Right coronoid of *Megalocoelacanthus dobiei* paratype AUMP 2834 in medial view (A), lateral view (B), and ventral view (C). Bottom row: left coronoid fragment AMNH 6843 in medial view (D), ventral view (E), and lateral view (F). Scale bar is for all figures.

Overall size is a labile feature in animals, but it is clear that *Megalocoelacanthus* was very large. The gross size is extrapolated from measured dimensions of the holotype left mandible (502 mm length) and right palate (395 mm dorsoventrally, 330 mm anteroposteriorly), the paratype complete right gular (481 mm length), and other bones, all compared with the corresponding bones in larger specimens of *Latimeria* (e.g., AMNH 56150) and *Mawsonia* (AMNH 12217, 12216). Allowing for some allometry and individual variability, an overall length of 3.5 m is estimated for the holotype specimen (Fig. 4). The additional six specimens reported here are of similar size, and certainly no less than 3.0 m long. This extremely large size appears to have evolved in *Megalocoelacanthus* independently of comparable maximum size (3.5 m lengths) in species of *Mawsonia* (Wenz, 1980, 1981; Maisey, 1986, 1991), which is a mid-Cretaceous (Albian-Turonian) genus from Brazil and North Africa. *Mawsonia* belongs to a monophyletic group that includes *Diplurus*, *Chinlea*, and *Axelrodichthys* (Forey, 1988; Maisey, 1991) but does not include *Latimeria*.

Latimeria attains lengths of ~180 cm (Bruton and Coetzee, 1991), nearly dou-

TABLE 1. LOCATION, AGE, AND COMPOSITION OF CRETACEOUS COELACANTH FOSSILS OF THE EASTERN UNITED STATES

No.	Locality	Stratum	Age	Material
CCK 88-2-1	Barbour Co., Ala., N. Fork Cowikee Ck.	Blufftown Fm.	Early Coniacian	Right and left pterygoquadrates, mandibles, and pectoral girdles, left operculum, hyoid plate, many branchial elements, dorsal fin spine, many unidentified bones
CCK 93-6-1	Russell Co., Ala., High Log Ck.	Blufftown Fm.	Early Campanian	Right quadrate fragment
CCK 93-13-1	Stewart Co., Ga., Ronnabatchee Ck.	Blufftown Fm.	Early Campanian	Right angular fragment
AUMP 3834	Dallas Co., Ala. Harrell Station	Mooreville Fm.	Early Campanian	Right rostrum, right coronoid, right and left pterygoquadrates and (five) metapterygoids, right gular, left operculum, right ceratohyal, single interhemitrun branchial
FMNH PF7524	Dallas Co., Ala., Harrell Station	Mooreville Fm.	Early Campanian	Right pterygoquadrate
AUMP 3943	Montgomery Co., Ala., Catoma Ck.	Tombigbee Mbr. of Eutaw Fm.	Late Santonian–Early Campanian	Right quadrate fragment
AMNH 6643	Marlboro, N.J., Big Brook	Marshalltown to Navesink Fms	Latest Campanian to mid-Maastrichtian	Ventral coronoid fragment

Note: CCK—Columbus (Georgia) College; AUMP—Auburn (Alabama) University Museum of Paleontology; FMNH—Field Museum of Natural History (Chicago); AMNH—American Museum of Natural History (New York).

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	Subtoroid
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	Intermediate	Small	Nonmarine	Subtriangular

*Ventral margin: straight, partial, or fully flanged.
†Relative dorsoventral height.
§Small: <25 cm; medium: 25–100 cm; large: 100–250 cm; giant: >250 cm.

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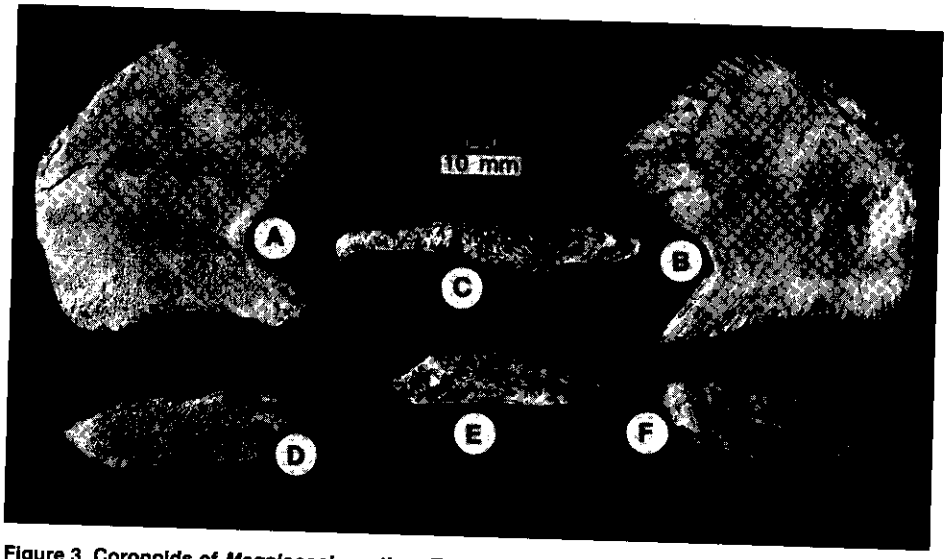

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FMNH P27524	Dallas Co., Ala., Harrell Station	Mooreville Fm.	Early Campanian	Right pterygoquadrate
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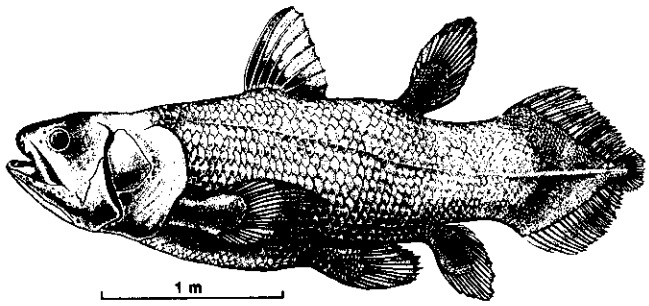

Figure 4. Reconstruction of *Megalocoelacanthus dobiei*. Reconstructed overall length approximately 3.5 m; head and pectoral regions based on holotype CC-88-2-1 and paratype AUMP 3834. Postpectoral regions based on morphology of *Latimeria*.

ble the size of *Macropoma,* previously thought to be its closest relative (Forey, 1984, 1988). The larger size of *Latimeria* compared with other genera in the clade, as well as the relatively young age of *Megalocoelacanthus,* suggests that the latter may be the proximal ancestor of the living coelacanth.

The left coronoid fragment AMNH 6643 (Fig. 3, D–F) is essentially indistinguishable from, although slightly larger than, the corresponding region on the well-preserved right coronoid of AUMP 3834 (Fig. 3, A–C). AMNH 6643 derives with certainty from a giant coelacanth with a coronoid indistinguishable from that of *Megalocoelacanthus,* but we hesitate to firmly assign the New Jersey specimen to *M. dobiei* on the basis of this single bone comparison. Nevertheless, AMNH 6643 is the youngest definite fossil coelacanth found so far.

CONCLUSIONS

Most of the giant coelacanth specimens were collected recently, but three were found misidentified in existing museum collections. The substantial amount of material now known from *Megalocoelacanthus dobiei* in the southeastern U.S. Coastal Plain suggests that the fish were common in the nearshore marine biota, and the New Jersey specimen suggests that they ranged widely. The sedimentary environments of the species occurrences include the open-marine carbonate shelf for the Mooreville Formation in western Alabama (Applegate, 1970), and nearshore, back-barrier, and estuarine environments for the Eutaw and Blufftown Formations in central and eastern Alabama, and western Georgia (Schwimmer, 1986; Case and Schwimmer, 1988). Thus, it is evident that these Late Cretaceous coelacanths favored marine environments similar to the habitats of the latest European coelacanth genus *Macropoma,* which is found in the Upper Cretaceous chalks of England (Woodward, 1909).

Although it seems odd that bones of such large creatures were unrecognized until recently, the sizeable sample now identified indicates that additional Late Cretaceous (and perhaps younger) coelacanth fossils are probably present but identified incorrectly in existing collections. The very large size of these coelacanth materials may have disguised their nature: indeed, the fossils could be mistaken for dinosaur or mosasaur bones. The presence of such large and apparently common fish in the marine shelf fauna requires reinterpretation of contemporary food webs in the Late Cretaceous nearshore biota of the eastern U.S. Coastal Plain.

ACKNOWLEDGMENTS

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