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Notes

Ornithosuchidae: a group of Triassic archosaurs with a unique ankle joint

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Abstract: The ornithosuchids were a group of archosaurs with body lengths ranging from 2 to 4 m recorded from Upper Triassic beds in Argentina and Scotland. The group was defined as a node-based clade including *Ornithosuchus longidens*, *Riojasuchus tenuisceps*, *Venaticosuchus rusconii* and all descendants of their most recent common ancestor. The ornithosuchids are diagnosed by the following apomorphies observed in the three known species of the clade: downturned premaxilla; premaxilla−maxilla contact with a diastema in the alveolar margin equal in length to two teeth; palatine−pterygoid fenestra; and orbit with a distinct ventral point surrounded by 'V'-shaped dorsal processes of the jugal. The most remarkable postcranial apomorphy of the group is the presence of the so-called crocodile reversed ankle joint, a condition that seems to be unique for the ornithosuchids among amniotans. The systematic history of Ornithosuchidae is complex and *Ornithosuchus* was allied with dinosaurs or phytosaurs prior to the implementation of numerical phylogenetic analyses. Currently, there is consensus that Ornithosuchidae is positioned within Pseudosuchia, but their phylogenetic position within the group remains strongly debated. Nevertheless, all hypotheses agree in inferring an extremely long ghost lineage at the base of the clade. The presence of derived pseudosuchians in the late Olenekian produces a ghost lineage of *c.*16−18 millions of years for Ornithosuchidae, indicating that only the late evolutionary history of the clade is currently sampled in the fossil record.

The pseudosuchians were the taxonomically and morphologically most diverse lineage of archosaurs during the Triassic Period (Brusatte *et al.* 2008), a time span that saw the origin and early evolutionary radiation of the stem lineages of most modern vertebrate clades (Sues & Fraser 2010). The fossil record of pseudosuchians is restricted to members of 'Rauisuchia' during the Early and Middle Triassic (Butler *et al.* 2011; Nesbitt *et al.* 2011). Indeed, it is not until the Late Triassic that members of Aetosauria, Phytosauria (recently considered as non-archosaur archosauriforms; Nesbitt 2011), Crocodylomorpha and Ornithosuchidae make their appearance in the sedimentary rocks record. With the exception of Ornithosuchidae, these pseudosuchian clades share a common morphological pattern in the tarsus, the so-called 'crocodile-normal' ankle joint, which consists of peg in the astragalus and a socket in the calcaneum (Chatterjee 1978). By contrast, a different tarsal morphology is present in ornithosuchids, the so-called 'crocodile-reversed' ankle joint, which is an apomorphic condition of the group (Chatterjee 1978; Brinkman 1981; Cruickshank & Benton 1985; Sereno 1991). The 'crocodile-reversed' ankle joint consists of a peg in the calcaneum and a socket in the astragalus (Chatterjee 1978). This hindlimb trait has captured the attention of several authors (e.g. Cruickshank & Benton 1985; Novas 1989; Sereno 1991; Parrish 1993), who considered ornithosuchids to be a pivotal clade for reconstructing the early evolutionary history of Pseudosuchia.

The group Ornithosuchidae was originally coined by Huene (1908) based only on *Ornithosuchus*. During the 1960s, the discovery of new pseudosuchians in the Triassic of northwestern Argentina increased the taxonomic content of the clade, with the addition of *Riojasuchus tenuisceps* and *Venaticosuchus rusconii* (Bonaparte 1967, 1970, 1972). The ornithosuchids were predatory pseudosuchians with a body length ranging from 2 to 4 m. The most diagnostic traits of these animals are, together with the peculiar tarsal anatomy, the presence of a downturned premaxilla and a diastema within the upper marginal tooth row below the external nares. Ornithosuchids are currently known from Upper Triassic beds of Scotland and Argentina (Fig. 1), indicating a wide palaeolatitudinal distribution.
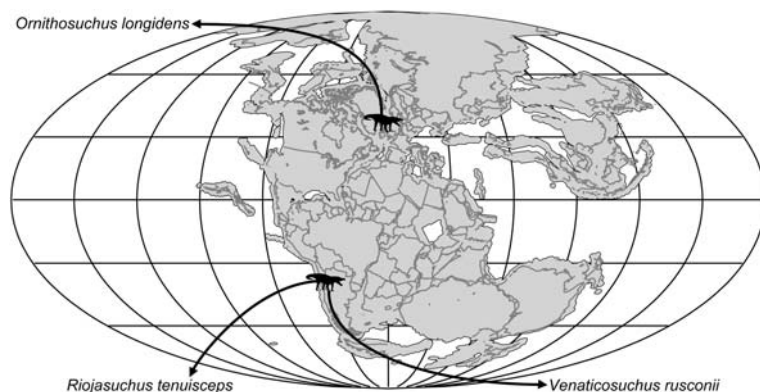
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Fig. 1. Palaeobiogeographical distribution of Ornithosuchidae across Pangaea during the Late Triassic (palaeomap for 230 Ma downloaded from the *Paleobiology Database*). Black ornithosuchid silhouettes indicate the procedence of *Ornithosuchus longidens* from Scotland and *Riojasuchus tenuisceps* and *Venaticosuchus rusconii* from Argentina.

Phylogenetic definition

Ornithosuchidae, Huene (1908). Node-based definition, *Ornithosuchus longidens* (Huxley 1877), *Riojasuchus tenuisceps* Bonaparte 1967, *Venaticosuchus rusconii* Bonaparte 1970 and all descendants of their most recent common ancestor, as defined by Sereno (1991). More recently, Benton (2004) redefined this clade as those taxa stemming from the last common ancestor of *Ornithosuchus longidens* and *Riojasuchus tenuisceps*, and sharing a more recent common ancestor with those species than with *Mystriosuchus planirostris (*Meyer 1863*), Stagonolepis robertsoni* Agassiz 1844 or Crocodylia. Sereno *et al.* (2005) considered Ornithosuchidae as the most inclusive clade containing *Ornithosuchus longidens* but not *Rutiodon carolinensis* Emmons 1856, *Aetosaurus ferratus* Fraas 1877, *Rauisuchus tiradentes* Huene 1942, *Prestosuchus chiniquensis* Huene 1942 or *Crocodylus niloticus* Laurenti 1768. Finally, Nesbitt (2011) employed a modified version of the definition provided by Sereno *et al.* (2005), including *Passer domesticus* Linnaeus 1758 as an external specifier. Considering the numerous definitions given of Ornithosuchidae over the last 20 years, we decided to follow temporal priority and use the original definition of Sereno (1991) as a node-based clade for the sake of stability.

The taxonomic content of Ornithosuchidae has not been modified over the last 40 years, being composed of *Ornithosuchus longidens*, *Riojasuchus tenuisceps* and *Venaticosuchus rusconii*. The clade Ornithosuchidae has been diagnosed recently by Nesbitt (2011: 194) on the basis of the following 13 synapomorphies, present in the most completely known species of the group (i.e. *Ornithosuchus longidens* and *Riojasuchus tenuisceps*): (1) premaxilla with three tooth positions; (2) premaxilla downturned; (3) premaxilla–maxilla contact with a diastema in the alveolar margin equal in length to two teeth (hereafter referred to as the 'subnarial gap'); (4) nasal-prefrontal contact absent; (5) postfrontal with a posterolateral process anteriorly inclined at an angle greater than 45°; (6) palatine–pterygoid fenestra present; (7) orbit with distinct ventral point surrounded by 'V'-shaped dorsal processes of jugal; (8) dentary–splenial mandibular symphysis present along one-third of the lower jaw; (9) cervical vertebrae have a middle portion of the ventral keel that extends ventral to the centrum rims; (10) pubis 70% or more of femoral length; (11) femoral anterior trochanter forms a steep margin with the shaft, but is completely connected to it; (12) astragalus–calcaneum with a ventral articular surface that is concavo-convex with the concavity on the astragalus ('crocodile-reversed' ankle joint); and (13) metatarsal V without a 'hooked' proximal end. Synapomorphies 2, 3, 6 and 7 can be recognized in the partial skull of *Venaticosuchus rusconii*. Thus, the remaining synapomorphies proposed by Nesbitt (2011) should be interpreted in a strict sense only as probable synapomorphies of Ornithosuchidae pending discovery of more complete material of *Venaticosuchus rusconii*.

Fossil record

Ornithosuchids are currently restricted to Late Triassic beds of South America and Europe (Table 1). *Ornithosuchus longidens* is known from numerous well-preserved specimens of different ontogenetic stages from the Lossiemouth Sandstone Formation of Moray, northeastern Scotland (Huxley 1877;

Table 1. *Taxonomic content of Ornithosuchidae Huene (1908) sensu Bonaparte (1971, 1972)*

Taxon	Occurrence	Age	Material
Ornithosuchus longidens (Huxley 1877)	Lossiemouth Sandstones Formation, Moray, Scotland	Late Carnian–earliest Norian	Partial skeletons and isolated elements
Venaticosuchus rusconii Bonaparte 1970	Ischigualasto Formation, La Rioja, Argentina	Late Carnian–earliest Norian	Partial skull (postcranial bones currently lost)
Riojasuchus tenuisceps Bonaparte 1967	Los Colorados Formation, La Rioja, Argentina	Middle Norian	Partial skeletons

Newton 1894; Walker 1964) (Fig. 2). The beds that yielded the specimens of *Ornithosuchus* have been correlated with the *Hyperodapedon* Assemblage Zone recognized in the South American Santa María and Ischigualasto formations based on the presence in the Lossiemouth Sandstone Formation of abundant remains of the derived rhynchosaur *Hyperodapedon gordoni* (e.g. Langer 2005). This correlation suggests a late Carnian–earliest Norian age of deposition for the Lossiemouth Sandstones Formation following the radioisotopic dates that constrain the age of the Argentinean Ischigualasto Formation (Rogers *et al.* 1993; Martínez *et al.* 2011). Thus, *Ornithosuchus longidens* is probably one of the oldest known members of the clade.

Venaticosuchus rusconii is known from a partial skeleton collected in the Ischigualasto Formation of La Rioja Province, northwestern Argentina. Bonaparte (1970) noted that the holotype and currently only known specimen of the species comprises a partial skull (Fig. 3b), an incomplete forelimb, and osteoderms. However, the postcranial remains could not be located within the collections of the Instituto 'Miguel Lillo' of Tucumán in 2011 and currently seem to be lost (von Baczko 2012). *Venaticosuchus rusconii* comes from a locality of the Ischigualasto Formation cropping out near to Cerro Las Lajas, which is several kilometres NW of the 'La Hoyada de Ischigualasto' in San Juan Province. The latter area has provided the vast majority of vertebrates collected from the Ischigualasto Formation and has been the focus of all previous stratigraphic studies of the formation. The type locality of *Venaticosuchus rusconii* was considered by Bonaparte (1970) to be situated within the middle part of the Ischigualasto Formation. However, Martínez *et al.* (2011) more recently indicated that there is currently insufficient stratigraphic evidence to determine the position of the Cerro Las Lajas locality within the Ischigualasto Formation. *Venaticosuchus rusconii* was found together with an associated fauna including the ornithischian *Pisanosaurus mertii* (Casamiquela 1967; Bonaparte 1976) and a basal crocodylomorph specimen (Bonaparte 1978, 1997; Ezcurra *et al.* 2008). Nevertheless, no

taxa that are widely employed in Triassic continental biostratigraphical correlations have been collected from the Cerro Las Lajas locality (e.g. rhynchosaurs, cynodonts), thus preventing accurate lateral correlation to the stratigraphic sequence of the 'La Hoyada de Ischigualasto' (Ezcurra 2012). Accordingly, the age of *Venaticosuchus rusconii* should be considered to be constrained only to that of the entire Ischigualasto Formation (i.e. late Carnian–earliest Norian; 232–225 million years ago (mya); Martínez *et al.* 2011).

Riojasuchus tenuisceps is represented by four specimens (Fig. 3a) from the uppermost levels of the Los Colorados Formation, as part of the so-called 'La Esquina Fauna' (Bonaparte 1972, 1982b) of La Rioja Province, northwestern Argentina. The 'La Esquina Fauna' has been dated recently as middle Norian (217–215 mya) based on magnetostratigraphic information (Santi Malnis *et al.* 2011) and, as a result, is the youngest ornithosuchid record. The holotype (PVL 3827) and a referred specimen (PVL 3828) of *Riojasuchus tenuisceps* are represented by fairly complete skeletons, while the other two referred specimens (PVL 3814 and 3826) are based on partial postcrania.

An isolated femur identified as a possible ornithosuchid was reported by Long & Murry (1995) from the Late Triassic Colorado City Formation (Otis Chalk Quarry 3) of the Dockum Group of Texas, southwestern USA. These authors referred this femur tentatively to the Ornithosuchidae because it was quite similar to that of *Ornithosuchus longidens*, sharing the presence of a well-developed anterior trochanter (Long & Murry 1995: 64). Furthermore, Long & Murry (1995) suggested that the Otis Chalk specimen resembled *Ornithosuchus longidens* more closely than *Riojasuchus tenuisceps*, because it was more gracile and possessed lower anterior and fourth trochanters. However, Nesbitt *et al.* (2010) noted that the Otis Chalk femur closely resembles that of silesaurid dinosauriforms and presents synapomorphies of the clade (e.g. absent posteromedial tuber, femoral head with a straight medial articular facet and a transverse straight groove on its proximal surface, distal
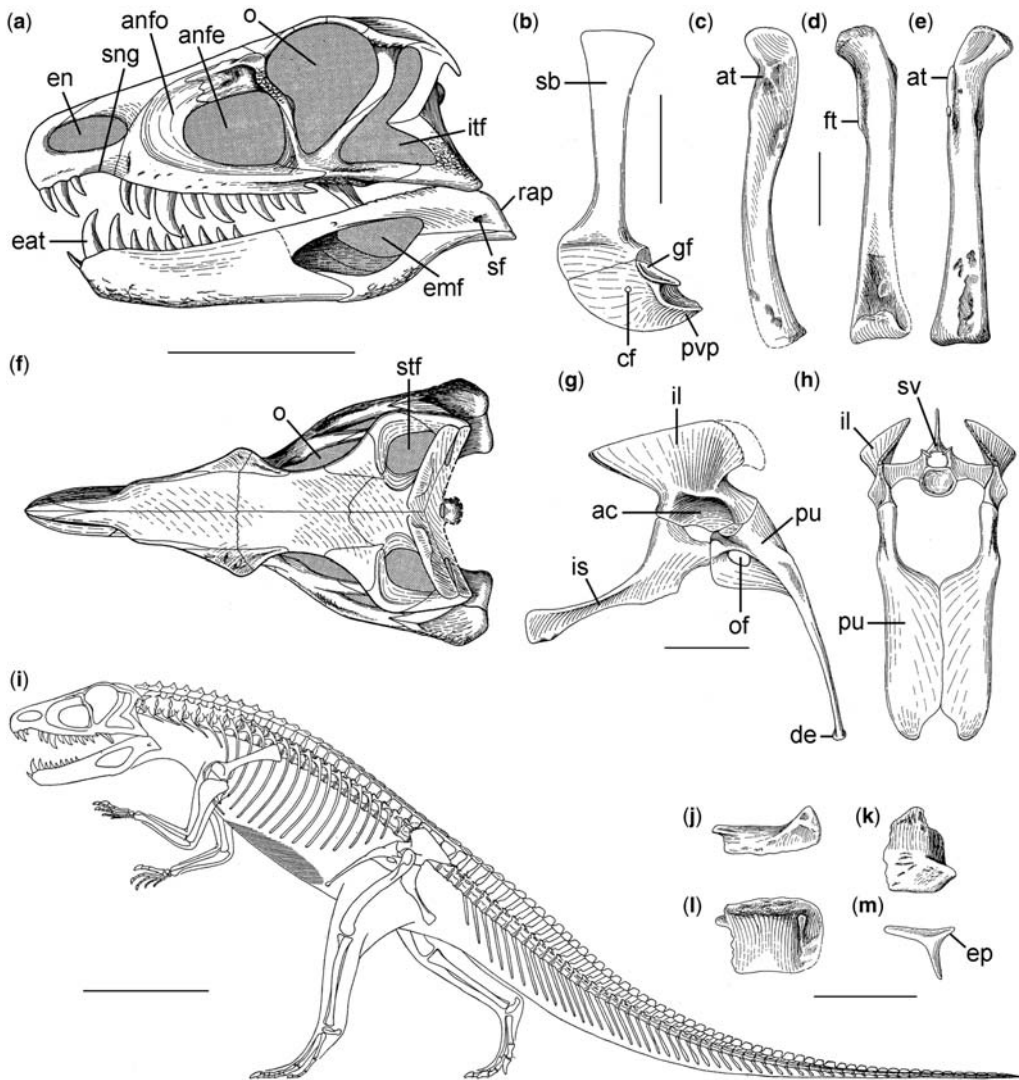
Fig. 2. Selected bones and skeletal reconstruction of *Ornithosuchus longidens* (Huxley 1877). Skull in left lateral (**a**) and dorsal (**f**) views. (**b**) Left scapula-coracoid in lateral view. Left femur in lateral (**c**), posterior (**d**) and anterior (**e**) views. Pelvic girdle in right lateral (**g**) and anterior (**h**) views. (**i**) Skeletal reconstruction in left lateral view. Fourth left cervical osteoderm in lateral (**j**) and ventral (**l**) views. Seventh right cervical osteoderm in dorsal (**k**) and posterior (**m**) views. (From Walker 1964.) *Abbreviations*: ac, acetabulum; anfe, antorbital fenestra; anfo, antorbital fossa; at, anterior trochanter; cf, coracoid foramen; eat, enlarged anterior dentary tooth; emf, external mandibular fenestra; en, external naris; ep, external prominence; ft, fourth trochanter; gf, glenoid fossa; il, ilium; is, ischium; itf, infratemporal fenestra; o, orbit; of, obturator foramen; pu, pubis; pvp, posteroventral process; rap, retroarticular process; sb, scapular blade; sf, surangular foramen; sng, subnarial gap; stf, supratemporal fenestra; sv, sacral vertebra. Scale bars: 10 cm (a, f, i); 5 cm (g, h); 2 cm (b, c–e); 1 cm (j–m).

condyles divided posteriorly between one-quarter and one-third the length of the shaft). Accordingly, these authors reinterpreted the Otis Chalk femur (together with other femora, tibiae and humeri from the same locality) as a possible distinct taxon of silesaurid dinosauriform.

Anatomy

Our understanding of ornithosuchid anatomy comes primarily from the partial skeletons of *Ornithosuchus longidens* and *Riojasuchus tenuisceps* (Walker 1964; Bonaparte 1972) (Figs 2–5). By contrast,
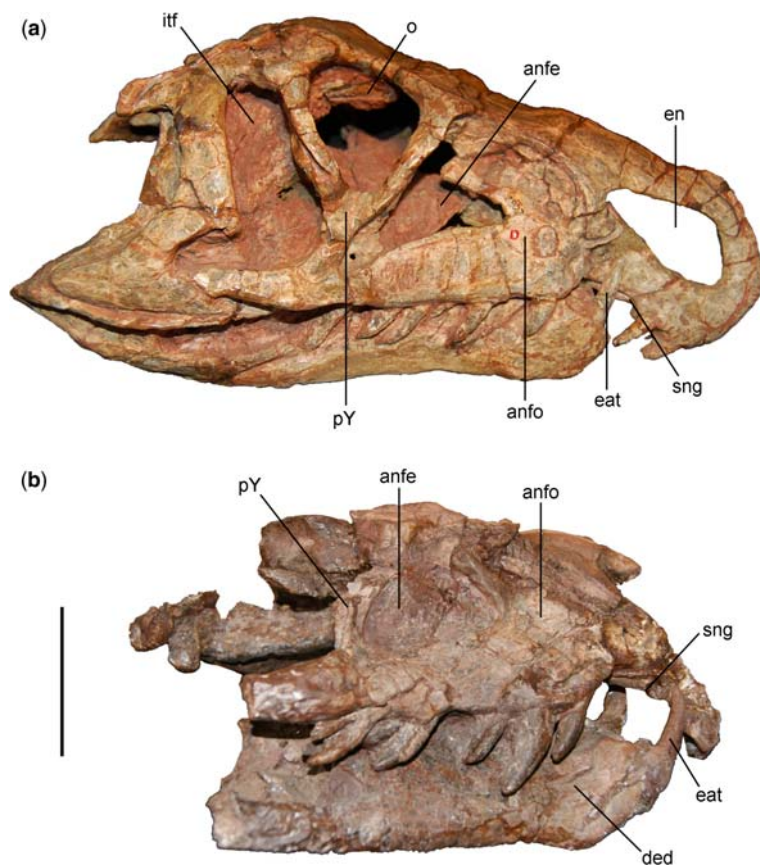
Fig. 3. Skulls of the holotypes of *Riojasuchus tenuisceps* Bonaparte 1967 (PVL 3827) (**a**) and *Venaticosuchus rusconii* Bonaparte 1970 (PVL 2578) (**b**) in right lateral views. *Abbreviations*: anfe, antorbital fenestra; anfo, antorbital fossa; ded, dorsoventrally expanded anterior end of dentary; eat, enlarged anterior dentary tooth; en, external naris; itf, infratemporal fenestra; o, orbit; pY, 'Y'-shaped ascending process of jugal; sng, subnarial gap. Scale bar: 5 cm.

Venaticosuchus rusconii is known only from highly incomplete cranial remains (Bonaparte 1970) (Fig. 3b). Thus, the present account of ornithosuchid cranial anatomy is based on all three known species but the postcranial morphology is based only on *Ornithosuchus longidens* and *Riojasuchus tenuisceps*.

The most conspicuous cranial features of ornithosuchids are a subtriangular skull in lateral view, with the height of the postorbital region considerably taller than that of the snout, a strongly downturned premaxilla that extends far beyond the anterior tip of the lower jaws, and the presence of a subnarial gap formed mainly by an edentulous region at the posterior end of the oral margin of the premaxilla (Figs 2 & 3: sng). The external naris is proportionally large in all three species (Figs 2 & 3: en), but longer than the antorbital fenestra in *Riojasuchus tenuisceps* and also probably *Venaticosuchus rusconii*. The antorbital fenestra is

proportionally small and surrounded by a well-developed antorbital fossa that covers most of the lateral surface of the maxilla in the three known ornithosuchid species (Figs 2 & 3: anfo). The jugal possesses a peculiar morphology, with a single 'Y'-shaped ascending process with two dorsal rami in *Riojasuchus tenuisceps* and *Venaticosuchus rusconii* (Fig. 3: pY) and with two distinct ascending processes in *Ornithosuchus longidens*. Each ascending ramus of the jugal contacts the lacrimal and the ventral process of the postorbital, respectively. The postorbital is a triradiate bone and the ventral process is particularly short in comparison with the height of the skull at that level in *Riojasuchus tenuisceps*. The quadratojugal is 'V'-shaped in lateral view, with an anterodorsally oriented dorsal process that contacts the ventral process of the squamosal at its most distal tip in both *Riojasuchus tenuisceps* and *Ornithosuchus*
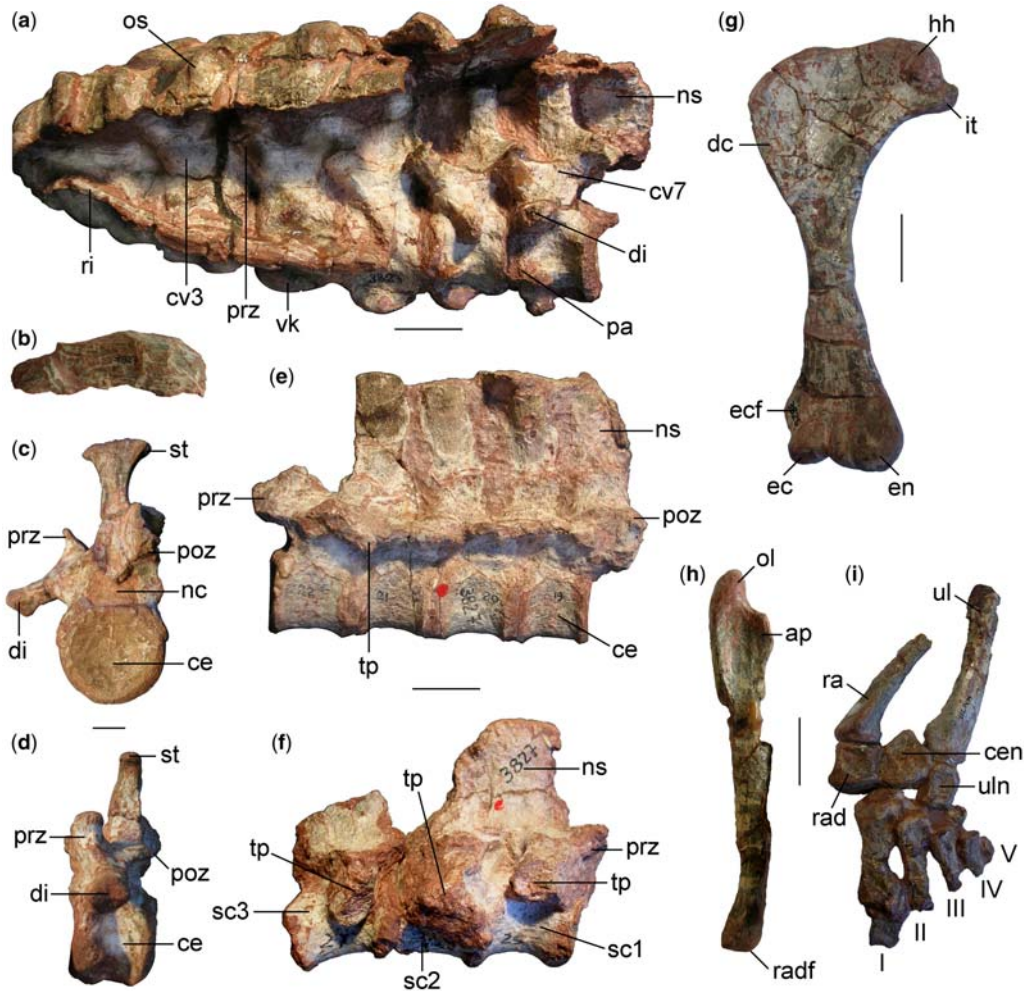
Fig. 4. Selected postcranial axial skeleton and forelimb elements of *Riojasuchus tenuisceps*. (a–f, i) PVL 3827, (g) PVL 3826 and (h) PVL 3828. (**a**) First seven cervical vertebrae, and eight cervical neural spine with articulated osteoderms in left lateral view. (**b**) Left osteoderm in dorsal view. Anterior dorsal vertebra in posterior (**c**) and lateral (**d**) views. (**e**) Articulated four middle dorsal vertebrae in left lateral view. (**f**) Articulated sacral vertebrae in right lateral view. (**g**) Right humerus in anterior view. (**h**) Left ulna in medial view. (**i**) Partial left forelimb in dorsal view. *Abbreviations*: I–V, first–fifth metacarpal; ap, anterior process; ce, centrum; cen, centrale; cv3, third cervical vertebra; cv7, seventh cervical vertebra; dc, deltopectoral crest; di, diapophysis; ec, ectepicondyle; ecf, ectepicondylar flange; en, entepicondyle; hh, humeral head; it, internal tuberosity; nc, neural canal; ns, neural spine; ol, olecranon; os, osteoderm; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; ra, radius; rad, radiale; radf, radiale facet; ri, rib; sc1–3, first–third sacral vertebra; st, spine table; tp, transverse process; ul, ulna; uln, ulnare; vk, ventral keel. Scale bars: 2 cm (a, e–i); 1 cm (b–d).

longidens (Figs 2a & 3a). At this point, the infratemporal fenestra is constricted by the ventral process of the squamosal and quadratojugal in both species. The supratemporal fenestra is small, dorsally oriented, and bordered by the parietal, postorbital and squamosal. The squamosal has a long posterior process that is extended beyond the posterior margin of the quadrate head in ornithosuchids, but the

condition of *Venaticosuchus rusconii* is unknown. The quadrate is posteriorly curved, mainly in *Riojasuchus tenuisceps*, resulting in an occipital condyle positioned considerably anteriorly to the craniomandibular joint. The palate of ornithosuchids does not bear teeth and differs from other archosaurs in the presence of a palatine–pterygoid fenestra. The lower jaw bears enlarged anterior teeth that fit
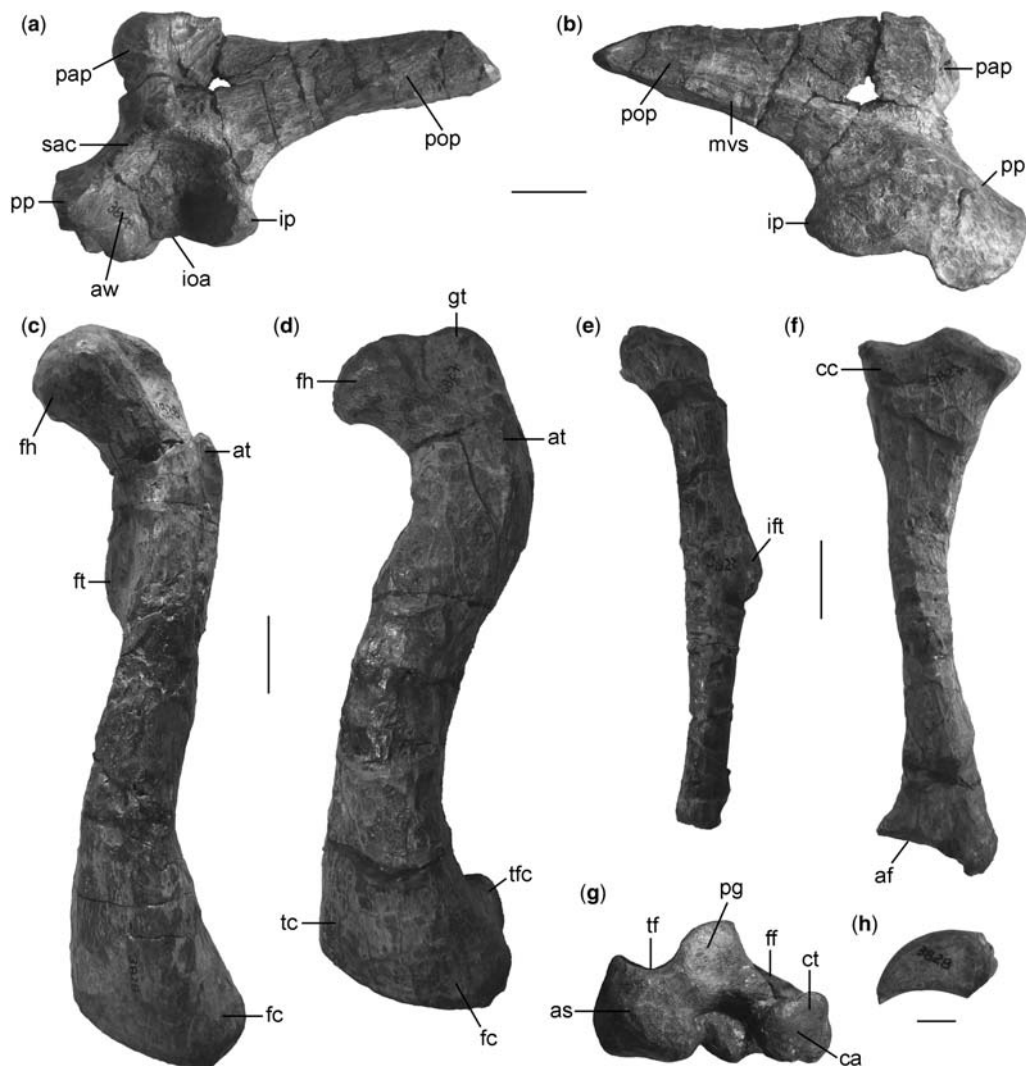
Fig. 5. Selected hindlimb and pelvic girdle elements of *Riojasuchus tenuisceps*. (a–c, h) PVL 3828 and (d–g) PVL 3827. Left ilium in lateral (**a**) and medial (**b**) views. Left femora in anterior (**c**) and anterolateral (**d**) views. (**e**) Left fibula in medial view. (**f**) Left tibia in lateral view. (**g**) Articulated astragalus and calcaneum in posterior view. (**h**) Pedal ungual phalanx in side view. *Abbreviations*: af, astragalar facet; as, astragalus; at, anterior trochanter; aw, acetabular wall; ca, calcaneum; cc, cnemial crest; ct, calcaneal tuber; fc, fibular condyle; ff, fibular facet; fh, femoral head; ft, fourth trochanter; gt, greater trochanter; ifc, iliofibular tubercle; ioa, incipiently open acetabulum; ip, ischiadic peduncle; mvs, medioventral shelf; pap, preacetabular process; pg, posterior groove; pop, postacetabular process; pp, pubic peduncle; sac, supra-acetabular crest; tc, tibial condyle; tf, tibial facet; tfc, tibiofibular crest. Scale bars: 2 cm (a–f); 1 cm (g–h).

into the transverse constriction present in the skull at the level of the subnarial gap in the three species. In *Riojasuchus tenuisceps* and *Venaticosuchus rusconii* the enlarged teeth occur in the first two dentary tooth positions, whereas in *Ornithosuchus longidens* the fang-like dentary teeth are the second and the third (Sereno 1991). The external

mandibular fenestra is oval and proportionally anteroposteriorly longer in *Riojasuchus tenuisceps* and *Venaticosuchus rusconii* than in *Ornithosuchus longidens* (Fig. 2a: emf).

The vertebral series is represented by 9 cervical, 14–15 dorsal, 3 sacral and 25–35 caudal vertebrae in *Riojasuchus tenuisceps* (Bonaparte 1972)

(Fig. 4). A similar condition is observed in *Ornithosuchus longidens*, with 9 cervical, 15 dorsal, 3 sacral and an unknown number of caudal vertebrae (Walker 1964). All vertebrae are short and tall, with elongate and vertically orientated neural spines (Fig. 4a, c–f). The axis of *Riojasuchus tenuisceps* is longer than the postaxial cervical vertebrae and has a well anteroposteriorly developed, blade-like neural spine. In *Riojasuchus tenuisceps*, the postaxial cervical vertebrae have weakly opisthocoelous centra with a well-developed ventral median keel (Fig. 4a: vk). These postaxial cervical vertebrae possess neural spines that are slightly transversely expanded at their distal ends in both *Riojasuchus tenuisceps* and *Ornithosuchus longidens* (Walker 1964; Bonaparte 1972) (Fig. 4a). The prezygapophyses are anterodorsally directed in the anterior and middle cervical vertebrae, but they are almost completely dorsally oriented in the anterior dorsal vertebrae of *Riojasuchus tenuisceps* (Fig. 4d: prz). The centra of the dorsal vertebra are spool-shaped and with subcircular articular facets (Fig. 4c). The spine tables are strongly transversely developed as 'T'-shaped structures in the anterior dorsal vertebrae of, at least, *Riojasuchus tenuisceps* (Fig. 4c: st). The spine tables are less conspicuously developed in the more posterior dorsal elements and absent in the posterior dorsal and sacral vertebrae of both species (Fig. 4e, f). The centra of the three sacral vertebrae are flattened ventrally. The caudal vertebrae also possess spool-shaped centra. There is one pair of paramedian osteoderms above each vertebra in ornithosuchids; these osteoderms have a simple ornamentation and bear a dorsolateral prominence on their external surfaces (Fig. 2m: ep; Fig. 4a, b).

The shoulder girdle of *Riojasuchus tenuisceps* has a deep glenoid fossa that is clearly delimited by strongly posteriorly developed supraglenoid and subglenoid lips. By contrast, the pectoral glenoid fossa of *Ornithosuchus longidens* is shallower. The scapula of *Ornithosuchus longidens* possesses a tall blade with a moderately anteroposteriorly expanded distal end. In both ornithosuchid species, the scapula has a moderately raised acromion and a subcircular and large subacromial depression. The coracoid is crescentic and has a long, tapering and posteriorly directed posteroventral (= sternal) process in both *Riojasuchus tenuisceps* and *Ornithosuchus longidens*. The coracoid foramen is oval and positioned far ventrally from the suture between the scapula and coracoid. The humeri of both species possess a similar morphology. The proximal end of the humeri has a well-developed deltopectoral crest (Fig. 4g: dc) and a strongly medially projected internal tuberosity (Fig. 4g: it). The proximal surface possesses a sigmoid profile in anterior view, with a dorsally inflated humeral head (Fig. 4g: hh).

The distal end of the humerus of *Riojasuchus tenuisceps* is thickened in the flexor–extensor direction and bears a distinct and rounded ectepicondyle and entepicondyle (Fig. 4g), but the condition in *Ornithosuchus longidens* is unknown. The radius and ulna are both slender and primarily cylindrical bones in both species. The radius is expanded at its distal end and the ulna has a well-developed olecranon process in *Riojasuchus tenuisceps* (Fig. 4h), but the olecranon is less developed in *Ornithosuchus longidens*. The proximal carpus of *Riojasuchus tenuisceps* consists of three bones – the radiale, the centrale (= intermedial: Bonaparte 1972) and the ulnare – which are small and cuboid in morphology and slightly dorsoventrally compressed (Fig. 4i). The carpal morphology of *Ornithosuchus longidens* is less well known, but the proximal carpals seem to have had a similar arrangement to that of *Riojasuchus tenuisceps*. In *Riojasuchus tenuisceps*, metacarpal I is long and stout, and metacarpals II–V become more slender towards the fifth metacarpal. The knowledge of the manual anatomy of *Ornithosuchus longidens* is more limited (Walker 1964), but the metacarpus seems to have been similar to that of the Argentinean species.

The pelvic girdle has a tall iliac blade with a well-developed postacetabular process that tapers posteriorly in both *Riojasuchus tenuisceps* and *Ornithosuchus longidens* (Figs 2g & 5a, b). In *Riojasuchus tenuisceps* the preacetabular process is strongly reduced and has a rounded anterior margin. By contrast, in *Ornithosuchus longidens*, the preacetabular process is squared and proportionally more anteriorly developed, but it does not exceed the anterior level of the pubic peduncle (Walker 1964). The acetabulum is bounded dorsally by a well-developed supra-acetabular crest and the acetabular wall is incipiently perforated at the contact between the ilium and ischium in both *Riojasuchus tenuisceps* and *Ornithosuchus longidens* (Figs 2g & 5a, b). The pubis of *Ornithosuchus longidens* possesses a large, oval obturator foramen in its proximal end (Fig. 2g). The pubic shaft of both ornithosuchid species is elongated and posteriorly curved. In *Ornithosuchus longidens*, at least, the pubis exhibits a small anteroposterior distal expansion. The ischium has a small obturator process in both species and is slightly dorsoventrally expanded at its distal end in *Ornithosuchus longidens*. The hindlimb has a sigmoidal femur, the proximal end of which is directed anteromedially (Fig. 5c, d). The anterior and greater trochanters are well developed, but the fourth trochanter is low in both species. The proximal end of the tibia is expanded anteroposteriorly and has a well-developed cnemial crest on its medial surface at the point at which the fibula articulates in *Riojasuchus tenuisceps* (Fig. 5f). The fibula of *Riojasuchus tenuisceps* possesses a

hypertrophied tubercle for the insertion of the *M. iliofibularis*. As discussed above, the tarsus of ornithosuchids is autapomorphic in possessing a crocodile-reversed ankle joint between the astragalus and calcaneum (Fig. 5g). The metatarsals are straight and elongate bones in both species. In *Riojasuchus tenuisceps* the metatarsal V is medially expanded at its proximal end and all the pedal phalanges are mediolaterally compressed (Fig. 5h).

Relationships and evolution

At the end of the 19th century, Newton (1894) described the remains of a diapsid reptile from the Late Triassic beds of Scotland and erected the new genus and species *Ornithosuchus woodwardi*. This new species was assigned provisionally to Dinosauria (Newton 1894). Boulenger (1903) reinterpreted *Ornithosuchus* as a member of Parasuchia (using this clade in a very different sense to that employed today), together with *Aetosaurus*, *Erpetosuchus*, *Stagonolepis* and '*Belodon*'. Huene (1908) coined the family Ornithosuchidae for *Ornithosuchus woodwardi*, *Scleromochlus taylori* and *Hallopus victor*, and also erected the order Ornithosuchia (Table 2). Subsequently, Broom (1913) recognized two different species within the genus *Ornithosuchus*, mostly based on size differences, and erected the new species *Ornithosuchus taylori*. Later, Huene (1921, 1939, 1956), Colbert (1952), Haughton & Brink (1954), Hoffsttetter (1955), Romer (1956) and Brink (1959) included several other species within Ornithosuchidae, namely *Saltoposuchus*, *Parringtonia*, *Erpetosuchus*, *Hesperosuchus*, *Stegomosuchus*, '*Mandasuchus*', *Euparkeria*, '*Browniella*' (=*Euparkeria sensu* Ewer 1965), *Cerritosaurus*, *Clarencea* (=*Sphenosuchus*) and *Prestosuchus*.

Walker (1964) conducted a detailed revision of the genus *Ornithosuchus* and rejected the validity of *Ornithosuchus taylori*, considering it a junior synonym of *Ornithosuchus woodwardi*. This author also recognized that the specimens belonging to *Dasygnathus longidens* Huxley 1877 are indistinguishable from that of *Ornithosuchus woodwardi*, and because *Dasygnathus* was preoccupied by a coleopteran insect he created the new combination *Ornithosuchus longidens* (Huxley 1877). Walker (1964) agreed with some previous authors in considering *Ornithosuchus* as an ancestral form of dinosaur (e.g. Newton 1894; Heilmann 1926), but further considered the ornithosuchids as a primitive group of 'carnosaurian' theropods. He considered that the family Ornithosuchidae was composed of *Ornithosuchus*, '*Sinosaurus*' and *Teratosaurus*. However, these latter two taxa were subsequently removed from the group (Romer 1966, 1968;

Charig 1969; Bonaparte 1969, 1972). Romer (1966) and Charig (1967) agreed in considering ornithosuchids as carnosaurian dinosaurs, but Reig (1961), Romer (1968) and Charig (1969) proposed instead that ornithosuchids were members of Pseudosuchia.

In the late 1960s, José Bonaparte enlarged the taxonomic content of Ornithosuchidae with the description of two new species from northwestern Argentina. First, Bonaparte (1967) described *Riojasuchus tenuisceps* from the Los Colorados Formation; subsequently, Bonaparte (1970) reported *Venaticosuchus rusconii* from the older beds of the Ischigualasto Formation. Following these discoveries, Bonaparte (1972) considered Ornithosuchia as an infraorder of Pseudosuchia, together with the infraorders Sphenosuchia and Proterochampsia. This author included several families within Ornithosuchia, namely Ornithosuchidae, Rauisuchidae, 'Pallisteriidae', 'Teleocratidae' and Scleromochlidae, but he only considered as members of Ornithosuchidae the genera *Ornithosuchus*, *Riojasuchus* and *Venaticosuchus*. Subsequently, Romer (1972*a*) considered Pseudosuchia to be composed of the families Ornithosuchidae and Scleromochlidae, and also included within Ornithosuchidae *Gracilisuchus* and probably *Parringtonia* and *Dyoplax*. Bonaparte (1975) conducted a revision of the family Ornithosuchidae and included within the group *Ornithosuchus longidens*, *Riojasuchus tenuisceps*, *Venaticosuchus rusconii* and *Gracilisuchus stipanicicorum*. Krebs (1976) agreed with the pseudosuchian assignment of Ornithosuchidae, but he also included a wide array of archosauriforms within the former group, such as Euparkeriidae, Rauisuchidae, Stagonolepididae, Erpetosuchidae and Scleromochlidae. Bonaparte (1982*a*) provided a reappraisal of the classification of the Thecodontia and included within Pseudosuchia the families Ornithosuchidae, Lagosuchidae, Euparkeriidae and Scleromochlidae.

Gauthier (1986) conducted the first comprehensive numerical analysis focused on the phylogenetic relationships among archosaurs. He found *Ornithosuchus longidens* to be placed at the base of the avian stem lineage (Gauthier 1986) (Fig. 6a), leading Gauthier & Padian (1985) to define the avian stem lineage of archosaurs as Ornithosuchia. The basal position of *Ornithosuchus longidens* within the avian stem lineage was also recovered by Benton & Clark (1988). However, subsequent phylogenetic analyses recovered ornithosuchids as members of the Pseudosuchia. Sereno & Arcucci (1990) recovered Ornithosuchidae within a polytomy at the base of the crocodile line of archosaurs (the crocodilian stem lineage), which they named Crurotarsi. Sereno (1991) obtained a similar result, but with ornithosuchids more closely related to Suchia (i.e. the least inclusive clade containing

Table 2. *Taxa once considered to be ornithosuchids*

Taxon	Occurrence	Age	Material	Current classification
Gracilisuchus stipanicicorum Romer 1972*b*	Chañares Formation, La Rioja, Argentina	Anisian–Ladinian	Partial skeletons	Early Suchia (Nesbitt 2011)
Parringtonia gracilis Huene 1939	Manda Beds Formation, Ruvuma, Tanzania	Late Anisian	Partial skeleton	Archosauria (Benton & Walker 2002)
Dyoplax arenaceous Fraas 1867	Schilfsandstein Formation, Baden-Württemberg, Germany	Early Carnian	Partial skeleton	Crocodylomorpha (Walker 1970)
'Sinosaurus triassicus' Young 1940	Lufeng Formation, Yunnan, China	Hettangian–Sinemrian	Fragmentary maxilla	Archosauria (Irmis 2004)
Teratosaurus suevicus Meyer 1861	Löwenstein Formation, Stuttgart, Germany	Middle Norian	Maxilla	Rauisuchidae (Brusatte *et al.* 2009)
Scleromochlus taylori Woodward 1907	Lossiemouth Sandstone Formation, Moray, Scotland	Late Carnian earliest Norian	Partial skeletons	Avemetatarsalia (Benton 1999)
Hallopus victor Marsh 1877	Morrison Formation, CO, USA	Kimm.–Tithonian	Partial postcranium	Crocodylomorpha (Walker 1970)
Saltoposuchus connectens Huene 1921	Löwenstein Formation, Pfaffenhofen, Germany	Norian	Partial skeletons	Crocodylomorpha
Erpetosuchus granti Newton 1894	Lossiemouth Sandstone Formation, Moray, Scotland	Late Carnian earliest Norian	Partial skeletons	Suchia (Benton & Walker 2002)
Hesperosuchus agilis Colbert 1952	Chinle Formation, AZ, USA	Norian	Partial skeletons	Crocodylomorpha (Walker 1970)
Stegomosuchus longipes Emerson & Loomis 1904	Portland Formation, MA, USA	Hettangian–Sinemurian	Partial skeleton	'Protosuchia' (Walker 1968)
'Mandasuchus tanyauchen' Charig 1956	Manda Beds Formation, Ruvuma, Tanzania	Late Anisian	Partial lower jaw and postcranial skeletons	Rauisuchia (Parrish 1993)
Euparkeria capensis Broom 1913	Burgersdorp Formation, Eastern Cape, South Africa	Anisian	Partial skeletons	Euparkeriidae
Cerritosaurus binsfeldi Price 1946	Santa Maria Formation, Rio Grande do Sul, Brazil	Middle–Late Triassic	Partial cranial and postcranial skeleton	Proterochampsidae (Bonaparte 1971)
Prestosuchus loricatus Huene 1938	Santa Maria Formation, Rio Grande do Sul, Brazil	Ladinian	Several skeletons	Rauisuchia
'Clarencea gracilis' Brink 1959	Upper Elliot Formation, Eastern Cape, South Africa	Hettangian–Sinemurian	Partial skull	*Sphenosuchus acutus* (Clark *et al.* 2000)

The definition and taxonomic content of each group under 'Current classification' follow those of the quoted author.
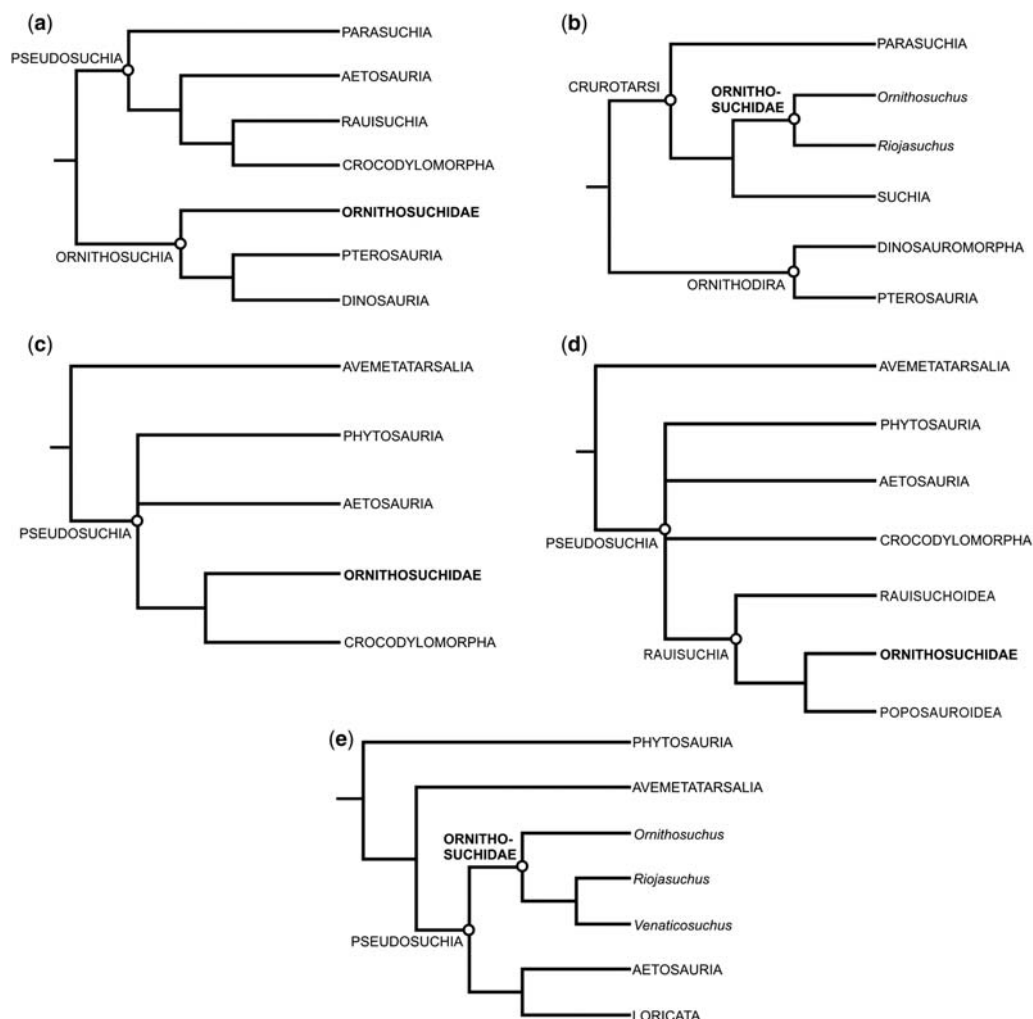*Abbreviations*: Kimm, Kimmeridgian.

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Fig. 6. Phylogenetic relationships of Ornithosuchidae: (**a**) Gauthier (1986); (**b**) Sereno (1991); (**c**) Juul (1994); (**d**) Butler *et al.* (2011) resulting from the revised analysis of the Brusatte *et al.* (2010) data set; (**e**) von Baczko (2012) modified from Nesbitt (2011).

Gracilisuchus stipanicicorum, Aetosauria, 'Rauisuchia', Poposauridae and Crocodylomorpha; Sereno 1991) than to Phytosauria (=Parasuchia) (Fig. 6b). By contrast, Parrish (1993) found ornithosuchids as the most basal crurotarsans. Juul (1994) recovered ornithosuchids as the sister group of a clade composed of Crocodylomorpha, *Postosuchus kirkpatricki* and *Gracilisuchus stipanicicorum* (Fig. 6c). Bennett (1996) placed Ornithosuchidae within a polytomy also composed of *Euparkeria capensis*, Pseudosuchia (i.e. Suchia + Phytosauria/Parasuchia) and Ornithodira (the avian stem lineage). In contrast to previous hypotheses, Benton (1999) and Benton & Walker (2002) found Ornithosuchidae within Suchia, being more closely related to 'rauisuchians' than to other pseudosuchians. However, Benton (2004) recovered ornithosuchids within a trichotomy also composed of a Parasuchia + *Gracilisuchus* clade and a group including Aetosauria, Crocodylomorpha and 'Rauisuchia'. Nevertheless, Nesbitt & Norell (2006), Nesbitt (2007) and Brusatte *et al.* (2010) found results congruent to those of Benton (1999); that is, that the ornithosuchids were closely related to 'rauisuchians' within Suchia. In particular, Brusatte *et al.* (2010) found Ornithosuchidae to be the sister taxon of the purported stem-aetosaur *Revueltosaurus*. Brusatte *et al.* (2010) and Nesbitt (2011) also corroborated the

monophyly of the group (i.e. *Riojasuchus tenuisceps + Ornithosuchus longidens*), but the latter author found ornithosuchids to be the most basal pseudosuchians, a position that is in agreement with the results reported by Parrish (1993). França *et al.* (2011) reanalysed a modified version of the data matrix of Brusatte *et al.* (2010) and found, for the first time, ornithosuchids as nested within a monophyletic Rauisuchia. However, the internal relationships at the base of Rauisuchia were depicted as a massive politomy in Brusatte *et al.* (2010). More recently, Butler *et al.* (2011) built a new database after the addition of more taxa and characters to the data set of Brusatte *et al.* (2010), and found ornithosuchids to be deeply nested within Pseudosuchia, as members of Rauisuchia and particularly the sister group of Poposauroidea (Fig. 6d). Thus, the results of França *et al.* (2011) and Butler *et al.* (2011) agree in the position of Ornithosuchidae within a monophyletic Rauisuchia. Finally, von Baczko (2012) included *Venaticosuchus rusconii* within the data matrix of Nesbitt (2011), and also recovered Ornithosuchidae as the most basal pseudosuchians and the Argentinean taxon as more closely related to *Riojasuchus tenuisceps* than to *Ornithosuchus longidens* (Fig. 6e). In summary, the current consensus is that ornithosuchids are a monophyletic group and are members of Pseudosuchia, but their phylogenetic position within Pseudosuchia remains contentious.

As a result, the current consensus establishes the inclusion of three species within Ornithosuchidae, *Ornithosuchus longidens*, *Riojasuchus tenuisceps* and *Venaticosuchus rusconii*. *Ornithosuchus longidens* differs from other ornithosuchids in the following features: minor cranial ornamentation on the dorsal surface of the frontals, parietals and anterior process of the postorbitals represented by small pits and shallow grooves; maxilla with a posterior prong; postorbital with a strong central horizontal crest; lower jaw with a ventral margin that is concave and elevated; surangular foramen positioned near the surangular–angular suture (Sereno 1991; Nesbitt 2011). *Riojasuchus tenuisceps* differs from other ornithosuchids in the following features: snout with a large overhanging anterior portion; antorbital fossa deep and extensively invading the horizontal process of the maxilla; base of the atlantal neural arch contacting at the midline (modified from Sereno 1991; Nesbitt 2011). Finally, *Venaticosuchus rusconii* differs from other ornithosuchids in the following features: basipterygoid processes ventrally directed; dentary with the dorsal margin of the anterior end dorsally expanded; articular without foramen in the medial surface; absence of a surangular foramen (von Baczko 2012).

The phylogenetic position of Ornithosuchidae within Pseudosuchia is currently open to debate. The most recent comprehensive archosaur phylogenies have found ornithosuchids as the sister group of Poposauroidea within the Rauisuchia (Butler *et al.* 2011, based upon a revision of the data set of Brusatte *et al.* 2010) or as the most basal pseudosuchians (Nesbitt 2011; see also Butler *et al.* 2011). Because of this phylogenetic uncertainty, the character evolution of ornithosuchid traits cannot be determined unambiguously. For example, the apomorphic crocodile-reverse ankle joint is inferred to be derived from the crocodile-normal ankle joint following some phylogenetic hypotheses (e.g. Juul

Fig. 7. Life reconstruction of *Riojasuchus tenuisceps*. Illustration by Rodrigo Vega.

1994; Nesbitt & Norell 2006; Brusatte *et al.* 2010), but would be inferred as independently acquired following other phylogenetic schemes (e.g. Parrish 1993). Beyond the uncertainty surrounding the higher-level phylogenetic affinities of Ornithosuchidae, all hypotheses agree on the presence of an extremely long ghost lineage at the base of the clade. The presence of an indeterminate paracrocodylomorph (*Vytshegdosuchus*) and a ctenosauriscid poposauroid (*Ctenosauriscus*) in the late Olenekian of Germany and Russia produces a ghost lineage of *c.* 16–18 millions of years for the ornithosuchid stem (Butler *et al.* 2011; Nesbitt 2011). Thus, it seems that only the late evolutionary history of the lineage is currently sampled in the fossil record.

The currently known ornithosuchids come from two palaeolatitudinally distant areas of Pangaea. *Ornithosuchus longidens* is known from a locality situated at a palaeolatitude of 35°N and *Riojasuchus tenuisceps* and *Venaticosuchus rusconii* from an area located at around 35°S during the Late Triassic (data taken from the Paleobiology Database). This disjunct distribution of ornithosuchids could be explained through either vicariance or a dispersal event, or a sampling bias reflecting an uneven record of the group in the rest of Pangaea during the Late Triassic. Recent palaeobiogeographical analyses found a cosmopolitan pattern for Middle Triassic tetrapods and palaeolatitudinally structured provincialism, with areas situated at roughly the same palaeolatitude possessing faunal assemblages more similar to each other during the Late Triassic (Ezcurra 2010). Because of the absence in palaeogeographical areas located close to the palaeo-Equator of several clades that are shared among middle and high palaeolatitudinal areas, Ezcurra (2010) hypothesized that these patterns could also be the result of vicariant events and/or local extinctions following the appearance of probable climatic barriers for tetrapod dispersal during the early Late Triassic. Accordingly, because ornithosuchids have not yet been recorded at low palaeolatitudes, the distribution of the group during the Late Triassic could be explained through this vicariant hypothesis, which implies that they should have a more global distribution during the Middle Triassic. However, these palaeobiogeographical hypotheses should be considered tentative because they can be easily biased by a sampling artefact, thus representing a non-biological signal, and cannot be tested until we have an improved taxonomic sample of ornithosuchids and evidence of their early evolutionary history.

Palaeobiology

Ornithosuchids are a group of pseudosuchians with body lengths ranging from 2 to 4 m (Fig. 7). The tooth crowns are labiolingually compressed, distally recurved and have fine denticles on both margins, indicating carnivorous habits for these animals. Walker (1964) and Bonaparte (1997) discussed the capability of ornithosuchids to adopt bipedal locomotion. These authors noted a considerable disparity between the fore- and hindlimbs and an elongated pubis and ischium. The external digits of the manus are reduced and would have been adapted for grasping rather than for use in locomotion (Walker 1964). The femur possesses a well-developed anterior trochanter, and the anterior caudal vertebrae present very high neural spines (Walker 1964). All these features led Walker (1964) to suggest that *Ornithosuchus* might have been facultative bipedal animals, acquiring an upright posture during fast gaits. However, these hypotheses should be tested in the future with more rigorous muscular reconstructions and biomechanical analyses.

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