Journal of Vertebrate Paleontology 22(3):548–563, September 2002

DISCOVERY OF MEGALOSAUR (DINOSAURIA, THEROPODA) IN THE MIDDLE BATHONIAN OF NORMANDY (FRANCE) AND ITS IMPLICATIONS FOR THE PHYLOGENY OF BASAL TETANURAE

RONAN ALLAIN
UMR 8569 du CNRS, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris, France

ABSTRACT—I report here on the discovery of the most complete megalosaurid skull known to date, from the Calcaire de Caen Formation of northwesten France. The specimen, which represents a new species is questionably referred to *Poekilopleuron*. It includes a nearly complete, unornamented skull, characterized by its low lateral profile. In addition to its historical significance, it provides additional characters that are crucial for reconstructing the phylogeny and biogeography of basal theropods. *Poekilopleuron*? *valesdunensis* new species is closely related to *Eustreptospondylus* and *Afrovenator*, and is united with *Torvosaurus* in the family of Megalosauridae. The Megalosauridae appear less derived than the Allosauroidea but resemble the Spinosauridae, with which they form the sister-group to the Neotetanurae. The proposed phylogenetic analysis hypothesizes two previously unrecognized major radiations of carnivorous dinosaurs.

INTRODUCTION

In 1824, William Buckland described several osseous elements of a great fossil lizard from the Stonesfield Slate of England, for which he coined the name *Megalosaurus*. These remains marked the discovery of a group of large, land-dwelling reptiles of Mesozoic age. Shortly thereafter, Richard Owen allied *Megalosaurus* with *Iguanodon* and *Hylaeosaurus* in a new taxon termed Dinosauria (Owen, 1842). Many theropod taxa of Late Triassic through Late Cretaceous age, based on incomplete or indeterminate material, have since been referred to the Megalosauridae (Huene, 1926, 1932). During the past 150 years, 'megalosaurid' remains have been reported from Middle to Late Jurassic strata in Normandy, including vertebrae and a hindlimb of *Streptospondylus altdorfensis* (Cuvier, 1824; Meyer, 1832; Allain, 2001); caudal vertebrae, gastralia, and the forelimb and pes of *Poekilopleuron bucklandii* (Eudes-Deslongchamps, 1838); and the braincase of *Piveteausaurus divesensis* (Piveteau, 1923; Taquet and Welles, 1977). In strata of similar age in England, many bones have since been referred doubtfully to *Megalosaurus* (Buckland, 1824; Owen, 1856, 1883; Philips, 1871; Waldman, 1974), and an incomplete skeleton has been described as *Eustreptospondylus oxoniensis* (Huene, 1926; Walker, 1964). Most of these species remain confusing and make difficult the elucidation of relationships within basal Tetanurae (Padian, 1997; Sereno, 1999).

The discovery in 1994 of many fragments of bones by A. Dubreuil, near the village of Conteville (Calvados, Normandy, France), led a team of the Muséum National d'Histoire Naturelle to carry out excavations. The locality yielded a skull and postcranial remains of a new theropod for which the cranial osteology and the phylogenetic affinity are described below.

Institutional Abbreviations—**BMNH** or **R**, British Museum of Natural History; **MNHN**, Muséum National d'Histoire Naturelle; OUM, Oxford University Museum.

STRATIGRAPHIC CONTEXT

The holotype specimen of the new theropod (MNHN 1998-13) was collected in the Pierre de Caen of the Calcaires de Caen Formation dated from the beginning of the Middle Bathonian (Dugué et al., 1998; Fig. 1). The Pierre de Caen is an homogeneous, fine-grained biomicrite, and this explains the excellent quality of preservation of the now acid-prepared cranial material. Postcranial remains are fragmentary due to previous quarrying. The precise stratigraphic position of the theropod material in the Middle Bathonian is indicated by the in-situ occurence of the zone ammonite *Procerites progracilis*. The associated fauna is also composed of other ammonites (*Procerites* sp., *Oxycerites* sp.), Pectinidae (*Entolium corneolum*), Pleuromyidae (*Pleuromya uniformis*), Pleurotomariidae (*Pyrgotrochus* sp.), Belemnitidae (*Belemnopsis fusiformis*), Terebratulidae (*Cererithyris intermedia*), Isognomonidae (*Gervillella acuta*), Limidae (*Limatula gibbosa*), Rhynchonellidae (*Kallirhynchia concinna*), Zeilleriidae (*Rugitela cadomensis*), elasmobranchs (*Paraorthacodus* sp., *Polyacrodus* sp.), actinopterygians (*Leptolepis* sp.), and drift wood. The bank in which the bones of the new theropod were collected is intersected by siliceous peg-like structures that characterize the top of the Pierre de Caen (Dangeard and Rioult, 1961) and thus confirm its early Middle Bathonian age (approximately 169 Ma). These siliceous features, perpendicular or oblique to the bedding plane, are interpreted as roots of mangrove trees and burrows (Dangeard and Rioult, 1961). If so, they indicate a low-energy, subtidal environment of deposition (Rioult, 1962; Dugué et al., 1998). Such an environment is consistent with the relative abundance of fossil vertebrates found in the Pierre de Caen. Teleosaur remains have been reported in the Pierre de Caen as early as 1812 by Cuvier in his 'Recherches sur les ossemens fossiles.'' Shortly after, Eudes-Deslongchamps (1838) described the remains of a ''large fossil saurian intermediate between the crocodiles and the lizards,'' in fact a theropod, for which he coined the name *Poekilopleuron bucklandii*. Except for several caudal vertebrae, and two gastralia, there is no comparable material, for the time being, between *Poekilopleuron bucklandii* and the new megalosaurid of Conteville. The affinity between the two taxa remains uncertain, but both being sympatric, the new specimen of Normandy is questionably referred to *Poekilopleuron*. Furthermore, a well developed additional spur, anterior to the neural spine has been observed on the neural arches of two middle caudal vertebrae of the new megalosaurid. Such an additional spur is unknown in *Poekilopleuron bucklandii* (Eudes-Deslongchamps, 1838:pl. 2, fig. 1; Allain and Chure, in press), and a new specific name is, thus, proposed for the new specimen. Further examination of the postcranial material of the new me-

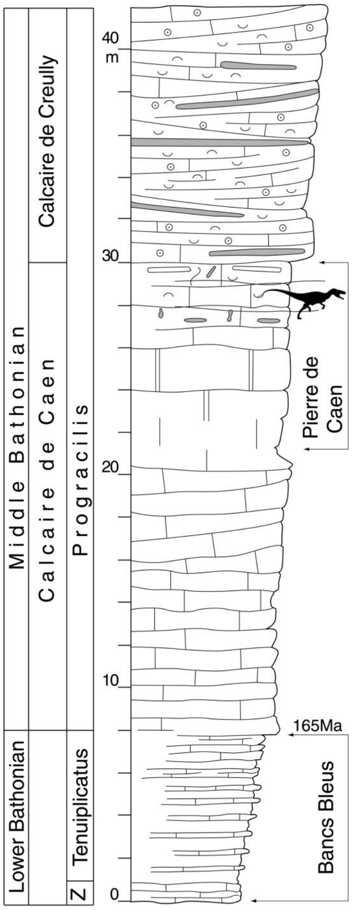

FIGURE 1. Synthetic section with Ammonite zones of the Lower to Middle Bathonian series in the region of Caen, Calvados, France. Measurements are in meters. The silhouette indicates the stratigraphic level of *Poekilopleuron*? *valesdunensis*. Modified from Dugué et al. (1998).

galosaurid from Conteville (now in preparation), could provide additional features to know if the two species are really cogeneric. A complete review of the genus *Megalosaurus* is now in progress and is beyond the scope of this paper. But it appears, as previously suggested by Rauhut (2000), that *Megalosaurus* which should be restricted to the lectotype dentary, is not diagnosable (Allain and Chure, in prep.).

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
SPINOSAUROIDEA Stromer, 1915
MEGALOSAURIDAE Huxley, 1869
POEKILOPLEURON incertae sedis Eudes-Deslongchamps, 1838

POEKILOPLEURON? *VALESDUNENSIS, SP. NOV.*

(Figs. 2–16)

Holotype—MNHN 1998-13, nearly complete skull and associated partial skeleton.

Type Locality—Conteville, Calvados, France.

Horizon and Age—Progracilis zone of the 'Calcaire de Caen' formation, Middle Jurassic (Middle Bathonian).

Etymology—From Val-es-Dunes, the Norman name of the battlefield near Conteville where the rebellious barons of the Bessin and the Cotentin were defeated by William the Conqueror in 1047 and where the holotype was found; *ensis*, from Latin.

Diagnosis—Tetanurine characterized by a very low skull, at least three times longer than high; parietals not visible in lateral view; a straight medial margin of the upper temporal fenestra; a well developed ventral process on the jugal ramus of the ectopterygoid; a deeply grooved posterior margin of the ectopterygoid ahead of the subtemporal fenestra; a double curvature of the anterodorsal margin of the maxillary nasal ramus; a postorbital ventral process with U-shaped cross section; the absence of a quadrate–quadratojugal fenestra; a large external mandibular fenestra; a mylohyoid foramen largely opened anteroventrally.

DESCRIPTION

General

The reconstructed skull (Fig. 2) is almost 50 cm long, with an orbital height of 15 cm. Among large theropod dinosaurs, only the specialized skull of the Spinosauridae (Charig and Milner, 1997) and that of *Afrovenator* (Sereno et al., 1994) present an orbital height that is less than one third the skull length. The absence of fusion between the frontoparietals, as well as between various elements of the braincase, indicates that the specimen was immature at the time of death. There are five major openings on each side of the skull. The external naris is 3 cm long and bounded by the nasal, the premaxilla and, to a lesser extent, by the maxilla. The external antorbital fenestra is 12 cm long and 9 cm high. It is bounded posteroventrally by the jugal. As in *Sinraptor* (Currie and Zhao, 1993a), *Carcharodontosaurus* (Sereno et al., 1996) and *Afrovenator*, the orbit is relatively short anteroposteriorly. The intertemporal bar is more reduced than in *Sinraptor*. The medial margin of the upper temporal fenestra, formed by the parietal and the frontal, is straight, whereas it is laterally deflected, at the level of the postorbital in other carnosaurs. There is neither horn, lacrymal, frontal or postorbital crest. The cranium is thus devoid of any ornamentation. Even a supraoccipital (nuchal) crest, present in all other large theropods, is lacking. The external mandibular fenestra is much larger than it is in *Allosaurus* (Madsen, 1976).

Premaxilla

Both premaxillae (48 mm broad) are partially preserved (Fig. 3). Each is pierced by about fifteen foramina for branches of the medial ethmoidal nerve and subnarial arteries (Currie anz Zhao, 1993a). The premaxillary body is longer than deep under the external naris, whereas it is deeper than long in *Ceratosaurus* (Gilmore, 1920), abelisaurids, *Torvosaurus* (Galton and Jensen, 1979; Britt, 1991), *Acrocanthosaurus* (Stovall and Langston, 1950; Harris, 1998; Currie and Carpenter, 2000) and tyrannosaurids. As in *Torvosaurus* (Britt, 1991) and tyrannosaurids, a broad foramen pierces the base of the nasal process of the premaxilla. The nasal process is at least 35 mm long and inclines posterodorsally at an angle of about 40° relative to the the premaxillary tooth row. As in *Allosaurus* and *Sinraptor*, the anteroventral margin of the premaxilla is vertical and shows an inflection point anteriorly to the base of the nasal process. This inflection is in a more posterodorsal position in *Torvosaurus* (Britt, 1991:fig. 3D). The flattened medial symphysis covers more than half of the medial surface and extends over the entire preserved part of the nasal process. Only the basal part of the maxillary process of the right premaxilla is preserved. The position of this process is, as in '*Megalosaurus*' *hesperis* (Waldman, 1974), intermediate between *Sinraptor* and *Allosaurus*. Although incomplete, the subnarial process is reminiscent of that observed in *Torvosaurus*, being less dorsally directed than

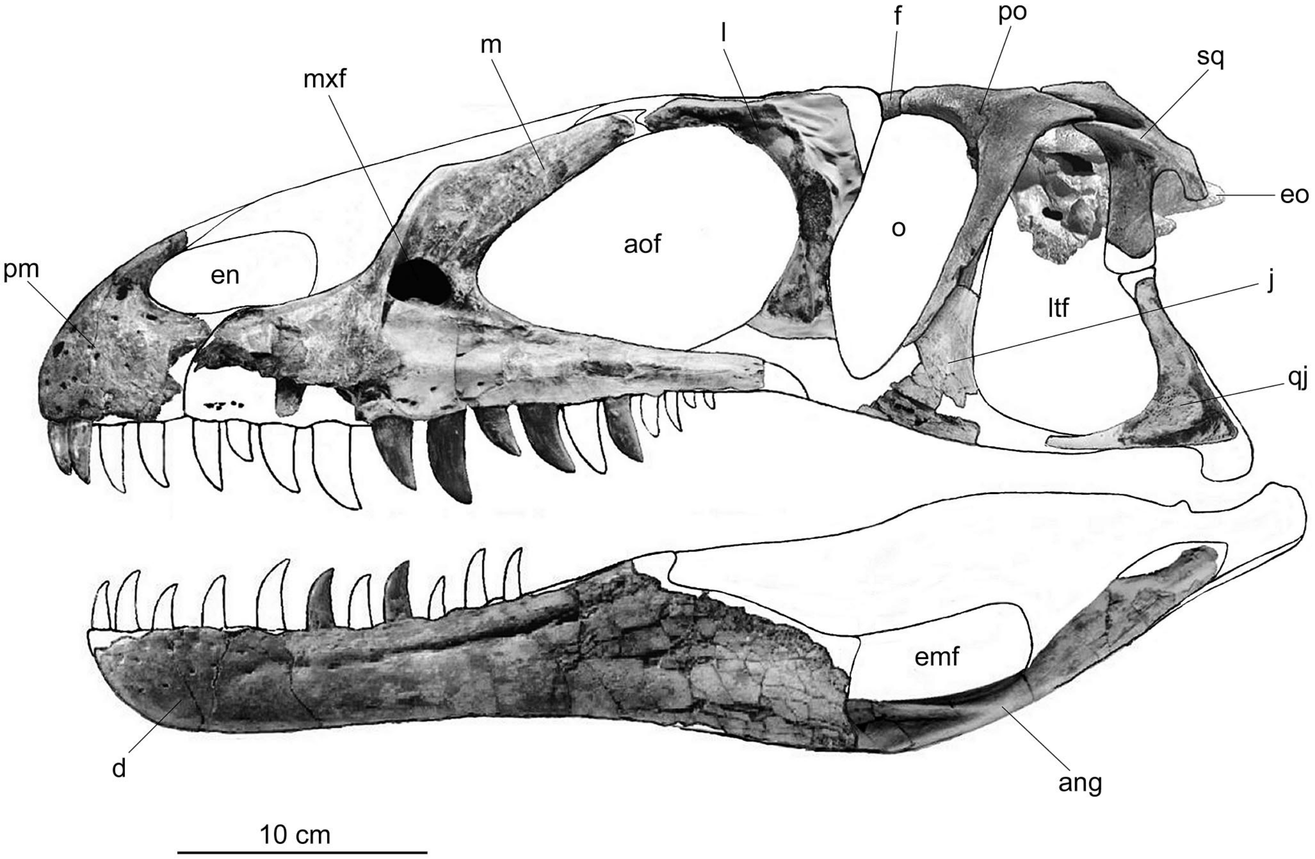

FIGURE 2. Skull of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13), in left lateral view. The premaxilla, maxilla, and lacrymal are mirror images of those of the right side. **Abbreviations**: **ang**, angular; **aof**, antorbital fenestra; **d**, dentary; **emf**, external mandibular fenestra; **en**, external naris; **f**, frontal; **j**, jugal, **l**, lacrimal; **ltf**, lateral temporal fenestra; **m**, maxilla; **mxf**, maxillary fenestra; **o**, orbit; **pm**, premaxilla; **po**, postorbital; **qj**, quadratojugal; **sq**, squamosal.

in *Sinraptor*. There are four premaxillary alveoli, a primitive condition for theropods. Only the first two left premaxillary teeth are preserved. The first three left and the second right alveoli house replacement teeth. The interdental plates are unfused. They increase posteriorly in height, and are all taller than long, whereas the second interdental plate of *Sinraptor* is longer than tall (Currie and Zhao, 1993a). The premaxillary teeth are laterally compressed and asymmetrical with the posterior carina pointing lingually as in *Torvosaurus*. These teeth are not D-shaped as in *Allosaurus* or Tyrannosauridae (Osborn, 1912). Both anterior and posterior carinae possess 11 denticles per 5 mm midway down each carina, but the anterior carina extends over approximately half of the tooth height from the tip.

Maxilla

The maxilla is more than 23 cm long (Fig. 4). As in '*Megalosaurus*' *hesperis*, *Torvosaurus*, and *Afrovenator*, its anterior ramus is longer than deep, and forms the ventral margin of the external naris. The lateral surface of the maxilla is rugose along its anterior edge, above the tooth row, where it is pierced by the superior labial foramina (Currie and Zhao, 1993). The rest of the lateral surface is smooth and only indented behind the nasal ramus, where it defines the extent of the antorbital fossa. Two fenestrae pierce the maxilla within the antorbital fossa. The promaxillary fenestra (Witmer, 1997) is not visible in lateral view, concealed by the lamina lateralis of the ascending ramus of the maxilla. The promaxillary fenestra inflates the portion of the maxilla flooring the naris, forming a distinctive vestivular bulla. The maxillary fenestra is large and more or less rounded in shape. It is closed medially, as in '*Megalosaurus*' *hesperis*, *Eustreptospondylus*, *Afrovenator*, and *Piatnitzkysaurus* (Bonaparte, 1986), whereas it is open in *Monolophosaurus* (Zhao and Currie, 1993), *Sinraptor* and *Allosaurus*. The margins of the alveolar ramus of the maxillary are regular, straight and converge posteriorly. In medial view, the superior margin is not indented to form a distinct border of the antorbital fenestra. Rather, the border extends only, in lateral view, in front of the external antorbital fenestra (Fig. 4A). This feature distinguishes *Poekilopleuron*? *valesdunensis* from '*Megalosaurus*' *hesperis* (R 333) in which, medially, the antorbital fossa is more developed ventrally and behind the ascending ramus. While the posterior margin of the ascending ramus of the maxilla has a regular curvature, its anterior margin presents an inflection at midheight. The angle formed between the anterior margin of the ascending ramus and the alveolar ramus is thus about 65°, anterior to the point of inflection and 30° thereafter. This double curvature of the ascending ramus is more conspicuous in *Poekilopleuron*? *valesdunensis* and '*Megalosaurus*' *hesperis* than in any other theropod. The medial surface of the maxilla has a prominent anterodorsal process (Fig. 4B). It contacts the premaxilla laterally, the vomer ventromedially and the opposite maxilla dorsomedially. This process is higher in position than that of *Sinraptor*, but lower than that of *Allosaurus*. The interdental plates are separated from each other. There are 13 laterally compressed maxillary teeth. As in the premaxillary teeth, the anterior carina extends onto only the distal part of the crown.

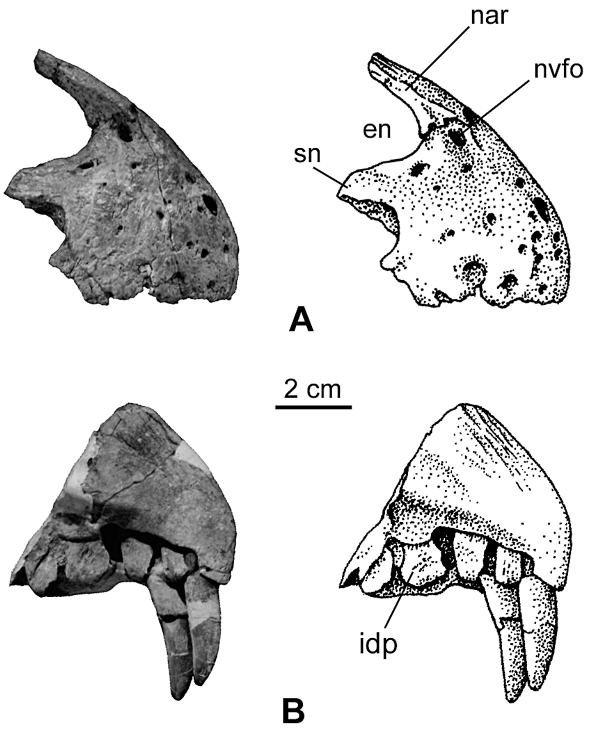

FIGURE 3. Premaxillae of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, right premaxilla in lateral view; **B**, left premaxilla in medial view. **Abbreviations**: **en**, external naris; **idp**, interdental plates; **nar**, nasal ramus; **nvfo**, neurovascular foramen; **sn**, subnarial process.

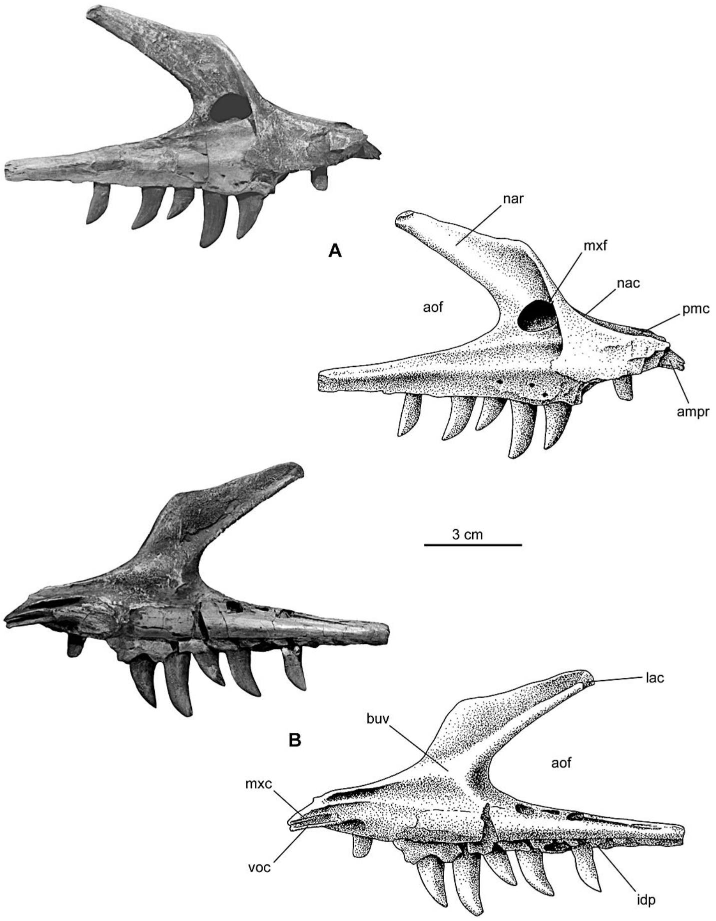

FIGURE 4. Right maxilla of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, lateral view; **B**, medial view. **Abbreviations**: **ampr**, anteromedial process; **aof**, antorbital fenestra; **buv**, bulla vestibularis; **idp**, interdental plates; **lac**, contact with lacrimal; **mxc**, maxillary contact on the anteromedial process of the maxilla; **mxf**, maxillary fenestra; **nac**, contact with nasal; **nar**, nasal ramus of maxilla; **pmc**, contact with premaxillary; **voc**, slot for vomer on anteromedial process of the maxilla.

Frontal

The two frontals are complete and well preserved. There is a deeply interdigitating transverse frontoparietal suture, which protrudes laterally into the upper temporal fenestra (Fig. 5A). The absence of fusion between the two frontals suggest that the individual was immature at the time of death. The interfrontal suture is straight anteriorly and slightly sinuous posteriorly. The frontals are quite similar in shape to those of *Eustreptospondylus* but are significantly thicker in this latter genus. As in *Allosaurus*, the median contact between the frontals is intricately sculptured (Fig. 5B), allowing no movement between the two frontals. As in *Herrerausurus*, *Ceratosaurus* and *Eustreptospondylus*, the associated frontals are longer than wide. The frontal thins anteriorly to underlap the nasal. Lateral to the frontonasal suture, a bony projection, with an associated cavity posteriorly, marks the deep sutural contact with the prefrontal. Behind this suture, the frontal makes a minimal contribution to the orbital rim. More posteriorly, at the level of the upper temporal fenestra, is the contact surface for the postorbital, similar to that for the prefrontal. Two depressions occur on the ventral surface of each frontal (Fig. 5C). The lateral one marks the dorsal portion of the orbit, whereas the medial one housed the paired olfactory nerves, and the olfactory bulbs. The deep notch located behind the orbit and medial to the frontopostorbital suture, indicates the contact for the laterosphenoid buttress.

Parietal

The parietals are unfused. Together the parietals are as long as wide, forming a flat platform 18 mm wide between the upper temporal fenestrae (Fig. 5A). There is neither a sharp sagittal crest, as in Tyrannosauridae and Troodontidae, nor a nuchal crest, which is present in all the other large carnivorous dinosaurs such as *Ceratosaurus*, *Majungatholus* (Sampson et al., 1998), *Allosaurus*, *Carcharodontosaurus*, *Sinraptor*, or *Tyrannosaurus*. Consequently, the parietal is not visible in lateral view (Fig. 2). The parietopostorbital and parietosquamosal contact surfaces are respectively reduced anteriorly and posteriorly. Ventrally, the ventral surface of the parietal contacts the prootic and the laterosphenoid buttress (Fig. 5C).

Lacrimal

The posterodorsal portion of the impression of the right lacrimal is missing (Fig. 6). As preserved, the lacrimal is approximately 9 cm long and 11 cm high. The nasal and jugal rami of the lacrimal meet at an angle of about 80°. The jugal ramus expands ventrally into a broad flange to articulate with the jugal, whereas the nasal ramus tapers anteriorly as in *Torvosaurus*, *Afrovenator*, and *Eustreptospondylus*. The posterior margin of the jugal ramus is uniformly concave in lateral view, whereas it has two concavities separated by a short process in *Acrocanthosaurus*, Sinraptoridae, Abelisauridae, and *Monolophosaurus*. In spite of the poor preservation of the lacrimal, there is no indication of a horn. Lacrimal horns are absent in several basal

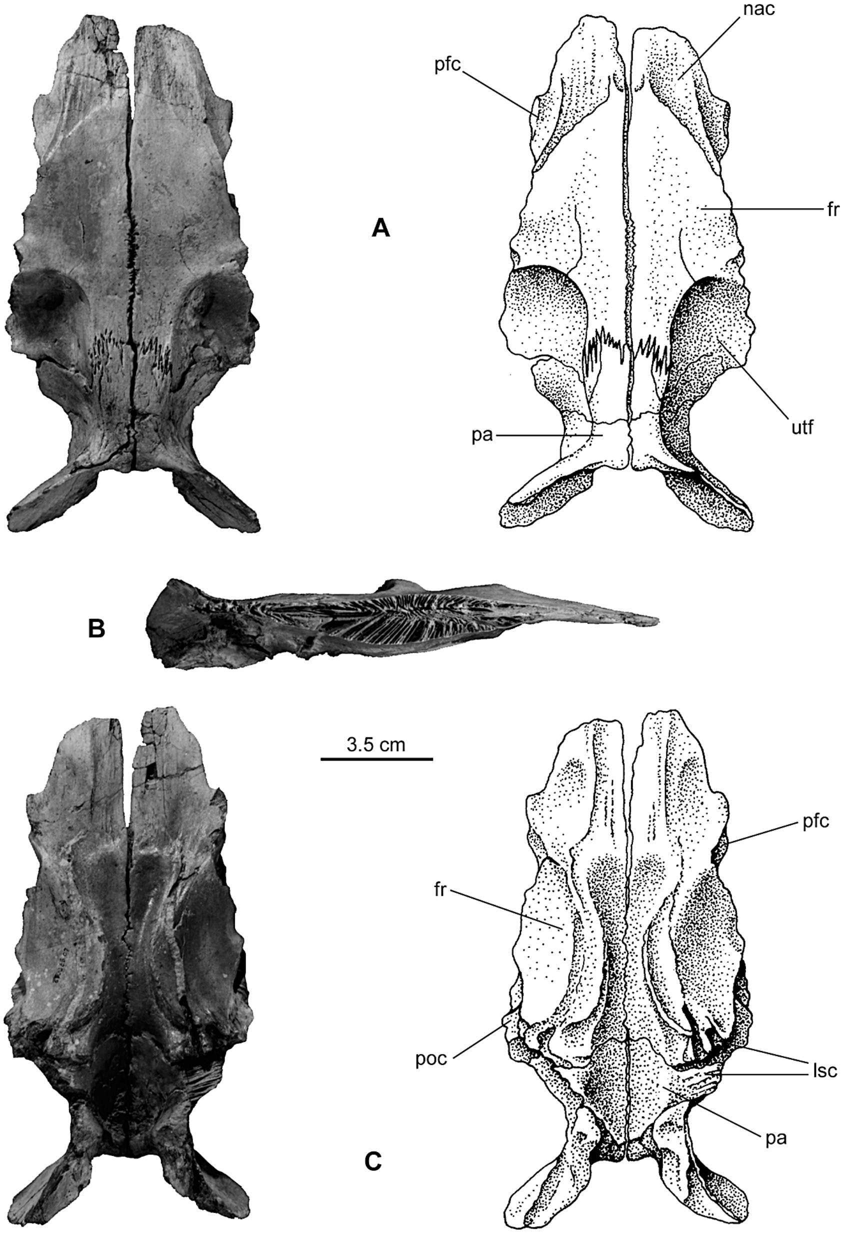

FIGURE 5. Frontoparietals of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, dorsal view; **B**, left frontoparietal in medial view; **C**, ventral view. **Abbreviations**: **fr**, frontal; **lsc**, contact with laterosphenoid; **nac**, contact with nasal; **pa**, parietal; **pfc**, contact with prefrontal; **poc**, contact with postorbital; **utf**, upper temporal fenestra.

tetanuran taxa (e.g., *Eustreptospondylus* and *Torvosaurus*), whereas they are small in Sinraptoridae, and prominent in *Allosaurus*, *Ceratosaurus* and *Monolophosaurus*. Following Britt's 'terminology' (1991), the medial blade of the jugal ramus of the lacrimal of *Poekilopleuron*? *valesdunensis* is anteroposteriorly broader than the lateral one, as in *Torvosaurus* and *Eustreptospondylus*. The lateral blade is more rounded dorsally in *Poekilopleuron*? *valesdunensis* than in *Eustreptospondylus*.

Postorbital

Both postorbitals are preserved. As in other basal theropods, the postorbital is a triradiate bone. Medially, a small foramen marks the meeting point of the three rami of the postorbital (Fig. 7B). The lateral surface of the supraorbital ramus is slightly rugose (Fig. 7A). This rugosity does not extend ventrally, as in *Allosaurus*, and forward to contact the lacrimal and prefrontal, as in *Acrocanthosaurus*, abelisaurids and carcharodontosaurids. The dorsal rim of the bone is smoothly rounded. Dorsally, the supraorbital ramus forms the anterolateral margin of the upper temporal fenestra. It contacts the frontal medially. The ventral ramus is 11 cm long, and curves slightly anteriorly. In contrast with members of Neotetanurae, it extends as far down as the ventral limit of the orbit and separates the orbit from the lateral temporal fenestra along its entire length. As in *Torvosaurus*, *Eustreptospondylus*, and *Afrovenator*, the ventral ramus is broader transversely than anteroposteriorly and U-shaped in cross section, with a backward concavity. The U-shaped groove, indicating the contact between the postorbital process of the jugal and the postorbital is 6 cm long. In distal

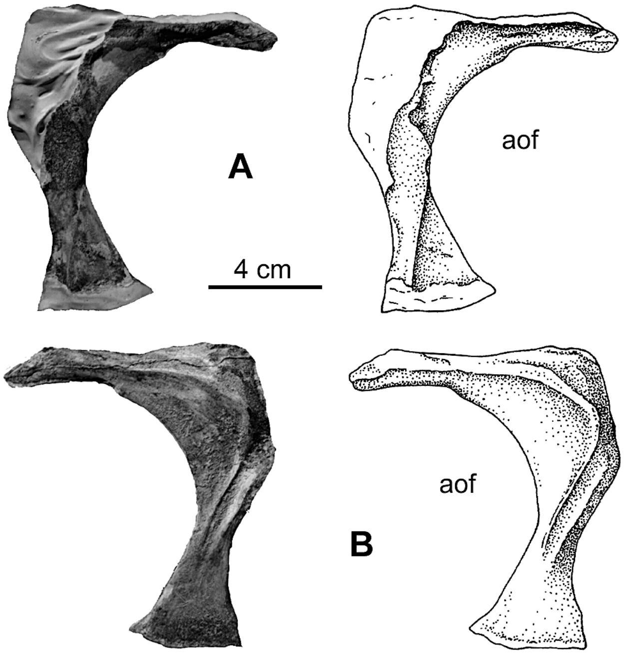

FIGURE 6. Right lacrimal of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, lateral view; **B**, medial view. **Abbreviation**: **Aof**, antorbital fenestra.

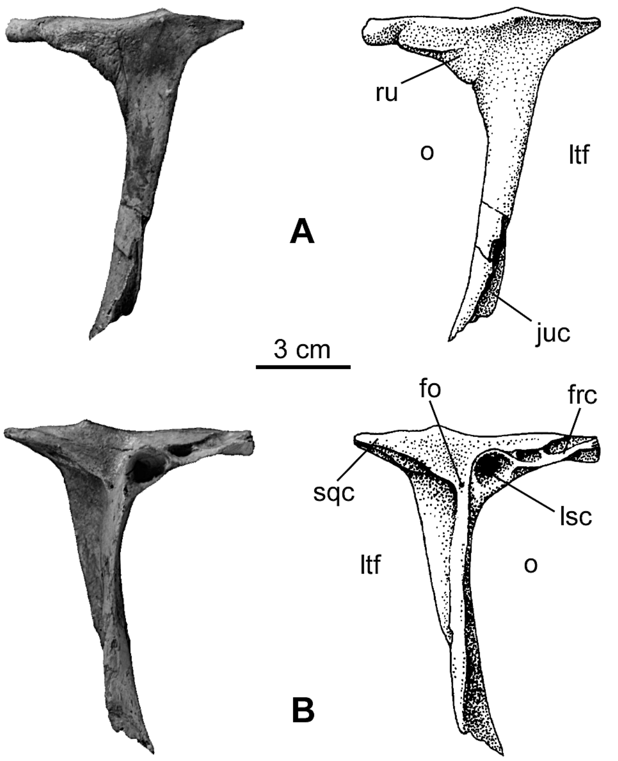

FIGURE 7. Left postorbital of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, lateral view; **B**, medial view. **Abbreviations**: **fo**, foramen; **frc**, contact with frontal; **juc**, contact with jugal; **ltf**, lateral temporal fenestra; **lsc**, contact with laterosphenoid; **o**, orbit; **sqc**, contact with squamosal; **ru**, orbital rugosity.

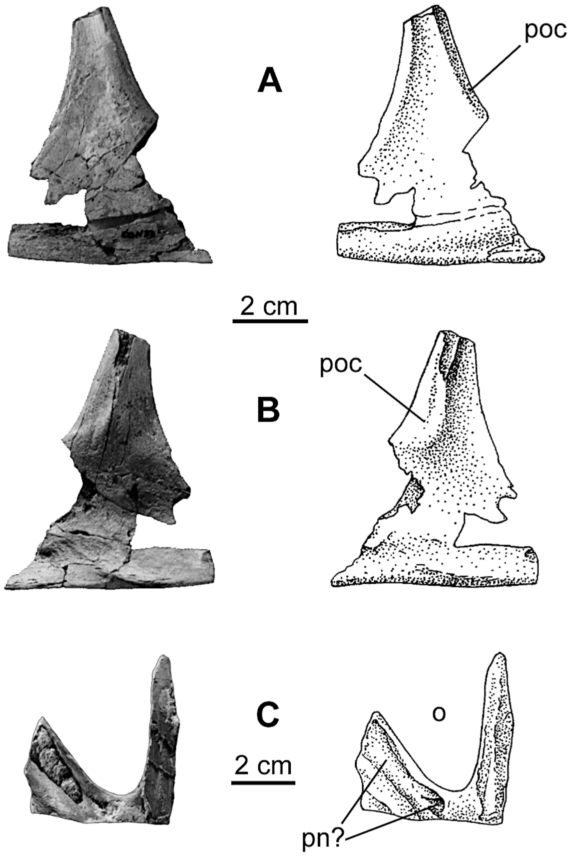

FIGURE 8. Jugals of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, right jugal in lateral view; **B**, right jugal in medial view; **C**, Suborbital part of the left jugal in lateral view. **Abbreviations**: **o**, orbit; **pn**, pneumatic opening; **poc**, contact with postorbital.

view, the medial margin of the U-shaped groove of *Poekilopleuron*? *valesdunensis* is more developed posteriorly than the lateral one. This condition is reversed in *Eustreptospondylus*. A medial cavity located at the top of the ventral ramus receives the buttress of the laterosphenoid. The 2.5 cm long intertemporal ramus of the postorbital inserts in a deep slot on the lateral suface of the intertemporal process of the squamosal. The entire intertemporal bar is thus 3 cm long. In *Sinraptor*, the intertemporal ramus of the postorbital has a limited lateral exposure.

Jugal

Two pieces of jugal could be identified: the postorbital process of the right jugal, with its surrounding part (Fig. 8A, B) and an impression of the suborbital part of the left jugal (Fig. 8C). Although incomplete anteriorly, the jugal takes part in the rim of the antorbital fossa. Laterally, an elongated depression and a small recess, both located anteroventral to the orbit, suggest the jugal was pneumatized. The postorbital process of the jugal is tall and slender and has a sloping contact with the postorbital bone, along its entire length. The ventral ramus of the postorbital wraps around the rounded anterior edge of the postorbital process of the jugal, onto the medial surface. This is a primitive characteristic. As with *Torvosaurus*, *Poekilopleuron*? *valesdunensis* shows little development of an outer, recessed postorbital facet on the jugal. The inner postorbital facet is more extensive than the outer one and, as in *Edmarka* (Bakker et al., 1992), it is composed by an elongated sulcus with an elevated posterior edge.

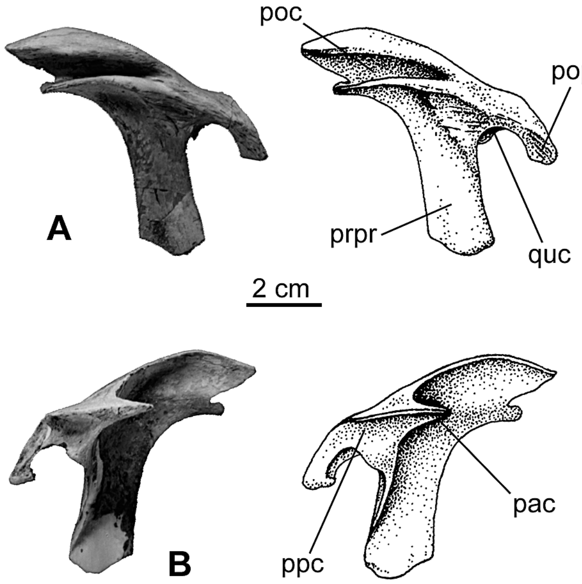

FIGURE 9. Left squamosal of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, lateral view; **B**, medial view. **Abbreviations**: **pac**, contact with parietal; **poc**, contact with postorbital; **popr**, postcotyloid process; **ppc**, contact with paroccipital process; **prpr**, precotyloid process; **quc**, quadrate contact.

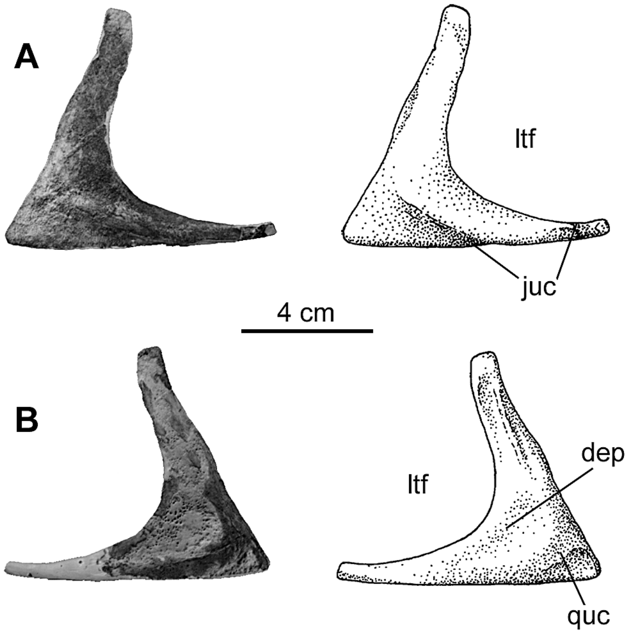

FIGURE 10. Right quadratojugal of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, lateral view; **B**, medial view. **Abbreviations**: **dep**, depression; **juc**, contact with jugal; **ltf**, lateral temporal fenestra; **quc**, contact with quadrate.

Squamosal

In lateral view, the squamosal is a triradiate bone that bounds the upper temporal fenestra posterolaterally and the lateral temporal fenestra posterodorsally. The intertemporal process of the squamosal has a deep, 3.5 cm long slot for the posterior ramus of the postorbital (Fig. 9A). The dorsal margin of the squamosal of *Poekilopleuron*? *valesdunensis* is strongly convex whereas it is slightly concave in *Eustreptospondylus*. The ventral process of the squamosal is indented by a deep quadrate cotylus and could be divided into pre- and postcotyloid processes. The head of the quadrate would have been exposed laterally between these two processes. The blade-like precotyloid process, which contacts distally the quadratojugal, is directed posteroventrally. Unlike more advanced theropods such as Allosauridae, *Monolophosaurus* and Tyrannosauridae, there is no anterior protrusion of the precotyloid process into the lateral temporal fenestra. The hook-like postcotyloid process has a weak ventral extension. The anteromedially projected, tapering parietal process extends along the dorsal surface of the paroccipital process (Fig. 9B). It seems to have a limited contact with the parietal.

Quadratojugal

As in most theropods, the quadratojugal is L-shaped and laterally compressed (Fig. 10A). Its anterior and dorsal rami are, respectively, 8.5 cm and 8 cm long, joining posteriorly at an angle of about 70°. A broad depression occurs on the medial surface of the quadratojugal, posteroventrally to the lateral temporal fenestra (Fig. 10B). Behind this depression, the surface of the bone is swollen where it contacts the quadrate. In contrast to the condition in *Allosaurus* (Madsen, 1976), this contact area is reduced and smooth, and would allow movements between these two bones. A strong quadratojugal–quadrate contact could, however, be size-related. The dorsal ramus is tapered, and the quadratojugal–squamosal contact is not obvious. This contact does not exist in Coelophysoidea, is broader in *Allosaurus* and reaches its maximum extension in Tyrannosauridae, in which it protrudes into the lateral temporal fenestra. The anterior ramus is tapered, and deeply grooved above and below the point where it joins the two prongs of the quadratojugal process of the jugal. It suggests that the uppermost prong of the quadratojugal process is shorter than the ventral prong, in contrast with *Torvosaurus* (Britt, 1991).

Quadrate

Only the fossil imprint of the pterygoid flange of the left quadrate has been recovered. Unlike *Allosaurus*, this flange extends anteriorly rather than obliquely toward the midline. In medial view, the posterior margin of the quadrate, joining the ventral condyles of the jaw articulation to the dorsal cotyle is convex, whereas it is concave in all others theropods except *Dilophosaurus*.

Ectopterygoid

The well-preserved hook-shaped left ectopterygoid was recovered (Fig. 11A). A deep pit invades the ectopterygoid medially and extends longitudinally over the entire length of the bone. Laterally, this recess reaches the base of the jugal process but, in contrast with *Sinraptor*, does not invade it. The recess is limited medioventrally by a bony lip, leading posteriorly to the ectopterygoid flange and anteriorly to the thin anteroventrally directed pterygoid process. The ectopterygoid recess is overhung dorsolaterally by a thin bone lamina. In dorsal view, this lamina is anteroposteriorly straight, whereas its posterior part is strongly deflected laterally in *Acrocanthosaurus* and *Allosaurus*, and medially in *Deinonychus* (Ostrom, 1969). In the same way, the ectopterygoid flange is straight and does not curve medially, as in *Allosaurus*, *Acrocanthosaurus* or *Sinraptor* (Fig. 11B). The jugal process emerges from the main body of the bone and is dorsoventrally flattened. An autapomorphic recess invades this part of the jugal process posteriorly ahead of the subtemporal fenestra. Further lateral, it becomes caudally recurved, the jugal process becomes strongly mediolaterally flattened where it contacts the medial surface of the jugal. In

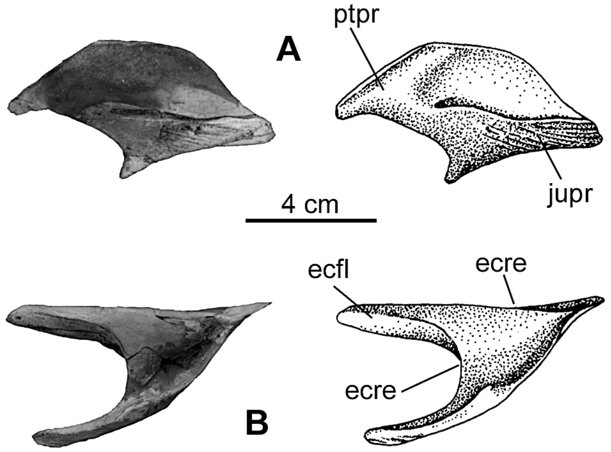

FIGURE 11. Left ectopterygoid of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, lateral view; **B**, ventral view. **Abbreviations**: **ecfl**, ectopterygoid flange; **ecre**, ectopterygoid recesses; **jupr**, jugal process; **ptpr**, pterygoid process.

lateral view, a small anteroventrally directed process, more developed than in any other theropod, emerges from the jugal ramus of the ectopyterygoid.

Braincase

The preserved remains of the braincase include both exoccipital–opisthotic complexes, the right laterosphenoid, the right prootic, the basioccipital and the parasphenoid (Fig. 12). The partial disarticulation of the braincase is consistent with the immaturity of the specimen. The basioccipital composes the largest part of the occipital condyle (Fig. 14A). Its dorsal surface, which makes a narrow contribution to the floor of the foramen magnum, is longitudinally depressed, giving the occipital condyle a heart-shaped aspect in posterior view. Ventrally, the basioccipital also forms the posterior portion of the basal tubera. In contrast with *Allosaurus* and *Sinraptor*, the basal tuber is wider than the transverse diameter of the occipital condyle. As in all theropods, except *Baryonyx* (Charig and Milner, 1997), the exoccipital and opisthotic are indistinguishably fused together. The paroccipital processes are strongly turned backwards, but not downwards as in Allosauridae, Carcharodontosauridae and *Sinraptor* (Fig. 13A, B). The exoccipitals are separated from each other on the midline by the supraoccipital and ventrally by the basioccipital. They only make a minor contribution to the dorsolateral corners of the occipital condyle. Laterally to the occipital condyle, three foramina lie in a depressed area between the base of the condyle and the paroccipital process. The two, more medial foramina are for branches of the hypoglossal nerve (XII): the first branch of the XIIth cranial nerve emerges through the smallest foramen, 2 mm below the second branch. More laterally, there is the larger vagus foramen for the exit of the jugular vein, and the vagus (X) and accessory (XI) cranial nerves. This foramen is divided internally into a medial and a lateral canal. The medial canal, traversed by the Xth and XIth nerves, extends to the otic capsule, where this two nerves consitute, with the glossopharingeal nerve (IX), a rounded metotic group. The IXth nerve and the posterior cerebral vein also enter the vagus foramen, from the otic capsule, but exit laterally, via the lateral canal, in the middle ear cavity. The prootic extends against the furrowed anterior surface of the opisthotic, over the proximal third of the length of the paraoccipital process (Fig. 14B). Below this contact, the opisthotic forms the posterior wall of the fenestra ovalis. The prootic bounds anterolaterally the fenestra ovalis. The trigeminal nerve (V) emerges from a large foramen between the prootic and the laterosphenoid. As in *Sinrator* and *Eustreptospondylus*, the separation of the ophthalmic branch of the trigeminal is incipient, the opening for the Vth cranial nerve being constricted in its midpart. In *Allosaurus*, *Acrocanthosaurus* and *Piveteausaurus* (MNHN 1920-7), this separation is complete. Between the fenestra ovalis and the foramen for the Vth nerve, just above the contact between the prootic, the parasphenoid and the basisphenoid, the prootic surrounds entirely the elongate foramen for the passage of the facial nerve (VII). The crista prootica is well-developed lateroventrally. In medial view, three foramina pass through the crista prootica below the foramen for the trigeminal nerve. The more posterior foramen is for the passage of the acoustic nerve (VIII), which emerged posterolaterally to the vestibule, medial to the fenestra ovalis. The foramen for the facial nerve (VII) originates from the acoustic fossa in the inner wall of the braincase, posteroventral to the trigeminal opening and anterior to that for the glossopharyngeal nerve. The anterior foramen for the abducens nerve (VI) passes down and forward from the floor of the braincase, through the prootic and not through the basisphenoid as it is the case in the Troodontidae (Currie and Zhao, 1993b). It exits dorsolaterally to the pituitary fossa, near the contact between the laterosphenoid, the prootic and the basisphenoid. In the inner wall of the prootic, posterodorsal to the trigeminal nerve and ventrally to the supraoccip-

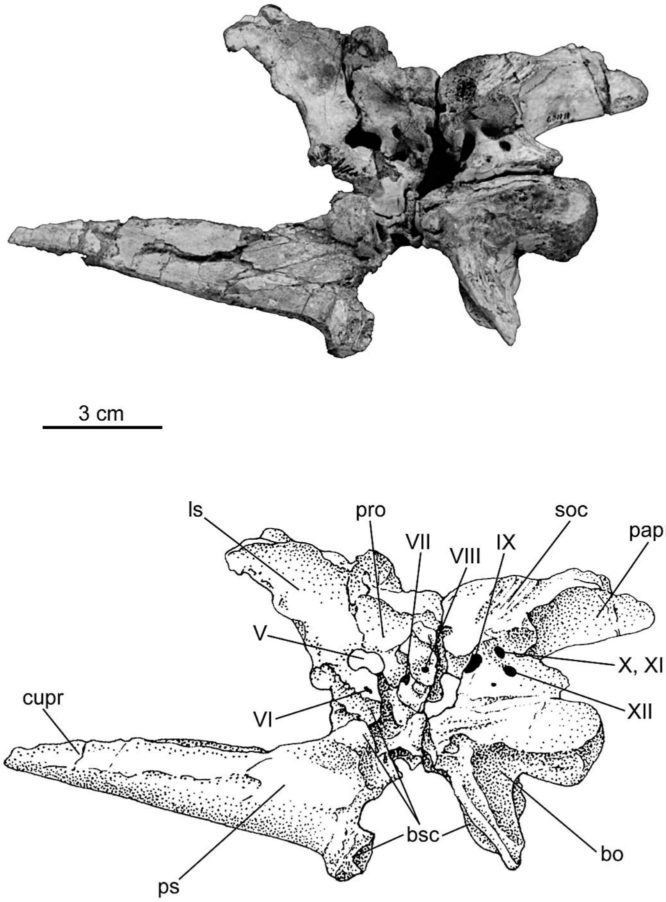

FIGURE 12. Reconstructed braincase of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13), in left medial view. **Abbreviations**: **bo**, basioccipital; **bsc**, contact with basisphenoid; **cupr**, cultriform process; **ls**, laterosphenoid; **papr**, paroccipital process; **pro**, prootic; **ps**, parasphenoid; **soc**, contact with supraoccipital; **V–XII**, cranial nerves.

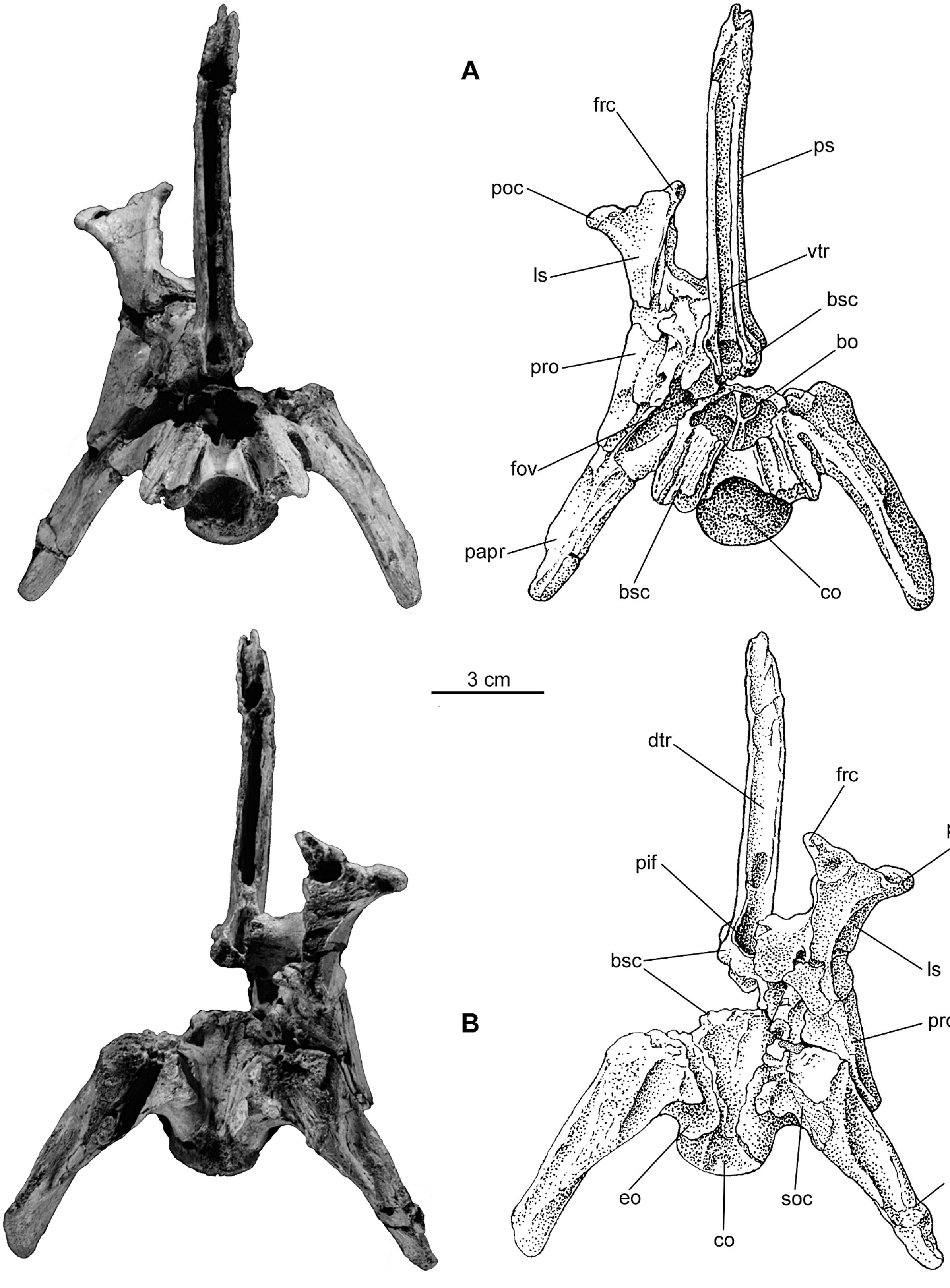

FIGURE 13. Reconstructed braincase of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, ventral view; **B**, dorsal view. **Abbreviations**: **bo**, basioccipital; **bsc**, contact with basisphenoid; **dtr**, dorsal trough of parasphenoid; **eo**, exoccipital; **fov**, fenestra ovalis; **frc**, contact with frontal; **ls**, laterosphenoid; **papr**, paroccipital process; **pif**, pituitary fossa; **poc**, contact with postorbital; **pro**, prootic; **ps**, parasphenoid; **soc**, contact with supraoccipital; **vtr**, ventral trough of parasphenoid.

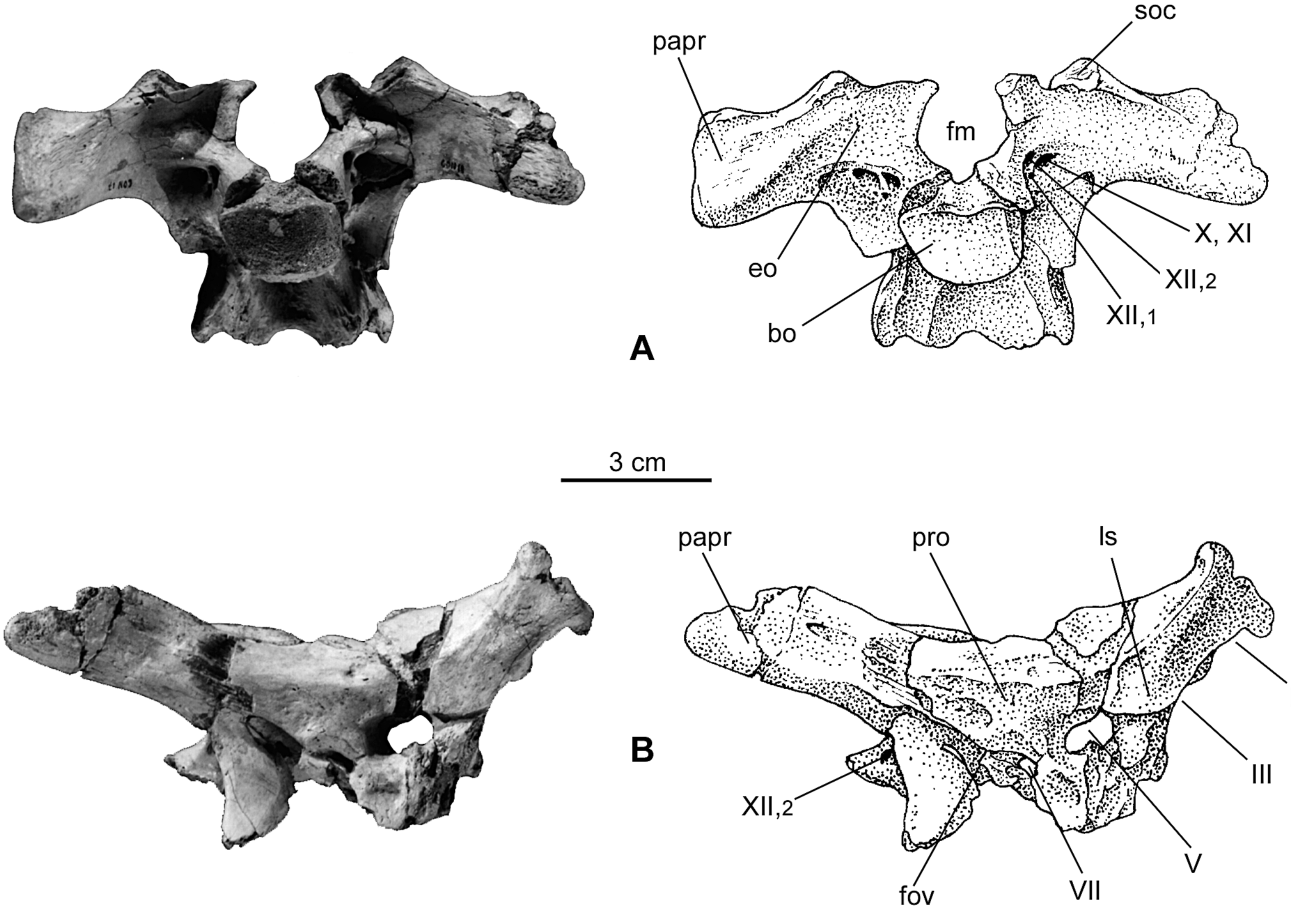

FIGURE 14. Reconstructed braincase of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, posterior view; **B**, lateral view. **Abbreviations**: **bo**, basioccipital; **eo**, exoccipital–opisthotic complex; **fm**, foramen magnum; **fov**, fenestra ovalis; **ls**, laterosphenoid; **papr**, paroccipital process; **pro**, prootic; **ps**, parasphenoid; **III**–**XII**, cranial nerves.

ital contact, a deep slot receives the median cerebral vein. The laterosphenoid forms the wall of the anterior part of the braincase, beneath the parietal. The anterodorsal process of the laterosphenoid has a distal bifid condyle for its contact with the postorbital and the frontal. There are two notches along the anteromedial margin of the laterosphenoid by which it contacts the orbithosphenoid. These notches form anterodorsally the posterior margin of the foramen for the trochlear nerve (IV) and ventrally, that of the foramen for the oculomotor nerve (III). In contrast with other known theropod braincases, the parasphenoid is not fused to the basisphenoid. While the parasphenoid fuses with the ventral surface of the basisphenoid during the late embryonic stages in crocodilians (Iordansky, 1973), this fusion is still incomplete in juvenile theropods. The parasphenoid contacts dorsolaterally the prootic, ventrally to the foramen for the facial nerve. The cultriform process is 8 cm long. A longitudinal trough runs along both the ventral and dorsal surface of the parasphenoid. The ventral trough is twice as deep as the dorsal one and extends over the entire length of the parasphenoid. In contrast to the condition in *Piveteausaurus*, the ventral trough does not widen posteriorly, and the thin bone lamina which form the lateral surfaces of the cultriform process are vertical and without a lateral concavity. Two aliform processes, located in each posteroventral corner of the lateral surface, contact the basisphenoid posteriorly. The dorsal trough for the trabecular cartilages of the interorbital septum is only 65 mm long. It is topped posteriorly by the pituitary fossa, which is pierced by two foramina for the merged internal carotids.

The braincase of an unnamed theropod (probably an allosaurid) from the Callovian of the Vaches Noires cliffs (Knoll et al., 1999) clearly differs from that of *Poekilopleuron*? *valesdunensis* in having, among other characters, a restricted participation of the supraoccipital in the rim of the foramen magnum and downturned paroccipital processes. Similarly, many characters (e.g., limited access of the frontal to the orbital rim, lateral extension of the frontal, absence of participation of the supraoccipital in the dorsal margin of the foramen magnum and more lateral orientation of the paroccipital processes) allow us to distinguish the braincase of *Piveteausaurus divesensis* from that of *Poekilopleuron*? *valesdunensis*.

Dentary

The left dentary is nearly complete, except in its posterior most part which is partially eroded (Fig. 15A). This bone is 29 cm long. Its depth is minimum (3.7 cm) at the level of the sixth and seventh alveoli. Its lower and upper margins are slightly concave in lateral view. The medial and lateral sides are flat and parallel. The dorsal margin of the lateral side is 6 mm higher than the medial one. The dentary deepens and widens anteriorly to the level of the fifth alveolus, to form the flat symphysial surface medially. The poorly defined interdentary symphysis allowed mobility between the lower jaws. The pos-

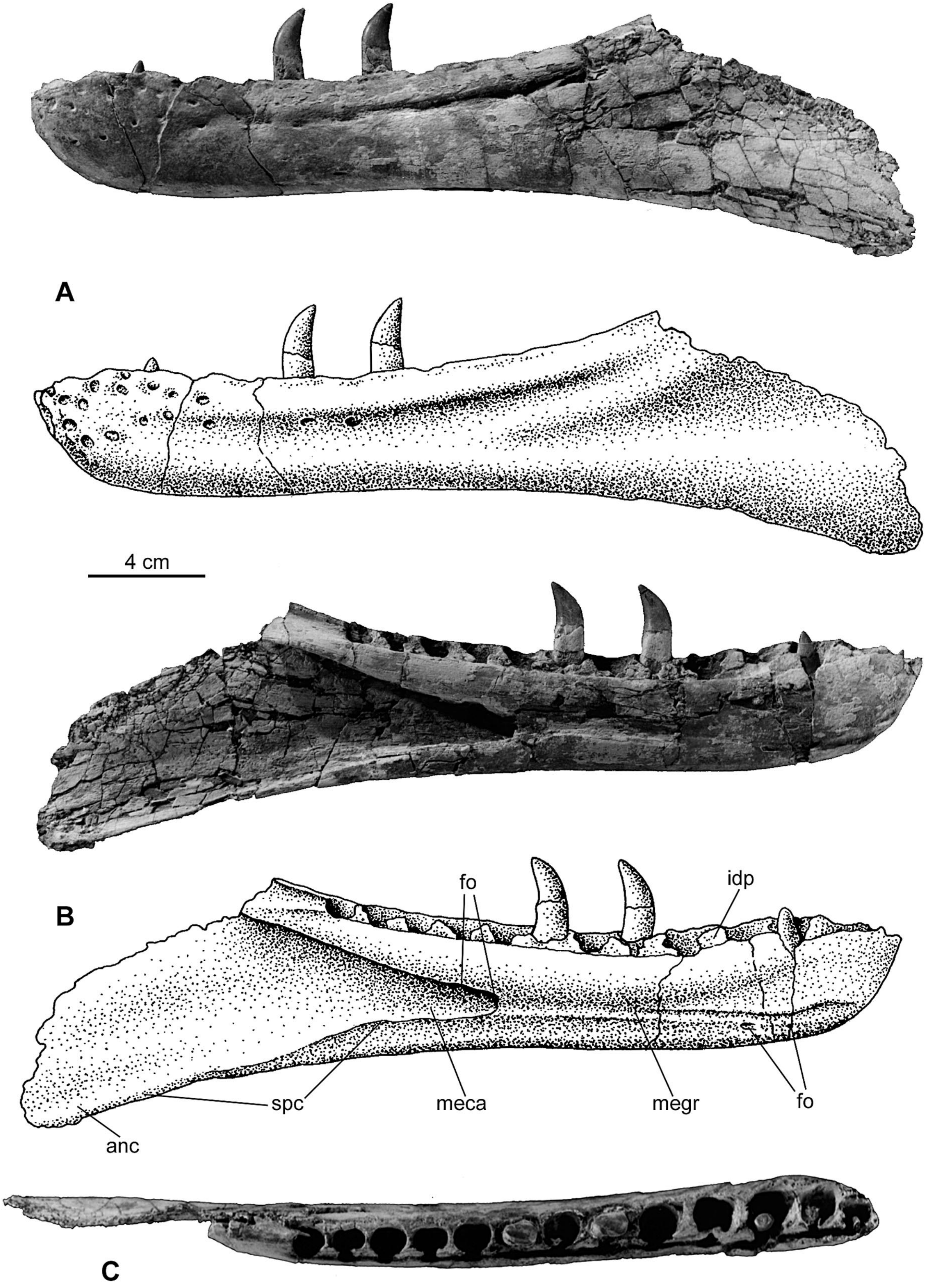

FIGURE 15. Left dentary of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, lateral view; **B**, medial view; **C**, dorsal view. **Abbreviations**: **anc**, contact with angular; **fo**, foramen; **idp**, interdental plate; **meca**, Meckelian canal; **megr**, Meckelian groove; **spc**, contact with splenial.

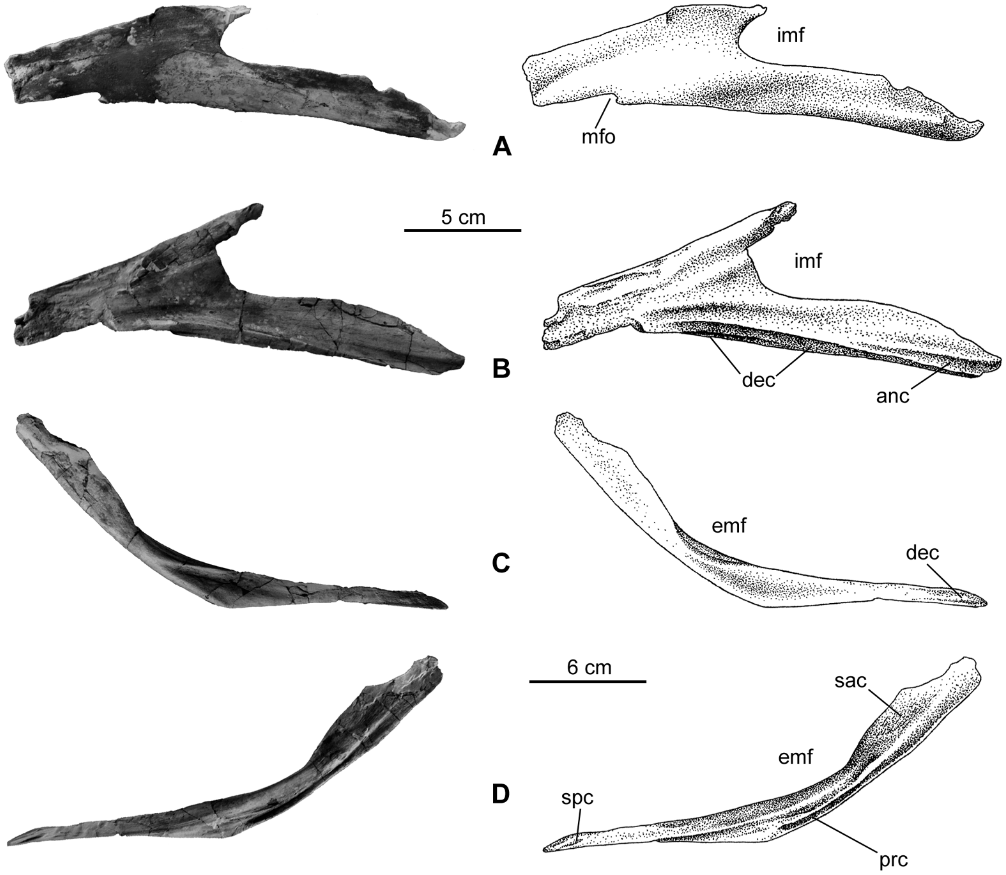

FIGURE 16. Splenials and right angular of *Poekilopleuron*? *valesdunensis*, new species (MNHN 1998-13). **A**, right splenial in medial view; **B**, left splenial in lateral view; **C**, right angular in lateral view; **D**, right angular in medial view. **Abbreviations**: **anc**, contact with angular; **dec**, contact with dentary; **emf**, external mandibular fenestra; **imf**, internal mandibular fenestra; **mfo**, mylohyoid foramen; **prc**, contact with prearticular; **sac**, contact with surangular; **spc**, contact with splenial.

terior dentary blade is slightly concave laterally, in its middle part. Its ventral and dorsal margins diverge posteriorly. In medial view, the ventral lip of the dentary blade thickens anteriorly and forms a slot for the anterior ramus of the angular (Fig. 15B). Further anteriorly, this bony lip bounds the Meckelian canal ventrally and contacts the splenial at the level of the eleventh alveolus. Like *Allosaurus* and *Sinraptor*, a foramen for the inferior alveolar nerve and the internal mandibulary artery pierces the bone beneath the ninth alveolus where the Meckelian canal passes between the splenial and dentary to become the Meckelian groove. A second, larger and more ventral foramen passes longitudinally through the body of the dentary and opens anteriorly near the end of the Meckelian groove. The Meckelian groove runs lengthwise along the medial surface of the dentary, slightly below its mid-height posteriorly, and near the ventral, rounded margin of the bone anteriorly. It is a shallow groove that is pierced anteriorly by two foramina. In contrast with *Sinraptor*, these foramina are not one above the other but one lies ahead the other. The lateral surface of the dentary is pierced by a row of mental foramina that are parallel to the dorsal margin of the bone for the inferior alveolar nerve. In the same way the most anterior part of the bone bears randomly distributed foramina for the passage of blood vessels and nerves. In dorsal view the 18,6 cm long dentary tooth row contains 13 alveoli like *Megalosaurus bucklandi*, while there are about 15 teeth in '*Megalosaurus*' *hesperis* (Walker, 1964; Waldman, 1974) (Fig. 15C). Two adult teeth are present in alveoli six and eight. Replacement teeth are also present in alveoli one, three and six. The interdental plates are unfused. The paradental groove for the dental artery runs lengthwise along the tooth row, between the bases of the interdental plates and the dorsal margin of the medial surface of the dentary. Like in other theropods, each alveolus communicates with the dental artery by means of a slot in its interdental plate. The adult teeth are 27 mm height and strongly compressed transversely. They are recurved in their apical part. Like in the premaxillary and maxillary teeth, the posterior margin of the dentary teeth is entirely serrated, while only two thirds of the anterior margin bears serrations.

Splenial

The splenial is virtually complete. It is a thin, triradiate bony plate, concave laterally and correspondingly convex medially. In contrast to *Ceratosaurus* and *Baryonyx*, its posterior margin is deeply notched to form the anterior margin of the internal mandibular fenestra. The notched splenial was found to be a neotetanurine feature in recent phylogenetic analyses (Sereno et al., 1996; Holtz, 2000) Anteriorly, the splenial extends to the level of the seventh dentary alveolus. The mylohyoid foramen is in an anterior position on the splenial and is opened anteroventrally (Fig. 16A). This foramen is absent in coelophysoids, completely surrounded by the splenial in *Ceratosaurus*, Abelisauridae, *Baryonyx*, and *Sinraptor*, and in a marginal position in *Allosaurus* and *Monolophosaurus*. In contrast with the condition in *Sinraptor* and *Allosaurus*, the posteroventral branch of the splenial is longer than the anterior one. A deep groove runs along the ventral margin of the spenial posteriorly to the mylohyoid foramen and anteriorly to the internal mandibular fenestra. It contacts the ventral lip of the dentary which bounds the Meckelian canal. The ventral margin of the spenial thickens posteriorly from this groove to form a shelf that receives the anterior end of the angular (Fig. 16B). The splenial does not wrap around the ventral margin of the dentary as in primitive theropods, such as *Herrerasaurus*, *Ceratosaurus* and coelophysoids, and *Monolophosaurus*, the Dromaeosauridae and the Troodontidae.

Angular

The boomerang-shaped angular is a bone plate, which is thickened ventrally below the external mandibular fenestra and slightly concave medially (Fig. 16C). The anterior blade of the angular is very thin and low. It is overlapped medially by the splenial and laterally by the dentary, but the surfaces of contact are smooth forming a sliding joint between these three bones. The thickened central portion of the bone forms the 5 cm long margin of the external mandibular fenestra. Medially, a shallow longitudinal groove for the articulation with the prearticular extends above the ventral margin of the angular (Fig. 16D). The posterior end of the bone bears longitudinal striations for the overlapping, immobile contact with the surangular. There is no anterior contact between the angular and the surangular, like in *Allosaurus*.

Surangular

Only a fossil impression of the medial surface of the right surangular is preserved. Like in all theropods, the dorsal border of the surangular is thickened and folded over medially to overhang the adductor fossa. Posteriorly, a medially extended hook-shaped process delimits the posterior margin of the adductor fossa and contacts the prearticular. The depth of the surangular above the external mandibular fenestra is lower than that in *Allosaurus* or *Monolophosaurus*.

METHODS

Previous phylogenetic analyses (Gauthier, 1986; Holtz, 1994, 2000; Sereno, 1999; Currie and Carpenter, 2000) have recognized two clades within the Theropoda: Tetanurae and Ceratosauria, the monophyly of this latter clade being questionned by recent works (Rauhut, 1998; Carrano and Sampson, 1999). Tetanuran synapomorphies of *Poekilopleuron*? *valesdunensis* include the position of the posteriormost maxillary tooth anterior to the orbit, pneumatic excavations within the jugal and lacrymal, and an overlapping articulation between the latter two elements. The relationships between *Poekilopleuron*? *valesdunensis* and other basal tetanurans were here assessed through a cladistic analysis of 45 cranial characters (Fig. 3A) (see Appendix 1 for character-state distributions). *Herrerasaurus* was retained as the outgroup to all other theropods, and *Ceratosaurus*, a non-tetanuran theropod, was included in this analysis as a second outgroup. The terminal taxa employed in this study were selected on the basis of completeness of their skulls. All characters were considered unordered. Character polarity was determined by outgroup comparison. Minimum-length trees were generated using the Branch-and-Bound and Heuristic algorithms in PAUP (Swofford, 1993). Characters were optimized under accelarated and delayed transformation. PAUP produced three equally parsimonious trees of 84 steps, with relatively high consistency and retention indices (C.I. = 0.67; R.I. = 0.778). The three resulting trees display similar topologies and differ only in the placement of *Afrovenator* relatively to *Poekilopleuron*? *valesdunensis* and *Eustreptospondylus* (see Appendix 1 for synapomorphies of each node). The tree allying the two european taxa is presented here (Fig. 17A).

DISCUSSION

The result supports the previously recognized monophyly of the two principal basal tetanuran clades: the Spinosauroidea (Sereno et al., 1998) and the Allosauroidea (Sereno et al., 1994, 1996; Harris, 1998; Currie and Carpenter, 2000). Unlike previous cladistic analysis (Sereno et al., 1996; Harris, 1998; Currie and Carpenter, 2000), the interrelationships of the Allosauridae, Carcharodontosauridae and Sinraptoridae are resolved. The allosaurids (*Allosaurus* and *Acrocanthosaurus*) are united on the basis of the exclusion of the basioccipital from the basal tubera; the configuration of the paroccipital process which curves below the level of foramen magnum; and the keyhole-shaped lateral temporal fenestra. The carcharodontosaurids (*Carcharodontosaurus* and *Giganotosaurus* [Coria and Salgado, 1995]), which share heavily sculptured facial bones, a suborbital flange on the postorbital and highly pneumatic braincase, appear, within allosauroids, more closely related to sinraptorids than to allosaurids (Fig. 17A). Several cranial features support spinosauroid monophyly, including the extension of the ventral ramus of the postorbital as far down as the ventral margin of the orbit, the rectangular shape of the anterior ramus of the maxilla, and a maximum height at the orbit that is less than one-third of the length of the skull. Spinosauroids include two clades, the long-snouted Spinosauridae and the Megalosauridae. Megalosaurids are characterized by the U-shaped cross section of the ventral ramus of the postorbital, the absence of quadrate fenestra and a supraoccipital crest on the parietal. This analysis suggests that megalosaurids can be divided into two subgroups, the North American Torvosaurinae (including *Edmarka rex*; Bakker et al., 1992), and the Megalosaurinae which include the European *Poekilopleuron* and *Eustreptospondylus*, and the Gondwanan *Afrovenator*. *Piatnitzkysaurus floresi* (Bonaparte, 1986) from the Middle Jurassic of Argentina and *Streptospondylus altdorfensis* (Allain, 2001) are also tentatively referred here to megalosaurids (see Appendix 4 for phylogenetic definitions). The existence of a geographic connection between Laurasia and Gondwana prior to the Late Jurassic opening of the Tethys could account for such a distribution. The relationships proposed above within the basal Tetanurae hypothesize two previously unrecognized major radiations of carnivorous dinosaurs (Fig. 17B). The first one occurred during the Early Jurassic before the breakup of Pangea and concerns the most basal tetanuran clade, the spinosauroids. Although the Early Jurassic theropod fossil record is poor, discoveries of basal Tetanurae in the Toarcian of North Africa (Jenny et al., 1980) and Antarctica (Hammer and Hickerson, 1994) are consistent with such a radiation.

During the Middle to Late Jurassic, allosauroids underwent a global radiation (Fig. 17B). By the Late Jurassic, coelurosaurs had also achieved a global distribution. Thus, the early evolution of avian coelurosaurs and the origin of birds participated in this second major radiation. At the same time, the European and North American megalosaurids apparently became extinct and *Afrovenator* is the only known Cretaceous survivor of a relatively uniform megalosaurid Early to Middle Jurassic radiation (Fig. 17B; Sereno et al., 1994). A similar Late Jurassic radiation has also been observed in neosauropod dinosaurs (Wilson and Sereno, 1998). Although this second major radiation takes place during the beginning of the breakup of Pangea, with the separation of the Gondwanan and Laurasian landmasses as early as the Callovian (Smith et al., 1994), the correlation of these two events remains difficult to establish. Assuming that I have correctly ascertained their phylogenetic relationships, and in spite of the land connections between North-

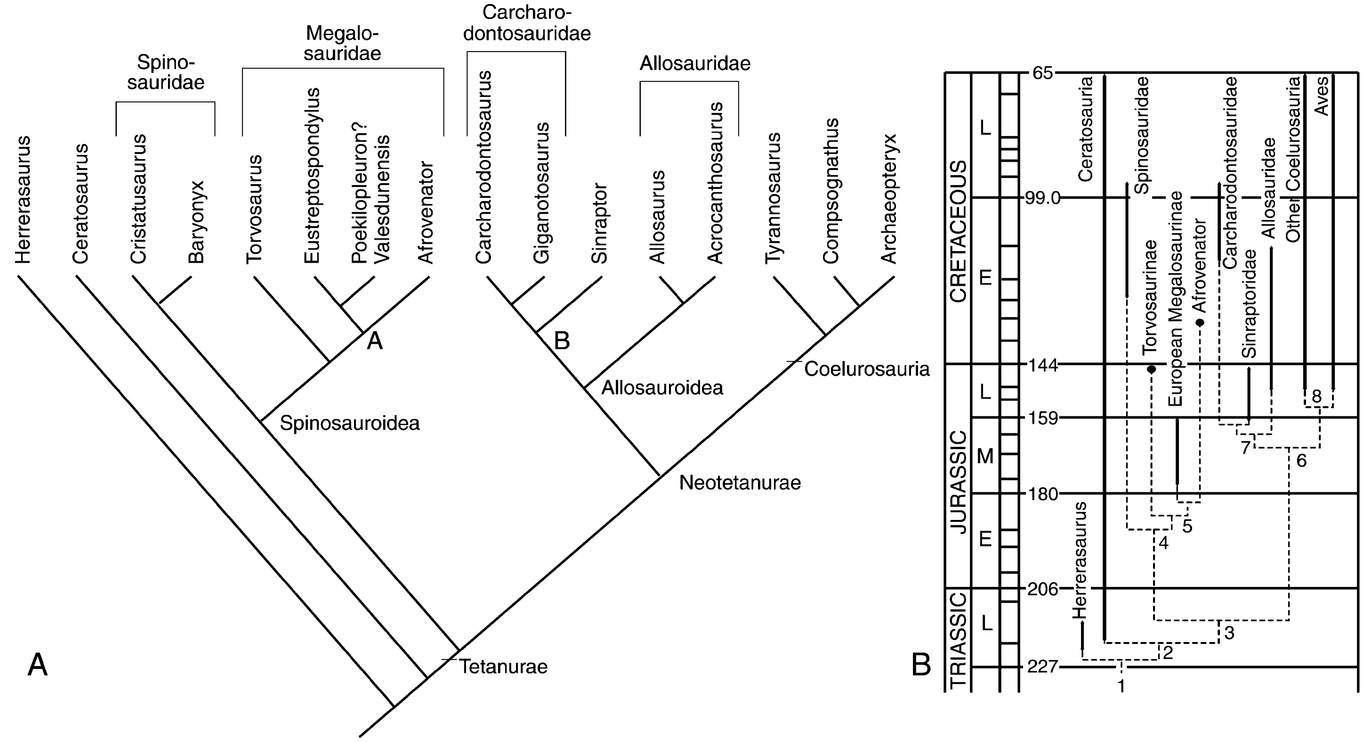

FIGURE 17. Phylogenetic and temporal relationships among basal theropods. **A**, one of the three most-parsimonious cladograms based on phylogenetic analysis of 44 cranial characters in 16 terminal taxa (see appendix), with *Herrerasaurus* and *Ceratosaurus* as successive outgroups (83 steps; C.I. = 0.66; R.I. = 0.77). **B**, phylogram based on the cladogram and recorded temporal ranges. **1**, Theropoda; **2**, Neotheropoda; **3**, Tetanurae; **4**, Spinosauroidea; **5**, Megalosauridae; **6**, Neotetanurae; **7**, Allosauroidea; **8**, Coelurosauria; **A**, Megalosaurinae; **B**, unnamed node.

ern and Southern continents suggested in previous works (Sereno et al., 1994, 1996), the families of large neotetanuran predators show an unexpectedly marked provincialism, with the Sinraptoridae (*Sinraptor*, *Yangchuanosaurus*) evolving in Asia, the Carcharodontosauridae (*Carcharodontosaurus* and *Giganotosaurus*) in Gondwana and the Allosauridae (*Allosaurus*, *Acrocanthosaurus*, *Neovenator*) in Europe and North America. The discovery of large theropod dinosaurs in the Jurassic of Africa would be decisive in elucidating the biogeographical history of the spinosauroids and basal Neotetanurae.

ACKNOWLEDGEMENTS

This work was partly supported by research grants from the EC TMR Programme (Natural History Museum) and from the Jurassic Foundation. I especially thank Philippe Taquet, who entrusted me with this new material. I thank André Dubreuil for discoveries and assistance; R. Vacant and M. Fontaine for the cranial restoration; D. Serrette and P. Loubry for the photographs; P. Taquet, A. Milner, P. Janvier, D. A. Russell, and C. Dal Sasso for valuable comments on various versions of the manuscript; T. Holtz, S. Sampson and T. Carr are thanked for their thorough reviews; A. Milner and S. Chapman for access to material in their care; P. Powell for the excellent unpublished documents on *Megalosaurus bucklandi* and for access to the collections of the Oxford University Museum; H. Gauthier, J.-C. Fischer, D. Dutheil and M. Rioult for helpful comments on regional geology, and invertebrate and fish identifications.

LITERATURE CITED

Allain, R. 2001. Redescription de *Streptospondylus altdorfensis*, le dinosaure théropode de Cuvier, du Jurassique de Normandie. Geodiversitas 23:349–367.

———, and D. J. Chure. 2002. *Poekilopleuron bucklandii* the theropod dinosaur from the Middle Jurassic (Bathonian) of Normandy. Palaeontology 45 in press.

Bakker, R. T., D. Kralis, J. Siegwarth, and J. Filla. 1992. *Edmarka rex*, a new, gigantic theropod dinosaur from the middle Morrison Formation, Late Jurassic of the Como Bluff outcrop region. Hunteria 2:1–24.

Bonaparte, J. F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropode, Cétiosauridés) du Jurassique moyen de Cerro Condor (Chubut, Argentine). Annales de Paléontologie 72:247–289.

Britt, B. B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. Brigham Young University Geology Studies 37: 1–72.

Buckland, W. 1824. Notice on Megalosaurus or great fossil lizard of Stonefield. Transactions of the Geological Socety of London 21: 390–397.

Carrano, M. T., and S. D. Sampson. 1999. Evidence for paraphyletic 'Ceratosauria' and its implications for theropod dinosaur evolution. Journal of Vertebrate Paleontology 19(3, suppl.):36A.

Charig, A. J., and A. C. Milner. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. Bulletin of the Natural History Museum 53:11–70.

Coria, R. A., and L. Salgado. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. Nature 377:224–226.

Currie, P. J., and K. Carpenter. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. Geodiversitas 22:207–246.

———, and X.-J. Zhao. 1993a. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30:2,037–2,081.

———, and ——— 1993b. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. Canadian Journal of Earth Sciences 30:2,231–2,247.

Cuvier, G. 1824. Recherches sur les ossemens fossiles. Paris, 2nd ed.

Dangeard, L., and M. Rioult. 1961. Observations nouvelles sur les accidents siliceux situés au sommet de la ''Pierre de Caen''. Bulletin de la Société Géologique de France 7:329–337.

Dugué, O., G. Fily, and M. Rioult. 1998. Le Jurassique des côtes du Calvados. Bulletin Trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre 85:1–132.

Eudes-Deslongchamps, J.-A. 1838. Mémoire sur le Poekilopleuron bucklandii, grand saurien fossile, intermédiaire entre les crocodiles et les lézards. Mémoires de la Société Linnéenne de Normandie 6: 1–114.

Galton, P. M., and J. A. Jensen. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. Brigham Young University Geology Studies 26:1–12.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds; pp. 1–55 *in* K. Padian (ed.), The Origin of Birds and the Evolution of Flight. California Academy of Science, San Francisco.

Gilmore, C. W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. Bulletin of the United Sates National Museum 110:1–154.

Hammer, W. R., and W. J. Hickereson. 1994. A crested theropod dinosaur from Antarctica. Science 264:828–830.

Harris, J. D. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and Paleobiogeographic implications, based on a new specimen from Texas. New Mexico Museum of Natural History and Science, Bulletin 13:1–75.

Holtz, T. R. 1994. The phylogenetic position of the Tyrannosauridae. implications for theropod systematics. Journal of Paleontology 68: 1,100–1,117.

——— 2000. A new phylogeny of the carnivorous dinosaurs. Gaia 15: 5–61.

Huene, F. von. 1926. The carnivorous Saurischia in the Jura and Cretaceous formations, principally in Europe. Revista del Museo de La Plata 29:35–167.

——— 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Monographien zur Geologie und Palaeontologie 4: 1–361.

Iordansky, N. N. 1973. The skull of the Crocodylia; pp. 201–262 *in* C. Gans and T. S. Parson (eds.), Biology of Reptilia. Academic Press, London and New York.

Jenny, J., C. Jenny-Deshusses, A. Le Marrec, and P. Taquet. 1980. Découverte d'ossements dans le Jurassique inférieur (Toarcien) du Haut Atlas central (Maroc). Comptes Rendus de l'Académie des Sciences 290:839–842.

Knoll, F., E. Buffetaut, and M. Bülow. 1999. A theropod braincase from the Jurassic of the Vaches Noires cliffs (Normandy, France): osteology and palaeoneurology. Bulletin de la Société Géologique de France 170:103–109.

Madsen, J. H. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological and Mineralogical Survey, Bulletin 109:1–163.

Meyer, H. von. 1832. Paleologica zur Geschichte der Erde. Frankfurt am Main, 560 pp.

Osborn, H. F. 1912. Crania of *Tyrannosaurus* and *Allosaurus*. American Museum of Natural History, Memoir 1, 30 pp.

Ostrom, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual threopod from the lower Cretaceous of Montana. Peabody Museum of Natural History Bulletin 30:1–165.

Owen, R. 1842. Report on British fossil reptiles. Report of the British Association for the Advancement of Science 11:60–204.

——— 1856. The fossil Reptilia of the Wealden Formations. Part III, *Megalosaurus bucklandi*. Palaeontographical Society, Monographs 9:1–26.

——— 1883. On the skull of *Megalosaurus*. Quarterly Journal of the Geological Society London 39:334–347.

Padian, K. 1997. Megalosaurus; pp. 415–417 *in* P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego.

Paul, G. S. 1988. Predatory dinosaurs of the world. Simon and Schuster, New York, 464 pp.

Philips, J. 1871. Geology of Oxford and the valley of the Thames. Clarendon Press, Oxford, 529 pp.

Piveteau, J. 1923. L'arrière crâne d'un dinosaurien carnivore de l'Oxfordien de Dives. Annales de Paléontologie 12:1–11.

Rauhut, O. 1998. *Elephrosaurus bambergi*, and the early evolution of theropod dinosaurs. Journal of Vertebrate Paleontology 18(3, suppl.):71A.

Rauhut, O. 2000. The interrelationships and evolution of basal theropods (Dinosauria, Saurischia). Ph.D. dissertation, University of Bristol, U.K., 440 pp.

Rioult, M. 1962. Sur l'âge du ''Calcaires de Caen'' et la stratigraphie du Bathonien de Normadie. Bulletin de la Société Linéenne de Normandie 2:51–61.

Sampson, S. D., L. M. Witmer, C. A. Forster, D. W. Krause, P. M. O'Connor, P. Dodson, and F. Ravoavy. 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. Science 280:1,048–1,051.

Sereno, P. C. 1999. The evolution of dinosaurs. Science 284:2,137–2,147.

———, A. L. Beck, D. B. Dutheil, B. Gado, H. C. E. Larsson, G. H. Lyon, J. D. Marcot, O. W. M. Rauhut, R. W. Sadleir, C. A. Sidor, D. D. Varricchio, G. P. Wilson, and J. A. Wilson. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. Science 282:1,298–1,302.

———, D. B. Dutheil, M. Iarochene, H. C. E. Larsson, G. H. Lyon, P. M. Magwene, C. A. Sidor, D. J. Varicchio, and J. A. Wilson. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differenciation. Science 272:986–991.

———, J. A. Wilson, H. C. E. Larsson, D. B. Dutheil, and H. D. Sues. 1994. Early Cretaceous dinosaurs from the Sahara. Science 266: 267–271.

Smith, A. G., D. G. Smith, and B. M. Funnel. 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, Cambridge and New York, 99 pp.

Stovall, J. W., and W. Langston. 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. American Midland Naturalist 43:696–728.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, version 3.1. Computer software and documentation distributed by Illinois Natural History Survey, Champaign, Illinois.

Taquet, P., and S. P. Welles. 1977. Redescription du crâne de dinosaure de Dives Normandie. Annales de Paléontologie 63:191–206.

Waldman, M. 1974. Megalosaurids from the Bajocian Middle Jurassic of Dorset. Palaeontology 17:325–340.

Walker, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurus. Philosophical Transactions of the Royal Society of London 248:53–134.

Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Memoirs of the Society of Vertebrate Paleontology 5:1–68.

Witmer, L. M. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Memoirs of the Society of Vertebrate Paleontology 3:1–73.

Zhao, X.-J., and P. J. Currie. 1993. A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30:2027–2036.

Received 30 November 2000; accepted 6 August 2001.

APPENDIX 1

Characters used in the theropod phylogenetic analysis. The following 45 characters correspond with scored character states that were used in the analysis of basal tetanuran relationships presented in Figure 3.

1. Premaxilla shape: longer than deep (0) or deeper than long (1) under the external naris.
2. Position of the posteriormost maxillary tooth: ventral (0); anterior (1) to the orbit.
3. Lacrimal pneumatic recess: absent (0); present (1).
4. Lacrimal–jugal articulation: overlapping (0); slotted (1).
5. Promaxillary recess: absent (0); reduced to a single foramen or a shallow depression (1); deep but closed medially (2); fenestra opened medially (3).
6. Additional openings within the antorbital fossa, in addition to the promaxillary fenestra: absent (0), present (1).
7. Extension of the promaxillary recess into maxillary anterior ramus: absent (0); present (1).
8. Ectopterygoid pneumatic recess extends deeply into the jugal process: no (0); yes (1).

9. Ectopterygoid pneumatic recess shape: elongate (0); subcircular (1).
10. Splenial with notched rostral margin of internal mandibular fenestra: absent (0), present (1).
11. Increase in the width of the anterior margin of the antorbital fossa: no (0); yes (1).
12. Frontal with deep cerebral fossa: no (0); yes (1).
13. Ventral extent of postorbital substantially above ventral margin of orbit: yes (0); no (1); no with postorbital process of jugal reduced or absent (2).
14. Nasal participation to antorbital fossa: no (0); yes (1).
15. Basioccipital participation in the basal tubera: yes (0); no (1).
16. Anterior end of upper and lower jaws: convergent (0). expanded into a premaxillary/dentary rosette (1).
17. Snout length: less (0); more (1) than three times the length of antorbital fenestra.
18. Prefrontal: large (0); reduced (1); absent (2).
19. Trigeminal nerve, separation of ophthalmic branch: absent (0); incipient (1); complete (2).
20. Bulla vestibularis: absent (0); present and closed (1); present and opened into the naris (2).
21. Associated frontals longer than wide: yes (0); no (1).
22. Splenial wraps around the ventral margin of the angular and dentary: yes (0); no (1).
23. Pneumatic openings associated with internal carotid artery canal: no (0); yes (1).
24. Frontal-prefrontal articulation peg-in-socket: no (0); yes (1).
25. Postorbital ventral process with U-shaped cross section: no (0); yes (1).
26. Quadrate foramen: present (0); absent (1).
27. Supraoccipital crest: absent (0), present (1).
28. Premaxillary tooth crowns: symmetrical (0); asymmetrical but transversally compressed (1); D-shaped (2).
29. Jugal pneumatic: no (0); yes (1).
30. Length of upper prong of quadratojugal process of jugal relatively to the lower prong: subequal (0); upper prong markedly shorter (1).
31. Squamosal ventral process anteroventrally directed: yes (0); no (1).
32. Paroccipital processes downturned: no (0); yes (1); yes and extending below the level of foramen magnum (2).
33. Width across the basal tuber: more (0) or less (1) than the transverse diameter of the occipital condyle.
34. Maximum height at the orbit is less (0) or more (1) than one third the skull length.
35. Expanded, circular orbit: absent (0), present (1).
36. Height of the skull anteriorly to the orbit superior or equal to the height of the skull posteriorly to the orbit: yes (0), no (1).
37. Shape of the maxillary anterior ramus: triangular or rounded (0), rectangular (1).
38. Postorbital-lacrimal contact: absent (0); present (1).
39. Suborbital flange on postorbital: absent (0); small (1); large (2).
40. Facial bones sculpturing: moderate (0); heavily sculptured (1).
41. Lateral temporal fenestra: large and triangular (0); keyhole shaped (1); constricted at midheight and reduced (2).
42. Braincase pneumatism: apneumatic (0), moderately pneumatic (1); highly pneumatic (2).
43. Occiput: nearly vertical (0); slopes posteroventrally (1).
44. External mandibular fenestra: large (0); reduced (1).
45. Participation of the supraoccipital to the dorsal margin of the foramen magnum: large (0); reduced or absent (1).

APPENDIX 2

Data matrix. Character state matrix for two outgroups (*Herrerasaurus* and *Ceratosaurus*), 14 ingroups, and 45 characters used in a phylogenetic analysis of basal Tetanurae (Fig. 3A).

	1	2	3	4	
	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5
Herrerasaurus	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 1 1 0 0 0 0	0 0 0 0 0
Ceratosaurus	1 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 1 0 0	0 0 0 0 0 0 1 0 0 0	1 0 0 1 0 0 0 0 0 0	0 1 0 0 ?
Afrovenator	? 1 1 1 2 1 0 ? ? ?	0 ? 1 1 ? 0 0 ? ? 1	? ? ? 1 1 1 ? ? 1 1	1 ? ? 0 0 0 1 0 0 0	0 ? ? ? ?
Torvosaurus	1 1 1 1 1 0 0 ? ? ?	0 ? 1 ? ? 0 0 ? ? 0	? ? 0 ? 1 1 ? 0 1 0	? ? ? ? ? ? 1 ? 0 0	0 ? ? ? ?
Poekilopleuron?	0 1 1 1 2 1 0 1 0 1	0 0 1 1 0 0 0 1 1 1	0 1 1 1 1 1 0 1 1 1	1 0 0 0 0 0 1 0 0 0	0 1 0 0 0
Eustreptospondylus	0 1 1 1 2 1 0 ? ? ?	0 0 1 1 0 0 0 1 1 1	0 ? 1 1 1 1 0 1 ? ?	1 0 0 0 0 0 1 0 0 0	0 1 0 ? 0
Cristatusaurus	0 1 ? ? 1 0 0 ? ? ?	0 ? ? 0 ? 1 1 ? ? 0	? ? ? ? ? ? ? 0 ? ?	? ? ? ? ? ? 1 ? ? 0	0 ? ? ? ?
Baryonyx	0 ? 1 1 ? ? 0 ? ? 0	? 0 ? ? 0 1 1 ? 0 0	0 1 ? 1 0 0 1 0 ? ?	? 0 0 0 ? 0 1 0 0 0	0 1 0 0 0
Carcharodontosaurus	? 1 1 1 2 0 1 ? ? ?	0 0 0 1 ? 0 0 1 2 0	1 ? 0 ? 0 ? 1 ? 1 1	? 1 ? 1 0 0 0 1 1 1	0 2 1 ? ?
Giganotosaurus	0 1 1 ? 2 0 1 ? ? ?	0 ? 0 1 0 0 0 1 ? ?	1 1 0 ? ? 0 1 1 ? ?	? 1 ? 1 0 0 0 1 1 1	0 2 1 ? 1
Allosaurus	0 1 1 1 3 1 1 1 0 1	0 0 0 1 1 0 0 1 2 2	1 1 1 1 0 0 1 2 1 1	0 2 1 1 0 0 0 0 0 0	1 1 0 1 1
Sinraptor	0 1 1 1 3 1 1 1 0 1	0 0 0 1 0 0 0 1 1 2	1 1 0 0 0 0 1 1 1 1	0 1 1 1 0 0 0 0 0 0	0 1 1 0 1
Acrocanthosaurus	1 1 1 1 3 1 1 1 0 1	0 0 0 1 1 0 0 1 2 ?	1 1 1 ? 0 0 1 1 1 1	0 2 1 1 0 0 0 1 0 0	1 1 0 1 1
Tyrannosaurus	0 1 1 1 3 1 1 1 1 1	1 1 0 0 0 0 0 1 2 2	1 1 1 0 0 0 1 2 1 1	0 0 0 1 0 1 0 0 (0 & 2) 0	2 1 0 1 1
Compsognathus	0 1 0 1 3 1 1 1 1 0	1 1 2 0 ? 0 0 1 ? ?	? 1 ? 0 0 0 0 0 ? 1	0 ? ? 1 1 1 0 0 0 0	? 1 0 1 1
Archaeopteryx	0 1 0 1 3 1 ? 0 1 0	1 ? 2 ? 0 0 0 2 1 ?	1 1 ? 9 0 ? 0 0 1 0	? 0 0 1 1 1 0 0 0 0	2 1 0 1 1

APPENDIX 3

Synapomorphies. List of synapomorphies (ambigous characters between brackets) of each node (optimized under accelarated character state transformation) in Fig. 3A.

Neotheropoda: 5, 18, 42, [27, 31, 34, 35, 36]
Tetanurae: 2, 4, 22, 29, [3, 8, 10, 23, 30]
Neotetanurae: 7, 21, 45, [5, 6, 19, 20, 31]
Coelurosauria: 9, 11, 12, 41, [31, 44]
Spinosauroidea: 13, 37, [24, 34]
Megalosauridae (Megalosaurinae, Torvosaurinae): 25, 26, [14, 19, 27]
Node A: (Megalosaurinae) [5, 20, 28]
Spinosauridae: 16, 17 [10]
Allosauroidea: 32, 33, [14, 28]
Node B (Carcharodontosauridae, Sinraptoridae): 43, [23]
Carcharodontosauridae: 39, 40, 42, [5, 6, 20, 38]
Allosauridae: 15, 32, 41, [24, 44].

APPENDIX 4

Phylogenetic definitions. Megalosauridae is defined here as *Poekilopleuron*? *valesdunensis*, *Torvosaurus* and *Afrovenator*, and all descendants of their common ancestor.

The Torvosaurinae are defined here as all Megalosauridae that are more closely related to *Torvosaurus* than to either *Poekilopleuron* or *Afrovenator*; this clade includes *Torvosaurus* and tentatively *Edmarka*.

The Megalosaurinae are defined here as all Megalosauridae that are more closely related to *Poekilopleuron* than to *Torvosaurus*. This clade includes *Eustreptospondylus*, *Poekilopleuron* and *Afrovenator*.