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ARTICLE

ANATOMY OF *EMEROLETER LEVIS* AND THE PHYLOGENY OF THE NYCTEROLETER PARAREPTILES

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ABSTRACT—The nycteroleter parareptiles have lately become the focus of increased attention, owing to their recently recognized sister-group relationship to pareiasaurs and the discovery an impedance-matching ear in members of the group. The Kotel'nich locality in central Russia dates to the early part of the Late Permian and preserves a diverse tetrapod fauna that includes the pareiasaur *Deltavjatia vjatkensis* and the nycteroleter *Emeroleter levis*. The latter taxon was previously known only from isolated crania, but recent excavations have produced additional material, including well-preserved postcrania, allowing a complete redescription. The skull of *Emeroleter* is typified by dermal sculpturing consisting of evenly spaced small, round pits and supratemporals that extend posterolaterally into broad horns. The quadratojugal is long and the posterior portion of the element curves dorsally into a pointed projection, an autapomorphy of the taxon. Postcranially, *Emeroleter* is very gracile with a long, sigmoid femur, and slender limbs, carpal, and tarsal elements. A reassessment of the Russian nycteroleters results in the synonymy of *Tokosaurus perforatus* with *Macroleter poezicus*. Phylogenetic analysis of parareptilian relationships using both parsimony and Bayesian inference yields a monophyly of 'nycteroleters' in parsimony, whereas the group is found to be paraphyletic with Bayesian inference. The genus *Bashkyroleter* is consistently paraphyletic. A clade consisting of the nycteroleters and pareiasaurs, here termed Pareiasauromorpha, is supported by both methods.

INTRODUCTION

Although the fossil remains of nycteroleter parareptiles have been known since the early part of the 20th century (Efremov, 1938), much about their diversity, interrelationships, and importance has only recently been elucidated. Recent studies have shown this group to be the sister taxon of the large herbivorous pareiasaurs (Tsuji, 2006; Müller and Tsuji, 2007). Despite this acknowledged importance, however, only one nycterleter taxon, Macroleter poezicus Tverdokhlebova and Ivakhnenko, 1984, has been described in detail, and the postcranial anatomy of the group remains poorly understood. The clade is currently recognized to contain eight taxa within six genera: Nycteroleter ineptus, Emeroleter levis, Bashkyroleter bashkyricus, Bashkyroleter mesensis, Tokosaurus perforatus, M. poezicus, Macroleter agilis, and Rhipaeosaurus tricuspidens (Reisz and Laurin, 2001; Ivakhnenko, 2008). There is also an unnamed nycteroleter recently identified from the Karoo Basin of South Africa (Cisneros and Tsuji, 2009). With the exception of the South African specimen and M. agilis, a taxon comprising one specimen from the Middle or Lower Permian of Oklahoma (see Reisz and Laurin [2001, 2002] and Lucas [2002] for debate regarding this matter), all other nycteroleters are known from the Middle and Upper Permian of Russia (Fig. 1A).

The first named nycteroleter, *Nycteroleter ineptus* Efremov, 1938, was discovered in the Mezen River Basin in the Arkhangel'sk Province in northern Russia (Efremov, 1938). *Macroleter poezicus* and *Bashkyroleter mesensis* are the two other nycteroleters found in this basin (Iyakhnenko, 2008). The age

of this assemblage is not well constrained, with localities that likely range in age from the upper Cisuralian to end-Guadalupian (dates based primarily on biostratigraphic correlations with other Late Permian faunas; Golubev, 2005). Three of the Russian nycteroleters, *Bashkyroleter bashkyricus*, *Tokosaurus perforatus*, and *Rhipaeosaurus tricuspidens*, belong to the Belebey fauna, which dates to the late Kazanian (upper part of the Roadian) (Modesto and Rybczynski, 2000). *Emeroleter levis* is the only nycteroleter known from Kotel'nich, a locality situated on the banks of the Vjatka River, in the Kirov Oblast. The Kotel'nich locality is earliest Lopingian in age, making *Emeroleter* the youngest known nycteroleter as well as only known Late Permian member of the group (Fig. 2).

Despite the relatively large number of taxa, it was only recently that most of the sufficiently known nycteroleters were included in a phylogenetic analysis (Müller and Tsuji, 2007). Whereas a parsimony analysis confirmed their monophyly, a Bayesian analysis with a related data set showed an alternative topology in which a monophyletic group containing *Macroleter poezicus* and *Tokosaurus perforatus* were related more closely to pareiasaurs than to the other nycteroleters, suggesting that nycteroleters, rather than being a monophyletic sister group to pareisaurs, formed a grade with respect to pareiasaurs (Tsuji et al., 2010).

The two non-Russian nycteroleters have either been considered in other works (Cisneros and Tsuji, 2009) or are currently under study (*Macroleter agilis*). However, with the exception of *Macroleter poezicus* (Tsuji, 2006), the anatomy of the Russian taxa has not been recently reviewed. In addition, continuing excavations in the Kotel'nich locality have unearthed well-preserved specimens of *Emeroleter levis*, which include postcranial remains. These new specimens permit the first in-depth examination of the postcranial skeleton of a nycteroleter. This paper describes the complete skeleton of

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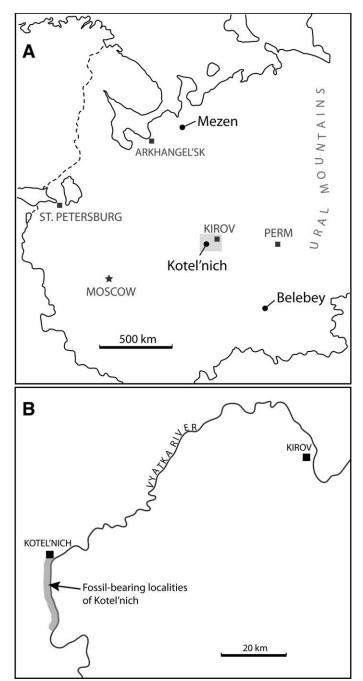


FIGURE 1. **A**, map of Western Russia showing nycteroleter-bearing localities (indicated by circles). Adapted from Modesto and Rybczyinski (2000). Shaded box in **A** represents **B**, map showing location of the town of Kotel'nich and the Kotel'nich localities.

Emeroleter levis from Kotel'nich, and redescribes in a comparative format the other Russian nycteroleter taxa. This new information is incorporated into a phylogenetic analysis of parareptilian relationships, and a revised taxonomy of the group is also provided.

Institutional Abbreviations—KPM, Kotel'nich Paleontological Museum, Kotel'nich, Russia; PIN, Paleontological Institute, Moscow, Russia; UTM, University of Toronto at Mississauga, Mississauga, Ontario, Canada.

Ma 251			Russian platform faunal assemblage			South African assemblage zone	Stratigraphic range of nycteroleters		
251		Lopingian			zniki nblage				
260-			i Ige		Sokolki	Dicynodon	rtus sensis cus levis		
			Sokolki Assembalge	Ilinskoe		Cistecephalus Tropidostoma	Nycteroleter ineptus Bashkyroleter mesensis r bashkyricus Macroleter poezicus perforatus us tricuspidens Emeroleter levis QR 3061		
	ian			Kotel'nich		Pristerognathus	Nycte Bashk bashk Macre erforat is tricu		
200	erm	าน	Isheevo Assemblage	Isheevo	Malaya Kinel	Tapinocephalus	nkyrolete ssaurus paeosaur		
		Guadalupian	ıer blage	Ocher	Mezen Assem- blage	Eodicynodon	Basl Macroleter agilis Tok		
271	(Gr	Ocher Assemblage		oly- herma				

FIGURE 2. Stratigraphic distribution of nycteroleter taxa. NMQR 3061 is the Karoo nycteroleter of Cisneros and Tsuji (2009). Adapted from Cisneros and Tsuji (2009).

Anatomical Abbreviations—a, angular; acr, acromion process; ar, articular; as-ca, astragalocalcaneum complex; atn, atlas neural arch; ati, atlantal intercentrum; axi, axial intercentrum; cbl, ceratobranchial; cl, clavicle; cle, cleithrum; d, dentary; dt, distal tarsal; ec, ectopterygoid; ect. for., ectepicodylar foramen; ent, entepicondyle; f, frontal; fe, femur; fib, fibula; gast, gastralia; h1, hyoid; hu, humerus; ic, intercentra; il, ilium; int, intermedium; j, jugal; la, lacrimal; la. for., lacrimal foramen; lum, lumbar series; m, maxilla; mc, metacarpal; mt, metatarsal; n, nasal; p, parietal; pal, palatine; pbs, parabasisphenoid; pf, postfrontal; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; ra, radius; rad, radiale; sa, surangular; sca, scapula; sp, splenial; sq, squamosal; st, supratemporal; sub. for., suborbital foramen; t, tabular; tib, tibia; ul, ulna; uln, ulnare; v, vomer.

TAXONOMIC HISTORY OF THE RUSSIAN NYCTEROLETERS

Nycteroleter ineptus was the first of the nycteroleters to be named and was considered by Efremov (1938) to be a member of Family Procolophonidae, Subfamily Nyctiphruretinae, with Nyctiphruretus acudens Efremov, 1938. Efremov (1940) then named two new forms from localities in the area around the town of Belebey: Rhipaeosaurus tricuspidens Efremov, 1940 and Nycteroleter (now Bashkyroleter) bashkyricus (Efremov, 1940). He included these taxa with N. ineptus and Nyctiphruretus in the subfamily Nyctiphruretinae. Chudinov (1955) named Rhipaeosaurus talonorophus (now Leptoropha talonophora), Nycteroleter kassini (now Nyctiboetus kassini), and Nyctiboetus liteus (now also Nyctiboetus kassini) and included these taxa with those already named in a new family—Rhipaeosauridae, moving the taxa out of Procolophonidae. Rhipaeosaurus (Leptoropha) talonorophus, however, was later identified as a seymouriamorph (reptiliomorph non-amniote tetrapod) and the

last two were synonymized with *Nyctiboetus kassini* and assigned to Anthracosauria (another group of reptiliomorph non-amniote tetrapod) (Ivakhnenko et al., 1997). Chudinov and V'yushkov (1956) named *Nycteroleter ultimus*, which is now considered *Karpinskiosaurus secundus*, a seymouriamorph. (*N. ultimus* was renamed *Raphanodon ultimus* by Ivakhnenko [1987], then the species was moved to *Karpinskiosaurus* by Bulanov [2002], and finally the taxon was synonymized with *K. secundus* by Klembara [2011].)

Like Efremov, Watson (1942) postulated a close relationship between *Nycteroleter* and *Nyctiphruretus*. Olson (1947), however, emphasized the similarities between *Nycteroleter* and seymouriamorphs. He placed all of these taxa along with diadectids, procolophonids, and pareiasaurs in a new subclass of Reptilia he coined Parareptilia. Romer (1956) held that *Nycteroleter* was a very primitive procolophonid and placed it in its own subfamily, Nycteroleterinae, within the family Procolophonidae. He considered *Rhipaeosaurus* to be closely related to *Nyctiphruretus* within the subfamily Nyctiphruretinae, with all of these along with pareiasaurs within the superfamily Procolophonoidea (though within Diadectomorpha). Kuhn (1969), on the other hand, on the basis of the large otic notch, assigned *Nycteroleter* to the Seymouridae, and asserted a close association between *Rhipaeosaurus* and pareiasaurs.

It was not until 1984 that additional taxonomic work was completed on the nycteroleters. *Macroleter poezicus* and *Tokosaurus perforatus* were erected by Tverdokhlebova and Ivakhnenko (1984). The authors placed *Macroleter* along with *Nycteroleter* into the Family Nycteroleteridae, and placed *Tokosaurus* in a family of its own—Tokosauridae. Finally in 1997, the nycteroleters *Emeroleter levis* and *Bashkyroleter mesensis* were named (Ivakhnenko, 1997). Ivakhnenko undertook at this point a taxonomic reassessment of the clade, coining a new genus (*Bashkyroleter*) for the new taxon *Bashkyroleter mesensis*. He also transferred '*Nycteroleter' bashkyricus* to this genus because he felt that these two taxa more closely resembled each other than either did the type species of *Nycteroleter*.

In the most recent review of the Russian nycteroleters (Ivakhnenko, 2008), they were included in a paraphyletic Nycteroleteroidea along with the lanthanosuchids, with a more in-

clusive group also containing the elginiid pareiasaur *Obirkovia* gladiator (Ivakhnenko, 2008). The names Nycteroleteroidea and Nycteroleteridae are attributed in this work to Romer (1956). See Table 1 for a summary of taxonomic history of the group.

The inclusion of nycteroleters in quantitative phylogenetic analysis (Lee, 1993, 1997a; deBraga and Rieppel, 1997) confirmed their placement within Parareptilia as close relatives of procolophonids. More recent analyses (Tsuji, 2006; Müller and Tsuji, 2007; Reisz et al., 2007; Tsuji et al., 2010) demonstrate a sistergroup relationship between nycteroleters and Pareiasauria.

Nyctiphruretus acudens has been considered closely related to the nycteroleters, but the most recent analysis of the taxon (Säilä, 2010a) recovers Nyctiphruretus as sister group to a nycteroleter-pareiasaur clade or alternatively as the sister taxon to procolophonids, but never within the nycteroleters.

THE KOTEL'NICH LOCALITY

Paramount to the redescription of Emeroleter levis are the extremely well-preserved fossils of the taxon recovered from the Kotel'nich locality. This locality is a practically continuous 18-20 km exposure of strata running south from Kotel'nich Port along the western bank of the Viatka River in the Kirov Region of western Russia (Fig. 1B). Fossils are preserved in a red mudstone (Coffa, 2007). Kotel'nich has produced a wide range of Permian amniotes, including the anomodonts Suminia getmanovi, Australobarbus kotelnitshi, and Vivaxosaurus permicus, the gorgonopsian Viatkogorgon ivakhnenkoi, the therocephalian Vyatkosuchus sumini, the biarmosuchian Proburnetia vyatkensis, and the parareptiles Nyctiphruretus acudens, Deltavjatia vjatkensis, and Emeroleter levis (Ivakhnenko et al., 1997). The Kotel'nich locality preserves an interesting parareptilian fauna, with three different groups co-existing: the last of the nycteroleters and one of the oldest pareiasaurs together with the enigmatic Nyctiphruretus. This parareptilian fauna is part of a very diverse, herbivore-dominated assemblage that includes the earliest-known arboreal amniote (Fröbisch and Reisz, 2009). The Kotel'nich strata are considered to be roughly correlated with the Pristerognathus Assemblage Zone of the Karoo Basin in South Africa (Golubev, 2005) (Fig. 2).

TABLE 1. Current nomenclatural status of Russian nycteroleters as well as other Russian taxa formerly associated with the group.

Valid nycteroleter taxa	Names no longer in use	Notes		
Nycteroleters Nycteroleter ineptus Rhipaeosaurus tricuspidens				
Bashkyroleter bashkyricus	Nycteroleter bashkyricus	N. bashkyricus moved to new genus		
Bushkyroteter bushkyricus	Nycleroteter bushkyricus	Bashkyroleter by Ivakhnenko (1997).		
'Bashkyroleter' mesensis				
Macroleter poezicus	Tokosaurus perforatus	T. perforatus synonymized with Macroleter poezicus in this work.		
Emeroleter levis		r		
Non-nycteroleters				
Leptoropha talonophora	Rhipaeosaurus talonorophus	R. talonorophus synonymized with L. talonophora by Ivakhnenko (1987).		
Nyctiboetus kassini	Nycteroleter kassini	N. kassini moved to genus Nyctiboetus by Ivakhnenko et al. (1997).		
Nyctiboetus kassini	Nyctiboetus liteus	N. liteus synonymized with N. kassini by Ivakhnenko et al. (1997).		
Karpinskiosaurus secundus	Nycteroleter ultimus,	N. ultimus moved to genus Raphanodon by		
1	Raphanodon ultimus,	Ivakhnenko (1987), then to		
	Karpinskiosaurus ultimus	Karpinskiosaurus by Bulanov (2002), finally synonymized with K. secundus by Klembara (2011).		

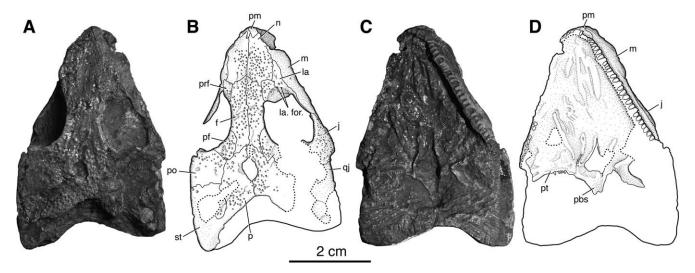


FIGURE 3. Emeroleter levis, PIN 2212/92, holotype. Photographs and interpretive drawings of skull in A, B, dorsal, and C, D, ventral views.

SYSTEMATIC PALEONTOLOGY

AMNIOTA Haeckel, 1866 REPTILIA Laurenti, 1768 PARAREPTILIA Olson, 1947 EMEROLETER LEVIS Ivakhnenko, 1997 (Figs. 3–10)

Revised Diagnosis—Medium-sized nycteroleter possessing the following autapomorphies: presence of unique sculpturing consisting of regularly spaced small, round pits in an otherwise smooth skull; posteriorly strongly elongated supratemporals that form long, narrow horns; enlarged, unsculptured otic notch extending almost to posterior rim of orbit; posterior end of quadratojugal curves upwards forming a small horn; middle pterygoid denticle ridge stretches from area of basipterygoid joint to posterior edge of choana and does not adjoin vomeropalatine ridge. Differentiated from other closely related parareptiles in the extremely gracile limb elements and sigmoidal curvature of the femur.

Holotype—PIN 2212/92, an isolated, dorsoventrally flattened skull (Fig. 3).

Referred Specimens—PIN 2212/14, partial skull (Fig. 4); PIN 2212/89, fragmentary skull; KPM uncat/E1, complete articulated skeleton (Fig. 5); KPM uncat/E2, mostly complete articulated skeleton and skull, part and counter part (Figs. 6–8); KPM uncat/E3, mostly complete skull and fragmentary postcranial remains (Fig. 9); KPM uncat/E4, partial articulated postcranial skeleton with partial skull.

Locality and Horizon—Vjatka River, Town of Kotel'nich, Kirov Province, Russia. Late Permian, earliest Lopingian (low-ermost upper Tatarian [Severodvinskian Gorizont], lowermost Wuchiapingian). Specimens are found in red mudstone in a series of localities that extend approximately 20 km along the western bank of the Vjatka River near Kotel'nich (Fig. 1B). Exposures are roughly correlated with the *Pristerognathus* Assemblage Zone of the South African Karoo Basin.

ANATOMICAL DESCRIPTION OF EMEROLETER LEVIS

Cranial Anatomy

The sculpturing on the dermal skull roof of *Emeroleter levis* is very distinctive, even among the other nycteroleters. The circular pits are small, very regular in size and distribution, and

form a very uniform pattern over the entire dermal skull roof. The skull itself is basically triangular in shape and is relatively gracile. A single median embayment of the posterior skull table in *Emeroleter* displays an extreme exaggeration of the morphology seen in other nycteroleters, a feature emphasized by the 'horn-like' morphology of the posterolateral corner of the skull table. All of the available specimens except for one partial skull are dorsoventrally crushed, making some of the cranial anatomy difficult to discern. There is an extremely sharp delineation between the skull roof and the cheek region, defined by a prominent ridge formed by the lateral edges of the postorbital and the supratemporal, and a severe undercut, ventral to which lies the otic notch. The cranial reconstruction in dorsal and lateral view (Fig. 10A, B) is based on all available specimens, but primarily PIN 2212/14, KPM uncat/E1, KPM uncat/E2, and PIN 2212/92.

Skull Roof—The premaxilla (Figs. 3, 5C, D, 6A, B) is the anterior-most element of the skull. The bone is triradiate in structure, with a dorsal process contacting the nasal, a lateral toothbearing portion that sutures with the maxilla, and a posterior process that forms the contact on the palate with the vomer. The dorsal process is thin and relatively tall, such that the nares point primarily anteriorly. It is noticeably more gracile than the dorsal process of the premaxilla seen in Macroleter poezicus (Tsuji, 2006). The slenderness of this dorsal process relative to the nasal and the maxilla also gives the anterior-most portion of the skull a pointed aspect in dorsal view (Fig. 3A, B). Ventral to the dorsal process of the premaxilla, a lateral process bears the anteriormost teeth in the upper jaw. There is space for at least four, and more likely five, teeth in the premaxilla, the same number found in the closely related M. poezicus and Bashkyroleter mesensis (Ivakhnenko, 1997). The palatal (posterior) process of the premaxilla contacts the vomer, but this suture is obscured, or this area is not preserved, in known specimens. The premaxilla itself is entirely unsculptured, unlike many of the other bones of the skull roof, a condition similar to that of the other known nycteroleters (Tsuji, 2006; Ivahknenko, 1997).

The maxilla (Figs. 3, 4, 6) bears the lateral tooth row in *Emeroleter*. There are 27 tooth positions in the holotype PIN 2212/92, although the posterior tip of the maxilla is missing on both sides, so a tooth position or two might be missing from this count. In the isolated skull of KPM uncat/E2, the full tooth row is not completely visible to the end of the maxilla and only approximately 22 tooth positions can be observed. Unlike other bones

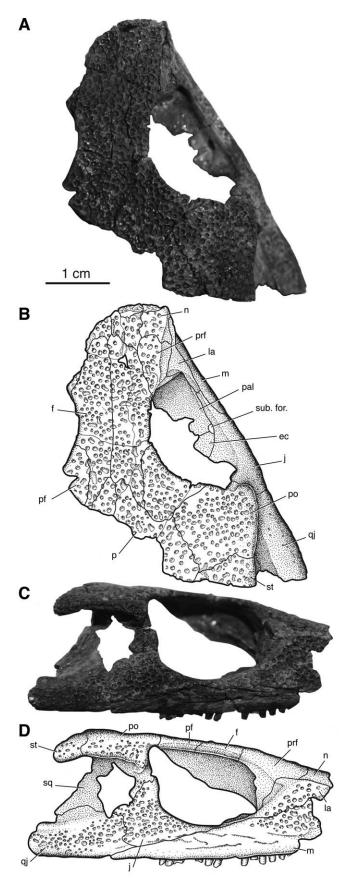


FIGURE 4. *Emeroleter levis*, PIN 2212/14. Photographs and interpretive drawings of skull in **A**, **B**, dorsal, and **C**, **D**, right lateral views.

of the skull roof, the maxilla of the small specimen of *Emeroleter* (KPM uncat/E2) does not bear the sculpturing pattern diagnostic for the taxon. Instead, the smooth lateral (external) surface of the maxilla is perforated by a series of small foramina, with a series running just above the tooth row and another patch just anterior to the suture with the lacrimal (Fig. 6E, F). As in all parareptiles, the anterior-most of these foramina is notably larger than the others (Laurin and Reisz, 1995). In the largest known Emeroleter specimen, PIN 2212/14, the maxilla is similar in form to that of *Macroleter*, in which the ventral part of the bone remains unsculptured, but with sculpturing appearing on the dorsal process. The maxilla itself has a relatively tall but wide dorsal process that contacts the nasal, excluding the lacrimal from reaching the naris, and forms the entire posterior, and a small bit of the dorsal, rim of the naris (Fig. 3A, B). The maxilla of Emeroleter has an exceptionally long posterior process that extends significantly past the end of the tooth row and forms a relatively long suture with the anterior process of the quadratojugal, completely excluding the jugal from the ventral cheek margin (Fig. 4C, D).

The teeth are simple, pointed, and conical. The anterior-most teeth on the maxilla are slightly recurved. There is no evidence of defined cutting edges, nor are vertical grooves present; a morphology assumed to represent infolding of the enamel seen on some specimens of *Macroleter* (Tsuji, 2006). Some of the maxillary teeth display a slight labiolingual compression in comparison with the premaxillary and more anterior maxillary teeth, a feature described by Ivakhnenko (1997) as a 'petaliform' expansion of the crowns.

The lacrimal (Figs. 3A, B, 4, 6A, B, E, F) partially underlaps the dorsal process of the maxilla and is at least externally excluded from the naris by the tall and wide dorsal process of the latter element (Fig. 3A, B). The ventral and posterior process of the lacrimal forms the anteroventral section of the orbital rim, with its posterior-most limit forming a short suture with the anterior process of the jugal. Within the orbital rim, the lacrimal bears two small foramina close to the dorsal edge of the bone, near its suture with the prefrontal (Fig. 3A, B). The section of the lacrimal that contributes to the orbital rim is unsculptured.

The nasal (Figs. 3A, B, 5C, D, 9) is a rectangular, sculptured element that forms the majority of the dorsal portion of the snout in *Emeroleter*. Its anterior end underlies the thin dorsal process of the premaxilla and forms the dorsal border of the naris. The nasal sutures with the frontal posteriorly, and along its lateral edge it meets the maxilla anteriorly (excluding the lacrimal from the naris) and the lacrimal posteriorly (Fig. 3A, B).

The prefrontal (Figs. 3A, B, 4, 5C, D, 6A, B, 9) makes up the anterodorsal border of the orbit. It is a small element that lies lateral to the frontal, and dorsal and posterior to the lacrimal. It contacts the nasal anteromedially. In *Emeroleter*, as in other nycteroleters, the prefrontal does not contact the postfrontal as it does in pareiasaurs (Lee, 1997a). The prefrontal has a ventrally directed process that lies within the orbital rim, lining the posterior edge of the lacrimal. This process makes contact with the palate, but this contact is not particularly strong (Fig. 4C, D).

The frontal (Figs. 3A, B, 4, 5C, D, 6A, B, 9) is a roughly rectangular bone that, unlike the condition in pareiasaurs, does form the dorsal-most portion of the orbital rim, excluding the prefrontal from contacting the postfrontal. It forms a long, straight suture with its counterpart at the midline of the skull. The regular sculpture of small round pits is present throughout the dorsal surface of the bone (Fig. 4A, B). The suture with the prefrontal is directed anteromedially, so that the frontal tapers to a blunt point anteriorly where it forms an interdigitating suture with the nasal

The parietal (Figs. 3A, B, 4A, B, 5C, D, 6A, B, 9) makes up the majority of the skull table. The parietal or pineal foramen is contained entirely within the paired parietals. In the smaller

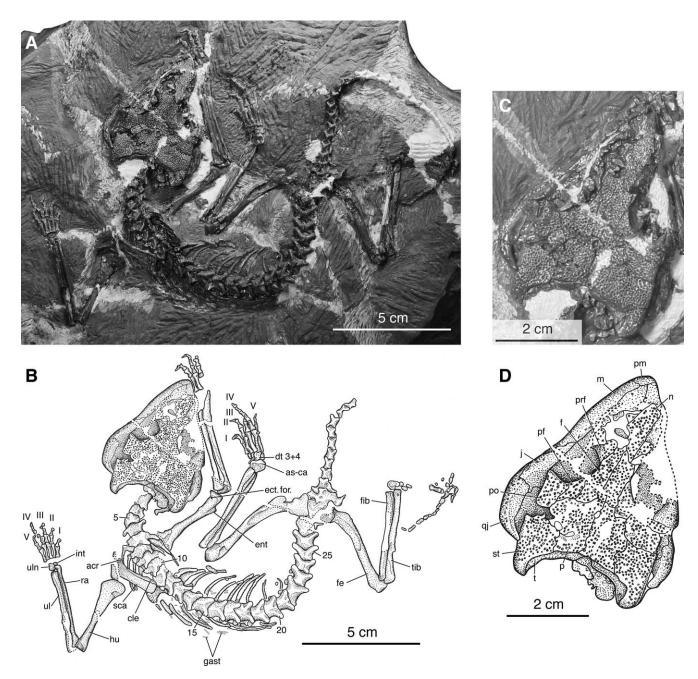


FIGURE 5. *Emeroleter levis*, KPM uncat/E1. Photographs and interpretive drawings of **A**, **B**, skeleton, and **C**, **D**, skull in dorsal aspect. Arabic numbers indicate presacral vertebrae. Roman numerals indicate digits.

skulls of *Emeroleter* the foramen is relatively small (Fig. 5C, D), but it is proportionately larger in specimens of larger size (Fig. 3A, B). The foramen lies anterior to the midpoint of the midline suture in the smaller specimen, KPM uncat/E1, whereas in the holotype PIN 2212/92 and PIN 2212/14 it is centered closer to the midpoint. In all cases, it appears to be displaced much further anteriorly within the parietal due to the deep embayment of the posterior edge of the skull table. The foramen itself is almost circular, contrasting with the teardrop shape seen in *Macroleter* (Tsuji, 2006). Anteriorly the parietal sutures with the frontal and laterally it forms a short suture with the postfrontal before forming a longer, posterolaterally directed suture with the postorbital (Fig. 4A, B). The last section of this lateral suture is made with

the supratemporal. The paired parietals meet in a straight median suture that is interrupted only by the parietal foramen (Fig. 5C, D). The parietal forms the majority of the posterior edge of the skull table. The edge itself is directed anteromedially such that it forms a wide 'V' in dorsal view. The parietal contacts the post-parietal and the tabular posteriorly.

Whereas no complete postparietal is preserved in known specimens of *Emeroleter*, this bone can be inferred to have been largely occipital and not integrated into the dermal skull roof.

The tabular (Fig. 5C, D), like that of *Macroleter*, is a small, thin bone that is located on the occipital region of the skull and is not integrated into the skull table. It instead runs posterior and slightly ventral to the parietal, making contact with a small

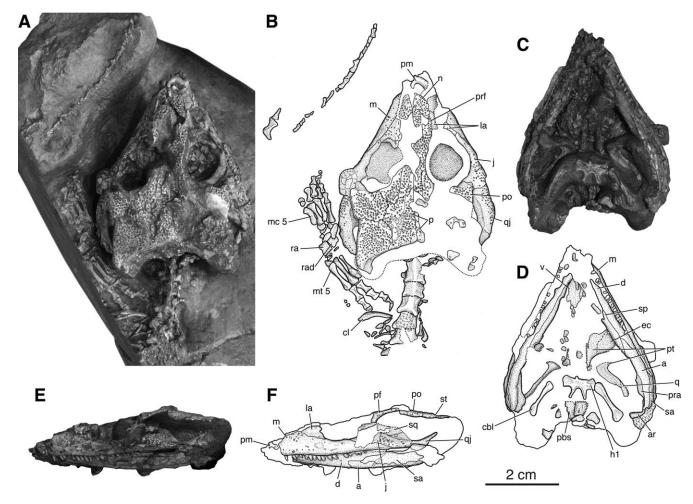


FIGURE 6. Emeroleter levis, KPM uncat/E2. Photographs and drawings of skull in A, B, dorsal, C, D, ventral, and E, F, left lateral views.

occipital flange of the supratemporal (Fig. 5C, D). The element does not bear the sculpturing seen on the bones of the skull table.

The presence of a large supratemporal (Figs. 3A, B, 5C, D, 6A, B) is characteristic of parareptiles (Laurin and Reisz, 1995), and this is no exception in *Emeroleter*, where the bone is proportionately larger than seen in other nycteroleters. The supratemporal forms a posterolateral 'horn' that curves slightly medially

at the tip (Figs. 5C, D, 6A, B). The supratemporal contacts the postfrontal anteriorly and the parietal medially. Posteriorly, it appears to make contact with the long, thin tabular. Laterally there is a distinct and severe undercut dorsal to the large temporal (or otic) notch below, with the supratemporal forming a prominent, thin, and sculptured laterally projecting ridge, continuing posteriorly from the postorbital. An unsculptured ventral

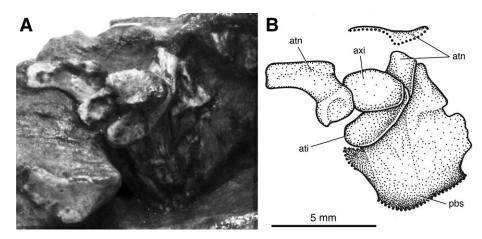


FIGURE 7. *Emeroleter levis*, KPM uncat/E2. **A**, photograph, and **B**, drawing of atlas-axis complex in ventral view.

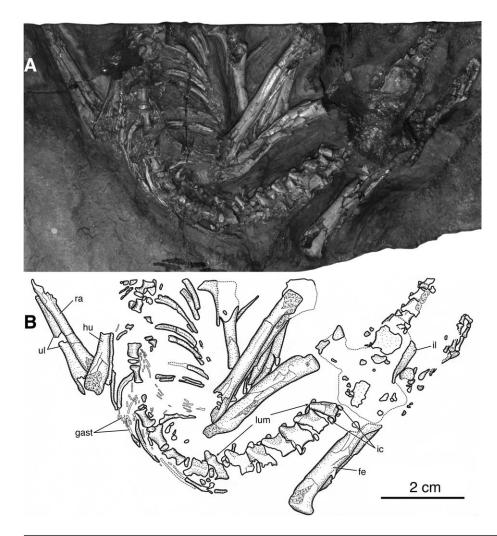


FIGURE 8. Emeroleter levis, KPM uncat/E2, postcranial skeleton. **A**, photograph, and **B**, drawing in dorsal aspect.

flange of the supratemporal takes part in the otic notch and forms a suture with the squamosal.

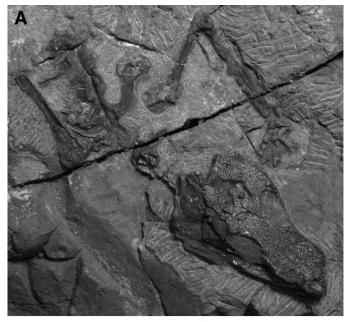
The postfrontal (Figs. 3A, B, 4, 5C, D, 6A, B, E, F, 9) is a triangular element that lies posterolateral to the frontal, anterolateral to the parietal, and medial to the postorbital, and as stated above, is excluded from contact with the prefrontal by a lateral extension of the frontal that forms part of the orbital rim (Fig. 3A, B). The postfrontal thus appears much broader than the prefrontal (Fig. 4A, B), the opposite of the arrangement seen in *Macroleter* (Tsuji, 2006). The postfrontal of *Emeroleter* bears the typical sculpturing on the dorsal surface of the element.

The postorbital (Figs. 3A, B, 4, 5C, D, 6A, B, 9) is a prominent bone that, as its name suggests, forms the posterior border of the orbit. It is subrectangular, contacting the supratemporal posteriorly, the parietal medially, the postfrontal anteromedially, and a small part of the jugal and the squamosal ventrally. The majority of the bone lies on the skull roof, but a process continues along the posterior rim of the orbit, extending ventrally to make contact with the thin dorsal process of the jugal (Fig. 4C, D). The postorbital is narrowly excluded from the unsculptured otic notch, but does form the anterodorsal limit of this feature. The bone is also sculptured on the external surface, except along the orbital rim where it is smooth.

The jugal (Figs. 3A, B, 4, 5C, D, 6A, B, E, F) is a lunate element that forms the posteroventral section of the orbital rim. The entire external surface of the bone is sculptured. The long anterior

process of the jugal forms a short suture with the posterior process of the lacrimal and the former bone is underlain by the maxilla for its entire length. In a morphology that differs from other nycteroleters, the jugal is excluded from the ventral border of the cheek by an extended maxilla-quadratojugal suture. Dorsally the jugal forms a short but interdigitating suture with the ventral process of the postorbital and the bone is thickened in this area. The dorsal process of the jugal is also angled posterodorsally, imparting a posterodorsal emargination to the shape of the orbit (Fig. 4C, D). The posterior edge of the jugal contacts the quadratojugal ventrally and the squamosal dorsally. The jugal also makes a small contribution to the palate in the form of a small, medially directed (alar) process located posterior to the ectopterygoid (Fig. 4A, B).

Whereas the lateral or external surface of the jugal is entirely sculptured, the squamosal (Figs. 4C, D, 6E, F), contained almost entirely within the otic notch, bears no sculpturing whatsoever (Fig. 4C, D). The element is basically semicircular, suturing with the supratemporal dorsally, the postorbital anterodorsally, the jugal anteroventrally, and the quadratojugal ventrally. The bone consists of a large plate that is angled medially towards its posterior end. The size of the otic notch is notable in this taxon, where it extends almost to the orbit anteriorly and far ventrally onto the quadratojugal. This structure, which implies the size of the tympanum, is much larger in proportion to the size of the skull than that observed in *Macroleter* (Tsuji, 2006). As the area of the



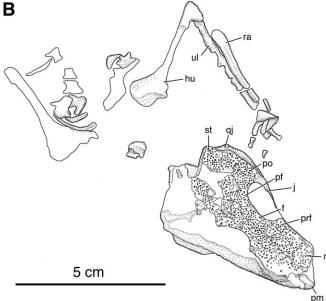


FIGURE 9. *Emeroleter levis*, KPM uncat/E3, anterior portion of skeleton. **A**, photograph, and **B**, drawing in dorsal aspect.

tympanum is related to the effectiveness of hearing (see Müller and Tsuji, 2007), the large tympanum seen in *Emeroleter* suggests that the hearing of this animal was even more acute than that of its close relative.

The quadratojugal (Figs. 4A, B, 5C, D, 6A, B, E, F) of *Emeroleter* is distinct from that of all other nycteroleters. The posterior process of the element tapers, and curves dorsally to form a small horn or spine, an autapomorphy of the taxon (Fig. 5C, D, 6E, F). The quadratojugal is also very long in *Emeroleter*. The ventral part of the element forms the posteroventral margin of the cheek and does not dip below the level of the tooth row, as is the case in *Macroleter* and the pareiasaurs (Lee, 1997b; Tsuji, 2006). Whereas the anterior and ventral-most portions of the element are sculptured, the horn and the dorsal external sur-

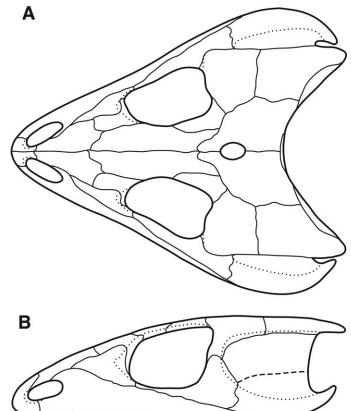


FIGURE 10. Reconstruction of the skull of *Emeroleter levis*. **A**, dorsal, and **B**, lateral views.

10 mm

face are a part of the smooth otic notch, with the sections separated by a noticeable ridge in addition to the change in texture (Fig. 4A, B).

Palate—The palate of *Emeroleter* is known only from two imperfectly preserved specimens so the detailed anatomy of this part of the skull cannot be fully described. In KPM uncat/E2, the hyoid apparatus and other bone fragments, in addition to the fragmentary nature of the palate itself, made it impossible to prepare this area fully. It appears that the field of small denticles present on the vomer, the palatine, and the anterior part of the pterygoid in *Macroleter* is not present in *Emeroleter*.

The vomer (Fig. 6C, D) is mostly obscured in the specimens currently known, but a portion of it can be seen in KPM uncat/E2. A row of small denticles is present on the medial edge of the vomer at the midline suture. The palatine (Fig. 6C, D) is also obscured. It is apparent that the raised row of denticles seen aligned anterolaterally on the pterygoid continue onto the palatine. Details of the morphology of the ectopterygoid cannot be discerned in the available specimens of *Emeroleter*, although a large suborbital foramen, contained between the ectopterygoid, palatine, and jugal can be seen in the dorsal view of the palate (Fig. 4A, B).

Portions of the pterygoid (Figs. 3C, D, 6C, D) have been preserved in KPM uncat/E2 and PIN 2212/92, visible in ventral view, though much of the morphology is still obscured by matrix. The transverse flange of the pterygoid is directed almost entirely laterally, and a row of sharp denticles can be seen lining the ventral

ridge, similar to the condition seen in *Macroleter* (Tsuji, 2006). A prominent row of denticles also lines the interpterygoid vacuity. A portion of the basicranial articulation formed with the parabasisphenoid of the braincase can be seen in PIN 2212/14, and it appears that the two elements are solidly sutured, such that no movement would have been possible between these bones (Fig. 3C, D). This morphology is shared with *Macroleter* and pareiasaurs, and differs from that seen in most other parareptiles where the basicranial articulation is mobile, or at least not tightly sutured (Lee, 1995). No epipterygoids are preserved or visible in any of the specimens of *Emeroleter*.

The pterygoid flange of the quadrate is very long, forming an extensive suture with the pterygoid, with the quadrate lying on the anterior surface of the latter element (Fig. 6C, D). A small sliver of the quadrate is exposed posterolaterally; however, the nature of the condyle for the articulation with the mandible cannot be seen.

Braincase—Known *Emeroleter* specimens comprise skulls that are missing most of the braincase or are prepared in situ with only the dorsal side exposed. Therefore, only a partial description of the braincase elements can be documented.

In parareptiles the parasphenoid and basisphenoid fuse into a single element, termed the parabasisphenoid (Figs. 3C, D, 6C, D). The anterior portion of this element has been preserved in the holotype PIN 2212/92. The general shape resembles an hourglass, with a flared anterior end and a constricted 'waist,' a morphology similar to other derived parareptiles (Carroll and Lindsay, 1985; Tsuji, 2006). As far as can be determined from the available specimens, there is no evidence of a cultriform process. A highly reduced or absent cultriform process is a condition shared with *Macroleter* (Tsuji, 2006), and there is also little evidence for the presence of a long cultriform process in the other nycteroleters (Ivakhnenko, 1997).

The nature of the paroccipital process, formed by the prootic and opisthotic, cannot be determined because the area is obscured by matrix in KPM uncat/E2. The supraoccipital and exoccipitals are also not visible in the available specimens and the basioccipital of KPM uncat/E2 is obscured by elements of the atlas-axis complex.

No stapes is preserved in known specimens of *Emeroleter*. This situation, along with a lack of exposure of other key braincase elements, allows for only limited comparisons with *Macroleter poezicus* regarding hearing ability. However, the large size of the otic notch and the similarity of the tympanic region of the skull and external braincase elements to those of *Macroleter* (Tsuji, 2006) indicate that *Emeroleter* had a very large tympanum, intimating that the latter taxon, like the former, had effective tympanic hearing (Müller and Tsuji, 2007).

Mandible—In specimens where it is present, the mandible of *Emeroleter* remains occluded to the skull. Therefore the morphology of some elements, particularly the medial elements, remains poorly known. The mandible is best preserved in KPM uncat/E2.

In KPM uncat/E2, the mandible is still occluded to the skull, leaving only the ventral and some of the lateral and medial surfaces of the dentary exposed (Fig. 6C, F). The dentary is the only tooth-bearing bone of the mandible, and like the rest of the mandibular elements, it is unsculptured along its length. The dentary constitutes the majority of the external surface of the mandible, with its posteroventral border formed by a long suture with the angular, and its posterodorsal border formed by a suture with the surangular. Medially the dentary is overlapped by the splenial, leaving it with minimal exposure on the ventral surface.

Only a sliver of the splenial (Fig. 6C, D) can be seen in ventral view in KPM uncat/E2. It is sutured to the anterior half of the dentary medially. Matrix and other fragments obscure the symphysis of the lower jaw in internal view, so it is not possible to

discern whether this element is excluded from the symphysis as it is in *Macroleter* (Tsuji, 2006).

The coronoid is not visible in *Emeroleter* specimens, and only a small sliver of the prearticular (Fig. 6C, D) is exposed in KPM uncat/E2 just internal to the angular and immediately anterior to the articular. The surangular (Fig. 6E, F) is long, and likely would have extended beyond the coronoid, as is the case in *Macroleter* (Tsuji, 2006). In KPM uncat/E2, it is possible to see a small shelf projecting laterally at the dorsal edge of the bone (Fig. 6E, F).

The angular (Fig. 6C, F) can be seen externally. It forms most of the posterior portion of the external surface of the mandible. The dorsal edge of the element forms a suture with the surangular, and ventrally (and slightly medially) the angular meets the prearticular. Posteriorly, the angular sutures with the articular (Fig. 6C, D).

A portion of the articular (Fig. 6C, D) is exposed in ventral view in KPM uncat/E2 (Fig. 6C, D). The element lies dorsal and posterior to the prearticular on the internal surface of the mandible, medial (internal) to the surangular and the angular. The bone articulates with the quadrate on the skull, but the nature of this articulation cannot be discerned. It is apparent, however, that the jaw articulation would have occurred at least as far posterior as the occiput.

Hyoid Apparatus-In KPM uncat/E2, the hyoid apparatus is preserved seemingly in place, and is mostly articulated (Fig. 6C, D). This structure has been described in a number of other parareptilian taxa, including the mesosaur Mesosaurus tenuidens (Modesto, 2006), Macroleter poezicus (Tsuji, 2006), some pareiasaurs (Lee, 1995), and the procolophonoids 'Owenetta' kitchingorium (Reisz and Scott, 2002), Sauropareion anoplus (Modesto and Damiani, 2007), and Procolophon trigoniceps (Carroll and Lindsay, 1985). The hyoid complex in parareptiles consists of three parts: the medial copula or corpus hyoideum, and a pair of lateral ceratohyals (or ceratobranchials). In KPM uncat/E2, the elements are well preserved. The copula resembles a bowtie, with a constricted middle and ends that flare laterally; however, in *Emeroleter* it also bears two posteriorly directed processes (Fig. 6C, D), a feature not present in the closely related *Macroleter* (Tsuji, 2006). The lateral ceratohyals (ceratobranchials) of *Emeroleter* are each longer than the copula itself. They are long and thin, with a slightly constricted middle. They appear to have articulated with the copula at its widest lateral section (Fig. 6C, D).

Postcranial Anatomy

The new specimens of *Emeroleter* allow a complete postcranial description of the taxon. The only other published data on nycteroleter postcrania are Chudinov's (1957) descriptions of the partial postcranium of '*Nycteroleter*' (now *Bashkyroleter*) bashkyricus and *Rhipaeosaurus tricuspidens*. The postcranium of *Emeroleter* is very gracile in form, with long and slender limb, carpus, and tarsal elements. It should be noted that the small size and extremely gracile nature of KPM uncat/E1 suggest that this specimen is possibly a subadult, which may have an influence on the nature of some of the observed morphology.

Axial Skeleton—The vertebral column (Figs. 5A, B, 6A, B, 8) of *Emeroleter* is not particularly distinct from that of other known nycteroleters. In KPM uncat/E1, 27 presacral vertebrae are present (Fig. 5A, B). The dorsal vertebrae have the swollen neural arches that are typical for parareptiles, with the postzygapophyses and areas around the neural arch being very well defined. This morphology is similar to that seen in seymouriamorphs (Romer, 1956), and many researchers have included the nycteroleters in the former group because of such morphological similarities. The neural spines of the vertebrae appear to be reduced in *Emeroleter*. In the well-preserved specimen KPM uncat/E1, the structure at the top of the neural arches can be

described as a thin anteroposteriorly directed ridge with only minimal elevation from the body of the neural arch (Fig. 5A, B). This condition is similar to that seen in *Macroleter* (L.A.T., pers. observ.) and seymouriamorphs.

The cervical portion of the vertebral column consists of approximately five or six vertebrae, which are not particularly elongate, and differ little in form from the rest of the dorsal vertebrae. A few elements of the atlas-axis complex are visible in posteroventral view in KPM uncat/E2 (Fig. 7). The paired atlantal neural arches take the form of a tall 'neck,' capped by a laterally projecting flat process. Slightly anterior to this structure is the probable atlantal intercentrum, which is ovoid in ventral view. A small, disarticulated element lying just medial to the atlantal neural arch is identified as the axial intercentrum (Fig. 7). The remaining elements of the atlas-axis complex are not visible.

A portion of the dorsal vertebral column can also be seen in lateral and ventral views in KPM uncat/E2. The centra bear a distinct ventral keel (Fig. 8), thereby differing from the morphology of the other known nycteroleters, e.g., *Macroleter poezicus* (Cisneros and Tsuji, 2009; L.A.T., pers. observ.), and demonstrating that the ventral part of the centrum lacking a keel is not a universal character among the nycteroleters.

Whereas the entire tail of *Emeroleter* is not preserved, in KPM uncat/E1 (Fig. 5A, B), what could possibly be the terminal caudal vertebra is preserved. The middle section of the tail is missing (and reconstructed in plaster) but the proximal and distal ends are preserved seemingly in place. In an approximate measurement, the tail is actually one-third longer than the presacral vertebral column, although the length of the missing vertebrae are only estimated, and an assumption has been made that the terminal section of the tail did not drift markedly from the anterior portion. However, considering the complete unaltered state of the rest of the skeleton, including the complete articulation of the manus and pes, this interpretation is reasonable.

The ventral aspect of the vertebral column is visible in KPM uncat/E2 such that the intercentra (Fig. 8) are also visible. These elements are similar in morphology to those of other known nycteroleters including *Macroleter* and the nycteroleter from South Africa (Cisneros and Tsuji, 2009), and are also similar to those of *Procolophon* (deBraga, 2003). The intercentrum is an elongated oval with pointed lateral ends, and was likely wedge-shaped in lateral view (Fig. 8).

A distinct sulcus is present on the ribs (Figs. 5A, B, 8) of *Emeroleter*, but they are otherwise fairly conservative. The heads of the ribs are broad (tall), bear holocephalus (single-headed) articulations with the vertebrae, and curve gently posteriorly. The presence of a lumbar region, with posterior dorsal vertebrae lacking ribs is a character that has been considered a synapomorphy of nycteroleterids (Lee, 1995), and this condition is also confirmed in KPM uncat/E1 and KPM uncat/E2. The posterior ribs are significantly shorter and more severely recurved than those around the anterior portion of the presacral vertebral column. There are approximately seven or eight posterior dorsal vertebrae that do not bear ribs (Figs. 5A, B, 8) and are here termed lumbar vertebrae.

The preservation and careful preparation of KPM uncat/E2 in oblique ventral view allows for the observation of gastralia (Fig. 8) in *Emeroleter*, and gastralia-like structures can also be seen in KPM uncat/E1 (Fig. 8). Although certainly not complete, a series of very thin rod-like structures lie ventral to the ribs, close to the vertebral column. Although gastralia are common structures in many Paleozoic anamniote tetrapods (Romer, 1956; Witzmann, 2007), they are not present as consistently in amniotes of the same age. Among parareptiles, gastralia have been described in *Mesosaurus tenuidens* and *Stereosternum tumidum* (Modesto, 1999, 2010), *Milleretta rubidgei* (Gow, 1972), and *Procolophon* (deBraga, 2003), but are seemingly absent in pareiasaurs. There is also no evidence of their presence in *Nyctiphruretus* or *Macro-*

leter (L.A.T., pers. observ.), although as they are such fine structures, they can easily be prepared away.

Appendicular Skeleton—The appendicular skeletal elements of *Emeroleter levis* are gracile, but relatively long in comparison with body size, particularly the elements of the manus and the pes. The lower limb is especially atypical for parareptiles in its proportions.

Portions of the scapulocoracoid are preserved in KPM uncat/E1. An element identified as a cleithrum can be seen lying along the anterior edge of the scapular blade (Fig. 5A, B). It is prominent, but does not cap the scapula anterodorsally as it does in the closest outgroups to Amniota, diadectomorphs and *Seymouria* (Laurin and Reisz, 1995). The scapula itself is long and thin, consisting of a flat plate of bone that flares only slightly at its dorsal end. There appears to be a small acromion process on the anterior part of the scapular blade, visible in KPM uncat/E1 (Fig. 5A, B).

Part of the left clavicle (Fig. 6A, B) can be seen in KPM uncat/E2, originating ventral to the vertebral column and then curving upwards and backwards where it would have attached to the scapula (Fig. 6A, B). The interclavicle is not exposed or preserved in any of the specimens of *Emeroleter*.

The humerus (Figs. 5A, B, 8, 9) of *Emeroleter* is very gracile, with the distal end only slightly flared. The ends are twisted at about 45° to each other. The proximal end is flared, and is much larger than the distal (Fig. 9). There does appear to be a groove representing the entepicondylar foramen seen in KPM uncat/E1, though the exact morphology is not clear as the entepicondylar foramen can be seen on the dorsal-most part of the anterior side of the bone (Fig. 5A, B).

The radius (Figs. 5A, B, 8, 9) is very long and gracile. It flares very slightly at the proximal end, but otherwise has very few features of note other than its extreme thinness.

The ulna (Figs. 5A, B, 8, 9) cannot be seen from all angles and is not completely exposed in any specimen. It is apparent, however, that the olecranon in specimen KPM uncat/E1 is not particularly tall or pronounced, with no noticeable sigmoidal notch (Fig. 5A, B), with which it would articulate with the trochlear condyle of the humerus. This articular surface appears to be restricted to the proximal end of the element in this specimen of *Emeroleter*, though the small size of the olecranon may also be an indication that this specimen could be subadult.

The manus (Figs. 5A, B, 6A, B) is relatively large, but also relatively robust in form. The elements of the proximal carpus are relatively large and appear to be fairly well defined. In KPM uncat/E1, there is a proximal element, most likely the ulnare, which is almost square in shape. A smaller, more medial element is most likely the intermedium (Fig. 5A, B). The entire manus appears to be mostly preserved in KPM uncat/E2, but the manus and the pes are overlapped so it is difficult to determine which element belongs to which (Fig. 6A, B). The metacarpals of Emeroleter are relatively slender compared to the condition seen in other derived parareptiles such as *Procolophon* (deBraga, 2003) and even the closely related Macroleter (L.A.T., pers. observ.), with a length more than 3 times the width. The phalanges are also relatively slender, being more than twice as long as wide, a condition that contrasts sharply with other derived parareptiles such as *Procolophon* and pareiasaurs (Boonstra, 1929). The probable manual phalangeal formula is 2-3-4-?5-3, which is typical for nonpareiasaurian parareptiles (Lee, 1995). The terminal phalanx of the manus takes the form of a claw and is not specialized in form.

The femur (Figs. 5A, B, 8) of *Emeroleter* is particularly long and gracile, with a slight sigmoidal curve evident in the shaft (Fig. 5A, B), similar to that seen in araeoscelidians (Sumida, 1997). The proximal end is also curved noticeably, with the head directed slightly medially and anteriorly. The morphology of the femur of *Emeroleter* differs significantly from that of

Rhipaeosaurus, which has a relatively robust shaft and widely flaring proximal and distal ends (Chudinov, 1957).

The tibia (Figs. 5A, B, 8) of *Emeroleter* is extremely long and gracile compared to other closely related parareptiles. There is no evidence of the presence of a significant cnemial crest. The expansion of the proximal end of the element where it articulates with the femur is also highly reduced (Fig. 5A, B).

The fibula (Figs. 5A, B, 8) is also very slender and elongate, with neither the proximal nor distal ends more than minimally expanded, contrasting with the more typical, robust basal reptilian form (Romer, 1956). The element is slightly shorter than the tibia in length, and is only slightly more slender. The ends of the bone are squared off, similar in form to the diapsid *Araeoscelis*, which also shares similar proportions of the tibia and the fibula (Reisz et al., 1984).

The pes (Figs. 5A, B, 6A, B, 8) is noticeably larger than the manus. In KPM uncat/E1, it appears that the astragalus and the calcaneum are either very closely sutured (in smaller individuals), or fused (in larger individuals), the condition present in *Macroleter* and also in pareiasaurs (Lee, 1995; Tsuji, 2006). The third and fourth distal tarsals are closely sutured and appear to form one larger element (Fig. 5A, B). The remaining distal tarsals are suboval and smaller. The metatarsals are elongate, and much longer than the phalangeal elements. The fourth metatarsal is the longest. The phalangeal formula of the pes is 2-3-4-?5-3, which is very close to 2-3-4-5-4, the most common count among early amniotes, and unlike the reduction of the phalangeal elements seen in pareiasaurs (Laurin and Reisz, 1995). Digit IV appears to be the longest. The metatarsals are much longer than the phalanges.

COMPARATIVE REDESCRIPTION OF OTHER RUSSIAN NYCTEROLETER PARAREPTILES

Only specimens of *Macroleter* and *Rhipaeosaurus*, along with a poorly preserved specimen of *Bashkyroleter bashkyricus*, have identifiable and associated postcrania, the whereabouts of which are currently known. In addition, other than *Macroleter poezicus*, none of the nycteroleter parareptiles have been described in a modern phylogenetic context, nor have they been defined autapomorphically. What follows is a comparative description of the Russian nycteroleter taxa.

SYSTEMATIC PALEONTOLOGY

AMNIOTA Haeckel, 1866 REPTILIA Laurenti, 1768 PARAREPTILIA Olson, 1947 NYCTEROLETER Efremov, 1938 NYCTEROLETER INEPTUS Efremov, 1938 (Fig. 11A)

Revised Diagnosis—*Nycteroleter ineptus* (Fig. 11A) is a parareptile with a low, elongate, triangular skull that is slightly wider posteriorly. It bears concavities along the lateral sutures of the parietal. Sculpturing typified by small, round pits, but differentiated from *Emeroleter* by their more inconsistent placement. Skull table flat in lateral view. Maxilla bears around 30 teeth.

Holotype—PIN 158/9, lost (Ivakhnenko, 1997).

Referred Specimens—PIN 3706/5, partial skull; PIN 3706/14, complete skull with lower jaw; PIN 104B/2005, partial skull.

Locality and Horizon—Mezen River Basin, Arkhangel'sk Province, Russia. Uppermost Kazanian or lowermost Tatarian, middle Permian (Ivakhnenko et al., 1997).

Notes—*Nycteroleter* was the first taxon of this group to be named. As noted above, the holotype specimen has since been lost.

Comparative Description—*Nycteroleter* is known only from the cranium. The skull is subtriangular, but slightly elongate with a relatively pointed snout and large, posteriorly emarginated or-

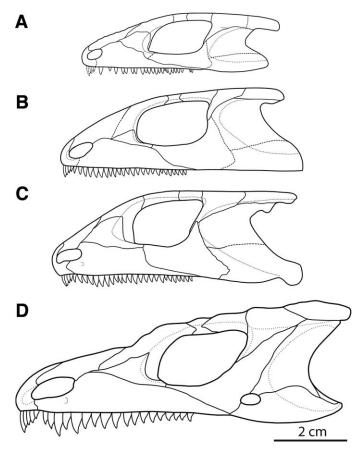


FIGURE 11. Reconstructions of nycteroleter skulls in lateral view. **A**, *Nycteroleter ineptus*, **B**, *Bashkyroleter bashkyricus*, **C**, '*Bashkyroleter mesensis*, and **D**, *Macroleter poezicus*. Based on Müller and Tsuji (2007).

bits, and a relatively low profile. Sculpturing of the dermal skull roof consists of closely spaced round pits with very little flat space in between, similar to that of *Emeroleter*, but the diameter of the pits in *Nycteroleter* is generally larger, and the surface of the skull roof is slightly textured, not smooth and flat as it is in *Emeroleter*. The temporal area and ventral cheek margin are incompletely known, but it appears that the otic notch is large, and the cheek is unfenestrated. The taxon has a higher number of maxillary teeth than all other nycteroleters except for *Emeroleter*, with the size of the teeth slightly increasing anteriorly, and the anterior-most teeth being slightly recurved.

RHIPAEOSAURUS TRICUSPIDENS Efremov, 1940

Revised Diagnosis—A large nycteroleter parareptile. Distinguished by the presence of slightly flattened, tricuspid teeth. Differentiated from other nycteroleters in its significantly larger size and associated increased robustness of the limb elements.

Holotype—PIN 164/2, mostly complete skeleton with partial skull consisting primarily of lower jaw.

Locality and Horizon—Belebey, upper Kazanian, middle Permian, Russia.

Notes—*Rhipaeosaurus* is the largest of the nycteroleters, and is known exclusively from the holotype specimen. Although Chudinov (1957) described a significant amount of material of this taxon, some of the holotypic material is missing or severely damaged, including the jaw fragments preserving the eponymous tricuspid teeth.

Comparative Description—Very little of the cranial anatomy of *Rhipaeosaurus* is known, but the dimensions of the postcranial elements indicate that it is the largest of the nycteroleters. What little is known of the cranium of the taxon, including the autapomorphy of the presence of tricuspid teeth, cannot be confirmed due to either degradation of the specimen or loss of key elements. The postcranium appears to be very similar to what is known for *Macroleter poezicus*, and a more detailed comparison of these two taxa may reveal a closer relationship between the two. As mentioned above, the astragalus and the calcaneum are two separate elements in *Rhipaeosaurus*, although they are closely sutured.

BASHKYROLETER Ivakhnenko, 1997 BASHKYROLETER BASHKYRICUS (Efremov, 1940) (Fig. 11B)

Revised Diagnosis—*Bashkyroleter bashkyricus* (Fig. 11B) is a parareptile with a slightly flattened, triangular skull, and a slightly rounded snout. Lower cheek margin extends posterior to skull table. Tooth number in the maxilla is 23–24. Sculpturing consisting of small rounded pits with flat areas in between sometimes raised into small bumps, giving the skull an uneven appearance.

Holotype—PIN 164/3, skull with lower jaw, disarticulated postcranium (whereabouts of postcranium unknown, having been separated from skull).

Referred Specimens—PIN 164/60, partial skull; PIN 164/4, partial postcranium.

Locality and Horizon—Belebey, upper Kazanian, middle Permian, Russia.

Note—Bashkyroleter bashkyricus was initially described as a species of the genus Nycteroleter (Efremov, 1940) and was assigned to a new genus following the discovery of B. mesensis, and the closer relationship between these two taxa was posited (Ivakhnenko, 1997). In addition to the cranial material, a small amount of postcranial material exists for this taxon (Chudinov, 1957).

Comparative Description—Bashkyroleter bashkyricus is known from only two specimens comprising cranial material, one of which is a poorly preserved partial skull. In general, the skull is relatively broad posteriorly compared to N. ineptus, and the posterior end of the quadratojugal extends posterior to the posterior-most extent of the supratemporals, a condition shared only with 'B.' mesensis. The orbits are large, but smaller in proportion to skull length than in *Emeroleter* and *Nycteroleter*. The anterior part of the maxilla retains some of its width in dorsal view, imparting a slightly rounded appearance to the snout. Similar to 'B.' mesensis, the suture between the maxilla and the lacrimal has a noticeable vertical 'step' partway along the suture, increasing dramatically in height over a short distance, rather than showing a gradual increase. There is a preserved partial postcranium of this taxon, though not much detail can be discerned. As in the other known nycteroleter taxa, there appear to be no ribs attached to the posterior dorsal vertebrae, though this condition could also be preservational in this case. PIN 164/4 shows that gastralia were present in this taxon.

'BASHKYROLETER' MESENSIS Ivakhnenko, 1997 (Fig. 11C)

Revised Diagnosis—'Bashkyroleter' mesensis (Fig. 11C) is a small parareptile with a skull that is almost an isosceles triangle in outline. Sculpturing consists of round pits of varying depths and sizes, which are more numerous in the area of the nasal and anterior edges of the frontal. Pits are present on parietal, postfrontal, and postorbital. Differs from the type species of this genus in the more circular parietal foramen, possessing larger and more elongated orbits, and morphology of sculpturing.

Holotype—PIN 162/30, almost complete skull.

Referred Specimens—PIN 3706/5, partial skull; PIN 3586/17, partial skull; PIN 3717/27, anterior part of juvenile skull; PIN 4541/3, partial skull; PIN 4541/4, partial skull.

Locality and Horizon—Mezen River Basin, Arkhangel'sk Province, Russia. Uppermost Kazanian or lowermost Tatarian, middle Permian (Ivakhnenko et al., 1997).

Note—The validity of 'Bashkyroleter mesensis' has been questioned based on the results of the first phylogenetic analysis to include the nycteroleters (Müller and Tsuji, 2007). A second analysis also indicated that the genus is in fact paraphyletic (Tsuji et al., 2010). As B. bashkyricus is the type species of the genus, 'B.' mesensis is here only provisionally assigned to Bashkyroleter, awaiting further analysis.

Comparative Description—'B.' mesensis is known from a number of well-preserved specimens, though all consist of cranial material only. The skull is triangular with a slightly rounded snout, slightly 'swollen' anterior to the orbits, and the skull is higher than that of other nycteroleters. The orbits are comparatively larger than those of B. bashkyricus. Sculpturing consists of round pits that are in general larger, shallower, and more diffuse than those of *Emeroleter* or *Nycteroleter*. The otic notch is large, with its anterior-most extent just ventral to the severe undercut of the dermal skull roof, similar to the condition seen in *Emeroleter*, and contrasting the condition seen in B. bashkyricus, where the otic notch reaches its anterior-most extent midway up the cheek. The maxilla has the same 'step' as in B. bashkyricus. As in Emeroleter, the maxilla forms all of the posterior and part of the dorsal edge of the naris. The quadratojugal extends slightly posterior to the skull table as it does in B. bashkyricus, but to a lesser extent than this latter taxon. The teeth of 'B.' mesensis differ significantly in size, and the posterior teeth tend to have slightly expanded crowns.

MACROLETER POEZICUS Tverdokhlebova and Ivakhnenko, 1984 (Fig. 11D)

Tokosaurus perforatus Tverdokhlebova and Ivankhnenko, 1984.

Revised Diagnosis—*Macroleter poezicus* (Fig. 11D) is a medium-sized parareptile that can be distinguished by the following cranial autapomorphies: basicranial articulation involving basipterygoid processes facing directly forward, with pterygoids meeting anterior to the articulation; sculptureless, round indentation centered just anterior to the fronto-parietal suture; posterior portion of the median suture between the two parietals highly depressed, giving the back of the skull roof a 'V'-shaped outline in occipital view.

Holotype—PIN 3586/1, an entire skeleton.

Referred Specimens—PIN 4543/3, mostly complete skull and postcranial material; UTM/Mezen/2001/1, complete skull and postcranial material; UTM/Mezen/2001/2, large skull, some postcranial material; UTM/Mezen/2001/3, skull and postcranial material anterior to pelvic girdle.

Locality and Horizon—Mezen River Basin, Arkhangel'sk Province, Russia. Uppermost Kazanian or lowermost Tatarian, middle Permian (Ivakhnenko et al., 1997).

Note—The cranial anatomy of *Macroleter poezicus* has been described in detail (Tsuji, 2006), and the description of some specimens preserving postcranial material is currently underway.

Comparative Description—The cranial anatomy of *Macroleter* is well known, and a growth series for the skull of this taxon exists (L.A.T., pers. observ.), but remains undescribed. *Macroleter* is larger than any of the nycteroleters described above. Overall, the skull is triangular, with a slightly rounded snout. The sculpturing of the taxon also consists of circular pits, though the size and space between them are generally greater than in other nycteroleter taxa. *Macroleter* also has small raised bosses present on the circumorbital elements of the skull. It is the only known

nycteroleter to possess temporal fenestration, in the form of a small, round fenestra contained between the jugal, the quadratojugal, and the squmosal. Some of the maxillary teeth have grooves running from the base of the tooth towards the crown (Tsuji, 2006). The postcranium is very similar to that known for *Rhipaeosaurus tricuspidens*, but the astragalus and calcaneum have fused in largest specimens of *Macroleter*, whereas these are separate, though closely attached elements in *Rhipaeosaurus* (L.A.T., pers. observ.).

Note—*Tokosaurus perforatus* was named by Tverdokhlebova and Ivakhnenko (1984) in the same publication as Macroleter poezicus. Tokosaurus was defined by the autapomorphies of a triangular temporal fenestra being present between the jugal and the quadratojugal, a slight difference in the shape and orientation of the otic notch, and the orientation of the quadrate bone. Upon recovery of more specimens of *Macroleter poezicus*, it has become clear that this taxon also has a small temporal fenestra that is contained between the jugal and the quadratojugal with a small dorsal contribution from the squamosal (Tsuji, 2006). The slight differences in the shape and angle of the otic notch can be attributed to preservational and ontogenetic factors, and the orientation of the quadrate does not differ sufficiently from that of Macroleter to justify placing this specimen (and a fragmentary referred specimen) in a distinct taxon. Therefore, Tokosaurus is declared to be a junior synonym of Macroleter poezicus. It is important to note that the two taxa are found in different regions— Macroleter in the Mezen Basin, whereas 'Tokosaurus' is found in the Orenburg region, which belongs to the Ocher subassemblage. Although this implies that they belong to two different faunas, these faunas are considered to be contemporaneous (Golubev, 2005).

PHYLOGENETIC ANALYSIS OF THE 'NYCTEROLETER' PARAREPTILES

Methods

Nycteroleters were first included in a phylogenetic analysis by Lee (1993). Before the inclusion of *Macroleter* in a phylogenetic analysis by deBraga and Rieppel (1997), only Nycteroleter ineptus was sufficiently known, and Nycteroleteridae was sometimes included as a single taxon, although most of the morphological information was based on Nycteroleter. The first analysis to contain the majority of the nycteroleter taxa was published by Müller and Tsuji (2007), and the first to use Bayesian analysis involved a variation of this matrix (Tsuji et al., 2010). Interestingly, the Bayesian analysis resulted in a slightly different topology than the parsimony tree with regards to the interrelationships of the nycteroleters. Rather than forming a monophyletic group, Macroleter poezicus and Tokosaurus perforatus (above considered a single taxon) were sister taxa to a monophyletic Pareiasauria, with the other nycteroleters forming a monophyletic clade sister to the Macroleter/Tokosaurus-pareiasaur clade. This result is intriguing, and the authors suggested that it may be caused by the lack of available postcranial information for the majority of the nycteroleters (Tsuji et al., 2010). Thus, the addition of postcranial data from Emeroleter has the potential to have a significant effect on the reported topology.

With the information derived from the morphological study of the new fossils described above, *Emeroleter levis* was rescored and included in the matrix of Tsuji et al. (2010). The other nycteroleter taxa were also reconsidered and rescored where appropriate, and *Rhipaeosaurus tricuspidens* was included for the first time in a phylogenetic analysis despite the incompleteness of the material. As described above, *Tokosaurus perforatus* is now considered to be a juvenile form, and a junior synonym of *Macroleter poezicus*.

The character matrix from Tsuji et al. (2010) was used as the basis for the reanalysis of parareptilian relationships.

Tokosaurus was removed from the matrix due to its synonymy with Macroleter as stated above, and Rhipeaosaurus tricuspidens was added. Emeroleter levis was rescored based on anatomical information gleaned from new material and a reexamination of previously described specimens. The matrix consists of 30 taxa (one outgroup taxon, Seymouria, and 29 ingroup taxa: Limnoscelidae, Diadectidae, Synapsida, Captorhinidae, Paleothyris, Araeoscelidia, "Younginiformes, Mesosauridae, Eunotosaurus, Millerettidae, Australothyris, Microleter, Nyctiphruretus, Eudibamus, Belebey, Acleistorhinus, Lanthanosuchus, Bradysaurus baini, Pareiasuchus peringueyi, Scutosaurus, Procolophon, Owenetta, Barasaurus, Macroleter poezicus, Bashkyroleter bashkyricus, 'Bashkyroleter' mesensis, Nycteroleter ineptus, Emeroleter levis, Rhipaeosaurus tricuspidens) and 136 parsimony-informative characters (list of characters, Appendix 1; character matrix, Appendix 2) were used in the analysis. Mesquite (Maddison and Maddison, 2009) was used to modify the matrix and prepare the data to be implemented into TNT. The analysis was completed using TNT (Goloboff et al., 2008), with 10,000 random addition sequences, using a heuristic search with all characters weighted equally and all characters unordered. A bootstrap analysis was also run in TNT with 5000 replicates to get some measure of support for the resulting topology.

Secondly, two Bayesian analyses of the same character matrix (Appendix 2) were performed using Mr Bayes version 3.2 (Ronquist and Huelsenbeck, 2003), both applying the Mk model, in accordance with Lewis (2001), consisting of 2,000,000 generations, sampled every 100th generation, with a burn-in of 2000 sampled trees, four chains and two runs, and a temperature of 0.2. The outgroup taxon was specified as Seymouria. Autapomorphies were not included in the analysis. The first Bayesian analysis implemented a gamma-shape parameter, whereas the second did not. The Bayes factor for each of these models was calculated using the method described by Kass and Raftery (1995) in order to determine which model of the two best fitted the data. Within each analysis, the runs of the differing models were compared for fit to the data by comparing the Bayes factor of the individual runs. The Bayes factor is a means of calculating the posterior probability that one of two theories is preferred given the data (Kass and Raftery, 1995), and is a generally accepted method of choosing between two models used in a Bayesian analysis. Though a number of methods have been developed for the calculation of the Bayes factor, some quite complex (Wasserman, 2000; Lartillot and Philippe, 2006), the calculation of the Bayes factor is most often done using the marginal likelihood estimation procedure, which involves comparing the estimation of the harmonic means of the two analyses. The difference between the log of the harmonic means of the analyses in question is then compared to a chart (found in Kass and Raftery, 1995) that assesses the probability of the data providing evidence against the null hypothesis (that no one method better explains the data than the other) (Kass and Raftery, 1995).

Results

Parsimony—Six equally most parsimonious topologies were found in the analysis, each consisting of 421 steps. The consistency index (CI) is 0.404, and the retention index (RI) is 0.679. Whereas all taxa considered nycteroleters (Nycteroleteridae) remained monophyletic, there is very little resolution within the group, with *Macroleter poezicus* appearing as the sister taxon to the other nycteroleters, which form an unresolved polytomy. The bootstrap shows very little support for the nodes within Parareptilia, with very few branches being recovered in 50% or more of the bootstrap replicates (Fig. 12).

A node comprising the nycteroleterids and pareiasaurs was recovered, which has also been recovered in all other recent

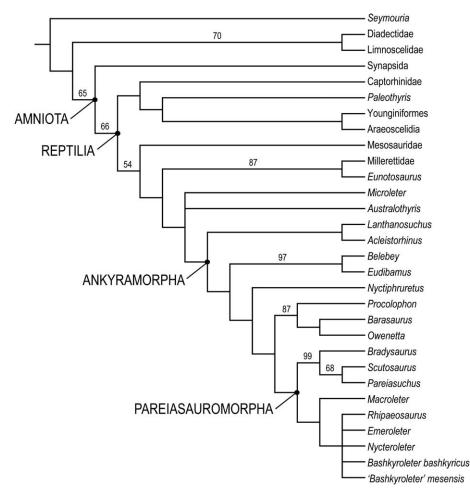


FIGURE 12. Strict consensus of the six most parsimonious topologies recovered from parsimony analysis of parareptilian relationships. Bootstrap support values above the branch leading to the node, listed when value is over 50%.

analyses of Parareptilia (Tsuji, 2006; Müller and Tsuji, 2007; Tsuji et al., 2010). Here this node is termed 'Pareiasauromorpha.' The taxon *Nyctiphruretus* also falls just outside of the clade consisting of procolophonoids and pareiasauromorphs, with bolosaurids and lanthanosuchids forming successive outgroups.

Bayesian—The results of each run of the Bayesian analysis is presented as a single topology consisting of a summary of the nodes resulting from the search. Both analyses recover Pareiasauromorpha, a monophyletic clade comprising the pareiasaurs and the 'nycteroleter' taxa, but similar to the topology recovered in the previous analysis of parareptile relationships using a Bayesian methodology (Tsuji et al., 2010), however, the 'nycteroleters' grade into the pareiasaurs rather than forming a clade. Rhipaeosaurus is the most basal member of the group, with 'B.' mesensis and Emeroleter forming a sister-group relationship, and B. bashkyricus and Nycteroleter forming another, and *Macroleter* constituting the sister taxon to pareiasaurs (Fig. 13A, B). In both Bayesian analyses Nyctiphruretus falls out basal to bolosaurids, but more derived than lanthanosuchids. The posterior probabilities of the clades are also not very high for many of the nodes. Although the placement of nycteroleter taxa is consistent between the two analyses, there are significant differences in the position of the more basal taxa between the analysis that used the gamma parameter (Fig. 13A) and the one that did not (Fig. 13B), and also differences in the posterior probabilities supporting nodes common between the two. Also, bolosaurids are the first outgroup to the clade comprising procolophonoids and pareiasauromorphs in the analysis using the gamma parameter (Fig. 13A), whereas bolosaurids actually form a clade with procolophonoids in the analysis without gamma (Fig. 13B). The log harmonic mean of the analysis in which the gamma-shaped parameter was applied is -1561.85, and -1572.46 with no model. Two times the difference between the two is 21.22, which implies that the iteration with the gamma parameter applied is strongly preferred for the present data set (against chart in Kass and Raftery, 1995).

DISCUSSION

Phylogenetic Analysis

The results of the phylogenetic analyses emphasize a lack of resolution—perhaps reflective of a lack of anatomical data—of the various taxa within Parareptilia. Whereas the addition of poorly known taxa such as *Rhipaeosaurus* adds more data into the analysis, the condition and the inability to score many characters for the taxon appears to make it ambiguous and also adds more uncertainty. It has been documented that a lack of resolution in phylogenetic analysis depends more on the number of characters that have been completely scored within taxa rather than on absolute missing data (Wiens, 2003). In this case, it is hoped that new material will help to further resolve some of the more ambiguous relationships.

The larger issue within the analysis is the topologic difference between the maximum parsimony and Bayesian analyses, in particular the relationships within the 'nycteroleters' and their relationship to Pareiasauria. The results of the Bayesian analysis

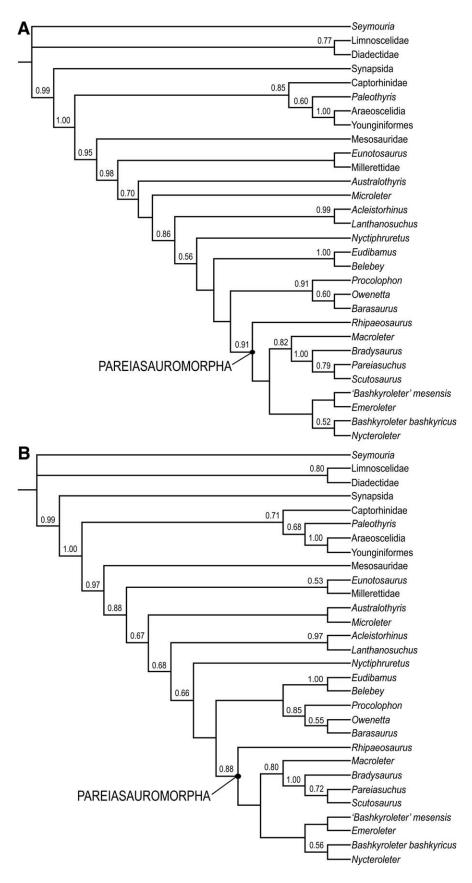


FIGURE 13. Cladogram of parareptilian relationships resulting from Bayesian analysis. **A**, with, and **B**, without application of a gamma parameter. Posterior probabilities above 0.5 listed on the branch leading to the node.

are not particularly surprising because there are certainly clear similarities between Macroleter poezicus and pareiasaurs (Tsuji, 2006). In the first Bayesian analysis of parareptilian relationships, Tsuji et al. (2010) suggested that the lack of information about the postcranium of other nycteroleters might have had an effect on the differences in topology, with *Macroleter* affiliating more closely with the pareiasaurs based solely on the presence of shared postcranial characters that could not be scored for the other nycteroleters. The addition of postcranial characters of Emeroleter appears, however, not to have affected the divergence between the parsimony and Bayesian topologies in the current analysis. The analyses are also on the whole equivocal regarding the paraphyly of the genus Bashkyricus, with the parsimony analysis not resolving any relationships between the nycteroleters other than Macroleter, and the Bayesian analysis suggesting only a poorly supported paraphyly of the genus. There is also a considerable difference in the analyses regarding the placement of Nyctiphruretus and its relationship to the more derived parareptiles (Procolophonoidea + Pareiasauromorpha), a result consistent with the recent redescription and phylogenetic analysis of the taxon (Säilä, 2010a). The only hope to find greater congruence between the two types of analyses is to include more data (more taxa and more characters as well finding additional fossils of known taxa with new morphological information) and to see if the topologies converge.

Nomenclatural Issues with the Nycteroleters

The present analysis of relationships using parsimony, including all adequately known nycteroleter parareptiles, appears to confirm their monophyly, whereas the Bayesian analysis indicates that they are paraphyletic. The conflicting topologies resulting from the two different methods of analysis have definite implications for the taxonomy of this group. Although inclusion of data from one taxon not included in the analysis (Macroleter agilis) may yet result in a convergence of the two topologies, as it currently stands, it is not possible to pick one result or method over another. The possibility that the nycteroleters grade into pareiasaurs as suggested by the Bayesian analysis makes the naming of the group awkward. Thus, we propose that the informal grouping, 'nycteroleters,' be retained to refer to the group of animals described herein, with the understanding that this might refer to a paraphyletic assemblage of taxa. A more inclusive taxon, Pareiasauromorpha, is used here for the monophyletic clade including Pareiasauria and the 'nycteroleters,' sister taxon to the Procolophonomorpha (Figs. 12, 13).

The Bayesian results also seem to confirm those of previous analyses, which suggest that the species of 'Bashkyroleter' (B. bashkyricus and B. mesensis) are paraphyletic, implying that one of the taxa requires a nomenclatural change. Because Bashkyroleter bashkyricus is the type species of the genus, it would retain the name and a new genus name should be created for 'Bashkyroleter' mesensis. However, these groupings are not very well supported, and for the time being we refrain from naming a new genus.

Locomotion and Lifestyle in Emeroleter levis

Emeroleter levis appears to be a very specialized form: the large size of the head in relation to the rest of the body, extremely gracile limbs, and long tail suggest a lifestyle different from that of many other parareptiles, including those to which it is most closely related. The very robust limbs and probable graviportal posture of pareiasaurs suggest a slow-moving habit (Romer, 1956), and certain derived procolophonids, including Procolophon (deBraga, 2003) and Leptopleuron (Säilä, 2010b), have been shown to possess specialized burrowing anatomy. The

femur and the humerus of *Emeroleter* are very gracile, with the shaft of the femur bearing a slightly sigmoid curve. This morphology is different from the postcranial skeleton of other known nycteroleters, namely Macroleter and Rhipaeosaurus, which are much more robust, though this difference could also be due in part to scaling; in general, larger animals tend to have more robust limb elements (Christian and Garland, 1996). The high ratio of the epipodial (lower limb segment) to the propodial (upper limb segment) (0.89 front, 1.08 hind) suggests certain rapidity of movement was present in *Emeroleter*, with nearly equal 'moment arms' for acceleration (Moermond, 1979), and indeed an increased length in the tibia in relation to femur and metatarsal length is correlated with increased sprint speed in modern Anolis (Vanhooydonck et al., 2006). This ratio is higher in Emeroleter than in other parareptiles such as Macroleter, pareiasaurs, and *Procolophon*, and is a ratio and morphology more similar to the diapsid Araeoscelis (Reisz et al., 1984).

The extremely large otic notch implies the presence of a large tympanum in Emeroleter, even compared to other nycteroleters such as Macroleter. This morphology indicates an enhanced ability to hear compared to its close relatives, because the effectiveness of impedance matching is a relationship between the size of the footplate of the stapes and the area of the tympanum (Hemilä et al., 1995; Müller and Tsuji, 2007). Although other elements necessary to confirm the presence of impedance-matching hearing cannot be directly observed in *Emeroleter*, the overall similarity of this animal to *Macroleter* implies that these elements were also present in the former taxon. It has been suggested that the origin of the tympanic ear in this group arose out the necessity for hearing prey (Müller and Tsuji, 2007), for better perception of sounds such as the 'buzzing' of insects (Clack, 1997, 2002). The apparent prominence of a hearing ability in *Emeroleter* combined with other features, such as palatal dentition and the possession of small, sharp marginal teeth, are strong indicators of an insectivorous diet (Modesto et al., 2009). This lifestyle differs quite considerably from that of pareiasaurs, but appears to be similar to many other Permian parareptiles (Modesto et al., 2009). The lightly built skeleton of *Emeroleter* indicates it was capable of relatively high speeds, and its sensitive hearing combined with the presence of relatively large orbits seem to support the inference of a nocturnal habit, a lifestyle already proposed for other members of the group (Müller and Tsuji, 2007).

CONCLUSION

The nycteroleters are a group of primarily Russian parareptiles that have been known since the first half of the 20th century, but only recently has their diversity and importance been recognized. Emeroleter levis is perhaps the most distinctive member of this group. New, well-preserved specimens from the Kotel'nich locality, including for the first time postcranial material, allow a more complete description of the taxon. Along with its distinctive sculpturing and relatively gracile postcranial skeleton, Emeroleter appears to have been a relatively fast-moving insectivore, one that was possibly nocturnal in habit. A comparative redescription of the Russian nycteroleters results in the synonymy of Tokosaurus perforatus with Macroleter poezicus. With all adequately known nycteroleter taxa included in a phylogenetic analysis for the first time, resolution among the members of the group still remains rather poor and conflicting parsimony and Bayesian topologies only add to the ambiguity, with the Bayesian analysis not supporting the monophyly of the clade. Despite more intensive research, however, the 'nycteroleters' as a whole still remain enigmatic, and further study of the postcranial anatomy of Macroleter poezicus and a more intensive study of Macroleter agilis from the Permian of Oklahoma can perhaps more fully resolve their relationships.

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LITERATURE CITED

- Boonstra, L. D. 1929. Pareiasaurian studies. Part III. On the pareiasaurian manus. Annals of the South African Museum 28:97–112.
- Bulanov, V. V. 2002. Karpinskiosaurus ultimus (Seymouriamorpha, Parareptilia) from the Upper Permian of European Russia. Paleontological Journal 36:72–79.
- Carroll, R. L., and W. Lindsay. 1985. Cranial anatomy of the primitive reptile *Procolophon*. Canadian Journal of Earth Sciences 22:1571– 1587
- Christian, A., and T. Garland Jr. 1996. Scaling of limb proportions in monitor lizards (Squamata: Varanidae). Journal of Herpetology 30:219–230.
- Chudinov, P. K. 1955. [Cotylosaurs of Russia]. Doklady Akademii Nauk SSSR 103:913–916. [Russian]
- Chudinov, P. K. 1957. [Cotylosaurs from the Upper Permian redbeds deposits of the preurals]. Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR 68:19–87. [Russian]
- Chudinov, P. K., and B. P. V'yushkov. 1956. [New data on small cotylosaurs from the Permian and Triassic of the USSR]. Doklady Akademii Nauk SSSR 8:547–550. [Russian]
- Cisneros, J. C., and L. A. Tsuji. 2009. Nycteroleter affinities of a Permian parareptile from the South African Karoo Basin. Acta Palaeontologica Polonica 54:165–169.
- Clack, J. A. 1997. The evolution of tetrapod ears and the fossil record. Brain, Behaviour, and Evolution 50:198–212.
- Clack, J. A. 2002. Gaining Ground: The Origin and Evolution of Tetrapods. Indiana University Press, Bloomington and Indianapolis, Indiana, 369 pp.
- Coffa, A. A. 2007. The Kotelnich Upper Permian reference section. Ph.D. dissertation, Monash University, Melbourne, Australia, 238 pp.
- deBraga, M. 2003. The postcranial skeleton, phylogenetic position, and probable lifestyle of the Early Triassic reptile *Procolophon trigoniceps*. Canadian Journal of Earth Sciences 40:527–556.
- deBraga, M., and R. R. Reisz. 1996. The Early Permian reptile *Acleistorhinus pteroticus* and its phylogenetic position. Journal of Vertebrate Paleontology 16:384–395.
- deBraga, M., and O. Rieppel. 1997. Reptile phylogeny and the interrelationships of turtles. Zoological Journal of the Linnean Society 120:281–354.
- Efremov, J. A. 1938. Some new Permian reptile of the USSR. Comptes Rendus (Doklady) 19:771–776.
- Efremov, J. A. 1940. New discoveries of Permian terrestrial vertebrates in Bashkiria and the Tchkalov Province. Comptes Rendus (Doklady) 27:412–415.
- Fröbisch, J., and R. R. Reisz. 2009. The Late Permian herbivore *Suminia* and the early evolution of arboreality in terrestrial vertebrate ecosystems. Proceedings of the Royal Society B 276:3611–3618.
- Golubev, V. K. 2005. Permian tetrapod stratigraphy; pp. 95–99 in S. G. Lucas and K. E. Zeigler (eds.), The Nonmarine Permian. New Mexico Museum of Natural History and Science Bulletin 30.
- Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.
- Gow, C. E. 1972. The osteology and relationships of the Millerettidae (Reptilia: Cotylosauria). Journal of Zoology 167:219–264.
- Haeckel, E. 1866. Generelle Morpholgie der Organismen. G. Reimer, Berlin, 574 pp.

- Hemilä, S., S. Nummela, and T. Reuter. 1995. What middle ear parameters tell about impedance matching and high frequency hearing. Hearing Research 85:31–44.
- Ivakhnenko, M. F. 1987. [Permian Parareptiles of USSR]. Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR 223:1–160. [Russian]
- Ivakhnenko, M. F. 1997. New Late Permian nycteroleterids from Eastern Europe. Paleontological Journal 31:552–558.
- Ivakhnenko, M. F. 2008. [Subclass Parareptilia]; pp 49–85 in M. F. Ivakhnenko and E. N. Kurochkin (eds.), [Fossil Vertebrates of Russia and Adjacent Countries: Fossil Reptiles and Birds, Part 1]. Geos, Moscow. [Russian]
- 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]
- Kass, R. E., and A. E. Raftery. 1995. Bayes factors. Journal of the American Statistical Association 90:773–795.
- Klembara, J. 2011. The cranial anatomy, ontogeny, and relationships of *Karpinskiosaurus secundus* (Amalitzky) (Seymouriamorpha, Karpinskiosauridae) from the Upper Permian of European Russia. Zoological Journal of the Linnean Society 161:184–212.
- Kuhn, O. 1969. Cotylosauria; in O. Kuhn (ed.), Handbuch der Paläoherpetologie, Part 6. Gustav Fischer Verlag, Jena, 164 pp.
- Laurenti, J. N. 1768. Classis Reptilium. Specimen medicum, exhibens synopsis Reptilium emendatum, cum experimentis circa venena et antidote Reptilium Austriacorum. Joan. Thomae, Nob. de Trattnern, Vienna.
- Laurin, M., and R. R. Reisz. 1995. A reevaluation of early amniote phylogeny. Zoological Journal of the Linnean Society 113:165–223.
- Lee, M. S. Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. Science 261:1716–1720.
- Lee, M. S. Y. 1995. Historical burden in systematics and the interrelationships of 'parareptiles.' Biological Reviews 70:459–547.
- Lee, M. S. Y. 1997a. Pareiasaur phylogeny and the origin of turtles. Zoological Journal of the Linnean Society 120:197–280.
- Lee, M. S. Y. 1997b. A taxonomic revision of pareiasaurian reptiles: implications for Permian terrestrial palaeoecology. Modern Geology 21:231–298.
- Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50:913–
- Lartillot, N., and H. Philippe. 2006. Computing Bayes factors using thermodynamic integration. Systematic Biology 55:195–207.
- Lucas, S. G. 2002. Discussion and reply. The reptile *Macroleter*: first vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. Discussion. Geological Society of America Bulletin 114:1174–1176.
- Maddison, W. P., and D.R. Maddison. 2009. Mesquite: A Modular System for Evolutionary Analysis. Version 2.72. Available at http://mesquiteproject.org. Accessed December 18, 2010.
- Modesto, S. P. 1999. Observations on the structure of the Early Permian reptile *Stereosternum tumidum* Cope. Palaeontologia Africana 35:7–19
- Modesto, S. P. 2006. The cranial skeleton of the Early Permian aquatic parareptile *Mesosaurus tenuidens*: implications for relationships and palaeobiology. Zoological Journal of the Linnean Society 146:345–368.
- Modesto, S. P. 2010. The postcranial skeleton of the aquatic parareptile *Mesosaurus tenuidens* from the Gondwanan Permian. Journal of Vertebrate Paleontology 30:1378–1395.
- Modesto, S. P., and R. Damiani. 2007. The procolophonoid reptile *Sauropareion anoplus* from the lowermost Triassic of South Africa. Journal of Vertebrate Paleontology 27:337–349.
- Modesto, S. P., and N. Rybczynski. 2000. The amniote faunas of the Russian Permian: implications for Late Permian terrestrial vertebrate biogeography; pp. 17–34 in M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, U.K.
- Modesto, S. P., D. M. Scott, and R. R. Reisz. 2009. Arthropod remains in the oral cavities of fossil reptiles support inference of early insectivory. Biology Letters 5:838–840.
- Moermond, T. C. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. Ecology 60:152–164.

- Müller, J., and L. A. Tsuji. 2007. Impedance-matching hearing in Paleozoic reptiles: evidence of advanced sensory perception at an early stage of amniote evolution. PLoS ONE 2(9):e889.
- Olson, E. C. 1947. The Family Diadectidae and its bearing on the classification of reptiles. Fieldiana: Geology 11:1–53.
- Reisz, R. R., and M. Laurin. 2001. The reptile *Macroleter*: first verte-brate evidence for correlation of Upper Permian continental strata of North America and Russia. Geological Society of America Bulletin 113:1229–1233.
- Reisz, R. R., and M. Laurin. 2002. Discussion and reply. The reptile *Macroleter*: first vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. Reply. Geological Society of America Bulletin 114:1177.
- Reisz, R. R., and D. Scott. 2002. Owenetta kitchingorum, sp. nov., a small parareptile (Procolophonia: Owenettidae) from the Lower Triassic of South Africa. Journal of Vertebrate Paleontology 22:244– 256.
- Reisz, R. R., D. S Berman, and D. Scott. 1984. The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. Journal of Vertebrate Paleontology 4:57–67.
- Reisz, R. R., J. Müller, L. Tsuji, and D. Scott. 2007. The cranial osteology of *Belebey vegrandis* (Parareptilia: Bolosauridae), from the Middle Permian of Russia, and its bearing on reptilian evolution. Zoological Journal of the Linnean Society 151:191–214.
- Romer, A. S. 1956. Osteology of the Reptiles. University of Chicago Press, Chicago, Illinois, 772 pp.
- Ronquist, F., and J. P. Huelsenbeck. 2003. Mr. Bayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.
- Säilä, L. K. 2010a. The phylogenetic position of *Nyctiphruretus acudens*, a parareptile from the Permian of Russia. Journal of Iberian Geology 36:123–143.
- Säilä, L. K. 2010b. Osteology of *Leptopleuron lacertinum*, a procolophonoid parareptile from the Upper Triassic of Scotland, with remarks on ontogeny, ecology and affinities. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 101:1–25.
- Sumida, S. S. 1997. Locomotor features of taxa spanning the origin of amniotes; pp. 353–398 in S. S. Sumida and K. L. M. Martin (eds.), Amniote Origins, Completing the Transition to Land. Academic Press, San Diego.
- Tsuji, L. A. 2006. Cranial anatomy and phylogenetic affinities of the Permian parareptile *Macroleter poezicus*. Journal of Vertebrate Paleontology 26;849–865.
- Tsuji, L. A., J. Müller, and R. R. Reisz. 2010. *Microleter mckinzieo-rum* gen. et sp. nov. from the Lower Permian of Oklahoma: the basalmost parareptile from Laurasia. Journal of Systematic Palaeontology 8:245–255.
- Tverdokhlebova, G. I., and M. F. Ivakhnenko. 1984. [Nycteroleterids from the Upper Permian of Eastern Europe]. Paleontologicheskii Zhurnal 1984:98–111. [Russian]
- Vanhooydonck, B., A. Herrel, R. Van Damme, and D. J. Irschick. 2006. The quick and the fast: the evolution of acceleration capacity in *Anolis* lizards. Evolution 60:2137–2147.
- Wasserman, L. 2000. Bayesian model selection and model averaging. Journal of Mathematical Psychology 44:92–107.
- Watson, D. M. S. 1942. On Permian and Triassic tetrapods. Geological Magazine 79:81–116.
- Wiens, J. J. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. Systematic Biology 52:528–538.
- Witzmann, F. 2007. The evolution of the scalation pattern in temnospondyl amphibians. Zoological Journal of the Linnean Society 150:815–834.

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APPENDIX 1. List of characters used in the phylogenetic analysis.

(1) Narial shelf: absent (0); present (1) (Laurin and Reisz, 1995:character 1).

- (2) Frontal orbital contact: absent (0); present (1) (Laurin and Reisz, 1995:character 2).
- (3) Frontal lateral lappet: absent (0); large, occupies at least one-third of the dorsal margin of the orbit (1) (deBraga and Reisz, 1996:character 7).
- (4) Pineal foramen position: in the middle of the body of the parietal (0); displaced posteriorly (1); displaced anteriorly and reaches level of orbit (2); absent (3) (deBraga and Rieppel, 1997:character 49, modified).
- (5) Postparietal: paired (0); median (1); greatly reduced or absent (2) (Laurin and Reisz, 1995:character 4, modified).
- (6) Postparietal position: dorsally exposed, integrated into skull table (0); occipital (1) (Laurin and Reisz, 1995:character 5).
- (7) Prefrontal-palatal contact: absent (0); weak (1); strong (2) (Laurin and Reisz, 1995:character 6).
- (8) Prefrontal medial flange: narrow (0); wide (1) (Laurin and Reisz, 1995:character 7).
- (9) Bulbous medial process of prefrontal: absent (0); present (1) (Laurin and Reisz, 1995:character 8).
- (10) Lacrimal narial contact: present (0); absent (1) (Laurin and Reisz, 1995:character 9).
- (11) Foramen orbitonasale: absent (0); represented by a medial indentation on the lacrimal and a dorsal indentation on the palatine (1); enclosed between prefrontal, lacrimal, and palatine (2) (Laurin and Reisz, 1995:character 10).
- (12) Jugal anterior process: does not extend to anterior orbital rim (0); extends at least to level of anterior orbital rim (1) (Laurin and Reisz, 1995:character 11).
- (13) Postorbital posterior process shape: slender, half as wide as it is long (0); increased width, parallelogram outline in lateral aspect (1) (deBraga and Reisz, 1996:character 14).
- (14) Squamosal-parietal contact: present (0); absent (1) (Laurin and Reisz, 1995:character 12).
- (15) Posterolateral corner of skull roof: formed by tabular (0); formed mostly by supratemporal (1); formed by parietal and small supratemporal or parietal alone (2) (Laurin and Reisz, 1995:character 15).
- (16) Tabular size: large and part of skull table (0); small and largely occipital (1); absent (2) (Laurin and Reisz, 1995:character 17).
- (17) Supratemporal size: large (0); small (1); absent (2) (Laurin and Reisz, 1995:character 18).
- (18) Premaxillary dorsal process: broad, narial opening faces predominantly laterally (0); narrow, narial opening faces anteriorly (1) (deBraga and Reisz, 1996:character 1).
- (19) Anterodorsal process of the maxilla: absent (0); present (1) (Laurin and Reisz, 1995; character 19, modified).
- (20) Anterior lateral maxillary foramen: equal in size to other maxillary foramina (0); larger than other foramina (1); the lateral surface of the maxilla lacks large foramina (2) (Laurin and Reisz, 1995:character 20).
- (21) Maxilla and quadratojugal: in contact (0); separated (1) (Laurin and Reisz, 1995:character 22).
- (22) Quadratojugal anterior extent: reaches posterior border of orbit (0); does not reach level of posterior border of orbit (1) (Laurin and Reisz, 1995:character 23, modified).
- (23) Caniniform region: present (0); absent (1) (Laurin and Reisz, 1995:character 24).
- (24) Single caniniform maxillary tooth: absent (0); present (1) (Laurin and Reisz, 1995:character 25).
- (25) Squamosal and post-temporal fenestra: separated (0); in contact (1) (Laurin and Reisz, 1995:character 26).
- (26) Quadratojugal shape: does not reach beyond the level of the ventral orbital margin (0); extends dorsally beyond the level of ventral orbital margin (1) (Laurin and Reisz, 1995:character 28, modified).

- (27) Quadratojugal ornamentation: confluent with the cheek and not ornate in any manner (0); ornamented, dermal protuberances project from its surface (1) (deBraga and Rieppel, 1997:character 43).
- (28) Upper temporal fenestra: absent (0); present (1) (Laurin and Reisz, 1995:character 29).
- (29) Ventral temporal emargination: absent (0); present and bounded ventrally, forming a lower temporal fenestra (1); present and open ventrally (2) (Laurin and Reisz, 1995:character 30, modified).
- (30) Postorbital contribution to lateral temporal fenestra: bordered by jugal, quadratojugal, squamosal, and postorbital (0); no contribution by postorbital (1) (deBraga and Reisz, 1996:character 20).
- (31) Quadratojugal-lateral temporal fenestra contribution: quadratojugal excluded from posterior border (0); quadratojugal contributes to lateral temporal fenestra (1) (de-Braga and Reisz, 1996:character 16).
- (32) Postorbital region of skull: length at least equals anteroposterior extension of orbit (0); postorbital region shorter than anteroposterior extension of orbit (1) (Laurin and Reisz, 1995:character 32).
- (33) Ventral margin of postorbital skull region: expanded below ventral extent of maxilla (0); rectilinear (1); emarginated (2) (Laurin and Reisz, 1995:character 33).
- (34) Quadrate lateral exposure: absent (0); present (1) (Laurin and Reisz, 1995:character 34).
- (35) Quadrate anterior process: long (0); short (1) (Laurin and Reisz, 1995:character 35).
- (36) Jaw articulation position: posterior to occiput (0); even with occiput (1); anterior to occiput (2) (Laurin and Reisz, 1995:character 36).
- (37) Posterior extension of orbit: absent (0); present (1) (Laurin and Reisz, 1995:character 37)
- (38) Dermal sculpturing: absent (0); tuberosities (1); tuberosities and pits (2); honeycomb pattern of ridges and pits (3) (Laurin and Reisz, 1995:character 38).
- (39) Sculpturing involving circumorbital bumps: no distinctive ornamentation (0); circumorbital tubercles (1) (Tsuji, 2006:character 45).
- (40) Posterior margin of skull roof: roughly straight (0); with a single, median embayment (1); embayed bilaterally (2) (Modesto, 1999:character 125).
- (41) Interpterygoid vacuity anterior extent: absent (0); reaches beyond posterior border of palatine (1); reaches level of palatine or less (2) (Reisz et al., 2007:character 39, modified).
- (42) Choana: parallel to maxilla; palatine forms its posterior edge only (0); curved posteromedially; palatine forms its posterior and part of its lateral edge (1) (Laurin and Reisz, 1995:character 40).
- (43) Alar flange of the vomer: absent (0); present (1) (Tsuji, 2006:character 50).
- (44) Arcuate flange of pterygoid: present (0); absent (1) (Laurin and Reisz, 1995:character 42).
- (45) Cranio-quadrate space: small, quadrate ramus of pterygoid and paraoccipital process of opisthotic converge posterolaterally (0); large, quadrate ramus of pterygoid and paraoccipital process of opisthotic are parallel to each other (1) (Laurin and Reisz, 1995:character 43).
- (46) Pterygoid anterior extent: reaches level of posterior end of choana (0); posterior to choana (1) (Laurin and Reisz, 1995:character 44).
- (47) Transverse flange of the pterygoid: large, approaches cheek, a noticeable lateral projection (0); small, does not approach cheek (1) (Lee, 1997a:character 19, modified).
- (48) Transverse flange of pterygoid orientation: directed posterolaterally or transversely (0); directed anterolaterally

- (1); directed anteriorly (2) (Laurin and Reisz, 1995:character 45, modified).
- (49) Transverse flange of pterygoid dentition: shagreen of denticles, no ventral ridge (0); single row of large teeth, no ventral ridge (1); edentulous with ventral ridge (2) (Laurin and Reisz, 1995:character 46).
- (50) Quadrate ramus of pterygoid: merges smoothly into transverse flange without distinctive excavation (0); deep excavation on posterolateral surface (1) (deBraga and Reisz, 1996:character 29).
- (51) Ectopterygoid dentition: present (0); absent (1) (Laurin and Reisz, 1995:character 48).
- (52) Ectopterygoid relationship to transverse flange: ectopterygoid anterolateral to transverse flange, does not contribute to flange (0); ectopterygoid makes contact with transverse flange (1) (deBraga and Reisz, 1996:character 33).
- (53) Suborbital foramen: absent (0); present (1); fenestra present (2) (Laurin and Reisz, 1995:character 49).
- (54) Basicranial articulation: kinetic/synovial (0); sutured and/or immobile (1) (Lee, 1997a:character 2, modified).
- (55) Length of basicranial articulation: restricted to anterolateral margin of the parasphenoid (0); extends over much of length of main body of parasphenoid (1) (deBraga and Reisz, 1996:character 36).
- (56) Parasphenoid pocket for cervical musculature: present (0); absent (1) (Laurin and Reisz, 1995:character 50).
- (57) Parasphenoid wings; present, parasphenoid broader posteriorly than long (0); absent, parasphenoid narrower posteriorly than long (1) (Laurin and Reisz, 1995:character 51, modified).
- (58) Cultriform process: longer than the body of the parasphenoid (0); shorter than the body of the parasphenoid (1); absent (2) (Laurin and Reisz, 1995:character 52).
- (59) Parasphenoid teeth: absent (0); present (1) (Laurin and Reisz, 1995:character 53).
- (60) Supraoccipital: absent (0); plate-like, no sagittal crest (1); body constricted at midline, forming sagittal crest (2) (de-Braga and Rieppel, 1997:character 56, modified).
- (61) Paroccipital process: vertically broad (0); anteroposteriorly expanded (1); narrow (2); tubular, composed of opisthotic (3) (Laurin and Reisz, 1995:character 56).
- (62) Paraoccipital process orientation: directed primarily laterally (0); oriented obliquely, at an angle of at least 45° from the horizontal plane of skull (1) (deBraga and Reisz, 1996:character 44).
- (63) Sutural contact between paroccipital process and dermatocranium: absent (0); present (1) (Laurin and Reisz, 1995:character 57, modified).
- (64) Otic trough in ventral flange of opisthotic: absent (0); present (1) (Laurin and Reisz, 1995:character 58).
- (65) Medial wall of inner ear (made of prootic): unossified (0); ossified with acoustic nerve foramina (1) (Laurin and Reisz, 1995:character 59).
- (66) Post-temporal fenestra: absent (0); small, diameter less than half the diameter of foramen magnum (1); large, diameter at least equal to foramen magnum (2) (deBraga and Rieppel, 1997:character 59).
- (67) Osseous contact between basioccipital and basisphenoid: present (0); absent (1) (Lee, 1993:character A3; scored as per Laurin and Reisz, 1995:character 61).
- (68) Occipital condyle shape: transversely broad (0); reniform to circular (1) (Laurin and Reisz, 1995:character 62).
- (69) Ventral exposure of basioccipital: contributes extensively to ventral surface of the braincase (0); restricted to condylar region (1) (deBraga and Reisz, 1996:character 37).
- (70) Ventral braincase tubera: absent (0); present and restricted to basioccipital (1); present, very large and restricted to basisphenoid (2); median (3) (Laurin and

- Reisz, 1995:character 63, modified; deBraga and Rieppel, 1996:character 65).
- (71) Lateral flange of exoccipital: absent (0); present (1) (Laurin and Reisz, 1995:character 64).
- (72) Quadrate condyle articular surfaces: strongly convex, anteroposteriorly longer than they are wide (0); nearly flat, anteroposteriorly shorter than they are wide (1) (Laurin and Reisz, 1995:character 65, modified).
- (73) Stapes: robust, greatest depth exceeding one-third of total length (0); slender, length at least four times depth (1); slender but short (2) (deBraga and Rieppel, 1997:character 45).
- (74) Stapedial dorsal process: ossified (0); unossified (1) (Laurin and Reisz, 1995:character 67).
- (75) Labyrinthodont infolding: present (0); absent (1) (Laurin and Reisz, 1995:character 68).
- (76) Morphology of marginal dentition: single cusp (0); two to seven cusps (1); more than seven cusps (2) (Lee, 1997a:character 59, modified).
- (77) Foramen intermandibularis: anterior symphysial foramen (0); two foramina, a symphysial and a posterior foramen located anterior to coronoid process (1); two foramina, a symphysial and a posterior foramen located located posterior to or at level of coronoid process (2) (Laurin and Reisz, 1995:character 69).
- (78) Meckelian fossa orientation: faces mediodorsally, prearticular narrow (0) faces dorsally, prearticular broad (1) (Laurin and Reisz, 1995:character 70).
- (79) Fossal meckelii: long, occupies at least 20% of lower jaw length (0); short, occupies less than 20% of lower jaw length (1) (Laurin and Reisz, 1995:character 71).
- (80) Surangular length: extends beyond coronoid eminence (0); does not extend beyond coronoid eminence (1) (Laurin and Reisz, 1995:character 72).
- (81) Accessory lateral shelf on surangular anterior to articular region: absent (0); present (1) (Laurin and Reisz, 1995:character 73).
- (82) Coronoid number: two or three (0); one (1) (Laurin and Reisz, 1995:character 74).
- (83) Prearticular extends: beyond the coronoid eminence (0); does not extend beyond coronoid eminence (1) (Laurin and Reisz, 1995:character 75, modified).
- (84) Retroarticular process: absent or small and narrow (0); transversely broad, dorsally concave (1) (Laurin and Reisz, 1995:character 76).
- (85) Retroarticular process composition: articular body (0); three or more elements (articular, prearticular, angular, and surangular) (1) (Laurin and Reisz, 1995:character 77).
- (86) Lateral shelf on articular region: absent (0); on articular (1); on surangular (2) (Laurin and Reisz, 1995:character 78).
- (87) Coronoid process: small or absent, composed of several elements (0); high process composed of coronoid only (1); high, composed primarily of dentary (2) (Laurin and Reisz, 1995:character 79, modified).
- (88) Splenial: contributes to symphysis (0); excluded from symphysis (1) (Laurin and Reisz, 1995:character 80).
- (89) Presacral vertebral count: more than twenty (0); twenty or less (1) (Laurin and Reisz, 1995:character 81).
- (90) Axial centrum orientation: in plane of axial skeleton (0); sloping anterodorsally (1) (Laurin and Reisz, 1995:character 82).
- (91) Atlantal neural arch: possesses epipophysis (0); lacks epipophysis (1) (Lee, 1995:475; scored as per Modesto, 1999:character 126).
- (92) Axial intercentrum: with rounded anteroventral edge (0); with strong anterior process (1) (Laurin and Reisz, 1995:character 84).

- (93) Atlantal pleurocentrum and axial intercentrum: separate elements (0); attached or fused (1) (Laurin and Reisz, 1995:character 85).
- (94) Trunk neural arches: swollen (0); narrow (1) (Laurin and Reisz, 1995:character 86, modified).
- (95) Ventral surface of anterior pleurocentra: uniform (0); bearing exavations on either side of flattened median crest (1) (Laurin and Reisz, 1995:character 87, modified).
- (96) Number of sacral vertebrae: one (0); two (1); three or more (2) (Laurin and Reisz, 1995:character 88).
- (97) Sacral rib distal overlap: broad with narrow gap between ribs (0); small or absent with wide gap between ribs (1) (Laurin and Reisz, 1995:character 89).
- (98) Transverse process or ribs: present only on a few anterior caudals (0); present on at least thirteen caudals (1) (Laurin and Reisz, 1995:character 90).
- (99) Caudal hemal arches: wedged between centra (0); attached to anterior centrum (1) (Laurin and Reisz, 1995:character 91).
- (100) Interclavicle: diamond-shaped (0); T-shaped, with long, slender lateral processes (1) (Laurin and Reisz, 1995:character 92).
- (101) Interclavicle attachment for clavicle: ventral sutural area (0); anteriorly directed groove (1); tightly sutured into plastron (2) (Laurin and Reisz, 1995:character 93).
- (102) Cleithrum: caps scapula anterodorsally (0); does not cap scapula at all (1); absent (2) (Laurin and Reisz, 1995:character 94).
- (103) Scapula: broad (0); narrow, thin (1) (Laurin and Reisz, 1995:character 96).
- (104) Supraglenoid foramen: present (0); absent (1) (Laurin and Reisz, 1995:character 97).
- (105) Glenoid: anteroposteriorly long, helical (0); short, bipartite (1) (Laurin and Reisz, 1995:character 98).
- (106) Acromion: absent (0); present (1) (Laurin and Reisz, 1995:character 99).
- (107) Sternum: not mineralized (0); mineralized (1) (Laurin and Reisz, 1995:character 100).
- (108) Supinator process: strongly angled relative to shaft, separated from it by groove (0); parallel to shaft, separated from it by groove (1); parallel to shaft, not separated from shaft (2) (Laurin and Reisz, 1995:character 101).
- (109) Ectepicondylar foramen: only groove present (0); groove and foramen present (1); only foramen present (2); both absent (3) (Laurin and Reisz, 1995:character 102).
- (110) Entepicondylar foramen: present (0); absent or not fully enclosed (1) (Laurin and Reisz, 1995:character 103).
- (111) Humerus: with robust heads and a short shaft (0); short and robust, without a distinct shaft (1); slender with long shaft (2) (Laurin and Reisz, 1995:character 104).
- (112) Olecranon process: large, proximal articular facet of ulna faces medially (0); small or absent (1) (Laurin and Reisz, 1995:character 105, modified).
- (113) Manual phalangeal formula: 2-3-4-5-3 (0); 2-3-4-4-3 (1); 2-3-3-3-3 or less (2) (Laurin and Reisz, 1995:character 106)
- (114) Dorsolateral shelf on iliac blade: absent (0); present (1) (Laurin and Reisz, 1995:character 107).
- (115) Iliac blade: low, with long posterior process (0); dorsally expanded, distally flaring (1) (Laurin and Reisz, 1995:character 108).
- (116) Acetabular buttress: small, overhangs acetabulum only moderately (0); large, overhangs acetabulum strongly (1) (Laurin and Reisz, 1995:character 109).
- (117) Oblique ventral ridge of femur (adductor crest): present (0); absent (1) (Laurin and Reisz, 1995:character 110).

- (118) Femoral proximal articulation: anteroposteriorly long (0); round (1) (Laurin and Reisz, 1995:character 111).
- (119) Greater trochanter of femur; absent (0); present on posterior edge of femur (1) (Laurin and Reisz, 1995:character 112).
- (120) Femoral shaft: short and broad (0); long and slender (1) (Laurin and Reisz, 1995:character 113).
- (121) Carpus and tarsus: short and broad (0); long and slender (1) (Laurin and Reisz, 1995:character 114).
- (122) Astragalus: absent (0); incorporates incompletely fused tibiale, intermedium, and perhaps centrale 4 (1); without traces of compound origin (2) (Laurin and Reisz, 1995:character 115).
- (123) Tibio-astragalar joint: flat (0); tibial ridge fits into astragalar groove (1) (Laurin and Reisz, 1995:character 116).
- (124) Astragalus and calcaneum: separate (0); sutured or fused (1) (Laurin and Reisz, 1995:character 117).
- (125) Medial pedal centrale: present (0); absent (1) (Laurin and Reisz, 1995:character 118).
- (126) Number of distal tarsals: five (0); four or less (1) (Laurin and Reisz, 1995:character 119).
- (127) Metapodials: not overlapping (0); overlapping (1) (Laurin and Reisz, 1995:character 121).
- (128) Pedal phalangeal formula: 2-3-4-5-3/4 (0); 2-3-4-4-3 (1); 2-3-3-4-3 or less (2) (Laurin and Reisz, 1995:character 122).

- (129) Ratio between length of metatarsal one to length of metatarsal four: at least 0.5 (0); less than 0.5 (1) (Laurin and Reisz, 1995:character 123).
- (130) Dorsal dermal ossifications: absent (0); present (1) (Laurin and Reisz, 1995:character 124).
- (131) Subtemporal process of jugal: present (0); absent (1) (Müller and Tsuji, 2007:character 131).
- (132) Suture between jugal and maxilla: straight, jugal thins out smoothly towards anterior direction (0); 'stepped,' anterior-most tip of jugal very narrow but expands broadly posteriorly along with a dramatic thinning of the posterior process of the maxilla (1) (Müller and Tsuji, 2007:character 133).
- (133) Temporal notch: present (0); absent (1) (Müller and Tsuji, 2007:character 134).
- (134) Temporal depression associated with posterolateral excavation: restricted to the posterior half of the cheek (0); closely approaches the orbital margin (1) (Müller and Tsuji, 2007:character 135).
- (135) Contact between maxilla and prefrontal: absent (0); present (1) (Müller and Tsuji, 2007:character 136).
- (136) Contribution of maxilla to external naris: maxilla is either excluded from naris or forms only its ventral/posterior edge (0); maxilla extends also to the posterodorsal margin of naris (1) (Müller and Tsuji, 2007:character 137).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis. **Abbreviations**: **A**, polymorphism for 0 and 1; **B**, polymorphism for 1 and 2; **Ba**, *Bashkyroleter*; **C**, polymorphism for 0 and 2; **D**, polymorphism for 0, 1, and 2; **E**, uncertainty for 0 and 1; **F**, uncertainty for 1 and 2.

	1	2	3	4	5	6	7
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Seymouria	0000001000	0000000000	000000000?	?00000300	0001000000	0000010000	3100000000
Limnoscelidae	0000110000	0111100000	010001000?	?000010001	1000000010	000000011	0001?00000
Diadectidae	0000111000	?0?1100000	011001000?	?001110102	1100000100	00000?0001	0001100000
Synapsida	A10B010000	0011100000	1A01000010	00A0010002	1000000010	00000A00A1	000A01010C
Captorhinidae	010C011000	1110221000	110110000?	?010110302	1001000000	??100110A1	2000?20100
Paleothyris	0101010000	?0?0211000	010110000?	?010110002	10?1000010	00?0001011	000??2?100
Araeoscelidia	0100010000	0A00211?00	0A01A00110	1010110002	10?10001A0	00200110A1	0000?2?100
Younginiformes	0100010001	0100211?10	0100100110	1011110001	1001000010	1120011001	2000?2?100
Mesosauridae	0100010001	?0?0110000	001010000?	?110010001	1001?00010	???0000001	000??2?100
Eunotosaurus	?10201????	?001110?1?	111011000?	?121020101	1?????001?	???0010001	100?????0?
Millerettidae	0101011001	2001110001	11A00100A0	0111020101	100000010	1010011011	0000021100
Australothyris	?1?E01F00?	2001110??1	0010?10010	1110120100	2000010011	10?0010111	0000?1?000
Microleter	1100111100	?0011?0?11	1110?10020	1120?20300	?0?0??01?1	3330033333	0033333333
Nyctiphruretus	0101112101	2011110111	0010010021	1110021100	1110100010	0010011101	10???2?100
Eudibamus	010???210?	?01?2?210?	?0101?00?1	11?000?000	??????1221	1??0001?0?	?0?????01?
Belebey	0101212100	2010202101	0010100011	1100011000	2000?11221	100000100?	3003330333
Acleistorhinus	011011???1	?011110111	0101110011	1010020101	1000100011	1111101111	0110?20010
Lanthanosuchus	0110211001	?01111011?	1110111011	1010000201	1000100011	1101111112	0110?1?01?
Bradysaurus	0002101000	?111120111	101000100?	?000020211	2110110111	1011011102	1010120100
Pareiasuchus	0002101000	?111110111	101000100?	?000020211	211011011?	1A11011102	1010?2?100
Scutosaurus	0002101000	?111110111	001000100?	?000020211	2110110111	1011011102	1010120100
Procolophon	11022?2111	2111110111	101001002?	?120021000	1000110121	1110010102	1010021101
Owenetta	1102002111	?111120111	100001002?	?120021000	1000110121	1110011102	1010?2?101
Barasaurus	110200?110	?011120111	101001002?	?120021001	100011012?	1110011102	101??2?101
Macroleter	0102A12101	2111110111	0100001011	1000011211	2110100010	1011001202	1010120100
<i>`Ba.'mesensis</i>	0100112101	2A11110111	110001100?	?0100?1201	2110100010	10?101120?	?01??2????
Ba.bashkyricus	0102?12101	2011110?1?	????0?100?	?000??1200	2?101?0011	??110?120?	?01???????
Nycteroleter	0100012101	2011110111	11100??0??	?000011201	2??0?00011	??1101120?	?????????0
Emeroleter	0102212101	2011110111	0110?1100?	?010011201	2??0??0010	??1101120?	???????1?0
Rhipaeosaurus	?????????	?????????	?????????	?????????	??????0010	??1?011?0?	????????00
	8 1234567890	9 1234567890	10 1234567890	11 1234567890	12 1234567890	13 1234567890	13 123456
Seymouria	0001000000	0000000000	0000000000	000000000	0100000000	?0?????000	000000
Limnoscelidae	00??001100	0000000000	01100100?0	0000000000	1001000000	01??0??000	001?00
Diadectidae	000000100?	0100000000	01100100:0	0000000000	1001100000	01?A0?0000	000000
Synapsida	000010D00A	A000?00001	00A1010000	0100000000	000000000A	A200000000	001?00
Captorhinidae	0000101000	0100?00001	0010010000	0B00000230	0000000000	0200100000	001?00
Paleothyris	?00010??00	01?0??0001	1011010000	0100000100	2000000001	1200101000	001?00
Araeoscelidia	000010?000	0100?00A01	0010010000	0100001BA0	2000001001	1210101010	001?00
Younginiformes	001110??0?	01?0?000??	00?1010101	01010011A0	0100111001	12101A1010	001?10
Mesosauridae	?00010??00	01?1000?01	1010010010	01010001A0	2100001101	0200100000	101?00
Eunotosaurus	??0110???0	???0??0?1?	???1011??0	0?11000110	0?0010?000	0200100000	?????0
Millerettidae	000110?000	0100?00001	0011011??0	0101000110	0?001??001	120010?010	101?00
Australothyris	010010??00	0?1000?0??	????????0	0????????	?????????	?????????	?0000?
Microleter	?0??10?001	0?00000???	?????????	?????????	?????????	?????????	100000
Nyctiphruretus	01??10??11	010110010?	???01211?1	1?10000100	00?0101001	0210000?00	101?10
Eudibamus	????102???	??10??200?	??0000?0?1	1?01?00131	2??1010111	1200100010	??????
Belebey	00??102011	0110?021??	???00?????	??0????1??	???00????1	????????0	101?00
Acleistorhinus	010010???1	0110?0?1??	?????????	?????????	?????????	?????????	101?10
Lanthanosuchus	11??10????	?????????	???0?????1	1?0??????	?????????	?????????	101?00
Bradysaurus	11?011?111	0111?1101?	1000021111	1111?10220	1120110000	020111?201	1?1000
Pareiasuchus	11??122111	0111?1101?	???002???1	?211110?21	1120110010	02011????1	1?1000
Scutosaurus	1101122111	0111?1101?	10000?11?1	?211110220	1120110010	020111?201	101000
Procolophon	01111021?1	1111101101	10?0121001	1211100200	0100110?01	020011?100	110000
Owenetta	00??102111	011110110?	?0?01210?1	?111?001?1	01?011??01	0?0?1????0	100000
Barasaurus	00??10????	????????01	10?01210?1	1111100101	01001?0001	0??11??000	100000
Macroleter	1?21102111	1110?0?101	1010021??1	1111?00120	01?0110001	0201110?00	100000
`Ba.'mesensis	?1??10?111	1110??????	?????????	?????????	?????????	?????????	010101
Ba.bashkyricus	?1??10?111	1110??????	?????????	?????????	?????????	?????????	0101?0
=	?1??10??11	1??0???1??	?????????	?????????	?????????	?????????	000100
Nycteroleter							
Emeroleter Emeroleter	11??10???1	1??0????0?	???002????	?11??10?00	21001???01	1201011000	100101