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Euparkeriidae

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Abstract: *Euparkeria capensis* has long been considered an archetype for the ancestral archosaur morphology, and has been placed just outside of crown Archosauria by nearly all cladistic analyses. Six species are currently considered to be putative members of a clade Euparkeriidae, and have been collected from Olenekian- or Anisian-aged deposits in South Africa (*Euparkeria capensis* – the only definitive member of the group), China (*Halazhaisuchus gaoensis*, *Wangisuchus tzeyii*, ‘*Turfanosuchus*’ *shageduensis*), Russia (*Dorosuchus neoetus*) and Poland (*Osmolskina czatkowicensis*). Four other species (*Turfanosuchus dabanensis*, *Xilousuchus sapingensis*, *Platyognathus hsui*, *Dongusia colorata*) were historically assigned to Euparkeriidae, but have been removed by recent work. Recent authors deemed *Osmolskina czatkowicensis* and *Dorosuchus neoetus* to be the most likely taxa to form a euparkeriid clade with *Euparkeria capensis*, but *Osmolskina czatkowicensis* and *Euparkeria capensis* were not found as sister taxa by the only cladistic analysis to have tested euparkeriid monophyly. *Euparkeria capensis* was small (<1 m), insectivorous or carnivorous, probably had vision adapted to low-light conditions and a semi-erect crocodile-like stance, and may have been facultatively bipedal. Bone histology demonstrates that *Euparkeria capensis* had a slow growth rate, which has been suggested to have been an adaptation to relatively stable environmental conditions.

Euparkeria capensis was a small (reaching c. 1 m in length: Ewer 1965; Remes 2007; Botha-Brink & Smith 2011, see Figs 1–4) non-archosaurian archosauriform (e.g. Nesbitt 2011), currently known from a single locality in the early Middle Triassic of South Africa (Broom 1913a, b; Ewer 1965; Senter 2003). The anatomy of *Euparkeria capensis* has been relatively comprehensively described (Broom 1913a, b; Haughton 1922; Ewer 1965; Gow 1970; Sereno & Arcucci 1990; Sereno 1991; Gower & Weber 1998; Senter 2003), although no comprehensive modern monographic treatment exists. The taxon is the only definite member of Euparkeriidae, and thus forms the focus of the group.

Several other species have been referred to Euparkeriidae (Tables 1, 2). The monophyly of a euparkeriid clade including putative euparkeriid species has not been thoroughly tested using modern phylogenetic techniques; indeed, the only cladistic analysis to date to include more than a single putative euparkeriid did not find a monophyletic grouping of *Osmolskina czatkowicensis* and *Euparkeria capensis*, although this analysis was not focused on the group (Ezcurra *et al.* 2010). *Euparkeria capensis* has been placed just outside Archosauria (using a crown group definition) in nearly all phylogenetic analyses of non-archosaurian archosauriforms (e.g. Gower & Wilkinson 1996; Nesbitt 2011). As a result, this species, and potentially other putative euparkeriids, is of great importance in understanding archosaurian origins, having long

been considered to represent something approaching the ancestral archosaurian body plan (e.g. Romer 1972). In this chapter, we provide a brief and preliminary review of previous work on the taxonomy, phylogenetics and geographic and stratigraphic distribution of *Euparkeria capensis* and other putative members of Euparkeriidae.

Phylogenetic definition

Euparkeriidae Huene 1920. Stem-based definition – the most inclusive clade containing *Euparkeria capensis* Broom 1913a but not *Crocodylus niloticus* Laurenti 1768 or *Passer domesticus* Linnaeus 1758. (new)

Comments

Euparkeriidae Huene 1920 has not previously been defined phylogenetically. At present, the confirmed taxonomic content of Euparkeriidae includes only *Euparkeria capensis*, although other species may ultimately prove referable to this clade (see below and Table 1).

Diagnosis

No extensive formal diagnoses of the genus *Euparkeria* or the species *Euparkeria capensis* have been provided. The most recent diagnosis of



Fig. 1. Holotype of *Euparkeria*, SAM-PK-5867, skull and partial skeleton. Image courtesy of S. Nesbitt. Scale bar: 50 mm.

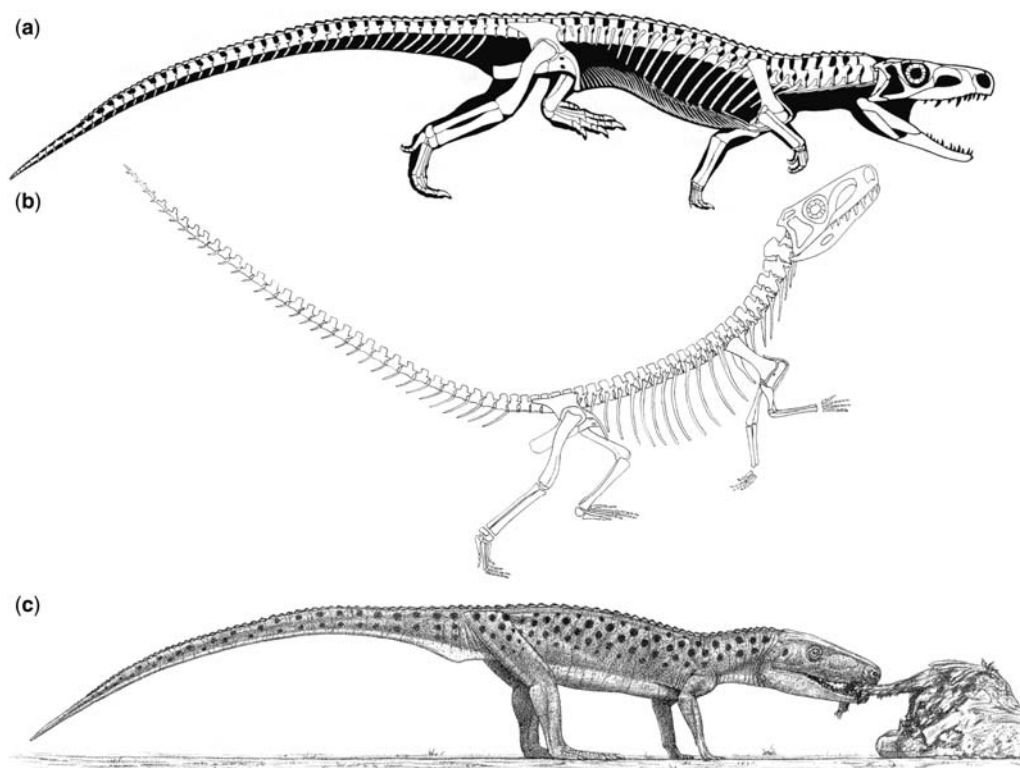


Fig. 2. Skeletal reconstructions of *Euparkeria* showing quadrupedal stance ((a) drawing courtesy and copyright of G. S. Paul) and bipedal stance ((b) from Ewer 1965), and life reconstruction of feeding *Euparkeria* ((c) from Paul 2002, drawing courtesy and copyright of G. S. Paul). The largest individuals of *Euparkeria* reached c. 1 m in length.

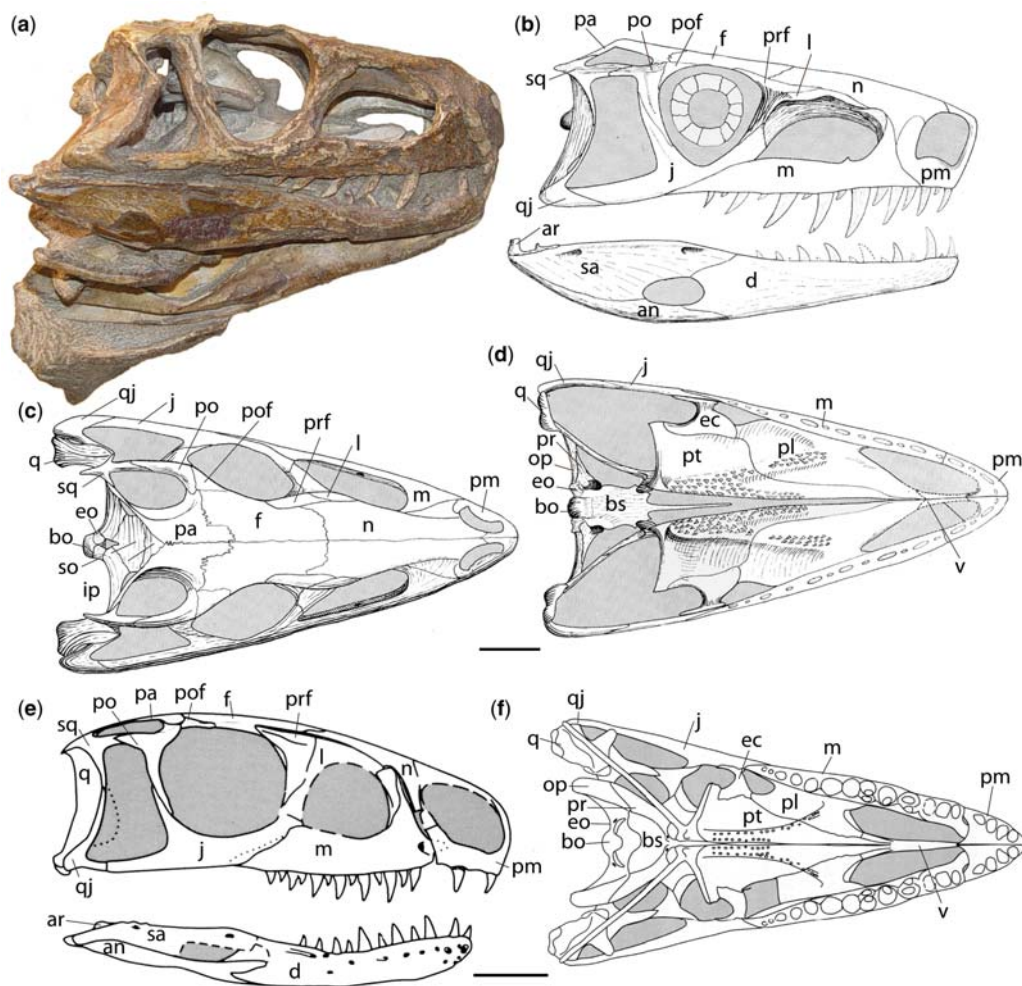


Fig. 3. Crania of *Euparkeria* and *Osmolskina*. Skull of holotype of *Euparkeria* SAM-PK-5867 in right lateral view (a, image courtesy of O. Rauhut); right lateral (b), dorsal (c) and ventral (d) skull reconstructions of *Euparkeria* from Ewer (1965); right lateral (e) and ventral (f) skull reconstructions of *Osmolskina* modified from Borsuk-Białnicka & Evans (2009). Scale bars: 10 mm; upper scale bar applies to (a–d), lower scale bar to (e, f). Abbreviations: an, angular; ar, articular; b, basioccipital; bs, basisphenoid; d, dentary; ec, ectopterygoid; eo, exoccipital; f, frontal; ip, interparietal; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; pa, parietal; pm, premaxilla; pof, postfrontal; po, postorbital; pl, palatal; pr, prootic; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sq, squamosal; v, vomer.

Euparkeriidae recognized no synapomorphies of the group, and instead species were assigned based on ‘a combination of plesiomorphic and apomorphic characters’ (Borsuk-Białynicka & Evans 2009; Borsuk-Białynicka & Sennikov 2009, p. 322). Borsuk-Białynicka & Evans (2009) and Borsuk-Białynicka & Sennikov (2009) diagnosed Euparkeriidae as differing from crown Archosauria in retaining the archosauriform plesiomorphies of an unossified median wall of the otic capsule and a lateral orientation of the calcaneal tuber (see Nesbitt

2011, characters 117, 377), differing from proterosuchids (but not other archosauriforms) in the possession of a vertically orientated basisphenoid and the absence of an astragalocalcaneal canal, and from erythrosuchids in a lighter skeletal construction, smaller skull and more elongate cervical vertebrae. Older diagnoses (e.g. Kuhn 1976) also did not establish unique synapomorphies of Euparkeriidae. Given the absence of clear synapomorphies uniting putative euparkeriid species, the monophyly of the group must be considered questionable (see below).

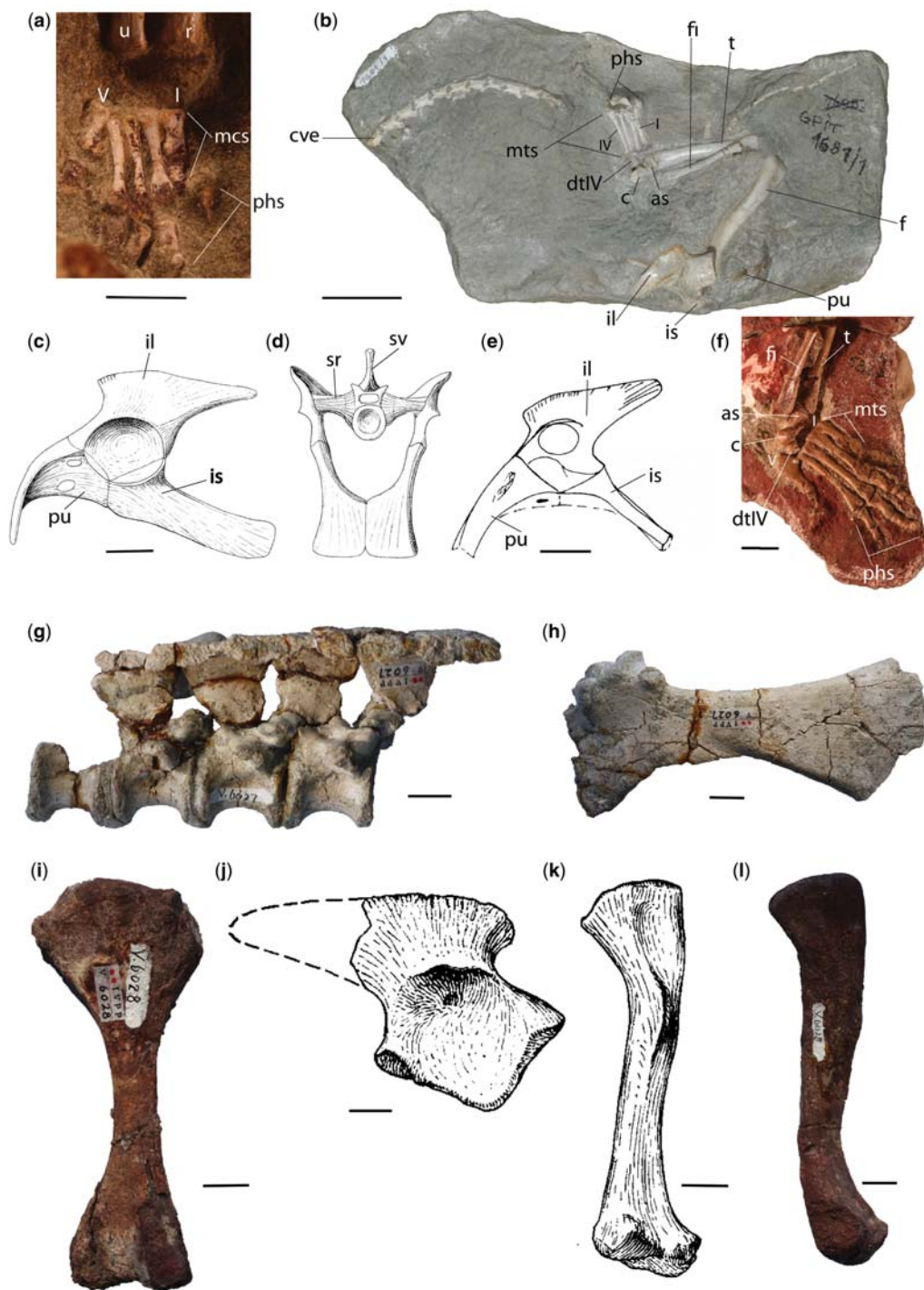


Fig. 4. Postcrania of definite and putative euparkeriids: (a) right metacarpus of *Euparkeria* (SAM-PK-13666, image courtesy of S. Nesbitt); (b) left pelvic girdle and hind limb, and caudal vertebrae of *Euparkeria* (GPIT 1681/1); left lateral (c) and anterior (d) views of reconstructed pelvic girdle of *Euparkeria* (from Ewer 1965, image courtesy of the Royal Society); (e) left lateral view of reconstructed pelvic girdle of *Osmolskina* (from Borsuk-Białynicka

Fossil record and distribution

The holotype and referred specimens of *Euparkeria capensis* were all collected from a single accumulation within the Burgersdorp Formation of the Beaufort Group, close to Aliwal North (see Ewer 1965; Arcucci pers. comm. 2012; R. Smith pers. comm. 2012), Eastern Cape Province, South Africa. This locality is within Subzone B of the *Cynognathus* Assemblage Zone (Hancox *et al.* 1995; Hancox 2000), the uppermost biozone of the Beaufort Group. Subzone B is defined on the basis of the first appearance datum of the mastodonsaurid temnospondyl *Xenotosuchus africanus* and includes the dicynodont *Kannemeyeria*, the cynodonts *Trirachodon*, *Cynognathus* and *Diademodon*, and the archosauriforms *Euparkeria* and *Erythrosuchus* as its typical faunal assemblage (Hancox 2000).

Although the *Cynognathus* Assemblage Zone has traditionally been considered to be entirely Early Triassic in age, recent work has suggested that Subzones B and C are actually Middle Triassic (Anisian) in age, with Subzone B potentially of early Anisian age (Hancox 2000). It should be noted, however, that direct (i.e. radioisotopic) dates, magnetostratigraphy and invertebrate/palynomorph biostratigraphic data are lacking, and that this age assignment is based almost entirely on long-range vertebrate biostratigraphy. The assignment of an early Anisian age to Subzone B (e.g. Hancox 2000) is based primarily on the fact that the vertebrate assemblage is dominated by a kannmeyeriid dicynodont (widely considered a 'typical' Middle Triassic group) and that Subzone B is placed stratigraphically between faunal assemblages that have been assigned to the late Olenekian (Subzone A) and the late Anisian (Subzone C), also on the basis of vertebrate biostratigraphy (Hancox 2000).

The putative euparkeriid *Osmolskina czatkowicensis* was collected from karstic deposits in southern Poland (Czatkowice locality), which formed during the Early Triassic within Early Carboniferous limestones (Borsuk-Bialynicka & Evans 2009). Dating has been based upon vertebrate biostratigraphy, with an initial date of early Olenekian presented on the basis of the presence of the dipnoan *Gnathorhiza* and the 'advanced evolutionary

level' of the procolophonids from this site (Borsuk-Bialynicka & Evans 2003). More recently, Shishkin & Sulej (2009) have argued for a late Olenekian date on the basis of comparisons of the temnospondyl assemblage from Czatkowice to that of Russia.

Material assigned to *Dorosuchus neoetus* was collected from the Donguz Gorizont of Orenburg Province, western Russia (Gower & Sennikov 2000). Four faunal assemblages have been recognized by Russian workers within the Triassic of European Russia, named on the basis of the dominant temnospondyl genera (Shishkin *et al.* 2000). Of these, the Donguz Gorizont is considered to be part of the *Eryosuchus* faunal assemblage, and has been dated as late Anisian based upon similarities between the temnospondyl assemblage and temnospondyl assemblages from the Muschelkalk of Germany, as well as the presence of an Anisian miospore assemblage in the lower parts of the Donguz (Shishkin *et al.* 2000). Other workers have considered the Donguz Gorizont to be broadly Anisian (e.g. Tverdokhlebov *et al.* 2003; Lucas 2010) or early Anisian (Rubidge 2005) in age.

The Chinese putative euparkeriids '*Turfanosuchus*' *shageduensis* and *Halazhaisuchus qiaoenensis* were both collected from the lower Ermaying Formation of Nei Mongol (Inner Mongolia) and Shaanxi provinces, China. The age of the lower Ermaying is estimated only on the basis of long-range vertebrate biostratigraphy, and has been correlated with Subzone B of the *Cynognathus* Assemblage Zone of South Africa on the basis of the presence of the dicynodont *Kannemeyeria* (Rubidge 2005). As a result, the formation appears to be of possible early Anisian age. Material assigned to *Wangisuchus tzeii* has been collected from the upper part of the Ermaying Formation in Shanxi Province. Rubidge (2005) assigned the upper Ermaying Formation to the late Anisian based on the presence of the dicynodont *Shansiodon*.

Palaeobiogeographically, putative euparkeriids have been recovered in both southern and northern palaeohemispheres, and through a broad range of palaeolatitudes (Fig. 5). During the Olenekian, the Czatkowice area was located at a palaeolatitude of c. 20°N (data from the *Paleobiology Database*), whereas during the Anisian, outgroups of the

Fig. 4. (Continued) & Sennikov 2009); (f) right pes of *Euparkeria* (SAM-PK-8309, image courtesy of S. Nesbitt); (g) posterior dorsal vertebrae of *Halazhaisuchus* (IVPP 6027, image courtesy of S. Nesbitt) in right lateral view; (h) left scapula of *Halazhaisuchus* (IVPP 6027, image courtesy of S. Nesbitt) in lateral view; (i) right humerus of '*Turfanosuchus*' *shageduensis* (IVPP V 6028, image courtesy of S. Nesbitt) in dorsal view; (j) right ilium of *Dorosuchus* (PIN 1579/161) in lateral view (from Sennikov 1989); (k) right femur of *Dorosuchus* (PIN 1579/161) in posteromedial view (from Sennikov 1989); (l) right femur of '*Turfanosuchus*' *shageduensis* (IVPP V 6028, image courtesy of S. Nesbitt) in posteromedial view. Scale bars: 10 mm (a, c–l); 50 mm (b). The same scale bar applies to (c) and (d). Abbreviations: a, astragalus; c, calcaneum; cve, caudal vertebrae; dt, distal tarsal; f, femur; fi, fibula; il, ilium; is, ischium; I, first; IV, fourth; mcs, metacarpals; mts, metatarsals; phs, phalanges; pu, pubis; r, radius; sr, sacral rib; sv, sacral vertebra; t, tibia; u, ulna; V, fifth.

Table 1. *Taxa currently considered putative members of Euparkeriidae*

Taxon	Occurrence	Age	Material
Unambiguous Euparkeriidae			
Euparkeriidae Huene 1920			
<i>Euparkeria</i> Broom 1913a (including <i>Browniella</i> Broom 1913b)			
<i>E. capensis</i> Broom 1913a (including <i>Browniella africana</i> Broom 1913b)	<i>Cynognathus</i> Assemblage Zone, Subzone B, Burgersdorp Formation, Eastern Cape, South Africa	Early Anisian	Holotype: SAM-PK-5867, relatively complete skeleton including the skull Hypodigm: at least 11 individuals including all skeletal elements excepting distal caudal vertebral series, proximal caudal intercentra, and distal portions of some ribs and chevrons
Possible Euparkeriidae			
<i>Dorosuchus</i> Sennikov 1989			
<i>D. neoetus</i> Sennikov 1989	Donguz Gorizont, Orenburg, Russia	Anisian	Holotype: PIN 1579/161, right ilium, femur, tibia Hypodigm: left and right ilia, right femur, tibia, braincase, sacral and caudal vertebrae
<i>Wangisuchus</i> Young 1964			
<i>W. tzeyii</i> Young 1964	Upper Ermaying Formation, Shanxi (Shānxī), China	Late Anisian	Holotype: IVPP V 2701, a left maxilla Hypodigm: one left and two right maxillae, teeth, vertebrae, limb bones, osteoderms
Unnamed genus ‘<i>Turfanosuchus</i>’ Young 1973)			
‘<i>Turfanosuchus</i>’ <i>shageduensis</i> Wu 1982	Lower Ermaying Formation, Nei Mongol (Nèi Měnggǔ), China	Early Anisian	Holotype and only known specimen: IVPP V 6028, right mandibular ramus, six cervical vertebrae, right scapula, coracoid, humerus, radius, ulna, femur, tibia and fibula
<i>Halazhaisuchus</i> Wu 1982			
<i>H. qiaensis</i> Wu 1982	Lower Ermaying Formation, Shaanxi (Shānxī), China	Early Anisian	Holotype and only known specimen: IVPP V 6027, 13 vertebrae, scapulae, humeri, left coracoid, radius and ulna, proximal portions of ribs
<i>Osmolskina</i> Borsuk-Białynicka & Evans 2003			
<i>O. czatkowicensis</i> Borsuk-Białynicka & Evans 2003	Czatkowice 1 locality, Unnamed Formation, Małopolska (Małopolskie), Poland	Olenekian	Holotype: ZPAL R-I/77, anterior of maxilla with nasal process Hypodigm: catalogued material includes 200 skull bones including braincase and mandible, 63 vertebrae, 12 scapulae, 10 ilia, four ischia, five pubes, 15 femora, 18 tibiae, radius fragments, ulna fragments, fibula fragments, tarsals including astragalus, calcaneum, four distal tarsals, further uncatalogued material

Burgersdorp Formation were located at a palaeo-latitude of c. 65°S and outcrops of the Donguz Gorizont and lower Ermaying Formation at c. 35–40°N.

In summary, the stratigraphic ages of *Euparkeria capensis* and all of the putative euparkeriids are

uncertain, largely because none of the formations from which putative euparkeriids have been collected have been dated directly, and estimates of their ages are therefore based almost exclusively upon long-range vertebrate biostratigraphy. Because

Table 2. *Taxa formerly assigned to Euparkeriidae, no longer considered as possibly referable to the group (additionally, 'Fukangolepis' barbaros was assigned to Euparkeriidae in a lapsus calami)*

Taxon	Occurrence	Age	Material	Revised taxonomic assignment
<i>Turfanosuchus</i>				
Young 1973				
<i>T. dabanensis</i> Young 1973	Kelamayi Formation, Xinjiang, (Xinjiāng) China	Middle Triassic	Holotype and only known specimen: IVPP V 3237, skeleton lacking left girdles and limbs	Pseudosuchia incertae sedis (Nesbitt 2011)
<i>Xilousuchus</i>				
Wu 1981				
<i>X. sapingensis</i> Wu 1981	Heshanggou Formation, Shaanxi, (Shǎnxī) China	Late Olenekian– Anisian	Holotype and only known specimen: IVPP V 6026, maxillae, premaxilla, lacrimal, nasal, dentary, articular, surangular fragment, splenial, braincase, axis, presacral vertebrae 3–11, sacral vertebra, two distal caudal vertebrae, cervical rib, dorsal rib, clavicle, ungula	Pseudosuchia: Poposaurioidea: Ctenosauriscidae (Butler <i>et al.</i> 2011; Nesbitt <i>et al.</i> 2011)
<i>Platyognathus</i>				
Young 1944				
<i>P. hsui</i> Young 1944	Zhangjiawa Member, Lufeng Formation, Yunnan, (Yúnnán) China	Early Jurassic (?Hettangian– Sinemurian)	Holotype: CRL V 71, anterior conjoined dentaries Neotype and only currently known specimen (holotype lost): IVPP V 8266, rostrum	Pseudosuchia: Crocodyliformes (Wu & Sues 1996)
<i>Dongusia</i>				
Huene 1940				
<i>D. colorata</i> Huene 1940	Donguz Group, Orenburg, Russia	Anisian	Holotype and only known specimen: PIN 268/2, single dorsal vertebra	Archosauriformes indet., <i>nomen</i> <i>dubium</i> (Gower & Sennikov 2000)

of the well-established problems with terrestrial vertebrate biostratigraphy (e.g. Rayfield *et al.* 2005, 2009; Irmis *et al.* 2010), these age assignments should be treated with caution. All putative euparkeriid occurrences can be broadly characterized as of Olenekian–Anisian age (and thus cluster around the Lower/Middle Triassic boundary).

Relationships and evolution

Taxonomy and phylogenetic position of Euparkeria capensis

Broom (1913a, b) described the first (and, to date, only definitive) euparkeriids *Euparkeria capensis* and *Browniella africana*, with Huene (1920) defining Euparkeriidae to include only these two

genera. Haughton (1922) referred the majority of the syntype material of *B. africana* to *Euparkeria capensis*, and designated an isolated femur as the lectotype of *B. africana*. However, this isolated femur is likely referable to Euparkeria, making *B. africana* a subjective junior synonym of *E. capensis*.

Early work hypothesized *Euparkeria capensis* to be close in morphology to the archetypal ancestor of several major archosaur groups (e.g. Romer 1972), based upon its supposedly generalized morphology. In cladistic analyses, *Euparkeria capensis* has consistently been placed high on the archosaur stem (see summaries in Gower & Wilkinson 1996; Benton 2004), usually as either the sister taxon of crown Archosauria (Benton & Clark 1988; Parrish 1993; Bennett 1996; Nesbitt *et al.* 2009) or the sister taxon of Archosauria + Proterochampsidae (Serenio & Arcucci 1990; Serenio 1991; Juul 1994;

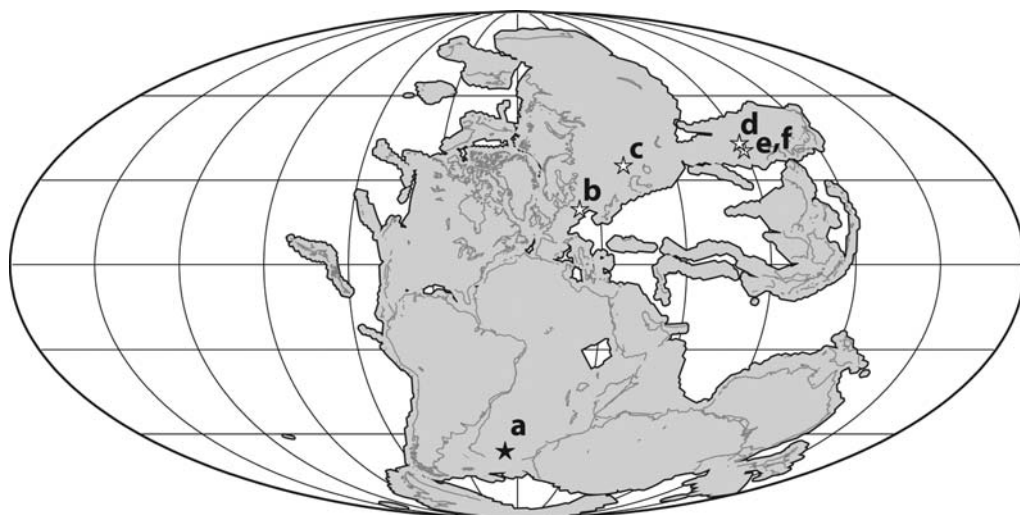


Fig. 5. Map showing distribution of putative euparkeriids. (a) *Euparkeria capensis*; (b) *Osmolskina czatkowicensis*; (c) *Dorosochus neoetus*; (d) *'Turfanosuchus' shageduensis*; (e) *Wangisuchus tzeiyii*; (f) *Halazhaisuchus qiaoenis*. Map produced using built in function from the Paleobiology Database.

Benton 1999; Parker & Barton 2008; Brusatte *et al.* 2010; Ezcurra *et al.* 2010), with Nesbitt (2011) finding *Euparkeria capensis* to be the sister taxon of Archosauria + Phytosauria (Fig. 6c). Nesbitt (2011) cited the following unambiguous characters as supporting the sister group relationship between *Euparkeria capensis* and Archosauria + Phytosauria (the latter clade was referred to as Crurotarsi by Nesbitt 2011): foramen on the medial side of articular; distal ends of neural spines of cervical vertebrae laterally expanded; neural spines of dorsal vertebrae with lateral expansion and flat dorsal margin; proximal end of fibula rounded/elliptical in proximal view; distal end of fibula asymmetrical in lateral view; posterior corner of dorsolateral margin of astragalus dorsally overlaps calcaneum more than anterior portion; calcaneal tuber shaft more broad than tall or roughly equal breadth and height.

The phylogenetic analysis of Dilkes & Sues (2009) was one of the few recent studies to find a markedly different position for *Euparkeria capensis*, with the taxon being placed outside of *Erythrosuchus africanus* + Archosauria, separated by at least four nodes from Archosauria (Fig. 6b). Dilkes & Sues (2009) proposed that this novel phylogenetic position relative to *Erythrosuchus africanus* resulted in part from the rescoring of a number of characters for the latter taxon; these included the absence of a parietal foramen (previously scored as present), presence of an antorbital fossa (previously scored as absent), presence of thecodont dentition (previously scored as absent), and

presence of dorsal osteoderms (previously scored as absent). A full assessment of the relative strengths of these competing phylogenetic hypotheses is currently complicated by their only partially overlapping character and taxon samples (e.g. Dilkes & Sues 2009; Nesbitt 2011). However, some of the scorings proposed for *Erythrosuchus africanus* were controversial, especially the presence of osteoderms (Gower 2003; Nesbitt 2011) and were changed in a recent analysis involving the first author (Dilkes & Arcucci 2012), which yielded a more conventional placement of *Euparkeria capensis* just outside crown archosaurs. Moreover, recent cladistic analyses that have attempted to build on the data set of Dilkes & Sues (2009) using increased character and taxon sampling have recovered *Euparkeria capensis* in a more conventional phylogenetic position, closer to crown Archosauria than *Erythrosuchus africanus* (Desojo *et al.* 2011; Ezcurra *et al.* 2010). Thus, the phylogenetic topology that places *Euparkeria capensis* outside of Archosauria, but more closely related to Archosauria than are erythrosuchids, remains the consensus hypothesis.

Some earlier authors have recovered *Euparkeria* in markedly different phylogenetic positions to the consensus viewpoint. Gauthier (1986) placed *Euparkeria capensis* within Archosauria, within the avian stem lineage, and as the sister taxon to the clade consisting of Ornithosuchidae + Ornithodira. Several workers, including Welman (1995), have posited that *Euparkeria capensis* is closely allied to (or directly ancestral to) birds, based on

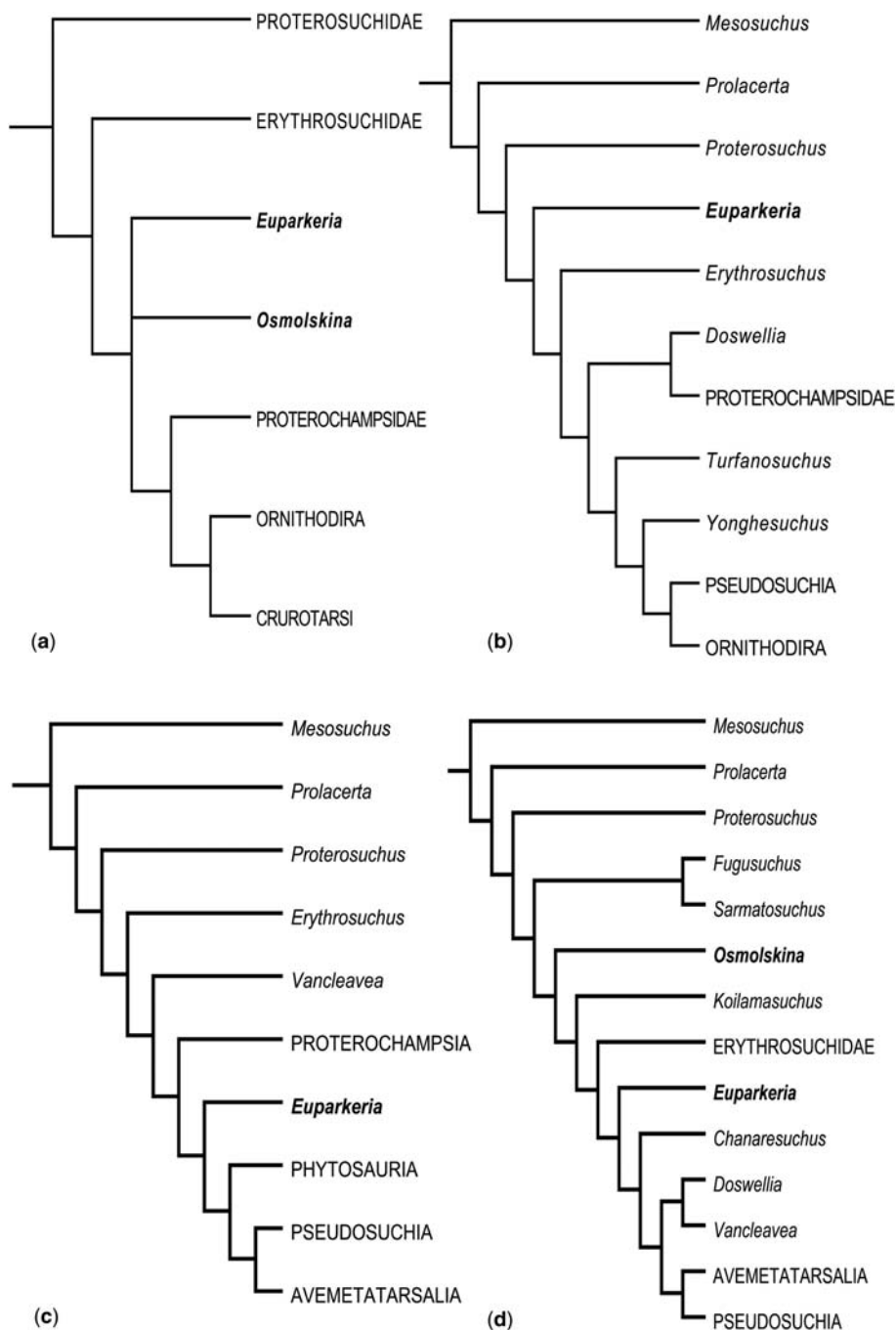


Fig. 6. The phylogenetic position of putative euparkeriids. (a) Simplified figure 1 from Borsuk-Bialynicka & Evans (2003) showing putative position of *Osmolskina* in a polytomy with *Euparkeria* and Archosauria+Proterochampsidae on Sereno's (1991) cladogram. (b) Simplified figure 16a from Dilkes & Sues (2009) showing position of *Euparkeria* on single most parsimonious cladogram – *Euparkeria* is placed further outside Archosauria here than in most recent analyses. (c) Simplified figure 51 from Nesbitt's (2011) analysis, showing the position of *Euparkeria* as sister to Archosauria + Phytosauria. (d) Simplified figure 7 from Ezcurra *et al.* (2010), placing *Osmolskina* further outside Archosauria than *Euparkeria* and thus failing to support monophyly of putative euparkeriids.

braincase morphology. Welman argued that dinosaur (and crocodylomorph) braincases were too derived to have given rise to those of birds, citing for example the passing of the palatine ramus of the facial nerve anterior to the otic capsule in *Sphenosuchus* and *Syntarsus*, but not in *Euparkeria* or birds, and the subdivision of the parasphenoid into basitemporal and pretemporal platforms. Welman's hypothesis was, however, convincingly dismissed by Gower & Weber's (1998) comprehensive reassessment of the braincase of *Euparkeria*. These authors demonstrated that Welman (who only investigated four taxa) presented no convincing evidence of synapomorphies uniting birds and *Euparkeria*, and found that crocodilians and birds are united to the exclusion of *Euparkeria* by three synapomorphies within the braincase, one of which ('presence of laterally positioned foramina in the parabasisphenoid for the entrance of the cerebral branches of the internal carotid arteries') exhibits no homoplasy.

Composition and position of Euparkeriidae

The only cladistic analysis to have included more than one putative euparkeriid (see Table 1 for listing of putative euparkeriids) was that of Ezcurra *et al.* (2010), which found that *Euparkeria capensis* and *Osmolskina czatkowicensis* Borsuk-Białynicka & Evans 2003 did not form a clade, with *Euparkeria capensis* placed slightly closer to Archosauria (immediately outside the clade including the proterochampsid *Chanaresuchus bonapartei* + Archosauria, as recovered by many other authors: see above) than *Osmolskina czatkowicensis* (placed immediately outside the clade including *Koilemasuchus gonzalezdiazi* + Erythrosuchidae + Archosauria) (Fig. 6d). *Osmolskina czatkowicensis* is the most recent taxon to be assigned to Euparkeriidae, and a non-numerical phylogeny presented by Borsuk-Białynicka & Evans (2003, 2009) placed *Osmolskina czatkowicensis* together with *Euparkeria capensis* as the sister taxon of Archosauria + Proterochampsidae, although no synapomorphies linking the two species were identified.

Dorosuchus neoetus Sennikov 1989 was assigned to Euparkeriidae by Sennikov (1989), who also erected two subfamilies: Euparkeriinae (composed of *Euparkeria capensis* and *Browniella africana*) and Dorosuchinae (composed of *Dorosuchus neoetus*, *Wangisuchus tzeyii*, *Xilousuchus sapingensis*, *Turfanosuchus dabanensis* and *Halazhaisuchus qiaoensis*). However, Gower & Sennikov (2000) cast doubt on the euparkeriid assignment of *Dorosuchus neoetus*, citing the lack of synapomorphies of the clade and the incompleteness of material. Borsuk-Białynicka & Evans (2003) and Borsuk-Białynicka & Sennikov (2009) proposed, however,

that the hypothesis that *Dorosuchus neoetus* is a euparkeriid is better supported than for all other taxa, with the exceptions of *Euparkeria capensis* and *Osmolskina czatkowicensis*, based on the generally similar morphology of all three taxa and the larger amount of material available compared to other putative euparkeriids.

Three Chinese species are considered as putative euparkeriids, but their assignment has also not been tested cladistically. *Wangisuchus tzeyii* Young 1964 was described and assigned to Euparkeriidae by Young (1964). Although multiple authors have doubted this placement (e.g. Kuhn 1976; Parrish 1993; Gower & Sennikov 2000; Nesbitt 2011), largely on the basis of the presence of a suchian calcaneum within material questionably referred to this taxon by Young (1964), further work on the holotype (a maxilla) and referred specimens are needed to preclude euparkeriid affinities. '*Turfanosuchus*' *shageduensis* Wu 1982 and *Halazhaisuchus qiaoensis* Wu 1982 were also assigned to Euparkeriidae upon initial description. '*T.*' *shageduensis* is probably generically distinct from *Turfanosuchus* (Gower & Sennikov 2000). Gower & Sennikov (2000) expressed doubts about the euparkeriid assignment of the Chinese taxa due to the incompleteness of material (see also Borsuk-Białynicka & Evans 2003).

Four other taxa have been placed in Euparkeriidae, but today these are generally agreed not to be assignable to the group (Table 2). *Dongusia colorata* Huene 1940 and *Platyognathus hsui* Young 1944 were referred to Euparkeriidae by Romer (1956) and Huene (1956), respectively. Both assignments were doubted by Kuhn (1976), who posited a crocodilian affinity for *Platyognathus hsui*, which was subsequently confirmed cladistically (Wu & Sues 1996). Kuhn deemed *Dongusia colorata* an indeterminate archosaur, with Gower & Sennikov (2000) regarding it as a *nomen dubium* of possible 'rauisuchian' grade. *Turfanosuchus dabanensis* Young 1973 was assigned to the clade by Young (1973), was redescribed by Wu & Russell (2001), and has been placed within Pseudosuchia by the most comprehensive and recent cladistic analyses (Nesbitt 2011; but see Parker & Barton 2008 for an alternative non-euparkeriid archosauriform placement). *Xilousuchus sapingensis* Wu 1981 was assigned to Euparkeriidae by Sennikov (1989), but recent analyses place it within Poposauroidae (Butler *et al.* 2011; Nesbitt 2011; Nesbitt *et al.* 2011). Additionally, '*Fukangolepis*' *barbaros* Yang 1978 was mentioned as possibly referable to the Euparkeriidae by Parrish (1986) in what was presumably a *lapsus calami* given that '*Fukangolepis*' *barbaros* is an indeterminate dicynodont skull fragment (Lucas & Hunt 1993) previously assigned by Young (1978) to Aetosauria.

Palaeobiology

Size, growth and reproduction

Euparkeria capensis was a small animal (largest known individuals reaching c. 1 m in length: Botha-Brink & Smith 2011). Using bone histology, Botha-Brink & Smith (2011) recognized that the known *Euparkeria capensis* specimens represent adult individuals. They found *Euparkeria capensis* to have had slower growth rates and therefore probably later sexual maturity than Early Triassic archosauromorph taxa such as the similarly sized *Prolacerta broomi* or crown-group archosaurs. They hypothesized that slower growth rates were reacquired in the more stable environment of the Middle Triassic (as opposed to rapid growth rates in the environmentally unstable Early Triassic: Smith & Botha 2005), where rainfall was more predictable, and juvenile and adult mortality hypothesized to have been lower (Botha-Brink & Smith 2011). *Euparkeria capensis* thus differed in growth strategies from both crown-group archosaurs and taxa further separated from Archosauria, emphasizing the previously noted variability and reversibility of growth rates within archosauriform phylogeny (de Ricqlès *et al.* 2008; Botha-Brink & Smith 2011).

Gait and stance

Based on forelimb to hindlimb and hind limb to trunk proportions, *Euparkeria capensis* has been proposed to have had a facultatively bipedal gait (Ewer 1965; Santi 1993). The osteoderms (by stabilizing the vertebral column as in modern crocodiles; Frey 1985) and elongate tail (by acting as a counterbalance to the elevated trunk) may have assisted with stability during bipedal locomotion (Ewer 1965; Santi 1993). However, no specific adaptations of the forelimb to bipedality have been recognized (Ewer 1965; Remes 2007). Moreover, caution is warranted given the proportionally elongate humerus when compared to those of bipedal dinosauromorphs and poposauroids (Remes 2007; Gauthier *et al.* 2011) and the proportionally large head that may have made the animal too front-heavy for sustained bipedality (Paul 2002).

Regarding stance, Ewer (1965) suggested that during slow, quadrupedal movement the femur would have been held largely horizontally, but that *Euparkeria capensis* was able to hold the femur in an adducted, near-vertical orientation when running, to facilitate bipedality. A sprawling to semi-erect posture of the humerus during locomotion (based on muscle reconstructions: Remes 2007) has similarly been proposed. *Euparkeria capensis* has also been proposed to have had a stance approaching the 'high walk' of juvenile crocodilians

(Paul 2002). Parrish (1986) also argued for a crocodilian-like 'semi-erect' gait. During locomotion, the calcaneal flange would have assisted in propulsion by providing a longer moment arm for the *peroneus longus* muscle, as it does in modern *Varanus* and analogous to the function of the calcaneal tuber in crocodiles (Sullivan 2010).

Behaviour

Euparkeria capensis was probably carnivorous or insectivorous based on its dental morphology (Ewer 1965; Senter 2003). If indeed carnivorous, *Euparkeria capensis* would probably have been restricted to medium- to small-sized prey in light of its own small size and the proposed absence of well-developed pterygoideus musculature (Ewer 1965).

Recent work examining sclerotic ring size suggests that *Euparkeria capensis* was scotopic (a large aperture for given focal length and retinal area, as measured by a large internal scleral-ring diameter in comparison to external diameter and orbit length) and thus probably nocturnal, or at least adapted to low-light conditions (Schmitz & Motani 2011). This supports work indicating stem archosaurs may have had visual pigments adapted for low light (Chang *et al.* 2002). The Karoo environment was at high latitude (c. 65°S; see below), and *Euparkeria capensis* may thus have experienced long periods of darkness and light in winter and summer, respectively (Schmitz & Motani 2011).

Future directions

It is currently not clear if Euparkeriidae as hypothesized is mono-, para- or polyphyletic, and substantial further work is needed to better understand the composition, within-group relationships and position on the archosauromorph tree of Euparkeriidae. Chinese and Russian material in particular requires further detailed anatomical study, and more detailed comparison with material of *Euparkeria capensis* is necessary to create accurate diagnoses, identify any possible synapomorphies of the clade, as well as to delineate autapomorphies for each of the putative euparkeriid taxa and thus stabilize their taxonomy. Subsequently, taxonomically and anatomically comprehensive numerical phylogenetic analyses are required to assess the composition of Euparkeriidae and the position of the various putative euparkeriids relative to both each other and to other archosauriform taxa. Improved biostratigraphy studies, and further work on functional morphology – especially locomotion – are also greatly needed. This work should, by helping to increase the accuracy of the archosauromorph tree and by

clarifying morphological features of these early taxa, serve to shed light on the rise of archosauromorphs and archosaurs, as timing, rate and mode of both functional and taxonomic diversification may be better understood.

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Appendix: Institutional abbreviations

CRL, Cenozoic Research Laboratory, National Geological Survey of China, Beijing, China; GPIT, Paläontologische Sammlung der Universität Tübingen; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; PIN, Paleontological Institute, Moscow, Russia; SAM, Iziko South African Museum, Cape Town, South Africa; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

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