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Reassessment of *Unaysaurus tolentinoi* (Dinosauria: Sauropodomorpha) from the Late Triassic (early Norian) of Brazil, with a consideration of the evidence for monophyly within non-sauropodan sauropodomorphs

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We present a systematic revision of the 'prosauropod' dinosaur Unaysaurus tolentinoi. Past phylogenetic treatments of this taxon have presented it as a key constituent of the low-diversity Plateosauridae. This clade, along with Massospondylidae, is currently regarded as a relatively non-controversial example of monophyly within non-sauropodan sauropodomorphs - an otherwise pectinate grade of animals from which the apically nested Sauropoda is derived. The inclusion of Unaysaurus within Plateosauridae is primarily dependent on similarities shared with the Northern Hemisphere taxon Plateosaurus, with a sister-taxon relationship between these taxa indicating the earliest known instance of Pangaean cosmopolitanism among early sauropodomorphs. However, an in-depth exploration of the character states that in the past have produced this relationship shows that many either present a complex distribution throughout early Sauropodomorpha, or are subject to ambiguities in the formulation and scoring of primary homologies. An updated cladistic analysis finds weak continued support for a sister-taxon relationship between Unavsaurus and Plateosaurus; however, this result is supported by synapomorphies that are either labile with respect to taxon inclusion, not exclusively restricted to the clade, or represented by character-state dichotomies of relatively subtle differentiation. These uncertainties aside, the validity of Unaysaurus tolentinoi remains supported by several unambiguous autapomorphies. Although strong anatomical evidence for monophyletic divergences amongst early sauropodomorphs remains elusive, the relatively low stratigraphical occurrence of Unaysaurus demonstrates that the typical 'prosauropod' bauplan – and hence habitual herbivory – had evolved by the early Norian.

Keywords: Sauropodomorpha; 'prosauropods'; Plateosauridae; Late Triassic; monophyly

Introduction

Interest in non-sauropodan sauropodomorph dinosaurs (henceforth referred to as 'prosauropods') is generally underscored via two oft-repeated introductory lines: (1) that they represent the first great radiation of dinosaurian herbivores (e.g. Barrett 2000; Barrett & Upchurch 2005, 2007; Barrett et al. 2011; McPhee et al. 2017), and (2) that they represent the ancestral stock from which sauropod dinosaurs - the Earth's largest terrestrial animals – arose (Yates et al. 2010; Pol et al. 2011; McPhee et al. 2014, 2015a; Otero et al. 2015). However, the contribution of various 'prosauropod' lineages to this latter phenomenon is obscured by continuing uncertainties regarding their interrelationships. The earliest hypotheses of 'prosauropod' paraphyly presented a fully pectinate arrangement, suggesting a continuous transformation series from the initial divergence of the group to the ultimate radiation of Sauropoda (Yates

2003a; Yates & Kitching 2003; cf. Upchurch et al. 2007). Most recent analyses, however, have indicated isolated monophyletic groupings of 'prosauropods', of which the Plateosauridae and Massospondylidae have received perhaps the most attention (Smith & Pol 2007; Yates 2007a; Apaldetti et al. 2011, 2012; Otero & Pol 2013; McPhee et al. 2015b; Chapelle & Choiniere 2018). Nonetheless, this consensus derives primarily from workers using iterations of the same cladistic data set (Yates 2007a), and it is possible that both clades are sensitive to taxon sampling and character conception (Sereno 2007; Upchurch et al. 2007; Apaldetti et al. 2014). Furthermore, although the monophyly and supporting characters of Massospondylidae have received focused discussion (e.g. Smith & Pol 2007; Apaldetti et al. 2011, 2012, 2014; McPhee et al. 2015b; Chapelle & Choiniere 2018), the putative monophyly of Plateosauridae has been less systematically explored a confusion compounded by the ambiguous status of

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several of its constituent taxa (i.e. *Plateosaurus engel*hardti, P. erlenbergiensis, P. gracilis, P. 'ingens').

Here we provide a detailed reassessment of the Brazilian 'prosauropod' *Unaysaurus tolentinoi* (Leal *et al.* 2004). *Unaysaurus* has been recovered as a member of the plateosaurid clade in the majority of cladistic analyses that have included it, and thus has direct bearing on assessing the 'reality' of this grouping. Furthermore, its early Norian age, along with its position at the base of the 'core prosauropods' (*sensu* Upchurch *et al.* 2007; see also Sereno 2007), provides valuable insight into the characters and character states of greatest relevance to understanding and reconstructing one of the most dramatic radiations of the Mesozoic.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; BP, Evolutionary Studies Institute, Johannesburg, South Africa (formerly Bernard Price Institute); MB.R., Museum für Naturkunde-Leibniz-Institut für Evolutions und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany; NMQR, National Museum, Bloemfontein, South Africa; PVL, Paleontología de Vertebrados, Instituto 'Miguel Lillo', San Miguel de Tucumán, Argentina; PVSJ, Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; UFSM, Laboratório de Estratigrafia e Paleobiologia, Universidade Federal de Santa Maria, Brazil; ULBRA, Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas-RS, Brazil.

Material and horizon

Originally introduced and briefly described by Leal et al. (2004), the holotype of Unaysaurus tolentinoi, UFSM11069, is a partial skeleton consisting of cranial, axial and appendicular material collected from the Caturrita Formation of south-eastern Brazil (Rio Grande do Sul state, Água Negra locality). The most recent assessment of the age of Unavsaurus suggested an early Norian position based on biostratigraphical correlation with other Caturrita Formation localities in which material potentially referable to Unavsaurus was found in association with the dicynodont Jachaleria (Müller et al. 2017a). This interpretation was tentatively corroborated by recent radioisotopic dating of an unrelated locality within the Caturrita Formation in which a single zircon yielded a maximum age limit of deposition of 225.42 Ma (Langer et al. 2018).

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Dinosauria Owen, 1842 Saurischia Seeley, 1887 Sauropodomorpha Huene, 1932 Unaysaurus Leal, Azevedo, Kellner & Da Rosa, 2004 Unaysaurus tolentinoi Leal, Azevedo, Kellner & Da Rosa, 2004 (Figs 1–13)

Revised diagnosis. The current study finds little disagreement with the initial diagnosis of Unaysaurus tolentinoi given in Leal et al. (2004, p. 3). However, several of the diagnostic statements require clarification. These are: (1) "presence of well-developed laterodorsally oriented process formed by frontal and parietal; medial depression on mediodorsal surface of the parietals". The supratemporal region of Unaysaurus is notable for possessing a supratemporal fossa that is deeply incised into the posterior surface of the frontal, continuing posteriorly as a strongly rimmed depression onto the mediodorsal surface of the parietal. This feature, in conjunction with a frontal-parietal suture located well back from the anterior-most margin of the supratemporal fossa, is seen only in Unavsaurus and a few other 'primitive' sauropodomorph taxa (e.g. Plateosaurus). However, Unaysaurus is unique in possessing a strongly developed eminence on the medial rim of the supratemporal fossa, at the frontal-parietal juncture, that protrudes laterally over the fossa; (2) "deep ventral depression on the basisphenoid". A basisphenoid recess is common throughout Sauropodomorpha (and other dinosaurs). However, Unaysaurus is notable for possessing an additional 'sub-recess' at the juncture of the basisphenoid and basioccipital, between the basal tubera pedicles of the basisphenoid. To the original diagnosis is added: (3) fine, bifurcating ridges housed within the ventral (= Meckelian) groove of the dentary, delimiting two small fossae/foramina.

Description

Comparative taxa mentioned throughout the description are listed in Table 1.

Cranial anatomy

Premaxilla. The left premaxilla is preserved in association with the left nasal and right maxilla (Fig. 1). It is missing the anteroventral corner of the main premaxillary body, from what was likely the anteriormost alveolus forward. It is thus difficult to assess

Table 1. Sources of a	comparative data	used in	this	study
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Taxon	Source(s)		
Aardonyx celestae	Various elements catalogued BP/1/5379-6893		
Adeopapposaurus mognai	Martinez 2009		
Anchisaurus polyzelus	Galton 1976; Yates 2004; Fedak & Galton 2007		
Antetonitrus ingenipes	BP/1/4952a, b, c; McPhee et al. 2014		
Blikanasaurus cromptoni	SAM-PK403		
Buriolestes schultzi	Müller et al. 2018a		
Coloradisaurus brevis	PVL 5904 (field no. 6); Apaldetti et al. 2012, 2014		
Efraasia minor	Bronzati & Rauhut 2017		
Eoraptor lunensis	Sereno et al. 2012		
Herrerasaurus ischigualastensis	Novas 1994; Sereno & Novas 1994		
Leonerasaurus taquetrensis	Pol et al. 2011		
Leyesaurus marayensis	Apaldetti et al. 2011		
Lufengosaurus huenei	Barrett et al. 2005; IVPP V15		
Massospondylus carinatus	BP/1/4934; Chapelle & Choiniere 2018		
'Melanorosaurus readi'	Yates 2007a; NMQR 1551, 3314		
Mussaurus patagonicus	Otero & Pol 2013		
Panphagia protos	Martinez & Alcober 2009		
Pantydraco caducus	Yates 2003a		
Pampadromaeus barberenai	ULBRA-PVT016		
Plateosauravus cullingworthi	SAM-PK3341-3356, 3602-3603, 3607-3609		
Plateosaurus spp.	Huene 1926; Galton 1985, 2001; Yates 2003b; Prieto-Márquez & Norell 2011		
'Riojasaurus incertus'	PVL 3808		
Sarahsaurus aurifontanalis	Rowe et al. 2010; Marsh & Rowe 2018		
Saturnalia tupiniquim	Langer 2003; Langer et al. 2007		
Yunnanosaurus huangi	Young 1942; Barrett et al. 2007		

whether the anterior tip of the snout was pointed as in Pampadromaeus, Plateosaurus and Yunnanosarus (Barrett et al. 2007; Cabreira et al. 2011; Prieto-Márquez & Norell 2011), a possibly plesiomorphic condition for Sauropodomorpha, or relatively dorsoventrally sheer as in Massospondylus (Chapelle & Choiniere 2018). There appears to have been a slight indentation between the anterodorsal (=nasal) ramus and the anterior margin of the snout, as is typical for most 'prosauropods'. The elongated nasal ramus curves posterodorsally over the external naris at an angle of about 40° to the main body of the premaxilla, terminating roughly level with the posterior tip of the posterior (=maxillary) ramus and adjacent to the posteroventrally displaced nasal - although a depression in the posteriormost third indicates the area of the ramus that would have been laterally overlapped by the nasal. As preserved, the distal end of the nasal ramus does not appear to have been obviously transversely expanded, contra the condition in, for example, Massospondylus and Plateosaurus. However, both adherent matrix and the nasal bone obscure a confident appraisal of this morphology. The lateral surface of the premaxilla is anteriorly pierced by a small sub-triangular excavation at the base of the nasal ramus, and ventrally by a subtle foramen close to the alveolar margin of the bone. A shallow external narial fossa extends along most of the anteroposterior length of the lateral surface. It is not delimited by a distinct lip and is hence somewhat inconspicuous,

especially as it progresses ventrally (see Discussion, below). It is likely that the anterior-most margin of the external naris was located posterior to the midpoint of the anteroposterior length of the premaxillary body, although this is ambiguous as preserved.

The undivided maxillary ramus of the premaxilla is similar to the elongate condition seen in *Plateosaurus*, contrasting with the anteroposteriorly short ramus observed in *Massospondylus*. Anteriorly, the maxillary ramus occupies roughly half the dorsoventral width of the premaxillary body, with the ventral surface of the former set at 90° relative to the posterior margin of the latter. The medial process (Fig. 2C), which forms the anterior portion of the palate, is observable at the level of the fourth premaxillary tooth. It is a sharp, medially pointing pyramidal process, although it is difficult to say how complete it is. The lateral alveolar margin extends ventrally about 0.5 cm below the medial margin.

Three alveoli are present (the fourth is likely missing), with the middle housing a broken tooth crown.

Maxilla. Both maxillae are present, with the right element adhered to the medial surfaces of the left premaxilla and nasal (Figs 1, 2). Neither is perfectly preserved, with the dorsal end of the ascending (=lacrimal) ramus broken in both elements and the right maxilla missing most of the posterior (=jugal) ramus.

The anterior (=premaxillary) ramus of the maxilla of *Unaysaurus* is sub-square-shaped with a length/height



Figure 1. A, left premaxilla and nasal of *Unaysaurus tolentinoi* (UFSM11069) in lateral view. B, right maxilla in lateral view and left premaxilla in medial view. Abbreviations: aof, antorbital fossa; ar, anterior ramus of the maxilla; ascr, ascending ramus of the maxilla; f, foramina; M, maxilla; medp, medial process of the premaxilla; mp, maxillary process of the nasal; mr, maxillary ramus of the premaxilla; N, nasal; nf, narial fossa; nr, nasal ramus of the premaxilla; pmp, premaxillary process of the nasal; posr, posterior ramus of the maxilla; Prm, premaxilla. Scale bars = 2 cm.



Figure 2. Left maxilla of *Unaysaurus tolentinoi* (UFSM11069) in (A) lateral, (B) medial (including line drawing) and (C) dorsal views. Abbreviations: amp, anteromedial process; aof, antorbital fossa; ascr, ascending ramus; ar, anterior ramus; fo, fossa; mns, maxillary nerve sulcus; posr, posterior ramus. Scale bar = 2 cm.

ratio of 1.25. This is relatively squat for 'prosauropods', with Plateosaurus (AMNH FARB 6810), Massospondvlus (BP/1/5241) and Aardonvx all displaying values closer to 1.4. The anterior ramus is marked at its dorsal margin by a laminar ridge that delimits a shallow lateral depression, representing the facet for reception of the maxillary ramus of the premaxilla and/or the posterior portion of the narial fossa. The shelf-like anteromedial process (=vomeral flange) extends from the base of the ascending ramus on its mediodorsal surface, reaching beyond the anteriormost point of the maxilla, as in other 'prosauropods' (e.g. Plateosaurus, Massospondylus). It has a convex medial margin and broadens anteriorly. In this respect it is closer in morphology to the anteromedial process of Plateosaurus, with the same process in Massospondylus tapering to a sharp anterior point. A narrow crevice separates the anteromedial process from the anterior end of the anterior ramus. Due to the relative anteroposterior shortness of the anterior ramus, the incompletely preserved ascending ramus rises from the main maxillary body at a point close to one-quarter of its total anteroposterior length, differing from other 'prosauropod' taxa in which the ascending ramus is positioned at closer to one-third of its length (Plateosaurus, Lufengosaurus, Massospondylus). In very basal taxa (e.g. Pampadromaeus) the ascending ramus is positioned even more anteriorly. The ascending ramus forms an angle of 80° with the posterior ramus of the maxilla. This is a slightly steeper angle than that observed in *Plateosaurus* ($\sim 60^{\circ}$).

Medially, the ascending ramus possesses a broad, dorsoventrally oriented sulcus that is delimited laterally by the laminar ridge that extends from the dorsal surface of the anterior ramus. This ridge adopts a wall-like morphology as it proceeds dorsally along the ascending process. The dorsal portions of the ascending processes of both maxillae are broken and possibly appressed to their respective maxilla (to the lateral alveolar margin in the case of the right, to the medial antorbital wall in the case of the left). The ascending ramus tapers dorsally as in most 'prosauropods' and possesses a thin ridge extending dorsoventrally along its lateral surface.

The anteroventral corner of the antorbital fenestra is delineated by a mediolaterally thin ridge that originates within the posterior half of the posterior ramus. At roughly the anteroposterior midpoint of the main maxillary body this ridge undergoes a dramatic dorsoventral expansion, forming the sheet-like anteromedial wall of the antorbital fossa. A similarly expansive medial wall of the antorbital fossa is seen only in Plateosaurus, Coloradisaurus, Aardonyx and NMQR 3314 ('Melanorosaurus') among basal sauropodomorphs. The ventral floor of the antorbital fossa is a transversely narrow platform formed of the flattened dorsal surface

of the maxillary posterior ramus. The left maxilla possesses two shallow fossae that excavate the medial wall of the antorbital fossa. The anterior excavation is sub-rectangular in shape and dorsoventrally more expansive than the anteroposteriorly elongate posterior depression. A similarly located depression is present on the antorbital fossa of Pampadromaeus (Cabreira et al. 2011). Beginning posterior to the posterior excavation, at roughly the anteroposterior midpoint of the posterior ramus, an elongated sulcus separates the medial antorbital wall from the maxillary body. This feature has been observed in a number of sauropodomorphs and is thought to have accommodated the passage of the maxillary branch of the trigeminal nerve (see Prieto-Márquez & Norell 2011). The dorsolateral margin of the posterior ramus, wherein it forms the ventral border of the antorbital fossa, is raised as a pronounced laterally projecting ridge. This ridge becomes progressively less pronounced towards the posterior end of the ramus, disappearing entirely towards the posterior end of the maxilla. The posterior ramus appears to have tapered dorsoventrally towards its posterior end, although this is ambiguous with respect to preservation.

The right maxilla possesses six (five in the left maxilla) foramina distributed along the mid-height of the lateral surface of the body. The alveolar margin is parallel with the ventral margin of the antorbital fenestra. As with the premaxilla, the lateral alveolar wall descends ventrally below the ventral margin of the medial wall. Nineteen alveoli are observable in the better preserved right maxilla, although it is likely that the true number was slightly higher.

Nasal. Only the anterior portion of the nasal is preserved (Fig. 1). The anterodorsal (=premaxillary) process is laterally bulged and projects towards the nasal ramus of the premaxilla. Its anterior-most point is broken. The sub-triangular anteroventral (=maxillary) process expands ventrally, nearly contacting the maxillary ramus of the premaxilla. However, it is not possible to determine whether these processes contacted in life, as in basal 'prosauropod' taxa such as *Plateosaurus* and *Efraasia* (Yates 2003b). The two anterior processes diverge at an angle of roughly 70°. The lateral surface of the anteroventral process is pierced by several minute foramina.

Frontal. Incomplete paired frontals are preserved articulated with their respective parietals (Fig. 3). The frontal counterparts meet at the midline via an open suture. Although much of the anterior portions are missing, including the prefrontal rami, the paired frontals appear

to have been lateromedially narrower anteriorly than posteriorly. The lateral margins are too poorly preserved to assess the frontal's contribution to the orbital border. Most of the dorsal surface of the frontal is planar and featureless. Posteriorly, each frontal articulates with the parietal via an irregular zigzag-like suture. The posterior portion of the frontal forms the anterior section of the supratemporal fossa complex. This manifests as a deep, crescentic excavation that penetrates anteriorly into the posterior surface of the bone and is roofed by a short curving lamina that is anteriorly bowed in dorsal view. Medially, this bow is bordered by a short, flange-like projection that contacts the parietal in the form of a laterally projecting, pointed prominence. In dorsal view, this prominence gives the anteromedial corner of the supratemporal fossa a 'scalloped' (sensu Yates 2007a, b) profile (see Discussion, below). Unfortunately, due to the ambiguous manner of preservation at the posterolateral ends of both frontals, it is not possible to determine whether the frontal reached all the way to the anterior margin of the supratemporal fenestra. Nonetheless, the frontal-parietal suture in Unaysaurus is remarkable for being posteriorly set back a considerable distance from the anterior-most margin of the supratemporal fossa. Although a similar morphology is observed in *P. erlenbergiensis*, the frontal-parietal suture in most 'prosauropods' tends to be located at approximately the same level as (or just behind) the anterior-most margin of the supratemporal fossa (e.g. *Massospondylus*, *Adeoppaposaurus*, *Coloradisaurus*).

The ventral surface of the frontal is marked by a shallow, semicircular concavity within its lateral half, which delimits the roof of the orbit. Anteriorly, an oval concavity, posteriorly delimited by a median ridge, represents the fossa for the olfactory bulb.

Parietal. Only the anterior-most portion of the left parietal is preserved (Fig. 3). The right is more complete, although missing much of its posterolateral corner (=squamosal ramus). It is not possible to assess the nature of the contact between the parietal and the postorbital. The parietal forms the medial wall of the supratemporal fenestra, which is present as a dorsoven-trally expansive wall that faces mainly dorsolaterally and then anterolaterally as the posterior body of the



Figure 3. Cranial elements of *Unaysaurus tolentinoi* (UFSM11069) in (A) 'top' and (B) 'bottom' views. Abbreviations: adr, anterodorsal ramus of the postorbital; ar, anterior ramus of the jugal; dr, dorsal ramus of the jugal; Ec, ectopterygoid; fob, fossa for olfactory bulb of frontal; Fr, frontal; Ju, jugal; me, medial eminence; qf, quadrate foramen; orb, orbit; Pa, parietal; Po, postorbital; pr, posterior ramus of the jugal; Pt; pterygoid; Qj, quadratojugal; Qr, right quadrate; stfe, supratemporal fenestra; stfo, supratemporal fossa; vr, ventral ramus of the postorbital. Scale bars = 2 cm.

partial undergoes a strong lateral curvature. This wall rises towards the dorsal surface of the parietal to form a sharply lipped rim that delimits the dorsal margin of the supratemporal fenestra. The dorsal surface of the parietal is transversely thin and considerably depressed. The presence of a median/sagittal crest cannot be evaluated due to its missing medial portion. The posterior surface is dorsoventrally extensive (although still wider than deep) and formed the anterior margin of the occipital region. This surface is particularly poorly preserved/ obscured by adherent matrix. The posterodorsal margin of the parietal is not dorsally projected.

Postorbital. The left postorbital is preserved close to the left supratemporal fenestra (Fig. 3). The anterodorsal ramus is incomplete, but the preserved portions suggest it was dorsoventrally and anteroposteriorly broad and plate-like, at least at its base. Its medial portion deflects ventrally, forming the lateral border of the supratemporal fenestra. Tracing a line across the dorsal margin of the preserved segment of the anterodorsal ramus suggests that it was likely dorsally raised with respect to the dorsal margin of the posterodorsal ramus, resulting in a 'stepped' dorsal margin in lateral view. This condition is similar to that of most 'prosauropods', but different from some taxa which have a mostly straight dorsal margin of the postorbital (e.g. Sarahsaurus). The posterodorsal ramus is missing. The ventral ramus is laterally concealed by matrix and other disarticulated cranial elements. Its medial surface is exposed and shows the typical anterodistal curvature forming the posterior margin of the orbit. The visible medial portion of the ventral ramus is primarily formed of a broad posteromedially facing facet that meets the posterior margin of the orbit as a sharp medial edge. The posteromedial facet of the ventral ramus bears a dorsoventrally oriented sulcus located towards its ventral end.

Jugal. An incomplete dorsal ramus of the left jugal is preserved (Fig. 3). The anterior and posterior rami left slightly informative impressions within the sedimentary matrix. A small sliver of the posterior ramus is ventrally appressed to a remnant of the quadratojugal anterior ramus. Based on the sediment impression, it is evident that the anterior ramus formed an angle of roughly 55° with the dorsal ramus. The posterior margin of the dorsal ramus forms an angle of approximately 70° with the anterior ramus of the quadratojugal. The dorsal ramus appears to have been the most well developed of the three rami. This contrasts with taxa such as Massospondylus (Chapelle & Choiniere 2018) and Plateosaurus (Prieto-Márquez & Norell 2011) in which the anterior ramus is the most well developed (although preservation remains an issue). The dorsal ramus possesses a distinct ridge that originates at the

anteroventral corner of its base and extends posterodorsally. This ridge borders a concave area that would have been overlapped by the ventral ramus of the postorbital.

Quadratojugal. Parts of the dorsal and anterior rami of the left quadratojugal are preserved, as well as impressions of these rami within the sedimentary matrix (Fig. 3). The anterior ramus is associated with a portion of the posterior ramus of the jugal. It is possible that the quadratojugal overlapped the jugal, although this is ambiguous as preserved. The dorsal ramus of the quadratojugal forms an angle of 70° with the anterior ramus. The contribution of the quadratojugal to the infratemporal fenestra cannot be evaluated due to poor preservation.

Ouadrate. An uninformative portion of the left quadrate is associated with the quadratojugal. The right quadrate is more complete, being exposed along most of its lateral and posterior surfaces, although it is partially concealed by a small vertebral centrum from an unrelated animal that is adhered to its proximal half. The element is further obscured by matrix and other disassociated skull bones. The lateral condyle of the distal end is obtusely rounded, a morphology possibly exaggerated by abrasion. The medial condyle is missing, so its relationship to the lateral condyle cannot be determined. The quadratojugal ramus (=lateral process) is appressed to the lateral surface of the pterygoid flange, and thus it is difficult to distinguish one from the other. A relatively deep, proximodistally oriented sulcus appears to have separated the quadrate head from the quadratojugal ramus, although the aforementioned centrum obscures the full extent of this sulcus. The pterygoid flange/quadratojugal ramus extends anteriorly at an angle roughly perpendicular to the transverse axis of the distal condyles. Although it cannot be established whether the preserved proximal terminus of the quadrate head represents the natural point of termination, the preserved anatomy nonetheless suggests that the pterygoid flange extended for less than 0.70 times the proximodistal length of the bone (~ 0.65). This metric is broadly consistent with that of other early sauropodomorphs. A rugose depression located on the main shaft just distal to the base of the quadratojugal ramus possibly represents the quadrate foramen (Fig. 3B). If this is the case, the quadrate foramen of Unaysaurus was incised into the main body of the quadrate, as in Saturnalia, Plateosaurus and Coloradisaurus. Although this differs from the condition in other basal sauropodomorphs in which the foramen is located on the quadrate-quadratojugal suture (e.g. Pantvdraco, Levesaurus, Sarahsaurus), a similarly positioned fossa was recently described for Massospondvlus (Chappelle & Choiniere 2018) and interpreted as a separate feature to the quadrate foramen (indicating a potential confusion with respect to this character).

Pterygoid. A partial left pterygoid is preserved (Fig. 3), although anatomical information is highly fragmentary. The ?vomeropalatine ramus is ventrally marked by a conspicuous crest, separating a flattened medial surface bearing a medial pendant process, and a slightly concave, plate-like lateral surface. In contrast to earliest sauropodomorphs, no evidence of palatal teeth can be seen. The ectopterygoid ramus expands laterally, forming a stout process connected to the vomeropalatine ramus.

Ectopterygoid. Only a remnant of the jugal ramus of the ectopterygoid is preserved (Fig. 3). It is a claw-shaped process, wide at the base and tapering distally, exposed on the infratemporal fenestra between the jugal and quadratojugal. It is similar to the slightly curved distal portion of the same process seen in other 'prosauropods' (e.g. *Efraasia, Massospondylus* [BP/1/5241], *Adeopapposaurus, Lufengosaurus*), although different from the strongly curved jugal ramus of the ectopterygoid of other non-sauropodan sauropodomorphs (e.g. *Pantydraco, Sarahsaurus*).

Basioccipital. A partial basioccipital is preserved, comprising most of the occipital condyle and the basioccipital component of the basal tubera (Fig. 4). The dorsal surface is very poorly preserved, offering little information. The occipital condyle is broader transversely than deep dorsoventrally and has a slight median crevice on its ventral margin. A similar indentation is observable in P. erlenbergiensis. The condylar neck is clearly defined, with its ventral surface delimited as a broad median ridge. The condyle is slightly transversely expanded relative to the neck. This is similar to the condition in Efraasia, but different to taxa in which both the condyle and condylar neck of similar width are (e.g. Massospondylus, Plateosaurus). The anteroventral portion of the basioccipital expands mediolaterally to form a large flange-like structure, which comprises the posterior portion of the basal tubera. This flange is saddle-shaped in anterior view, with a concave median notch bound laterally by the obliquely sloping faces of the basal tubera. This notch is less developed than the deep recess present in Massospondylus, which is more deeply incised into the body of the basioccipital. This morphology appears to have been mostly absent in *P. erlenbergiensis*, which presents a more transversely straight ventral contact between the basioccipital and basisphenoid in posterior view. The transversely straight anteroventral margin of the basioccipital of Efraasia also lacks a median notch (Bronzati & Rauhut 2017; see also Yates [2010] for comments on variability in this structure). The anterior surface of the basioccipital is marked by a central concavity, which extends dorsally from the median notch. This concavity represents the posterior boundary of the basisphenoid recess (see below). The anterolateral surfaces of the basioccipital contact the basisphenoid portion of the basal tubera. The contact between the basioccipital and basisphenoid is relatively uniform in ventral aspect, forming a straight suture line between the tubera (although see Discussion, below).

Parabasisphenoid. The basisphenoid and parasphenoid are fused as a single element (Fig. 4). Unfortunately, most of the parasphenoid rostrum (=cultriform process) has been destroyed since the original description, and thus no further information is available.

The basisphenoid portion of the basal tubera is in contact with, but not fused to, the anterior margin of the basioccipital component of the basal tubera. The tubera represent the ventral termini of posterolaterally flaring peduncles that occupy the posterior half of the ventral body of the basisphenoid and laterally bound the central anterior concavity of the basioccipital. The left peduncle is separated from the basioccipital component of its basal tuber via a conspicuous lateral crevice, a morphology that appears less marked in the right tuber (possibly due to differential preservation). As in Massospondylus and Coloradisaurus, the basal tubera of Unavsaurus appear to have been discrete, rounded apices, as opposed to the irregular series of minute projections described for P. erlenbergiensis. As preserved, the basisphenoid component of the basal tubera extends ventral to the basioccipital component and terminates in a more acute, laterally extensive tip. The lateral margins of the tubera peduncles are shallowly concave and form paired, bony laminae that extend anteroventrally towards the base of the basipterygoid processes (Fig. 4B). These laminae bound the three major fossae of the parabasisphenoid: ventrally, they bound the two (left and right) triangular dorsolateral fossae delimited posteriorly by the tuber peduncles and anteriorly by the ridges extending dorsolaterally from the bases of the basipterygoid processes. These fossae are thought to house the lateral passage of the internal carotid artery (Gow 1990; Chapelle & Choiniere 2018), a feature that is topologically equivalent to the 'anterior tympanic recess' described in other dinosauriforms (Bronzati & Rauhut 2017). Laterally, the laminae bound a large ventral recess delimited posteriorly by the anterior wall of the basioccipital and anteriorly by the transverse ridge extending between the bases of the basipterygoid processes. This recess is excavated by an additional subfossa on the sagittal midline of its posterior end, at the juncture between the basisphenoid and the basioccipital. A basisphenoid ventral recess is a common feature in



Figure 4. Braincase of *Unaysaurus tolentinoi* (UFSM11069) in (A) ventral, (B) lateroventral, (C) left lateral and (D) posterior views. Abbreviations: atr, anterior tympanic recess; Bo, basioccipital; bpt, basipterygoid process; bsr, basisphenoid recess; bt, basal tubera; cp, cultriform process; dtr, dorsal tympanic recess; mn, median notch of the basioccipital; oc, occipital condyle; otc, otosphenoidal crest; Pbs, parabasisphenoid; Pr, protic; ssr, subsellar recess; sur, sub-recess. Scale bars = 2 cm.

Sauropodomorpha, with the morphology of Unaysaurus broadly intermediate between the thickly walled recess of Massospondylus (Chapelle & Choiniere 2018) and the broad, laminae-bounded recess of Coloradisaurus (Apaldetti et al. 2014). In contrast, both P. erlenbergiensis and Efraasia are notable for exhibiting relatively shallow (and, in the former, possibly absent) basisphenoid recesses. In P. erlenbergiensis a highly striated sheet of bone connects the basal tubera to the basipterygoids. The relative depth of the basisphenoid recess in Unaysaurus, in combination with its extension to the posterior-most margin of the bone, is possibly autapomorphic among basal Sauropodomorpha.

The ventral surface between the bases of the basipterygoid processes, immediately anterior to the transverse ridge, is excavated to an equivalent degree to the anterior portion of the basisphenoid recess described above (i.e. presence of a subsellar recess *sensu* Bonzati &

Rauhut [2017]). Although incompletely preserved, it appears that this recess terminated anteriorly via the merging of the ventrolateral walls of the base of the cultriform process, as described by Bronzati & Rauhut (2017). The dorsal surface of the cultriform process is positioned at least as high as, if not higher than, the dorsal margin of the dorsolateral fossae. Its ventral margin is roughly level with the ventral margins of the basal tubera and slightly below the ventral margin of the occipital condyle. Although this is consistent with the 'stepped' morphology seen in Plateosaurus and Coloradisaurus, the condition in Unavsaurus is much less developed than in those taxa (see Discussion, below). Existing photographs indicate that the left basipterygoid process (now broken, missing) was lateroventrally (and possibly slightly anteriorly) oriented, distally bulged, and with a sulcus extending along its anterior margin.

Prootic. A partial right prootic is articulated ventrally with the clinoid process (forming the roof of the dorsolateral fossa of the parabasisphenoid), and dorsally with a ventral portion of the parietal (Fig. 4). The lateroventral surface of the preserved portion of the prootic is marked by a large facet-like concavity, which is here interpreted as the dorsal tympanic recess. Near to the posteromedial corner of this recess is the foramen for the facial nerve (cranial nerve VII), which is bounded by sharp ridges. The ventral portion of the otosphenoidal crest is preserved as a pronounced ridge extending ventrally from the posterior margin of the dorsal tympanic recess.

Mandible

Dentary. The right and left dentary are preserved in articulation with other mandibular bones (Fig. 5). The left one is more complete and forms the primary basis

for the following description. The dentary is deeper posteriorly than anteriorly. Its anterior end, including the symphysis, is ventrally deflected and dorsoventrally expanded. This produces a concave ventral margin of the dentary in lateral view. A notably expanded anterior end of the dentary is rare among non-sauropodan sauropodomorphs, although it is observable in Pradhania (Kutty et al. 2007), Mussaurus (Pol & Powell 2007) and, to a lesser extent, Plateosaurus. The alveolar margin also deflects ventrally at the tip, forming a dorsally convex edge. The lateral surface of the dentary is laterally bulged at the mid-length and bounded dorsally by a shallow longitudinal concavity. A serially arranged group of small foramina, located close to the alveolar margin of the bone, extends along the anterior third of the dentary.

The medial surface of the anterior end of the dentary is peculiar in *Unaysaurus*. A triangular sheet of bone



Figure 5. Mandible elements of *Unaysaurus tolentinoi* (UFSM11069). Left dentary in (A) lateral and (B) medial views. Right dentary in (C) lateral, (D) medial and (F) medioventral views. E, right surangular in lateral view. Abbreviations: hy, hyoid; ic, intercoronoid; mg, mandibular glenoid; mkg, Meckelian groove; sp, splenial; ve, ventral eminence; vf, ventral fossae. Scale bars = 2 cm.

extends posteroventrally from the mandibular symphysis and terminates as a sharp, elongated point within the Meckelian groove. The sheet of bone is delimited dorsally by a faint, anterodorsally inclined sulcus. The medial surface of the symphysial region is marked by a pronounced sulcus that extends posteroventrally along the anteroventral corner of the mandibular symphysis. Immediately posterior to this sulcus the ventral margin of the dentary bifurcates with the thinner, medial arm of this bifurcation dividing the anterior end of the Meckelian groove. This produces two narrow foramina – one anteromedial to the birfurcation, and one bounded by its respective branches. Both excavations extend posteriorly and continue as a single groove (i.e. the Meckelian groove) along the ventral margin of the dentary.

The lateral and medial walls of the dentary, bounding the tooth row, are of subequal dorsal height (although the former appears to be raised very slightly relative to the latter). The first dentary tooth is positioned well back from the anterior tip of the dentary; however, a toothless alveolus was probably present anterior to this tooth, meaning that there was only a very small gap (less than one tooth's width) between the beginning of the dentary tooth row and the tip of the dentary. Including the putative anterior-most socket, there are 20 alveoli observable in the better preserved left dentary.

Splenial. Partial splenials are associated with the medial surfaces of both dentaries, albeit dislocated from its original position with respect to the left dentary (Fig. 5). The posterior portion of the right splenial is closely appressed to the right dentary. The splenial is anteroposteriorly elongate and medially concave. Its ventral margin is transversely thicker than the dorsal one. The presence of a mylohyoid foramen cannot be confirmed.

?Intercoronoid/hyoid. The left ?intercoronoid is an elongated, rod-like bone that is preserved on the medial side of the left dentary (Fig. 5). If interpreted correctly, it has dislocated from its original position wherein it braced the medioventral edge of the tooth row, and lies at an oblique, posteroventral-to-anterodorsal angle along the dentary. A similarly shaped rod of bone is appressed to the lateroventral edge of the same dentary. This possibly represents the intercoronoid of the opposite mandible, although its slightly more robust, bowed morphology suggests it could instead be a hyoid element.

Post-dentary bones. The posterior region of the mandible is poorly preserved, and the individuation of the post-dentary bones is difficult. The surangular is dorsally convex, the anterior eminence of which appears to have projected higher than the level of the glenoid articulation (Fig. 5). The posterior surangular crest

manifests as the thickened posterodorsal border of the bone and is pierced by a tiny anteroposteriorly elongated foramen. Laterally, the posterior end of the crest roofs an anteroposteriorly elongated sulcus posterior to the presumed position of the mandibular fenestra. The mandibular glenoid is a small, medially facing cupshaped facet positioned on the posterodorsal corner of the surangular. Its dorsolateral edge forms an elevated rim. The angular is featureless except for a posterodorsally inclined ridge towards the ventral margin of the bone, which delimits a subtriangular lateral depressed area. The articular cannot be distinguished from other post-dentary bones. The retroarticular process is not preserved.

Dentition

The premaxilla probably housed four alveoli, the anterior-most of which was located in the missing portion of the bone. Interdental plates are situated lingually to the tooth row and arranged in an alternating pattern with respect to each tooth. These plates are apically triangular and connected to the tooth row via a broad basal pedicle. They are roughly one-quarter the apicobasal length and half the mesiodistal width of the teeth they lingually brace. Similar interdental plates are present in Plateosaurus and have been described for Lufengosaurus (Barrett et al. 2005). They are either absent in Massospondylus, or present as an uninterrupted sheet of bone (Chapelle & Choiniere 2018). The morphology of the premaxillary teeth is difficult to ascertain due to only the basal half of a single tooth (probably the third) being present. This tooth is sub-circular in cross-section, being slightly longer mesiodistally than labiolingually.

The maxillary teeth present the typical morphology for early sauropodomorphs more derived than the basalmost members of the group, which still have teeth relatively undifferentiated from the plesiomorphic dinosaur condition (e.g. Buriolestes). The anterior maxillary teeth display a subtle distal recurvature, a morphology that becomes progressively less pronounced moving posteriorly along the tooth row. Despite this slight recurvature, both mesial and distal margins are convex in labial/ lingual view. A strong constriction is evident between base and crown in labial/lingual view, although this is more marked in more posterior maxillary teeth. Accordingly, the anterior maxillary teeth appear apicobasally elongate relative to the more posterior elements. The lingual surfaces of the maxillary teeth are relatively flat compared to labial surfaces, which display a slight convexity (both apicobasally and mesiodistally). This imparts a subtle 'D'-shaped morphology to the cross-section of the teeth, a morphology observed in the dentition of numerous other 'prosauropods'. Serrations extend for at least two-thirds the length of the maxillary tooth crowns and

are present on both mesial and distal edges. These serrations are of the typical level of development for basal sauropodomorphs, being relatively coarse (cf. the hyperfine serrations of carnivorous dinosaurs) and angled at about 45° relative to the long axis of the tooth. The anterior maxillary teeth are slightly imbricating, with the distal edges labially overlapping the mesial edges of the following tooth. There is no evidence of longitudinal fluting (*sensu* Yates 2007a) or enamel wrinkling in any of the preserved teeth. There are no obvious occlusal wear facets.

The dentary teeth are less well preserved. The anterior elements are slightly procumbent, although this is primarily a result of the ventral deflection of the anterior dentary body. As in the anterior maxillary teeth, the second preserved (complete) dentary tooth has a more convex mesial than distal margin, with the more posterior teeth relatively symmetrical in labial/lingual view. The nature of the serrations concurs with those of the maxillary teeth; however, the lingual surfaces of the dentary teeth are slightly more convex, so that the teeth are elliptical in cross-section.

Vertebral column

Axis. The axis is the only element from the cervical series preserved for *Unaysaurus*. It is adhered at a perpendicular angle to a block of articulated remains containing four dorsal vertebrae, a dorsal rib and the dorsal end of the left scapular blade (Fig. 6). The axis is overlying the posterodorsal corner of the scapular blade.

Only the centrum and the neural arch are preserved. The axial intercentrum and the atlantal centrum (odontoid process), usually fused to the axis, are not preserved. The centrum is elongated, with its anteroposterior length at least 2.5 times the dorsoventral height of the posterior surface. However, as the anterior-most margin of the centrum is not preserved, it is possible that this ratio was even higher. The lateral surface of the centrum (only the left side is visible) is marked by a pronounced longitudinal sulcus that extends from the anterodorsal tip of the centrum to the posterior articular facet. The dorsal border of this sulcus is formed of the crested rim than extends along the dorsal margin of the centrum. Ventrally, it is delimited by a putative parapophyseal facet, which is present as an anteroposteriorly elongate swelling at the dorsoventral midpoint of the anterior end of the centrum, and a rod-like ridge similarly positioned at the posterior end of the centrum. The latter feature is separated from the posterior margin of the centrum via the strong transverse expansion of the outer rim of the articular facet. The ventral margin of the centrum is transversely compressed, producing a sharp keel-like

feature along its anteroposterior length. The posterior articular facet is well excavated.

The neural arch is only partially preserved, missing sections of both the dorsal margin of the neural spine and the postzygapophyses. The neural arch is connected to the centrum through an unfused sinuous suture. The presence of a distinct, slit-shaped foramen, separating the posterodorsal margin of the centrum from the posteroventral margin of the neural arch, is possibly related to this lack of fusion between the two main vertebral bodies. The neural arch was possibly longer than the centrum, although this is difficult to confirm given the state of preservation. The prezygapophysis is a platelike swelling located anteriorly at the mid-height of the neural arch, on the cusp of an oblique shelf extending from the base of the neural spine. It does not appear to have reached the anterior-most margin of the neural spine. The prezygapophysis is connected to the postzygapophysis via a low longitudinal lamina. The surface of the neural arch immediately ventral to this lamina is shallowly concave.

The anterior tip of the axial neural spine forms a sharp point separated from the neural canal roof by a small, notch-like indent on the anterodorsal margin of the latter. Poor preservation precludes an assessment of the dorsal profile of the neural spine, i.e. whether it possessed a distinct posterodorsal slope as in the majority of basal dinosaurs (Müller et al. 2017b). The midpoint of the base of the neural spine, between the pre-and postzygapophyses, is shallowly excavated. The posterior margin of the neural spine exhibits a gradual ventral slope towards the posterior end of the arch, bifurcating into two elongate laminae that straddle the dorsal margin of the postzygapophyses, i.e. the epipophyses. The better preserved right postzygapophysis suggests that the epipophysis may have extended beyond its posterior-most margin, although this can only be stated tentatively. The interpostzygapophyseal fossa is deeply incised into the neural arch. The right postzygapophysis is sub-triangular in lateral view and expands well posterior to the posterior edge of the centrum. The neural canal is half the height of the anterior articular facet of the axial centrum and roughly circular in outline.

Dorsal vertebrae and ribs. The dorsal vertebrae are irregularly preserved, with the more anterior elements tending to be in better condition than the more posterior elements. Furthermore, a combination of adherent matrix, dorsal ribs, and the above-mentioned fragment of scapular blade, as well as articulation between the vertebrae, hinders a full assessment of the anatomy of many of the elements.

Ten dorsal vertebrae, discovered in articulation, are preserved in the holotype of *Unaysaurus* (Figs 6, 7).



Figure 6. Axis of *Unaysaurus tolentinoi* (UFSM11069) in left lateral view (A). Anterior dorsal vertebrae of *Unaysaurus tolentinoi* (UFSM11069) in (B) ventral, (C) right lateral, (D) left lateral and (E) posterior views. Abbreviations: acdl, anterior centrodiapophyseal lamina; aidf, anterior infradiapophyseal fossa; D1, ?first dorsal vertebra; D2, ?second dorsal vertebra; D3, ?third dorsal vertebra; ls, lateral sulcus; nc, neural canal; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; poz, postzygapophysis; pp, parapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis. Scale bars = 2 cm.

The precise position of these elements within the dorsal series cannot be established with certainty. Nonetheless, the position of the left scapular blade, as well as the relative anteroposterior shortness of the neural spine of the second preserved dorsal vertebra, suggests that the preserved elements begin at the anterior-most point of the dorsal column. This is further supported by the placement of their respective parapophyses. In the first preserved dorsal vertebra (only posterior half present) the right parapophysis is clearly observable within the lateral depression of the centrum, i.e. far back from the anterior edge, and makes no meaningful incursion onto the respective neural arch. This combination of features is generally associated with anterior-most dorsal elements (e.g. *Ruehleia* MR.R.4718.41-42; *Plateosaurus engelhardti* MB.R. 4430.22-25; *Adeopapposaurus* PVSJ 610). Therefore, for ease of description, this element will be referred to as D1 from this point on.

The amphicoelous dorsal centra are shorter than the axial centrum. Ventrally, the centra are transversely



Figure 7. Middle dorsal vertebrae of *Unaysaurus tolentinoi* (UFSM11069). Dorsal vertebrae ?4–7 in (A) right lateral and (B) dorsal views. Dorsal vertebrae ?8–9 in (C) left lateral, (D) right lateral and (E) posterior views. Dorsal vertebra ?10 in (F) right lateral and (G) left lateral views. Abbreviations: acdl, anterior centrodiapophyseal lamina; cidf, central infradiapophyseal fossa; dia, diapophysis; hyp, hyposphene; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pidf, posterior infradiapophyseal fossa; podl, postzygodiapophyseal lamina; poz, postzygapophysis; pp, parapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis. Scale bars = 2 cm.

constricted, resulting in a lateromedial breadth at midlength of less than half the lateromedial width of the articular facets. No ridge or keel is present on the ventral surfaces of any of the centra within the assemblage, including the anterior-most elements. This is somewhat atypical for a 'prosauropod', with most forms (e.g. Massospondylus - Cooper 1981; Lufengosaurus - Young 1941) displaying pronounced keels on the underside of the vertebrae at the cervicodorsal transition; although note that only D1 is keeled within the dorsal series of P. engeldhardti (MB R 4430 skelett C) and Adeopapposaurus (Martinez 2009). The lateral surfaces of all dorsal centra are excavated by shallow depressions, as per the condition for all early saurischians. The articular facets of all preserved dorsal centra are considerably higher dorsoventrally than transversely wide. The anteroposterior length of all dorsal centra is approximately 1.3 times the dorsoventral height of their posterior ends.

As stated above, the rugosely textured parapophysis of the first dorsal vertebra is located in a central position on the lateral surface of the centrum, directly below its contact with the neural arch. In D2, the parapophysis is in a similar position axially, although the dorsal corner of the parapophysis is positioned on the base of the neural arch. In D3, the parapophysis has moved to an intermediate position between the anterodorsal midpoint of the centrum and its anterior margin, although the majority of the process is still restricted to the centrum. In D4 and D5, the parapophysis has essentially migrated to the anterodorsal corner of the centrum and is divided roughly between the centrum and neural arch. It merges along its anterior border with the anterior centrodiapophyseal lamina/paradiapophyseal lamina (ACDL/PPDL; Wilson 1999), although this part of both D4 and D5 is obscured by both an adherent dorsal rib and poor preservation. The parapophysis appears to have migrated entirely to the neural arch from at least D7, although the subtle swelling of the anterodorsal corner of the centrum of D6 does not necessarily pertain to the parapophysis. In D8 and the remaining two preserved dorsal vertebrae, the parapophysis is positioned directly between the central infradiapophyseal fossa and the prezygapophysis, forming much of the ventral border of the anterior infradiapophyseal fossa.

Although preservation remains a persistent issue, it is nonetheless clear that the system of diapophyseal laminae is well developed in all preserved dorsal vertebrae of *Unaysaurus*, with the distribution of prezygodiapophyseal, anterior and posterior centrodiapophyseal, and postzygodiapophyseal laminae consistent with those of other sauropodomorphs (Wilson 1999; Yates *et al.* 2012). It is not possible to determine at what precise point the prezygodiapophyseal lamina (PRDL) disappears – although, if present, it is certainly much reduced by D8, with the right prezygapophysis of this element presenting a distinct laminar ridge that extends from the lateral margin of the zygapophysis, terminating at a point immediately medial to the dorsal corner of the parapophysis.

From the eighth dorsal onwards (although probably earlier) the parapophysis makes unambiguous contact with the ACDL, forming much of the anteroventral wall of the middle centrodiapopyseal fossa and thus rendering this laminar process the PPDL. The deep posterior infradiapophyseal fossa is medially walled by the peduncle of the neural arch and is particularly well preserved in D9. No preserved dorsal vertebrae show evidence of the accessory lamina dividing this fossa that has been described in other dinosaurs/sauropodomorphs (e.g. *Eucnemesaurus*: Yates 2007b).

The orientation of the diapophysis in most of the dorsal elements has clearly been affected by postmortem distortion. Specifically, the diapophyses on the right side of the vertebral column are dorsally raised at a much steeper angle than on the left side of the column. The well-preserved left lateral surface of D9 bears a transverse process that projects entirely laterally, an orientation that is likely to have characterized the transverse processes of most of the dorsal series. Its lateral surface forms a smooth, anterodorsally facing area for attachment to the rib head.

All prezygapophyses are elliptical to triangular in lateral view, have dorsomedially facing articular facets angled at about 50°, and project anterior to the anterior margins of their respective centra. Interestingly, D9 possesses a low prezygoparapophyseal lamina that originates at the dorsoventral midpoint of the parapophysis and extends a short distance along the lateral surface of the main body of the prezygapophysis. This lamina, together with the parapophysis, the subtle spinoprezygapophyseal lamina, and what is possibly the remnants of a low PRDL, frame a distinct concavity at the anterodorsal portion of the neural arch, just behind the prezygapophyses.

The postzygapophyses of most elements are obscured by either poor preservation or articulation with the adjoining element. Nonetheless, it is evident that the interpostzygapophyseal fossa is more deeply incised into the neural spine than the interprezygapophyseal fossa, as is typical for basal Sauropodomorpha. The morphology of the hyposphene is similarly difficult to reconstruct, although the right postzygapophyseal facet of D9 preserves the broken prezygapophysis of D10 in articulation, which in turn is bound medially by a triangular wedge of bone, demonstrating the clear possession of hyposphene-hypantrum articulations. The hyposphene appears to have been much shallower dorsoventrally than the sub-circular neural canal. Measuring from the dorsal margin of the postzygapophysis to the floor of the neural canal, the neural arch is lower than the posterior articular facet of the centrum, differing from the dorsoventrally elongate condition in later sauropodiforms (e.g. *Antetonitrus*, *Pulanesaura*; McPhee & Choiniere 2017).

The morphology of the dorsal neural spines is difficult to fully assess in most of the dorsal vertebrae, although the neural spines of D2 through D6 appear to be mainly complete. The anteroposterior length of the neural spine of D5 (the best preserved of the middle elements) is 1.7 times its dorsoventral height. In terms of general morphology the preserved dorsal vertebrae possess low, sub-rectangular neural spines that are considerably lower than the centrum. The posterior margin of the neural spine of D5 is slightly concave, with a sharper posterodorsal corner than anterodorsal corner. Although the dorsal margin of this element is faintly bulged transversely towards its posterior end, no dorsal vertebra of *Unaysaurus* displays unambiguous spinal tables at the dorsal summit of its neural spine, including the relatively well-preserved spine of D2.

The dorsal ribs are unremarkable for Sauropodomorpha, being comprised of a short, tab-like tuberculum and much more medially expansive capitulum. Pronounced sulci are observable on both anterior and posterior surfaces of the most complete rib attached to the block of four articulated vertebrae.

Caudal vertebrae and haemal arches. Twenty-nine middle-to-posterior caudal vertebrae are preserved (Fig. 8). The more anterior preserved centra are almost twice as long anteroposteriorly than dorsoventrally deep. The centra become proportionally lower moving posteriorly along the caudal series, and also decrease in absolute anteroposterior, dorsoventral and lateromedial dimensions. The centra are rod-like in ventral view, lacking the strongly constricted outline of the dorsal vertebrae. Although a subtle sagittal indentation is observed in some (but not all) of the more anterior elements, this is considerably less developed than the true sulcus present in the anterior caudal vertebrae of some sauropodomorphs (contra Müller et al. 2018b). The articular facets are slightly excavated, and the ventral border of the posterior ends of the centra is not beveled for chevron attachment.

The neural arch is dorsoventrally shorter than the centrum. No evidence of a transverse process is seen posterior to the fifth preserved caudal vertebra. The prezygapophyses are laterally bulged, separated by a



Figure 8. Caudal vertebrae of *Unaysaurus tolentinoi* (UFSM11069). Middle caudal vertebrae in (**A**) right lateral, (**B**) left lateral and (**C**) lateroventral views. Distal caudal vertebrae in right lateral view (**D**). Extreme distal caudal vertebrae in right lateral view (**E**). Abbreviations: ch, chevron, prz, prezygapophyses; poz, postzygapophysis; tp, transverse process. Scale bars = 2 cm.

rounded interprezygapophyseal fossa, and the articular facets are directed medially. They are short, overlapping approximately 10% of the preceding centrum. The neural spine is a short process that is directed posterodorsally. It is positioned posteriorly upon the arch, close to the short and sub-triangular postzygapophyses. There is no marked evidence of an anterior median ridge extending from the base of the neural spine towards the prezygapophyses (although this is probably more common on more anterior-to-middle caudal vertebrae).

Several haemal arches are preserved with the caudal vertebrae. The more anterior elements have more robust peduncles and their distal end is transversely flattened, giving them a plate-like appearance in lateral view. There is no evidence of a distinct anterior process. The haemal canal is roofed by a bony bridge connecting the proximally bifurcating peduncles. The more posterior haemal arches are proportionally shorter and more anteroposteriorly expanded at their distal portion in relation to the more anterior elements.

Pectoral girdle

Both scapulocoracoids are preserved (Fig. 9). The following description assumes a vertical orientation of the scapula, with the top of blade positioned dorsally and the acromial area positioned ventrally. The majority of the description focuses on the better preserved right scapulocoracoid.

The scapula is strongly bowed in anterior/posterior view, with the ventral base of the lateral surface of the blade representing the convex apex of this bowing. The main body of the scapula is formed by the glenoid articulation, the acromion process and the area of contact with the coracoid. Most of its lateral surface is occupied by the acromion fossa. The long axis of this fossa is oriented anteroposteriorly, extending from the anterior-most margin of the scapular glenoid to the anterior apex of the acromion process.

The acromion process is stout and anteriorly projected at a right angle with respect to the long axis of the scapular blade. The thin ridge connecting the anterior tip of the acromion process to the blade rises at an angle of $\sim 55^{\circ}$ relative to the long axis of the scapula. This compares to an angle of roughly 60-65° in most other basal sauropodomorphs (e.g. Massospondylus, Coloradisaurus, Lufengosaurus). The main body of the acromion process is divided into distinct dorsal and ventral facets due to the anterior extension of the preglenoid ridge. The scapular glenoid is a rounded, posteroventrally facing facet that is borne on a transversely robust, peduncle-like strut of bone. This region represents the thickest part of the element. The scapula exhibits a mound-like ventral swelling at the point of contact with the coracoid, at the level of the coracoid foramen.



Figure 9. Scapulocoracoid of *Unaysaurus tolentinoi* (UFSM11069). A, left scapula in lateral view. B, right scapula in lateral view. C, right scapulocoracoid in medial view. D, right coracoid and detail of acromial region of right scapula in lateral view. Abbreviations: acp, acromion process; af, acromion facet; cf, coracoid foramen; cor, coracoid; ct, coracoid tubercle; gl, glenoid; sb, scapular blade. Scale bars = 2 cm.

An oval aperture occurs between this swelling and the anterolateral margin of the acromion fossa. However, the differential development of this feature (being much more evident in the right element), suggests augmentation by preservational processes. The anteroposterior length of the ventral end of the scapula is 0.41 times its total dorsoventral length.

The scapular blade extends dorsally from the acromial region as a thin, plate-like spine with concave anterior and posterior margins. The minimum anteroposterior length of the blade at its mid-length is 0.13 times the total dorsoventral length of the bone, similar to the gracile scapulae of other sauropodomorphs (e.g. Adeopapposaurus, Coloradisaurus, Seitaad, Plateosaurus) and differing from more robust ones which have a ratio >0.2 (e.g. Antetonitrus, Lessemsaurus). Its lateral surface has a very shallow dorsoventral sulcus extending over the mid-length of the blade. The posterior border of the medial surface possesses a low ridge that extends from the dorsal end of the glenoid peduncle to a point ventral to the mid-length of the scapular blade. This ridge delimits an equally subtle sulcus that mirrors the dorsoventral extent of the lateral sulcus. The dorsal end of the scapular blade presents the typical anteroposterior expansion of sauropodomorph scapulae. The precise dimensions of this expansion are difficult to assess due to the missing anterodorsal corner of the right scapula and the axis covering the posterodorsal corner of the left; however, the latter element yields a tentative estimate of 0.35 (i.e. slightly less than the ventral expansion).

The suture between the scapula and coracoid is still clearly visible. The latter bone is a kidney-shaped element that is anteroposteriorly longer than dorsoventrally deep. Similar to the ventral end of the scapula, the coracoid is transversely thinnest at its anterior end and thickest at its posterior end, whereupon it forms the coracoid component of the glenoid fossa. It is subtly concave medially, with a similarly subtle convexity to the lateral surface. The coracoid foramen is a circular aperture situated at the anteroposterior mid-length of the element, a few millimetres ventral to the scapulocoracoid suture. In the right coracoid, the aperture is directed anterodorsally, passing from the lateral surface through to the medial. The glenoid articular facet faces posterodorsally and is sub-elliptical in outline. It is of similar, if slightly smaller, dimensions to the scapular component of the glenoid, and is somewhat less laterally inclined than the latter. The glenoid is laterally bordered by a thick rim. The coracoid tubercle is present as a pronounced lateral swelling immediately ventral to the glenoid, occupying most of the posterior end of the coracoid. Unavsaurus does not appear to have possessed the discrete, posteroventrally facing facet between the glenoid and coracoid tubercle that is present in a number of 'prosauropods' (e.g. *Riojasaurus*, *Sarahsaurus*).

Forelimb

Humerus. Both humeri are present, with the right element the better preserved of the two (Fig. 10). In overall appearance, the humerus of Unaysaurus is consistent with the anatomy seen in the majority of basal sauropodomorphs, with a mediolaterally expanded proximal half, narrow midshaft, and less expanded distal half. The proximal half is rotated roughly 40° relative to the transverse axis of the distal condyles, although this angle becomes progressively higher towards the anterolateral margin of the proximal head due to the strong anterior deflection of the deltopectoral crest. As previously described by Remes (2008), the proximal humeral head of Unavsaurus is relatively low in anterior-posterior view, lacking the strong proximal doming of other sauropodomorphs (e.g. Yunnanosaurus, Antetonitrus). In this respect, Unaysaurus was considered most similar to Plateosaurus (see also McPhee et al. 2015b). Nonetheless, it should be noted that the degree of proximal vaulting in several other 'prosauropod' taxa (e.g. Efraasia, Plateosauravus; see Remes 2008, fig. 7.5) is not conspicuously greater than that observed for Unaysaurus. The proximal surface of the head is rugosely textured throughout its length, a feature related to the epiphyseal-like cartilage plates inferred for extinct archosaurs (Bonnan et al. 2010). The proximal head expands posteriorly, making a strong incursion onto the posteroloateral surface of the proximal shaft. This swelling is restricted to an area roughly congruent with the transverse margins of the humeral shaft. The medial (= internal) tuberosity is posteriorly deflected from the long axis of the proximal head at an angle of about 20° . This deflection, in combination with the posterior swelling mentioned above and the anterior projection of the deltopectoral crest, imparts a sigmoid proximal profile to the humeral head (when viewed proximally).

The medial edge of the proximal surface of the humerus slopes mediodistally at an angle of 30° , whereas the medial margin of the proximal shaft flares proximomedially at a similar angle. The right angle at which these two edges meet forms the main body of the medial tuberosity. The posterolateral surface of the medial tuberosity exhibits a shallow sulcus, possibly related to the attachment of the M. scapulohumeralis posterior (Otero *et al.* 2017). However, the same area of the left humerus does not appear to have been as deeply recessed, suggesting the possibility of post-mortem bone collapse – although much of the medial tuberosity is missing in the left element.



Figure 10. Forelimb elements of *Unaysaurus tolentinoi* (UFSM11069). Right humerus in (A) proximal, (B) lateral, (C) anterior, (D) medial and (E) posterior views. Right ulna (left) and radius (right) in (F) proximal, (G) lateral, (H) anterior, (I) medial, (J) posterior and (K) distal views. Abbreviations: ap, anterior process; cf, cuboid fossa; dpc, deltopectoral crest; ec, entepicondyle; mt, medial tuberosity; olc, olecranon process; pmp, posteromedial process. Scale bars = 2 cm.

The deltopectoral crest forms the lateral margin of the proximal end of the humerus and projects mainly anteriorly and slightly laterally relative to the transverse axis of the distal condules. It has two major components: a transversely thin proximal portion that is angled slightly medially relative to the proximodistal long axis of the humerus, and a transversely wider distal portion that is angled slightly laterally relative to the proximodistal long axis. The anterior profile of the deltopectoral crest thus exhibits a mild sinuosity, as is observed to varying degrees in all basal sauropodomorphs (particularly pronounced in Riojasaurus and Coloradisaurus). The robust distal portion represents the most strongly anteriorly projecting part of the deltopectoral crest, forming a sub-rectangular tab in lateral view. A similar profile is observed in most other 'prosauropods'.

On the medial surface of the deltopectoral crest, the juncture of its thin and thick portions produces a shallow groove that extends distally and is primarily delimited by the transverse expansion of the distal half. A distinct sinuous ridge is observable on the lateral surface of the deltopectoral crest, originating at roughly the proximodistal midpoint of the thin proximal portion of the crest and extending posterodistally towards the juncture of the crest with the main body of the humeral shaft. This ridge terminates in a distinctive pit-shaped fossa which is positioned level with the anterodistal corner of the deltopectoral crest. These features (putatively autapomorphic for Unavsaurus: Leal et al. 2004) are observable on both humeri and are likely associated with the M. deltoides musculature. There is no sign of a paramarginal sulcus or similar feature bordering the anterolateral margin of the crest in either humerus (as in Antetonitrus, for example). Measured from the proximal-most point of the humeral head to the point where the deltopectoral crest remerges with the humeral shaft, the crest is just under half (~ 0.48) the total proximodistal length of the humerus. This ratio is fairly typical for 'prosauropods', with the majority of taxa possessing a deltopectoral crest that extends for roughly 45-55 times the total length of the humerus (e.g. Leonerasaurus, Antetonitrus, Lufengosaurus, Efraasia).

The humeral shaft is a sub-circular strut of bone that undergoes a gradual transverse expansion along its medial and lateral margins to form the distal condyles. The anterior face of the distal end is marked by the presence of a deep cuboid (= intercondylar) fossa. Although clearly well developed, probable bone collapse and the differential preservation of this feature across both humeri precludes a better understanding of its morphology. Likewise, the shallow depression generally observed on the posterior face of the distal end has clearly been exaggerated by bone collapse in both humeral elements. The ulnar and radial condyles are of subequal size in distal view, with the former having slightly greater dimensions. A distinct entepicondyle is present on the mediodistal corner of the ulnar condyle, observable as a sheer mediodistally facing facet. The transverse width of the distal end is 0.32 times the proximodistal length of the humerus.

Radius. The preserved radius is the accompanying antebrachial element to the right ulna (Fig. 10). It is a simple, rod-like bone with expanded proximal and distal ends and a straight, slender shaft. The proximal end forms an anteroposteriorly elongated ellipse in proximal view, being 2.2 times longer anteroposteriorly than transversely wide. In lateral view the proximal end is gently saddle-shaped, with proximally raised anterior and posterior corners. The posterior corner, in addition to being raised to a higher proximal level than the anterior corner, also exhibits a strong posterior projection. In contrast, the anterior projection of the anterior end is proportionally much less acute. An acutely raised posterior (=posterolateral) corner of the proximal radius appears to be plesiomorphic for Sauropodomorpha (or a slightly less inclusive grouping, see the conditions in Adeopapposaurus and Mussaurus), and is reduced in the 'near-sauropod' Antetonitrus. Curiously, the condition appears to 'reverse' in later sauropods, with the anterior/ medial corner of the proximal radius developing into a pronounced 'medial process' (e.g. Wilson & Sereno 1998; Upchurch et al. 2015).

Consistent with the distortion experienced by the ulna, the bone surfaces directly beneath the proximal end of the radius are transversely crushed. The remaining, uncrushed part of the shaft is circular in cross-section. The shaft bows slightly medially towards the distal end. The distal articular surface is of generally much more robust proportions than the proximal end and more circular in distal outline. A series of fine, vertical striations skirt the distal rim of the shaft along its entire circumference. The posterior corner of the distal articular surface is proximally raised relative to the anterior corner. A very low crest originates from this raised corner and extends a short distance along the posteromedial margin of the distal radial shaft. This crest coincides with the area of the distal radius that made the most obvious contact with the distal ulna. The distal articular surface is primarily flat and rugose.

Ulna. The complete right ulna is 0.72 times the length of the humerus (Fig. 10). This is a relatively high ratio for Sauropodomorpha, with most 'prosauropods' typically displaying a ratio of about \sim 0.6 (e.g. *Riojasaurus*, *Antetonitrus*). The proximal articular surface is anteroposteriorly elongate (with an anteroposterior length by

maximum transverse breadth ratio of 1.95) and presents a relatively sigmoid outline in proximal view. The proximal surface comprises an anteriorly projecting anterior process, a bulbous lateral process and the proximally domed olecranon process. The anterior process is a triangular wedge of bone that tapers anteriorly to a rounded point. Its proximal surface is gently convex, which produces a shallow transverse trench between the base of the anterior process and the main area of the proximal surface (i.e. the olecranon process). The anterior process displays a subtle lateral deflection which, together with the lateral process, delimits a shallow radial fossa. The depth of this fossa is variable throughout Sauropodomorpha, with its incipient development generally associated with basal sauropodiform taxa close to Sauropoda (e.g. Yates et al. 2010; Otero & Pol 2013). The majority of the lateral margin of the proximal end of the ulna is occupied by the lateral process, which is a hemispherical swelling overhanging the lateral surface of the ulnar shaft. As in most very basal sauropodomorphs, the medial surface of the proximal ulna is relatively anteroposteriorly uniform, lacking the discrete medial process (=ridge) observed in a number of derived non-sauropodan sauropodiforms (e.g. Aardonyx, Antetonitrus). However, the posterior-most corner of the proximal end abruptly tapers to a sharp point, forming a small 'posterior process' which is likely homologous to the medial ridge of later forms. The olecranon process is of the typical condition for basal Sauropodomorpha, being moderately developed and uniformly convex in all dimensions. Its medial margin terminates somewhat more abruptly than the lateral due to the absence of a lateral process-like feature in that region of the bone.

The ulnar shaft tapers strongly from the proximal end, becoming progressively anteroposteriorly restricted towards the distal end. Its proximal half is strongly transversely compressed. However, this has clearly been exaggerated by taphonomic crushing, a phenomenon that is evidenced by the large excavated area on the medial surface of the proximal half of the shaft. Although a slight recess in this region of the ulna is common, the uneven bone surface and artificial ridging points to the influence of diagenetic processes. The same crushing is potentially responsible for shifting the typical proximal anterior process posteriorly. Likewise, the sharp lip that the proximal lateral process forms above the lateral surface of the shaft has potentially been exaggerated by taphonomic crushing.

The distal end of the ulna is slightly twisted relative the proximal end. Accordingly, the distal half of the shaft undergoes a modest transverse expansion when viewed anteriorly. On the anterior-most corner of the distal end, a few millimetres above the distal articular surface and in direct line with the anterior tip of the proximal anterior process, there is a circular rugose pit. This is likely the attachment scar for the ulnoradial ligaments. The distal articular surface is softly convex transversely and sub-ovoid in distal view.

Manus. The manus of *Unaysaurus* is represented by the complete first, second and fourth metacarpals, as well as the proximal end of the third metacarpal; the penultimate phalanx of the pollex; several non-terminal phalanges tentatively assigned to the hand; and two ungual phalanges missing their distal tips (Fig. 11). The latter two elements are assigned to the hand primarily because they possess large flexor tubercles, and presumably represent the two unguals assigned to the hand in the original description. In the absence of strong evidence to the contrary, all elements are interpreted as belonging to the right manus.

Metacarpal I is 0.7 times the length of metacarpal II, although its maximum proximal breadth is subequal to that metacarpal. Its proximal articular surface is sub-triangular in outline with a dorsoventrally deep lateral end and dorsoventrally shallower medial end that terminates in a rounded medial margin. The lateral margin of the proximal surface is proximally elevated and divided into two distinct lobes that are separated by a distinct notch. These tubercles laterally bound a shallow concavity located centrally on the proximal surface. Given the disarticulated state of the metacarpus, it is not possible to determine whether the proximolateral edge of the first metacarpal was inset into the carpus, as in the majority of 'prosauropods' (Sereno 2007). However, articulation of metacarpal II with the lateral surface of metacarpal I suggests a more 'natural' alignment if the former is positioned 0.5 cm or so below the proximal surface of the latter. This would thus leave space for the second distal carpal to articulate between the proximolateral edge of metacarpal I and the proximal surface of metacarpal II. This is further supported by the excavated area observable on the proximal half of the lateral surface of metacarpal I, suggesting accommodation for the medioventral corner of the proximal surface of metacarpal II. However, these considerations remain mainly speculative for the time being. The maximum proximal breadth of metacarpal I is 0.73 times the proximodistal length of the bone. This falls within the plesiomorphic range for Sauropodomorpha and is similar to metrics observed in Plateosaurus (Huene 1926), Adeopapposaurus (PVSJ 610: 0.75) and Anchisaurus (Galton 1976).

Both medial and lateral margins of the shaft of metacarpal I are transversely waisted and concave in dorsal/ventral view. The minimum transverse width of the shaft is 0.53 times the total proximodistal length of



the bone. Both dorsal and ventral surfaces of the shaft of metacarpal I bear a longitudinal sulcus. Its distal articular condyles are asymmetrical in both transverse and sagittal planes, with the lateral ginglymoid articulation and its collateral pit transversely, proximodistally and dorsoventrally deeper than the corresponding structures on the medial condyle. This condition is observed in most 'prosauropods' (e.g. *Plateosaurus* – Huene 1926; *Mussaurus* – Otero & Pol 2013). In contrast, derived, 'near-sauropod' taxa such as *Antetonitrus* (McPhee *et al.* 2014) possess a metacarpal I in which the medial condyle, although still proximally raised relative to the lateral, is roughly volumetrically equivalent in overall size to the latter.

The first phalanx of digit I is slightly longer proximodistally than the respective metacarpal. It is proximally asymmetrical, with the ventral portion of its medial articular facet strongly projected ventrally. This projection lends the medial facet a dorsoventrally 'stretched' appearance, contrasting with the more typically semi-circular lateral facet. The ginglymoidal ridge separating the proximal articular facets is low-to-absent in the very centre of the proximal surface, but expands ventrodorsally to form proximodorsal and proximoventral 'heels' that articulate with the intercondylar groove of the distal articular portion of metacarpal I. The ventral heel extends further proximally than the dorsal heel and is thus the larger of the two. The distal condyles are twisted about 25° clockwise relative to the dorsoventral midline of the proximal articular surface. This metric is relatively low, with most 'prosauropods' displaying a first manual phalanx that is twisted longitudinally to around 45-60° (e.g. Adeopapposaurus - PVSJ 610). Phalanx I.1 of the putative basal sauropodomorph Eoraptor is twisted to approximately 35° (Sereno et al. 2012), whereas the same element in Plateosaurus was also only twisted $\sim 30^{\circ}$ (Mallison 2010, fig. 6). It is possible, therefore, that the low value observed for Unaysaurus represents an incipient twisting as opposed to a reversal of the apomorphic state. The collateral pits are larger than those of metacarpal I. The ventral margins of the distal condyles are enlarged relative to the dorsal margin, with the former making a proportionally greater incursion onto the ventral surface of the shaft. This pattern is observed in other preserved phalanges. The medial condyle is slightly larger than the lateral one.

The proximal surface of metacarpal II is sub-rhomboidal in outline, with the dorsal margin slightly transversely wider than the ventral margin. The dorsolateral corner (=dorsolateral flange) projects as an acute proximal flange. Except for its ventral border, which rises as a slight crest, the proximal surface is mostly flat. The maximum proximal breadth of metacarpal II is 0.53 times the total proximodistal length of the bone. The lateral surface of its shaft is slightly concave. The dorsal surface possesses a shallow, sub-triangular fossa proximally, and a distal 'C'-shaped extensor fossa. The proximal half of the medial surface is also subtly concave where it contacts the metacarpal I. The medioventral corner of the shaft, directly beneath proximal surface, does not possess a projecting tubercle as seen in some sauropodiform taxa (e.g. Antetonitrus, Sefapanosaurus; McPhee et al. 2014). The ventral surface has a shallow distal flexor excavation. The distal articular portion is considerably wider transversely than dorsoventrally deep. It is trapezoidal in distal outline, with the ventral surface of the condules transversely expanded relative to the dorsal surface. There is no marked asymmetry between the medial and lateral condyles, although the latter is slightly more robust than the former and its collateral ligament appears to have been more developed.

The proximal articular surface of metacarpal III is subtriangular in outline (as in *Adeopapposaurus*, for example), rather than trapezoidal, as seen in other sauropodomorphs (e.g. *Plateosaurus* – Huene 1926; *Mussaurus* – Otero & Pol 2013). The absence of the distal half makes orientation of the element difficult. Two sides of the triangular proximal part of the shaft are deeply excavated, although the fossa on the broader ?ventral surface has potentially been exaggerated by post-depositional crushing. This same crushing has potentially affected the general morphology of the proximal surface.

Metacarpal IV is considerably more slender than metacarpal II. Its proximal surface is sub-triangular, with the longest edge facing ventrolaterally, as in other basal sauropodomorphs. The medioventral corner is more broadly rounded than either the dorsomedial or dorsolateral corner, the latter being the most acute. The proximal area of the shaft lacks fossae on any of its surfaces. The majority of the shaft is proximodistally straight with a marked narrowing towards the distal end. The distal flexor fossa is

Figure 11. Manual elements of *Unaysaurus tolentinoi* (UFSM11069). **A**, right metacarpal I in (left to right) ventral, dorsal, lateral, medial, proximal (top) and distal (bottom) views. **B**, right metacarpal II in (left to right) ventral, dorsal, lateral, medial and proximal views. **C**, right metacarpal IV in (left to right) ventral, dorsal, lateral, proximal (top) and distal (bottom) views. **E**, phalanx I.1 in (left to right) ventral, dorsal, lateral, medial, proximal (top) and dorsal (bottom) views. **E**, phalanx I.1 in (left to right) ventral, dorsal, lateral, medial, proximal (top) and distal (bottom) views. **F**, ungual phalanx ?I.2 in (left to right) lateral, medial and proximal views. **G**, ungual in ?medical (top) and ventral (bottom) views. **H**, isolated non-terminal manual phalanx. **Abbreviation: ft**, flexor tubercle. Scale bars = 2 cm.

faint. The distal articular portion is asymmetrical, the medioventral corner of the medial condyle projected medially as a short pyramidal process. The medial collateral pit is sub-quadrangular and distally open.

Several isolated non-terminal phalanges are also preserved. Two of them are roughly of the same absolute length as the first phalanx of digit I and probably belong to digit II. Indeed, their articular areas are compatible both with one another and with the distal articular area of metacarpal II. The more distal (i.e. phalanx II.2), better preserved of these two elements is the most gracile element amongst the preserved manual phalanges. It has a proximal articular surface that broadly mirrors that of phalanx I.1, with a medial articular facet that is transversely attenuated relative to the lateral articular facet. However, it lacks the twisted offset between the proximal and distal ends observed in the former. The shorter, more squat-shaped phalanges are probably associated with either digits III or IV.

The proximal portions (missing most of the distal tip) of two ungual phalanges are preserved. One is slightly smaller than the other and they are tentatively assigned to digit I and II, respectively. The degree of overall curvature for both elements cannot be assessed due to the missing distal portions. The proximal articular surfaces of both elements are considerably taller dorsoventrally than transversely wide. The proximal articular surface of the larger ungual (i.e. phalanx I.2) is more concave in mediolateral view than that of the smaller ungual (i.e. phalanx II.3). The dorsal extensor process overhangs the proximal surface in both elements and is more robustly developed in phalanx I.2. This process represents the proximal-most point of both elements. Flexor tubercles are well preserved on both elements and, as in all early sauropodomorphs, are much more developed than in the pedal unguals. Consistent with the condition of the extensor process, the flexor process of phalanx I.2 is much more robustly developed than in phalanx II.3. Both elements have well-developed haemal grooves on the medial and lateral surfaces.

Hind limb

Tibia. Fragments of both tibiae are present (Fig. 12). The right tibia is missing much of the proximal half, while its distal end has experienced a modest degree of erosion. The left is only represented by the distal end, although this is in a generally better state of preservation than the same region of the right tibia.

The distal half of the preserved right tibial shaft is sub-circular in cross-section, being slightly wider transversely than anteroposteriorly deep. The anterior face of the shaft is divided into relatively discrete anteromedial and anterolateral facets, separated by a low midline ridge (slightly biased towards the lateral side) that extends proximally from the anterior-most corner of the distal end (i.e. anterior ascending process). The anteromedial facet is separated from the posterior surface via a similarly acute marginal edge. The distal end of the anterolateral surface is partly crushed in both elements, but it appears to have housed a proximodistally elongate oval fossa within the groove that extends proximally from the juncture between the distal ascending and descending processes.

The distal surface of the tibia is transversely wider than anteroposteriorly long. In general outline, the distal articular surface of the tibia is broadly intermediate between the square- distal end of basal dinosaurs (e.g. Herrerasaurus, Saturnalia, Panphagia), and the more transversely elongate distal tibia observed in most 'prosauropod' taxa (e.g. Massospondylus, Adeopapposaurus). This appears to be due to the medial expansion of the medial (=anteromedial) corner of the distal end. However, the 'posteromedial' corner of the distal end remains positioned closer to the transverse midline of the posterior surface. This has the overall effect of producing a sub-triangular distal end of the tibia in Unaysaurus, as opposed to the more sub-rectangular outline typical of 'prosauropods' (e.g. Coloradisaurus, Mussaurus, Lufengosaurus). It also means that the posteromedial surface of the distal shaft is of similar proportions to the posterolateral, whereas in most 'prosauropods' the posterolateral surface is the more expansive.

The medial half of the distal articular surface is unevenly preserved in both elements, although it appears to have been mostly flat. A slight concavity is present at the posterodistal margin (at the juncture of the two surfaces described above), which accommodated a posterior swelling on the posterodorsal margin of the astragalus. The lateral half of the distal articular surface is divided into the two distinctive facets that comprise this region of the sauropodomorph distal tibia: the anterior ascending process (which articulated with the ascending process of the astragalus) and the posterior descending process. The morphology of articular facets of these processes is obscured by poor preservation; nonetheless, it is clear that the posterior descending process would have laterally extended well beyond the lateral margin of the anterior ascending process, as in the majority of non-sauropodiform sauropodomorphs.

Astragalus. The right astragalus is complete except for the lateral-most margin (including the fibular articular area) (Fig. 12). It is transversely elongated and dorsoventrally deepest at in the region of anterior ascending process. The anteromedial corner is sub-triangular in proximal view, forming an acutely projecting angle that marks the anterior limit of the astragalus. The posteromedial corner, in contrast, is much less sharp,





Figure 12. Tibiae and astragalus of *Unaysaurus tolentinoi* (UFSM11069). Distal left tibia in (A) posterior, (B) anterior and (C) distal views. Right tibia in (D) anterior, (E) posterior, (F) medial and (G) distal views. Right astragalus (H) in (left to right) anterior, posterior, dorsal, ventral and medial views. Abbreviations: aap, anterior ascending process of the distal tibia; ap, astragalar ascending process; dp, descending process of the distal tibia; mp, medial process. Scale bars = 2 cm.

forming a rounded arc wherein the posterior side gradually merges with the medial. Although the medial margin (='condyle') is anteroposteriorly enlarged relative to the incomplete lateral margin, being approximately 1.3 times the length of the latter, it is unlikely to have approached the ratio of 1.6 that Müller *et al.* (2018b) cite as a diagnostic feature of their Unaysauridae.

Α

В

C

The astragalus thins dramatically towards the posterior margin in medial view, while also undergoing a modest dorsal inflection. This morphology lends a lacriform medial outline. The relationship between the dorsal inflection of the posteromedial corner observed here and the distinct 'pyramidal process' described for *Coloradisaurus* (Apaldetti *et al.* 2012) is ambiguous, with both conditions potentially representing variants of the same morphology. Nonetheless, it is this morphology that produces the respective concavity on the distal surface of the tibia.

Most of the medial half of the dorsal surface of the astragalus is occupied by a shallow fossa bounded posteriorly by the raised posteromedial corner, and anteriorly by the dorsoventrally expansive anterior margin. It is this fossa that receives the medial portion of the distal tibia. The lateral half of the dorsal surface is marked anteriorly by the astragalar ascending process, the dorsal surface of which appears to have merged gradually with the medial body of the astragalus. However, this can only be stated equivocally due to the missing lateral portion. The ascending process occupies over half the anteroposterior depth of the dorsal surface of the astragalus. A tiny foramen possibly (it might be a preparatory artifact) pierces the anterodorsal face of the ascending process, just below the articular facet. A larger, less ambiguous foramen is located on the posterior surface of the ascending process, directly at its base. This foramen is elliptical in outline and penetrates the bone medioventrally. Posterior to this foramen, the body of the astragalus narrows dramatically to form a dorsoventrally thin laminar shelf - the surface for articulation with the posterior descending process of the tibia.

The ventral surface of the astragalus is a rugose roller joint. In ventral view its anterior margin is straight to weakly concave, whereas its posterior margin is strongly convex. The ventral surface is slightly concave transversely, and strongly convex anteroposteriorly.

Pes. The pes is represented by fragmentary remains from both feet, including six partial metatarsals (Fig. 13). Most phalanges were found isolated and scattered within the matrix and cannot be confidently referred to any digit.

The distal ends of both first metatarsals are present. The right element is badly crushed. The left metatarsal is preserved in articulation with the first phalanx of digit I. Its medial condyle is much reduced in size compared to the lateral, and less distally extensive. Accordingly, the collateral ligament pit of the latter is of much greater size. The ventral margin of the medial condyle is ventrally projected to form a pyramidal process below the collateral pit, as in other 'prosauropods' (e.g. *Adeopapposaurus* – PVSJ 568). The shallow extensor fossa is sub-triangular. The articulated phalanx is elongate and slender, but its relative proportions with regard to the first metacarpal cannot be evaluated.

The proximal ends of the right second and third metatarsals are preserved in articulation. These elements are relatively poorly preserved, presenting uneven bone surfaces and other signs of distortion.

The proximal surface of metatarsal II is medially concave, where it would have articulated the proximal end of metatarsal I. Unfortunately, much of the dorsolateral corner of its proximal end is eroded, so the condition of the lateral surface cannot be fully determined. The ventrolateral corner terminates in a considerably more acute angle than the other two preserved corners of the proximal surface of that metatarsal. The proximal part of the shaft is transversely compressed, clearly as a result of diagenetic distortion. The proximal end of metatarsal III is less completely preserved than that of metatarsal II, with a badly eroded dorsal edge. It appears to have been mainly triangular in proximal outline, with a short ventral border and longer medial and dorsolateral sides. The preserved proximal segment of the shaft is badly crushed, being especially prominent on the lateral surface.

Two isolated distal metatarsal portions are interpreted as the associated condylar ends of the right metatarsal II and III. They are closely matched in morphology, with shallow extensor fossae and sub-equally sized medial and lateral condyles that are slightly laterally deflected relative to the long axis of the shaft. The lateral collateral ligament pit of metatarsal II is deeper than the corresponding structure in metatarsal III. The ventral corner of the lateral condyle of metatarsal III terminates in a sharp point, descending ventral to the ventral margin of the medial condyle. The produces a more trapezoidal distal outline compared with the sub-rectangular outline of metatarsal III.

The metatarsus of the left pes is represented by the distal ends of the third and fourth metatarsals. The shafts are slightly wider transversely that dorsoventrally deep. In general morphology they are identical to the distal metatarsal portions described above, with the exception of the shallower collateral pits of metatarsal IV. The distal outlines of metatarsals II through IV are considerably broader transversely than deep dorsoventrally.

All preserved pedal phalanges are longer proximodistally than transversely wide. This includes a sequence of two phalanges articulated with an incomplete ungual, suggesting that none of the penultimate phalanges of *Unaysaurus* were proximodistally shortened.

The one complete pedal ungual is probably from the third or fourth digit. It is not strongly curved, and the flexor area is only faintly projected. It is subcircular in proximal outline, with equally sized articular facets.

Discussion

'Prosauropod' interrelationships and the Plateosauridae

Establishing the interrelationships of less-inclusive groups within 'Prosauropoda' is confounded by a host of issues for which there is currently no simple solution.



These issues pertain to several well-voiced concerns, including: (1) confusions and disagreements in character conception/inclusion; (2) large amounts of missing data for many key specimens; (3) a paucity of detailed information (including specimen access) for several Chinese taxa (e.g. Yimenosaurus, Jingshanosaurus, Gongxianosaurus, Kunmingosaurus, Chuxiongosaurus, Chinshakiangosaurus); and (4) the potentially chimerical nature of several operational taxonomic units (OTUs), such as Massospondvlus (Chapelle & Choiniere 2018); Riojasaurus (McPhee et al. 2015b; McPhee & Choiniere 2017), Coloradisaurus (Apaldetti et al. 2014) and Plateosauravus (McPhee et al. 2017). In addition to these concerns, and perhaps underpinning them, is the famous morphological conservativeness of 'prosauropods', which makes it difficult to isolate obvious divergences from the generic condition.

Recent assessments have tended to divide non-sauropodan sauropodomorphs into three informal groups: (1) a grade of very basal 'stem' forms little differentiated from the primitive dinosaurian condition (e.g. Buriolestes, Saturnalia, Eoraptor, Panphagia); (2) a central suite of 'gracile' (probably habitually bipedal and herbivorous) forms comprising the taxa that generally constitute the plateosaurid and massospondylid clades ('core prosauropods' sensu Upchurch et al. 2007; see also Sereno 2007); and (3) a pectinate array of 'robust' (probably mostly quadrupedal) basal sauropodiforms representing progressively proximate outgroups to Sauropoda (e.g. Upchurch et al. 2007; Yates 2007a; Otero et al. 2015; McPhee et al. 2015a, b). However, whereas it has recently been suggested that the lattermost taxon can be recognized with respect to an apomorphic suite of features related to forelimb parasagittalism (McPhee & Choiniere 2017), determining clear boundaries between the other three groups represents a far greater challenge.

Although the total functional disparity of craniodental characters for non-sauropodan sauropodomorphs has recently been reported to be relatively high (Button *et al.* 2017), this variation is expressed mainly via autapomorphic outliers, whereas morphological disparity values (based on discrete characters) from across the skeleton show clear morphospace divisions between only basal Saurischia, 'prosauropods' and sauropods *sensu stricto* (McPhee *et al.* 2017). Thus, evidence for monophyletic groupings within 'Prosauropoda' is generally inferred from subtle changes in the cranial

architecture (e.g. nature of contact between elements; position and shape of fenestrae/fossae relative to other landmarks) and the relative proportions of specific parts of the postcranial skeleton (e.g. inter/intra-element ratios of the limbs; height/length of the major vertebral components). However, many of these features present either a confused or an unclear distribution throughout the group, or occur along a graded continuum.

The above concerns have a bearing on the hypothetical monophyly of Plateosauridae. This clade is generally constituted of (1) the various species that currently comprise the Plateosaurus complex (P. engelhardti, P. gracilis, P. 'ingens', P. erlenbergiensis, P. 'longiceps'; Galton 1985, 2001; Moser 2003; Yates 2003b; Prieto-Márquez & Norell 2011) and (2) Unavsaurus (and possibly the fragmentary Indian genus Jaklapallisaurus: Novas et al. 2010). Although Plateosaurus is in serious need of revision - an undertaking far beyond the scope of this paper – the clade Unavsaurus + Plateosaurus is nonetheless primarily the result of previously inferred cranial similarities between Unavsaurus and P. engelhardti. The latter is represented in the current cladistic data set mainly by the informal neotype SMNS 13200 (Huene 1926; Yates 2003b), with cranial scorings undoubtedly augmented by the near-identical P. erlenbergiensis (AMNH FARB 6810), for which a detailed cranial description exits (Prieto-Márquez & Norell 2011; treated as a separate OTU in Chapelle & Choiniere [2018]). During the course of the current study, examination of the McPhee et al. (2018) matrix revealed several character states were observed to be shared between Unaysaurus and Plateosaurus to the exclusion of most other 'prosauropods'. However, the synapomorphic status of several of these features remains contentious, with some either displaying a more complex distribution within 'prosauropods' or being subject to the uncertainties that arise from inter-worker subjectivity and/ or ambiguities in the specimen/source providing the observation. These characters are discussed in detail below, followed by an updated cladistic analysis.

Contact between maxillary ramus of the premaxilla and maxillary (anteroventral) ramus of the nasal (Character [Ch.] 8). *Plateosaurus* shares with early dinosaurs (e.g. *Herrerasaurus*, *Eoraptor*) an external naris in which the posterior border is composed entirely of the respective rami of the premaxilla and nasal. In contrast,

Figure 13. Pedal elements of *Unaysaurus tolentinoi* (UFSM11069). **A**, right metatarsal II and III in (left to right) proximal, medial, lateral and posterior views. **B**, central right distal metatarsal in (left to right) dorsal and distal views. **C**, central right distal metatarsal in (left to right) lateral, posterior, dorsal and distal views. **D**, distal left metatarsal I and articulated pedal phalanx I.1 in medial (left) and dorsal (right) views. **E**, central left metatarsal and associated phalanx in dorsal view. **F**, central left metatarsal in dorsal (left) and lateral (right) views. **G**, articulated phalanges with partial ungual in dorsal (left), ventral (right) and side (bottom) views. **H**, ungual in proximal and side views. **I**, isolated ?distal phalanx in (left to right) dorsal, ventral and side views. Scale bars = 2 cm.

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these rami fail to meet along the ascending ramus of the maxilla in most other sauropodomorphs. Although *Unaysaurus* was originally reconstructed (Leal *et al.* 2004, fig. 2) in such a way as to suggest contact between the premaxilla and nasal (and was scored accordingly), this cannot be stated with certainty given the preservation of the holotypic snout. In addition to the nasal likely having been ventrally offset relative to its position in life, *Unaysaurus* also appears to have lacked the anteroventrally elongate nasal maxillary ramus seen in *Plateosaurus* (i.e. *P. erlenbergiensis*; AMNH FARB 6810; Prieto-Márquez & Norell 2011, fig. 6).

Development of external narial fossa (Ch. 11). Previously scored as well developed (1) in Unaysaurus and Plateosaurus (and also Coloradisaurus, Efraasia and Eoraptor), and as absent to weak (0) in forms such as Massospondylus, Adeopapposaurus and Aardonyx, this character refers to the degree to which the recess surrounding the narial fenestra is demarcated by an obvious rim, with emphasis on the anteroventral and posterior margins. In Plateosaurus (AMNH FARB 6810) this rim is obvious, with a sharply incised anteroventral corner of the fossa. However, in no other (non-sauropod) taxon in the data set is this morphology as marked. In Unavsaurus, although the narial ramus of the premaxilla possesses a pronounced ridge that extends along its length and partially roofs the dorsal margin of the external narial fossa/fenestra (probably relatively typical for most forms), the anteroventral corner of the fossa grades smoothly with the premaxillary body. In other taxa (e.g. Coloradisaurus) this region of the cranium is too poorly preserved to confidently assess the condition of this feature. This character, therefore, appears to be highly sensitive to the vagaries of preservation and interpresonal interpretation (i.e. in determining what is, and what is not, 'well developed'), and should be treated with caution.

Antorbital fossa (Ch. 34). One of the more striking similarities between Unaysaurus and Plateosaurus is the expansive sheet of bone occupying the anteroventral region of the antorbital fenestra. This sheet of bone effectively forms the medial wall of the antorbital fossa, and in most forms is present as no more than a crescentic depression bounding the posterior margin of the lacrimal (dorsal) ramus of the maxilla (e.g. Adeoppaposaurus, Massospondylus). Although Coloradisaurus (PVL 3967) has the same condition as Plateosaurus and Unaysaurus, it also shares a host of cranial features with the former, suggesting a closer relationship than implied by most recent analyses (see Apaldetti et al. 2014). Stranger is the presence of a similar structure in the relatively 'derived' non-sauropodan sauropodiforms Aardonyx (Yates et al. 2010) and NMQR 3314 (='*Melanorosaurus*'; see Yates [2007a] and McPhee *et al.* [2017]). Further work is required to address the plausibility of a homoplastic distribution of this relatively marked morphology (one of the less ambiguous transformations within the data set) relative to the effects of other poorly understood and/or problematic character formulations.

Frontal contribution to the supratemporal fenestra (Ch. 61). Previously scored as present (1) in Plateosaurus and Unaysaurus (and Jingshanosaurus impossible to confirm – and Xingxiulong – contingent on the interpretation of Wang et al. [2017, fig. 3e, f]), this character has a particularly confusing history. In most early dinosaurs the supratemporal fossa extends as a depressed area of bone onto the posterodorsal surface of the frontal. Much rarer is the condition in which the frontal makes unambiguous contact with the fenestra itself. Huene's (1926, pl. 1, fig. 4) illustration of Plateosaurus (SMNS 13200) clearly shows the frontal reaching the anterior margin of the supratemporal fenestra, a condition that appears to be supported with respect to photographs BWM has of this skull. Although the frontal-parietal suture of Unavsaurus appears to have extended markedly close to the supratemporal fenestra, the preserved condition does not permit a confident assessment of its condition. As currently understood, this feature is autapomorphic for *Plateosaurus* (and possibly Xingxiulong) within non-sauropodan Sauropodomorpha. Nonetheless, Plateosaurus and Unavsaurus are notable for sharing a deeply excavated, scarp-like anterior margin of the supratemporal fossa (Chapelle & Choiniere 2018, ch. 63) that is set well anterior of the parietal-frontal suture.

'Scalloped' medial margin of the supratemporal fossa. The frontal-parietal contact along the medial margin of the supratemporal fossa in *Unaysaurus* is unusual in that it bears a pointed eminence that projects laterally towards the fenestra. Yates (2007a, b) included this morphology as a character in his matrix, with the 'scalloped' condition scored as present in *Unaysaurus* and *P. engelhardti*. However, in no known specimen of *Plateosaurus*, with many lacking any suggestion of the feature altogether (e.g. *P. erlenbergiensis* – AMNH FARB 6810). As currently observed, a well-developed medial eminence of the infratemporal fenestra appears to be an uncontroversial autapomorphy of *Unaysaurus*.

Shape of the braincase. Yates (2004) originally homologized the variation in sauropodomorph braincase anatomy as a multistate (three-part) character. More recently, this character was compartmentalized into several two-state transformations following a reductive coding strategy by Chapelle & Choiniere (2018; see

also below). In general, this variation pertains to the relative positions of the occipital condyle, basal tubera, basipterygoid processes and cultriform process (=parasphenoid rostrum), with Unavsaurus and Plateosaurus (and Coloradisaurus and Lufengosaurus) displaying the 'stepped' condition whereby the occipital condyle is raised dorsal to the other constituent braincase processes. Although the updated character scheme reflects the previous scorings, it is worth noting that the dorsal offset between the occipital condule and the floor of the braincase is not as marked in Unaysaurus as it is in Plateosaurus or Coloradisaurus (being especially pronounced in the latter). Qualitatively, the condition in Unavsaurus is closer to that of Massospondylus than Coloradisaurus. The phylogenetic signal in braincase anatomy thus expresses little in terms of driven trends with respect to recent hypotheses of 'prosauropod' relations (see Apaldetti et al. 2014 for further discussion).

Cladistic analysis

In order to explore the effects of our revised understanding of Unaysaurus on current hypotheses of early sauropodomorph relationships, updated scorings for the taxon were entered into a version of the character-by-taxon matrix of McPhee et al. (2018). The primary revisions to this matrix pertained to the character observations and character-state formulations recently given in Bronzati & Rauhut (2017) and Chapelle & Choiniere (2018). From Chapelle & Choiniere (2018), characters 48, 58, 63, 77, 78, 90, 91, 94, 97 and 104 (sensu that study) were included. From Bronzati & Rauhut (2017), characters 85, 366 and 367 (sensu that study) were included. Excluded were characters pertaining to the 'scalloped' medial margin of the supratemporal fenestra (autapomophic for Unaysaurus), the shape of the braincase (divided into multiple states in Chapelle & Choiniere [2018]) and the septum spanning the interbasipterygoid (due to reasons stated in Bronzati & Rauhut [2017]).

Additionally, with a single exception (see below), all characters pertaining to the basal tubera were removed on the grounds that no unambiguous homology statement(s) can be made regarding their various manifestations. Some sauropods (e.g. Camarasaurus - Madsen et al. 1995) have well-developed tubera borne on lateral bifurcating protrusions formed of both the basioccipital and basisphenoid. In more basal sauropodomorphs only the basisphenoid possesses pedicle-like tubera, which in most taxa are only subtly differentiated from the ventral ridge that transversely connects the tubera components of the bassiocciptal. In some 'prosauropod' taxa (e.g. Anchisaurus, Massospondvlus) this ridge is excavated by a median notch of variable development, suggesting the incipient development of the more marked separation seen in eusauropods like Mamenchisaurus (Ouyang & Ye 2002).

Thus, previous character-state formulations (see discussion in Yates 2010) have attempted to homologize the degree to which either (1) the basioccipital components of the basal tubera continue to extend medially independent of the basisphenoid components; and/or (2) or the basioccipital makes an anteromedial incursion between the basisphenoid tubera (see Bronzati & Rauhut 2017). However, as the basisphenoid is the only structure that forms obvious tuber pedicles early in sauropodomorph evolution, the basioccipital component of the basal tubera tends to be more medially extensive in all known 'prosauropod' taxa (in some taxa, e.g. Unaysaurus and Massospondylus, this results in the anterior face of the basioccipital 'opening' into the recess formed of the bifurcating basisphenoid pedicles). Furthermore, the posterolateral bifurcation of the basisphenoid tubera pedicles means that the degree of anteromedial incursion made by the tubera components of the basioccipital often depends on (1) the manner in which the braincase is oriented and (2) subjective interpretation of the point of termination of the basioccipital tubera, with the subtle manifestations of this feature precluding obvious character state dichotomization. As recently demonstrated by Bronzati & Rauhut (2017), it is only with the loss of obvious basisphenoid tuber pedicels in Neosauropoda (e.g. Tornieria) that this median incursion is lost entirely (the basioccipital-basisphenoid contact being transversely ventrally continuous in these forms). Thus, the only meaningful (i.e. potentially synapomorphic) variation appears to be whether or not the ridge connecting the basioccipital tubera is broken by an obvious excavation (Ch. 89 this analysis), and this too is highly variable in expression (Unavsaurus, cf. Massospondylus).

Finally, on account of both its completeness and stratigraphical position (Santa Maria Formation) directly below the succession in which *Unaysaurus* was found, the newly described *Buriolestes* (Müller *et al.* 2018a) was also added to the data set.

The phylogenetic matrix, comprising 61 OTUs and 378 characters, was analysed with TNT v. 1.5 (Goloboff & Catalano 2016) using a heuristic search of 1000 replicates of Wagner trees followed by tree bisection and reconnection with 10 trees saved per replication. Characters were equally weighted with 43 multistate characters treated as ordered (Supplementary material S2). The initial analysis resulted in 112 most parsimonious trees (shortest 1357 steps; consistency index [CI]: 0. 326; retention index [RI]: 0.683), the strict consensus of which resulted in a large polytomy with the relationships of most 'core prosauropods' unresolved (Fig. 14A). A majority rule consensus tree (Fig. 14B) returns the 'typical' topology of most recent analyses (e.g. Apaldetti et al. 2011, 2012; McPhee et al. 2014, 2015b; Otero et al. 2015; McPhee & Choiniere 2017).



Figure 14. Results of cladistic analysis. **A**, abbreviated (beginning with Dinosauria) strict consensus of 112 most parsimonious trees. Numbers above branches = bootstrap values >50%; numbers below branches = Bremer supports >1. **B**, majority consensus (all unmarked nodes 100%) of **A**. Node numbers: 1, Sauropodomorpha; 2, Plateosauridae; 3, Massospondylidae; 4, Sauropodiformes. See text for further details.

Exploratory deletions to the matrix indicate how labile the data set remains: for example, the exclusion of Coloradisaurus, which displays disparate phylogenetic signals between the cranium (PVL 3967) and postcranium (PVL 5904) (Apaldetti et al. 2014), returns a resolved strict consensus tree broadly compatible with the majority rule consensus tree of the previous analysis. Additionally, the removal of the relatively unstable and highly incomplete Seitaad (Sertich & Loewen 2010) returns a similar consensus topology. Although the application of alternative optimisation protocols (e.g. Bayesian/likelihood) may help to 'solve' this lack of resolution, this simply shifts discussion to whether parsimony represents a more efficacious approximation of evolutionary process than its alternatives (e.g. Wright & Hillis 2014; O'Reilly et al. 2016) a possibly unresolvable obstacle and one that ignores more fundamental concerns regarding the metaphorical concessions inherent in current manifestations of 'treethinking' (Rieppel 2006, 2010, 2011). Moreover, the issues outlined at the beginning of this discussion are largely independent of the choice of grouping algorithm.

The above uncertainties aside, the position of *Unaysaurus* remains relatively stable throughout the various iterations of the matrix, being consistently recovered in its 'traditional' position as the sister taxon to *Plateosaurus*. Within the context of the initial (non-reduced) analysis, this relationship (Plateosauridae) is supported by unambiguous synapomorphies only of the humerus: a transversely flattened (i.e. non-convex) humeral head (a character introduced by McPhee *et al.* [2015b] in an effort to homologize observations presented in Remes [2008]), and distal condyles with a transverse width (only minimally) less than 0.33 times total humeral length (present also in several other non-sauropod taxa).

Other supporting synapomorphies that occurred with the removal of the abovementioned taxa included (1) presence of a large, triangular antorbital fossa (present also in several other sauropodomorphs); (2) ventral margin of the occipital condyle dorsal to the proximal base of the basipterygoid processes (see Discussion, above); and (3) laminae/ridges extending from the basipterygoid processes onto the cultriform process anteromedially converging (character adopted from Bronzati & Rauhut [2017]). A further possible supporting character, not optimized as an unambiguous synapomorphy in the current analysis (but treated as a diagnostic feature of *Unaysaurus* in Leal *et al.* [2004]), is the presence of a deep, sharp-rimmed excavation on the posterior surface of the frontal, representing the anterior margin of the supratemporal fossa. This is coupled with the relatively posterior position of the frontal-parietal suture within the supratemporal fossa complex. However, as a similar morphology is observed in the Carnian-aged *Buriolestes* (Müller *et al.* 2018a), it remains possible that this feature is plesiomorphic for the group.

Thus, there are currently few supporting characters of the Plateosauridae clade that are either wholly exclusive to the clade or strongly (i.e. likely to be immune to worker subjectivity) differentiated from the condition in other closely related sauropodomorphs. Obviously, this comes with the usual qualification that additional discoveries (and, specifically, more complete specimens of Unavsaurus) will likely alter our understanding of the constituency and relationships this taxon in the future. This was demonstrated very recently with the introduction of Macrocollum, also from the Caturrita Formation (Müller et al. 2018b). In that study Unaysaurus was resolved as the sister taxon to Macrocollum within a putative Unavsauridae, itself sister clade to the Plateosauria sensu Yates (2007a, b). Although the sister relationship between the two Caturrita taxa is not surprising given their equivalence in horizon and general morphological similarities, the validity of the unavsaurid clade (which also included Jaklapallisaurus) once again hinges on the strength of its supporting synapomorphies. For example, the single stated 'unaysaurid' synapomorphy of a medial end of the astragalus that is at least 1.6 times the anteroposterior length of the lateral end cannot be confirmed in Unaysaurus (see Description, above), and an enlarged medial portion is also observed in more distantly related taxa such as Blikanasaurus.

Although this part of the sauropodomorph tree clearly remains highly labile with respect to both taxon and character sampling strategies, with even relatively wellestablished groups like the Massospondylidae subject to potential collapse, the difficulty of distinguishing both *Unaysaurus* and Plateosauridae from the generalized 'prosauropod' condition does have a more positive corollary: that it can be viewed as a good indication that this bauplan, and its attendant demonstration of increasing specializations towards obligate herbivory, appears to date back to at least the outset of the Norian. This further underscores the importance of the South American landmass as a key source of insight into the timing, and potential origins, of the radiation of the dominant terrestrial animals of the Mesozoic.

Conclusions

As mentioned in the original description of Unavsaurus (Leal et al. 2004), determining the interrelationships of the sauropodomorph dinosaurs generally typified as 'prosauropods' is beset by a number of issues, foremost amongst them being the large amount of missing information for many taxa, as well as the persistent difficulty of isolating unambiguous morphological divergences between closely related forms. The above discussion on the Plateosauridae exemplifies these difficulties, with the small clade exhibiting modest support via a number synapomorphies that are labile with respect to taxon inclusion, not exclusively restricted to the clade, or represented by character-state dichotomies of relatively subtle differentiation.

Unaysaurus is part of a growing assemblage of sauropodomorph dinosaurs from the Brazilian Late Triassic (e.g. Cabreira *et al.* 2016; Pretto *et al.* 2019) that demonstrate surprising degrees of both morphological disparity and dietary experimentation within the early history of the clade. This record provides valuable insight into the adaptive environment in which the classically 'prosauropodan' bauplan was taking shape, with taxa like Unaysaurus and Macrocollum providing our strongest evidence that several characteristic features of the group – habitual herbivory amongst them – were already well-established by the outset of the Norian.

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Supplemental material

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