The vertebrate fauna of the Upper Permian of Niger. VI. First evidence of a gorgonopsian therapsid

Tara M. Smiley , Christian A. Sidor , Abdoulaye Maga & Oumarou Ide

Published online: 02 Aug 2010.

Submit your article to this journal

View related articles

THE VERTEBRATE FAUNA OF THE UPPER PERMIAN OF NIGER. VI. FIRST EVIDENCE OF A GORGONOPSIAN THERAPSID

TARA M. SMILEY,[1] CHRISTIAN A. SIDOR,[*,1] ABDOULAYE MAGA,[2] and OUMAROU IDE[2]; [1]Burke Museum and Department of Biology, University of Washington, Seattle, Washington, 98195, USA., casidor@u.washington.edu, tsmiley@u.washington.edu; [2]Institut de Recherches en Sciences Humaines, Université Abdou Moumouni de Niamey, République du Niger

Upper Permian terrestrial faunas are well known from the rocks of southern Africa and the Cis-Ural region of Russia (Parrish et al., 1986; Rubidge and Sidor, 2001). In these regions, tetrapod assemblages are dominated by therapsids, with 'mammal-like reptiles' often constituting upwards of 80 percent of the preserved fauna (Kitching, 1972; Colbert, 1986; Ivakhnenko et al., 1997; Sidor and Smith, 2007). Gorgonopsian therapsids were the dominant large bodied carnivores of the Upper Permian and are relatively abundant in the lower Beaufort Group of South Africa, where over 600 gorgonopsian fossils are known and 25 genera currently recognized (Sigogneau-Russell, 1989; Rubidge and Sidor, 2001; Nicolas, 2007).

The occurrence of similar fossils at high latitudes in both the Northern and Southern Hemispheres suggests that Upper Permian therapsids were unrestricted in their dispersal capability (Parrish et al., 1986; Smith et al., 2006; Kemp, 2006). However, the paucity of low latitude localities potentially undermines this assumption. Upper Permian tetrapods have been discovered in two regions of paleoequatorial Pangea, the Argana Formation of Morocco and the Moradi Formation of Niger (e.g., Jalil and Dutuit, 1996; Sidor et al., 2005). These two localities have yielded tetrapod assemblages that are strikingly different from coeval high latitude localities in that they preserve an abundance of captorhinids and pareiasaurs, but seemingly lack therapsids.

Field work in the Moradi Formation in 2003 and 2006 has uncovered evidence of therapsids (Fig. 1). An upper jaw fragment, including the roots of a large canine and two postcanine teeth, is described here (Fig. 2). Unfortunately, the present material does not permit a generic identification to be made, although its morphology and size are suggestive of the gorgonopsian subfamily Rubidginae. In addition, we describe an isolated canine (Fig. 3), likely belonging to Gorgonopsidae or to another therapsid group. The recognition of gorgonopsians in the Moradi Formation fauna helps to fill a previously empty terrestrial carnivorous ecological niche and sheds light on the influence of climate on the distribution patterns of therapsids during this important stage of vertebrate evolution.

Institutional Abbreviations—GPIT, Geologisch–Paläontologisch Institut der Universität Tübingen; **MNN**, Musée National du Niger, Niamey; **UWBM**, Burke Museum of Natural History and Culture, Seattle.

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905
GORGONOPSIA Seeley, 1895
GORGONOPSIDAE Lydekker, 1890
cf. RUBIDGINAE Sigogneau, 1970

Material—MNN MOR99, portion of upper jaw of a large gorgonopsian preserving the left maxilla, anterior portion of the left palatine, and posterior portion of the vomer; MNN MOR90, isolated canine. Casts of both specimens are housed at the UWBM.

Locality and Horizon—The upper jaw, MNN MOR99, was collected from dark reddish-brown mudrocks of the Moradi For-
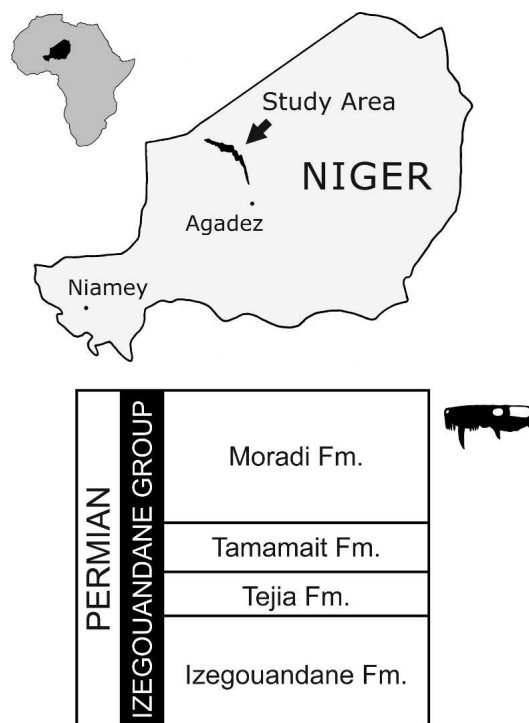

FIGURE 1. Geographic position of the study area and generalized stratigraphy of the Permian Izegouandane Group of Niger. Skull icon denotes approximate stratigraphic level of the gorgonopsian fossils. See O'Keefe et al. (2005:fig. 1) for a detailed locality map. **Abbreviation**: **Fm.**, formation.
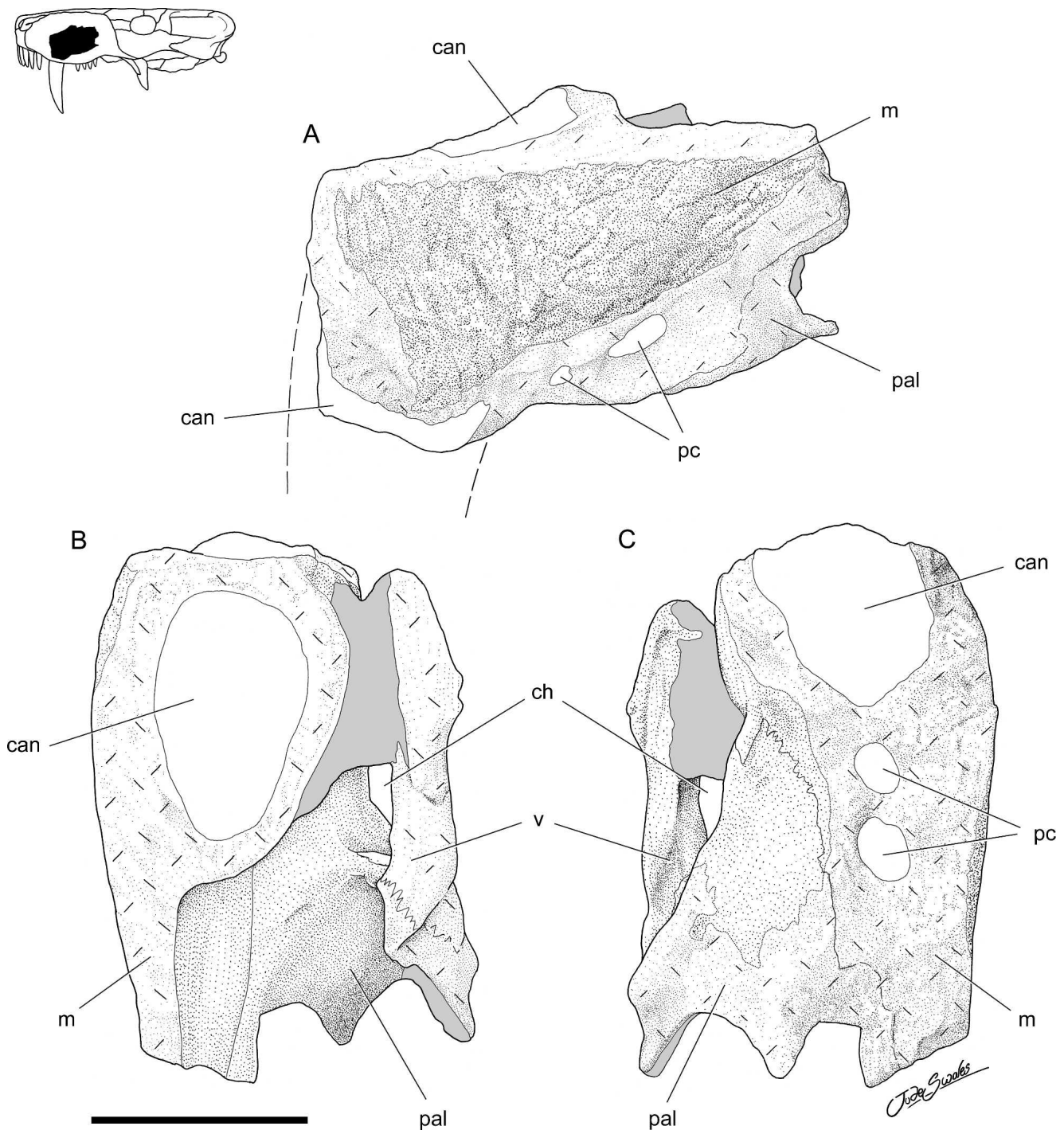
*Corresponding author.

FIGURE 2.   Indeterminate gorgonopsian (MNN MOR99) from the Upper Permian Moradi Formation of Niger. Drawing of the specimen in: **A**, lateral; **B**, dorsal; **C**, ventral views. Gray indicates remaining matrix. Crosshatching indicates broken or eroded surface. Scale bar equals 5 cm. Inset skull of *Leontocephalus intactus* (from Kemp, 1969) shows preserved portion of skull. **Abbreviations**: **can**, canine; **ch**, choana; **m**, maxilla; **pal**, palatine; **pc**, postcanine; **v**, vomer.

mation, (18° 31.113′ N, 7° 33.186′ E), approximately 20 km west of Arlit, Agadez Department, northern Niger (Fig. 1). The canine, MNN MOR90, was collected from an intraformational conglomerate of the Moradi Formation approximately 30 km southeast of Arlit (18°47.719′ N, 7°12.064′ E). Paleontological evidence suggests a Late Permian age for the formation (Taquet, 1972; de Ricqlès and Taquet, 1982).

Description

Upper Jaw—MNN MOR99 consists of a rectangular piece of the snout that includes portions of three bones, the left maxilla, left palatine, and vomer (Fig. 2). The specimen was found with its dorsal surface exposed and suffers from post-fossilization breaks on all surfaces except along the lateral face and deep in the
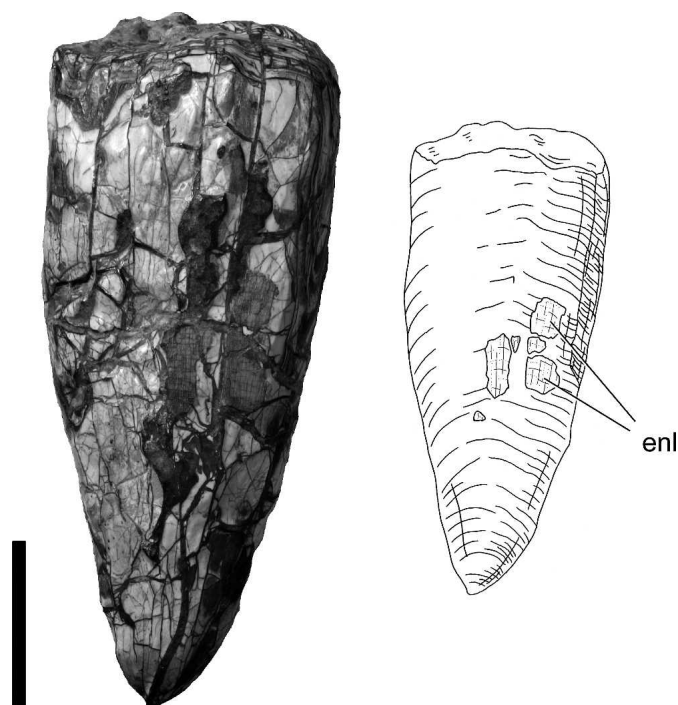
FIGURE 3. Photograph and interpretive drawing of the isolated canine (MNN MOR90) from the Upper Permian Moradi Formation of Niger. Scale bar for photograph equals 2 cm. **Abbreviation**: **enl**, enamel.

palate. The most prominent feature of the specimen is the root of an extremely large canine. Comparing MNN MOR99 against the complete skull of the gorgonopsian, *Dinogorgon quinquemolaris* (GPIT K16), gives an estimated total skull length of 45-50 cm for the former. Due to the preservation of the specimen, the dorsal surface of the fossil represents an unusual view of the palate, best comparable to that of *Leontocephalus intactus*, figured in Kemp (1969:fig. 7). Framed by the maxilla, palatine, and vomer, a portion of the left choana is preserved (Fig. 2B, C).

The maxilla preserves a rugose lateral surface (Fig. 2A). The medial surface of this element can be seen partially in dorsal view and is smooth, scooping concavely posterior to the root of the canine to meet the palatine (Fig. 2B). The root of the canine is best exposed along the dorsal margin of the maxilla (Fig. 2B), where it is oval in cross-section, with a major axis diameter of 5.5 cm and a minor axis diameter of 3.5 cm. As preserved, the canine root embedded in the maxilla measures 6.5 cm in length, but is less well exposed along the broken ventral surface (Fig. 2C). The portion of the maxilla housing the canine bulges medially into the choana when viewed either dorsally (Fig. 2B) or ventrally (Fig. 2C). The impression of a blood vessel is preserved along the medial margin of the maxillary bulge. It is 4 mm in width and runs along an antero-ventral to postero-dorsal path. In ventral view, the maxilla narrows posterior to the canine and contains the roots of two postcanine teeth exposed along its broken margin (Fig. 2C). The postcanines are relatively small and exit the broken ventral maxillary surface at the same angle as the much larger canine.

Deep in the palate, a suture separates the maxilla and palatine in dorsal view (Fig. 2B). The palatine broadens slightly towards its broken posterior edge, approaching the midline of the skull. The smooth dorsal surface of the palatine is interrupted by a ridge that runs medio-laterally through the center of the bone. The lateral end of the ridge is accompanied by a small groove on its anterior side. The suture between maxilla and palatine can be seen in ventral view, closely following the medial and ventral

edge of the broken surface of the maxilla (Fig. 2C). The ventral surface of the palatine is more textured than its dorsal surface, and may include a small foramen just medial to the suture between the palatine and the maxilla.

The vomer is a thin bone, preserved best in the vicinity of the maxillary bulge. A suture between the palatine and left portion of the vomer is exposed on the same plane as the preserved dorsal margin of the maxilla (Fig. 2B). The vomer is present medial and anterior to the palatine and comes within one cm of the medial bulge of the maxilla (Fig. 2B, C). The post-choanal portion of the vomer is restricted to the area along the midline, notably lacking a large lateral process. The suture between the vomer and the palatine can be followed entirely along the broken medial margin of the specimen.

Canine—A large, isolated canine was found weathered out of an intraformational conglomerate. Its external surface is highly eroded and cracked, although maintaining its original form (Fig. 3). The tooth is oval in cross-section, with a major axis diameter of 3.5 cm and a minor axis diameter of 2 cm. As preserved, the tooth is 8.5 cm from base to tip. Small areas of enamel are preserved, but no serrations remain along the carinae.

DISCUSSION

Identification—Both MNN MOR90 and MNN MOR99 are referable to the Therapsida on the basis of their enlarged canines. Among Paleozoic tetrapods, distinct canines are a synapomorphy of therapsids and are possessed by no true reptiles (Kemp, 1982; Rubidge and Sidor, 2001). Furthermore, the exaggerated size of the canines in both specimens is diagnostic of the Gorgonopsidae (Kemp, 1982; Sigogneau-Russell, 1989). The possession of highly reduced and laterally placed postcanines in MNN MOR99 confirms this placement and excludes dicynodonts from consideration (Kemp, 1969; Cluver and King, 1983; MacLean, 1986). Additional gorgonopsian features present in MNN MOR99 can be seen in dorsal and ventral view (Fig. 2B, C). The palatine broadens extensively posterior to the choana, reaching far medially with no contribution from the pterygoids. Although the midline is not preserved in this specimen, the medial extent of the palatine suggests that the palatines met at the midline, blocking contact between the pterygoids and vomer, a distinguishing feature of this pair of bones in gorgonopsians not seen in other therapsids, such as therocephalians (Sigogneau-Russell, 1989; Rubidge and Sidor, 2001). The reduction of the post-choanal portion of the vomer provides further evidence for the presence of this gorgonopsian feature. Although MNN MOR90 is more fragmentary, the large canine is diagnostic certainly of therapsids, if not gorgonopsians as well. If correctly attributed to the Gorgonopsia, the Moradi specimens are most similar in overall size to those of the gorgonopsian subfamily Rubidginae (Sigogneau, 1970).

Biostratigraphy—The Moradi Formation is poorly constrained biostratigraphically, but the discovery of a gorgonopsian fossil reinforces its currently accepted Late Permian age (Taquet, 1972; de Ricqlès and Taquet, 1982; Sidor et al., 2005). Previous data used to support this age include the presence of the Triassic ichnotaxon *Cheirotherium* in the overlying Téloua 1 Formation (Ginsburg et al., 1966) and the occurrence of Early Permian palynomorphs in the Tarat Formation, which underlies the Izegouandane Group (Broutin et al., 1990). Additional corroborating evidence includes the recognition that all other recognized Gondwanan formations preserving captorhinid fossils are considered to be Late Permian in age (Kutty, 1972; Jalil and Dutuit, 1996; Gow, 2000; Modesto and Smith, 2001).

The recognition of a large gorgonopsian further supports a Late Permian age for the Moradi Formation. Although the first gorgonopsians appear in the Middle Permian *Tapinocephalus* Assemblage Zone of South Africa (Rubidge, 2005), they are

represented by relatively small specimens and it is not until the *Cistecephalus* and *Dicynodon* biozones that rubidgines are found. In addition, all gorgonopsian fossils found outside South Africa (e.g., from Russia, Tanzania, or Zambia), are considered Late Permian in age (Sigogneau-Russell, 1989; Ivakhnenko et al., 1997; Rubidge and Sidor, 2001; Rubidge, 2005).

Low Latitude Upper Permian Tetrapod Faunas—Nonmarine rocks comparable to the Moradi Formation in both age and paleolatitude crop out in the western Upper Atlas mountains of Morocco (Jalil and Dutuit, 1996; Jalil, 1999). Due to their deposition in the paleoequatorial region of Pangea, both the upper part of Member T2 of the Argana Formation of Morocco and the Moradi Formation of Niger record climatic conditions that differ strongly from their high latitude counterparts. Models of climatic conditions in central Pangea during the Late Permian suggest that the region was extremely seasonal and highly arid (Rees et al., 2002; Gibbs et al., 2002). These models are supported by recent field work, the findings of which confirm a warm and arid climate characterized by strongly seasonal precipitation (Smith et al., 2007; Steyer et al., 2007; Tabor et al., 2007). Late Paleozoic paleoclimate indicators from Niger indicate climatic deterioration from humid, nearly ever-wet conditions during Pennsylvanian/Early Permian time to harsh, hyperarid 'wet desert' conditions during the Late Permian deposition of the Moradi Formation (Smith et al., 2007; Tabor et al., 2007).

The distinct climate of equatorial Pangea is reflected in the comparable faunas of the Argana and Moradi formations. The Moradi fauna consists of two herbivorous reptiles, the giant captorhinid *Moradisaurus grandis* and the pareiasaur *Bunostegos akokanensis*, as well as two temnospondyls, *Nigerpeton ricqlesi* and *Saharastega moradiensis* (Taquet, 1969; de Ricqlès and Taquet, 1982; Sidor et al., 2003; O'Keefe et al., 2005; Damiani et al., 2006; Steyer et al., 2006). Like the Moradi, the tetrapod fauna of the Argana Formation is not therapsid dominated, but rather composed of amphibians, captorhinids, and pareiasaurs (Jalil and Dutuit, 1996; Jalil and Janvier, 2005). To date, the Argana fauna consists of the diplocaulid amphibian *Diplocaulus minimus*, the captorhinid *Acrodonta irheri*, and at least one pareiasaur, *Arganaceras vacanti*, which is superficially similar to *Bunostegos* in several features (Jalil, 1999; Jalil and Dutuit, 1996; Jalil and Janvier, 2005).

The discovery of gorgonopsian therapsids in the Moradi Formation represents a new geographic record for the group, but is not entirely unexpected. As carnivores, gorgonopsians should be less affected by latitude than Permian herbivores, who likely track the distribution of their preferred vegetation type. For example, dicynodonts have long been associated with the *Glossopteris*-dominated flora of southern Pangea (King, 1992; Rayner, 1992), which has led some workers to hypothesize that their less common occurrence in Permian strata of Russia might be related to its different flora (Modesto et al., 1999). The Late Permian is marked by several distinct floral provinces (Rees et al., 2002) and preliminary data suggest that despite being located on the African plate, the Moradi Formation corresponds to the Euramerican, not Gondwanan, province (C. Looy, pers. comm.; Broutin et al., 1990). Dicynodonts therefore might have been excluded from the Moradi tetrapod fauna not only due to climatic restrictions on dispersal, but also because of a lack of an available niche, with the endemic pareiasaurs and moradisaurines better adapted to the local conifer flora. Further study of the Moradi Formation should lead to a better understanding of the relationship between floral and faunal distributions, including their relationship to broad-scale patterns of Permian climate.

Note added in proof—One of us (CAS) recently had the opportunity to visit the Museum national d'Histoire naturelle (Paris) and, with the kind permission of P. Taquet, examine material collected from the Moradi Formation in the late 1960s. We have come to the conclusion that the supposed dicynodont skull mentioned several times in the literature (e.g., de Ricqlès and Taquet, 1982:47, Taquet 1967:417, 1978:338) cannot be referred to the Therapsida. Instead, we believe the specimen to represent the braincase of a large reptile, perhaps *Bunostegos*. As such, the gorgonopsian described herein is the only therapsid identified from the Permian of Niger.

LITERATURE CITED

Broom, R. 1905. On the use of the term Anomodontia. Records of the Albany Museum 1:266–269.

Broutin, J., J. Doubinger, M. O. Elhamet, and J. Lang. 1990. Comparative palynology in the Permian of Niger (Western Africa) and the Peritethysian realm—stratigraphic and phytogeographic implications. Review of Palaeobotany and Palynology 66:243–261.

Cluver, M. A., and G. M. King. 1983. A reassessment of the relationships of the Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. Annals of the South African Museum 91:195–273.

Colbert, E. H. 1986. Therapsids in Pangaea and their contemporaries and competitors; pp. 133–145 in N. Hotton III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), The Ecology and Biology of Mammal-like Reptiles. Smithsonian Institution Press, Washington and London.

Damiani, R., C. A. Sidor, J. S. Steyer, R. M. H. Smith, H. C. E. Larsson, B. Gado, A. Maga, and O. Ide. 2006. The vertebrate fauna of the Upper Permian of Niger. V. The primitive temnospondyl *Saharastega moradiensis*. Journal of Vertebrate Paleontology 26:559–572.

Gibbs, M. T., P. M. Rees, J. E. Kutzbach, A. M. Ziegler, P. J. Behling, and D. B. Rowley. 2002. Simulations of Permian climate and comparisons with climate-sensitive sediments. The Journal of Geology 110:33–55.

Ginsburg, L., A. F. de Lapparent, B. Loiret, and P. Taquet. 1966. Empreintes de pas de vertébrés tétrapodes dans la série continentale à l'ouest d'Agadès (République du Niger). Comptes Rendus de l'Académie des Sciences de Paris, Série D 263:28–31.

Gow, C. E. 2000. A captorhinid with multiple tooth rows from the Upper Permian of Zambia. Palaeontologia Africana 36:11–14.

Ivakhnenko, M. F., V. K. Golubev, Y. M. Gubin, N. N. Kalandadze, I. V. Novikov, A. G. Sennikov, and A. S. Rautian. 1997. Permian and Triassic tetrapods of Eastern Europe. GEOS, Moscow, 216 pp. [Russian]

Jalil, N-E. 1999. Continental Permian and Triassic vertebrate localities from Algeria and Morocco and their stratigraphical correlations. Journal of African Earth Sciences 29:219–226.

Jalil, N-E., and J. M. Dutuit. 1996. Permian captorhinid reptiles from the Argana Formation, Morocco. Palaeontology 29:907–918.

Jalil, N-E., and P. Janvier. 2005. Les pareiasaures (Amniota, Parareptilia) du Permien supérieur du Bassin d'Argana, Maroc. Geodiversitas 27:35–132.

Kemp, T. S. 1969. On the functional morphology of the gorgonopsid skull. Philosophical Transactions of the Royal Society of London Series B 256:1–83.

Kemp, T. S. 1982. Mammal-like reptiles and the origin of mammals. Academic Press, London, 363 pp.

Kemp, T. S. 2006. The origin and early radiation of the therapsid mammal-like reptiles: a palaeobiological hypothesis. Journal of Evolutionary Biology 19:1231–1247.

King, G. M. 1992. The palaeobiogeography of Permian anomodonts. Terra Nova 4:633–640.

Kitching, J. W. 1977. The distribution of the Karroo vertebrate fauna.

Bernard Price Institute for Palaeontological Research Memoir 1: 1–131.

Kutty, T. S. 1972. Permian reptile fauna from India. Nature 237:462–463.

Lydekker, R. 1890. Catalogue of the fossil Reptilia in the British Museum (Natural History), Part 4. Longmans, London, 259 pp.

MacLean, P. D. 1986. Neurobehavioral significance of the mammal-like reptiles (therapsids); pp. 1–21 in N. Hotton III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), The Ecology and Biology of Mammal-like Reptiles. Smithsonian Institution Press, Washington and London.

Modesto, S. P., B. S. Rubidge, and J. Welman. 1999. The most basal anomodont therapsid and the primacy of Gondwana in the evolution of the anomodonts. Proceedings of the Royal Society of London B 266:331–337.

Modesto, S. P., and R. M. H. Smith. 2001. A new Late Permian captorhinid reptile: a first record from the South African Karoo. Journal of Vertebrate Paleontology 21:405–409.

Nicolas, M. V. M. 2007. Tetrapod biodiversity through the Permo-Triassic Beaufort Group (Karoo Supergroup) of South Africa. Ph.D. dissertation, University of the Witwatersrand, Johannesburg, 312 pp.

O'Keefe, F. R., C. A. Sidor, H. C. E. Larsson, A. Maga, and O. Ide. 2005. The vertebrate fauna of the Upper Permian of Niger—III, Morphology and ontogeny of the hindlimb of *Moradisaurus grandis* (Reptilia, Captorhinidae). Journal of Vertebrate Paleontology 25: 309–319.

Parrish, J. M., J. T. Parrish, and A. M. Ziegler. 1986. Permian-Triassic paleogeography and paleoclimatology and implications for therapsid distribution; pp. 109–131 in N. Hotton III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), The Ecology and Biology of Mammal-like Reptiles. Smithsonian Institution Press, Washington and London.

Rayner, R. J. 1992. *Phyllotheca*: the pastures of the Late Permian. Palaeogeography, Palaeoclimatology, Palaeoecology 92:31–40.

Rees, P. A., A. M. Ziegler, M. T. Gibbs, J. E. Kutzbach, P. J. Behling, and D. B. Rowley. 2002. Permian phytogeographic patterns and climate data/model comparisons. Journal of Geology 110:1–31.

Ricqlès, A. de, and P. Taquet. 1982. La faune de vertébrés du Permien supérieur du Niger. I. Le Captorhinomorphe *Moradisaurus grandis* (Reptilia, Cotylosauria)—Le crâne. Annales de Paléontologie (Vert.-Invert.) 68:33–106.

Rubidge, B. S. 2005. Re-uniting lost continents—Fossil reptiles from the ancient Karoo and their wanderlust. South African Journal of Geology 108:135–172.

Rubidge, B. S., and C. A. Sidor. 2001. Evolutionary patterns among Permo-Triassic therapsids. Annual Review of Ecology and Systematics 32:449–480.

Seeley, H. G. 1895. Researches on the structure, organization and classification of the fossil Reptilia. IX, section I. On the Therosuchia. Philosophical Transactions of the Royal Society of London B 185: 987–1018.

Sidor, C. A., D. C. Blackburn, and B. Gado. 2003. The vertebrate fauna of the Upper Permian of Niger—II, Preliminary description of a new pareiasaur. Palaeontologia Africana 39:42–52.

Sidor, C. A., F. R. O'Keefe, R. Damiani, J. S. Steyer, R. M. H. Smith, H. C. E. Larsson, P. C. Sereno, O. Ide, and A. Maga. 2005. Permian tetrapods from the Sahara show climate-controlled endemism in Pangaea. Nature 434:886–889.

Sidor, C. A., and R. M. H. Smith. 2007. A second burnetiamorph from the Upper Permian Teekloof Formation of South Africa and its associated fauna. Journal of Vertebrate Paleontology 27:420–430.

Sigogneau, D. 1970. Révision systématique des Gorgonopsiens sud-africains. Cahiers de Paléontologie, Paris, 416 pp.

Sigogneau-Russell, D. 1989. Theriodontia I; pp. 1-127 in P. Wellnhofer (ed.), Encyclopedia of Paleoherpetology, Part 17B. Gustav Fischer, Stuttgart, Germany.

Smith, R. M. H., B. S. Rubidge, and C. A. Sidor. 2006. A new burnetiid (Therapsida: Biarmosuchia) from the Upper Permian of South Africa and its biogeographic implications. Journal of Vertebrate Paleontology 26:331–343.

Smith, R. M. H., C. A. Sidor, N. J. Tabor, J. S. Steyer, and D. S. Chaney. 2007. Vertebrate taphonomy of a Permian "wet desert" in central Pangea. Journal of Vertebrate Paleontology 27(3, Supplement): 150A.

Steyer, J. S., R. Damiani, C. A. Sidor, F. R. O'Keefe, H. C. E. Larsson, A. Maga, and O. Ide. 2006. The vertebrate fauna of the Upper Permian of Niger. IV. *Nigerpeton ricqlesi* (Temnospondyli: Cochleosauridae), and the edopoid colonization of Gondwana. Journal of Vertebrate Paleontology 26:18–28.

Steyer, J. S., G. Gand, R. Smith, C. Sidor, N. Tabor. 2007. The first tetrapod trackways from the Paleozoic of West Africa: one step towards reconstructing the landscape of central Pangea. Journal of Vertebrate Paleontology 27(3, Supplement):152A.

Tabor, N., S. Thomas, C. Sidor, C. Looy, and J. S. Steyer. 2007. Paleoclimatic indicators from the Moradi Formation of Niger indicate progressive aridification of central Pangea during the Permian. Journal of Vertebrate Paleontology 27(3, Supplement):156A.

Taquet, P. 1967. Découvertes paléontologiques récentes dans le Nord du Niger. Pp. 415-418. Problèmes actuels de Paléontologie (Évolution des Vertébrés). Éditions du Centre National de la Recherche Scientifique, Paris.

Taquet, P. 1969. Première découverte en Afrique d'un reptile captorhinomorphe (Cotylosaurien). Comptes Rendus de l'Académie des Sciences, Paris D 268: 779–781.

Taquet, P. 1972. Un exemple de datation et de correlation stratigraphique basé sur les Captorhinomorphes (Reptiles cotylosauriens). Mémoires du Bureau de Recherches Géologiques et Minières 77:407–409.

Taquet, P. 1978. Niger et Gondwana. Annales de la Société Géologique du Nord 97:337–341.