

A DYROSAURID CROCODYLIFORM BRAINCASE FROM MALI

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ABSTRACT—A well-preserved crocodyliform specimen from the Maastrichtian or Paleocene of Mali preserves the braincase and posterior dermatocranium. It is referred to Dyrosauridae on the basis of several derived features (a prominent anterior process of the postorbital, discrete occipital processes on the exoccipitals, significant quadratojugal contribution to jaw joint) and tentatively referred to *Rhabdognathus* on the basis of supratemporal fenestra shape. The lacrymal and prefrontal are relatively short compared with those published for other dyrosaurids. The palatines border the internal choanae anteriorly, and the choanae are divided by a midline septum derived from the pterygoids. The prefrontal pillars are mediolaterally broad and contact the palate ventrally. One stapes is preserved in place. The basicranial pneumatic system is very unusual, in that the anterior and posterior branches of the median eustachian canal are both separate at the palatal surface, and the pterygoids form part of the border for the anterior branch. The lateral eustachian openings lie within fossae on the lateral surface of the braincase and face laterally, with a descending process of the exoccipital nearly intersecting the opening. The braincase and surrounding dermal bones are elongate anteroposteriorly, and the postorbital's posterior ramus extends along the posterodorsal margin of the infratemporal fenestra. The quadrate ramus projects ventrally. These observations clarify character optimizations in previous phylogenetic analyses of Crocodyliformes.

INTRODUCTION

DYROSAURIDAE IS an extinct clade of tube-snouted crocodyliforms known from the Late Cretaceous through Late Eocene. Dyrosaurids are best known from marginal marine sediments of northern Africa and southwestern Asia, in units deposited by the Tethys Sea (Piveteau, 1935; Swinton, 1950; Arambourg, 1952; Halstead, 1975; Buffetaut, 1976a, 1976b, 1977, 1978, 1980; Storrs, 1986; Buffetaut et al., 1990; Langston, 1995). They are also known from the Late Cretaceous of North and South America (e.g., Troxell, 1925; Parris, 1986; Argollo et al., 1987; Gasparini and Spalletti, 1990; Gasparini, 1996; Denton et al., 1997; Wu et al., 2001), again in marginal marine or shallow marine deposits.

Dyrosaurids are prominent in the crocodyliform systematic literature. A long tubular snout is characteristic of several Mesozoic crocodyliform taxa, including Thalattosuchia, Pholidosauridae, Dyrosauridae, and one or more crown-group crocodylian lineages. Historically, these were thought to represent multiple independent derivations of the long-snouted morphology, which is generally regarded as a modification for piscivory (Langston, 1973; Buffetaut, 1982). Early parsimony analyses corroborated this hypothesis, indicating that dyrosaurids were more closely related to living crocodylians than to pholidosaurids or thalattosuchians (Benton and Clark, 1988; Norell and Clark, 1990). But more recent cladistic work groups thalattosuchians, pholidosaurids, and dyrosaurids together (Clark, 1994; Wu et al., 1997, 2001; Larsson, 2000). Although the characters uniting these taxa might be regarded as modifications for a long snout (and therefore not independent; Langston, 1973), this group remains stable in parsimony analysis even when allowances are made for convergence in the rostrum (Clark, 1994).

The subject of the present paper is a well-preserved dyrosaurid braincase from the Pgi (Bassot et al., 1981) rocks of Mali, which are the equivalent of "Terrecht 1" (Monod, 1939; see also Péré-baskine, 1932; Radier, 1959; and Bellion et al., 1989, 1992). These strata have been broadly mapped as Maastrichtian-Danian and consist of a series of shales, sandstones, and limestones. The specimen was recovered on a joint expedition in 1999 by the Centre National de la Recherche Scientifique et Technologique du Mali and Stony Brook University. The locality ("Mali-5") is situated on an extensive broad, flat plain covered with low, gray,

largely calcareous boulders (Fig. 1). One of these boulders contained the entire, virtually undistorted skull and was removed en bloc and prepared in acid. Other fossils in the boulder included a very small (<5 cm) vomerine dentition of a pycnodont neopterygian. Aggressive searching for other fossils in the area yielded no other traces of bone on the surface.

The locality "Mali-5" from which the specimen derives is in the vicinity of the village of Asler and is characterized by a pale yellow, sandy limestone, which displays less than 0.5 m of vertical relief and very limited exposure. The only fossil material identified from this unit is the dyrosaurid skull, some fragmentary oyster shells, and a small pycnodont fish. Given the limited exposure and paucity of datable fossil material (separate investigations of samples from this locality by Amnon Rosenfeld and Marie Pierre Berggren yielded no microfossils), we infer this locality to be of shallow marine origin but cannot presently provide a more precise date than Maastrichtian-Paleocene.

Based on morphology, we tentatively refer this specimen to *Rhabdognathus*, a dyrosaurid known previously from the Early Eocene of Mali (Buffetaut, 1980), Tunisia (Bergouinioux, 1955, 1956; Buffetaut, 1978), and Nigeria (Swinton, 1930). On this basis, we suspect the rocks to be of Paleocene or Early Eocene age; but this should be verified using non-reptilian temporal indicators.

This specimen allows a complete description of the occipital region of the skull. It also preserves features that prompt recodings in previous assessments of dyrosaurid relationships. Given the paleobiogeographic distribution of Dyrosauridae and its evident survivorship across the Cretaceous-Tertiary boundary, a well-tested phylogenetic hypothesis for the group contributes to the census of taxa affected by this extinction event, which is one of the five most dramatic of the Phanerozoic.

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Benton and Clark, 1988

MESOEUROCODYLIA Whetstone and Whybrow, 1983

DYROSAURIDAE de Stefano, 1903

cf. RHABDOGNATHUS Swinton, 1930

cf. RHABDOGNATHUS sp.

Specimen.—CNRST-SUNY (Centre National de la Recherche Scientifique et Technologique du Mali—Stony Brook University)—190.

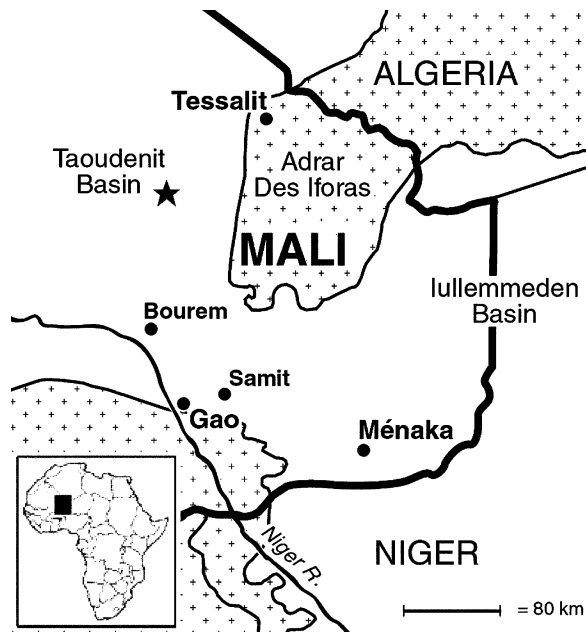


FIGURE 1—Locality Mali-5, which produced the dyrosaurid, is located on the western side of the Adrar des Iforas mountains in the vicinity of the village of Asler.

General form and preservation.—The braincase and posterior dermatocranium are largely complete and undistorted, missing only the left quadrate ramus (Figs. 2, 3). A small amount of bone is missing from the anterolateral rim of the left orbit, making the anterior ramus of the jugal appear more slender than natural. The left stapes is preserved (Fig. 4), although not in life position (see below). As with other dyrosaurids, the occipital region is elongate relative to the condition typically found in shorter-snouted crocodyliforms.

A portion of the tubular rostrum is preserved anterior to the orbits, with ten complete maxillary alveoli preserved on either side, but it is not known how much of the anterior portion is missing. If the maxilla had up to 24 alveoli, as reported for *Rhabdognathus* by Buffetaut (1980), then more than half of the snout is missing. But in the skull figured by Buffetaut (1980), the snout margins were still flared along the posteriormost ten alveoli, whereas they become parallel anteriorly in the present specimen.

Major cranial openings.—The orbits are circular in outline and project dorsolaterally. The margins are everted, but not telescoped as in extant *Gavialis*. The posterolateral corner is disrupted by the robust anterior process of the postorbital bar typical of dyrosaurids (Buffetaut, 1976a, 1979; Clark, 1994). The process is completely preserved only on the left side (Fig. 2.2), where it nearly contacts the jugal ventrally, subdividing the orbit into a circular anterior region and posterior triangular region. Sereno et al. (2001) indicated the presence of this feature in several non-dyrosaurid taxa (e.g., *Sarcosuchus*, *Goniopholis*, *Araripesuchus*), but we regard the postorbital in these forms as having a sharply squared-off anterolateral margin without a process.

The infratemporal fenestrae are oblong and approximate an isosceles triangle in outline, with the long axis projecting posteriorly. The right fenestra is more than four times longer than its greatest dorsoventral extent, and the ventral margin is concave as a result of the lower temporal bar's undulation. The fenestra extends posteriorly below the external otic recess (Fig. 3.3)—an unusual feature, as the fenestra is generally located in front of the

recess in other crocodyliforms. The right fenestra is bound anteriorly and posterodorsally by the postorbital, posteriorly by the quadratojugal, and ventrally by the quadratojugal and jugal. Elongation of the infratemporal fenestra may be responsible for the extremely long posterior ramus of the postorbital, which extends ventrally below the otic recess. We cannot tell if a quadratojugal spine was present.

The external otic recess is circular, bound posterodorsally by the squamosal and anteroventrally by the quadrate (Fig. 3.2, 3.3). The squamosal-quadrate suture passes dorsally along the posterior margin of the recess. A thin lamina emerges from the quadrate at the posteroventral surface of the recess, forming an extension of the floor of the cranioquadrate canal. There is no preotic siphonial opening. The opening to the mastoid antrum is visible through the otic recess on the right side.

The supratemporal fenestrae are long and narrow (Fig. 3.1). Their separation is best described as a sagittal crest, in contrast with the flattened frontal-parietal deck found in most crocodyliforms. The sagittal crest's dorsal surface is elevated posteriorly, with distinct fossae at the anteromedial corners. The fenestral rims are bound anteromedially by the frontal, posteromedially by the parietal, anterolaterally by the postorbital, and posterolaterally by the squamosal; within the fenestra itself, the quadrate and laterosphenoid form much of the medial wall. Within the supratemporal fenestrae, the temporal canal is a circular hole that is bordered by the squamosal and parietal ventrally.

The suborbital fenestrae are slender and extend anterior to the prefrontal pillars (Fig. 3.4). The medial margin of each fenestra is linear, and the lateral margin is concave; both anterior and posterior corners are acute. The internal choanae form a single D-shaped medial opening, bordered anteriorly by the palatines and posteriorly by the pterygoids. The anteriormost extent lies between, rather than behind, the suborbital fenestrae. This probably reflects a posterior extension of the suborbital fenestrae in dyrosaurids rather than an anterior shift in the position of the choanae. There is a thin midline septum within the choanal aperture comprised of the pterygoids.

The foramen magnum is bound dorsally by the exoccipitals and ventrally by the basioccipital.

Cranial bones.—The nasals are imperfectly preserved, but on this specimen are narrow and expand slightly posteriorly. Each terminates as an acute wedge, with the prefrontal and lacrymal forming the lateral margin of the wedge and the frontal forming the medial margin, separating the two nasals posteriorly.

The maxillae are also incomplete. They contact the nasals medially and the lacrymals, prefrontals, frontal, and jugals posteriorly. There is a short posterior process of each maxilla along the anterior margin of each lacrymal. Ten alveoli are completely preserved on the left side, with an eleventh partially preserved anterior to these. The alveoli are small and circular, and the teeth preserved project ventrally from each alveolus. The toothrow extended posteriorly behind the postorbital bar, and the maxilla contributes to the lower temporal bar. The anteriormost preserved alveoli are separated by broad sulci; posteriorly, there are deep occlusal pits between the alveoli.

The lacrymal is a triangular element passing anteriorly along the lateral margin of the nasal. It extends farther anteriorly than the prefrontal and is approximately as long as the orbit. There is a short maxillary process at the anterior tip of the lacrymal (Fig. 3.1); this has not been reported previously for a dyrosaurid, but is evident in at least one of the specimens of *Dyrosaurus phospathicus* figured by Bergounioux (1956, plate 4, fig. 3). The lacrymal ducts are represented by a series of small foramina perforating each lacrymal posteriorly within the orbit.

The prefrontal is slender and triangular in dorsal view, lodged between the frontal and nasal medially and the lacrymal laterally.



FIGURE 2—cf. *Rhabdognathus*, skull in (1) dorsal, (2) left lateral, (3) right lateral, (4) ventral, and (5) posterior view.

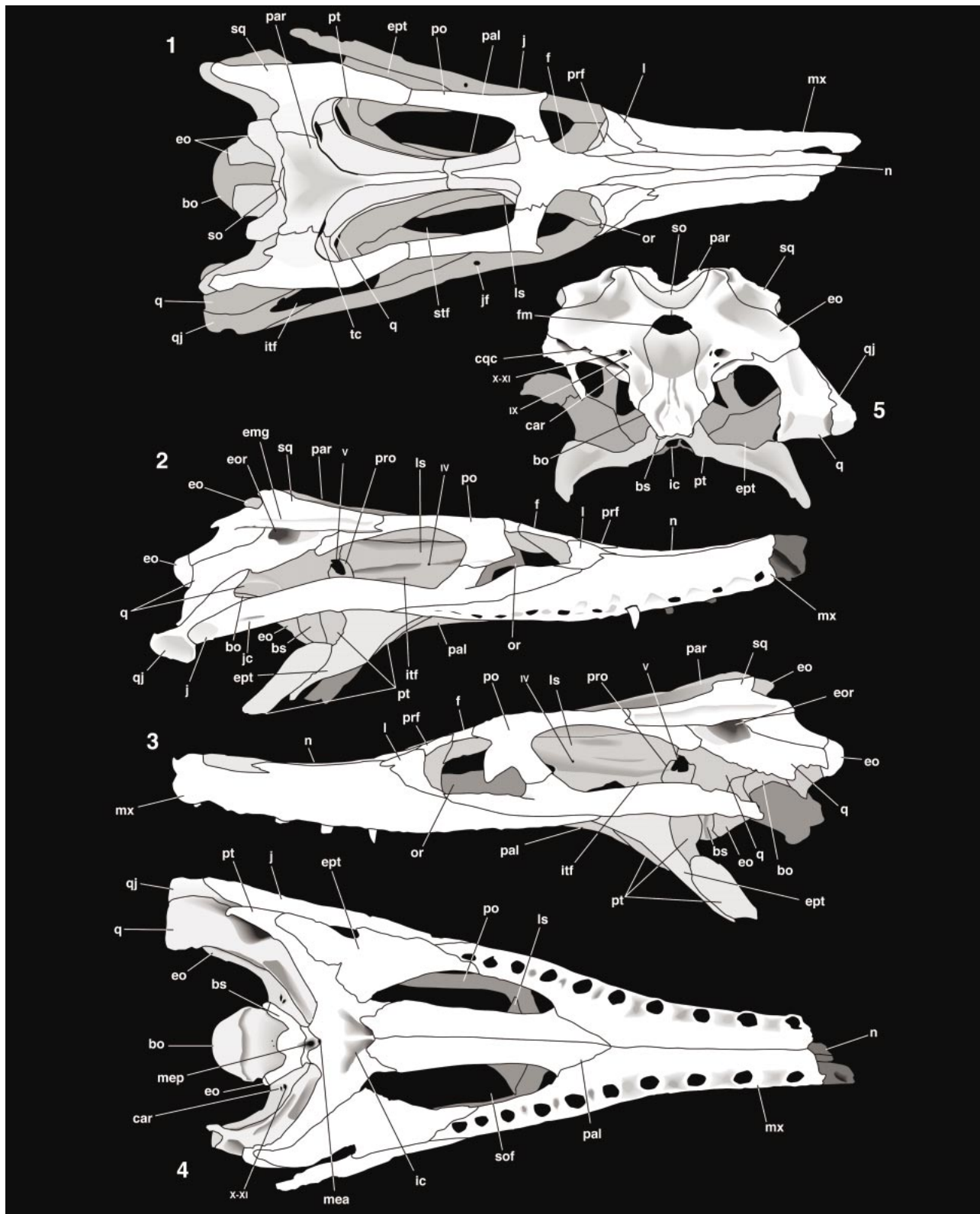


FIGURE 3—cf. *Rhabdognathus*, line interpretation of skull showing cranial sutures in (1) dorsal, (2) left lateral, (3) right lateral, (4) ventral, and (5) posterior view. Abbreviations: bo, basioccipital; bs, basisphenoid; car, carotid foramen; cqc, cranioquadrate canal; emg, groove on squamosal for ear muscles; eo, exoccipital; eor, external otic recess; ept, ectopterygoid; fm, foramen magnum; ic, internal choanae; itf, infratemporal fenestra; j, jugal; jc, concavity on lateral surface of jugal; jf, jugal foramen; f, frontal; l, lacrymal; ls, laterosphenoid; mea, median eustachian opening (anterior branch); mep, median eustachian opening (posterior branch); mx, maxilla; n, nasal; or, orbit; pal, palatine; par, parietal; po, postorbital; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; qj, quadratejugal; so, supraoccipital; sof, suborbital fenestra; sq, squamosal; stf, supratemporal fenestra; tc, temporal canal. Exit foramina for cranial nerves are identified by Roman numerals.



FIGURE 4—cf. *Rhabdognathus*, close-up of left otic recess showing stapes (st). Other abbreviations as in Figure 3.

Each bears a broad descending process (the prefrontal pillar) that contacts the palatine. The prefrontal pillar is mediolaterally broad, and unlike the distinct pillars of most crocodyliforms, it merges very gradually with the posterior lamina of the prefrontal. The medial process below the olfactory groove is dorsoventrally deep, and each meets its counterpart at the midline.

Both the prefrontal and lacrymal have rather broad laminae within the orbital space. In this regard, they are similar to the prefrontal and lacrymal of extant *Gavialis*. But there is an important difference. In *Gavialis*, the prefrontal and lacrymal are broad within the orbital space because the anterior and lateral margins of the orbit are upturned, increasing the surface area of the bones comprising the orbital margin (including the prefrontal and lacrymal). Hence, parts of the “laminae” in *Gavialis* are homologous with the posterior or ventral surfaces of the prefrontal and lacrymal in other crocodyliforms. The orbital margin is barely upturned in *Rhabdognathus*, and the breadth of these bones is formed by laminae extending ventrally.

The anterior ramus of the jugal forms the lateral margin of the orbit and extends slightly anteriorly beyond the orbit’s anterior limit, where its ventral suture with the maxilla merges with the maxillolacrymal suture (Fig. 3.2, 3.3). Along the orbital rim, the anterior ramus is very thin in cross-section. This is most evident on the right side, where the lateral orbital rim is undamaged. It forms the lower half of the robust, columnar postorbital bar, the ventral margin of which is nearly flush with the lower temporal bar. The surface of the bar is offset from the lateral surface of the lower temporal bar by approximately 1 cm, but the surfaces themselves are continuous and there is no deep sulcus separating the postorbital and lower temporal bars.

The posterior jugal ramus forms the temporal bar and is D-shaped in cross section, with the lateral surface forming the flat side of the “D.” It bears a shallow concavity on its lateral surface, ventral to the infratemporal fenestra (Fig. 3.3). There are small foramina on the medial surface ventral and anterior to the postorbital bar that may be homologous with the anterior jugal sphenoidal foramen described by Brochu (1997) for eusuchians and

a larger opening on the dorsolateral surface of the temporal bar. The posterior ramus continues beyond the posterior margin of the infratemporal fenestra. It does not extend to the end of the quadrate ramus, but there is a distinct oval, concave rugosity at the posterior tip of the jugal, immediately anterior to the quadrate condyle.

The postorbital forms the dorsal half of the postorbital bar and bears an anterior process within the orbital space. It does not contact the parietal. The dorsal rami are slender and contact the frontal medially and the squamosal posteriorly, forming the anterolateral border of the supratemporal fenestra. The posterior dorsal ramus is extremely long and reaches the level of the otic recess (Fig. 3.3). It forms much of the posterodorsal margin of the infratemporal fenestra. There is a small fossa on the postorbital’s surface at the anteromedial corner of the supratemporal fossa for the laterosphenoid’s capitate process.

Other longirostrine crocodyliforms lack this elongation of the postorbital. The postorbital passes dorsally over the long anterior ramus of the squamosal in thalattosuchians, and the postorbital does not extend along the posterior margin of the fenestra (e.g., Telles Antunes, 1967; Vignaud et al., 1993). Although the gavialoid infratemporal fenestra is large relative to its counterpart in other crocodylian lineages, gavialoids follow the plesiomorphic eusuchian pattern in which the postorbital passes medially along the surface of the squamosal’s anterior ramus, and the postorbital does not extend beyond the dorsal angle of the infratemporal fenestra. A posterior process along the infratemporal fenestra’s posterodorsal margin is seen in derived alligatoroids (Brochu, 1999).

The fused frontal is cruciform in dorsal view, with an acute anterior process separating the nasals and a very slender posterior process forming the anterior one-third of the sagittal crest. Lateral processes for the postorbitals are short, and a broad sutural contact with the laterosphenoid occurs within the supratemporal space. A deep midline groove on the frontal’s ventral surface indicates the pathway of the olfactory tract. There is damage to the center of the sagittal crest, obscuring any posterior division to enclose the

tip of the parietal's anterior process, an unusual condition reported by Langston (1995) for other dyrosaurid material.

The fused parietals form the posterior two-thirds of the sagittal crest, expanding posteriorly to form a flattened, sculpted deck behind the supratemporal fenestrae adjacent to the squamosals. There is a V-shaped groove on the dorsal surface of the parietal extending a short distance toward the sagittal crest. There is also a deep sulcus at the posterior end of the parietal, giving the skull deck the appearance of bearing two prominent bulges along the posterior edge in posterior view. The parietal is exposed on the occipital surface of the skull and separates the dorsal skull table surface from the supraoccipital, as in other dyrosaurids (Lavocat, 1955; Langston, 1995). Swinton (1930) interpreted the ventral flange of the dyrosaurid parietal exposed on the occipital surface as a dermosupraoccipital.

The squamosal bears a pair of dorsal rami—one anteriorly, contacting the postorbital, and a shorter, more robust posteromedial ramus contacting the parietal. The anterior ramus does not pass laterally against the postorbital, as it does in eusuchians. The squamosal extends posteroventrally from the skull deck anterolateral to the paroccipital process. The lateral margin of the squamosal portion of the skull deck bears a long groove for support of the ear-flap muscles; but unlike the grooves of nearly all longirostrine crocodyliforms, the groove in this specimen does not flare anteriorly (Figs. 3.2, 3.3, 4). The squamosal and parietal contact each other in two places on the surface of the infratemporal fenestra—dorsal to the temporal canal and ventral to it, preventing the quadrate from forming part of the temporal canal's margin.

The left stapes is preserved within the left otic aperture (Fig. 4). The visible portion is a slender rod 2 mm in diameter, flaring slightly at its distal tip. Matrix covers the floorplate of the stapes and the fenestra ovalis.

The quadratojugal bears a very slender anterodorsal process forming the posterodorsal margin of the infratemporal fenestra. This is preserved only on the right side. It would have contacted the postorbital one-third of the way up the infratemporal fenestra's margin, blocking the squamosal and quadrate from the fenestra's border, but the dorsalmost portion of the process has broken away. Contact surfaces for the quadratojugal can be seen both on the anterior margin of the quadrate and the ventralmost tip of the postorbital.

The quadratojugal broadly meets the jugal laterally. The jugal's posterior process tapers posteriorly, and the quadratojugal forms the posteroventral corner of the infratemporal fenestra. The quadratojugal continues anteriorly medial to the jugal for half of the lower temporal bar's length. Posteriorly, the quadratojugal also forms a substantial portion of the quadrate condyle, as in other dyrosaurids (Langston, 1995). In fact, nearly half of what would be the lateral hemicondyle in a crown-group crocodylian is comprised of the quadratojugal. The condylar surface for the articular on the quadrate is continuous with an identical surface on the quadratojugal.

The palatines lie between the suborbital fenestrae, with the anterior palatine processes forming a short V-shaped wedge. This is typical of long-snouted crocodyliforms, though the relative length of the process is shorter here than in most longirostrine forms.

The ectopterygoid forms the medial border for the posterior-most maxillary alveolus, and there is no maxillary apron separating the ectopterygoid from the alveolar border. Much of the ectopterygoid lies along the medial surface of the temporal bar, but although the ectopterygoid extends anteriorly beneath the postorbital bar, it forms no part of the postorbital bar itself. The ectopterygoid's medial bar is thick and oval in cross-section, becoming a posterior process at the lateral side of each pterygoid wing terminating in an acute posteroventrally-projecting process.

This process is complete only on the left side, but although it appears to reach the tip of the pterygoid wing, this is the result of damage to the pterygoid.

The pterygoids are fused along the midline. The wings are slender and covered ventrally largely by the ectopterygoids (Fig. 3.4); in most crocodyliforms, the ectopterygoids would only form the ventrolateral-most border of each wing. The wings' posterior margins are concave in ventral view. The pterygoids extend anteriorly, forming the roof of the nasopharyngeal duct and tapering to a point as they pass anteriorly over the palatines beyond the prefrontal pillars. The pterygoids themselves do not actually contact the prefrontal pillars. The thin septum dividing the nasopharyngeal duct and visible within the choana (Fig. 3.4) is composed of the pterygoids. The pterygoid is concave behind the choanae, forming a shallow groove that Buffetaut (1982) interpreted as an extension of the choanae themselves, allowing the choanae to communicate with the median eustachian openings.

The laterosphenoid is extremely elongate relative to that of other crocodyliforms, a feature that distinguishes the dyrosaurid braincase (Langston, 1995). The laterosphenoids meet along the midline ventral to the olfactory foramen, the anterior margins flaring slightly around the paired optic foramina. The capitate processes are small and visible through the supratemporal fenestrae dorsally (Fig. 3.1), fitting within fossae in the postorbitals. The anterior margins of the processes trend anteromedially. A series of shallow anteroposterior grooves along the ventrolateral surface of each laterosphenoid may indicate the external pathways of the branches of the trigeminal nerve. There is no laterosphenoid bridge forming a discrete foramen for the ophthalmic branch; rather, all branches merged posteriorly, and the common groove emerges from the anteroventral margin of the foramen ovale. A small foramen pierces the laterosphenoid's surface and indicates the trochlear (IV) nerve's exit (Fig. 3.3). Each laterosphenoid contacts its corresponding quadrate posterodorsally, the pterygoid posteroventrally below the foramen ovale, and the basisphenoid ventrally.

The prootic is exposed on the braincase lateral wall, where it can be seen rimming the foramen ovale and extending ventrally toward the basisphenoid (Fig. 3.2, 3.3). Whether the prootic meets the basisphenoid externally cannot be determined.

On the braincase lateral wall, the quadrate forms the posterodorsal quarter of the foramen ovale's margin and contacts the laterosphenoid and prootic anteriorly. The quadrate laps laterally over the pterygoid, forming a U-shaped process. A deep sulcus separates the quadrate from the basisphenoid and exoccipital posteriorly.

The main body of the quadrate lies ventral to the squamosal and anterolateral to the exoccipital. It nearly encircles the external otic recess, and there is a shallow sulcus anterior to the aperture itself. The cranioquadrate canal opens between the quadrate and exoccipital posteroventrally on the occipital surface and communicates with the otic recess. The quadrate ramus projects ventrally. The sulcus separating the lateral and medial hemicondyles is modest. Although the medial hemicondyle is dorsoventrally deep, it is much narrower mediolaterally than its lateral counterpart. A single robust muscle-attachment ridge lies on the ramus' anteroventral surface and extends almost to the supratemporal fenestra.

The quadrate ramus of hatchling crocodylians projects ventrally and rotates to a posterior projection in adult specimens (personal obs. and H. Larsson, personal commun.). The adult condition is clearly seen in mature *Gavialis* (Fig. 6.1). But the quadrate is not reflected posteriorly in dyrosaurids, and the ramus maintains a relationship similar to that of very young crown-group crocodylians (Fig. 6.2). This condition is also seen in a wide array of noncrocodylian crocodyliforms (Clark, 1994).

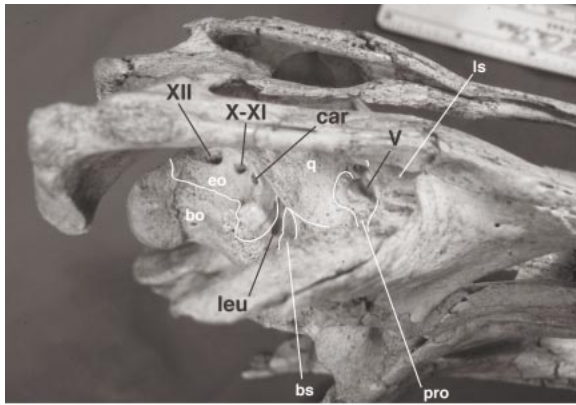


FIGURE 5—cf. *Rhabdognathus*, right ventrolateral view, showing position of lateral eustachian opening (leu). Other abbreviations as in Figure 3.

The supraoccipital is exposed as a crescentic bone ventral to the parietal and dorsal to the exoccipitals. Its external surface is concave, and the lateral tips extend dorsally to the posttemporal fenestrae, although the floor of each fenestra is actually comprised of the exoccipital (see below). The supraoccipital can also be seen through the external otic recess and temporal canal.

Each exoccipital bears a prominent posterior process dorsally. Each process floors the posttemporal fenestra, and although the supraoccipital laps over the ridge extending ventrally from each process, it does not contribute to the fenestra's margin. Deep concavities lie on the exoccipital's surface between these processes (which are typical of dyrosaurid braincases; Thevenin, 1911; Swinton, 1930; Buffetaut, 1976a; Langston, 1995; Denton et al., 1997) and the posterolaterally-directed paraoccipital processes, imparting a distinct U-shape to the occipital plate in dorsal or ventral view. The paraoccipital process bears a rugosity at the distal tip and a notch along the ventral margin, where it roofs the cranioquadrate canal.

The exoccipitals are pierced by four sets of foramina lateral and ventral to the occipital condyle (Fig. 3.5). The medialmost is for the hypoglossal nerve (XII). The vagus (X) and accessory (XI) nerves evidently exited through a common opening with the jugular vein ventrolateral to the hypoglossal foramen; the glossopharyngeal (IX) nerve foramen lies within a common fossa with the vagus/jugular foramen, but the two foramina are widely separated externally. The posterior carotid foramen lies directly ventral to the vagus/jugular foramen adjacent to a deep sulcus separating the exoccipital from the quadrate; it lies dorsal to the basisphenoid's posterior exposure.

The exoccipitals form the dorsal and lateral margins of the foramen magnum and extend onto the dorsal surface of the basioccipital, extending posteriorly to the occipital condyle. They also project ventrally, each bearing a broad ventral process that contributes to the basioccipital tubera. In this regard, they are similar to the exoccipitals of gavialoids. In *Gavialis*, the exoccipitals appear at the anterolateral corner of each tuber and their ventral exposure is modest. In at least some dyrosaurids (including the present material), they lie at the posterolateral tips of each tuber and have a more extensive ventral exposure (Fig. 3.4). The exoccipitals evidently do not contribute to the tubera in thalattosuchians (e.g., figures in Telles Antunes, 1967) or pholidosaurs (Köken, 1887).

The basisphenoid's anterior exposure is long, extending along the midline between the laterosphenoids and pterygoids. The cultriform process is missing. A distinct sulcus separates the basisphenoid from the pterygoid anteriorly, and a small foramen (probably for the abducens nerve) pierces the suture immediately

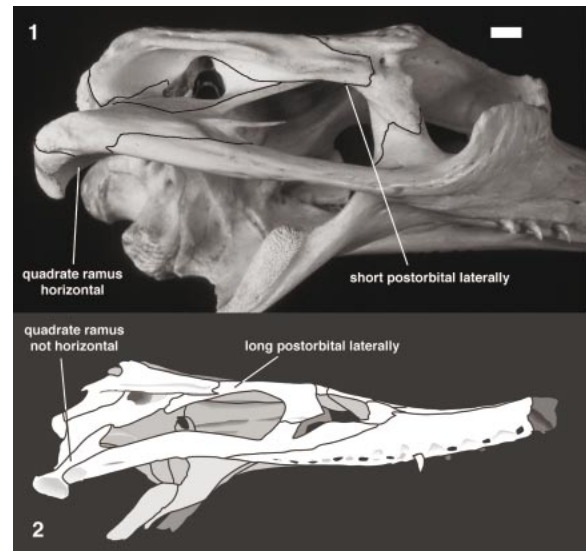


FIGURE 6—Differences in cranial elongation in (1) *Gavialis* (Texas Memorial Museum m-5485; scale = 1 cm) and (2) cf. *Rhabdognathus*.

ventral to the pterygoid-laterosphenoid contact. Details of the sella turcica cannot be seen.

The basisphenoid is also exposed posteriorly encircling the braincase, extending dorsally to approximately the level of the occipital condyle with crescentic exposures wedged between the basioccipital and pterygoid (Fig. 5).

The basioccipital forms most of the occipital condyle and continues ventrally on the occipital surface toward the palate (Fig. 3.5). The basioccipital tubera are V-shaped in ventral and W-shaped in posterior view, with a ventromedial rugosity and lateral tips that lie dorsal to the midpoint. A pair of grooves extends along the posterior surface toward the medial rugosity, and a pair of (presumably) vascular foramina pierces the surface dorsal to these grooves.

Pneumaticity.—As with all crocodyliforms, the chondrocranium is invested with a series of internal recesses that presumably communicated with the pharynx in life. These can be seen externally as the median and lateral eustachian openings found in virtually all crocodyliforms. In most forms, the median eustachian opening splits into anterior and posterior rami. The posterior ramus penetrates the basioccipital, and the anterior ramus—which itself splits into paired lateral rami (as does the posterior ramus)—passes through the basisphenoid (Owen, 1850; Colbert, 1946; Walker, 1990). In hatchling crocodylians, the anterior-posterior split is visible externally. But the basisphenoid (which borders the median eustachian opening anteriorly) and the basioccipital (which borders the median eustachian opening posteriorly) extend ventrally during ontogeny in eusuchians, and usually only a single opening is visible externally in mature specimens (with the exception of caimans—Brochu, 1999). A single common opening is often seen in other crocodyliforms, including most thalattosuchians (Walker, 1990).

The lateral eustachian openings also usually lie along the basioccipital-basisphenoid suture on either side of the median opening. Each leads dorsally to a rhomboid sinus between the basioccipital and exoccipital, which also communicates with the posterior ramus of the median canal.

The present specimen bears median and lateral eustachian openings, but their placement and relationship to cranial bones is different from that reported for other taxa. The median openings are visible ventrally in an anteroposteriorly long oval behind the

TABLE 1—Revised codings for Dyrosauridae based on the matrix used by Clark (1994) and Buckley and Brochu (1999). Matrix has 110 characters; see Clark (1994) and Buckley and Brochu (1999) for character details.

	1	1	2	2	3	3	4	4	5	5
5	0	5	0	5	0	5	0	5	0	5
111??	1?101	00101	11000	10001	11101	00110	12110	10100	11120	11?10
								1	1	1
6	6	7	7	8	8	9	9	0	0	1
0	5	0	5	0	5	0	5	0	5	0
11?10	?1010	1301?	3?00?	?2?00	0????	????0	100??	????1	?1000	00100

choanae, and the anterior and posterior branches are both visible (Figs. 2.4, 3.4). The basisphenoid appears to form the wall separating the branches, and the posterior branch is bordered posteriorly by the basisphenoid, but the anterior wall of the anterior branch is comprised of the pterygoid.

Piveteau (1935) was unable to locate the lateral eustachian openings in a braincase of *Dyrosaurus*, but Buffetaut (1982) stated that they are visible in lateral view. Lavocat (1955) figured them lying significantly dorsal to the median opening and visible when the braincase was viewed anteriorly, but not posteriorly. The present specimen confirms Buffetaut's and Lavocat's observations—the lateral eustachian openings are located immediately posterior to the basisphenoid/basioccipital suture on the lateral surface of the basioccipital (Fig. 5). They open *laterally*—an unusual condition, as the lateral eustachian foramina usually open ventrally or ventrolaterally in crocodyliforms. They cannot be seen when the skull is observed in posterior or ventral view. Although they penetrate the basioccipital, the external fossae for the foramina are each bound by the basisphenoid anteriorly and the exoccipital posteriorly.

These conditions may apply to some general level within Dyrosauridae. A *Dyrosaurus phosphaticus* braincase from the Eocene of Algeria figured by Buffetaut (1982) shows a pair of foramina behind the choanae, presumably representing the anterior and posterior median eustachian openings, though the sutural relationships were not drawn (and have evidently been difficult to reconstruct in the braincase of that taxon; Piveteau, 1935). An isolated braincase from the Cretaceous dyrosaurid *Hyposaurus rogersii* from New Jersey (AMNH 2545) does not preserve the median openings, but it does preserve the lateral openings, confirming their communication with the rhomboid sinus and suggesting exoccipital participation with the external rim of the opening (personal obs.). *Terminonaris* is the only putative dyrosaurid reported with a more general crocodyliform condition—a single median eustachian opening and lateral eustachian openings visible in ventral view (Wu et al., 2001).

These conditions contrast with those found in most other longirostrine crocodyliforms. Thalattosuchians and gavialoids both have single median openings and lateral openings that open ventrally (Eudes-Deslongchamps, 1863; Westphal, 1962; Telles Antunes, 1967; Wenz, 1968; Walker, 1990; personal obs.). The anterior and posterior rami are visible externally in *Gavialis*, but this results from elongation of the braincase (which widens the median opening) and dorsoventral shortening of the basisphenoid and basioccipital (which brings the ramification closer to the surface).

Pholidosaurids also have single median openings, but they may share one interesting similarity with dyrosaurids—the lateral eustachian opening assumes a lateral rather than ventral position. Köken (1887) reported the lateral eustachian opening to be lying within a shallow sulcus on the lateral surface of the braincase in *Pholidosaurus meyeri* from the Lower Cretaceous of Germany, a condition strikingly similar to that seen in the present specimen. It is unclear from his description whether the exoccipital played

any role in the lateral opening's margin. This may not be a consistent feature within Pholidosauridae, as the lateral openings were reported as taking a ventral position in the Upper Jurassic pholidosaurid *Sumosuchus junggarensis* of China by Wu et al. (1996).

PHYLOGENETIC ANALYSIS

Character coding.—The character states preserved in this specimen bear upon codings in published matrices used to explore crocodyliform phylogenetics, most of which are based on a matrix presented by Clark (1994). To explore the possible impact of this new information, we recoded Dyrosauridae as indicated below in the modified version of Clark's 1994 matrix used by Buckley and Brochu (1999). These new codings are presented in Table 1.

Clark (1994) coded dyrosaurids as having smooth rather than ornamented bone (character 1). Although this might be a matter of degree, the dermal bones of the skull deck in this specimen are clearly ornamented except on the surface of the sagittal crest. This is especially true on the dorsal surface of the postorbital and squamosal, where discrete pits and grooves are apparent. Similar features are visible on the frontal and dorsal bones of the snout, but they are less prominent and, on the maxilla, become shallow grooves.

Clark's character 11 expressed contact or lack of contact between the nasal and lacrymal. This was left as unknown for dyrosaurids in the original matrix. The lacrymal and nasal contact each other in the present specimen, and based on published figures, evidently did so in other dyrosaurids as well.

One of the characters ambiguously supporting long-snout monophyly is the absence of contact between the prefrontal pillar and the palate (Clark's character 15). This feature was coded as unknown in *Sokotosuchus* and *Dyrosaurus*. But the prefrontal pillar contacts the palate in the specimen described here. If conditions in cf. *Rhabdognathus* apply to all dyrosaurids, absence of pillar-palate contact would diagnose a more inclusive clade including only pholidosaurids and thalattosuchians.

Similarly ambiguous for long-snout monophyly is a rod-shaped lower temporal bar (Clark's character 18). This was coded as unknown in the dyrosaurids in Clark's analysis. The lower temporal bar of this specimen is distinctly mediolaterally flattened, and not rodlike as in thalattosuchians (or in *Gavialis*).

The postorbital bar of extant crocodylians bears a distinct vascular foramen on the lateral surface immediately below the skull table. This was expressed as character 27 in Clark (1994) and left unknown in dyrosaurids. Multiple foramina are present on the postorbital bar in the present specimen, but it is unclear whether these are homologous with the vascular structures seen in crocodylians. As an experiment, we coded this character as present (and homologous with the crocodylian vascular foramen) in dyrosaurids.

The pterygoid of the present specimen has a similar relationship to the braincase as in extant crocodylians—it makes a robust contact with the laterosphenoid and forms the ventral margin of the foramen ovale. This is not universally true in crocodyliforms,

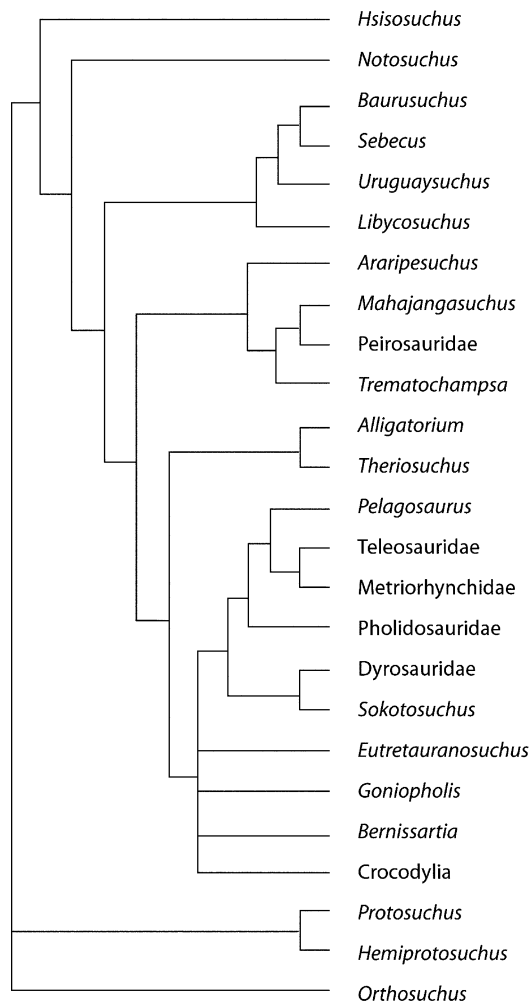


FIGURE 7—Strict consensus of three equally most parsimonious trees for mesoeucrocodylians. Matrix is based on Clark (1994) and Buckley and Brochu (1999); see text for details.

as the pterygoid in basal groups is largely restricted to the palate and suspensorium. We can thus resolve the coding for Clark's character 38, which expressed this distinction.

Parsimony analysis.—The modified matrix used here includes 22 ingroup taxa, three outgroup taxa (*Orthosuchus*, *Protosuchus*, and *Hemiprotosuchus*), and 110 characters. The characters are largely based on Clark (1994) with a few recodings, along with additional characters as discussed by Buckley and Brochu (1999). It was subjected to maximum parsimony analysis using PAUP* (ver. 4.08b; Swofford, 2001). One hundred heuristic searches were run with the starting order of taxa randomized for each iteration, both with and without the new codings for Dyrosauridae.

The topological results are identical whether information from cf. *Rhabdognathus* is included or not. In both cases, three most parsimonious trees were recovered. The strict consensus (Fig. 7) is consistent with the results reported by Clark (1994) and Buckley and Brochu (1999)—Dyrosauridae and *Sokotosuchus* are sister taxa, and these together are the sister group to a clade including pholidosaurids and thalattosuchians. The strict consensus shows this longsnout clade as part of a polytomy with *Eutretraurosuchus*, *Goniopholis*, *Bernissartia*, and *Crocodylia*; in two of the three trees, the longirostrine clade was the sister group to

Crocodylia, and in the third it was closer to *Eutretraurosuchus* and *Goniopholis*.

The only numerical difference is a one-step length increase between the original matrix and the matrix including new information. The original tree length was 222 steps, with a consistency index (excluding autapomorphies) of 0.500 and retention index of 0.683. With the new codings, length was 223 steps, consistency index was 0.498, and retention index was 0.682. This reflects two independent derivations (or a derivation and a loss) of the vascular foramen on the postorbital bar, although as noted above the foramina on the dyrosaurid postorbital bar may not be homologous with those of crocodylians.

Although this new information does not influence optimal topology, it does resolve character state ambiguity. A rod-like temporal bar and a prefrontal pillar not contacting the palate diagnose either the clade including all slender-snouted forms or the clade including only the thalattosuchians and pholidosaurids. Because of the basal position dyrosaurids and *Sokotosuchus* adopt within the longirostrine clade, adding information about the prefrontal pillar and lower temporal bar resolves the transitions to the less inclusive clade.

DISCUSSION

Taxonomic affinities.—Present dyrosaurid taxonomy is highly dependent on the snout and lower jaw. Indeed, the lack of anatomical overlap between many dyrosaurid holotypes is a general problem that makes interpretation of the group's history difficult. As the rostrum and mandible were not preserved in the present material, referral to any previously described dyrosaurid species is extremely difficult.

The supratemporal fenestrae are anteroposteriorly elongate in all dyrosaurids; in fact, they are always longer than the orbit, even though they were coded otherwise in Clark's (1994) matrix. However, the degree of elongation is more extreme in the present material than in most dyrosaurids. The width/length ratio of the fenestra is 0.44 in *Sokotosuchus* (Buffetaut, 1979), 0.45 in *Phosphatosaurus* (Buffetaut, 1980), and 0.40 in *Hyposaurus* (Parris, 1986; Denton et al., 1997). It varies in *Dyrosaurus*, depending on whether you derive the measurements from figures in Bergouinioux (1956; 0.49), Thevenin (1911; 0.46) or Buffetaut (1979; 0.41). In the present specimen, it is 0.36; this is most similar to that for *Rhabdognathus*, which has a width/length ratio of 0.33 based on Buffetaut (1980). This is a problematic character to use for two reasons: 1) the ratios we report are based on measurements from published photographs or reconstructions, and 2) we would expect the shape of the fenestra to vary ontogenetically (Mook, 1921; Kälin, 1933). Nevertheless, the supratemporal fenestrae of the present specimen and those of *Rhabdognathus* as figured by Buffetaut (1980) are narrow relative to those of other dyrosaurids.

The present specimen shares with *Rhabdognathus* a virtually unsculpted sagittal crest. Small depressions are found on the frontal and parietal at the anterior and posterior ends of the crest, where it begins to flare laterally, but the crest itself is smooth. The sagittal crests of other dyrosaurids bear small pits along their lengths.

One interesting difference between the present specimen and most other dyrosaurids is the brevity of the lacrymal and prefrontal. As reported by Thevenin (1911) and Bergouinioux (1956), the prefrontal is approximately as long as the orbit in *Dyrosaurus phosphaticus*. This is also true for the prefrontal of *Phosphatosaurus*, based on the reconstruction published by Buffetaut (1978). The prefrontal is shorter than the orbit in the present specimen, and the length of the lacrymal approximates that of the orbit. A similar condition is found in *Terminonaris robusta*, which has recently been reinterpreted as a dyrosaurid (Wu et al., 2001),

though the lacrymal in that form is longer than the orbit. In this sense, the specimen described here is similar to derived gavialoids (such as *Gavialis*), although the lacrymal and prefrontal are long and slender in basal gavialoids, such as *Thoracosaurus*. Furthermore, the maxillary process within the lacrymal seems bound entirely by the lacrymal in the present specimen, whereas it may lie between the lacrymal and nasal in the *Dyrosaurus* specimen figured by Bergounioux (1956, plate 4); closer examination of Bergounioux's specimen is warranted. We do not know how the lacrymal and prefrontal are configured in previously described specimens of *Rhabdognathus*.

Given the lack of overlap between the material described here and holotypes used by previous workers, we choose not to erect a new taxon at this time. We tentatively refer this material to *Rhabdognathus* on the basis of the shape of the supratemporal fenestra. Hopefully, future collections will clarify the taxonomic identities of relevant specimens.

Phylogenetic implications.—Strict parsimony analyses of the most comprehensive matrices for crocodyliform relationships (Clark, 1994) support the monophyly of a clade including thalattosuchians (Metriorhynchidae, Teleosauridae, *Pelagosaurus*), known primarily from the Jurassic; Pholidosauridae, known from the Late Jurassic and Early Cretaceous; and Dyrosauridae. These taxa share a long, tubular rostrum, and prior studies argued for a more distant relationship between them (e.g., Buffetaut, 1982; Norell and Clark, 1990; Larsson, 2000), with the thalattosuchians adopting a basal position relative to other mesoeucrocodylians and with goniopholidid affinities for the pholidosaurids. The trees supported by Clark's matrix would indicate a single derivation of a tubular snout among noncrocodylian mesoeucrocodylians, whereas earlier hypotheses suggested at least three.

Single derivation was regarded as troublesome by Clark (1994) for several reasons. Not only does the result run counter to most previous considerations, the characters supporting monophyly of the long-snout clade are homoplastic. Moreover, because the latest-occurring members (dyrosaurids) adopt a basal position relative to pholidosaurids and thalattosuchians, this tree also raises stratigraphic incongruence questions.

We presently face an interesting problem. Most of our discomfort with the optimal trees comes from preconceived notions. Multiple derivations of a long snout have been so central to the general crocodyliform phylogenetic paradigm that any alternative hypothesis immediately strikes us as "wrong," even if we have no logical basis for rejecting it. The analysis presented here shows that filling in some blanks in the current matrix will not overturn the optimal hypothesis it supports.

Because phylogeny-based *a posteriori* tests of character correlation (e.g., Maddison, 1990, 2000; Pagel, 1994) have not been conducted for these taxa, suspicions that character nonindependence is responsible for allying these lineages (or even arguments that certain characters are related to long-snoutedness in the first place) remain speculative. We also face a numerical problem with this issue, as the long-snouted taxa are all restricted to a single clade. Tests of character correlation only work if the characters in question show multiple derivations (Maddison, 1990).

More detailed understanding of crocodyliform phylogeny is necessary to understand the evolution of snout morphology, but it will have additional benefits. For example, counts of taxa over time suggest that crocodyliforms suffered a very modest decrease in diversity across the Cretaceous-Tertiary boundary and a more significant decrease at the end of the Eocene (Vasse and Hua, 1998; Markwick, 1998). The Eocene diversity drop may correspond with the extinction of dyrosaurids. But to date, none of the studies addressing this issue have included the unsampled diversity (ghost lineages) implied by phylogeny. If, as suggested by Buffetaut (1978), some of the later-occurring dyrosaurids (such

as *Rhabdognathus*) are basal to other dyrosaurids, we would have to account for multiple lineages, not just one, crossing the Cretaceous-Tertiary boundary.

The analysis presented here shows that expansion, rather than modification, of currently-available data matrices is the next step. Part of this effort should involve better and more precise taxon sampling. Our analysis assumes monophyly of groups such as Pholidosauridae and Metriorhynchidae; while these assumptions may be valid, they should be tested by breaking these groups down into smaller OTU's (preferably species). Furthermore, many crocodyliforms that might prove relevant to this question have not yet been included. These include several "goniopholidid" taxa. Interestingly, as noted by Buckley and Brochu (1999), removal of dyrosaurids and pholidosaurids from the matrix results in a set of trees in which thalattosuchians are basal to other mesoeucrocodylians. This is congruent with earlier noncladistic suggestions that thalattosuchians were "primitive" mesoeucrocodylians. On the surface, it appears that dyrosaurids, pholidosaurids, or both are responsible for drawing thalattosuchians crownward. Pholidosaurids have been viewed as goniopholidid relatives (e.g., Buffetaut, 1982), and inclusion of more goniopholidid taxa (especially narrow-snouted taxa such as *Vectisuchus*) could be pivotal. We also believe that current matrices can be improved through better character sampling. Closer examination of crocodyliform skeletons will surely provide a larger suite of potentially informative characters.

We hope that new discoveries, such as the braincase reported here, will add to the available pool of material from which characters can be drawn. The locality from which this specimen came should be explored for additional material, both for the sake of phylogenetics and to assist comparisons with other published dyrosaurids. We also hope that future stratigraphic work will help pinpoint the locality's age, which will be necessary to understand how crocodyliform diversity has changed over time.

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