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Acknowledgements This collaboration was facilitated by the Meeting of Young Researchers in the Earth Sciences (MYRES) held in La Jolla, California, in August 2004. This work was supported by a grant from IGPP Los Alamos.

Competing interests statement The authors declare that they have no competing financial interests.

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Permian tetrapods from the Sahara show climate-controlled endemism in Pangaea

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New fossils from the Upper Permian Moradi Formation of northern Niger^{1–6} provide an insight into the faunas that inhabited low-latitude, xeric environments near the end of the Palaeozoic era (~251 million years ago). We describe here two new temnospondyl amphibians, the cochleosaurid *Nigerpeton ricqllesi* gen. et sp. nov. and the stem edopoid *Saharastega moradiensis* gen. et sp. nov., as relicts of Carboniferous lineages that diverged 40–90 million years earlier^{7–9}. Coupled with a scarcity of therapsids, the new finds suggest that faunas from the poorly sampled xeric belt that straddled the Equator during the Permian period^{10–12} differed markedly from well-sampled

faunas that dominated tropical-to-temperate zones to the north and south^{13–15}. Our results show that long-standing theories of Late Permian faunal homogeneity are probably oversimplified as the result of uneven latitudinal sampling.

For over 150 yr, palaeontologists have understood end-Palaeozoic terrestrial ecosystems largely on the basis of Middle and Late Permian tetrapod faunas from southern Africa. The fauna of these rich beds, particularly South Africa's Karoo Basin, has provided fundamental insights into the origin of modern terrestrial trophic structure¹⁶ and the successive adaptations that set the stage for the subsequent mammalian radiation¹³. A Karoo-like tetrapod fauna has been found across coeval Gondwanan rocks in Brazil, India, Mozambique, Tanzania, Zambia and Zimbabwe. A remarkably similar amniote fauna is known from China, Germany, Laos, Russia and Scotland, although these Laurasian strata host different amphibian groups⁹. The cosmopolitan fauna recorded across Pangaea provides compelling evidence for the unrestricted dispersal of tetrapods during the Middle and Late Permian period. We report here on the discovery of new fossils from West Africa that reveal a highly unusual fauna that has important implications for this interval of vertebrate evolution.

Temnospondyli Zittel, 1888

Edopoidea Romer, 1945

Nigerpeton ricqllesi gen. et sp. nov.

Etymology. *Niger*, for the country, and *herpeton* (Greek), meaning crawler; *ricqllesi*, named for Armand de Ricqlès.

Holotype. MNN MOR69 (Musée National du Niger, Niamey), partial skull and associated atlas vertebra.

Referred material. MNN MOR70, a larger skull preserving most of the left side of the palate, skull roof and lower jaw; MNN MOR83, three isolated sacral neural arches with associated ribs; MNN MOR82, partial femur.

Horizon and locality. Collected from a thin conglomerate in the Upper Permian Moradi Formation, approximately 20 km west of Arlit, north-central Niger.

Diagnosis. Edopoid temnospondyl distinguished from all other edopoids by the unique presence of a highly reduced supratemporal bone, lateral swelling of the maxilla that accommodates two or three fangs medial to the marginal tooth row, maxillary and dentary tooth rows with sporadic appearance of 'doubled' tooth positions, medially positioned premaxillary fangs, and anterior premaxillary vacuities for accommodation of mandibular fangs. Further distinguished from the cochleosaurids *Chenoprosopus* and *Cochleosaurus* by its larger size, extreme preorbital length (~70% of total skull length), anteroposteriorly short skull table, broad sphenethmoid, and the presence of an anterior palatal vacuity.

Saharastega moradiensis gen. et sp. nov.

Etymology. *Sahara*, for the Sahara Desert, and *stega* (Greek), meaning roof; *moradi*, the formation from which the fossil was recovered, and *ensis* (Latin), meaning place or locality.

Holotype. MNN MOR73, nearly complete skull lacking lower jaws.

Horizon and locality. Collected from dark reddish-brown flood-plain deposits of the Moradi Formation, approximately 20 km west of Arlit, north-central Niger.

Diagnosis. Distinguished from all other temnospondyls by the unique presence of an extensive tongue-and-groove articulation between the premaxilla and maxilla, and tabulars with exceptionally large, blunt-ended 'horns' that are directed both laterally and ventrally. Further distinguished from all other edopoids by the following unique combination of characters: orbits broadly separated and close to skull margin, pineal foramen absent, basicranial articulation sutural, fossa subrostralis media present, transverse tooth row present, palatal tusks highly reduced or absent, supraoccipital ossified.

The Upper Permian Moradi Formation of northern Niger is a 100-m-thick succession of fluvial sediments that were deposited as the result of reactivated strike-slip faults bounding the Izégouan-

dane Basin^{1,2,6}. The upper portion of the formation consists of fossiliferous overbank deposits laid down by meandering streams that flowed into a closed, semi-arid continental basin. Although Moradi Formation rivers were sourced in more humid uplands, palaeopedogenic carbonate horizons in the floodplain sediments indicate that basinal conditions were very dry. On a regional scale, palaeoclimatic reconstructions suggest that desert-like conditions prevailed over central and western Africa during Late Permian times^{10–12}. Previously reported members of the Moradi tetrapod fauna include the giant captorhinid *Moradisaurus grandis*^{2,3,5} and the pareiasaur *Bunostegos akokanensis*⁴.

The two amphibians described here are the first temnospondyls known from the Upper Permian of West Africa and the most

primitive temnospondyls from Gondwana. The skull of *Nigerpeton ricqlesi* has crocodilian proportions and size, reaching an adult length of at least 65 cm (Fig. 1a–c, g). In dorsal view (Fig. 1a, b), it is sub-triangular with an elongate, rounded snout and relatively small orbits and external nares. The latter are retracted posteriorly to a position above the maxillary tooth row and open dorsolaterally. The orbits are placed in the posterior one-fifth of the skull and restrict the skull table and its complement of dermal elements to a comparatively small area. As in other cochleosaurids, a characteristic pattern of dermal sculpturing and broad depressions adorns the skull roof. The snout of *Nigerpeton* has paired anterior premaxillary vacuities (av; see Fig. 1) that accommodated the tips of hypertrophied mandibular fangs, a feature common to Triassic

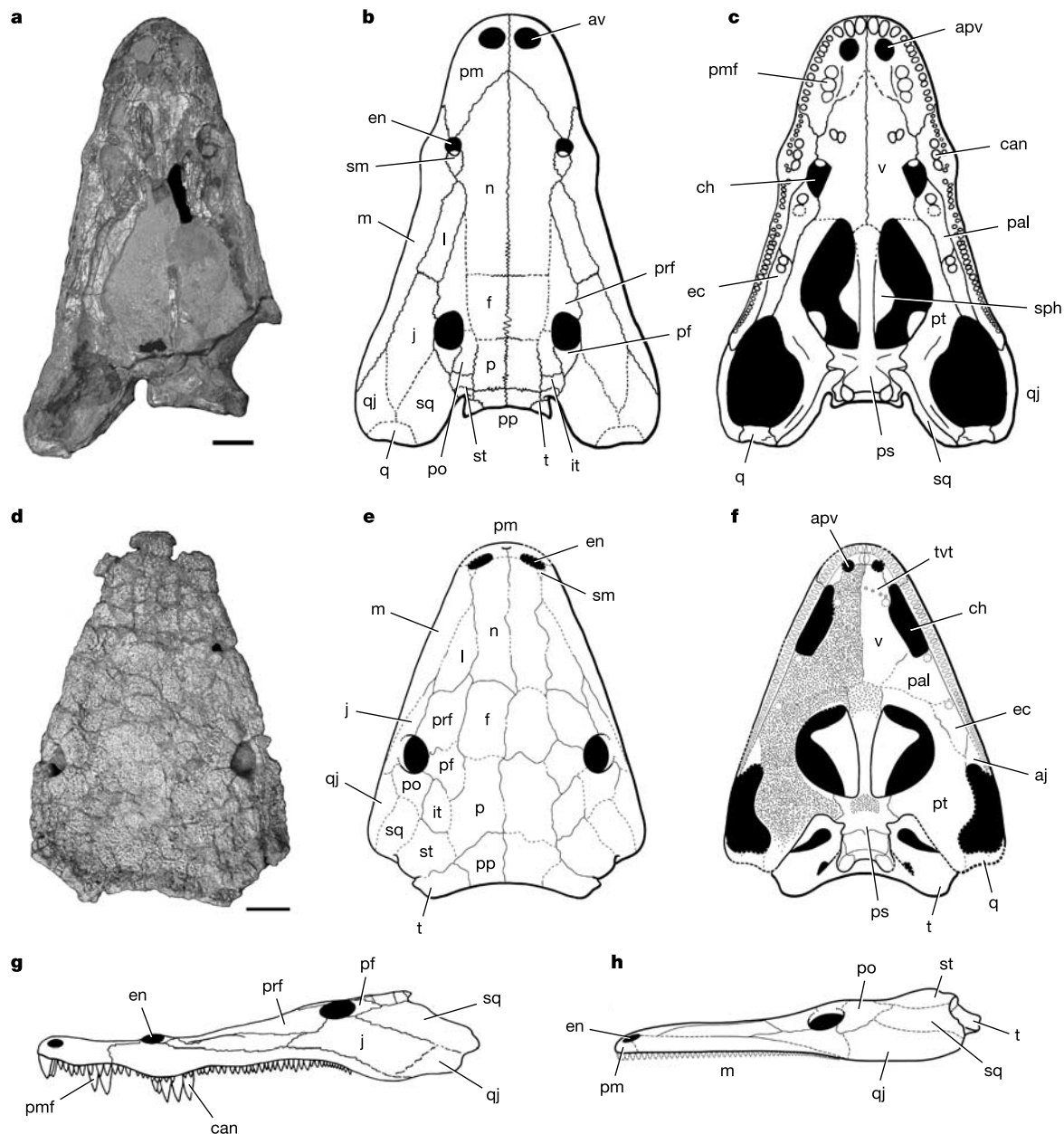


Figure 1 New edopoid temnospondyls from the Moradi Formation. **a**, Photograph of MNM MOR69 in dorsal view. **b, c, g**, Reconstruction of *Nigerpeton ricqlesi* in dorsal (**b**), ventral (**c**) and lateral (**g**) views. **d**, Photograph of MNM MOR73 in dorsal view. **e, f, h**, Reconstruction of *Saharastega moradiensis* in dorsal (**e**), ventral (**f**) and lateral (**h**) views. Scale bars, 5 cm. aj, alary process of jugal; apv, anterior palatal vacuity; av, anterior vacuity in skull roof; can, hypertrophied caniniform region; ch, choana; ec, ectopterygoid;

en, external naris; f, frontal; it, intertemporal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; pmf, premaxillary fang; po, postorbital; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sm, septomaxilla; sph, sphenethmoid; sq, squamosal; st, supratemporal; t, tabular; tv, transvomerine tooth row; v, vomer.

mastodontosaurids^{17–19} but unknown among primitive temnospondyls, including cochleosaurids. In palatal view (Fig. 1c), *Nigerpeton* displays small, rounded interpterygoid vacuities that are placed in the posterior half of the skull. Anterior to them, the vomers form broad, plate-like elements that separate the posteriorly tapering choanae. The dentition is highly specialized. Anteriorly, the premaxilla bears three enlarged marginal teeth as well as three, medially positioned, palatal fangs. Lateral to the choana, the maxilla has a well-defined swelling that houses three caniniform teeth as well as the smaller teeth of the marginal tooth row. This degree of heterodonty is exceptional among temnospondyls.

The skull of *Saharastega moradiensis* is broadly triangular in outline and shallow in profile, with a moderately long snout (Fig. 1d–f, h). The orbits are posteriorly positioned and face almost wholly laterally. An unusual aspect of the skull is the extreme shortening of the suspensorium, which results in an anteriorly

positioned jaw articulation. As in other edopoids, the pineal foramen and lateral line sulci are absent, the lacrimal is excluded from the anterior margin of the orbit by a contact between the prefrontal and jugal, and an intertemporal ossification is present. The morphology of the tabular of *Saharastega* is markedly different from that of all other temnospondyls; its 'horn' is a very long, robust flange of bone with a blunt end. Orientated ventrolaterally, the horn partially underlaps the posterior margin of the supratemporal. The palate of *Saharastega* has small, rounded interpterygoid vacuities positioned mainly in the posterior half of the skull, paired anterior palatal vacuities, small subtemporal vacuities, and extremely long choanae. A dense field of small denticles uniformly covers the palatal bones, and there is only tenuous evidence for the presence of palatal fangs on the vomers, palatines, or ectopterygoids. *Saharastega* is unique among primitive temnospondyls in possessing a transvomerine tooth row (vtv; see Fig. 1), which is a derived character typical of more advanced temnospondyls^{17–19}.

Several cranial features unite *Nigerpeton* and *Saharastega* with the basal temnospondyl clade Edopoidea^{7–9}. Our phylogenetic analysis indicates that *Saharastega* is the sister taxon of Edopoidea, whereas *Nigerpeton* nests within the clade as the sister taxon to the Late Carboniferous genus *Chenoprosopus* (Fig. 2; see also Supplementary Information for details of analysis). Edopoids were previously restricted to a narrow latitudinal band straddling the palaeoequator in the Late Carboniferous and Early Permian of Euramerica^{7–9}. The discovery of edopoid amphibians in the Moradi Formation implies a stratigraphic gap of at least 40 million years between the early

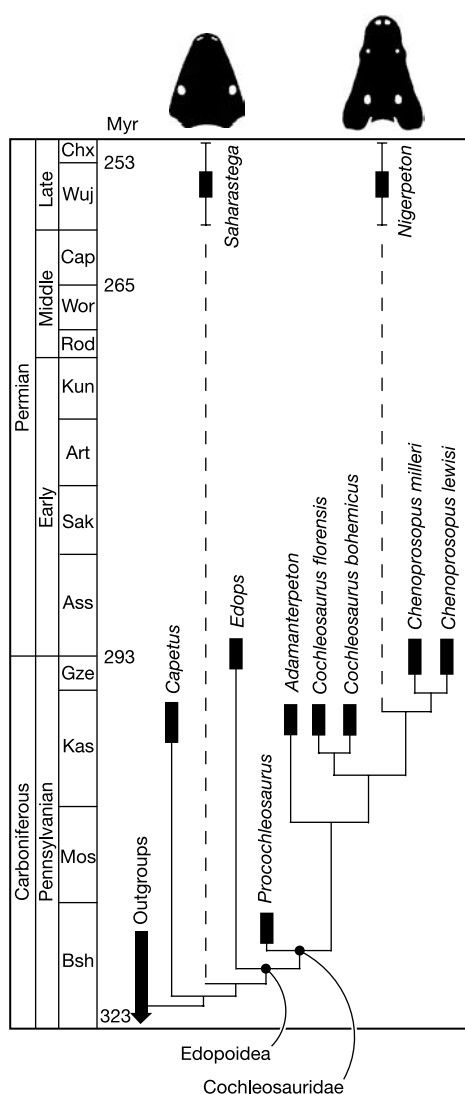


Figure 2 Phylogenetic position of *Nigerpeton ricqlesi* and *Saharastega moradiensis* among basal temnospondyl amphibians based on maximum parsimony analysis (see Supplementary Information for details of analysis). Error bars indicate approximate uncertainty in the age of the Moradi Formation^{2–5}. Stratigraphic distribution of remaining taxa is based on previous studies^{7–9}. Myr, million years. Bsh, Bashkirian; Mos, Moscovian; Kas, Kasimovian; Gze, Gzelian; Ass, Asselian; Sak, Sakmarian; Art, Artinskian; Kun, Kungurian; Rod, Roadian; Wor, Wordian; Cap, Capitanian; Wuj, Wujiaopingian; Chx, Changxingian.

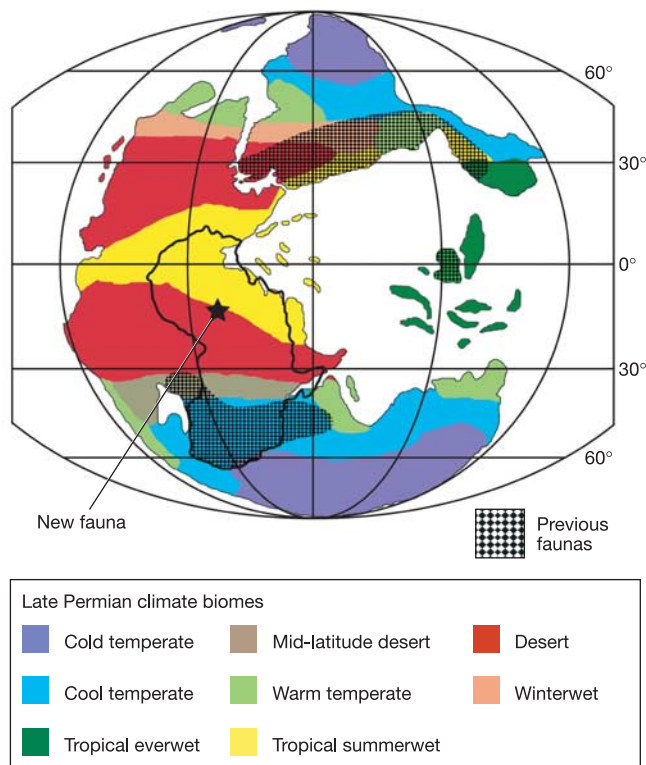


Figure 3 Palaeogeography¹² and palaeoclimatology^{10,11} of the Late Permian showing the geographical distribution of tetrapod faunas^{7–9,13–24}. The distribution of previously recognized, therapsid-dominated faunas is shown by the hatched pattern, and comprises dicynodont herbivores, other therapsid taxa and advanced temnospondyls. The southern range is based on occurrences from South America, southern Africa and India; the northern range is based on European, Russian and Chinese records; the eastern range is based on Laotian records. The new fauna from the Moradi Formation of Niger (star) is characterized by primitive edopoid amphibians, pareiasaurian reptiles and moradisaurine captorhinid reptiles. The modern outline of Africa is highlighted.

appearing Euramerican members of this group and the new African species (Fig. 2). The Moradi amphibians probably represent relicts of a basal group that had long gone extinct elsewhere. In all other regions of Pangaea, more advanced temnospondyls form the bulk of amphibian diversity during the Late Permian, with archegosauroids, dvinosaurians, eryopoids and dissorophoids present in Russia and China, rhinesuchids and archegosauroids present in southern Africa and South America^{9,17–20}, and advanced stereospondyls present in Australia²¹.

Therapsid-dominated faunas composed of the same, or closely related, species have long been known from areas as distant as South Africa and Russia^{13–15,22,23}, and indicate that long-distance, bidirectional north–south exchange was commonplace on Pangaea during the Permian period. In these faunas, dicynodonts are the dominant large-bodied herbivores and advanced temnospondyls represent the principal aquatic predators. Despite its central geographical location (within 15° of the palaeoequator), the fauna from Niger does not overlap at the generic level with the higher-latitude faunas. Dicynodonts have yet to be described from the Moradi Formation^{2–6}, and we found no evidence for their presence, despite intensive fieldwork. Instead, an abundance of captorhinid and pareiasaurian herbivore remains suggests that these taxa were the chief plant consumers^{3–5}.

Climate seems to have had an important role in isolating tetrapods from low latitudes from those at mid- and high latitudes during the Late Permian period (Fig. 3). Geological data and climate simulations suggest that desert-like conditions replaced a more moderate climate in central Pangaea by Middle Permian times^{10–12}. Along with the markedly different floral provinces that characterize northern and southern continents during the Late Permian¹¹, this change in climate may have isolated pockets of a once widespread tetrapod fauna⁹. This hypothesis accounts for the early divergence of the new temnospondyls from Niger, the highly autapomorphic anatomy of the contemporary reptiles^{3–5}, and the similar captorhinid/pareiasaur fauna recovered from low palaeolatitudes in Upper Permian rocks in Morocco^{14,24}.

The degree to which climate influenced the evolutionary biogeography of terrestrial vertebrates towards the end of the Permian period has been previously underestimated because of uneven latitudinal sampling. Mid-to-high-latitude faunas in Russia and South Africa, although fossil-rich and comparatively well known, may have evolved under similar climatic conditions and were probably linked by coastal migration routes. Our discoveries reveal a surprisingly distinctive Permian terrestrial community at low palaeolatitude, and highlight the influence of climate change on large-scale patterns of biotic evolution. □

Received 18 October 2004; accepted 25 January 2005; doi:10.1038/nature03393.

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Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank A. Beck, D. Blackburn, J. Conrad, A. Dindine, E. Duneman, B. Gado, T. Lyman, G. Lyon, R. Sadlier and G. Wilson for assistance in the field; A. Crean, E. Love, V. Heisey and J. Groenke for fossil preparation; and S. Spilkevitz for help with Fig. 3. We thank H. Salissou of the Ministère des Enseignements Secondaire et Supérieur, de la Recherche et de la Technologie for permission to conduct fieldwork. We acknowledge the National Geographic Society for support.

Competing interests statement The authors declare that they have no competing financial interests.

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Hair cell synaptic ribbons are essential for synchronous auditory signalling

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Hearing relies on faithful synaptic transmission at the ribbon synapse of cochlear inner hair cells (IHCs)^{1–3}. At present, the function of presynaptic ribbons at these synapses is still largely unknown^{1,4}. Here we show that anchoring of IHC ribbons is impaired in mouse mutants for the presynaptic scaffolding protein Bassoon. The lack of active-zone-anchored synaptic ribbons reduced the presynaptic readily releasable vesicle pool, and impaired synchronous auditory signalling as revealed by