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The vertebrate fauna of the Upper Permian of Niger – VIII. *Nigerpeton ricqlesi* (Temnospondyli: Cochleosauridae) and tetrapod biogeographic provinces

La faune de Vertébrés du Permien supérieur du Niger – VIII. Nigerpeton ricqlesi (Temnospondyli: Cochleosauridae) et les provinces biogéographiques des tétrapodes

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ABSTRACT

The Moradi Formation of northern Niger preserves a rare glimpse of tetrapods inhabiting the low paleolatitude regions of Pangea during Late Permian times. In contrast to the broadly distributed and dicynodont-dominated Karoo fauna known from southern Pangea (e.g., South Africa, Tanzania, Zambia, and Malawi), recent work has shown that (1) Moradi tetrapods are endemic, and (2) the taxonomic composition of the Moradi fauna is unlike that of any other Upper Permian fauna. In this contribution, I describe new cranial material of the derived cochleosaurid *Nigerpeton ricqlesi*. I also compare the Moradi tetrapod assemblage to five other Upper Permian assemblages with bipartite taxon–locality occurrence networks. At the genus level, the Moradi appears unconnected to any other locality, which underscores its endemic nature. In contrast, southern Pangean assemblages display high levels of connectedness and low percentage of endemic genera (except for the Karoo Basin of South Africa, which is likely the result of its more intense sampling). I infer that the fauna of the Moradi Formation was not part of the same faunal province that dominated southern Pangea, but evidence for linking it to the faunal assemblage of the Ikakern Formation of Morocco is currently equivocal.

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R É S U M É

La formation de Moradi, dans le Nord du Niger, garde un aperçu rare des tétrapodes habitant les régions de basses paléolatitudes de la Pangée, pendant le Permien supérieur. Au contraire de la faune du Karoo, largement distribuée et à dominance de dicynodontes, bien connue dans la Pangée méridionale (à savoir l'Afrique du Sud, la Tanzanie, la Zambie et le Malawi), une récente étude a montré (1) que les tétrapodes de Moradi sont endémiques et (2) que la composition taxonomique de la faune de Moradi est différente de celle de toute autre faune du Permien supérieur. Dans cet article sera décrit le nouveau matériau crânien du cochléosauridé dérivé *Nigerpeton ricqlesi*. L'assemblage des tétrapodes de Moradi sera aussi comparé à cinq autres assemblages du Permien supérieur, avec des réseaux d'occurrence taxon–localité. Au niveau du genre, la faune de Moradi apparaît comme non connectée à toute autre localité, ce qui souligne sa nature endémique. En revanche, les assemblages de la Pangée méridionale présentent de hauts niveaux de connectivité et un pourcentage bas de genres endémiques (exception faite du bassin du Karoo en Afrique du Sud, ce qui résulte

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vraisemblablement d'un échantillonnage plus intense). L'auteur en déduit que la faune de la formation de Moradi n'a pas fait partie de la même province faunique prédominante de la Pangée méridionale, mais l'évidence de son lien avec l'assemblage faunique de la formation d'Ikakern au Maroc est actuellement équivoque.

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1. Introduction

Jouliá (1960) published the first notice of vertebrate fossils from the Permian Moradi Formation of northern Niger. Shortly thereafter, French paleontologists mounted three short expeditions in the late 1960s, but named and described only a single taxon, the large captorhinid reptile, *Moradisaurus grandis* (de Ricqlès and Taquet, 1982; Taquet, 1967, 1969). A photo of a pareiasaur skull from the same formation was later published by Taquet (1976), but this specimen was neither named nor described.

More recent fieldwork in the Moradi Formation was conducted in 2000, 2003, and 2006. Research based on the new collections has clarified the unique composition of the tetrapod fauna, with four additional taxa now recognized: the stem-edopoid, *Saharastega moradiensis*, the cochleosaurid, *Nigerpeton ricqlési*, the pareiasaur, *Bunostegos akokanesis*, as well as an indeterminate rubidgine gorgonopsid (Damiani et al., 2006; Sidor et al., 2003, 2005; Smiley et al., 2008; Steyer et al., 2006; Tsuji et al., 2013). These results suggest that the Moradi tetrapod fauna differed substantially from those known elsewhere during Late Permian times (Rubidge, 2005). For example, dicynodont herbivores, which numerically dominate southern African assemblages (Nicolas and Rubidge, 2010; Sidor and Smith, 2007; Smith, 1993; Smith et al., 2012), have yet to be recognized from the Moradi Formation (Smiley et al., 2008).

Because no physical barrier, such as a mountain range or epicontinental seaway, separated tetrapods in Niger from those in southern Africa during the Permian, Sidor et al. (2005) suggested that climatic conditions were probably responsible for limiting the intermixing of taxa. Indeed, climate simulations have suggested that central Pangea experienced desert-like conditions (Gibbs et al., 2002; Kiehl and Shields, 2005; Rees et al., 1999, 2002) and recent geological work has found evidence for arid to hyper-arid conditions during Moradi deposition (Smith et al., 2009; Tabor et al., 2011). In addition, although paleobotanical data is limited (Looy et al., 2009), it appears that Moradi vegetation did not conform to the *Glossopteris*-dominated flora that typified southern Pangea (Pigg and Trivett, 1994), which might help to explain the lack of dicynodont herbivores. The climate-controlled endemism hypothesis of Sidor et al. (2005) suggests that tetrapods of Late Permian age are known from two biomes within the African portion of Pangea: a southern cool temperate biome (e.g., Karoo Basin of South Africa, Luangwa Basin of Zambia; Ruhuhu Basin of Tanzania) and a low latitude desert biome (e.g., Moradi Formation of Niger and possibly the Ikakern Formation of Morocco).

This contribution has two aims. First, I describe recently prepared material of *N. ricqlési*, a cochleosaurid

temnospondyl from the Moradi Formation of Niger, highlighting newly recognized features of its cranial anatomy. Second, I apply a network visualization approach for Permian tetrapod biogeography. I use the latter to compare the Upper Permian faunal assemblage from Niger with those of other contemporary basins across Africa.

2. Systematic paleontology

TEMNOSPONDYLI Zittel, 1887–1890

EDOPOIDEA Romer, 1945

COCHLEOSAURIDAE Broili in Zittel, 1923

Nigerpeton ricqlési Sidor et al., 2005

Holotype. Musée National du Niger (MNN) MOR69, partial skull preserved in dorsal view with associated atlas vertebra.

Referred material. MNN MOR70, incomplete skull; MNN MOR82, isolated femur; MNN MOR83, three sacral neural arches and ribs; MNN MOR108, incomplete skull.

Distribution and age. All material of *Nigerpeton* comes from the upper one-third of the Moradi Formation (Fig. 1), which is considered Late Permian in age (Sidor et al., 2005; Tabor et al., 2011; Taquet, 1972), approximately 20 km west of Arlit, Niger. Detailed locality data is available to qualified researchers at the MNN or by contacting C.A.S.

Revised diagnosis. Cochleosaurid distinguished by the following autapomorphies: orbits posteriorly positioned with elongated preorbital region (~70% total skull length); tusks on palatal surface of premaxilla; premaxilla-maxilla suture located anterior to external naris; external naris surrounded by thickened bone; lateral swelling on maxilla; two or three maxillary tusks positioned lateral to choana; vomerine tusks positioned anterior to choana; supratemporal highly reduced; deep occipital region; lateral line system present in adult.

Description and comparisons. MNN MOR108 was collected during fieldwork in 2006. A number of additional smaller fragments representing much of the mid-portion of the skull were also recovered, but could not be reunited with the snout figured here (Figs. 2 and 3) because of their advanced degree of weathering. Nonetheless, the material described here can be unambiguously referred to *N. ricqlési* because the maxilla is laterally swollen at the level of the external naris and because of the presence of an enlarged premaxillary tusk on the palate (Steyer et al., 2006). In addition, it shows the anterior displacement of the vomerine tusks seen in MNN MOR70 (Steyer et al., 2006: fig. 2b). In most regards, MNN MOR108 conforms to the anatomy previously documented for *Nigerpeton*, so this description will focus on areas preserving new information. All of the cranial material attributed to *N. ricqlési* (MNN MOR69, MOR70,

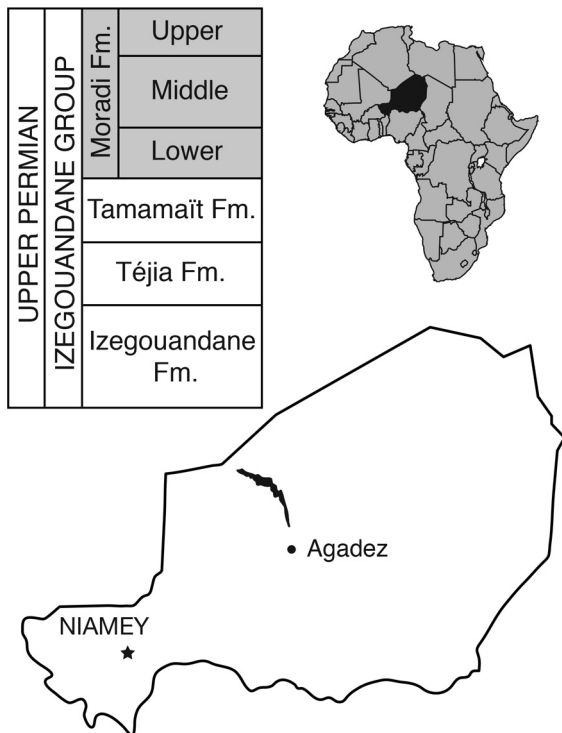


Fig. 1. Geographic position of the study area and generalized stratigraphy of the Permian Izegouandane Group of Niger. Filled area within country outline of Niger indicates mapped extent of the Izegouandane Group (Tabor et al., 2011). Abbreviation: Fm., Formation.

Fig. 1. Position géographique de la région étudiée et stratigraphie généralisée du groupe d'Izegouandane au Niger. La zone noire à l'intérieur de l'esquisse du Niger indique l'étendue cartographiée du groupe d'Izegouandane (Tabor et al., 2011). Abréviations : Fm., formation.

MOR108) is roughly equivalent in size and suggests an adult skull length of approximately 65–75 cm.

In dorsal view (Figs. 2A and 3A), MNN MOR108 displays a pair of anteriorly diverging ridges that bound a broad central depression, as in other cochleosaurids (Godfrey and Holmes, 1995; Langston, 1953; Sequeira, 2004). The anterior rim of the depression has been weathered, but the central region is well preserved and apparently lacks the lower relief of dermal sculpturing noted in some taxa (e.g., species of *Cochleosaurus*; Godfrey and Holmes, 1995; Sequeira, 2004). It is also worth noting that *Nigerpeton* differs from all other cochleosaurids in that a groove is developed between the ridge and the external naris, likely as a result of the thickened bone surrounding the external naris.

Steyer et al. (2006) described the presence of paired vacuities on the anterior skull roof of *Nigerpeton* for the accommodation of mandibular fangs. This feature was considered unique among cochleosaurids, although it was incompletely preserved on both of the specimens then available (MNN MOR69, MOR70). The current specimen unmistakably lacks this feature. On the right side, the premaxilla is well preserved and a fenestra is clearly lacking. However, on the left side the tip of a tooth is visible in a matrix-filled area. I suspect that the dermal bone was thin in this area as the result of a fossa on its ventral surface,

and that the appearance of the tooth and matrix are the result of mild erosion on the dorsal surface. The presence of anterior skull roof vacuities is likely related to individual or ontogenetic variation, and therefore its recognition as an autapomorphy of *Nigerpeton* should be considered questionable.

Although the margin of the skull roof is slightly eroded, the left external naris is well preserved. The opening sits in the middle of a tall, rounded protuberance formed by the maxilla, premaxilla, septomaxilla, and nasal. The depth of the surrounding bones forms a vertical opening, but one that is transversely oblong. A deep, smooth trough extends anterolaterally from the narial opening onto the skull roof. This structure, which was presumably related to respiration, was not preserved in previously described specimens of *Nigerpeton* and has not been recognized on any other cochleosaurid, where the narial margin is typically round and the surrounding bones flat. Uniquely in *Nigerpeton* among cochleosaurids, the maxilla-premaxilla suture along the lateral margin of the skull is positioned well anterior to the external naris (Fig. 3A).

In ventral view (Figs. 2B and 3B), the anterior part of the left hemi-mandible is visible, as well as most of the anterior palate. Sutures are difficult to discern, but the vomer undoubtedly forms most of what is preserved. Posteriorly, a broad embayment with a lightly ornamented roof is present between the choanae. The lateral margins of the embayment are formed by well-developed ridges that parallel the medial margin of each choana. Other cochleosaurids are known to have a depression in this region (e.g., *Cochleosaurus florensis*; Godfrey and Holmes, 1995: fig. 1), although a transverse ridge does not form its anterior margin in MNN MOR108. The central portion of the preserved palate is flat. On the right side, the root of a large premaxillary palatal tusk is present and surrounded by a raised, semicircular ridge.

The base of a large maxillary caniniform tooth is present lateral to each choana, and two (right side) or three (left side) vomerine teeth are present more anteriorly. As noted by Steyer et al. (2006), *Nigerpeton* is unique among cochleosaurids in having vomerine tusks that are displaced rostrally from the anterior margin of the choana. Although imperfectly preserved, the vomerine teeth have a circular cross-section but are slightly recurved. Just posterior to each cluster of vomerine teeth is a replacement pit. A large, isolated tooth is preserved on its side on the palate and represents the first well-preserved tooth of *Nigerpeton*. It measures 4.5 cm from tip to root and preserves a thin layer of enamel. A well-defined carina is visible, but serrations are absent.

3. Faunal analysis

3.1. The endemic Moradi Formation tetrapod fauna

Previous studies have highlighted the unique species recorded in the Moradi Formation (Damiani et al., 2006; O'Keefe et al., 2005; de Ricqlès and Taquet, 1982; Sidor et al., 2003, 2005; Steyer et al., 2006; Tsuji et al., 2013). In addition, each Nigerien species is also usually very distinctive. For example, the current study of *N. ricqlès*

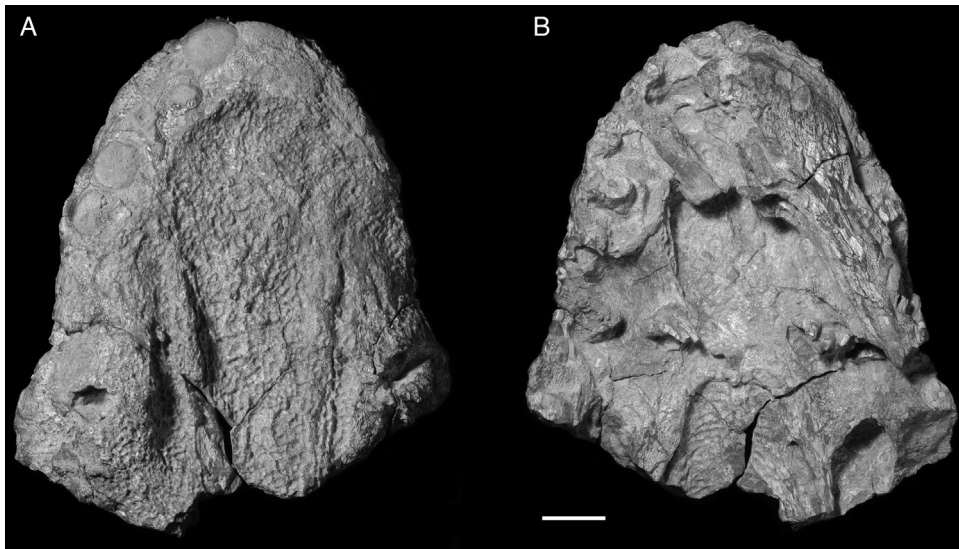


Fig. 2. The snout of *Nigerpeton ricqlesi* (MNN MOR108). A. Dorsal view. B. Ventral view. Scale bar equals 3 cm.
Fig. 2. Musée de *Nigerpeton ricqlesi* (MNN MOR 108). A. Vue dorsale. B. Vue ventrale. Barre d'échelle = 3 cm.

suggests that it can be diagnosed by at least ten cranial autapomorphies. Similarly, a recent study of the pareiasaur *Bunostegos akokanensis* noted nine cranial autapomorphies (Tsuji et al., 2013). It is also worth noting that dicynodonts are missing from the Moradi, and that pareiasaurs and large captorhinids appear to have filled the herbivorous tetrapod niche. All of these factors, in addition to the long ghost lineages inferred for some lineages, led Sidor et al. (2005) to consider the Moradi tetrapod fauna as an endemic assemblage likely isolated from the remainder of Pangea by the

xeric conditions inferred for central Pangea (Gibbs et al., 2002; Kiehl and Shields, 2005; Rees et al., 1999, 2002; Smith et al., 2009; Tabor et al., 2011).

3.2. Network visualization of Upper Permian tetrapod biogeography

A taxon-locality occurrence network can be used to compare the fauna of the Moradi Formation to those from five other areas preserving Upper Permian assemblages,

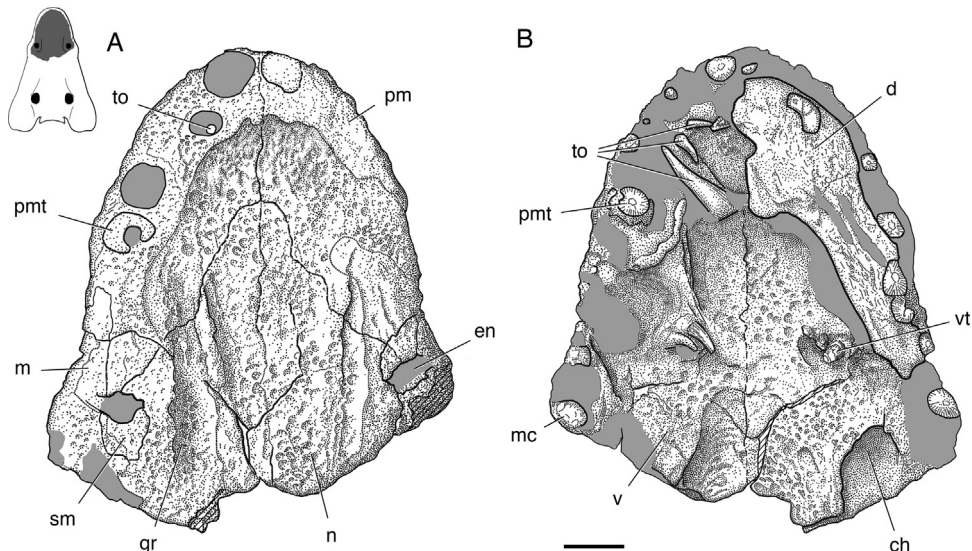


Fig. 3. The snout of *Nigerpeton ricqlesi* (MNN MOR108). A. Dorsal view. B. Ventral view. Gray indicates remaining matrix. Skull outline redrawn from Steyer et al. (2006). Abbreviations: ch, choana; d, dentary; en, external naris; gr, groove; m, maxilla; mc, maxillary caniniform tooth; n, nasal; pm, premaxilla; pmt, premaxillary tusk; sm, septomaxilla; to, tooth; v, vomer; vt, vomerine tusk. Scale bar equals 3 cm.
Fig. 3. Musée de *Nigerpeton ricqlesi* (MNN MOR 108). A. Vue dorsale. B. Vue ventrale. Les zones grisées indiquent la matrice restante. Le dessin du crâne a été réalisé d'après Steyer et al. (2006). Abréviations: ch, choane; d, dentaire; en, narine externe; gr, sillon; m, maxillaire; mc, dent de maxillaire, en forme de canine; n, nasal; pm, pré-maxillaire; pmt, défense de pré-maxillaire; sm, septomaxillaire; to, dent; v, vomer; vt, défense vomérine. Barre d'échelle = 3 cm.

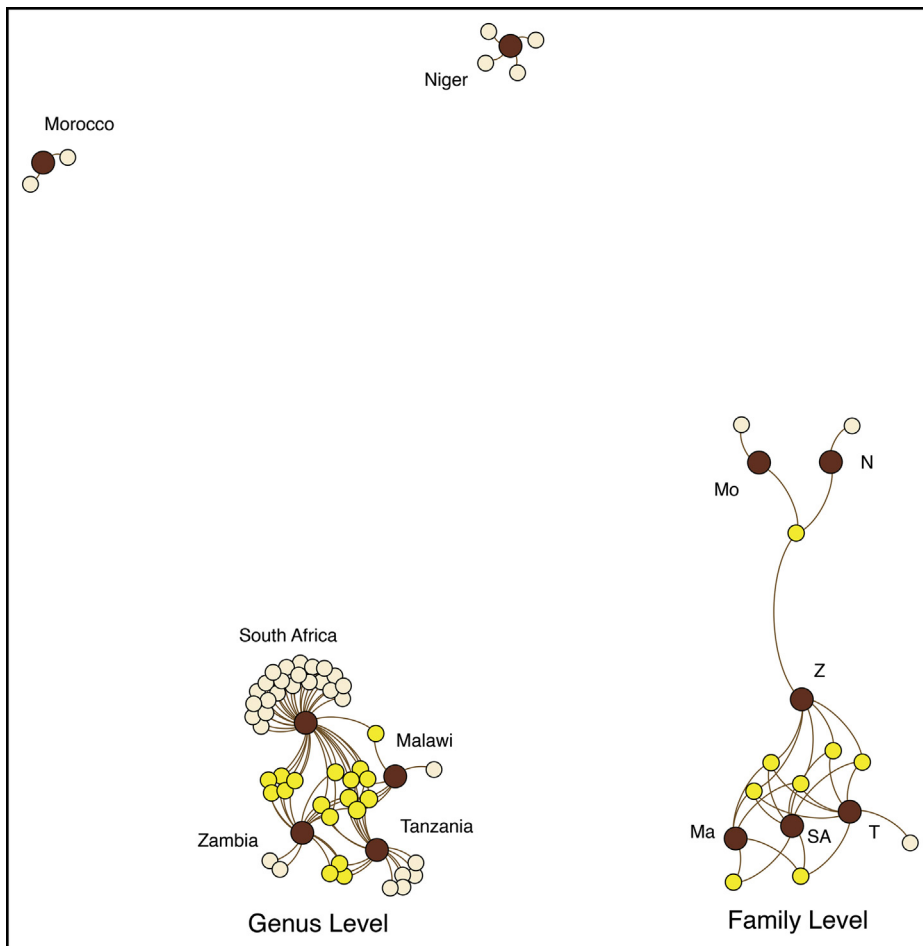


Fig. 4. Bipartite network representation of Late Permian tetrapod occurrences. Large circles represent localities and small circles represent taxa. Yellow filled circles denote taxa that occur at more than one locality. A taxon is connected to a locality if it occurs there. Corresponding occurrence data are given in [Tables 1 and 2](#). Abbreviations: Ma, Malawi; Mo, Morocco; N, Niger; SA, South Africa; T, Tanzania; Z, Zambia.

Fig. 4. Représentation du réseau bipartite des occurrences de tétrapodes du Permien supérieur. Les grands cercles représentent les localités et les petits cercles les taxons. Les cercles jaunes correspondent aux taxons observés dans plus d'une localité. Un taxon est connecté à une localité s'il y a été trouvé. Les données correspondantes d'occurrences sont fournies dans les [Tableaux 1 et 2](#). Abréviations : Ma, Malawi ; Mo, Maroc ; N, Niger ; SA, Afrique du Sud ; T, Tanzanie ; Z, Zambie.

namely the: Ikakern Formation of Morocco, Chiweta beds of Malawi, *Cistecephalus* Assemblage Zone (AZ) of South Africa, Upper Madumabisa Mudstone Formation of Zambia, and Usili Formation of Tanzania. The last four areas are well-correlated biostratigraphically ([Angielczyk et al., in press](#); [Rubidge, 2005](#); [Sidor et al., 2010, 2013](#)). In contrast, as noted by [Lucas \(2006\)](#), the Ikakern and Moradi formations defy direct correlation, but are nonetheless typically considered Upper Permian because of their faunal content (e.g., the presence of pareiasaurs) and intra-basinal stratigraphic relationships ([Jalil, 1999](#); [Jalil and Janvier, 2005](#); [Sidor et al., 2005](#); [Taquet, 1972](#)). Comparison to overlying *Dicynodon* AZ faunas would restrict the number of comparisons made, as this biozone is exclusively known from South Africa, but would not significantly change the results shown here (i.e., [Fig. 4](#)), because both the *Cistecephalus* and *Dicynodon* AZs are dominated by dicynodonts and have similar

community structure ([Nicolas and Rubidge, 2010](#); [Smith et al., 2012](#)).

Here I use a bipartite network, where localities and taxa are both represented by nodes, for biogeographic analysis ([Sidor et al., 2013](#); [Vilhena et al., 2013](#)). The six localities included in this analysis are represented by red circles in [Figs. 4 and 5](#). Taxa, represented by small circles in [Figs. 4 and 5](#), are connected to localities if they occur there. For ease of recognition, taxa that occur at more than one locality are shown in yellow. In this visualization structure, an endemic assemblage appears as an isolated locality sharing no taxa with other localities. I used the data matrices in [Tables 1 and 2](#) to produce genus and higher-level occurrence networks ([Fig. 4](#)). The composition of higher taxa (e.g., Captorhinidae) was based primarily on the genus-level records in [Table 1](#) (i.e., *Captorhinus*, *Moradisaurus*). These taxonomic levels of analysis were used as a heuristic and are a way to bring some phylogenetic information to

$$\text{Biogeographic Connectedness} = \frac{O - N}{LN - N}$$

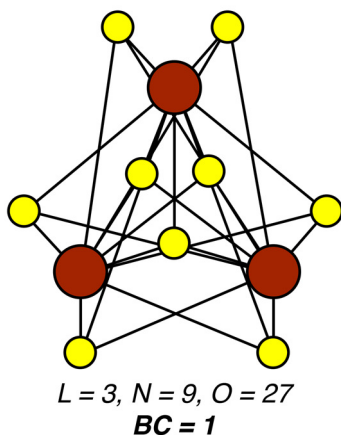
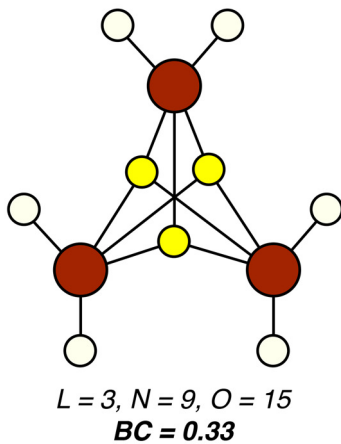
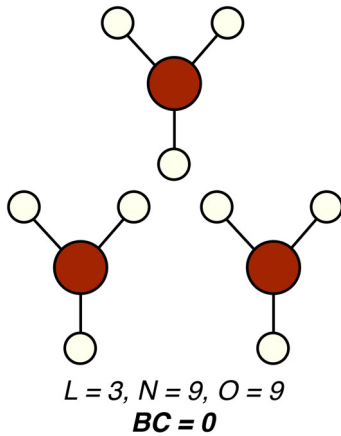


Fig. 5. Taxon-locality occurrence networks depicting increased levels of connectedness. Large circles represent localities and small circles represent taxa. Yellow filled circles denote taxa that occur at more than one locality. A taxon is connected to a locality if it occurs there. Abbreviations:

an essentially non-phylogenetic type of analysis. Moreover, they permit the inclusion of data that could not otherwise be included (i.e., fossils not referable to genera, but to higher level clades). As has been recognized in other analyses using higher taxa, the taxonomic units included in each analysis do not represent equivalent phylogenetic groups (Sepkoski and Kendrick, 1993).

At the finest level of taxonomic resolution, a clear pattern emerges: therapsid-dominated faunas are highly connected across the four southern African localities and the faunas of Morocco and Niger are endemic and thus isolated in the graph space (Fig. 4). Out of 54 genera analyzed, 19 showed at least two occurrences but the majority (35) was endemic to a single locality. In addition to the fossil records of Niger and Morocco showing entirely endemic genera, a large percentage of genera also uniquely occurs in South Africa (59%, 22 of 37 genera). This is likely due to the intensive history of fossil collecting and paleontological work in the Karoo (Sidor et al., 2013; Smith et al., 2012).

A slightly coarser level of analysis permits the inclusion of several records that are referable to family or superfamily, but are too incomplete for a generic identification (see Table 2 legend; Fig. 4). Only 11 taxa are recognized and the number of endemics is reduced to three (Diplocaulidae, Peltobatrachidae, Edopoidea). The fact that all three of these are amphibians (i.e., non-amniote tetrapod) supports Milner's (1993) suggestion that species tied to water for reproduction might be prone to increased isolation and hence biogeographic endemism. The only other non-amniote clade included, Rhinesuchidae, occurs in only two regions: Malawi and South Africa. Morocco and Niger retain the highest levels of endemic family-level taxa (33% and 25%, respectively).

Networks are commonly used by ecologists to depict trophic relationships within a community. One metric developed for such studies is connectance, or the number of connections present in a network compared to the number that could conceivably occur (Dunne et al., 2002). More densely connected networks are thought to be more stable or resilient to species loss (Roopnarine et al., 2007). Sidor et al. (2013) developed the corresponding metric for bipartite taxon-occurrence networks, which they termed biogeographic connectedness (BC). BC scores, which range from zero to one, indicate variation along an axis from endemic to cosmopolitan structure. Examples are shown in Fig. 5. When $BC=0$, each locality hosts an endemic community. In contrast, when $BC=1$, all taxa occur at all localities (i.e., communities are cosmopolitan). When compared to similar species-level southern Pangean data in Sidor et al. (2013), the inclusion of data from Niger and Morocco reduce overall BC for the Late Permian.

BC, biogeographic connectedness; L, number of localities; N, number of taxa; O, number of occurrences.

Fig. 5. Réseaux d'occurrence taxon-localité, représentant les niveaux croissants de connectivité. Les grands cercles représentent les localités et les petits cercles les taxa. Les cercles jaunes correspondent aux taxa observés dans plus d'une localité. Un taxon est connecté à une localité, s'il y a été trouvé. Abréviations : BC, connectivité biogéographique ; L, nombre de localités ; N, nombre de taxa ; O, nombre d'occurrences.

Table 1

Genus-level occurrence data for 54 Late Permian tetrapods used to construct the bipartite network shown in Fig. 4. “0” denotes absence and “1” denotes presence. Taxa are based on occurrences in the Late Permian *Cistecephalus* Assemblage Zone of South Africa and its recognized temporal equivalents in southern Africa (i.e., Chiweta beds, Malawi; Upper Madumabisa Mudstone Formation, Luangwa Basin, Zambia; Usili Formation, Ruhuhu Basin, Tanzania). Tetrapod records from the Ikakern Formation of Morocco and the Moradi Formation of Niger are included for comparison, but no direct biostratigraphic correlation is implied. The bulk of the occurrence records are from key publications (Angielczyk et al., in press; Rubidge, 2005; Germain, 2010; Sidor et al., 2010, 2013), although gorgonopsians have been ignored because of their unresolved alpha taxonomy. MAL 290 was identified as a new biarmosuchian by Jacobs et al. (2005).

Tableau 1

Données d'occurrences genre-niveau pour 54 tétrapodes du Permien supérieur, utilisés pour construire le réseau bipartite, présenté sur la Fig. 4. «0» représente l'absence et «1» la présence. Les taxons sont basés sur les occurrences, au Permien supérieur, de la zone-assemblage à *Cistecephalus* d'Afrique du Sud et ses équivalents temporels reconnus en Afrique méridionale (à savoir les couches Chiweta, Malawi; la formation Mudstone de Madumabisa, bassin de Luangwa en Zambie; la formation Usili, bassin de Ruhuhu, en Tanzanie). Les archives de tétrapodes en provenance de la formation Ikakern au Maroc et de la formation de Moradi au Niger sont incluses pour comparaison, mais n'impliquent aucune corrélation biostratigraphique directe. La plupart des occurrences répertoriées proviennent de publications clé (Angielczyk et al., sous presse; Rubidge, 2005; Germain, 2010; Sidor et al., 2010, 2013), bien que les gorgonopsiens aient été ignorés en raison de leur taxonomie alpha non résolue. MAL 290 a été identifié en tant que nouveau biarmosuchien par Jacobs et al. (2005).

Taxon	Morocco	Niger	Zambia	Tanzania	Malawi	S. Africa
<i>Diplocaulus</i>	1	0	0	0	0	0
<i>Saharastega</i>	0	1	0	0	0	0
<i>Nigerpeton</i>	0	1	0	0	0	0
<i>Rhinesuchus</i>	0	0	0	0	1	1
<i>Peltobatrachus</i>	0	0	0	1	0	0
<i>Anthodon</i>	0	0	0	0	0	1
<i>Arganaceras</i>	1	0	0	0	0	0
<i>Bunostegos</i>	0	1	0	0	0	0
<i>Nanoparia</i>	0	0	0	0	0	1
<i>Pareiasaurus</i>	0	0	0	1	0	1
<i>Pareiasuchus</i>	0	0	1	0	0	1
<i>Pumiliopareia</i>	0	0	0	0	0	1
<i>Captorhinus</i>	0	0	1	0	0	0
<i>Moradisaurus</i>	0	1	0	0	0	0
MAL 290	0	0	0	0	1	0
<i>Herpetoskylax</i>	0	0	0	0	0	1
<i>Lemurosaurus</i>	0	0	0	0	0	1
<i>Lycaenodon</i>	0	0	0	0	0	1
<i>Paraburnetia</i>	0	0	0	0	0	1
<i>Aulacephalodon</i>	0	0	0	0	0	1
<i>Basilodon</i>	0	0	0	0	0	1
<i>Cistecephaloides</i>	0	0	0	0	0	1
<i>Cistecephalus</i>	0	0	0	0	0	1
<i>Compsodon</i>	0	0	1	0	0	1
<i>Dicynodon</i>	0	0	1	1	0	0
<i>Dicynodontoides</i>	0	0	1	1	1	1
<i>Diictodon</i>	0	0	1	0	0	1
<i>Dinanomodon</i>	0	0	0	0	0	1
<i>Emydops</i>	0	0	1	0	0	1
<i>Endothiodon</i>	0	0	1	1	1	1
<i>Euptychognathus</i>	0	0	0	1	0	1
<i>Galepus</i>	0	0	0	0	0	1
<i>Geikia</i>	0	0	0	1	0	0
<i>Katumbia</i>	0	0	1	1	0	0
<i>Kawingasaurus</i>	0	0	0	1	0	0
<i>Keyseria</i>	0	0	0	0	0	1
<i>Kitchinganomodon</i>	0	0	1	0	1	1
<i>Myosauroides</i>	0	0	0	0	0	1
<i>Odontocyclops</i>	0	0	1	0	0	1
<i>Oudenodon</i>	0	0	1	1	1	1
<i>Pachytelos</i>	0	0	0	1	0	0
<i>Pristerodon</i>	0	0	1	1	0	1
<i>Rhachiocephalus</i>	0	0	0	1	0	1
<i>Syops</i>	0	0	1	0	0	0
<i>Akidnognathus</i>	0	0	0	0	0	1
<i>Euchambersia</i>	0	0	0	0	0	1
<i>Hofmeyria</i>	0	0	0	0	0	1
<i>Ictidostoma</i>	0	0	0	0	0	1
<i>Ictidosuchoides</i>	0	0	0	0	0	1
<i>Ictidosuchops</i>	0	0	0	0	0	1
<i>Miroenthes</i>	0	0	0	0	0	1
<i>Silphoictoides</i>	0	0	0	1	0	0
<i>Theriongnathus</i>	0	0	1	1	0	0
<i>Procyonosuchus</i>	0	0	1	1	0	1

Table 2

Family-level (or above) occurrence data for eleven Late Permian tetrapod clades used to construct the bipartite network shown in Fig. 4. “0” denotes absence and “1” denotes presence. Occurrences are based on the genus-level data presented in Table 1 with two exceptions. First, gorgonopsids were recorded to be present in Zambia, Tanzania, Malawi, and South Africa based on data in Sigogneau-Russell (1989). Second, occurrence records for some generically-indeterminate material that can be identified to family could be included: Moroccan captorhinids (Jalil and Dutuit, 1996) and Nigerian gorgonopsids (Smiley et al., 2008).

Tableau 2

Données d'occurrences famille-niveau (ou au-dessus) pour 11 clades de tétrapodes du Permien supérieur, utilisés pour construire le réseau bipartite présenté sur la Fig. 4. « 0 » représente l'absence et « 1 » la présence. Les occurrences sont basées sur les données genre-niveau fournies par le Tableau 1, avec deux exceptions. D'abord, les gorgonopsidés ont été répertoriés comme présents en Zambie, Tanzanie, Malawi et Afrique du Sud d'après les données de Sigogneau-Russell (1989). Ensuite, les occurrences répertoriées pour du matériel indéterminé du point de vue générique qui peut être identifié à la famille pourraient être incluses : captorhinidés du Maroc (Jalil et Dutuit, 1996) et gorgonopsidés du Niger (Smiley et al., 2008).

Taxon	Morocco	Niger	Zambia	Tanzania	Malawi	S. Africa
Diplocaulidae	1	0	0	0	0	0
Edopoidea	0	1	0	0	0	0
Rhinesuchidae	0	0	0	0	1	1
Peltobatrachidae	0	0	0	1	0	0
Pareiasauridae	1	1	1	1	0	1
Captorhinidae	1	1	1	0	0	0
Biarmosuchia	0	0	0	1	1	1
Dicynodontia	0	0	1	1	1	1
Gorgonopsidae	0	1	1	1	1	1
Therocephalia	0	0	1	1	0	1
Cynodontia	0	0	1	1	0	1

One would expect a strong relationship between the taxonomic level of an analysis and BC, as higher taxa subsume larger and larger numbers of species. Not surprisingly, for the data used here, genus and family analyses yield BC values of 0.10 and 0.36, respectively. More importantly, however, the use of higher taxa allows for the inclusion of specimens that cannot be referred to genera or species. For example, the current state of gorgonopsid alpha-taxonomy makes the assignment of specimens to species (or genera) very difficult, but this clade was clearly widespread (Table 2). The inclusion of phylogenetic information into bipartite taxon-occurrence networks, perhaps through the differential weighting of connections, is an important goal for the development of this model of biogeographic analysis.

4. Discussion

Biogeographic analysis of paleontological data always assumes, at least to some degree, that the distribution of fossils at localities is due to genuine differences in the geographic ranges of the species involved. However, it is clear that the absence of an occurrence could alternatively be due to poor sampling. For example, the Chiweta beds of Malawi are very limited in mapped area (<4 km²) and collecting effort. A single early collection (Dixey, 1926; Haughton, 1926) of 19 specimens recognized dicynodont, temnospondyl, and gorgonopsid taxa, and more recent collecting (Jacobs et al., 1990, 2005) added several more dicynodont specimens of previously recognized taxa as well as a new biarmosuchian. However, the lack of therocephalian and cynodont records might not be unexpected if Chiweta rocks preserves an assemblage like the *Cistecephalus* AZ of South Africa, where museum records indicate that dicynodont fossils outnumber those of therocephalians and cynodonts by roughly 38 or 385 to 1, respectively (Smith et al., 2012: table 2.3). Sidor et al. (2013) introduced a bootstrapping procedure to mitigate the

effects of incomplete sampling on inferred biogeographic structure, but care must be taken when interpreting patterns based on the absence of occurrence. In the case of the Moradi Formation, the presence of large-bodied pareiasaurs offer a degree of taphonomic control on the absence of dicynodonts, as these taxa are known to co-occur elsewhere during the Permian (Nicolas and Rubidge, 2010; Smith et al., 2012).

The use of bipartite networks to visualize the geographic occurrence of tetrapods seems intuitive. At a glance, the reader has an impression of the relative sampling of taxa from localities, the relative number of endemics, and how many taxa are shared between two or more localities. In addition to the taxonomic analysis shown here, taxon-locality occurrence networks could be used to show how patterns of biogeographic distribution changed in a historical analysis of sampling (e.g., Weishampel, 1996), which could lead to an understanding of whether there is a relationship between fossil abundance and breadth of geographic distribution. Most importantly, analysis of successive time intervals could provide a macroevolutionary perspective on how mass extinctions affect the continuity or breakup of faunal provinces (Sidor et al., 2013; Vilhena et al., 2013).

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