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The vertebrate fauna of the Upper Permian of Niger — II, Preliminary description of a new pareiasaur

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The skull of a new pareiasaur, *Bunostegos akokanensis* gen. et sp. nov., is described on the basis of a partial skull from the Upper Permian Moradi Formation of north-central Niger. Autapomorphies of the genus include the presence of three hemispherical bosses at the tip of the snout, an enlarged laterally projecting supraorbital boss positioned on each postfrontal, and additional, smaller bosses on the squamosal and supratemporal bones. *Bunostegos* is further characterized by a tab-like process of the nasal that articulates with the frontal, a pineal foramen located equidistant between the parietal-frontal and parietal-postparietal sutural contacts, a postparietal that is excluded from the caudal margin of the dorsal skull roof, and a blunt interpterygoid vacuity. The discovery of *Bunostegos* suggests an unsuspected degree of biogeographic endemism for central West Africa during the Late Permian.

Keywords: Permian, Moradi Formation, West Africa, Niger, Pareiasauria, Parareptilia.

INTRODUCTION

The Beaufort Group of South Africa chronicles an important period of vertebrate evolution — the assembly of an herbivore-based terrestrial ecosystem during the Middle and Late Permian (Olson 1962; Bakker 1972; Reisz & Sues 2000). Although perhaps best known for its therapsid ('mammal-like reptile') fauna (Hancox & Rubidge, 2001; Rubidge & Sidor, 2001), the Beaufort Group also enjoys the greatest diversity of pareiasaur taxa in the world. Rubidge (1995) conservatively listed four pareiasaur genera from South Africa, whereas Lee's (1997b) more recent taxonomic revision recognized at least eight genera comprising ten species. Importantly, the results of Lee's (1997b) study imply the sympatric co-occurrence of pareiasaur herbivores: three genera co-occur within the *Tapinocephalus* Assemblage Zone (AZ), four within the *Cistecephalus* AZ, and two within the *Dicynodon* AZ. Elsewhere in the world, pareiasaur remains are less abundant: three taxa are known from China, two taxa from Russia, and one each from Brazil, Germany, Morocco, Scotland and Zambia (Lee 1997b; Lee *et al.* 1997; Jalil 2001). Here we provide a preliminary description of an unusual new pareiasaur from the Republic of Niger that suggests a distinct biogeographic province for West Africa near the close of the Palaeozoic Era (Sidor *et al.* 2003).

The history of fossil discovery in the Moradi Formation of Niger was reviewed by de Ricqlès & Taquet (1982). Although they discussed the collection of abundant vertebrate remains on expeditions in 1966, 1967 and 1969, the only taxon to be formally named and described to date is the large captorhinomorph *Moradisaurus grandis* (Taquet 1969; de Ricqlès & Taquet, 1982). A pareiasaur skull from the Moradi Formation was figured by Taquet (1972: pl. 1), but it was neither named nor described.

In November of 2000, a University of Chicago team led by P. Sereno revisited the Moradi Formation. They discovered a locality northwest of Agadez that produced the skulls of a new temnospondyl amphibian and the pareiasaur described in this contribution.

MATERIAL

The specimen was collected from an intraformational conglomeratic unit of the Moradi Formation. The skull was preserved palate-up and had been eroded down to the level of the orbit. As a consequence, the lower jaw is absent and much of the palate is preserved only as impression. The specimen was prepared at the Smithsonian Institution's National Museum of Natural History in Washington, D.C.

SYSTEMATIC PALAEONTOLOGY

Pareiasauria Seeley, 1888

***Bunostegos akokanensis* gen. et sp. nov.**

Etymology. Buno, knobby (Greek); *stegos,* roof (Greek), referring to its identification as a pareiasaur and the knobby bosses that adorn the skull roof; Akokan, a town close to the type locality; *-ensis* (Latin), place or locality.

Diagnosis. Medium-sized pareiasaur with three hemispherical bosses located at the anterior end of the snout; nasal with a posterolateral tab-like process articulating with the frontal; elongate, laterally projecting postfrontal bosses overhanging orbits; hemispherical supratemporal boss located at posterolateral corner of skull roof; postfrontal and supratemporal bosses with neck separating globular head from skull roof; pineal foramen equidistant from frontoparietal and parietal-postparietal sutures.

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Holotype. MNN-MOR72, a nearly complete cranium that has been eroded ventrally.

Type Locality. Coordinates 18°47′01″N, 7°11′49″E, west of Arlit, Agadez Prefecture, Republic of Niger (Fig. 1). The locality lies in a conglomeratic layer of the Moradi Formation, which is believed to be uppermost Permian, based on biostratigraphic data (Taquet 1972).

DESCRIPTION

Preservation

MNN-MOR72 consists of a partial skull and several 'skins' of bone that preserve the external surface of the dorsal skull roof and temporal regions. Erosion has separated these 'skins' from the remainder of the skull by a gap of between 0–2 cm, leaving only an endocast of the skull in certain places. The conglomeratic nature of the surrounding matrix, coupled with the specimen's relatively spongy, pachyostotic bone, has made preparation and interpretation extremely difficult. In particular, this mode of preservation has limited our recognition of sutures between skull elements. Some sutures are visible on the internal surface of the 'skins' of bone, whereas others are visible on what remains of the skull itself. Rarely is a suture visible on the true external surface of the skull, which precludes a direct comparison with the pattern of other pareiasaurs.

The palate and ventral surface of MNN-MOR72 is extremely damaged, being planed-off by erosion. Some bone and several sutures are evident in ventral view, although the majority of the palate is preserved only as impression. Substantial adhering matrix surrounds the occipital region and obscures this region's structure. Further preparation of the occiput is risky due to the thin skull roof bones in this region.

Figures 2, 3, and 4 show MNN-MOR72 with several of the 'skins' of bone in place. Because the external surface of these 'skins' is backed by an approximately even amount of matrix, we believe that the overall shape of *Bunostegos* is well portrayed. In the figures we have attempted to reconstruct the outline of the skull and project the placement of sutures onto its external surface. Caution should be used when comparing the sutural configuration of *Bunostegos* to that of other pareiasaurs because all of the sutures we illustrate are deep to some level (i.e., they are not on the true external surface of the bone).

Skull roof

Although its overall appearance is peculiar, *Bunostegos* is a pareiasaur based on its possession of the following diagnostic characters: anapsid cranium, single fused postparietal located on the skull roof, medially directed posterior choanae, and prefrontal-postfrontal sutural contact (Lee 1997a). Figures 2–4 demonstrate the important features of the genus, including three supranasal bosses, laterally elongated supraorbital bosses formed by the postfrontals, and additional bosses extending laterally from the supratemporals. The shape and distribution of these features is unique to *Bunostegos* and absent in all other pareiasaur genera.

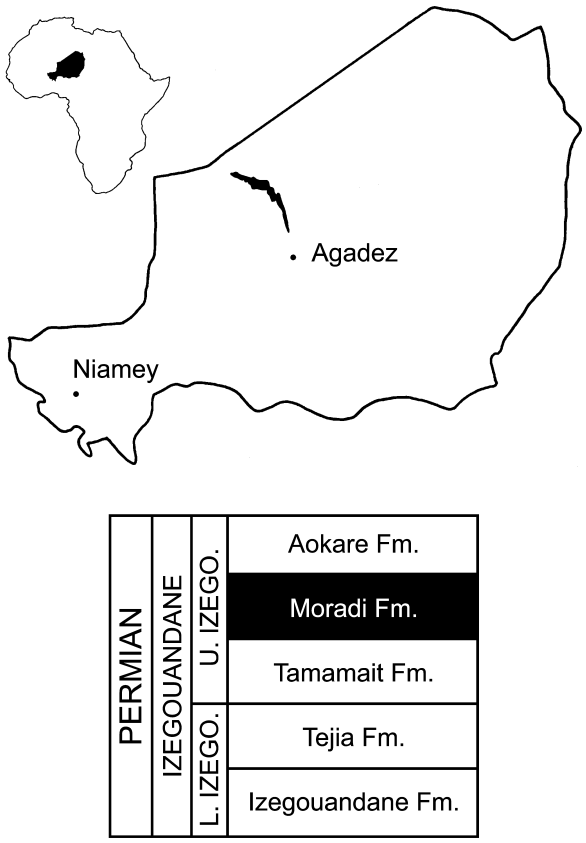


Figure 1. Geography and generalized Permian stratigraphy of the Republic of Niger. The position of Permian rocks is highlighted within the outline of Niger. Abbreviations: Fm. = Formation, Izego. = Izegouandane, L = Lower, U = Upper. Stratigraphic subdivisions based on Ministère des Mines et de l'Hydraulique, Direction des Mines et de la Géologie (1977).

Only the dorsal process of the premaxilla is preserved. Ventrally this element is so badly eroded that the tooth-bearing ramus of the premaxilla is completely absent. The nasal descends along the posterior margin of the premaxilla's dorsal process and may exclude the premaxilla from participating in the preserved anterior margin of the external naris. A similar condition was illustrated by Boonstra (1934: Pl. 2) for *Dolichopareia angusta* (now *Nochelesaurus angusta*; Lee 1997b). In anterior view, the pair of premaxillae form an inverted triangle that nearly reaches the base of a median boss.

The maxilla is typically a large, tooth-bearing element in pareiasaurs that makes up much of the lateral surface of the snout. In addition, it forms much of the posterior margin of the external naris. In *Bunostegos,* the external naris is incomplete and it is difficult to determine how much, if any, of the maxilla remains. This uncertainty is complicated by the poor delineation of the nasal and lachrymal bones.

Three hemispherical bosses are positioned at the rostral end of the skull roof: one boss is median and two are parasagittal. The median boss projects the furthest anteriorly and is slightly smaller than the other two swellings. In *Pareiasuchus nasicornis,* Lee *et al.* (1997) describe paired bosses above the external nares as separate ossifications sutured to the nasals. *Elginia mirabilis* also bears paired bosses above the external nares, although these are considered to be formed by the nasals (Spencer & Lee

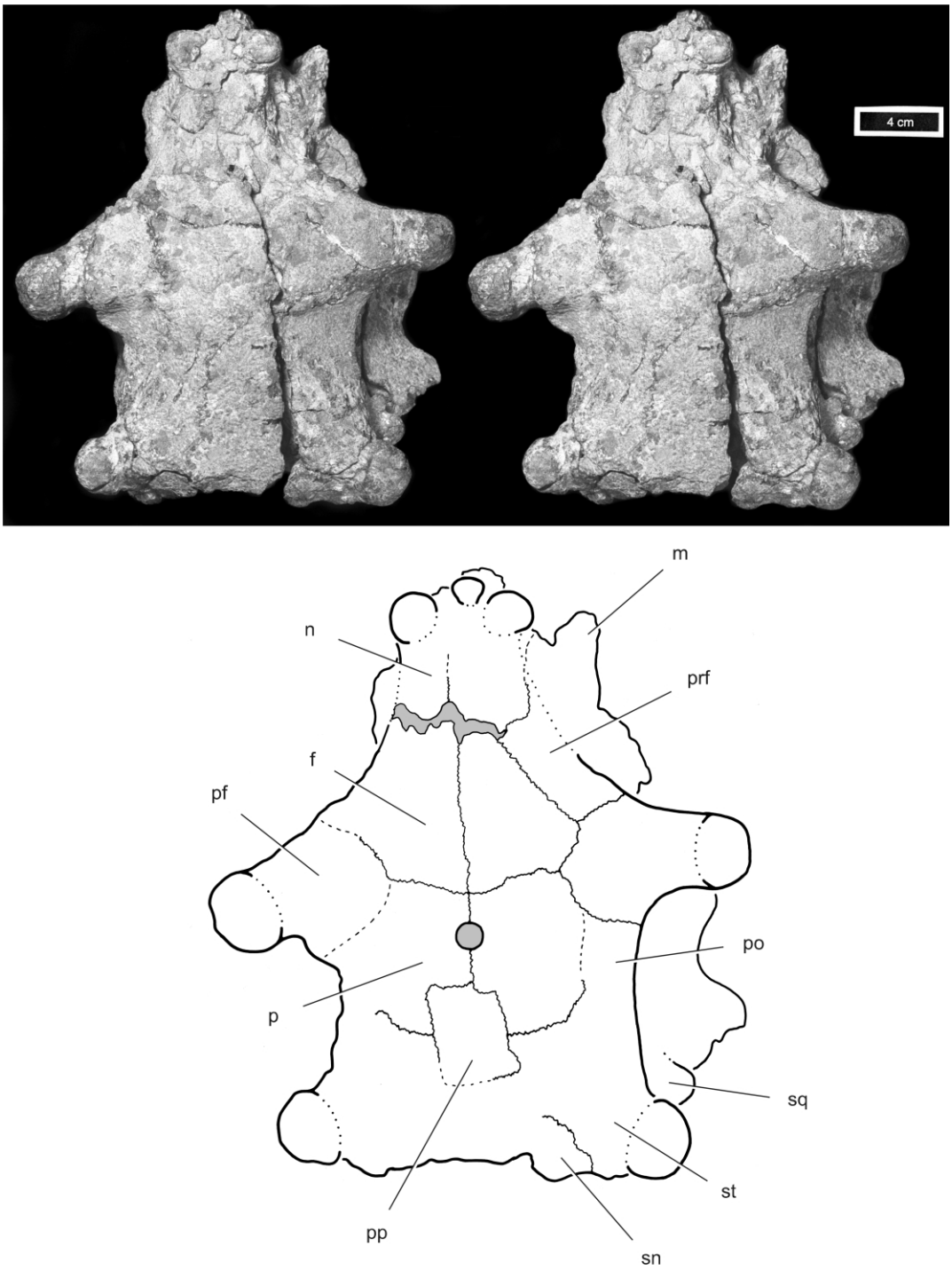


Figure 2. Stereophotographs and interpretive line-drawing of the skull of *Bunostegos akokanensis* (MNN-MOR72), gen. et sp. nov., in dorsal view.

2000; D. Maxwell, pers. comm.). We are unable to determine the precise location or osteological identity of the three bosses in *Bunostegos* because the relevant sutures are not visible.

The snout has been slightly flattened dorsoventrally and sheared to the left. This deformation has stretched the snout and widely separated the nasal from the frontal. The suture between these two elements can been seen as a transversely oriented gap, just anterior to the level of the orbit. On either side, the nasal bears a small, caudally directed tab at its posterolateral corner that slots into a corresponding socket on the frontal. A short contact between the nasal and prefrontal is visible on the right side. Only a small portion of the contact between the nasal and lachrymal can be made out on the left side.

The anatomy of the prefrontal is more clearly exposed on the right side. On the skull roof, the prefrontal contacts the frontal along an anteromedially directed suture arising from the triple junction between the frontal, prefrontal, and postfrontal. The prefrontal's suture to the nasal is visible as a short contact, mostly located along the lateral surface of the snout. In dorsal view, the prefrontal-postfrontal contact is visible along the anterior margin of the supraorbital boss. Inside the orbit, the prefrontal can be seen to contact the lachrymal at the level of the orbit's midpoint.

The left lachrymal can be distinguished by virtue of its suture with the prefrontal and nasal, although its

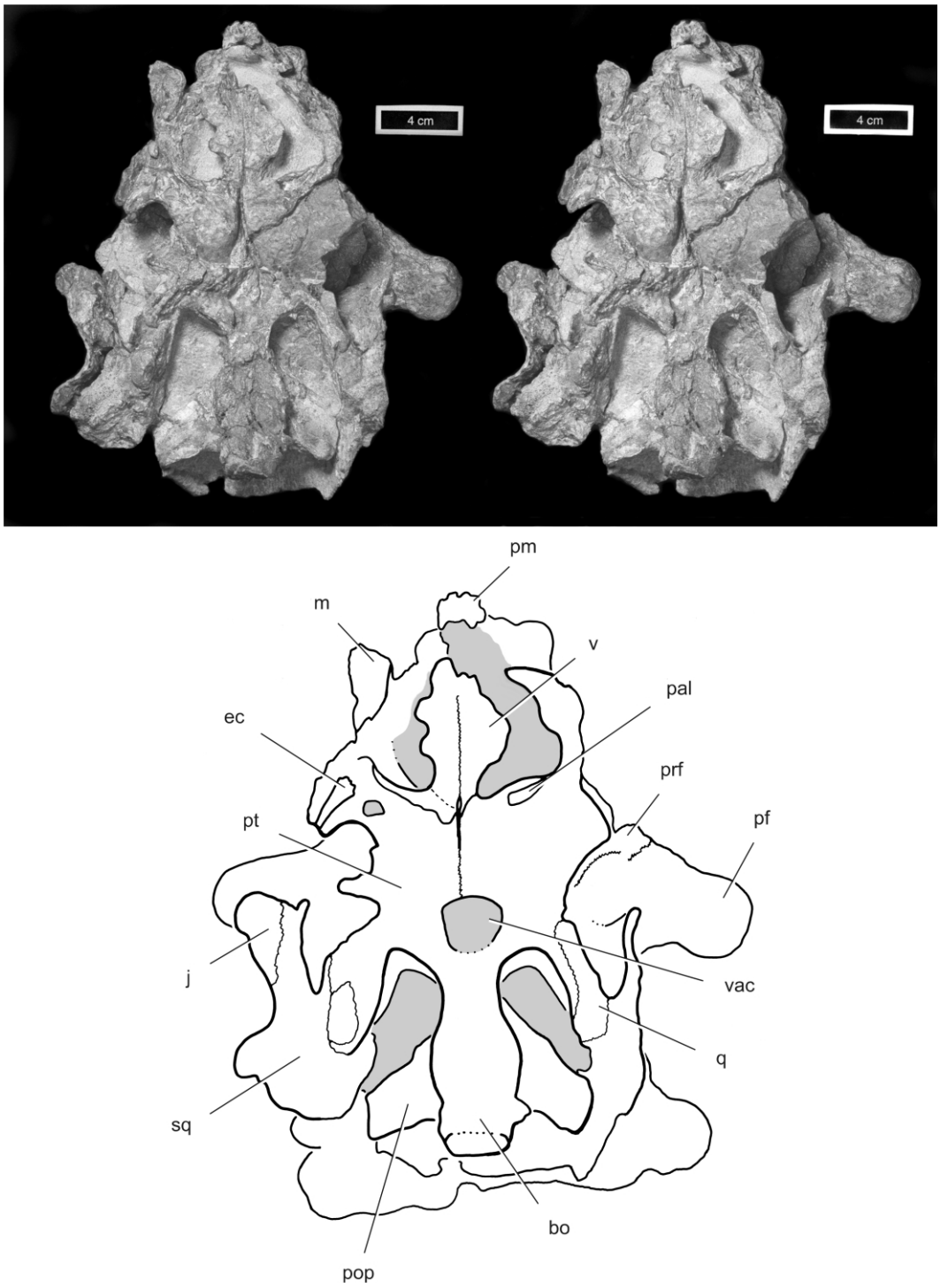


Figure 3. Stereophotographs and interpretive line-drawing of the skull of *Bunostegos akokanensis* (MNN-MOR72), gen. et sp. nov., in ventral view.

presumed ventral contact with the maxilla and jugal could not be determined. The lachrymal forms a portion of the orbital margin inferior to that of the prefrontal. This contact occurs approximately halfway up the left orbit's anterior border and then continues anteriorly and slightly upwards, where the nasal descends onto the lateral surface of the snout.

Owing to the degree of erosion, the suborbital portion of the jugal is absent on both sides of MNN-MOR72. However, on the right side, a well-defined suture with the postorbital is present on the inside of one of the 'skins' of bone and verifies that the jugal formed the inferior one-half of the orbit's posterior margin. Because the relevant sutures are not visible, it is impossible to determine if the jugal is present anteroventral to the orbit.

As discussed above, the frontal's contact with the nasal is represented by a large, transverse gap on the dorsal surface of the snout. Further posteriorly, the frontal-parietal suture is also oriented roughly transversely, but it is located further back, in line with the posterior one-quarter of the orbit. The frontal-parietal contact bends slightly anteriorly as it progresses away from the sagittal plane, such that its full extent resembles a shallow 'U'. In dorsal view, the frontal-postfrontal contact is nearly as long as the frontal-prefrontal contact. Typically in pareiasaurs, the latter contact is the substantially longer of the two (Lee

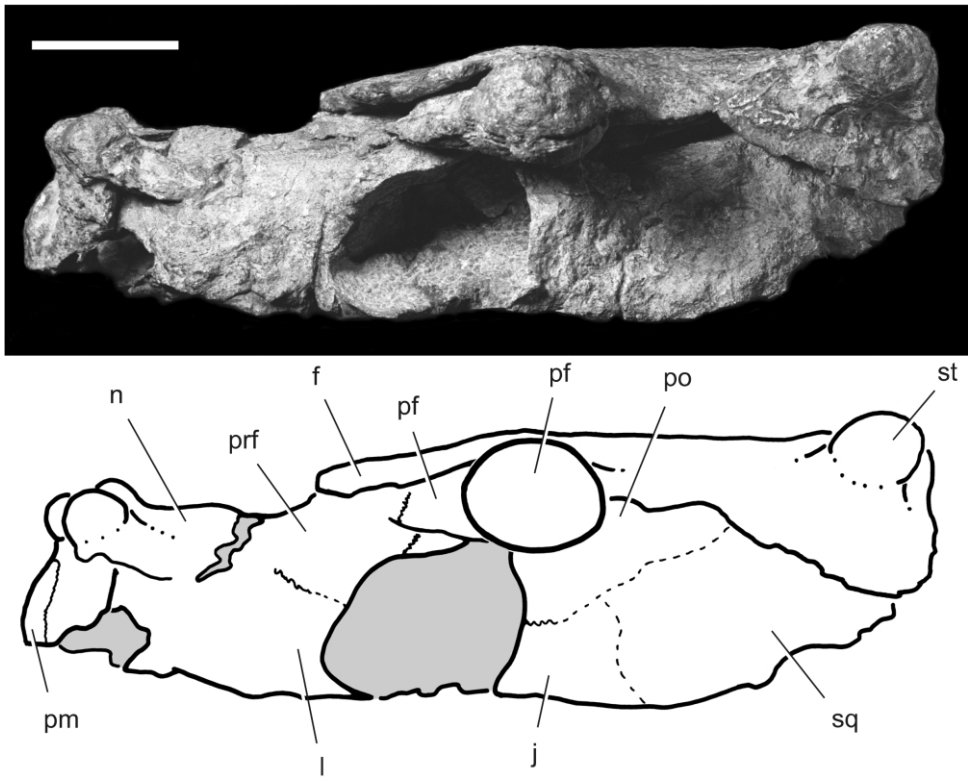


Figure 4. Photograph and interpretive line-drawing of *Bunostegos akokanensis* (MNN-MOR72), gen. et sp. nov., in lateral view. Scale bar = 4 cm.

1997: fig. 4). As a result of the long frontal-prefrontal contact, the dorsal margin of the orbit is composed almost exclusively of an enlarged postfrontal in *Bunostegos.* The postfrontal supports a greatly enlarged boss that extends laterally and expands distally to form two regions: a discrete neck and globular head. The postfrontal boss obscures the orbit in dorsal view. This condition is unknown in other pareiasaurs but superficially resembles reconstructions of *Elginia* (Spencer & Lee 2000). However, these reconstructions may be misleading because the dorsolateral skull roof has been anterolaterally displaced in the type specimen of *Elginia,* thus giving the false impression that the orbits were dorsally obscured in this taxon (D. Maxwell, pers. comm.). The sutural contacts of the prefrontal, postfrontal, and postorbital cannot be discerned in *Elginia* (D. Maxwell, pers. comm.), but it is clear that the postfrontal is not enlarged to the extent found in *Bunostegos.*

Anatomical information regarding the postorbital comes from both sides of the skull. In lateral view (Fig. 4), this element occupies roughly the upper half of the orbit's posterior border, sandwiched between the postfrontal, above, and the jugal, below. In dorsal view, the limits of the postorbital are more difficult to make out, although it presumably contacted the postfrontal, parietal, and supratemporal. On both sides, the dorsal portion of the jugal is preserved in articulation with the postorbital, but the remainder of the jugal has been lost due to the erosion of the cranium's ventral surface.

An internal suture is visible between the right supratemporal and right squamosal on the relevant 'skin' of bone. Although little detail can be made out, the position of this suture indicates that the squamosal supports a dorsolaterally projecting boss just ventral to the large supratemporal boss. Other swellings along the posterior margin of the squamosal might have been present, but this region is incompletely preserved. Anteriorly, the squamosal forms the broad plate of bone behind the orbit, although its contacts with the postorbital and jugal are uncertain.

The parietal is a large, flat bone of the posterior skull roof. It contacts the frontal anteriorly and the postfrontal anterolaterally. The lateral margin of the parietal is unclear, although we suspect it contacted the postorbital along a roughly longitudinal suture, as indicated in Fig. 2. The posterolateral portion of the skull table is poorly preserved, so it is impossible to determine if the usual parietal-supratemporal contact is present in *Bunostegos.* More medially, however, the parietal can be seen to contact the median postparietal. Between the two parietal bones, a circular parietal foramen is present. This foramen is located equidistant from the frontal-parietal and parietal-postparietal contacts, which is approximately in line with the posterior margin of the orbit.

The postparietal is a median, rectangular element located on the skull roof. The anterior one-half of this element is enclosed within the parietals by a clearly defined suture. It is more difficult to determine the posterior extent of the postparietal. However, the remnants of a transversely oriented suture seem to indicate that the posterior border of the postparietal was located on the skull roof. That is, the postparietal was excluded from the caudal margin of the dorsal skull roof. Among pareiasaurs, this condition is observed only in *Elginia,* where it is due to the 'supernumerary' elements contacting each other on the midline (Lee 1997b; Spencer & Lee 2000). Enlarged 'supernumerary' elements are known in both *Elginia* and the 'Kupferschiefer pareiasaur' (referred

to *Parasuchus geinitzi* by Wild 1985). We suspect that a similar condition was present in *Bunostegos,* although a midline suture between the enlarged 'supernumerary' elements cannot be observed on either the skull roof or corresponding 'skin' of bone.

The supratemporal is poorly delimited on the skull roof. In the region where the supratemporal would be expected, a large boss projects laterally from the posterolateral skull roof. Similar to the supraorbital boss, the supratemporal boss has a distinct neck and terminates in a bulbous head. A portion of the medial boundary of the right supratemporal is visible on the underside of the relevant 'skin'. This suture indicates that the 'supernumerary' element was a broad bone that extended nearly to the supratemporal boss. The posterior border of the skull is transversely oriented and extends caudally to overhang and obscure the occipital condyle in dorsal view.

Palate

The ventral cranial morphology of *Bunostegos* is difficult to compare with that of other pareiasaurs because erosion has removed most of the palatal surface of the skull. Portions of both vomers are present but their ventral surfaces have been eroded to such an extent that it is impossible to discern the presence of vomerine teeth. Anteriorly, erosion has destroyed the contact between each vomer and its corresponding premaxilla. As in all pareiasaurs, the choanae are large, C-shaped openings that curve medially at their posterior margin.

At the posterior end of the choanae, a fragment of the palatine is preserved on both sides. The right palatine is more complete, and contacts either the maxilla or lachrymal deep within the choana.

An extremely fragmentary portion of the right ectopterygoid is present but little morphology is preserved (Fig. 3). Between the ectopterygoid and palatine, a remnant of the posterior palatal foramen may be present.

The palatal ramus of the pterygoid is preserved mostly as an impression of its internal (i.e. dorsal) surface. The right transverse flange of the pterygoid is partially preserved and an impression of the left transverse flange is also present. These may provide a good indicator of the lateral extent of the pterygoids and suggest that they failed to reach the cheek, as in other pareiasaurs. A small section of both pterygoids is present near the midline, and shows that these elements were sutured together until the interpterygoid vacuity. On the left side, the margin of this vacuity is reasonably well preserved and shows it to be relatively blunt anteriorly. In this respect, the interpterygoid vacuity of *Bunostegos* is most similar to that of *Deltavjatia* and *Bradysaurus.* A portion of the quadrate ramus of the pterygoid is present on both sides. These form the lateral aspect of the cranioquadrate space and are clearly sutured to their respective quadrates posterolaterally.

The ventral surface of the basisphenoid is highly eroded. In the region of the interpterygoid vacuity, remnants of the parasphenoid rostrum are present, but no detail can be made out. There is a distinct constriction of the basisphenoid posterior to the basicranial articulation. This condition is present in basal pareiasaurs such as *Bradysaurus* and *Nochelesaurus* (Lee 1997a).

The position of the contact between the basioccipital and basisphenoid cannot be determined because of damage in this region. Further posteriorly, the basioccipital is represented by the occipital condyle, which is circular in posterior view and bears a deep notochordal pit. Contacts between the basioccipital and exoccipitals cannot be seen.

The paroccipital process of the opisthotic is relatively well preserved and visible primarily in ventral view. As a consequence of its deeper position within the skull, it was spared the erosion affecting the remainder of the palate. The ventral surface of the paroccipital process is a gently concave plate that is angled posteroventrally. When viewed from below, the paroccipital process is directed posterolaterally from the braincase and abuts the medial surface of the squamosal distally.

Only the dorsal ramus of the quadrate is preserved in *Bunostegos.* It is represented by a posterolaterally oriented vertical lamina that broadens slightly towards the region of the jaw articulation. Although only visible in section, the left quadrate can be distinguished by a change in bone texture and is slotted between the remnants of the quadrate ramus of the pterygoid medially and the squamosal laterally. If the orientation of the quadrate dorsal ramus reflects the position of the more ventral portions of this bone, it may indicate that the articular surface of the quadrate was located in a position nearly level with the anteroposterior midpoint of the basisphenoid. This configuration is atypical for pareiasaurs, where the quadrate rami are more transversely oriented and the jaw articulation is located at the level of the interpterygoid vacuity. Only in *Pareiasuchus nasicornis* is the jaw articulation located further posteriorly, just anterior to the basisphenoid-basioccipital suture (Lee *et al.* 1997).

DISCUSSION

Fauna of the Moradi Formation

The tetrapod fauna of the Moradi Formation now consists of two large-bodied, herbivorous reptiles: the pareiasaur *Bunostegos akokanensis,* and the multiple tooth-rowed captorhinid, *Moradisaurus.* The skull figured by Taquet (1976) either represents an additional species of pareiasaur from the Moradi fauna, or pertains to *Bunostegos.* A second pareiasaur occurring in the same beds would not be unexpected, given the fauna of the Karoo (Rubidge 1995; Lee 1997b).

The unnamed pareiasaur (Taquet 1976) is similar to *Bunostegos* in that its orbits are obscured in dorsal view by enlarged and laterally projecting bosses, although these do not appear to bear a distinct neck and spherical end. An additional similarity is that the region of the nasal bears an enlarged boss rostrally. However, as figured by Taquet (1976) the occipital condyle is visible in dorsal view, which suggest the absence of large supernumerary elements. The degree to which damage has influenced the overall shape of the figured skull is unclear. Overall, the smaller supraorbital bosses and the apparent shortening of the dorsal skull roof may indicate that Taquet's (1976) speci-

men is a different morphotype of *Bunostegos,* but this cannot be confirmed with certainty.

The Late Permian has been interpreted as a time of broad cosmopolitanism among terrestrial vertebrates (Olson 1962; Romer 1973). Faunal similarity, including the presence of shared genera in coeval South African, Indian, Zambian, and Russian rocks (Rubidge 1995; Ivachnenko *et al.* 1997; Ray 1999; Battail 2000), argues for relatively unrestricted dispersal among land-living tetrapods. It is surprising, then, to discover a West African fauna that fails to share genera with the stratigraphically thick and palaeontogically well known Beaufort Group (Sidor *et al.* 2003). Moreover, in contrast to the dicynodont-dominated faunas known elsewhere, the herbivores of the Moradi Formation are predominantly captorhinids, represented by *Moradisaurus,* and pareiasaurs, represented by *Bunostegos.* A similar condition occurs in the Upper Permian Argana Formation of Morocco, where the material identified as captorhinid by Jalil & Dutuit (1996) actually includes both captorhinid and pareiasaur remains (M. Lee, pers. comm.). Although based on preliminary data, we suggest that North and West Africa might have hosted an endemic tetrapod fauna (Sidor *et al.* 2003; see also Jalil 1999, 2001). This hypothesis requires testing by the further collection of vertebrate remains and the recognition of a plausible isolation mechanism for this section of Pangea.

Relationships of *Bunostegos*

Lee (1997a) presented the first cladistic analysis of pareiasaur interrelationships using data from both the cranial and postcranial skeletons. His analysis included 16 pareiasaur terminal taxa, which represented most of the described taxa at the time. The primary conclusions of this and the analysis of Lee (1995) were the paraphyly of pareiasaurs with respect to turtles and the recognition of several subclades within Pareiasauria. Lee's (1997a) detailed phylogenetic work has established a framework within which *Bunostegos* may be tentatively placed.

Bunostegos presents features of both primitive and derived pareiasaur taxa (Lee 1997a). For example, the shape of the interpterygoid vacuity is similar to *Deltavjatia* and *Bradysaurus,* both of which are stem pareiasaur taxa (Lee 1997a). *Elginia mirabilis,* a small anomalous pareiasaur from the Upper Permian of Scotland, shares two interesting characters with *Bunostegos*: postparietals that are excluded from the caudal border of the dorsal skull roof by enlarged 'supernumerary' elements, and enlarged squamosal and supratemporal bosses. *Bunostegos* may also resemble *Pareiasuchus nasicornis* from the Upper Permian of Zambia (Lee *et al.* 1997) if its anterior nasal bosses are discrete ossifications and its quadrate articular surfaces were displaced posteriorly. The ingroup relationships of the clade including both *Elginia* and *Pareiasuchus* ('Clade E' of Lee 1997a) are tenuous as they are presently supported by only a few characters. This diverse pareiasaur clade is the sister taxon to the clade to which turtles may belong. As the above comparisons attest, the phylogenetic affinities of *Bunostegos* are presently unresolved.

A new season of fieldwork was conducted in the Moradi Formation in March–April of 2003 (Sidor *et al.* 2003). Additional pareiasaur material was collected, including three partial skulls and substantial postcranial remains. We believe that most of this material will, upon preparation, be found to pertain to *Bunostegos.* This new material should shed much needed light on the detailed anatomy of this taxon and its phylogenetic relationships to other pareiasaurs. In addition, the identification of additional tetrapod taxa will provide data for the biogeographic endemism hypothesis proposed herein.

ABBREVIATIONS

bo	basioccipital
ec	ectopterygoid
f	frontal
j	jugal
l	lachrymal
m	maxilla
MNN	Musée National du Niger
n	nasal
p	parietal
pal	palatine
pf	postfrontal
pm	premaxilla
po	postorbital
pop	paroccipital process of opisthotic
pp	postparietal
prf	prefrontal
pt	pterygoid
q	quadrate
sn	'supernumerary element'
sq	squamosal
st	supratemporal
v	vomer
vac	interpterygoid vacuity

We thank P. Sereno for the opportunity to prospect the Moradi Formation in 2000, and the other team members (A. Beck, J. Conrad, E. Duneman, D. Duthiel, M. Hettwer, H. Larsson, G. Lyon, T. Lyman, R. Sadleir, and G. Wilson) for their interest in Permian vertebrates and dedication during the expedition. We are indebted to I. Kouada and the Government of Niger for permission to conduct fieldwork, E. Love for preparation of the *Bunostegos* holotype, and the David and Lucile Packard Foundation, the National Geographic Society, and the Pritzker Foundation for funding (to P. Sereno). Finally, we acknowledge R. Reisz, M. Lee, and B. Rubidge for their editorial contributions.

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