

## PELAGOSAURUS TYPUS BRONN, 1841 (MESOEUCROCODYLIA: THALATTOSUCHIA) FROM THE UPPER LIAS (TOARCIAN, LOWER JURASSIC) OF SOMERSET, ENGLAND

STEPHANIE E. PIERCE and MICHAEL J. BENTON

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ, United Kingdom, S.Pierce@bristol.ac.uk, Mike.Benton@bristol.ac.uk

**ABSTRACT**—The thalattosuchian crocodyliform *Pelagosaurus typus* Bronn, 1841 is fully documented and described from the Upper Lias (Toarcian, Lower Jurassic) of England. The material under study is part of a historical collection made by Charles Moore (1814–1881) at Strawberry Bank (Ilminster, Somerset, England) around 1848. Apomorphic features of the genus include: sculpturing on almost the entire skull and mandible with extensive sculpturing on the prefrontal, lachrymal, frontal, parietal, temporal arcade and the posterior extent of the mandible; 30 piercing teeth on each side of the upper and lower jaws; small, shallow, egg-shaped antorbital fenestra present within the lachrymal and maxilla; supratemporal fenestrae short anteroposteriorly; paired frontal; anterior margin of internal choana tapers anteriorly between the paired palatines; and presence of a choanal septum on the palatine and pterygoid. *Pelagosaurus* was a small, exceedingly long-snouted, gracile crocodyliform whose diet probably consisted of small fishes, crustaceans and possibly insects. The small-bodied fish *Leptolepis* is confirmed as part of its diet as a specimen is found in the rib cage of a small juvenile *Pelagosaurus*. Laterally placed eyes suggest that this species actively pursued its prey rather than sitting and waiting at the water surface. The phylogenetic position of *Pelagosaurus* has been debated. *Pelagosaurus* possesses the majority of teleosaurid apomorphies, including: four premaxillary teeth; small prefrontal; lachrymal visible in dorsal aspect; presence of mandibular fenestrae; dermal armor; and a straight tail; however, these are all plesiomorphic for the Crocodyliformes in general. There also appear to be problems when defining the proposed metriorhynchid features of *Pelagosaurus* (i.e., broad nasal, large frontal, lateral orbit, sclerotic ring and arrangement of prefrontal-lachrymal). Moreover, characters that have been used in past cladistic analyses are either incorrect or too simplistic. Accordingly, *Pelagosaurus* is considered to belong to the *Thalattosuchia incertae sedis* until a more thorough phylogenetic investigation is conducted.

### INTRODUCTION

One of the most intriguing groups to evolve during the Mesozoic was the Thalattosuchia, longirostrine marine crocodyliforms. The two thalattosuchian families, the Teleosauridae and Metriorhynchidae, appear in abundance in the Lower Jurassic of Western Europe (Carroll, 1988). These crocodiles diversified and dispersed throughout the Jurassic with specimens recorded from Russia (Hua et al., 1998), South America (Gasparini and Dellapé, 1976; Gasparini and Díaz, 1977; Vignaud and Gasparini, 1995; Gasparini et al., 2000, 2005), North Africa (Fara et al., 2002), Mexico (Frey et al., 2002), and Cuba (Gasparini and Iturralde-Vinent, 2001). The teleosaurs were large nearshore animals characterised by extreme elongation of the snout, extensive dermal armor, and a 'generalised' postcranial skeleton. Conversely, the metriorhynchids were smaller offshore animals that became highly adapted to an aquatic lifestyle with loss of dermal armor, paddle-like limbs, and a caudal tail fin.

Thalattosuchians form an important part of an exceptional assemblage of marine reptiles that have been recovered from the Upper Lias (Toarcian; Lower Jurassic) of England and Western Europe (Benton and Taylor, 1984; Walkden et al., 1987). Notably common in the marine fauna of Germany and France is the monotypic genus *Pelagosaurus* Bronn, 1841 (Westphal, 1961, 1962). This animal was originally described by Eudes-Deslongchamps (1863; 1877) based on incomplete cranial and postcranial remains from Normandy, France. Since these initial investigations, few authors have examined the anatomy of *Pelagosaurus* in any detail (Duffin, 1979b). Most studies have focused on a select number of morphological characters (e.g., position of orbits) in order to resolve the phylogenetic affinity of *Pelagosaurus* within the Thalattosuchia; however, little consensus has been achieved (e.g., Westphal, 1962; Buffetaut, 1982; Clark, 1994). Thus, an up-to-date description of *Pelagosaurus* seems warranted and will provide a valuable source of information towards unravelling thalattosuchian systematics.

Although common in Western Europe, *Pelagosaurus* has gone almost unnoticed in the English Toarcian. Duffin (1979a, b) was the first to highlight a collection of beautifully preserved specimens from the Ilminster succession of the Upper Lias (Fig. 1) discovered by Charles Moore around 1848 (cf. Moore, 1852). Twenty-four specimens referable to *Pelagosaurus typus* are present in the Moore Collection (Bath Royal Literary and Scientific Institute, BRLSI) making it the most significant collection of *Pelagosaurus* material in England and indeed in Western Europe. Remarkably, this material has never been properly described or figured.

Moore's (1852) first reference to the *Pelagosaurus* material was in a comprehensive paper about the paleontology of the Middle and Upper Lias. He drew attention to three particularly well-preserved individuals (one of which is a "baby Saurian") and assigned them to the genus *Teleosaurus*. In subsequent papers, Moore placed the Ilminster specimens in the species *Teleosaurus temporalis* (Moore, 1866, 1870). The true taxonomic identity, however, was not realized until Eudes-Deslongchamps (in a lost manuscript) described the juvenile and proposed the name *Pelagosaurus moorei* (Wilson, 1893; Duffin, 1979a,b). Following this account, the crocodyliforms of the Ilminster succession were referred to two species of *Pelagosaurus*, *P. moorei*, and *P. typus* (Moore, 1879; Wilson, 1893; Woodward, 1893; Arkell, 1933); however, no further detailed examination of the material was ever undertaken.

Duffin (1978), in an account of the vertebrate faunas collected by Charles Moore, remarks that recent reviews of fossil crocodyliforms failed to mention the existence of these spectacular *Pelagosaurus* specimens (Westphal, 1961, 1962; Steel, 1973). Duffin (1979a) undertook a historical review of the material collected by Moore, providing a detailed literature survey. Furthermore, in a companion paper, Duffin (1979b) presented a description of the juvenile's skull and reassigned the material to *Pelagosaurus typus*. In the same article, Duffin (1979b:477) states, "the complete collection will be dealt with thoroughly in a later paper. . ." This, however, was never realized.

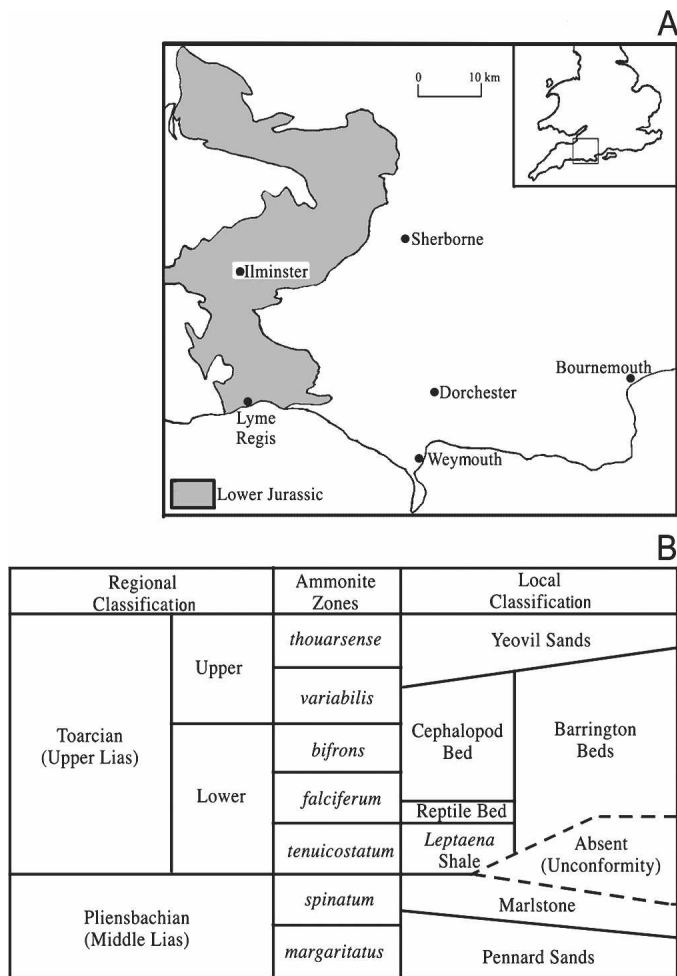


FIGURE 1. **A**, Geographical location of Ilminster in Somerset, England; **B**, Stratigraphy of the Middle and Upper Lias deposits in Somerset, England. (Modified from Bennett, 1987.)

The purpose of the present study is to fulfill Duffin's (1979b) proposal that the Charles Moore *Pelagosaurus* collection deserves to be properly figured and described. The main intent is to provide a thorough, modern, detailed anatomical description of *Pelagosaurus typus*, supplying both pictures and drawings of the collection and an idealized reconstruction of the skull and postcranial skeleton. As a result, the Moore collection of Upper Lias crocodyliforms will finally be accurately documented and figured and the occurrence of *Pelagosaurus* in the English Toarcian substantiated. The paleoecology of *Pelagosaurus* will also be considered. Additionally, a breakdown of the characteristics of the families Teleosauridae and Metriorhynchidae will be offered and the controversy over the affinity of *Pelagosaurus* within the Thalattosuchia will be discussed.

#### SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES sensu Benton and Clark, 1988  
 MESOEUCROCODYLIA sensu Benton and Clark, 1988  
 THALATTOSUCHIA Fraas, 1901  
*PELAGOSAURUS* Bronn, 1841

**Type species**—*Pelagosaurus typus*.

**Holotype**—Teylers Museum, Haarlem, Nr. 2744.

**Range**—Upper Lias; Toarcian; Lower Jurassic.

**Distribution**—Western Europe; England, France, and Germany.

**Revised Diagnosis**—Features shared with teleosaurids include four premaxillary teeth; small prefrontal; lachrymal visible in dorsal aspect; sagittal crest made up of equal portions of the frontal and parietal; absence of supraorbital constriction on the frontal; presence of mandibular fenestrae; dermal armor; straight tail. Features shared with metriorhynchids include: broad nasals; large frontal; lateral orbits; sagittal crest broad and sculpted; jugal vertically oriented; and scapula symmetrical in lateral view. Apomorphic features include: sculpturing on almost the entire skull and mandible, with extensive sculpturing on the prefrontal, lachrymal, frontal, parietal, temporal arcade and the posterior extent of the mandible; 30 piercing teeth on each side of the upper and lower jaws; small, shallow, egg-shaped antorbital fenestra present within the lachrymal and maxilla; supratemporal fenestrae short anteroposteriorly; paired frontal; anterior margin of internal choanae tapers anteriorly between the paired palatines; presence of a choanal septum on the palatine and pterygoid.

#### *PELAGOSAURUS TYPUS* Bronn, 1841 (Figs. 2–8)

**Diagnosis**—As for genus.

**Locality**—Charles Moore collected the *Pelagosaurus* specimens from Strawberry Bank, north of Ilminster, Somerset, England (National Grid Reference ST 361148; Duffin, 1979b) (Fig. 1a). The skeletal remains are contained within featureless limestone nodules; these nodules were extracted from the thin bed of yellow limestone or Reptile Bed ("Fish and Saurian" Bed of Moore, 1866) of the Junction Bed, Upper Lias (Toarcian; Lower Jurassic) (Cope et al., 1980; Bennett, 1987). The fossil-rich Reptile Bed is within the lower part of the Upper Lias within the *falciferum* ammonite zone (Fig. 1b). The Strawberry Bank quarry has long since been built over.

**Referred Specimens**—The Moore collection at the BRLSI is composed of four isolated skulls and associated postcranial skeletal elements along with two articulated specimens, one of which is a small juvenile. All specimens are preserved in three dimensions, but the degree of preparation varies. The specimens examined include: M1397 (lower jaw fragment with teeth), M1410 (dentary, scapula, vertebrae, and ribs), M1411 (skeletal fragments in matrix), M1412 (skull with cervical vertebrae), M1413 (skull), M1414 (cervical vertebrae), M1415 (upper and lower jaw fragment with teeth), M1416 (skull, vertebrae and ribs), M1417 (cervical rib, scutes, ilium, and femur), M1418 (articulated juvenile skull and postcranium), M1419 (dorsal vertebrae, ribs, sacral vertebrae, pubis, ischium, femur and caudal vertebrae), M1420 (skull in ventral view, sacral vertebrae, pubis, hind limb elements), M1421 (ilium and hind limb elements), M1422 (dorsal vertebrae and ribs), M1423 (dentary fragment), M1424 (dentary, scapula, metacarpal, scutes, ammonites, and brachiopods), M1425 (dorsal vertebrae), M1426 (vertebrae, scutes and limb elements), M1427 (dentary fragment with teeth, M1428 (lower jaw fragment) M1429 (surangular, angular, humerus, ribs and scutes), M1430 (scutes, dorsal ribs, metatarsal), M1431 (ribs and scutes), M3578 (articulated skull and postcranium).

#### DESCRIPTION

##### Skull and Mandible

The skull (Fig. 2) is narrow, exceedingly long and highly sculptured. It gradually broadens toward the orbits and then narrows very slightly backwards. The snout is long and tubular and two thirds the length of the entire skull. The external nares are terminal and face anterodorsally. The snout is oval in cross-sectional view. The laterally placed orbits and supratemporal

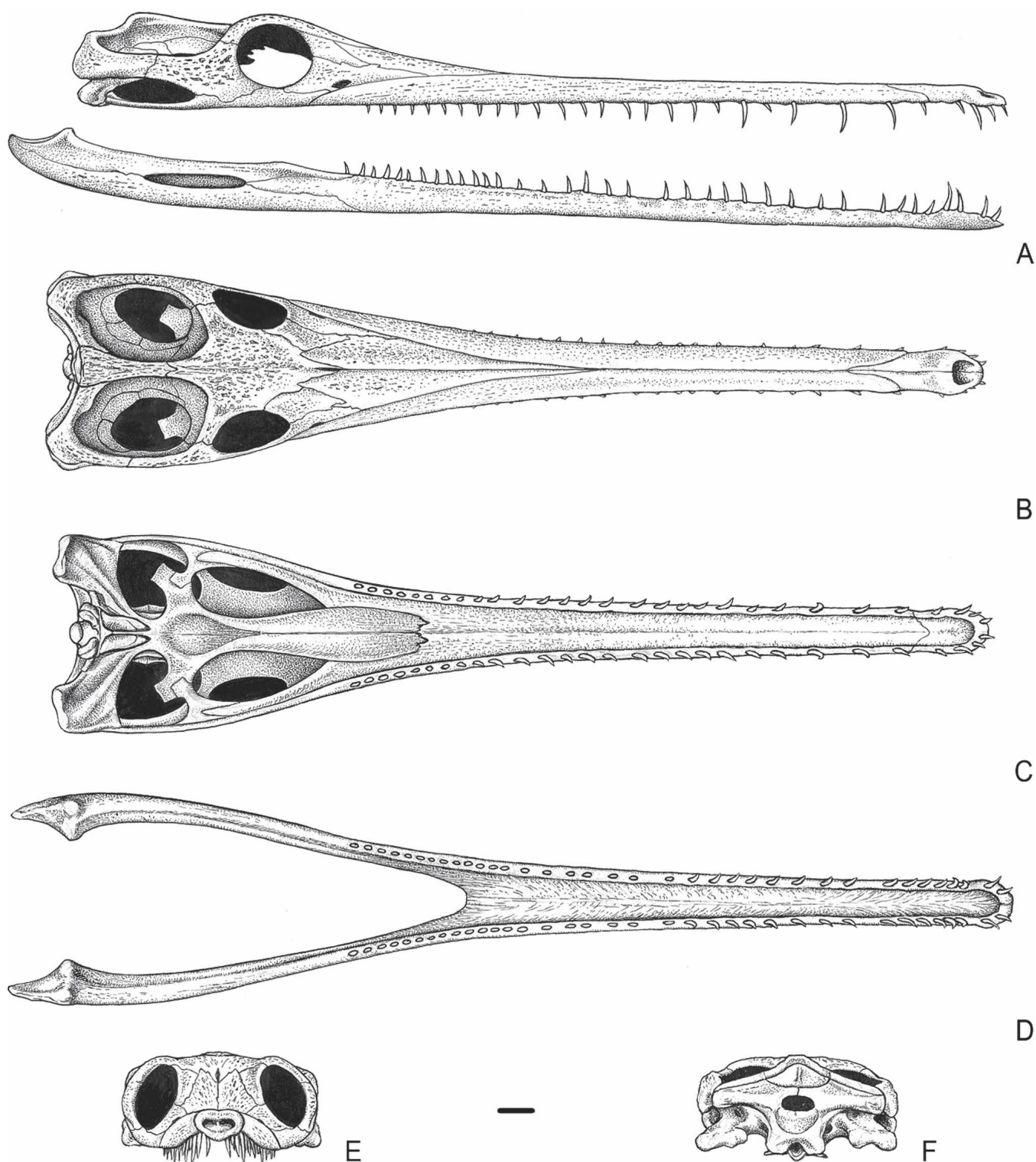


FIGURE 2. Reconstruction of the skull and mandible of *Pelagosaurus typus* from the Toarcian of Somerset, England, in various views. **A**, lateral skull and mandible; **B**, dorsal skull; **C**, ventral skull; **D**, dorsal mandible; **E**, anterior skull; **F**, posterior skull. Scale bar equals 1 cm. (Drawing by ©John Sibbick).

fenestrae are of similar size and shape. Behind the orbits, the skull is very short and the posterior extent is not flared. Laterally, the posterior aspect of the skull is relatively deep as compared to the snout. The mandible is long, narrow, and greatly flattened in cross-sectional view. The dentary comprises two

thirds of the entire lower jaw. Each dentary ramus diverges at a 45-degree angle from the midline. The mandible terminates in short, somewhat dorsally curved retroarticular processes.

**Premaxilla**—The premaxilla is paired, well developed, and completely envelops the external nares opening (Figs. 3A, B; 4,

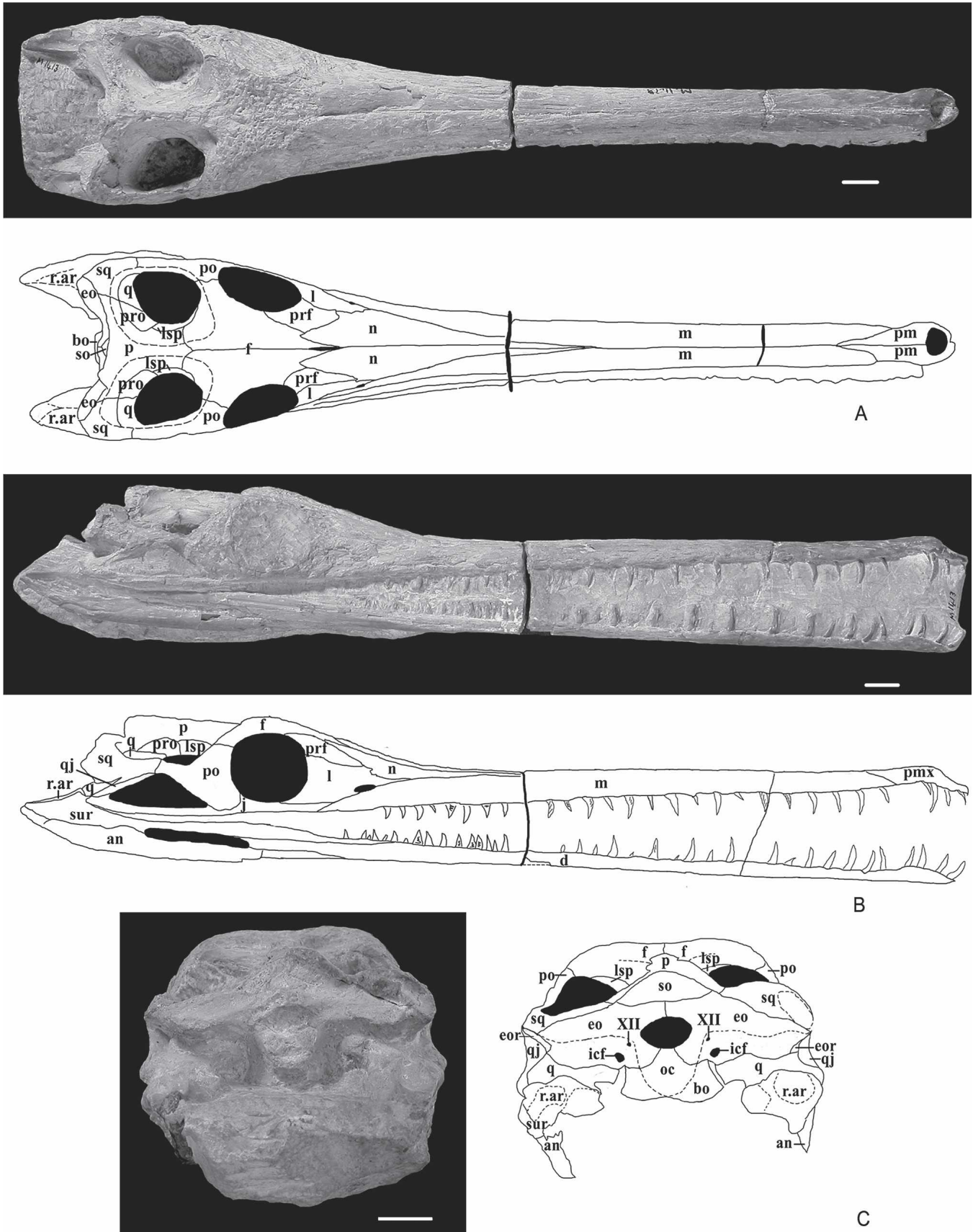


FIGURE 3. *Pelagosaurus typus* (M1413) from the Toarcian of Somerset, England; photographs and interpretive drawings of the skull and mandible in various views. **A**, dorsal skull; **B**, lateral skull and mandible; **C**, occipital skull. **Abbreviations:** an, angular; bo, basioccipital; d, dentary; eo, exoccipital; eor, external otic recess; f, frontal; j, jugal; icf, internal carotid foramina; l, lachrymal; lsp, laterosphenoid; m, maxilla; n, nasal; oc, occipital condyle; pm, premaxilla; p, parietal; po, postorbital; prf, prefrontal; pro, prootic; q, quadrate; qj, quadratojugal; r.ar, retroarticular process; so, supraoccipital; sq, squamosal; sur, surangular; XII, foramina for cranial nerve seven. Scale bar equals 1 cm.

5A). The anterior termination is smooth and rounded. The narial opening is positioned in the first one third of the premaxilla, is sub-ovate in outline, and opens anterodorsally. The region containing the narial opening is deflected ventrally, creating a scooped appearance. Dorsally, the premaxilla has a long posterior process that extends between the anterior ends of the maxillae, isolating the maxillae from the nares. The posterior process does not reach the nasal bones. The dorsal contact with the maxillae is V-shaped, with the apex pointed posteriorly. From the lateral perspective the premaxilla-maxilla suture is straight and inclined posteriorly. There are four premaxillary teeth, with the third tooth being the largest and the fourth tooth the smallest. A large notch or diastema exists between the fourth premaxillary tooth and first maxillary tooth, which serves to receive the third and fourth tooth on the dentary. The contact with the maxillae on the palatal/ventral surface cannot be discerned, but is expected to form a V-shaped suture, the apex of which would have been pointed anteriorly. The foramen incisivum is not preserved.

**Maxilla**—The maxilla is an exceedingly long, paired bone that forms the greater part of the snout (Figs. 3A, B; 4, 5A). Dorsally, the maxillae are lightly sculptured and meet one another for approximately half their length, isolating the nasals from the premaxillae. The anterior end is separated by the ascending process of the premaxilla and plunges anteroventrally in a smooth arch terminating in the centre of the diastema. The posterior end is separated by the anterior process of the nasal and descends posteroventrally in a smooth arch underneath the nasal, lachrymal, and jugal, and ends anterior to the orbit. The suture with the nasal is extensive and V-shaped, with the apex pointing anteriorly. The maxilla contributes to the anterior portion of the small, shallow, egg-shaped antorbital fenestra halfway down its contact with the lachrymal. Contact with the jugal is minimal. The margin of the maxillary tooth row is straight, devoid of swellings over the teeth, and contains approximately 25 teeth and replacement teeth. The teeth come to an end approximately at the maxilla-jugal contact.

Ventrally, the maxillae have broad palatal processes, which

are sutured along their midline making up a considerable portion of the secondary palate (Fig. 6). There is a central groove and two lateral grooves running down the entire length of the central axis. Posteriorly, the maxillae form three processes. A mid-sagittal (palatal) process and two lateral (ectopterygoid) processes. The mid-sagittal process extends between the palatines for a short distance, forming a V-shaped suture, the apex of which points posteriorly. The medial edges of the lateral processes contribute to the anterolateral margin of the triangular palatal fenestrae while the lateral edges contact the jugal. At their posterior extent, the lateral processes become sutured to the ectopterygoids.

**Nasal**—The paired nasals are relatively long and broad (Figs. 3A, B; 4, 5A). They do not reach the premaxilla and therefore do not contribute to the external narial opening. Dorsally, the nasals are roughly triangular and are in contact for most of their length. The anterior (maxillary) process is narrow, pointed, and inserts between the posterior ends of the maxillae. The nasals broaden posteriorly and form the greater part of the posterodorsal portion of the snout. Their broadest point is at the junction between the nasal, lachrymal, and prefrontal, with the nasal slightly wrapping around the anteroventral end of the prefrontal. After this point, the nasals become constricted and continue between the prefrontal bones, eventually stretching out into two long posterior (frontal) processes. Combined, the posterior processes form an M-shape, with the ascending tips of the M surrounded by the frontal bone; the descending tip of the M forms a deep V-shaped suture with the frontal, the apex of which is pointed anteriorly. Sculpturing increases in intensity from the anterior to posterior ends of the nasals.

**Lachrymal**—The lachrymal is large, deep dorsoventrally, and is visible on the dorsal surface of the skull (Figs. 3A, B; 4, 5A). It tapers anteriorly and inserts between the nasal and maxilla. The posterior portion of the small, shallow, egg-shaped antorbital fenestra is situated within the lachrymal about halfway down the lachrymal-maxillary contact. The dorsal margin is sinuous and is capped by the nasal and prefrontal. The ventral edge is straight and lined by the jugal bone. Posteriorly, the lachrymal

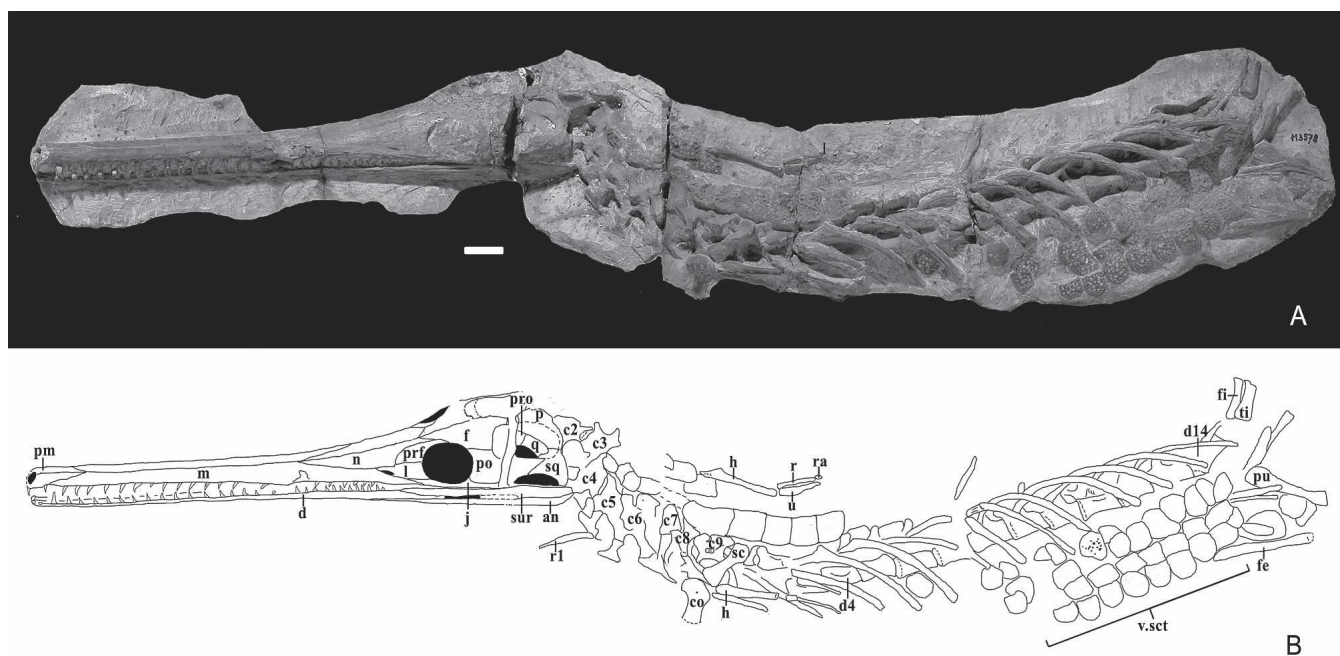


FIGURE 4. *Pelagosaurus typus* (M3578) from the Toarcian of Somersset, England; articulated small adult. **A**, photograph; **B**, interpretive drawing. **Abbreviations:** an, angular; c2-c9, cervical vertebrae 2-9; co, coracoid; d, dentary; d4, dorsal vertebra 4; d14, dorsal vertebra 14; f, frontal; fe, femur; fi, fibula; h, humerus; j, jugal; l, lachrymal; m, maxilla; n, nasal; pm, premaxilla; p, parietal; po, postorbital; prf, prefrontal; pro, prootic; pu, pubis; q, quadrate; r1, cervical rib 1; r, radius; ra, radial; sc, scapula; sq, squamosal; sur, surangular; ti, tibia; u, ulna; v.sct, ventral scutes. Scale bar equals 1 cm.

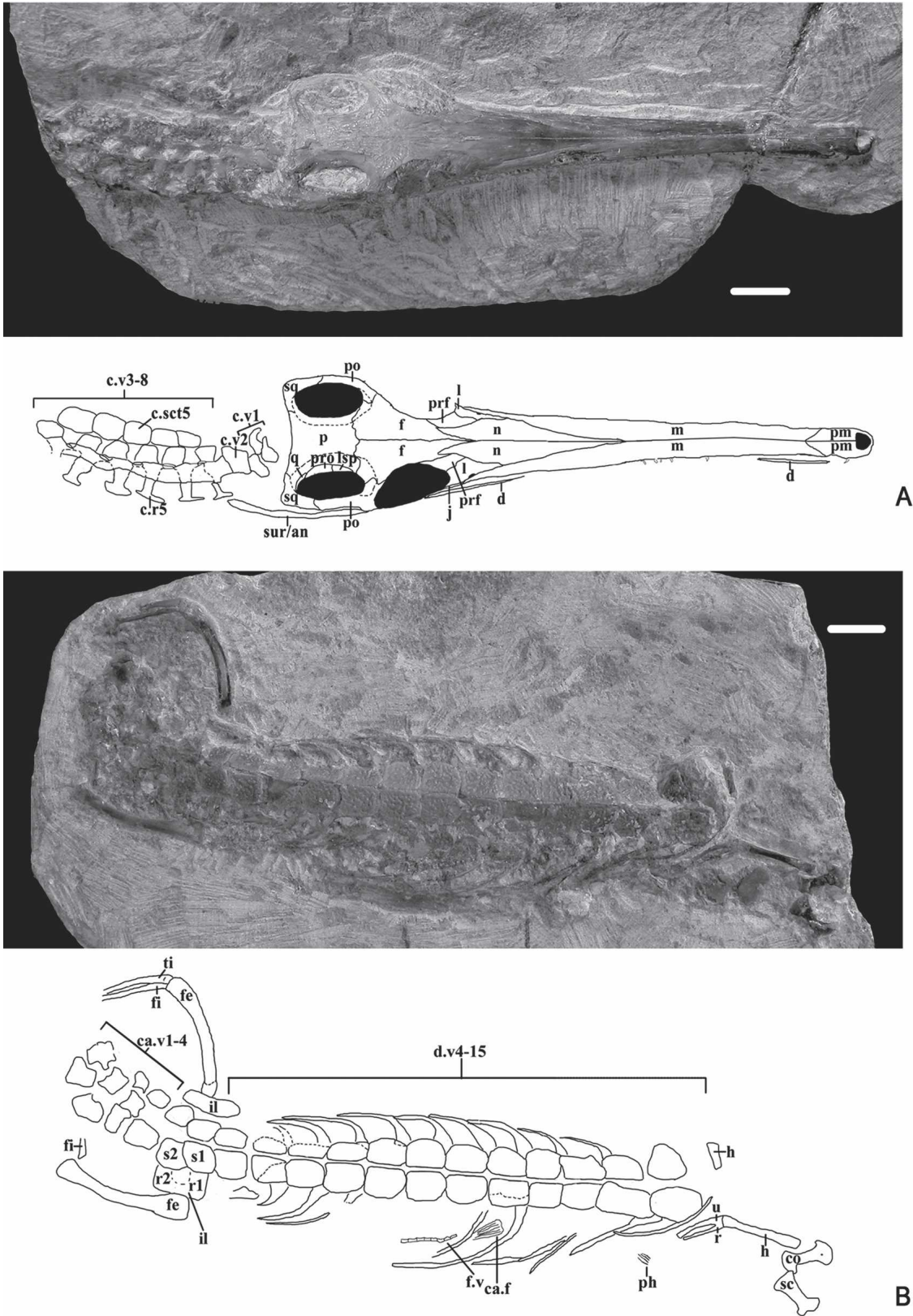


FIGURE 5. *Pelagosaurus typus* (M1418) from the Toarcian of Somerset, England; articulated juvenile. **A**, photograph and interpretive drawing of the skull and cervical vertebrae and ribs; **B**, photograph and interpretive drawing of the dorsal postcranial anatomy including the limbs. **Abbreviations:** an, angular; c.sct5, cervical scute five; c.r5, cervical rib five; ca.f, *Leptolepis* caudal fin; ca.v1-4, caudal vertebrae and scutes one to four; co, coracoid; d, dentary; d.v4-15, dorsal vertebrae, ribs and scutes four to fifteen; f, frontal; fe, femur; fi, fibula; f.v, *Leptolepis* dorsal vertebrae; h, humerus; il, ilium; j, jugal; l, lachrymal; lsp, laterosphenoid; m, maxilla; n, nasal; ph, phalanges; pm, premaxilla; p, parietal; po, postorbital; prf, prefrontal; pro, prootic; q, quadrate; r, radius; r1-r2, sacral ribs one and two; s1-s2, sacral vertebral scutes one and two; sc, scapula; sq, squamosal; sur, surangular; ti, tibia; u, ulna. Scale bar equals 1 cm.

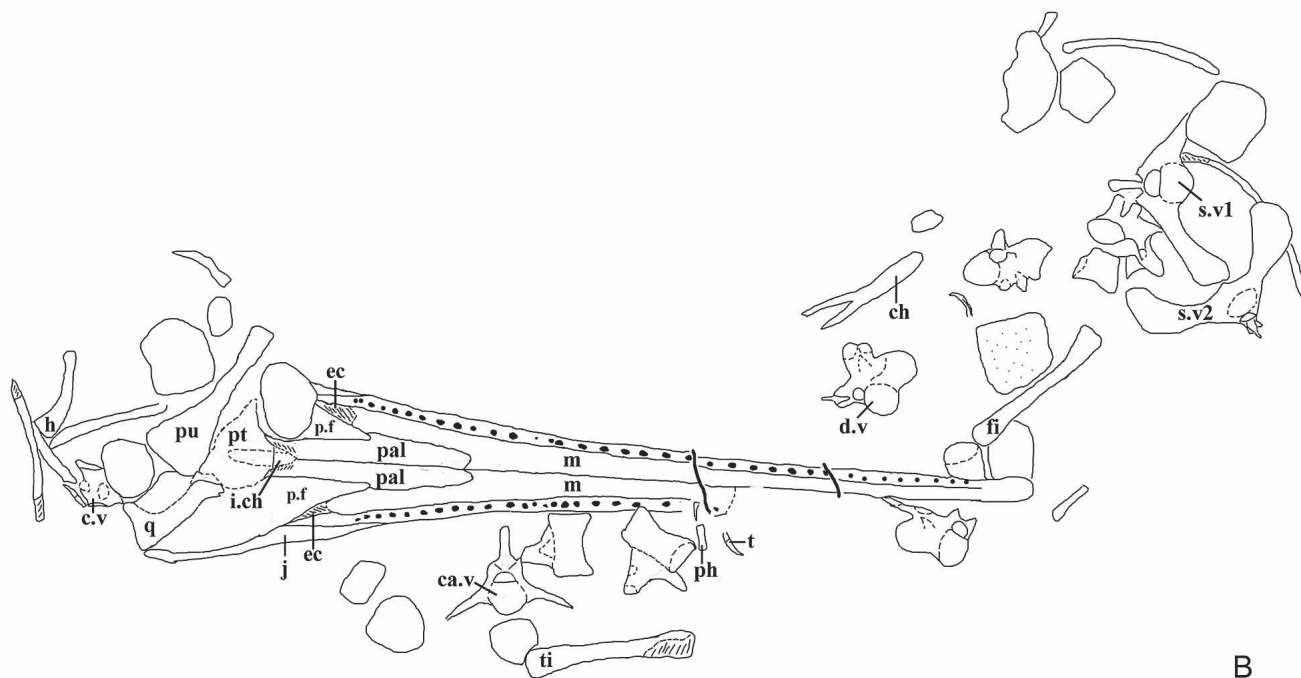


FIGURE 6. *Pelagosaurus typus* (M1420) from the Toarcian of Somerset, England; photograph and interpretive drawing of the skull in ventral view with associated postcranial elements. **Abbreviations:** *ca.v*, caudal vertebra; *ch*, chevron; *c.v*, cervical vertebra; *d.v*, dorsal vertebra; *ec*, ectopterygoid; *h*, humerus; *i.ch*, internal choanae; *j*, jugal; *fi*, fibula; *m*, maxilla; *pal*, palatine; *p.f*, suborbital fenestra; *ph*, phalanx; *pt*, pterygoid; *pu*, pubis; *q*, quadrate; *s.v1*, sacral vertebra one; *s.v2*, sacral vertebra two; *t*, tooth; *ti*, tibia. Scale bar equals 1 cm.

broadens, becomes sculptured, and forms the anteroventral border of the orbit.

**Prefrontal**—The prefrontal is crescent-shaped, broadening posteriorly (Figs. 3A, B; 4, 5A). The narrow anterior tip is partly surrounded by the nasal bone, while the broad posterior edge forms the anterodorsal margin of the orbit. The dorsal margin is convex and lined by the nasal anteriorly and the frontal posteriorly; conversely, the ventral margin is concave and sutured to

the lachrymal. Sculpturing is evident and increases in intensity around the orbit. The prefrontal is large, but not a prominent element in proportion to other cranial bones.

**Jugal**—The jugal is slender, long, and straight (Figs. 3B, 4). It progresses up the posterodorsal margin of the maxilla for a short distance, terminating just posterior to the antorbital fenestra. The jugal forms the ventral border of the orbit and the ventral portion of the infratemporal fenestra. About half way down its

extent, the jugal sends a short, laminar ascending (postorbital) process posterodorsally; this process runs medial to the descending (jugal) process of the postorbital and forms a convex-concave suture with this bone. The jugal ceases just prior to the most posterior tip of the infratemporal fenestra in an oblique suture with the quadratojugal.

**Frontal**—The frontal is broad and paired in both the juvenile and adult forms. It forms a rectangular plate with four radiating processes (Figs. 3A, 4, 5A). The anterior (nasal) process stretches deep between and beneath the nasal bones. The posterior (parietal) process forms the anterior portion of the parietal crest, meeting the parietal in a V-shaped suture, the apex of which points anteriorly; this suture continues on to the medial surface of the supratemporal fenestra. The two lateral (postorbital) processes form the posterodorsal border of the orbit and contact the postorbital bone in an irregular suture. There is a broad interorbital space, as the orbits are situated laterally on the skull. The frontal forms more than one half the skull roof, is highly sculptured, and borders the dorsal part of the orbit as well as the anteromedial component of the supratemporal fenestra.

**Parietal**—The sculptured parietal is an unpaired, highly constricted tri-radiate bone (Figs. 3A, B; 5A). The anterior (frontal) process forms a long and narrow parietal crest that stretches between the supratemporal fenestrae. The two lateral (squamosal) processes are slender and frame the posteromedial portion of the supratemporal fenestrae; posteriorly, they suture to the underlying supraoccipital and exoccipitals, preventing the supraoccipital from contributing to the dorsal skull roof. Additionally, the lateral processes contact the squamosal in a simple anteriorly-posteriorly directed suture. Within the supratemporal fenestra, the parietal defines the dorsomedial rim, contacting the laterosphenoid, prootic, and quadrate along its ventral margin and the squamosal at its posterior extent. There is no evidence of a posttemporal fenestra.

**Postorbital**—The postorbital is a sculptured tri-radiate bone; it forms the posterior border of the orbit, the anterolateral margin of the supratemporal fenestra, and the anterodorsal margin of the infratemporal fenestra (Figs. 3A, B; 4, 5A). Its ascending (frontal) process meets the frontal in an irregular anteriorly-posteriorly directed suture, while the descending (jugular) process articulates with the jugal in a convex-concave suture. The postorbital 'bar' is composed almost entirely of the postorbital bone in lateral aspect with very little contribution from the jugal. It is laminar and wide anteroposteriorly. The posterior (squamosal) process forms approximately two thirds of the supratemporal bar and tapers posteriorly to meet the squamosal in an oblique suture.

**Squamosal**—The sculptured squamosal forms a constricted arch at the back of the skull (Figs. 3A, B; 4, 5A). It borders the posterolateral portion of the supratemporal fenestra, but is excluded from the infratemporal fenestra by the quadratojugal. The anterior (postorbital) process of the squamosal forms one third of the supratemporal bar and contacts the postorbital in an oblique suture. The medial (parietal) process is short, narrow, and contacts the parietal in a simple anteriorly-posteriorly directed suture. A very small posterolateral process is present which extends above the paroccipital process. The squamosal contacts the quadrate on its posteroventral surface and ventrally within the supratemporal fenestra.

**Quadratojugal**—The quadratojugal is a small splint of bone, which is situated in an inclined plane (Fig. 3B). It forms the posterodorsal portion of the infratemporal fenestra. Dorsally, it contacts the squamosal in a long, straight suture and terminates at the postorbital/squamosal junction. Ventrally, the quadratojugal meets the jugal in an oblique suture. The medial side of the quadratojugal is sutured to the quadrate. There is no anterior process projecting into the infratemporal fenestra.

**Quadrate**—The quadrate is inclined anteriorly, displacing the mandibular condyle slightly beyond the level of the occipital condyle (Figs. 3B, C). It is not deflected laterally and therefore does not form a lateral shelf beneath the squamosal. The anterior surface lies in tight contact with the squamosal and prootic within the supratemporal fenestra. Posteriorly, the quadrate is sutured to the ventral surface of the exoccipital. Laterally, the quadrate contacts the quadratojugal and the posterior tip of the jugal. The dorsal surface is in intimate contact with the paroccipital process of the exoccipital. The mandibular condyle of the quadrate faces posteriorly and has a medial indentation.

**Supraoccipital**—The supraoccipital is a small, triangular wedge of bone (Figs. 3A, C). It is surrounded by the exoccipitals ventrally and the parietal dorsally, and does not contribute to the dorsal skull roof or the foramen magnum. No evidence of a posttemporal fenestra can be observed between the supraoccipital and the parietal.

**Exoccipital**—The exoccipitals are sutured together above the foramen magnum, excluding the supraoccipital from that opening (Figs. 3A, C). The paraoccipital processes are long, thin plates that have become deflected into the horizontal plane; this rotation causes the ventral margin to form a prominent ridge that overhangs the quadrate. A significant gap exists between the paraoccipital process and the quadrate. The ventral margin is sutured to the dorsal surface of the quadrate at the level of the basal tubera. The exoccipitals meet the basioccipital in an oblique suture on the ventrolateral margin of the foramen magnum. A small circular opening for cranial nerve XII is visible lateral and ventral to the foramen magnum; below that, a large oval opening for the internal carotid foramen is present.

**Basioccipital**—The basioccipital forms the ventral margin of the foramen magnum (Figs. 3A, C). The occipital condyle is large, somewhat square in outline, and deflected ventrally. Laterally, there are two large basal tubera that hang below the level of the occipital condyle and the palatal complex.

**Laterosphenoid/Prootic**—The laterosphenoid and prootic border the ventral margin of the medial portion of the supratemporal fenestra (Figs. 3A, B, 5A). They are sutured to the parietal above. The anterior end of the laterosphenoid contacts the frontal, while the posterior end of the prootic lies above the quadrate. The laterosphenoid and prootic contact each other in a vertical suture.

**Palatine**—The paired palatines are rectangular in shape (Fig. 6). They are sutured to one another along the midline except at their most anterior and posterior ends. The free anterior tips are smooth and rounded and separated by the mid-sagittal (palatine) process of the maxillae. At the posterior end, the ventral surface of the palatines diverge and form a V-shape with the apex pointed anteriorly while the dorsal surface remains in contact down the midline; the dorsal surface contacts the pterygoid in a straight horizontal suture within the depression of the internal choanae, and a choanal septum is present. The palatines are widest at their midpoint where they surround the anterior tips of the suborbital fenestrae. They also form the medial margins of the suborbital fenestrae. The exit for the internal choanae begins where the palatine posterior ends diverge. The internal choana sits in a shallow depression between the junction of the palatine and pterygoid.

**Pterygoid**—The pterygoid is a tri-radiate, single element (Fig. 6). It is exceedingly small and does not exhibit lateral descending flanges. The pterygoid contacts the palatines in a horizontal suture in the centre of the internal choana depression and contributes to the choanal septum. The majority of the anterior end is bowl-shaped and forms the posterior aspect of the internal choana depression. The transverse process is very small and has been broken away on each side; however, it would have contacted the ectopterygoid on its anterolateral edge. The posterior

extent is not preserved, but would most likely have been short, contacting the basisphenoid in a horizontal suture.

**Ectopterygoid**—The ectopterygoids are broken away; however, remnants of the anterior sutures with the maxillae are still evident (Fig. 6). The anterior (maxillary) process is fairly large and triangular in shape. It attaches to the posterior, edentulous portion of the maxilla. Additionally, the ectopterygoid forms the posterolateral margin of the palatal fenestra.

**Vomer**—The vomer is not visible on the palatal surface and therefore does not appear to contribute to the secondary palate (Fig. 6).

**Dentary**—The dentary bone is elongate and forms the majority of the mandibular complex (Figs. 3B, 4). Its dorsoventral profile is extremely shallow, more so than the opposing snout. The dorsal margin is straight except for the anterior tip where there exists a convex peak incorporating the third and fourth tooth; this convexity on the dentary inserts into the opposing concavity on the premaxilla/maxilla above and gives the appearance that the anterior teeth fan out anteroventrally. The mandibular symphysis terminates approximately three fourths down its length, with each dentary bone diverging from one another at a 45-degree angle. As the dentition ceases, the dentary becomes surrounded by the surangular above and the angular below, both sutures being straight and horizontal. The posterior extent of the dentary contributes to the anterior border of the elongate, sub-oval mandibular fenestra. There appear to be at least 36 alveoli. The teeth vary in size, but generally decrease in size posteriorly and become very small at the back of the dentary; additionally, the teeth are widely spaced anteriorly and become closely packed further back.

**Surangular**—The surangular is a long, thin element that forms the dorsal and posterior margin of the mandibular fenestra (Figs. 3B, 4). Anteriorly, the surangular tapers and terminates on the dorsal surface of the dentary just prior to the last visible tooth. Behind the mandibular fenestra, the surangular contacts the angular in an undulating suture. At the articular fossa, the surangular meets the articular and becomes marginally deflected dorsally, forming the dorsolateral portion of the short retroarticular process. The dorsal edge and its contact with the coronoid cannot be determined, as it is not exposed on any of the specimens. The surangular is sculptured at its posterior end.

**Angular**—The angular is a long, thin element that forms the ventral margin of the mandibular fenestra (Figs. 3B, 4). Anteriorly, it thins and sutures to the ventral edge of the dentary bone, terminating at the level of the lachrymal-maxilla-nasal junction. Just posterior to the mandibular fossa, the angular widens briefly. At the level of the articular fossa, the angular curves gently in a dorsal arch and forms the ventrolateral and posterior portion of the short retroarticular process. The angular is sculptured at its posterior end.

**Articular**—The articular extends posteriorly in a long, broad retroarticular process (Figs. 3A–C). The process curves gently dorsally and has a mid-sagittal ridge that separates two shallow concave grooves from one another. The articular fossa faces anterodorsally; it has a medial prominence that divides the fossa into a lateral and medial concavity for reception of the quadrate. A large transverse crest separates the articular fossa from the retroarticular process. The medial surface cannot be discerned.

**Splenial**—The splenials are not observable on any of the specimens, as the matrix in this area has not been removed.

### Postcranium

The postcranial skeleton is long and gracile (Fig. 7). The overall characteristics of the vertebrae, ribs and limbs are 'conservative,' and reflect the plesiomorphic character states found among most basal mesoeucrocodylians. A single row of dermal scutes runs along each side of the dorsal vertebral column; they increase

in size toward the sacrum and then decrease in size along the tail. A dermal ventral shield sits along the sternum and is composed of an array of scutes. All the centra are amphicoelous. The forelimbs are less than two thirds the length of the hindlimbs.

**Cervical Vertebrae and Ribs**—There are nine cervical vertebrae (Figs. 4, 5A). The centra are hourglass-shaped and amphicoelous, being slightly concave both anteriorly and posteriorly. The neural spine is square to triangular in outline and low as compared to the dorsal vertebrae. On each side of the ventral surface of the centrum, near the anterior end, is a small facet to which the lower branch of the cervical rib attaches; on the anterior end of the neural arch is a short, blunt transverse process for the reception of the upper branch of the cervical rib. There appears to be a slight ventral swelling in the hypapophysis area. Both the pre- and postzygapophyses are angled at 45 degrees. The atlas-axis complex is not well preserved; however, the lateral process of the atlas is long and the axis is larger than the third cervical vertebra. The first and second ribs are long and bear one articulation surface. The remaining ribs are T-shaped and bear two articulation surfaces.

**Dorsal Vertebrae and Ribs**—There are 15 dorsal vertebrae (Figs. 4, 5A, 8B). The centra are hourglass-shaped and amphicoelous. The length of the centrum increases slightly posteriorly. The neural spine is triangular, but somewhat longer and taller than cervicals and the angle of pre- and postzygapophyses approach vertical. The transverse processes are long, horizontal and broad anteroposteriorly; they contain two rib articulation surfaces. The anterior articulation is shorter and contacts the head of the rib while the posterior one is much longer to contact the tubercle of the rib. The ribs curve posteroventrally. The length and thickness of the ribs increases posteriorly, with numbers 13–15 decreasing in size. The number of ribs contacting the sternum cannot be observed.

**Sacral Vertebrae and Ribs**—There are two sacral vertebrae, with the second slightly bigger than the first (Figs. 5B, 6, 8B). The centra are hourglass-shaped and amphicoelous. The neural spine is long and low. The ribs curve strongly ventrally, hanging below the level of the centrum. The second rib is thicker than the first and is more expanded at its lateral end. There is an oval gap between the ribs.

**Caudal Vertebrae and Ribs**—The exact number of caudal vertebrae cannot be determined; however, it can be assumed that there were at least 15 as the tail would have been longer than the dorsal body. The centra are hourglass-shaped and amphicoelous and the neural spine is rectangular in outline (Figs. 5B, 6, 8B). The transverse processes are long and narrow anteroposteriorly; they end in a rounded tip and deflect ventrally below the level of the centrum. The pre- and postzygapophyses approach vertical. Cheverons are present and display the typical Y-shape.

**Scapula/Coracoid**—The scapula is a flat, paddle-shaped element (Figs. 4, 5B). The distal end is slightly expanded, flat and plate-like while the proximal end is thicker and bifurcated to incorporate the notch-like glenoid fossa. The proximal contact with the coracoid is extensive and is deflected somewhat anterodorsally. The coracoid is elongate, plate-like, and hourglass-shaped, being expanded at both ends. Both the proximal and distal expansions are of similar size and form a rounded convex outline. There is a small coracoid foramen on the proximal end in the center of the expansion.

**Humerus/Radius/Ulna**—The humerus is long and slender and more or less straight (Figs. 4, 5B, 8A). The proximal articulation is larger than the distal and incorporates a large delto-pectoral crest. The ulna is slightly longer and thicker than the radius and forms the greater part of the elbow and wrist joint. It is somewhat curved. The proximal articulation is larger than the distal articulation. The radius has a straight cylindrical shaft. Both the proximal and distal articulations are of similar size.

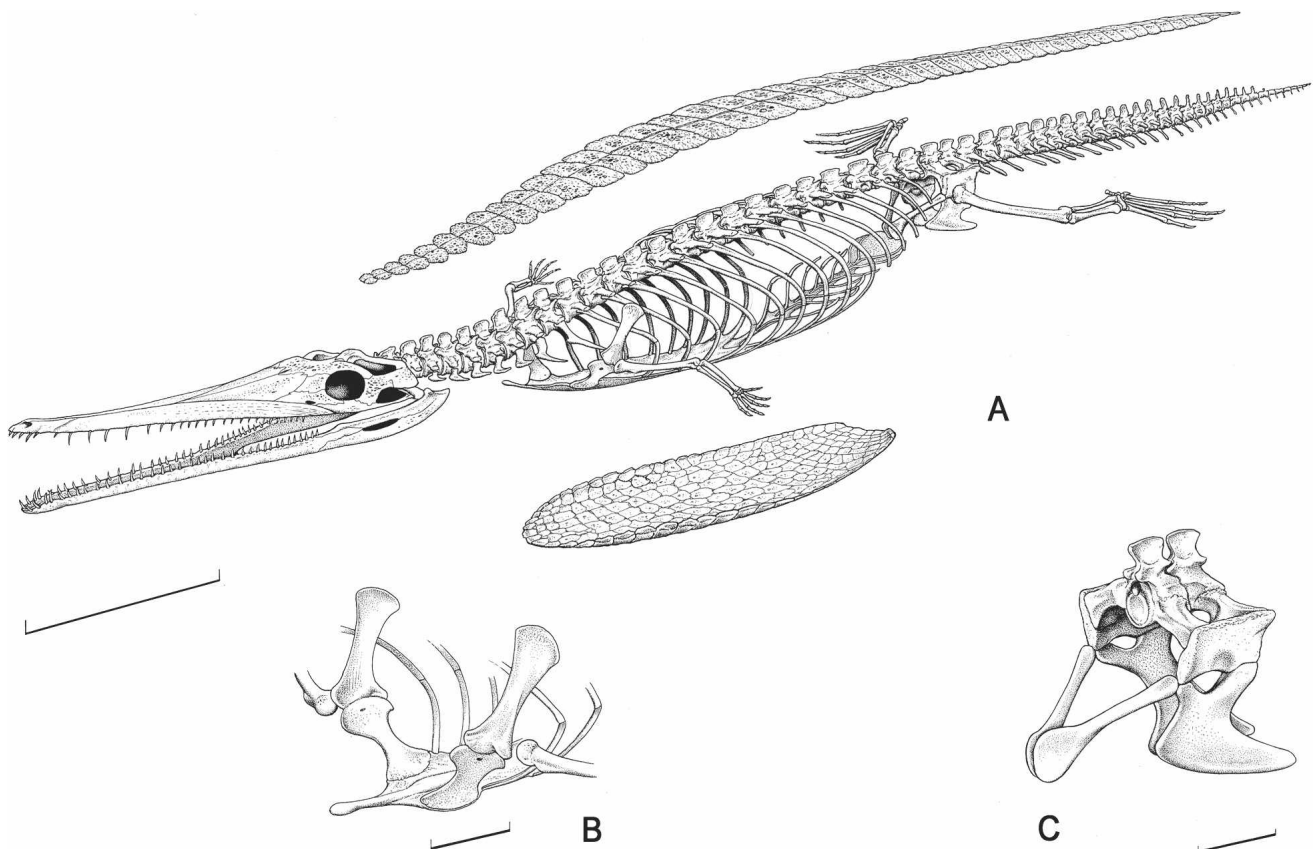


FIGURE 7. Reconstruction of the postcranial anatomy in *Pelagosaurus typus* from the Toarcian of Somerset, England, with special reference to the pectoral and pelvic girdles. **A**, articulated skull and postcranial skeleton (Scale bar equals 10 cm); **B**, pectoral girdle (Scale bar equals 3 cm); **C**, pelvic girdle (Scale bar equals 3 cm). (Drawing by ©John Sibbick).

**Ilium/Pubis/Ischium**—The ilium is a square element with a shallow acetabular depression on its lateral surface (Figs. 4, 5B, 8). The dorsal edge is smooth and fairly straight; the anterior end is rounded while the posterior end projects caudally in a small pointed process. The ventral edge has a W-shaped outline with the pubis connecting anteriorly and the ischium posteriorly. There is a small central notch that forms the dorsal rim of the acetabular foramen. The pubis is long and plate-like. The proximal end is slender and rod-like, while the distal end is greatly expanded and straight along its ventral rim. The ischium is triangular in outline. The proximal end is thick, narrow and circular in cross-sectional view; there is a central notch that forms the ventral border of the small acetabular foramen and separates the proximal end into two processes. The anterior process is much smaller than the posterior process, causing the foramen to sit anteriorly. The distal portion of the ischium fans out and is plate-like. The anterior edge is short and rounded while the posterior edge is long and stretches out caudally.

**Femur/Tibia/Fibula**—The femur is a typical sigmoid shape (Figs. 4, 5B, 6, 8A). It is thicker and significantly longer than the humerus. The proximal articular end is expanded and semi-elliptical; it narrows posteriorly and forms a large trochantral ridge, which runs one third down the shaft. The distal articular end is not preserved. The tibia is somewhat longer and thicker than the fibula. The shaft of the tibia is very slightly sigmoid in outline. Its proximal end forms the majority of the knee joint. The fibula is more or less straight and its articular ends are of similar size.

**Carpals/Tarsals**—The carpals and tarsals are not observed on any of the specimens.

**Metacarpal/Metatarsal/Phalanges**—All the metacarpals, metatarsals, and phalanges are long and slender (Fig. 8A). Due to disarticulation, their relationships to one another cannot be determined.

**Osteoderms**—A row of dorsal osteoderms sits on either side of the vertebral column (Figs. 4, 5, 7A). They increase in size towards the sacrum and then decrease in size down the tail. The osteoderms are situated between the neural spines. The posterior margins overlap the anterior margins of each subsequent osteoderm. The medial margin is straight and the lateral margin is rounded. They are subrectangular in shape and display a honeycomb pattern, but have no dorsal keel. The actual arrangement of the osteoderms on the ventral surface is not ascertainable; however, they most likely would have created a shield that stretched across the sternum.

## DISCUSSION

### Paleoenvironment

During the Lower Jurassic, shallow epicontinental seas spilled out of the Tethys and Proto-Atlantic and spread across England. These extensive shallow waters, which supported a rich diversity of marine life, stimulated crocodyliforms to invade the sea and exploit this new ecological niche. The paleogeographic map of the Lower Jurassic (Smith et al., 1973) shows that Somerset, England was at about 26 degrees north of the paleo-equator and was surrounded on all sides, apart from the south-east, by a continental land mass. Somerset was, therefore, in or near the tropics; daytime water temperatures, especially in shallower wa-

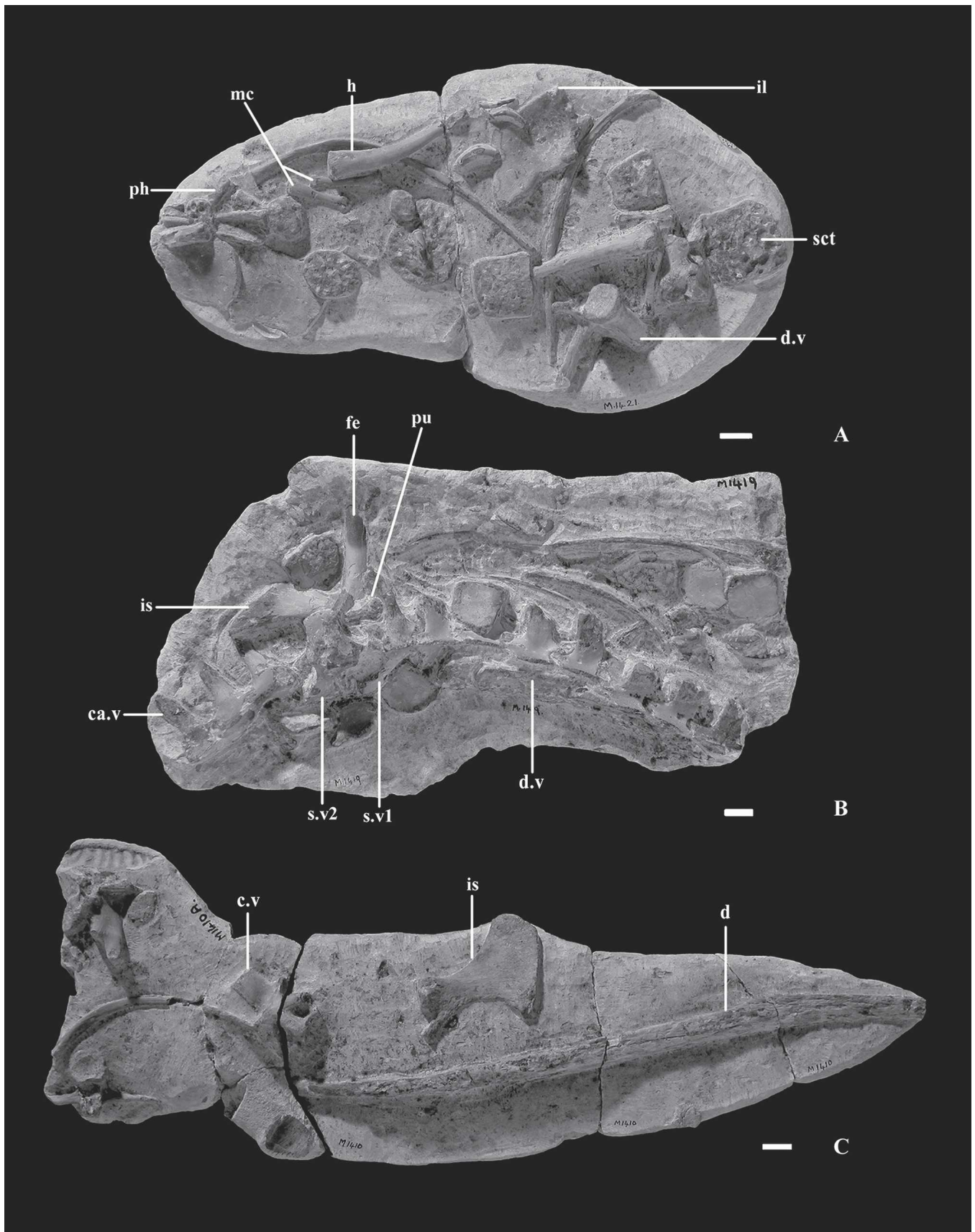


FIGURE 8. Postcranial remains of *Pelagosaurus typus* from the Toarcian of Somerset, England, highlighting the pelvic girdle elements. **A**, limestone nodule M1421; **B**, limestone nodule M1419; **C**, limestone nodule M1410. **Abbreviations:** **c.v**, cervical vertebra; **ca.v**, caudal vertebra; **d**, dentary; **d.v**, dorsal vertebra; **fe**, femur; **h**, humerus; **il**, ilium; **is**, ischium; **mc**, metacarpals; **ph**, phalanx; **pu**, pubis; **sct**, scute; **s.v1**, sacral vertebra one; **s.v2**, sacral vertebra two. Scale bar equals 1 cm.

ter, would thus have been high. A modern analogue is the Persian Gulf, which currently lies between 24 and 26 degrees north of the equator, as Somerset did 200 Ma ago. Additionally, the surrounding land mass of the Persian Gulf is arranged similarly, with access to the major seaway to the south-east (Bennett, 1987).

### Paleobiology

*Pelagosaurus* lived and foraged within the shallow warm waters of the Toarcian. Although it would have emerged from the water to lay eggs and to rest, the majority of time would have been spent in the water (Fig. 9). The rigid body of *Pelagosaurus*, with its array of dorsal and ventral osteoderms, is similar to that of teleosaurids and modern crocodilians and, therefore, would have supported an axial subundulatory mode of swimming (Massare, 1988); however, the more gracile and streamlined body form of *Pelagosaurus* would have provided greater agility in the water column as compared to its lumbering relatives. Although the maximum sustained swimming speed is consistent with a slow sustained swimmer rather than a high-speed pursuit predator (according to Massare, 1988), the presence of large laterally placed eyes and a long, thin, gracile body are reminiscent of a pursuit predator, rather than a predator that sits and waits at the water surface. Accordingly, *Pelagosaurus* probably fed by slowly stalking its prey, then attacking with a fast sideways sweep of the head, and capturing a fish or other food item on the many small piercing teeth within its elongate jaws.

The diet of *Pelagosaurus* probably consisted of small fishes, crustaceans and possibly insects. All of these animals are common in Toarcian rocks and are found in close association with the *Pelagosaurus* material from Ilminster. Predation on the small-bodied fish *Leptolepis* is evident, as a small juvenile *Pelagosaurus* contains a specimen, which includes a vertebral column and caudal fin, within its rib cage (Fig. 5B). The diet of gharials, modern long snouted-crocodilians, is comparable. Young gharials prey primarily on small invertebrates, like insects and larvae

and also small frogs, while the mature adults feed almost solely on fish. Their skull anatomy is ideally suited for this diet as their characteristic long thin snouts afford less resistance than broad-snouted forms in the water. As such, gharials, and in turn *Pelagosaurus*, are able to make fast sweeping motions with their heads in order to snap up fish within the water column (Cogger and Zweifel, 2003).

### Phylogenetic Relationship

The phylogenetic affinity of *Pelagosaurus* has been in a state of confusion ever since its first discovery. Originally, it was thought to belong to the Family Teleosauridae based on overall anatomical similarities to *Teleosaurus* (Eudes-Deslongchamps, 1863, 1877) and its Toarcian age. Westphal (1961, 1962) maintained a teleosaurid classification after analyzing the taxonomy of Upper Lias marine crocodyliforms and Duffin (1979b), in his description of the juvenile specimen from the Moore Collection, also allocated *Pelagosaurus* to the Family Teleosauridae. Mercier (1933) proposed an alternate interpretation by placing *Pelagosaurus* in the Family Metriorhynchidae. Buffetaut (1980, 1982) and Vignaud (1995) supported this hypothesis by considering *Pelagosaurus* to be a primitive metriorhynchid and extending the origin of the family back into the Toarcian. Modern cladistic studies offer yet a third proposition, with *Pelagosaurus* falling out as the sister group to both the Teleosauridae and the Metriorhynchidae (Benton and Clark, 1988; Clark, 1994; Buckley et al., 2000; Wu et al., 2001; Tykoski et al., 2002; Pol, 2003).

Buffetaut's (1980, 1982) argument for a metriorhynchid affinity of *Pelagosaurus* is based on its broad nasals, large frontals, lateral orbits, sclerotic rings, and a similar arrangement of the prefrontal-lachrymal when compared to the metriorhynchid *Teleidosaurus*. We disagree with this view. Although the nasals in *Pelagosaurus* are relatively broad with respect to overall skull proportions, they are by no means as large as those in the metriorhynchids. The nasals of metriorhynchids are so broad that they form most of the dorsal aspect of the snout, with little

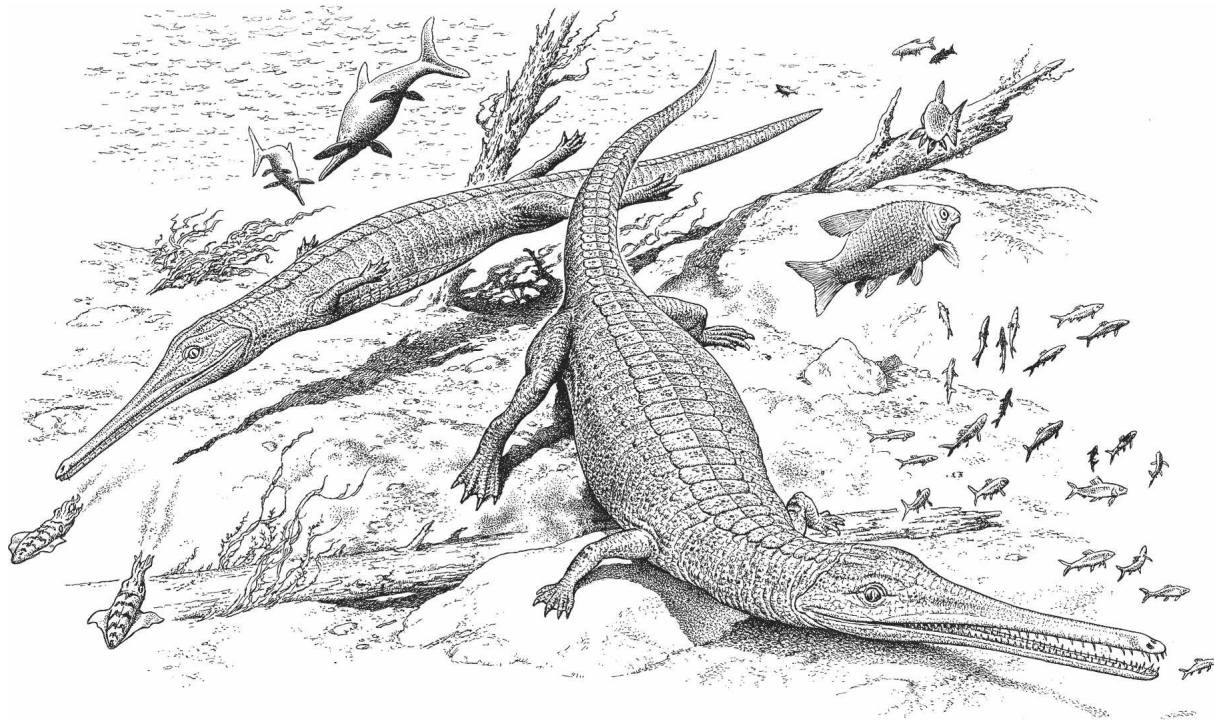


FIGURE 9. Flesh reconstruction of *Pelagosaurus typus*. Copyrighted drawing by John Sibbick.

contribution from the maxillae and no contribution from the lachrymals. In *Pelagosaurus*, the nasals, maxillae and the lachrymals form the dorsal surface of the snout, very much as in teleosaurids. The frontal bone is moderately larger in *Pelagosaurus* than in teleosaurids; this seems to be a function of the more laterally situated orbits and the reduced posterior aspect of the skull. However, the frontal in *Pelagosaurus* does not contain the marked supraorbital lateral constriction seen in metriorhynchids. The orbits are confined to the lateral aspect of the skull in *Pelagosaurus* and metriorhynchids by the larger frontal and the vertical orientation of the jugal, which becomes splayed in teleosaurids; however, the orbits in metriorhynchids are also restricted by the greatly enlarged prefrontal bones. The presence of sclerotic rings in *Pelagosaurus* is debatable, as none of the specimens in the Moore Collection or in Eudes-Deslongchamps (1863; 1877) descriptions show them. Finally, while *Pelagosaurus* and *Teleidosaurus* appear very similar in the prefrontal-lachrymal area, the phylogenetic position of *Teleidosaurus* as a metriorhynchid remains suspect (Steel, 1973).

Thus, we question Buffetaut's (1980, 1982) proposed metriorhynchid features of *Pelagosaurus*. Moreover, *Pelagosaurus* does not encompass the most conspicuous metriorhynchid apomorphies such as three premaxillary teeth, extreme enlargement of the prefrontals, absence of the mandibular fenestrae, lack of dermal armor, and bent caudal vertebrae that create a tail fin. With all of this taken into account it could appear that *Pelagosaurus* is more closely allied to the Teleosauridae than the Metriorhynchidae. *Pelagosaurus* has the majority of teleosaurid features, including four–five premaxillary teeth, small prefrontal, lachrymal visible in dorsal aspect, presence of the mandibular fenestrae, dermal armor, and a straight tail. However, all of these characteristics are plesiomorphic for the Crocodyliformes and therefore are not phylogenetically informative. Consequently, the teleosaurid affinity of *Pelagosaurus* is not currently supported by any apomorphic features.

A modern cladistic hypothesis (based on Clark, 1994) recovers three characters in support of *Pelagosaurus* (P) as the sister group to the two main thalattosuchian families Teleosauridae (T) and Metriorhynchidae (M): external surface of cranial and mandibular bones smooth (T&M) or heavily ornamented, with deep grooves and pits (P); parietal with broad, sculpted region separating fossae (P) or with a sagittal crest (T&M); and anterior and posterior scapular edges symmetrical in lateral view (T&M) or anterior edge more strongly concave than posterior edge (P). Further examination of the character matrix reveals five additional characters that vary among *Pelagosaurus*, Teleosauridae, and Metriorhynchidae: postorbital medial to jugal (T) or lateral to jugal (P&M); frontal narrow between orbits, similar to nasal breadth (T) or broad, about twice nasal breadth (P&M); frontal paired (P) or fused (T&M); cranial nerves IX–XI pass through common large foramen vagi in otoccipital (P) or cranial nerve IX passes medial to nerves X and XI in separate passages (T&M); and mandibular fenestra present (P&T) or absent (M).

A critical examination of these characters alongside the fossil material from this study, the Leeds Collection at the British Museum of Natural History, and the literature, shows that most of these characters are either too simplistic or inaccurate. If present, cranial sculpturing in teleosaurids appears mainly on the frontal bone (Antunes, 1967; Godefroit et al., 1995; Walkden et al., 1987) and in metriorhynchids, such as *Metriorhynchus superciliosus*, appears on the prefrontal, frontal, parietal and the temporal arcade (Andrews, 1913); however, some metriorhynchids like *Geosaurus araucanensis* (Gasparini and Dellapé, 1976) are almost devoid of cranial sculpturing. *Pelagosaurus*, on the other hand, has sculpturing on almost the entire skull and mandible, with extensive sculpturing on the prefrontal, lachrymal, frontal, parietal, temporal arcade and the posterior extent of the mandible.

Scoring the parietal of *Pelagosaurus* as broad instead of forming a sagittal crest is incorrect. The sagittal crest in teleosaurids is usually a very thin ridge, with the frontal and parietal being of similar width (Andrews, 1913; Antunes, 1967). That of metriorhynchids is broader, flatter, and sometimes sculpted, with the frontal portion of the crest wider than the parietal portion (Andrews, 1913; Gasparini and Dellapé, 1976; Gasparini and Díaz, 1977). The parietal area of an adult *Pelagosaurus* can be considered to be somewhat intermediate between these two conditions; the parietal and frontal are of similar width as in teleosaurids, but appear to be more broad, flat, and sculpted as in metriorhynchids. Alternatively, the parietal of a juvenile *Pelagosaurus* is a very broad and flat plate. Therefore, with respect to Clark's (1994) character states, the parietal area in *Pelagosaurus* should either be considered a sagittal crest or both a sagittal crest and a broad plate if ontogeny is considered.

The overall form of the scapula in *Pelagosaurus* is very similar to that seen in metriorhynchids (Mateer, 1974), being symmetrical and somewhat flat and paddle-shaped. On the other hand, the scapula in teleosaurids is asymmetrical, being greatly expanded only on one side of the distal end (Mateer, 1974). Additionally, the postorbital in teleosaurids does not sit medial to the jugal (Antunes, 1967). In fact, the ascending process of the jugal is very small in teleosaurids and is overlapped by the large postorbital bone, which stretches along the entire posterior border of the orbit (pers. obs.). Hence, both the scapula and postorbital characters appear to have been coded incorrectly.

Finally, the character describing the width of the frontal is misleading. It is unclear whether or not the character refers to one nasal bone or both in combination; additionally, it is uncertain where the frontal is being measured (i.e., between the orbits or at the contact with the postorbital). If only one nasal bone is considered, the frontal of *Pelagosaurus* is considerably larger whether it is measured between the orbits or at the postorbital contact; however, if both nasals are assessed (at their widest point) they are of similar size to the frontal at the orbit, but only half the width at the postorbital contact. With reference to teleosaurids, the width of one nasal bone is half the size of the frontal at the orbit and at least one third the size at the postorbital contact while the width of both nasal bones is larger than the frontal at the orbit and about two thirds the size at the postorbital contact (Andrews, 1913; Godefroit et al., 1995; Walkden et al., 1987). Alternatively, in European metriorhynchids the width of one nasal bone is greater than the frontal at the orbit and half the width at the postorbital contact while the width of both nasal bones is twice the size of the frontal at the orbit and about the same size at the postorbital contact (Andrews, 1913; Wenz, 1968). As the frontal bone is relatively short in South American and Mexican metriorhynchids (Frey et al., 2002; Gasparini and Dellapé, 1976; Gasparini and Díaz, 1977) the width of the frontal at the orbits and at the postorbital contact is almost the same; so, the width of one nasal bone is half that of the frontal and the width of both nasal bones is about the same size. Therefore, the character describing the width of the frontal bone is confusing and does not reflect the differences observed among the Thalattosuchia.

Consequently, based on the information available, *Pelagosaurus* should be considered to belong to the Thalattosuchia incertae sedis until a more thorough investigation is conducted. What is ultimately needed is a detailed examination of the interrelationships of the Thalattosuchia by separating each family out into its component species and performing a comprehensive cladistic analysis. As past cladistic studies have only broken down the Thalattosuchia into its constituent groups, anatomical characteristics of the Teleosauridae and Metriorhynchidae have been grossly generalised and do not reflect the variability present. As such, it is necessary to survey all teleosaurid and metriorhynchid specimens in order to create an accurate, phylogenetically infor-

mative data matrix (see Gasparini et al., 2006). Considering the tentative position of thalattosuchians within the Mesoeucrocodylia (Antunes, 1967; Buffetaut, 1982; Benton and Clark, 1988; Wu et al., 1997, 2001; Buckley et al., 2000; Ortega et al., 2000; Sereno et al., 2001; Tykoski et al., 2002) and their affinity to other longirostrine crocodyliforms (Wu et al., 1997, 2001; Sereno et al., 2001; Brochu et al., 2002; Pol, 2003), an ingroup cladistic study will not only clarify the position of *Pelagosaurus*, but will also elucidate thalattosuchian hierarchical relationships while discovering synapomorphies that might be useful in resolving broader evolutionary uncertainties.

#### ACKNOWLEDGMENTS

We thank John Sibbick for his wonderful artwork, Matthew Williams and the BRLSI for lending us the specimens for this study, and Stéphane Jouve for supplying information from Paris. Our appreciation goes to Ryosuke Motani, Diego Pol, Stéphane Jouve, and an anonymous reviewer for their insightful comments on this manuscript. Additional recognition goes to Eric Buffetaut for help in compiling a library on crocodyliforms and to Chris Duffin for encouraging further study of the specimens. S.E. Pierce extends gratitude to the Overseas Research Scholarship, University of Bristol Postgraduate Scholarship, and the Natural Sciences and Engineering Council (NSERC) PGS D Scholarship for helping to fund this project.

#### LITERATURE CITED

- Andrews, C. W. 1913. A descriptive catalogue of the marine reptiles of the Oxford Clay, 2. British Museum (Natural History), London. 206 pp.
- Antunes, M. T. 1967. Um Mesosquiano do Liásico de Tomar (Portugal): Considerações sobre a origem dos crocodilos. *Servicos Geologicos de Portugal, Memoria* 13:1–66.
- Arkell, W. J. 1933. The Jurassic System in Great Britain. Oxford University Press, Oxford, 681 pp.
- Bennett, R. M. 1987. The palaeoenvironment and diagenesis of the Upper Lias cephalopod bed in S. E. Somerset. Ph.D thesis, University of Bristol, Bristol, England, 239 pp.
- Benton, M. J. and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia; pp. 295–338 in M.J. Benton (ed.), *The phylogeny and classification of the tetrapods, Vol. 1. Amphibians, Reptiles, Birds*. Systematic Association Special Volume 35A. Clarendon Press, Oxford.
- Benton, M. J. and M. A. Taylor. 1984. Marine reptiles from the Upper Lias (Lower Toarcian, Lower Jurassic) of the Yorkshire coast. *Proceedings of the Yorkshire Geological Society* 44:399–429.
- Brochu, C. A., M. L. Bouaré, F. Sissoko, E. M. Roberts, and M. A. O'Leary. 2002. A dyrosaurid crocodyliform braincase from Mali. *Journal of Paleontology* 76:1060–1071.
- Bronn, H. G. 1841. Über die fossilen Gaviale der Lias-Formation und der Oolithe. *Archiv für Naturgeschichte, Berlin* 8:77–82.
- Buckley, G. A., C. A. Brochu, D.W. Krause, and D. Pol. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature* 405:941–944.
- Buffetaut, E. 1980. Position systématique et phylogénétique du genre *Pelagosaurus* Bronn, 1841 (Crocodylia, Mesosuchia), du Toarcian d'Europe. *Geobios* 13:783–786.
- Buffetaut, E. 1982. Radiation évolutive, paléocécologie et biogéographie des crocodiliens méso-suchiens. *Mémoires de la Société Géologique de France* 42:1–88.
- Clark, J. M. 1994. Patterns of evolution in Mesozoic Crocodyliformes; pp. 84–97 in N.C. Fraser and H-D. Sues (eds.), *In the shadow of the dinosaurs: Early Mesozoic tetrapods*. Cambridge University Press, Cambridge and New York.
- Cogger, H., and R. Zweifel. 2003. *Encyclopedia of Reptiles & Amphibians: A comprehensive illustrated guide by international experts* (third edition). San Francisco, CA: Fog City Press.
- Cope, J. C. W., T. A. Getty, M. K. Howarth, N. Morton, and H. S. Torrens. 1980. A correlation of Jurassic rocks in the British Isles; Part One: Introduction and Lower Jurassic. *Geological Society, Special Report No.14*, 73 pp.
- Duffin, C. J. 1978. The Bath Geological Collections. The importance of certain vertebrate fossils collected by Charles Moore: an attempt at scientific perspective. *Geological Curators Group Newsletter* 2: 59–67.
- Duffin, C. J. 1979a. The Bath geological collections. The Moore collection of Upper Liassic crocodiles: A history. *Geological Curators Group Newsletter* 2:235–252.
- Duffin, C. J. 1979b. *Pelagosaurus* (Mesosuchia, Crocodylia) from the English Toarcian (Lower Jurassic). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1979:475–485.
- Eudes-Deslongchamps, J. A. E. 1863. Mémoire sur les Téléosauriens de l'époque Jurassique du Département de Calvados. *Mémoires de la Société Linnéenne de Normandie* 13:1–138.
- Eudes-Deslongchamps, E. E.1877. *Le Jura Normand*, 4. F. Savy (ed). Paris. 60 pp.
- Fara, E., M. Ouaja, E. Buffetaut, and D. Srafi. 2002. First occurrences of thalattosuchian crocodiles in the Middle and Upper Jurassic of Tunisia. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2002:465–476.
- Fraas, E. 1901. Die Meerkrokodile (Thalattosuchia n.g.), eine Sauriergruppe der Juraformation. *Jahreshefte des Vereins für vaterländische Naturkunde Württembergs*, 57:409–418.
- Frey, E., Buchy, M-C., Stinnesbeck, W., and J. G. López-Oliva. 2002. *Geosaurus vignaudi* n. sp. (Crocodyliformes: Thalattosuchia), first evidence of metriorhynchid crocodyliforms in the Late Jurassic (Tithonian) of central-east Mexico (State of Puebla). *Canadian Journal of Earth Sciences*, 39:1467–1483.
- Gasparini, Z. B. de, and D. Dellapé. 1976. Un nuevo cocodrilo marino (Thalattosuchia, Metriorhynchidae) de la formation Vaca Mueta (Jurásico, Tithoniano) de la Provincia de Neuquén (Republica Argentina). *Primer Congreso Geológico Chileno (2-7 Agosto 1976, Santiago)*, 1–21.
- Gasparini, Z. B. de, and G. C. Díaz. 1977. *Metriorhynchus casamiquelani* n. sp. (Crocodylia: Thalattosuchia), a marine crocodile from the Jurassic (Callovian) of Chile, South America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 153:341–360.
- Gasparini, Z. B. de, and M. A. Iturralde-Vinent. 2001. Metriorhynchid crocodiles (Crocodyliformes) from the Oxfordian of western Cuba. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 9: 534–542.
- Gasparini, Z. B. de, P. Vignaud, and G. Chong. 2000. The Jurassic Thalattosuchia (Crocodyliformes) of Chile: A palaeobiogeographic approach. *Bulletin de la Société Géologique de France*, 171:657–664.
- Gasparini, Z. B. de, M. Cichowolski, and D. G. Lazo. 2005. First record of *Metriorhynchus* (Reptilia: Crocodyliformes) in the Bathonian (Middle Jurassic) of the Eastern Pacific. *Journal of Paleontology*, 79:801–805.
- Gasparini, Z. B. de, D. Pol, and A. Spalletti. 2006. An unusual marine crocodyliform from the Jurassic-Cretaceous Boundary of Patagonia. *Science*, 311:70–73.
- Godefroit, P., P. Vignaud, and A. Lieger. 1995. Un Teleosauridae (Reptilia) du Bathonien Supérieur Lorrain (France). *Bulletin de la Société de Géologie*, 104:91–107.
- Hua, S., P. Vignaud, and V. Efimov. 1998. First record of Metriorhynchidae (Crocodylomorph, Mesosuchia) in the Upper Jurassic of Russia. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1998:475–484.
- Mateer, N. J. 1974. Three Mesozoic crocodiles in the collections of the Palaeontological Museum, Uppsala. *Bulletin of the Geological Institutions of the University of Uppsala, New Series*, 4:53–72.
- Massare, J. A. 1988. Swimming capabilities of Mesozoic marine reptiles: Implications for method of predation. *Paleobiology*, 14:187–205.
- Moore, C. 1852. On the palaeontology of the Middle and Upper Lias. *Proceedings of the Somersetshire Archaeological and Natural History Society* 3:61–76.
- Moore, C. 1866. On the Middle and Upper Lias of the South West of England. *Proceedings of the Somersetshire Archaeological and Natural History Society* 13:119–244.
- Moore, C. 1870. On a specimen of *Teleosaurus* from the Upper Lias. *Reports of the British Association for the Advancement of Science, Exeter*, 97pp.
- Moore, C. 1879. Excursion to Bath, Whit Monday, June 2<sup>nd</sup> and the following day. *Proceedings of the Geologists' Association* 6:196–201.
- Ortega, F., Z. Gasparini, A. D. Buscalioni, and J. O. Calvo. 2000. A new species of *Araripesuchus* (Crocodyliforma, Mesoeucrocodylia)

- from the Lower Cretaceous of Patagonia (Argentina). *Journal of Vertebrate Paleontology* 20:57–76.
- Pol, D. 2003. New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil. *Journal of Vertebrate Paleontology* 23:817–831.
- Sereno, P. C., H. C. E. Larsson, C. A. Sidor, and B. Gado. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science* 294:1516–1519.
- Smith, A. G., J. C. Briden, and G. E. Drewry. 1973. Phanerozoic World Maps, in *Organisms and Continents Through Time*. Special Papers in Palaeontology 12, Palaeontological Association, London, pp. 1–42.
- Steel, R. 1973. Crocodylia. *Handbuch der Paläoherpetologie* [Encyclopedia of Paleoherpertology] 16. Gustav Fischer Verlag, Stuttgart, Portland-USA, 116pp.
- Tykoski, R. S., T. B. Rowe, R. A. Ketcham, and M. W. Colbert. 2002. *Calsoyasuchus valliceps*, a new crocodyliform from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology* 22:593–611.
- Vignaud, P. 1995. Les Thalattosuchia, crocodiles marins du Mésozoïque: systématique, phylogénétique, paléoécologie, biochronologie et implications paléogéographiques. Ph.D. thesis, University of Poitiers, France.
- Vignaud, P., and Z. B. de Gasparini. 1995. New *Dakosaurus* (Crocodylomorpha, Thalattosuchia) in the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences de Paris, Série 2A*, 322:245–250.
- Walkden, G. M., N. C. Fraser, and J. Muir. 1987. A new specimen of *Steneosaurus* (Mesosuchia; Crocodylia) from the Toarcian of the Yorkshire coast. *Proceedings of the Yorkshire Geological Society* 46:279–287.
- Wenz, S. 1968. Contribution à l'étude du genre *Metriorhynchus*: Crâne et moulage endocranien de *Metriorhynchus superciliosus*. *Annales de Paléontologie*, 1968:149–183.
- Westphal, F. 1961. Zur Systematik der deutschen und englischen Lias Krokodilier. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 113:207–217.
- Westphal, F. 1962. Die Krokodilen des deutschen und englischen oberen Lias. *Palaeontographica, Abteilung A*, 118:1–96.
- Wilson, E. 1893. Fossil types in the Bath Museum. *Proceedings of the Bath Natural History and Antiquarian Field Club* 7:270–292.
- Woodward, H. B. 1893. The Lias of England and Wales (Yorkshire excepted). *Memoirs of the Geological Survey, U.K. Jurassic rocks of Britain III*, 399 pp.
- Wu, X.-C., H.-D. Sues, and Z.-M. Dong. 1997. *Sichuanosuchus shuhanensis*, a new ?Early Cretaceous protosuchian (Archosauria: Crocodyliformes) from Sichuan (China), and the monophyly of Protosuchia. *Journal of Vertebrate Paleontology* 17:89–103.
- Wu, X.-C., A. P. Russell, and S. L. Cumba. 2001. *Terminonaris* (Archosauria: Crocodyliformes): New material from Saskatchewan, Canada, and comments on its phylogenetic relationships. *Journal of Vertebrate Paleontology*, 21:492–514.

Submitted 17 November 2005; accepted 25 May 2006.