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THE VERTEBRATE FAUNA OF THE UPPER PERMIAN OF NIGER. IV. *NIGERPETON RICQLESI* (TEMNOSPONDYLI: COCHLEOSAURIDAE), AND THE EDOPOID COLONIZATION OF GONDWANA

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ABSTRACT -We describe the edopoid temnospondyl *Nigerpeton ricqlesi* from the Upper Permian Moradi Formation of northern Niger on the basis of two partial skulls and tentatively associated postcranial material. This crocodile-like taxon displays several edopoid characters states such as a long prenarial region with enlarged premaxillae, elongated vomers, large, posteriorly tapering choanae. and a jugal that broadens anteriorly. *Nigerpeton* possesses a unique carnivorous dentition. lt is autapomorphic in its possession of an extremely elongate snout bearing a maxillary bulge that accommodates three hypertrophied caniniform teeth. inner premaxillary tusks, and anterior paired fenestrae, which pierce the skull roof. ln addition, both the maxilla and dentary tooth rows show the sporadic appearance of 'doubled' tooth positions. The lateral-line system is present at the adult stage, which suggests an aquatic habitat for this taxon. A phylogenetic analysis of Edopoidea and its relatives places *Nigerpeton* as the sister taxon to the Permo-Carboniferous genus *Chenoprosopus* from the U.S.A. As with other members of the Moradi tetrapod fauna, the discovery of *Nigerpeton* strengthens support for the hypothesis that West Africa hosted an endemic fauna at the close of the Paleozoic Era. Biogeographically, we propose that Late Carboniferous and Permian edopoids were geographically widespread and that they twice crossed the Central Pangean mountain chain (between Laurussia and Gondwana) during their evolution. This distribution was later fragmented with the onset of Late Permian climatic warming.

INTRODUCTION

Temnospondyls from the Permian of Africa are known from Malawi (Watson, 1962), South Africa (Damiani and Rubidge, 2003), and Tanzania (Panchen, 1959). Taquet (1978) was the first to mention the existence of temnospondyl remains from Upper Permian rocks in northern Niger. Captorhinid, pareiasaur, and probable anomodont fossils were also mentioned, but not described (Taquet, 1978). In their detailed description of the skull of the captorhinid *Moradisaurus grandis,* Ricqles and Taquet (1982) reported the collection of numerous temnospondyl remains during three expeditions to the Moradi Formation in the late 1960s. They provisionally attributed these fossils to the Rhinesuchoidea on the basis of their age and large size.

Fieldwork was recently undertaken in the Moradi Formation in 2000 and 2003. In addition to new material of the captorhinid *Moradisaurus grandis* (O'Keefe et al., in press) and the pareiasaur *Bunostegos akokanensis* (Sidor et al., 2003a), fossils representing two new temnospondyl genera were collected Sidor et al., 2003b; Sidor et al., 2004). These were named and briefly described by Sidor et al. (2005) as *Nigerpeton ricqlesi* and *Saharastega moradiensis.* The latter taxon was described in detail by Damiani et al. (in press) based on a near-complete skull lacking lower jaws. In contrast to the rhinesuchids that dominate southern African assemblages, *S. moradiensis* was considered to be related to the edopoids, a group of Late Carboniferous to Early Permian forms.

In this contribution, we provide a full description of the remains of *Nigerpeton ricqlesi.* As with *Saharastega,* this taxon increases African temnospondyl biodiversity and adds to the complexity of the geographic distribution of this group during the Late Permian.

Institutional Abbreviations-AMNH, American Museum of Natural History, New York; **MCZ,** Museum of Comparative Zoology, Harvard University, Cambridge; **MNHN**, Museum national d'Histoire naturelle, Paris; **MNN**, Musee National du Niger, Niamey.

SYSTEMATIC PALEONTOLOGY

TEMNOSPONDYLI Zittel, 1887-1890
EDOPOIDEA Romer, 1945
COCHLEOSAURIDAE Broili in Zittel and Broili, 1923

COCHLEOSAURINAE Broili in Zittel and Broili, 1923

Definition--A node-based taxon including *Cochleosaurus* and *Chenoprosopus* and all descendants of their most recent common ancestor.
Diagnosis--Cochleosaurids diagnosed by the following synapomorphic characters: depression in vomer anterior to choana (character 21 in the present phylogenetic analysis, unambiguous synapomorphy of the clade); elongate and narrow sphenethmoid (character 32, state 2, unambiguous synapomorphy of the clade); and pineal foramen closed in skulls greater than 120 mm in midline length (character 1, convergent with *Saharastega).*

NIGERPETON RICQLESJ Sidor et al., 2005
(Figs. 1-3)

Holotype--MNN MOR69, partial adult skull preserved in dorsal view (45 em in midline length) and associated atlas vertebra. The posterior region of the skull roof is weathered away, so that the posterior part of the palate is directly visible in dorsal view (Fig. 1).
Type Locality and Horizon--Collected froin a layer of intraformational conglomerate in the Moradi Formation, (18° 47.00' N, 7° 11.833' E), approximately 20 km west of Arlit, Agadez Department, northern Niger (see Damiani et al., in press, for a map of the study area). The age of the Moradi Formation is poorly constrained, although it is typically considered latest Permian (Taquet 1972, 1978).
Referred Material--From a nearby locality (18° 47.515' N, 7° 11.160' E) of the Moradi Formation: MNN MOR70, a larger adult skull (56 em midline length) preserving most of the left side of the palate, skull roof, and lower jaw. Some isolated postcranial elements, found close to the referred skull, are tentatively considered as referred associated material: three sacral neural arches and their associated ribs (MNN MOR83), as well as an isolated femur (MNN MOR82). Casts of parts of the referred skull are deposited in the MNHN.
Diagnosis--Cochleosaurine distinguished by the following autapomorphic characters: orbits positioned far posteriorly, leading to an extremely elongated preorbital region (-70% of total skull length); tip of snout pierced by paired vacuities for accommodation of mandibular fangs; supratemporal bone highly reduced; lateral swelling of maxilla at level of external nostril; maxilla bearing two or three medially positioned fangs at level of maxillary swelling; sporadic appearance of 'doubled' tooth positions on both maxilla and dentary tooth rows; medially located, premaxillary fangs present; high occipital and posterior regions of skull; lateral-line system present in adult.

DESCRIPTION

Preservation

The holotypic material was found eroding out of the surface of a thin conglomeratic red sandstone. The heterogeneous clasts of the sandstone matrix are composed of silicified and indurated clay pebbles. The matrix was removed mechanically.
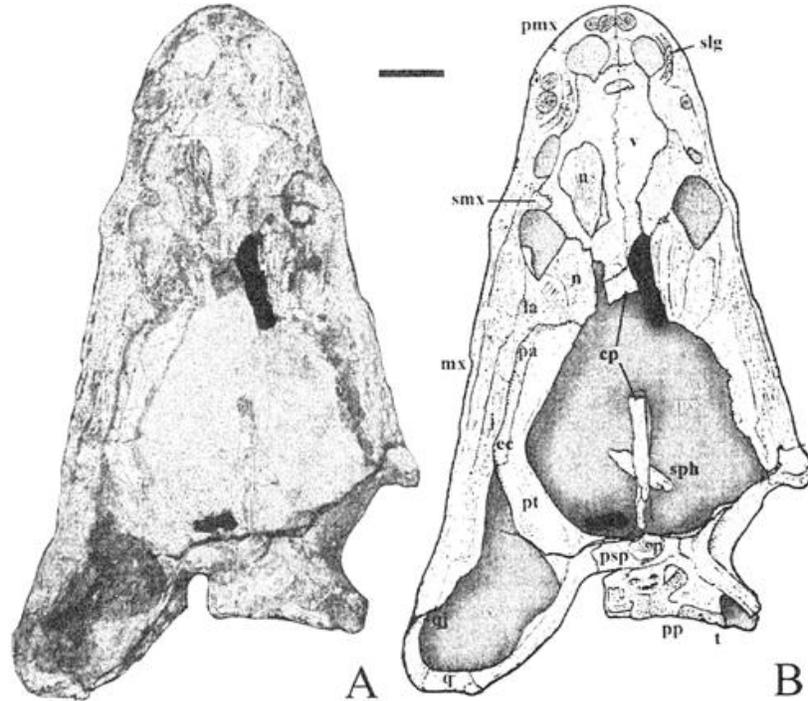

FIGURE 1. Holotype of *Nigerpeton ricqlesi* Sidor et al., 2005 (MNN MOR69), in dorsal view. A, photograph as preserved; B, interpretive drawing. Scale bar equals 5 em. Sedimentary matrix in grey, cracks in hatching. Abbreviations: apv, anterior paired vacuity; bo, basioccipital; ch, choana; cp, cultriform process of the parasphenoid; do, dentigerous ossicles; ec, ectopterygoid; en, external nostril; f, frontal; fm, foramen magnum; in, internal nostril; ipv, interpterygoid vacuity; it, intertemporal;j,jugal; Ia, lacrimal; mx, maxilla; n, nasal; pmx, premaxilla; p, parietal; pa, palatine; pf, prefrontal; po, postorbital; pof, postfrontal; pp, postparietal; psp, parasphenoid; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; slg, sensory line groove; smx, septomaxilla; sph, sphenethmoid; sq, squamosal; st, supratemporal; stv, subtemporal vacuity; t, tabular; v, vomer.

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The holotype consists of a partial skull and associated atlas. The skull roof is mainly missing, leaving the posterior part of the palate and the interpterygoid fenestrae visible in dorsal view. The dermal skull bones are silicified and missing their true external surface. Weathering has polished the internal aspect of the remaining bone, leaving an irregular eroded surface with numerous pits and lines of various sizes. However, some sutures are still visible. Matrix remains in some natural openings such as the choanae and the interpterygoid and subtemporal fenestrae. The skull has undergone post-mortem compaction in its left anterior and occipital parts. The occiput, partly eroded, remains difficult to interpret. The jugal, quadrato-jugal, and a part of the quadrate branch of the pterygoid are lacking on the right side. A deep crack runs transversely across the posterior part of the skull. The associated atlas was found immediately posterior to the skull.

The referred material was found lying in ventral view and consists of the left half of a skull and portions of its corresponding mandible. This half skull is relatively well preserved but very fragmented, a network of fissures being visible on both its dorsal and ventral sides. Each skull fragment was prepared separately and then reassembled in three dimensions. Although much of the skull was reconstructed, the tip of the snout and the region surrounding the orbit remain missing. The dorsal ornamentation of most of

the skull bones is preserved, except for the dorsally elevated fronto-parietal region, which is slightly eroded. Three presacral vertebrae with their associated ribs and an isolated femur were found within a meter of the skull and are tentatively considered as associated postcranial elements.

Skull--General Morphology

In general outline, the skull (Figs. 1-4) of *Nigerpeton ricqlesi* is triangular and elongate in shape. It ranges from 45 (MNN MOR69) to 56 em (MNN MOR70) in midline length. The dermal bones are 2 to 6 mm in thickness. The lateral margins of the skull are straight except at the level of the external nostrils where distinct lateral bulges are visible, an autapomorphic condition of this cochleosaurine. A similar, albeit less pronounced, maxillary bulge is figured in *Edops* (Romer and Witter, 1942). The preorbital region is very elongate but lacks concave margins, as independently occurs in some archegosaurians and trematosaurians (Steyer, 2002). The orbits are dorsally elevated, widely separated on the skull roof, and very posteriorly located, leading to an extremely short postorbital region, a typical condition of cochlea-saurids (Milner and Sequeira, 1998). Remarkably, the preorbital region in *Nigerpeton* corresponds to more than 80% of the skull length, a record within edopoids. The tip of the snout is rounded and pierced by two circular anterior paired vacuities for symphyseal tusks, as in some mastodonsaurids (Schoch and Milner, 2000; Damiani, 2001). This character is therefore autapomorphic for *Nigerpeton*. The posterior portions of the skull roof and occipital region are very high. The skull decreases in height anteriorly, lead-ing to a relatively flat and extended plate corresponding to the anterior region of the snout. MNN MOR70 shows that the rim of the external nostril was elevated above the remainder of the relatively flat snout. Also in MNN MOR70, deep and wide longitudinal canals are visible and separated by pronounced longi-tudinal ridges (a cochleosaurid synapomorphy according to Milner and Sequeira, 1998).

Typical temnospondyl ornamentation is visible on the skull roof and mandible; it largely consists of a honey-comb pattern grooves at the periphery and toward the inner part of the bone. The latter type of ornament, more visible on the type MNN MOR69 because of its surface weathering, has been regarded as indicative of bone areas that undergo 'intensive growth' (Bystrow, 1935). The premaxillary, maxillary, and nasal regions, which bear this type of ridge-and-groove ornamentation, therefore correspond to a strong zone of intensive growth, as is the case in the other edopoids. The heavy sculpturing pattern of these dermal bones and the high degree of ossification of the cranial and postcranial material indicate an adult age of the specimens (Steyer, 2000).

The lateral-line system is visible in *Nigerpeton,* and corresponds to an additional autapomorphy of this cochleosaurid (edopoids are characterized by absence of lateral-line canals according to Rieppel, 1980). Canals are deeply impressed on the external surface of the skull of MNN MOR69, which underwent dorsal weathering. They are also visible on the surface of the skull and (partly) the mandible in MNN MOR70. The canals are deep (3-6 mm) and wide (3-10 mm). The preorbital canals are located in the anterior part of the snout. The narrowest canals partly turn around the anterior paired vacuities, and posteriorly split into two sulci toward the nostrils. These deep, infranarial canals are only visible on the weathered surfaces of MNN MOR69, and do not appear on the surface of the intact bones. They are S-shaped and continuous but show a pitted ornamentation, as is the case in many temnospondyls. A large and deep depression, located posteromedial to the anterior paired vacuities, could be a transverse prenarial sulcus. Four wide, deep, and longitudinal supranarial canals (two per side) are parallel to the midline suture. They are elongate, but not strongly curved as in brachyopoids (sensu Warren and Marsicano, 2000), trematosauroids, or metoposaurids (Schoch and Milner, 2000). Another transverse depression, positioned posteromedial to the orbits, could be a transverse supraorbital sulcus. The lateral-line system on the mandible may correspond to a wide but shallow canal on the lateral surface of the angular. This relatively straight canal parallels, but is ventrally offset from, the angular-dentary suture. The preservation of the mandible does not permit further interpretation.

Skull Roof

In the skull roof (Figs. 1A-3A), the prenarial region of the snout is very elongated, and mainly composed of an extended premaxilla. The latter is more elongate marginally than medially, a synapomorphy of edo-poids (Milner and Sequeira, 1998). Although the medial suture of the premaxilla is not complete poster-iorly, its ratio of lateral to medial length is estimated at more than 1.5 (around 2), a synapomorphy of the Cochleosaurinae. The premaxilla in *Nigerpeton* housed approximately 18 teeth, as in *Cochleo-saurus florensis* (Rieppel, 1980; Godfrey and Holmes, 1995). The premaxilla of *Chenoprosopus* bears at least 20 teeth (Hook, 1993). The two anteriormost premaxillary teeth are enlarged into tusks (see dentition below).

The external nostril is small, circular, and laterally positioned, as is the case in the edopoids (Milner and Sequeira, 1998). It is dorsally elevated above the snout and opens laterally toward the bulged region of the maxilla. The septomaxilla, nasal, and premaxilla are higher and deeper around the nostril, but the maxilla is shallower and depressed. The latter forms a wide, deep trough from the anterolateral margin of the nostril to the border of the skull. The triangular septomaxilla is visible on the skull roof, as is the case in many temnospondyls. In MNN MOR69, the posterior border of the nostril can be seen to overlap the anterior margin of the choana in dorsal view. Also in MNN MOR69, the nostrils are posteriorly eroded, so that their posterior borders look artificially pointed because they also comprise the margins of the choanae.

The location of the orbits in *Nigerpeton* is based on MNN MOR70, where the ventral and postero-dorsal margins of the left orbit are preserved. Based on the preserved circumference, the orbit was small and located far posteriorly and dorsally. In addition, the orbit appears to have faced laterally, an autapomorphic condition among cochleosaurids.

A suture starting from the anterolateral margin of the orbit is interpreted as the jugal-prefrontal suture, suggesting that the lacrimal was excluded from contributing to the orbital margin, as in edopoids and eryopoids (Milner and Sequeira, 1998; Werneburg and Steyer, 1999). The lacrimal-jugal suture, partly visible anterolateral to the orbit, looks rather long, another edopoid synapomorphy according to Milner and Sequeira (1994, 1998). The jugal is thus very anterolaterally expanded, as is the case in *Saharastega* (Damiani et al., in press). Based on the phylogenetic position of *Saharastega* and *Nigerpeton,* we suggest that a jugal that extends anterior to the orbits is not an unambiguous synapomorphy of the stereospondy-lomorphs (contra Yates and Warren, 2000:92). The very elongate and relatively narrow maxilla extends posterior to the orbit. Unlike the nasal, the posterior part of the frontal's dorsal surface is slightly eroded and lacks its superficial ornamentation. Although obscured by weathering, the nasofrontal suture appears to have been located in the posterior region of the snout, leading to the recognition of a huge nasal that occupies a major part of the snout.

The skull table (i.e., the postorbital part of the skull) is partially preserved on both MNN MOR69 and MOR70. It is extremely short and narrow, another autapomorphy of *Nigerpeton,* and its posterior border is slightly concave. The dorsal surface of some bones (e.g., frontal, parietal, postparietal) has been differentially eroded because of the weathering of this very elevated skull region.

The postorbital is relatively small and triangular. The preserved posterior portion of the postfrontal is sub-quadrate, but its anterior branch that contributes to the orbital margin is missing. A small intertemp-oral is visible, as is the case in several unrelated primitive temnospondyls, including edopoids (Gubin et al., 2000; Sequeira, 2004, Damiani et al., in press). The intertemporal is relatively short, a feature that is unusual among the taxa that retain this skull roof element and could be related to the extreme shortening of the skull table. The supratemporal is small and subtriangular. The parietal is large (relative to the skull table size), slightly elongate and subrectangular, whereas the postparietal is shorter, as is the case in euskelians (Yates and Warren, 2000) and other basal temnospondyls such as *Onchiodon* (JSS, pers. obs.). The transverse suture between the supratemporal and parietal lies within the posterior half of the orbits, and not posterior to them, as in *Chenoprosopus.* Although the interparietal suture is clearly visible on MNN MOR70, a pineal foramen is not apparent on the skull roof. However, the eroded skull table of the

smaller MNN MOR69 suggests a very small pineal foramen, albeit at a much deeper level within the braincase. The loss or reduction of the pineal foramen is typical of adult edopoids (Steen, 1938).

The left otic notch, visible on both MNN MOR69 and MOR70, is triangular and relatively wide. It is shallower and wider than that of eryopoids (Werneburg and Steyer, 1999; and Milner, pers. comm., 2004). Together with the tabular and the squamosal, the supratemporal contributes to the border of the otic notch, as in many adult non-stereospondyl temnospondyls that possess a relatively deep otic notch. The anterior rim of the otic notch is vertical and does not show any regularly oblique and smooth area (i.e., the excavatio oticalis sensu Schoch, 1997) as in mastodonsauroids (Schoch, 1997; Damiani, 2001) and *Microposaurus* (Damiani, 2004). The preserved part of the squamosal is posteriorly expanded until its contact with the quadrate. The latter is robust and visible in dorsal view. The jaw articulation is located far posteriorly, as is the case in many temnospondyls (e.g., *Edops craigi,* Romer and Witter, 1942; *Microposaurus casei,* Damiani, 2004).

Palate

The palate (Figs. 1B-3B) of *Nigerpeton* is visible on both the ventral and dorsal sides of MNN MOR69 (depending on the degree of erosion of the skull roof), and on the ventral side of MNN MOR70. It is heavily ossified, but some sutures between individual bones are visible. The paired anterior palatal fossae are relatively close to each other. The palatal side of the snout is mainly composed of markedly elongated vomers, a synapomorphy of the cochleosaurids (Milner and Sequeira, 1998). The typical complement of tusks is present on the palate, although dentides are absent. The premaxilla bears three large tusks on each side; two marginal ones at the tip of the snout, and an inner tusk, which is flanked anteriorly and posteriorly by two replacement alveoli. The vomer-maxillary suture is relatively long. This suture appears shorter in *Cochleosaurus* (Godfrey and Holmes, 1995:fig. 1). An ovoid and relatively elongated depression of the premaxilla is visible between its most posterior replacement tusk alveoli and the vomer-maxillary suture.

The vomers form a remarkably elongated plate. Their ventral surface is relatively flat but shows a ventral ridge that laterally borders the choana. Due to poor preservation, it is not clear whether this bone contributes the anterior margin of the interpterygoid vacuities. The vomer does not contact the ectopterygoid, as in the dvinosaurian *Neldasaurus* (Chase, 1965). Two vomerine tusks are present in this element's anterior portion. These tusks are anterior to the choana, as in *Chenoprosopu.s,* and lie obliquely relative to the premaxillary depression described above.

The choanae are located in the mid-length of the snout, at the level of the bulged maxillary margin. The prechoanal region of the palate is therefore very long, a situation that represents a synapomorphy of Cochleosauridae (Milner and Sequeira, 1998). The choana is relatively small and elongate, but wider anteriorly than posteriorly (another cochleosaurid synapomorphy according to Hook, 1993). It is relatively shorter than that of *Chenoprosopus* (Hook, 1993) or *Saharastega* (Damiani et al., in press). The pterygoid does not contribute to the margin of the choana, as in *Capetus* (Sequeira and Milner, 1993).

The palatine is elongate, narrower and longer than that of other edopoids (including *Saharastega;* Damiani et al., in press). It widens anteriorly at the level of its tusk and replacement alveoli. The ectopterygoid is also narrow but shorter than the palatine (as is the case in *Adamanterpeton),* and has subparallel lateral margins (i.e., without widened extremities). Its tusk and replacement alveoli are smaller than those of the palatine. The posterior margin of the palatine appears to contribute to the subtemporal fenestra, which indicates that a ventral alary process of the jugal is not clearly present, as is the case, for example, in *Edops* (Romer and Witter, 1942).

The interpterygoid vacuities are longer than wide, but form less than 50% of the skull length. The vacuities are relatively wide (i.e., maximum width greater than 50% of the skull midwidth), as in *Saharastega* and other Cochleosaurinae. Their width is maximum in their mid-posterior part. These vacuities are open below the posterior part of the snout and the orbits, the posterior rims of these openings being at approximately the same level. The orbits are therefore partly visible in ventral view within the
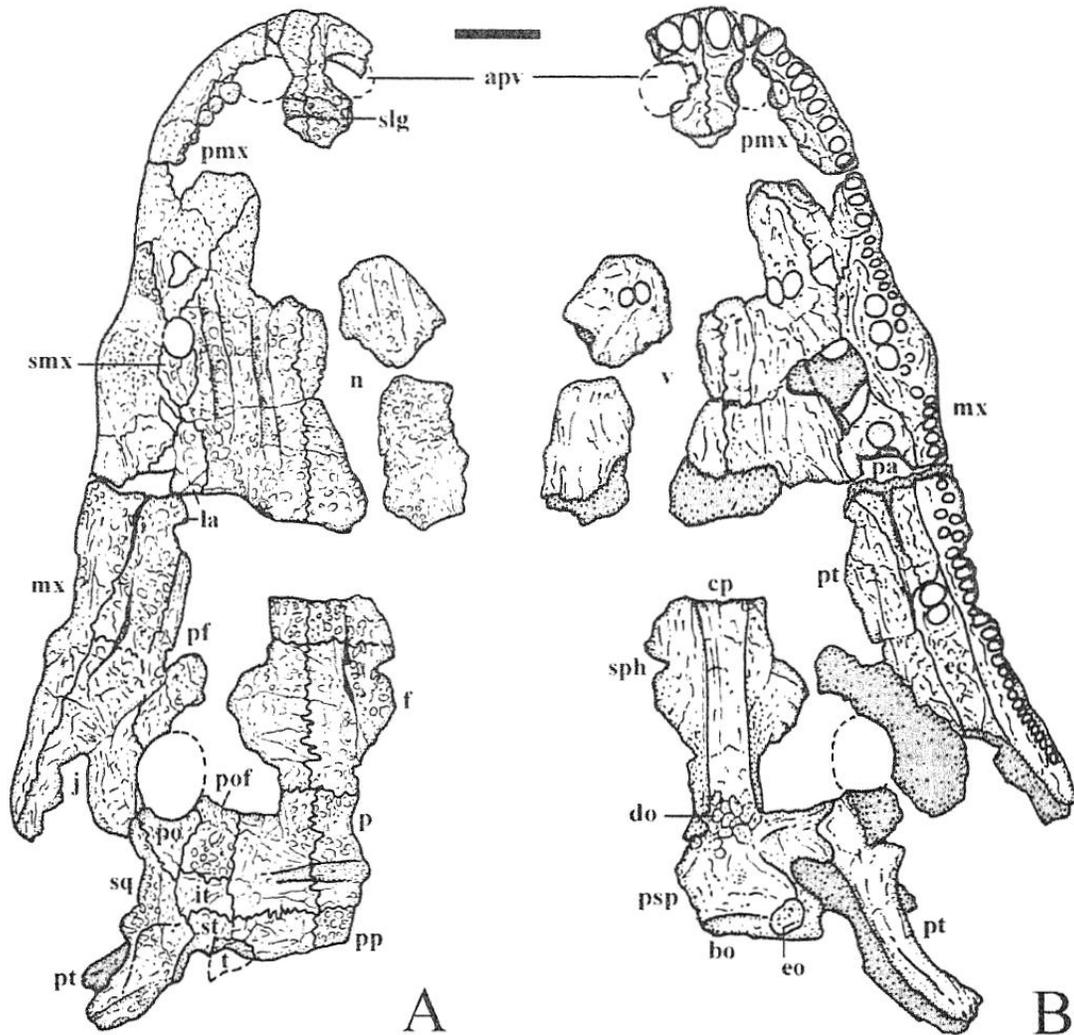
FIGURE 2. Referred specimen of *Nigerpeton ricqlesi* Sidor et al., 2005 (MNN MOR70): interpretive drawings of dorsal (A) and ventral (B) views (ventral surface of the skull roof is shaded grey). Scale bar equals 5 em. Abbreviations given in Figure 1.

interpterygoid fenestrae. The fenestrae are not semi-circular (as in *Adamanterpeton* and *Saharastega),* but rather sub-triangular in shape, their posterior extremities being more rounded than the anterior ones, as is the case in the other Cochleosaurinae.

The subtemporal vacuities are best displayed on the left side of MNN MOR69. They are very elongate, as a result of the posterior position of the suspensorium, with a maximum length almost equal to that of the interpterygoid vacuities. Their anterior extremity is constricted by the palatine ramus of the pterygoid, the lateral expansion of the quadratojugal, and possibly the posterior extremity of the ectopterygoid. According to their large size and the posterior position of the suspensorium, the vacuities may be largely open below the skull roof.

The parasphenoid, which is best preserved in MNN MOR70, is robust and does not show ornamentation on its ventral surface. The parasphenoid plate is sub-rhombic, with two prominent, lateral basipterygoid branches contacting the pterygoid. The suture with the pterygoid, located in the anterior half of the plate, is S-shaped but mainly convex, as is the case in primitive temnospondyls (Yates and Warren, 2000; Schoch and Milner, 2000). As in *Edops* (Romer and Witter, 1942) and *Saharastega* (Damiani et al., in press), foramina for the internal carotid artery are not visible on the ventrolateral side of the parasphenoid
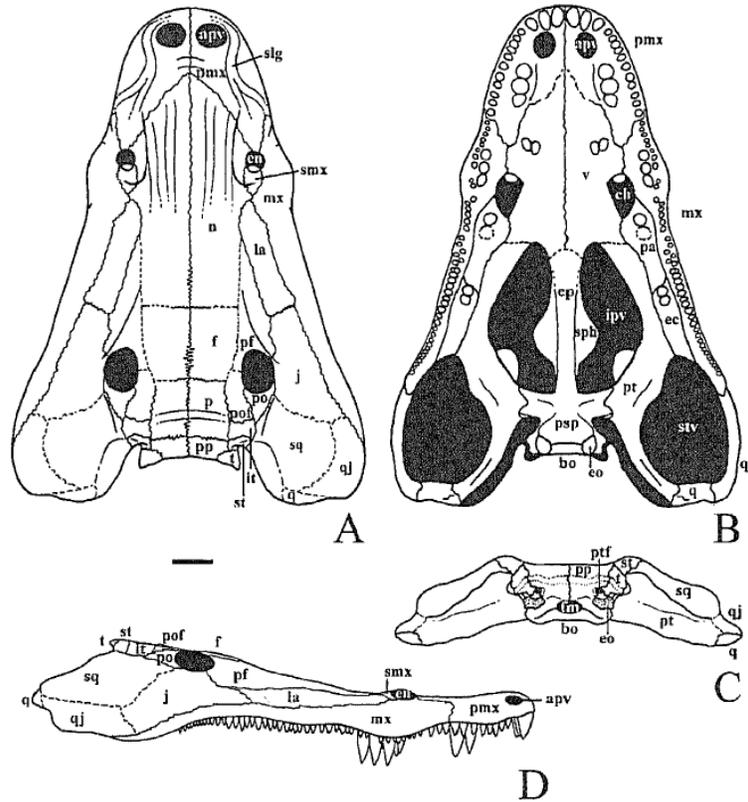
FIGURE 3. Reconstruction of *Nigerpeton ricqlesi* Sidor et al., 2005 based on MNN MOR69 and MOR 70. Reconstruction of the skull in dorsal (A), palatal (B), occipital (C), and lateral (D) views. Scale bar equals 5 cm. Abbreviations given in Figure l.

plate. However, these foramina could be tentatively recognized on the vertical sides of the parasphenoid lateral branches, which therefore suggests an arterial pathway similar to that of *Eryops* (Yates and Warren, 2000:fig. 5). The cultriform process is relatively high and narrow in its posterior half, where it keeps the same width and has a triangular section. Here it bears a ventral longitudinal crest that remains relatively smooth, i.e., not as sharp and high as the 'medial keel' of some stereospondyls (e.g., *Watson-isuchus, Wantzosaurus;* JSS, pers. obs.). Although the anterior extremity of the cultriform process is not preserved, the crest apparently disappears anteriorly, as the entire cultriform process flattens and widens. The posteriormost part of the cultriform process seems covered by a patchwork of small pelicular ossicles that are cemented by the matrix. Although they appear to lack concentric or pitted ornamentation on their ventral surface, these circular or subpolygonal flat bones could be tentatively referred to dentigerous ossicles like those observed within the interpterygoidal fenestrae of primitive temnospondyls, including *Chenoprosopus* (Hook, 1993:fig. 2A; Schoch and Milner, 2000:fig. 37).

A transversely expanded sphenethmoid lies lateral to the flanks of the cultriform process of the para-sphenoid. This element is rhomboidal, with flat, laterally expanded 'wings,' as in *Adamanterpeton* and *Saharastega.*

As in all temnospondyls, the pterygoid in *Nigerpeton* is robust and triradiate. Its ornamentation con-sists of slight elongated grooves. and ridges, as shown in dorsal view on MNN MOR69. The palatine and quadrate rami are very elongated, the elongation of the latter being linked with the posterior extension of the suspensorium. The palatine ramus is longer and flatter than the quadrate one, yet the latter is slender and more regularly curved than the former. The pterygoid flange is only visible on the quadrate ramus, which remains very high. No cristae arc visible on the ventral surfaces of either ramus of the pterygoid, unlike the condition in many adult stereospondyls (Damiani, 2001; Steyer, 2003). The palatine ramus of the pterygoid borders the interpterygoid vacuity anteriorly, thus excluding the palatine from its margin, as

is the case in non-stereospondyl temnospondyls (Yates and Warren, 2000). The palatine ramus widens anteriorly, as in *Adamanterpeton.*

Occiput

The occiput (Figs. 1B-3B, 3C) of *Nigerpeton* is incomplete in both specimens, and although it is three-dimensionally preserved in MNN MOR70, it remains difficult to interpret because of its state of fragmentation. The occiput is relatively high for a nonstereospondyl or a non-euskelian temnospondyl. In occipital view, the posterodorsal parts of the skull bones appear thick (around 6 mm) relative to the total occipital height. Lateral to the occiput, the robust quadrate is sub-cyclindrical, dorsally expanded, and shows well-developed sutures with the quadratojugal and the pterygoid. Although the quadratojugal is partially preserved in MNN MOR69, no paraquadrate foramen is visible, the absence of which is considered a primitive character state for temnospondyls (Yates and Warren, 2000; contra Sequeira, 2004). The dorsal plate of the tabular, which did not undergo compaction in MNN MOR69, is backwardly directed, another primitive character state for the temnospondyls (Steyer, 2002). Its paroccipital (or parotic) process is ventrally robust and contacts the exoccipital, as appears to be the case in *Saharastega* (Damiani et al., in press) but not *Edops* (Romer and Witter, 1942). The rounded post-temporal fenestra is therefore small, the exoccipital being also ventrally well ossified. The exoccipital is generally well preserved, but its articular condyle is not present. The condyle was evidently composed mainly of a median basioccipital, here lacking, a primitive condition for the tetrapods (Ruta et al., 2003). According to the inner curvature of the exoccipitals, the foramen magnum appears to have been circular and relatively large. No cristae or laminae are visible in occipital view, whereas many stereospondyls show such structures on the postparictal, tabular, and/or squamosal.

Mandible

The mandible of MNN MOR70 is preserved only in its anterior, mid-anterior, and posterior part. These three parts are separated by non-preserved gaps.

The anterior preserved part corresponds to the symphyseal extremity of the dentary, which bears one or two symphyseal tusks and possibly a large replacement alveolus (see dentition below). The symphyseal suture is relatively long, as is the case in the sterenspondyls and the edopoids.

The mid-anterior preserved part is composed of. the dentary (mostly labially) and the anterior part of the splenial (mostly lingually). Its dorsal margin is depressed to mirror the outline of the bulged maxilla, giving the skull a crocodile-like appearance in lateral and anterolateral views (Fig. 4). As with upper marginal dentition, it bears a marginal tooth row consisting of some irregular or 'doubled' tooth positions, an autapomorphic condition of *Nigerpeton.* The mandibular canal is visible at both extremities of this fragment; its section is anteriorly small and subtriangular but posteriorly large and high.

The posterior preserved part of the mandible is composed of a large part of the angular and the posterior end of the dentary. Both the dcntary and angular show an external ornamentation that is typical for temnospondyls. As with the maxilla, the dentary is elongated posteriorly (it terminates at the level of the orbits) and relatively shallow in lateral view. This suggests a relatively shallow mandible, at least in its anterior half, as is the case in *Adamanterpeton* and *Cochleosaurus.* The mandibles of *Procochleosaurus* (Sequeira, 1996), *Edops* (Romer and Witter, 1942) and *Chenoprosopus* (Langston, 1953; Hook, 1993) are more robust and deep.

Dentition

The dentition of *Nigerpeton* is one of the most specialized among temnospondyls and suggests a highly carnivorous ecology for this taxon. Although complete teeth are not known, visible sections throughout the tooth row show that the dentition was typically rounded in cross section, as in non-stereospondyl temnospondyls. In contrast, stereospondyl teeth are often antero

FIGURE 4. Restoration of the skull of *Nigerpeton ricqlesi* Sidor et al., 2005. With the courtesy of Franck Limon Duparcmeur, sculptor. A color version of this figure is available as supplementary data at www.vertpaleo.org/jvp/JVPcontents.html.

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posteriorly compressed (Schoch and Milner 2000; Steyer and Damiani, 2005).

The premaxillary teeth have cross-sectional diameters ranging from 6 to 19 mm. The two anteriormost teeth are enlarged into tusks. Anterior premaxillary tusks are also known in *Microposaurus* (Damiani, 2004). Posterior to the premaxillary marginal tusks, the tooth size decreases slightly until the level of the vomerine tusks, then increases until the maxillary tusks, then regularly decreases until the posterior end of the maxilla. The largest tusks (19 mm in basal section) of *Nigerpeton* appear on the inner portion of the premaxilla, anterior to its posterolateral depression and posterior to the anterior palatal vacuities. These inner tusks are bordered anteriorly and posteriorly by two large tooth replacement alveoli. This pattern, unique among temnospondyls, represents an autapomorphy of *Nigerpeton.*

The maxillary teeth have cross-sectional diameters ranging from 3 to 10 mm. Lateral to the choana, the maxilla thickens to form a well-defined swelling that accommodates three hypertrophied caniniform teeth in addition to the usual marginal tooth row. These tusks represent another autapomorphic condition of *Nigerpeton.* Labially, another irregular 'row' of teeth is visible on this bulged region of the upper jaw. This tooth 'patch' is also visible at the same occluded level on the lower jaw, on the midpart of the dentary. The vomer, palatine, and ectopterygoid also bear tusks. Neither denticles nor organized tooth rows are visible on the palate. The vomerine tusks (two per vomer) are relatively small (about 7 mm in basal section), and lie anterior to the choana without bordering it, as is surprisingly the case in metoposaurids (Schoch and Milner, 2000).

The anterior portion of the mandible also bore one or two huge symphyseal tusks that pierced the skull roof via an anterior vacuity, as is the case in the mastodonsaurids (Schoch and Milner, 2000; Damiani, 2001).

The complex dentition of *Nigerpeton* consists of numerous and variably sized marginal and palatal tusks. This degree of heterodonty is exceptional among temnospondyls, and is probably linked with the ability of the animal to catch and maintain prey in the mouth before swallowing.

Postcranial Skeleton

The atlas, found just behind the skull of MNN MOR69, consists of a well-ossified and disk-shaped intercentrum (47 rom wide and 40 mm high). It has a subtriangular profile of 21 mm in ventral length, and shows a possible attachment surface for the pleurocentrum in its right medial side. Its anterior face is concave whereas its posterior face is straight to convex.

Three presacral vertebrae and their associated ribs (MNN MOR83), as well as an isolated femur (MNN MOR 82), were found within a meter of the referred skull (MNN MOR70) and are tentatively referred to *Nigerpeton.* The vertebrae consist of isolated neural arches, the shape of which is typical for temnospondyls. The prezygapophyses are well developed, with their contact face with the corresponding postzygapophyses being very elongate. The neural spines are elongate and posterodorsally oriented. They have a losange-shaped cross section, and widen transversely and dorsally. Their upper surface is hence twice as wide as their inferior surface. Their lateral crests end in relatively smooth dorsolateral apophyses, which are a typical adult character for the temnospondyls (Steyer, 2000). The diapophyses are not pre-served, but the transverse processes, although partially broken, seem to extend between 90 (typical for the presacral arches) and 140 degrees (typical for the caudal arches) from the body of the arch. Together with the small size and the slight curvature of the associated ribs, this suggests that the vertebrae are anteriorly located along the vertebral column.
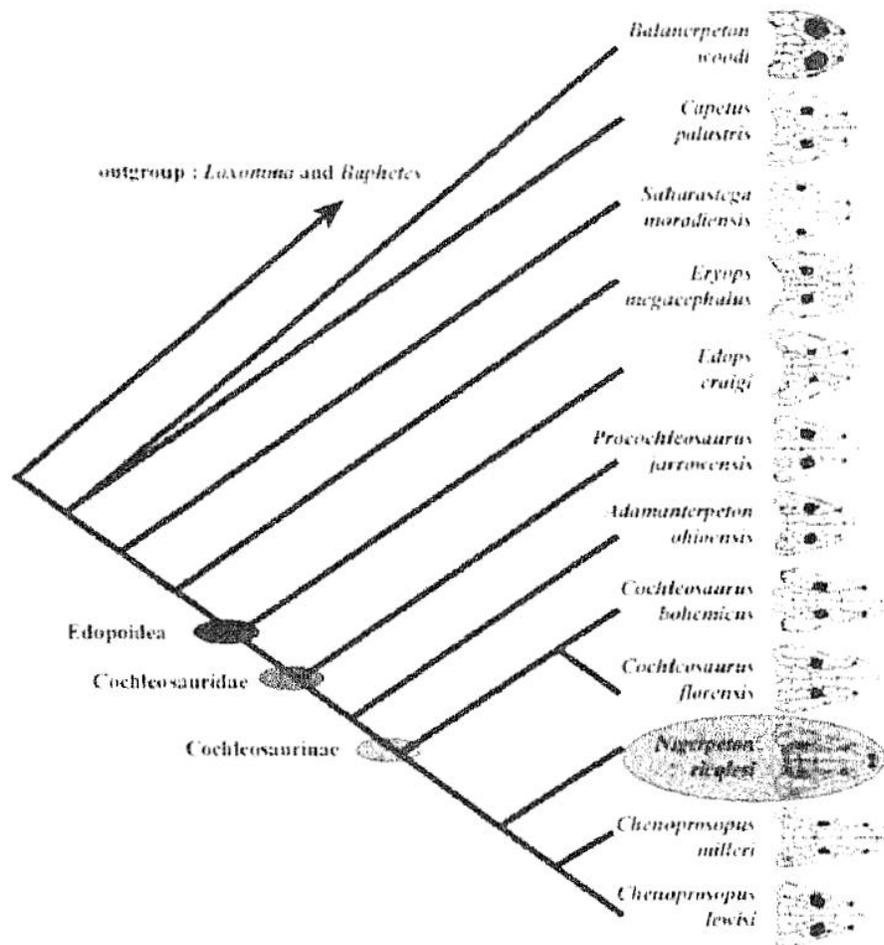

FIGURE 5. Phylogenetic position of *Nigerpeton ricqlesi* Sidor et al., 2005, among edopoids and relatives. Skulls are not to scale.

DISCUSSION

Phylogenetic Position

The phylogenetic analysis performed here is intended to test the phylogenetic position of *Nigerpeton* within the edopoids rather than to analyze the interrelationships of Paleozoic temnospondyls. Forty-two homologous and independent characters (see Appendix 1) were polarized in 14 terminal taxa according to the outgroup criterion. The character matrix (Appendix 2) is the same as that of Sidor et al. (2005), except that *Eryops* Cope, 1877, was included and *Dendrerpeton* was excluded from this analysis. Following Sequeira (2004) and Milner (pers. comm., 2005), *Loxomma* and *Baphetes* were used as outgroups. The matrix was assembled using NDE (Nexus Data Editor) version 0.5.0.
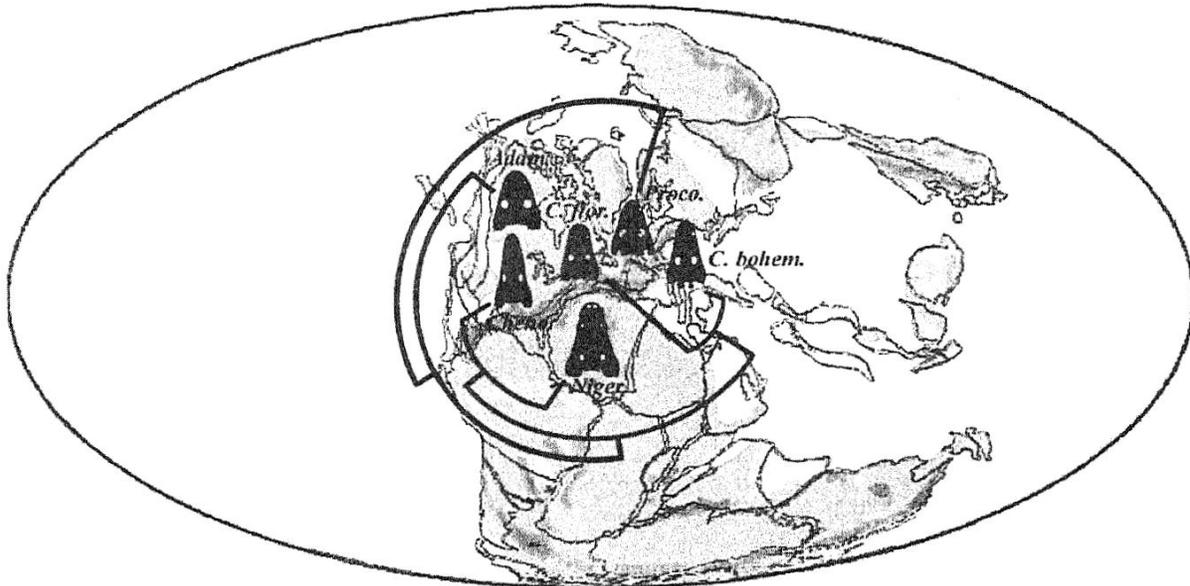

FIGURE 6. Biogeography of the cocbleosaurids at the end of the Permian. Evolutionary tree obtained from Figure 5; paleogeographic map from Scotese (2001): plains in clear grey, reliefs in dark grey. Skulls are not to scale. The American *Chenoprosopus* is here represented by the species C. *milleri.* Abbreviations: *Adam., Adamanterpeton; Cheno., Chenoprosopus;* C. *bohem., Cochleosaurus bohemicus;* C. *flor., Cochleosaurus florensis; Niger., Nigerpeton; Proco., Procochleosaurus.*

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In a recent redescription of *Cochleosaurus bohemicus,* Sequeira (2004) proposed a phylogeny of 17 basal temnospondyls (included edopoids) based on an analysis of 61 characters. Her cladistic analysis addressed the systematic relationships of the edopoids proposed by Godfrey and Holmes (1995) and by Milner and Sequeira (Sequeira and Milner, 1993; Sequeira, 1996; Milner and Sequeira, 1998). It should be noted that, prior to the analysis of Sequeira (2004), none of the previous phylogenetic analyses was computer-assisted. Our analysis is therefore based on the matrix of Sequeira (2004), with fewer (and different) non-edopoid taxa and fewer characters.

The matrix presented in Appendix 2 was analyzed with Windada version 1.00.08 (Nixon, 1999-2002), using the heuristic search of the most parsimonious tree(s) and the following options for character optimization: tree max: 1000000; replications: 1000; mult*max*. The analysis generated four mostparsimonious trees (MPTs) (length 105 steps; consistency index 0.46; retention index 0.58). The choice of first outgroup *(Loxomma* or *Baphetes)* did not affect the topology of the resulting trees. The differences between the four MPTs is related to (1) the position of *Balanerpeton* and *Capetus,* and (2) the monophyly of *Cochleosaurus.* However, as the monophyly of *Cochleosaurus* has been amply demonstrated (Rieppel, 1980; Sequeira, 2004; Sidor et al., 2005), we prefer to adopt the MPT in which *Cochleosaurus bohemicus* and C. *florensis* form a clade. This MPT is shown in Figure 5.

The MPT figured here is congruent with that of Sequeira (1996, 2004) and Sidor et al. (2005) in that the Edopoidea are composed of *Edops* plus the cochleosaurids. This clade is characterized by four unambiguous synapomorphies (characters 9, 15 [state 2], 25, and 30; see Appendix 1). Cochleosauridae are composed of .*Procochleosaurus* and *Adamanterpeton,* plus the cochleosaurines, and are characterized by two unambiguous synapomorphies (characters 27, 39). The genera *Cochleosaurus* and *Chenoprosopus* are both monophyletic and belong to the Cochleosaurinae (see diagnosis of the latter in the Systematic Paleontology section). The Nigerien taxa *Nigerpeton* and *Saharastega* do not form an African clade: *Saharastega* is the sister taxon to th~ clade composed of *Eryops* and the edopoids; *Nigerpeton* is the sister taxon of *Chenoprosopus* within the Cochleosaurinae. Interestingly, *Saharastega* occupies a more basal position in this analysis than in that of Sidor et al. (2005) or Damiani et al. (in press), where it is a stem edopoid. This slight difference is due to the i.nclusion of *Eryops* in our analysis, and our MPT supports previous analyses that show a close relationship between the edopoids and the eryopoids (Sequeira, 1996; Milner and Sequeira, 1998).

The Edopoid Colonization of Gondwana

As with the pareiasaur *Bunostegos akokanensis* and the temnospondyl *Saharastega moradiensis,* the discovery of *Nigerpeton* strengthens support for the hypothesis that West Africa hosted an endemic fauna at the close of the Paleozoic Era (Sidor et al., 2003a; Damiani et al., in press). *Nigerpeton* and *Saharastega,* which are from the same Moradi locality, are the only Late Permian temnospondyls from northern and western Africa. The Moradi temnospondyl fauna is distinctly Euramerican in aspect (Damiani et al., in press), unlike the stereospondyl-dominated southern and eastern African faunas (Anderson and Cruickshank, 1978; Milner, 1993). The edopoids are traditionally considered components of the Euramerican Pennsylvanian-Early Permian fauna (the Edaphosaur-Nectridean faunal province sensu Milner, 1993). *Saharastega* is the youngest known basal temnospondyl and the only edopoid relative known from Gondwana. *Nigerpeton* is currently the geologically youngest cochleosaurid and the only known cochleasaurid from Gondwana. Consequently, they represent both a southern (i.e., geographic) and a Late Permian (i.e., temporal) extension of the Edaphosaur-Nectridean province of Milner (1993). All cochlea-saurids except *Nigerpeton* are Pennsylvanian or Early Permian taxa from North America and Europe. Biogeographic optimization would therefore place the origin of the cochleosaurid clade somewhere in Euramerica (the oldest known cochleosaurid is *Procochleosaurus* from the Early Pennsylvanian of Ireland).

Paleogeographic reconstructions of Pangea suggest the presence of an equatorial mountain chain resulting from the collision of Laurussia with Gondwana (the Central Pangean Mountains sensu Scotese, 2001), with an estimated altitude of more than 2000 m at the level of western Africa during the end of the Permian (Ziegler et al., 1997). According to the results of the phylogenetic analysis performed here (Fig. 5), *Saharastega* represents an early temnospondyl branch (sister taxon of the clade *Eryops* + edopoids) and *Nigerpeton* is the sister taxon of *Chenoprosopus* from the Permo-Carboniferous of the United States. These relationships imply that the edopoids (and relatives) crossed the equatorial mountain chain at least twice during their evolution (Fig. 6). These two dispersal episodes could have taken a long time, because the temporal gap between the Euramerican and African taxa is at least 40 Ma (Sidor et al., 2005). According to its morphology, *Saharastega* was more terrestrially adapted, whereas *Nigerpeton* (with its longirostral skull and sensory line canals) was probably more dependent on or restricted to the fluviatile system of this inner mountain chain. The African colonization of the edopoids (and relatives) probably occurred under tropical or sub-tropical climates (i.e., from the Pennsylvanian to the Early-Middle Permian), and this once widespread distribution was later fragmented with the onset of Late Permian climatic warming (Ziegler et al., 1997; Fluteau et al., 2001; Rees et al., 2002; Sidor et al., 2005).

ACKNOWLEDGMENTS

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APPENDIX 1

Description of characters used in the phylogenetic analysis. All characters were given the same weight and were treated as unordered and non-additive.

(1) Pineal foramen in skulls ≥ 120mm midline length: open (0); closed (1).
(2) Lacrimal: entering orbit margin (0); not entering (1).
(3) Jugal: excluded from cheek margin (0); entering cheek margin separating maxilla from quadratojugal (1).
(4) Nasals: not contacting maxilla (0); contacting it (1).
(5) Preorbital length: short, less than 40% of skull length, as measured from tip of snout to anterior margin of orbit and middle of quadrate (0); intermediate, between 45-55% of skull length (1); long, greater than 60% of skull length (2).
(6) Postparietallappets: absent (0); present (1).
(7) Jugal-lacrimal contact: short (0); extensive (1).
(8) Postorbital with finger-like posterior process: absent (0); present (1).
(9) Premaxillary elongation: absent, marginal length equal to medial length (0); present, margin length much great than medial length (1).
(10) Maximum length of external naris: much less than half orbit length (0); approximately half orbit length (1).
(11) Width of skull table relative to maximum skull width: wide, ≥ 65% (0); narrow, less than 60% (1).
(12) Jugal deep below orbit (vs narrow process): < 50% orbit diameter (0); ≥ 50% (1).
(13) Jugal alary process on palate: absent (0); present (1).
(14) Prefrontal/postfrontal suture: middle of orbit (0); in anterior half of orbit (1).
(15) Septomaxillary: small, entirely within narial margin (0); barely exposed on dorsal surface (1); triangular, substantially exposed on dorsal skull surface (2).
(16) Squamosal-intertemporal contact: absent (0); present (1).
(17) Premaxillary alary process: absent (0); present (1).
(18) Width of interpterygoid vacuity: width ≥ total skull table width (0); < half of skull table width (1).
(19) Anterior palatal fossa: absent (0); present (1).
(20) Anterior extent of pterygoid: contacting contralateral pterygoid on midline anterior to cultriform process (0); contacting cultriform process, not meeting on midline (1); extending anteriorly but not contacting cultriform process or contralateral pterygoid (2).
(21) Depressions in vomers anterior to choanae: absent (0); shallow, dished depressions present (1).
(22) Vomerine denticle patch: uniformly distributed on body of vomer (0); denticles restricted to posterior vomerine surface (1); denticles absent (2).
(23) Denticles along quadrate ramus of pterygoid: extend (0); absent (1).
(24) Vomerine fangs: larger than marginal teeth (0); same size or smaller than marginal teeth (1).
(25) Upper marginal teeth near premaxillary-maxillary suture: not enlarged (0); enlarged (1).
(26) Pterygoid posterolateral edge: expanded into gently convex flange (0); extending at almost right angle to quadrate ramus (1).
(27) Prechoanal length of vomer: less than postchoanal length (0); greater than or equal to postchoanal width (1).
(28) Premaxillary tooth number: fewer than 20 (0); greater than 20 (1).
(29) Vomerine fang pair: aligned parallel to marginal tooth row (0); not parallel (1).
(30) Vomerine ridges radiating towards snout margins anterior to choanae: absent (0); present (1).
(31) Basicranial joint: mobile, unfused (0); sutural (1).
(32) Sphenethmoid: rhomboidal (0); almost square (1); elongate and narrow (2).
(33) Parasphenoid denticles: restricted to discrete zone (0); shagreen covering much of ventral surface (1); absent (2).
(34) Shape of choana: as wide anteriorly as posteriorly (0); wider anteriorly than posteriorly (1).

(35) Location of parasphenoid carotid grooves: lying posteromedial to basipterygoid process (0); curving far around basipterygoid process (1).

(36) Anterior splenial: excluded from jaw symphysis (0); entering jaw symphysis (1).

(37) Number of teeth in dentary: fewer than 48 (0); greater than 48 (1).

(38) Para-articular (chordatympanic) foramen: present (0); absent (1).

(39) Zone of subdued dermal ornament adjacent to midline suture: absent (0); present (1).

(40) Position of interpterygoid vacuities: in posterior half of skull (0); in anterior half of skull (1).

(41) Position of quadrate condyles relative to exoccipital condyles: posterior (0); at same level (1); anterior (2).

(42) Position of external naris: terminal (0); partially retracted (1); retracted well back from tip of snout (at least 15% of skull length) (2).

APPENDIX 2

Character-taxon matrix used for phylogenetic analysis. Matrix from Sidor et al. (2005) plus *Eryops* and the outgroups *Loxomma* and *Baphetes,* but without *Dendrerpeton.* Polarization of the characters inapplicable to the outgroup taxa (characters 18, 40) is based on *Balanerpeton.*

Taxon	1111111111222222222233333333333444 123456789012345678901234567890123456789012
Loxomma	0000010?0001101?00-000?1000?00000100??10-00
Baphetes	0001010100011101000-0002100000000?20010?0-00
Balanerpeton woodi	00000000000000000000201000000010100000010000
Capetus palustris	00101010000101100001021100000001??0??0??000
Saharastega moradiensis	11??2011010?10???11?000?010??01100????0110
Edops craigi	01001011111101201100010110001011011011000002
Procochleosaurus jarrowensis	?1101011?011?12011??????10???????????0?1???
Adamanterpeton ohioensis	01101?1110111120110101011110110011?00011?2
Cochleosaurus bohemicus	11101111101111201101110111101112010011112
Cochleosaurus florensis	111011111011112011011101111011020110111102
Nigerpeton ricqlesi	1101201011110?21111?1211111101011210101?1102
Chenoprosopus milleri	11111000101111211101110011111101220?1101102
Chenoprosopus lewisi	?11111001010?110110212?1111100???0??1011?1
Eryops megacephalus	0100201101110110110202110000100020101?0002