Osteology and phylogenetic relationships of *Tehuelchesaurus benitezii* (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia

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The diversification and early evolution of neosauropod dinosaurs is mainly recorded from the Upper Jurassic of North America, Europe, and Africa. Our understanding of this evolutionary stage is far from complete, especially in the Southern Hemisphere. A partial skeleton of a large sauropod from the Upper Jurassic Cañadón Calcáreo Formation of Patagonia was originally described as a 'cetiosaurid' under the name *Tehuelchesaurus benitezii*. The specimen is here redescribed in detail and the evidence presented indicates that this taxon is indeed a neosauropod, thus representing one of the oldest records of this clade in South America. A complete preparation of the type specimen and detailed analysis of its osteology revealed a great number of features of phylogenetic significance, such as fully opisthocoelous dorsal vertebrae, the persistence of true pleurocoels up to the first sacral vertebra, associated with large camerae in the centrum and supraneural camerae, and an elaborate neural arch lamination, including two apomorphic laminae in the infradiapophyseal fossa. The phylogenetic relationships of this taxon are tested through an extensive cladistic analysis that recovers *Tehuelchesaurus* as a non-titanosauriform camarasauromorph, deeply nested within Neosauropoda. Camarasauromorph sauropods were widely distributed in the Late Jurassic, indicating a rapid evolution and diversification of the group.

INTRODUCTION

Sauropod dinosaurs are one of the most prominent components of vertebrate faunas from the Middle Jurassic to the end of the Mesozoic. The group first appears close to the Triassic/Jurassic boundary (Buffetaut *et al*., 2000; Yates & Kitching, 2003), and all major lineages were established by the Late Jurassic, with the diversification of Neosauropoda probably happening in the Middle Jurassic (Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002; Upchurch, Barrett & Dodson, 2004). However, this radiation is so far mainly documented from Upper Jurassic rocks of western North America (the Morrsion Formation; Foster, 2003), Europe (especially Portugal; Antunes & Mateus, 2003), and Tanzania (Tendaguru Formation; Bussert, Heinrich & Aberhan, 2009). These localities provide the bulk of evidence upon which our current understanding of the Jurassic diversification and early evolution of Neosauropoda has been based.

In South America, identifiable Jurassic sauropod remains have been reported only from the Early–Middle Jurassic of Central Patagonia (Chubut

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Province, Argentina). These remains consist of non-neosauropod eusauropods such as *Amygdalodon patagonicus* Cabrera 1947, from the Toarcian–Aalenian Cerro Carnerero Formation (Cabrera, 1947; Casamiquela, 1963; Rauhut, 2003a), and *Volkheimeria chubutensis* Bonaparte, 1979, *Patagosaurus fariasi* Bonaparte, 1979, and two undescribed taxa from the ?Bajocian–Callovian Cañadón Asfalto Formation (Bonaparte, 1979, 1986a; Rauhut, 2003b; Pol, Rauhut & Carballido, 2009). The sauropod record in the Upper Jurassic of Patagonia is also restricted to the province of Chubut, from where *Brachytrachelopan mesai* Rauhut *et al*., 2005, a dicraeosaurid neosauropod from the probably Oxfordian–Tithonian Cañadón Calcáreo Formation (see below), was recently described (Rauhut *et al*., 2005).

Tehuelchesaurus benitezii was described by Rich *et al*. (1999) based on a partially articulated skeleton, allegedly found in the Middle Jurassic Cañadón Asfalto Formation. Rich *et al*. (1999) considered *Tehuelchesaurus* to be a non-neosauropod eusauropod (a 'cetiosaurid' in the traditional sense), closely related to the Chinese Middle Jurassic sauropod *Omeisaurus*, and, on that basis, argued that it represented evidence for a global Middle Jurassic sauropod fauna. In this paper, we review the stratigraphic provenance, anatomy, and phylogenetic relationships of this taxon.

GEOLOGICAL AND PALAEONTOLOGICAL CONTEXT

The type specimen of *Tehuelchesaurus benitezii* was found in the Estancia Fernández, some 25 km north to the village of Cerro Cóndor (Fig. 1). The specimen comes from a sequence of lacustrine and fluvial sediments that unconformably overly the volcanic and volcanoclastic rocks of the Lonco Trapial Formation, which is Middle Jurassic in age (Page *et al*., 1999). This sequence belongs to a series of lacustrine, fluvial, and overbank deposits that were traditionally regarded as part of the Cañadón Asfalto Formation (Turner, 1983; Silva Nieto *et al*., 2002), a Middle Jurassic unit defined on the basis of lacustrine sequences south of Cerro Cóndor (Stipanicic *et al*., 1968; Tasch & Volkheimer, 1970). Figari & Courtade (1993) argued that two different sections can be distinguished in the Cañadón Asfalto Formation, a Middle Jurassic, mainly lacustrine lower section, and an Upper Jurassic, lacustrine to fluvial upper section (see also Page *et al*., 1999). This upper section differs from the lower section in its sedimentology, tectonic structures, age, and vertebrate fauna (Figari & Courtade, 1993; Rauhut, 2006a, b; Rauhut & López-Arbarello, 2008), so that the distinction of a separate formation, as advocated by Proserpio (1987), seems justified (see also Volkheimer *et al*., 2009). Thus, the type of *Tehuelchesaurus* comes from the Cañadón Calcáreo Formation *sensu* Proserpio (1987). The exact age of the unit is still debated. Proserpio (1987) indicated a Late Jurassic age for the unit, and a tuff from the basal section of the formation yielded a Tithonian age (147 ± 3 Ma; Rauhut, 2006b). In contrast, Volkheimer *et al*. (2009) argued for a lowermost Cretaceous (Valanginian) age on the basis of palynological data from the central part of the type section of this formation. However, a new SHRIMP date from the same section, a few metres above the level that yielded the pollen of Volkheimer *et al*., gave an uppermost Oxfordian to lowermost Kimmeridgian age (155.5 Ma; Cúneo & Bowring, 2010). Thus, although
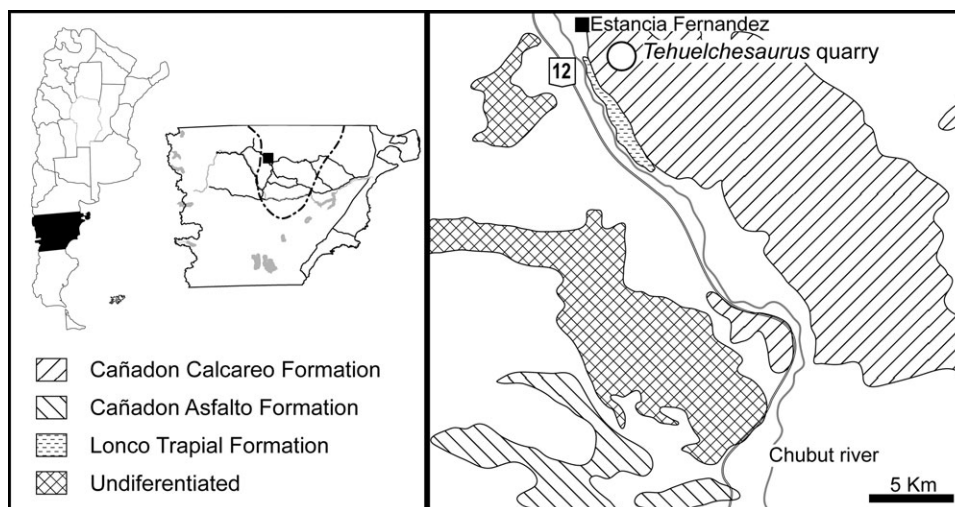

Figure 1. Map of Argentina and Chubut Province, showing the Somuncurá – Cañadon Asfalto Basin (dashed line) and a geological map of the outcrops where *Tehuelchesaurus* was collected. Geological map adapted from Rauhut (2003b).
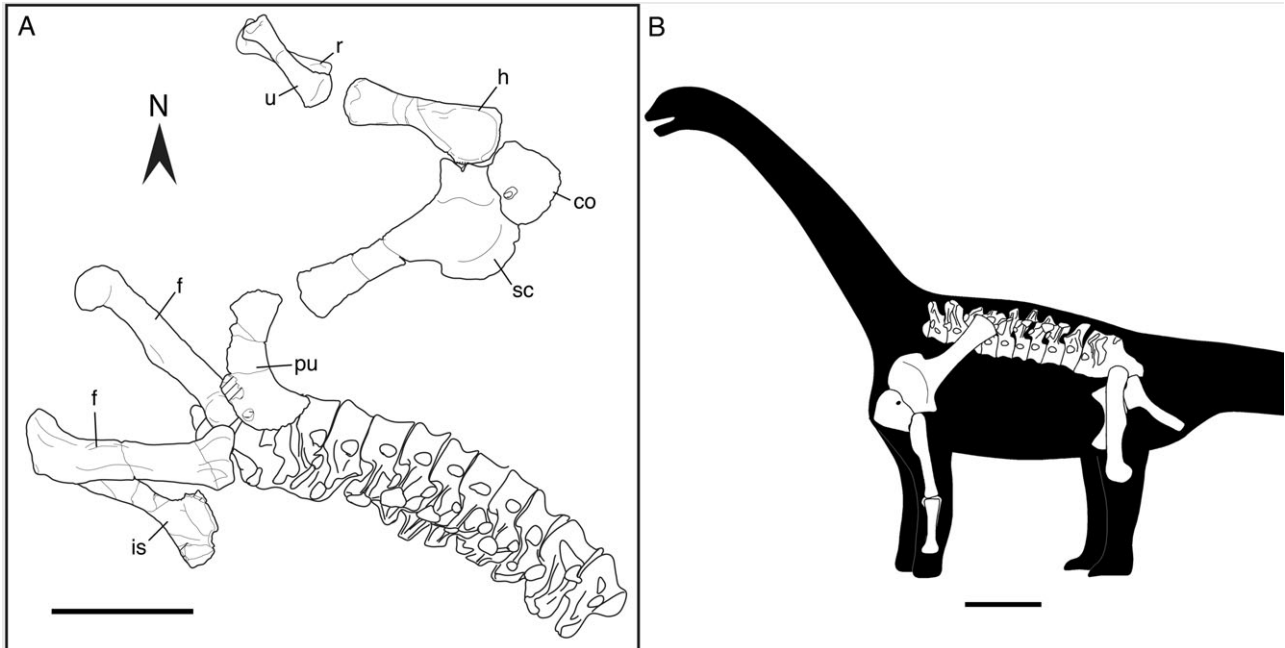
Figure 2. A, schematic drawing of the type specimen of *Tehuelchesaurus* as found in the quarry, showing the semi-articulated position of the skeleton. B, outline reconstruction of *Tehuelchesaurus*, indicating recovered elements (rib fragments not shown). Scale bars = 100 cm. For abbreviations see text.

this radiometric date came from an area some 30 km to the south of the type locality of *Tehuelchesaurus*, this taxon seems to be definitely Late Jurassic (Oxfordian–Tithonian) in age.

The most abundant vertebrate fossils from the Cañadón Calcáreo Formation are fishes from the basal lacustrine part. Two species of basal teleosts and one coccolepid have been described (Bordas, 1942; Bocchino, 1967; López-Arbarello, 2004), and at least one new species of teleost and some rare 'holosteans' are also present (López-Arbarello, Rauhut & Moser, 2008). The tetrapod fauna from this formation is still poorly known and only dinosaurs have been reported so far. Apart from *Tehuelchesaurus*, sauropods are represented by the dicraeosaurid *Brachytrachelopan mesai* (Rauhut *et al.*, 2005) and a brachiosaurid (Rauhut, 2006a), and theropods are known from several teeth and some cranial and postcranial fragments (O.W.M.R., pers. observ.).

The holotype of *Tehuelchesaurus* was found as a partial articulated skeleton in a lacustrine silt–sandstone at the base of the Cañadón Calcáreo Formation, some 15–20 m above the discordant contact with the volcanic and volcanoclastic rocks of the Lonco Trapial Formation [note that the stratigraphic section figured by Rich *et al.* (1999: fig. 3) represented a composite sequence with the assumed stratigraphic position of *Tehuelchesaurus*]. The specimen was found lying on its right side, with the vertebral column completely in articulation and the girdle and limb bones only slightly displaced (Fig. 2A). At least most of the missing parts, especially the cervical vertebrae and tail, were probably lost due to recent erosion, rather than before or at the time of burial. At the time of the original description (Rich *et al.*, 1999), the presacral vertebrae were only superficially prepared. Recent preparation of the vertebral column revealed many details of vertebral anatomy that are of importance for the systematic placement of the taxon; thus, the following description will focus on vertebral anatomy, but also provide additional comments on important characters of the limbs and girdles. The skin impressions found in association with the specimen were recently described by Giménez (2007). For additional information and especially measurements of the appendicular elements see Rich *et al.* (1999).

INSTITUTIONAL ABBREVIATIONS

CMU, Chengdu Univesity Museum, Chengdu, China; IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; PVL, Paleontología de Vertebrados, Fundación Miguel Lillo, Tucumán, Argentina; ZDM, Zigong Dinosaur Museum, Zigong, China.

ANATOMICAL ABBREVIATIONS

4tr, fourth trochanter; ac, acromion; acdl, anterior centrodiapophyseal lamina; acpl, anterior centroparapophyseal lamina; al, accessory lamina; apcdl, accessory posterior centrodiapophyseal lamina; atpol, accessory intrapostzygapophyseal lamina; aut 1, autapomorphic lamina 1; aut 2, autapomorphic lamina 2; corf, coracoid foramen; cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal lamina; dep, depression of the infraprezygapophyseal fossa; dp; diapophysis; dpc, deltopectoral crest; epc, epicondyle; fbc, fibular condyle; gl, glenoid; hh, femur head; hyp, hypantrum; ilpd, iliac peduncle; indf, infradiapophyseal fossa; inpf, intraprezygapophyseal fossa; ippf, infraparapophyseal depression; obf, obturator foramen; opl, internal opening of the pleurocoel; pcdl, posterior centrodiapophyseal lamina; pcpl; posterior centroparapophyseal lamina; pl, pleurocoel; plf, pleurocoel fossa; podl, postzygodiapophyseal lamina; poz, postzygapophysis; pp, parapophysis; ppdl, paradiapophyseal lamina; prdl, prezygodiapophyseal lamina; prpl, prezygoparapophyseal lamina; prz, prezygapophysis; pupd, pubic peduncle; rac, radial condyle; spdl, spinodiapophyseal lamina; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tbc, tibial condyle; tpol, intrapostzygapophyseal lamina; tprl, intraprezygapophyseal lamina; ulc, ulnar condyle.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA OWEN, 1842

SAURISCHIA SEELEY, 1887

SAUROPODOMORPHA HUENE, 1932

SAUROPODA MARSH, 1878

EUSAUROPODA UPCHURCH, 1995

NEOSAUROPODA BONAPARTE, 1986B

MACRONARIA WILSON & SERENO, 1998

CAMARASAUROMORPHA SALGADO, CORIA & CALVO, 1997

TEHUELCHESAURUS RICH *ET AL*., 1999

Type species: Tehuelchesaurus benitezii Rich *et al*., 1999

Diagnosis: As for type and only known species.

TEHUELCHESAURUS BENITEZII RICH *ET AL*., 1999

Holotype: MPEF-PV 1125, partial postcranial skeleton (Fig. 2B), including 10 articulated presacral vertebrae plus an eroded element, 4 sacral vertebrae, parts of the sacricostal yoke, several ribs, right scapulacoracoid, right humerus, left radius and ulna,

fragment of right ilium, right pubis and fragment of left pubis, left ischium and shaft of right ischium, both femora, and skin impressions.

Emended diagnosis: The taxon can be diagnosed by the autapomorphic presence of two accessory laminae in the infradiapophyseal fossa of the middle dorsal vertebrae. The accessory lamina 1 runs posterodorsally from the paradiapophyseal lamina and merges dorsally with the accessory lamina 2, which in turn runs posteroventrally from this point to the posterior centrodiapophyseal lamina. Further apomorphies include the presence of an accessory and laterally oriented lamina on the lateral surface of the intrapostzygapophyseal lamina and the strongly anteroposteriorly expanded and very robust distal end of the humerus. *Tehuelchesaurus* further differs from all other sauropods in the unique combination of the following characters: absence of the prezygoparapophyseal lamina in the middle and posterior dorsal vertebrae (reverse of the plesiomorphic sauropodomorph condition; see discussion below); presence of an accessory posterior centrodiapophyseal lamina, giving the impression of a ventrally bifurcated pcdl (convergently acquired in Titanosauria); a single intrapostzygapophyseal lamina in at least the mid-dorsals (uncertain in other dorsals; convergently present in diplodocids and some basal taxa) that supports the weakly developed hyposphene in middle and posterior dorsal vertebrae; neural spines of dorsal vertebrae longer anteroposteriorly than wide transversely (reversal to the ancestral sauropodomorph condition, also present in *Jobaria* (Sereno *et al*., 1999) and *Galvesaurus* (Barco, 2009); absence of lateral expansion in the dorsal end of the neural spine of dorsal vertebrae; absence of postspinal lamina in dorsal neural spines; greatest anteroposterior width of the acromion process of the scapula over the glenoid almost four times the minimum width of the shaft.

Comments: Rich *et al*. (1999) gave a differential diagnosis for *Tehuelchesaurus*, only distinguishing it from the allegedly closely related *Omeisaurus* and from the 'cetiosaurs' *Barapasaurus* and *Patagosaurus*. However, all the characters used in their diagnosis have a much broader distribution within sauropods, and neither any specific one of these characters nor their combination is unique for *Tehuelchesaurus*. Upchurch *et al*. (2004) noted that the characters given by Rich *et al*. (1999) were insufficient to diagnose the taxon and suggested the unusual, anteroposteriorly broad morphology of the distal humerus as a possible autapomorphy of *Tehuelchesaurus*. Although the morphology of the distal humerus might partially be due to preservational

artefacts, the presence of two small posterior condyles separated by a broad groove and the very deep distal end of this bone might indeed represent further autapomorphies of *Tehuelchesaurus*.

Type locality and horizon: Estancia Fernandez, 43°10′S, 69°15′W. Lacustrine silt- and sandstones, partially tuffaceous, at the basis of the Cañadón Calcáreo Formation, most probably Oxfordian–Tithonian (see above).

DESCRIPTION

AXIAL SKELETON

The vertebral column is represented by ten dorsal and four anterior sacral vertebrae (Figs 3–13), which were found in articulation. A further vertebral fragment, collected from the surface, was identified as an anterior caudal by Rich *et al*. (1999: 79), but rather represents a poorly preserved fragment of one of the anteriormost dorsals. Thus, the total number of dorsal vertebrae was at least 11. For reasons of convenience of description, the dorsal vertebrae preserved in articulation are numbered consecutively from 1 to 10, starting with the anteriormost vertebra, as was done also by Rich *et al*. (1999). The preservational quality of the bone is generally good, but most vertebrae show signs of lateromedial compression and suffered from erosion of their left sides and neural spines. Therefore, the following description is mainly based on the right side of the vertebrae. The terminology of vertebral laminae in the description follows Wilson (1999) and that of vertebral fossae follows Makovicky (1997).

General features

As noted by Rich *et al*. (1999), all presacral vertebrae are opisthocoelous, although the fully articulated state of the vertebral column makes a precise evaluation of the extent of their anterior convexity impossible in most vertebrae (see below). The centra are slightly higher than wide and this difference becomes less evident in posterior dorsals, although the transverse compression could have distinctly affected these proportions in different regions of the dorsal column (see below). The central length slightly increases from D1 to D3 and then gradually decreases, whereas the central height increases gradually and constantly from D1 to D10. The vertebral centra have a transversely convex ventral surface, unlike the ventrally flattened centra of some basal sauropods (e.g. Jain *et al*., 1979). Well-developed pleurocoels are present throughout the dorsal series and in the first sacral vertebra. These pleurocoels are subovoid in shape, having rounded anterior and posterior margins. Con-

trary to Rich *et al*. (1999), these true pleurocoels are pneumatic cavities that invade the centra and form large camerae (*sensu* Wedel, Cifelli & Sanders, 2000). The camerae extend anteriorly, posteriorly, ventrally, and dorsally from the pleurocoel and seem to be deeper in the anterior half (see below).

The neural arches have a relatively constant height, but vary from being subequal to lower (measured from the floor of the neural canal to the dorsal border of the proximal basis of the transverse process) than the vertebral centra toward the posterior dorsals (mainly because of the dorsoventral increase in the height of the centra). The lateral sides of the neural arches bear a large infradiapophyseal fossa. In most vertebrae this fossa bears a small, deep depression with well-defined margins that is located below the diapophysis and anterior to the posterior centrodiapophyseal lamina (PCDL), herein referred to as the posterodorsal depression. This depression has a similar topographical position as the large and deep lateral depressions present in some basal eusauropods (e.g. *Barapasaurus*, *Cetiosaurus*, *Patagosaurus*; Jain *et al*., 1979; Bonaparte, 1986b, 1999; Upchurch, 1998; Upchurch & Martin, 2002, 2003). These depressions are developed as deep, but superficial depressions in the anterior dorsals in *Patagosaurus* and *Barapasaurus* (Jain *et al*., 1979; Bonaparte, 1986b, 1999), and seemingly in all dorsals in *Cetiosaurus* (Upchurch & Martin, 2002), whereas they are developed as large lateral foramina that lead into large supraneural camerae in the posterior dorsals in the former two genera. Large, paired supraneural camerae are also present in *Tehuelchesaurus*, as in many other eusauropods, including neosauropods (e.g. *Diplodocus*, *Camarasaurus*; Bonaparte, 1999). These cavities are positioned medial to the deep posterodorsal depressions, although the preservation of the specimen does not allow determination of whether the supraneural camerae communicate with the exterior through a supraneural foramen, as in *Barapasaurus* (Jain *et al*., 1979) and *Patagosaurus* (Bonaparte, 1986a). The neural canal has been plastically deformed in some vertebrae, but some are seemingly undistorted and have a semicircular shape (being slightly wider than high), rather than being high and slit-like as in *Barapasaurus* (Jain *et al*., 1979) and *Amygdalodon* (Rauhut, 2003a). A vertical ridge extends dorsally above the neural canal on the anterior side of anterior dorsal vertebrae [i.e. the ventral end of the intraprezygapophyseal lamina (TPRL); see below] and is bounded by large depressions that extend laterally onto the anterior surface of the neural arches.

The zygapophyses are relatively large, broad, and oval-shaped in the anterior dorsals, but they become gradually smaller in more posterior vertebrae.

The zygapophyses project anteriorly and posteriorly, slightly exceeding the level of the anterior or posterior rim of the vertebral centra (excluding its convex anterior articular surface). The articular facets of the pre- and postzygapophyses are obliquely inclined at an angle of approximately 30° from the horizontal, as in most neosauropods. In most vertebrae, a lateral expansion of the ventral end of the prezygapophysis is present and most probably represents the lateral face of the hypantrum. Although these expansions are well developed in most vertebrae, the hyposphene–hypantrum system seems to be weakly developed, as can be observed in D9. A single lamina that joins the hyposphene with the neural canal is present and interpreted as the intrapostzygapophyseal lamina (TPOL), following Wilson (1999). The development of this lamina increases markedly in posterior vertebrae (see below).

The parapophyses are placed on the neurocentral junction in D1 and D2, whereas in more posterior elements they reach a position slightly above the half-height of the neural arch in D4–D8, but are more ventrally placed again in the last dorsals. The transverse processes and diapophyses are damaged in most vertebrae, but where they are preserved, they are short and massive and directed laterally, rather than dorsolaterally. The articulations for the capitula of the dorsal ribs on the parapophyses are concave, whereas those for the tubercula on the transverse processes are convex. The lateral surfaces of the neural arches bear well-developed lamination, which changes considerably along the preserved region of the dorsal series (see below).

The lamina that is most consistently developed in all dorsal vertebrae is the PCDL, although its presence cannot be determined in D10. This lamina is robust and slightly inclined anterodorsally in the anteriormost vertebrae, but almost vertical in more posterior elements and connects the ventral side of the diapophysis with the dorsal rim of the vertebral centrum. The Paradiapophyseal lamina (PPDL) is also well developed in all vertebrae in which the parapophysis is located above the neurocentral suture (D3–D10). This lamina is directed anterodorsally, so that the parapophysis overhangs the centrum anteriorly. A low, stout, laterally rounded centropostzygapophyseal lamina (CPOL) is present in the infrapostzygapophyseal fossa from D2 to the last presacral element, varying only in the dorsoventral placement of its anteroventral point of origin (see below). Well-developed, more or less horizontal prezygodiapophyseal and postzygodiapophyseal laminae (PRDL and PODL) are present in all dorsals, the former being much shorter and robust than the latter. Two autapomorphic laminae of *Tehuelchesaurus* are present between the PCDL and the paradiapophyseal

lamina (PPDL). The development of these laminae and their exact positions (as well as that of other laminae) varies along the dorsal series and will be described in detail for the respective elements below. No complete neural spine is preserved, but parts of this structure can be observed in D1–D8, with D6 apparently presenting an almost complete spine, which is not bifurcated. As is usual in eusauropods, neural spine lamination is well developed, but contrary to most neosauropods (Upchurch *et al*., 2004) prespinal and postspinal laminae are absent. Spinoprezygapophyseal and spinopostzygapophyseal laminae (SPRL and SPOL) are well developed, but, in contrast to many sauropods (Wilson, 2002), the latter is not subdivided into a lateral and a posterior spinopostzygapophyseal lamina.

Dorsal 1 (Fig. 3)

The ventral margin of the centrum of D1 is approximately 1.25 times longer than the dorsal margin (Table 1), indicating that the dorsal vertebral column flexed dorsally towards the dorsal–cervical junction. D1 is the only vertebra in which the complete anterior articular surface is exposed. This surface is strongly convex, showing the ophistocoelous condition of anterior dorsals of *Tehuelchesaurus*. The length of the anterior articular condyle is approximately 50% the centrum length.

Deep pleurocoels invade the centrum and expand within it, forming several large pneumatic camerae. Left and right camerae are separated by well-developed and thick bony septa. They are exposed on the dorsal surface of the anterior articular condyle of the centrum through a broken area, providing a longitudinal section of these camerae at different dorsoventral heights. The left camera is exposed at midheight of the centrum (at the level of the pleurocoel). The camera extends anteriorly from the pleurocoel, is lateromedially narrow and elongated, and extends throughout most of the articular condyle. The anterior region of the right camera is exposed at a more dorsal level, close to the dorsal edge of the centrum. At this level the anterior camera is anteroposteriorly shorter (extending only within the articular condyle) and wider transversely than in the more ventral level exposed on the left side. It shows fragments of a thin parasagittal septum that seems to (at least partially) divide the camera. The left camera is also exposed posterior to the pleurocoel, where it is broad and lacks a well-defined contour. The dorsal extension of this part of the camera seems to invade the neural arch (as observed on the medial surface of pedicels of the right neural arch). In contrast to the derived condition of *Brachiosaurus*, as well as more derived titanosauriforms (Wedel *et al*., 2000; Wedel, 2003a, b), this vertebra does not have a camellate structure

Table 1. Measurements (cm) of the vertebrae of *Tehuelchesaurus benitezii*

Vertebra	Length of centrum*	Anterior height of centrum	Posterior height of centrum	Height of neural arch	Length of neural arch
1	19†, 23.5‡	*c.* 21.5	*c.* 25.5	27	32.5
2	25	24.5	24.5	26.5	*c.* 36.5
3	*c.* 26	24	25	25	*c.* 33
4	24	25	27	26	37
5	*c.* 24	26.5	27	26	*c.* 35
6	22	26	30	25	33.5
7	21	28	30	24	31
8	22	27	32.5	27	d
9	*c.* 21.5	32	33.5	d	d
10	19.5	*c.* 33	*c.* 32	d	d
S1	18.5	d	d	d	d
S2	21	30	25.5	d	d
S3	19.5	25.5	d	d	d

*Length at about mid-height of centrum, excluding the anterior convexity.
†Dorsal length.
‡Ventral length.
d, damaged or deformed. Centrum width has not been evaluated as all vertebrae are more or less compressed transversely.

either in the condyles or in the zygapophyses. Therefore it resembles the condition of several non-titanosauriform neosauropods (e.g. *Camarasaurus*, *Galvesaurus*; Wedel, 2003a; Barco, 2009). The pleurocoel is enclosed in a large depression delimited dorsally by the posterior centroparapophyseal lamina (PCPL) and the parapophysis (Fig. 3). This depression has an acute posterior border produced by the almost horizontal orientation of the PCPL, although the posterior margin of the pleurocoel itself is rounded. This character also contrasts with the derived acute posterior edge of the pleurocoels present in Titanosauriformes (e.g. *Brachiosaurus*, *Chubutisaurus*, *Saltasaurus*).

The parapophysis is entirely placed on the centrum, and a stout centroprezygapophyseal lamina (CPRL) originates from the dorsal rim of the centrum above it, being directed anterodorsally along the anterior margin of the neural arch (Fig. 3). The four diapophyseal laminae that characterize the presacral vertebrae of most eusauropods (Wilson, 1999) are present and well developed in this vertebra. A robust PCDL is anterodorsally oriented (nearly 45°) and is almost parallel to the CPRL (Fig. 3). Although the contact of the PCDL with the diapophysis is broken, it is evident that this lamina forms the vertical axis of the T-shaped diapophysis. The anterior centrodiapophyseal lamina (ACDL) runs posterodorsally from the lower third of the CPRL to approximately the half height of the PCDL (Fig. 3), being oriented at an angle of 45° with respect to the longitudinal axis. The ACDL of this vertebra is relatively reduced, as the anteroposterior length of its neural arch is much smaller than in subsequent vertebrae. However, the ACDL is much more robust than its homologous structure, the PPDL, in the other dorsals. The two other laminae are the PRDL and the PODL, the former being more robust and shorter than the latter and forming the horizontal axis of the T-shaped diapophyseal process.

Two large triangular fossae are present on the lateral surface of the neural arch, located one above the other and separated by the ACDL (Fig. 3). The dorsal fossa is bounded by the CPRL anteriorly, the ACDL posteroventrally, the dorsal portion of the PCDL posteriorly, and the PRDL dorsally. The apex of this triangular fossa is directed ventrally, whereas it is broad dorsally. The extension of this fossa is much greater than in the two subsequent vertebrae, expanding over approximately half of the height of the neural arch. Given the position and development of this fossa in the subsequent vertebrae (D4–D5; see below), we refer to this fossa as the infraprezygapophyseal fossa (INPF; Fig. 3). This fossa bears a small but distinct posterodorsal depression in its posterior half, just above the point of contact between the ACDL and the PCDL. As noted above, this depression might represent a lateral exit of an extensive supraneural camerae, but the presence of such camerae in this vertebra cannot be established with certainty (they are absent in the anterior dorsals in some advanced, non-neosauropodan eusauropods; see Upchurch & Martin, 2002). The lower triangular fossa (infradiapophyseal fossa; INDF) is bordered by
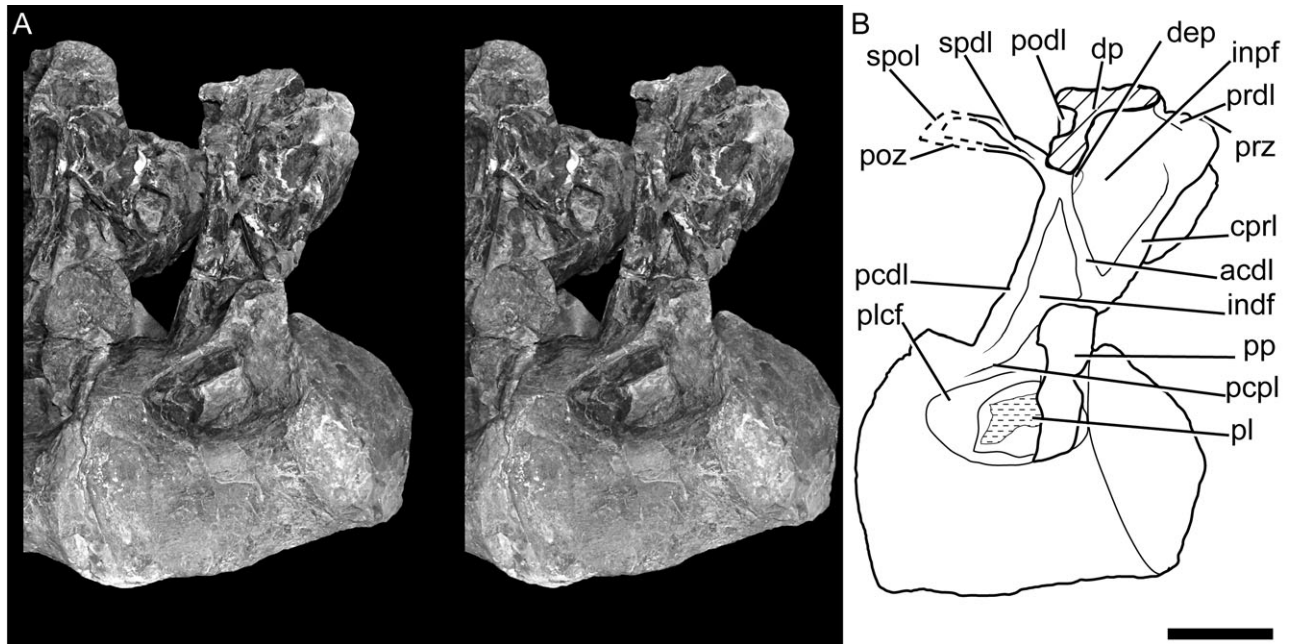
Figure 3. *Tehuelchesaurus benitezii*, ventrolateral view of the first preserved vertebra. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

the PCDL posteriorly, the ACDL anteriorly, the parapophysis anteroventrally, and the PCPL postero-ventrally. This fossa is small but deep and is much smaller than those of subsequent vertebrae, given the relatively lower position of the ACDL in dorsal 1.

The anterior surface of the neural arch becomes progressively wider dorsally, leading to the prezyga-pophysis (Fig. 3), which is completely preserved on the right side of the vertebra. The postzygapophyses are placed posteriorly, close to the level of the diapo-physis in the next vertebra (D2). Due to the articu-lation with the subsequent vertebra, their articular surfaces cannot be observed, but the posterior and lateral surfaces of the right postzygapophysis and the posterior base of the neural spine, which was posi-tioned posteriorly above the postzygapophysis, are well preserved and bear the basal part of the SPOL and spinodiapophyseal laminae (SPDL). Only a minor portion of the SPOL is preserved in D1 and resembles the condition in more posterior vertebrae, in which this lamina is more completely preserved (see below). The SPDL of this vertebra is oriented at an angle of approximately 25° from the longitudinal axis, thus being more horizontal than the SPDL in subsequent elements. A small triangular fossa is present on the lateral surface of the postzygapophyses, within the lateral recess formed by the dorsal junction of these two laminae. This fossa becomes progressively deeper anteromedially and is undivided, in contrast to the condition of subsequent vertebrae (see below). A

similar depression is also present in other vertebrae (D2–D3) and may represent an autapomorphic char-acter of *T. benitezii* (Fig. 4).

Dorsal 2 (Fig. 4)
This vertebra and D3 differ considerably from each other and from dorsal 1, thus representing a transi-tional series between the morphology of the anterior dorsals and the mid to posterior dorsal vertebrae. The centrum length of D2 is similar to the ventral length of D1, but unlike this vertebra there is no difference in the centrum length at its dorsal and ventral edges. A deep pleurocoel is enclosed in a large and posteri-orly acute depression that is approximately 1.3 times larger than that of D1. This depression is delimited dorsally by a stout PCPL (Fig. 4). This lamina is not horizontal as in D1, but is slightly inclined antero-dorsally, as the parapophysis is placed more dorsally. The parapophysis is located at the level of the neu-rocentral suture, having almost 80% of its dorsoven-tral extension placed on the neural arch. The articular surface of the parapophysis is large and comma-shaped, having an acute ventral edge and a rounded dorsal edge (Fig. 4). This contrasts with the parapophysis of the preceding vertebra (which is sig-nificantly smaller) and with that of the subsequent vertebrae (which are oval in shape).

The neural arch of D2 is anteroposteriorly longer than that of D1 but shows the same basic lamina-tion pattern, with the addition of accessory laminae
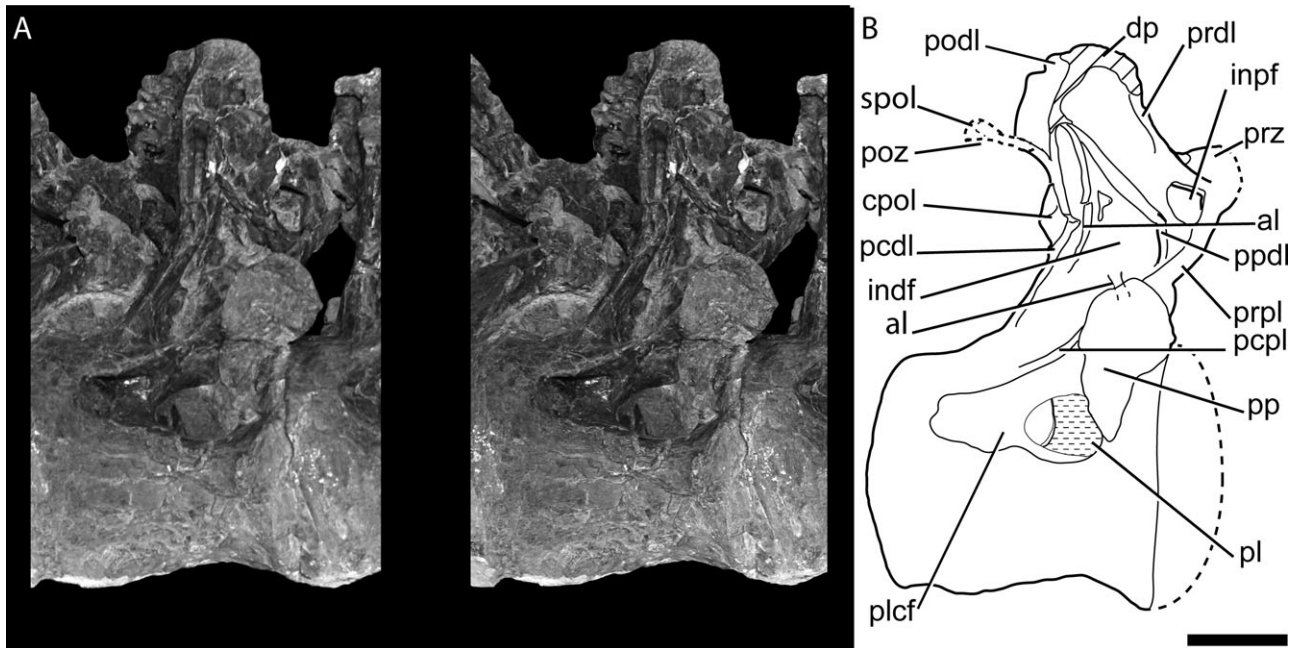
Figure 4. *Tehuelchesaurus benitezii*, ventrolateral view of the second preserved vertebra. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

and an associated fossa. The prezygoparapophyseal lamina (PRPL) of D2 is well developed and forms the anterior margin of the lateral surface of the neural arch (Fig. 4), but it is less robust, shorter, and more anteriorly directed than that of D1. A similar difference is present in the PCDL of D1 and D2, in which it has a sharp ventral end and dorsally reaches the diapophysis, forming a prominent vertical base of this process. An additional lamina extends ventrally from the dorsal end of the PCDL of D2 and runs parallel to it, along its anterior margin. A small, trough-shaped concavity is present between the two laminae along their dorsal half (Fig. 4). The ventral end of this lamina seems to be incomplete and may have been displaced from its natural position, given that this region of the neural arch seems to be broken and slightly deformed. The lamina that corresponds to the ACDL in the first dorsal is here better understood as PPDL, as the parapophysis has almost entirely moved onto the neural arch. It is significantly different from the corresponding lamina of the preceding vertebra. First, it is more dorsally located, running from the midpoint of the CPRL to the accessory lamina described above (close to the dorsal end of the PCDL). Second, the orientation of the PPDL is more horizontal than the ACDL in D1. Third, the anteroventral end of the PPDL is less robust than that of the homologous lamina in D1, forming a thin and sharp lamina. Fourth, the posterodorsal end of the PPDL is robust but not as developed as in D1. Rich *et al*.

(1999: fig. 7) labelled a more ventrally placed lamina, which extends from the posterodorsal rim of the parapophysis as 'ventral part of broken infraprezyga-pophyseal (ACDL) lamina' in this vertebra. However, repreparation of the vertebra revealed that this lamina is indeed not broken, but represents a short additional lamina (see below). The PODL and the PRDL of D2 are well developed and form the horizontal laminae of the diapophyseal process. The PRDL is more developed in this vertebra than in subsequent elements.

The lateral surface of the neural arch of D2 bears a series of depressions and fossae that differ from those of other elements. The most extensive of these is a large trapezoidal fossa enclosed by the PCDL (posteriorly), PPDL (anterodorsally), PRPL (anteriorly), PCPL (posteroventrally), and the parapophysis (anteroventrally). This depression is much larger than the lower fossa of D1 and is also interpreted as the infradiapophyseal fossa (Fig. 4). Within this fossa, three distinct depressions are present. The largest of them extends over the posterodorsal corner and excavates the base of the anterior surface of the PCDL (and its accessory lamina). This depression is dorsally bounded by the PPDL and is in identical topographical position as the posterodorsal depression developed in more posterior dorsals (see below). A distinct, kidney-shaped depression is present in the postero-ventral end of the infradiapophyseal fossa. This depression is approximately 5 cm long and relatively
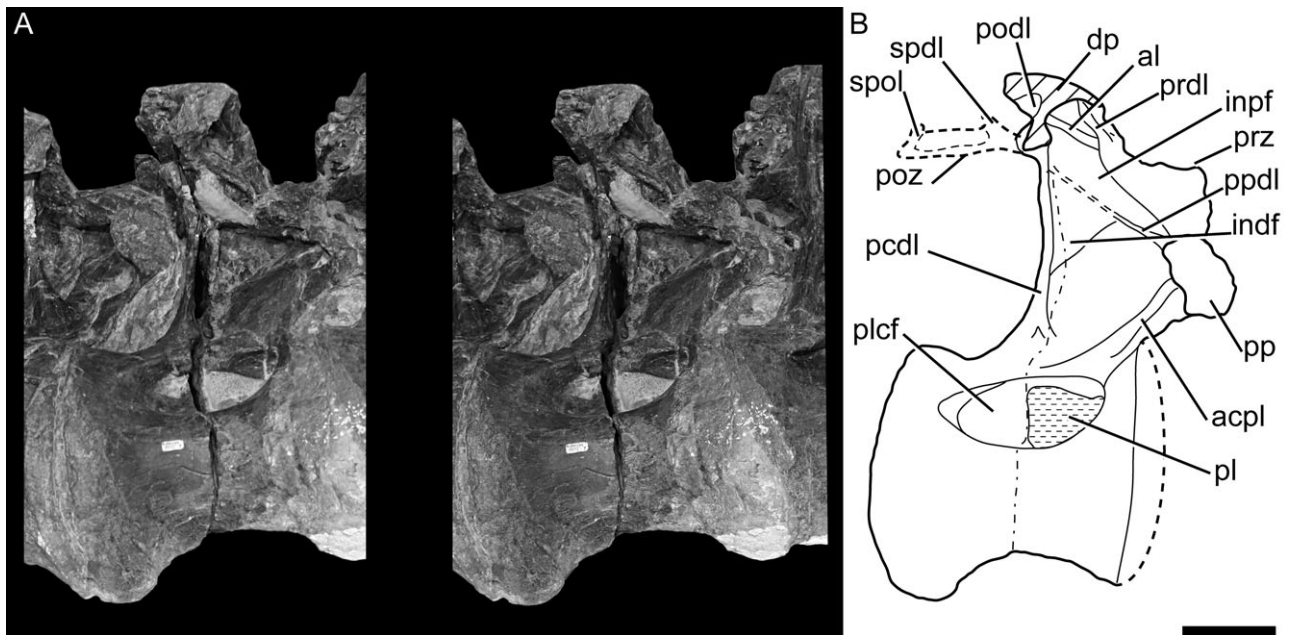
Figure 5. *Tehuelchesaurus benitezii*, ventrolateral view of the third preserved vertebra. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

shallow, but is only present in this vertebra. The third depression is developed at the anteroventral corner of the infradiapophyseal fossa. This depression excavates the posterior surface of the base of the parapophysis and is dorsally bounded by an accessory lamina. This lamina [referred to as the ACDL by Rich *et al*. (1999)] originates in the posterodorsal corner of the parapophysis and becomes rapidly lower posterodorsally, disappearing at about mid-length between the parapophysis and the PCDL within the infradiapophyseal fossa (Fig. 4). The infraprezygapophyseal fossa of D2 is much more reduced than in D1. This fossa is deep, subcircular (Fig. 4), and is enclosed between the PPDL and the PRPL along its ventral half. The dorsal border of this rounded fossa forms a sharp edge that is oriented horizontally, 5 cm below the PRPL. The lateral surface of the neural arch also bears a shallow and elongated concavity that runs enclosed between the PPDL and the PRDL.

The dorsal surface of the right prezygapophysis cannot be observed because it is in natural articulation with the postzygapophysis of D1, but the anterior surface of the prezygapophyseal process is well exposed in this vertebra. The lateral half of this process is convex (as in D1) but the medial half is markedly concave. This concavity represents the circumneural cavity (*sensu* Bonaparte, 1999) and is located dorsal to the neural canal. The dorsal limit of this concavity is formed by the medial region of the prezygapophysis, which seems to lack a hypantrum. The left and right circumneural cavities are separated

from each other by a sharp vertical strut of the TPRL. The dorsal (paired) part of the TPRL is not preserved in this vertebra. The postzygapophyses of D2 are badly damaged, except for their medial sides and articular surfaces (still in articulation). The medial surfaces of both postzygapophyses are almost in contact with each other. The postzygapophyseal process is supported by a well-developed CPOL, not observed in the previous vertebra (D1). This lamina is thin and delicate in comparison with the CPOL of subsequent vertebrae and extends from the mid-height of the PCDL posterodorsally to the anteroventral rim of the postzygapophysis (Fig. 4). The postzygapophysis is connected to the dorsal end of the PCDL by an accessory lamina that runs horizontally and flares anteriorly. This accessory lamina is located dorsal to the CPOL, and a deep depression is enclosed between them.

Dorsal 3 (Fig. 5)
This vertebra was cut transversally at the level of the PCDL (Fig. 5) at the time this specimen was collected, although this lamina is only broken at its ventral end. The pleurocoel present in this vertebra has a similar anteroposterior length as that present in D2, but they differ in their general shape. The pleurocoel of this vertebra has the major dorsoventral height at its posterior end and not at the anterior end as in D2. Although a pleurocoel fossa is present, its dorsal edge is formed by a pronounced edge, which obviously corresponds to the PCPL, but does not take the form

of a true lamina; this lamina is thus absent in this and all subsequent vertebrae. The fossa is developed as a small posterior depression that is distinctly and abruptly inset from the lateral surface of the centrum. The vertebral centrum is cut transversally at the level of the anterior margin of the pleurocoel posterior fossa. Several isolated spaces filled with sediments are observed in this cross-section, which are interpreted as pneumatic cavities [camerae in the sense of Wedel (2003a, b); Wedel *et al.*, 2000]. These small spaces are present both in the centrum and in the neural arch. The latter obviously represent small supraneural camerae that are separated by a stout midline septum. The small size of these camerae, also in comparison with their development in more posterior dorsals (see below), is consistent with the observation that such camerae are usually first developed in more posterior dorsals in some non-neosauropodan basal eusauropods, such as *Patagosaurus* and *Barapasaurus* (see Upchurch & Martin, 2002). The pneumatic cavities in the centrum of D3 are markedly smaller than those observed in D1 (and D8), but this difference is interpreted as a product of the posterior location of the breakage in the former, rather than a decrease in pneumaticity. This is in accordance with the observation that the pneumatic cavities become smaller posteriorly in D1, as described above.

The lateral surface of the neural arch has a different lamination pattern than the preceding vertebrae, and is unique in having an accessory lamina absent in all other preserved vertebrae (see below). Additionally, two other incipiently developed laminae are present in D3, which are topographically homologous with two well-developed autapomorphic laminae present in subsequent vertebrae. Therefore, these laminae are also interpreted as autapomorphic.

The parapophysis is entirely placed on the neural arch, so that the ACDL is divided in two laminae (Wilson, 1999), the ACPL that connects the parapophysis with the anterior centrum edge, and the PPDL that connects the parapophysis to the diapophysis. The ACPL runs posteroventrally from the parapophysis to the centrum and forms an angle of approximately 35° with the longitudinal axis. The articular surface of the parapophysis is oval, with its major axis is oriented anteroventrally–posterodorsally. In this vertebra the PPDL connects the parapophysis with the ventralmost part of the diapophysis, where the PCDL forms the ventral pillar of this process (Fig. 5). In contrast, the PPDL of subsequent vertebrae extends from the posterodorsal rim of the parapophysis to the anterior part of the diapophysis at the contact with the PRDL (see below). Although the right PCDL is partially broken, especially at its ventral end, it seems that this lamina was not very robust. The ventral end of the PCDL can be seen on

the left side of this vertebra. This lamina has an expanded and bifurcated ventral end, separated by a triangular depression. The anterior branch is rounded whereas the posterior branch is thinner and sharper (Fig. 5), as in titanosaurs (Salgado *et al.*, 1997). These two branches fuse gradually dorsally, forming a single PCDL that connects to the ventral side of the diapophysis. According to Salgado, Apesteguía & Heredia (2005), the posterior branch corresponds to the original PCDL, whereas the anterior branch represents an accessory posterior centrodiapophyseal lamina (APCDL). As in D2, the PRDL is present in this vertebra but this lamina is less developed, being lower and broader than that of D2. Consequently, the T-shaped diapophysis is less evident in lateral view in D3. A triangular infradiapophyseal fossa is present in this vertebra (Fig. 5). This fossa is broad and becomes progressively deeper toward its dorsal edge. Its ventral limit is not well defined, but the fossa becomes gradually shallower ventrally, in contrast to the condition of the preceding vertebra, in which this fossa is clearly delimited by the PCPL. The infradiapophyseal fossa is enclosed by the PPDL anterodorsally and PCDL posteriorly (Fig. 5). A deeper and triangular posterodorsal depression is present within the infradiapophyseal fossa. This depression is defined by the PCDL posteriorly, the PPDL dorsally and a posteromedially oriented bony crest anteroventrally (Fig. 5). Two autapomorphic laminae are present in the anterodorsal margin of the infradiapophyseal fossa and below the PPDL. These laminae are incipient ridges and their topographical position is the same as that of the well-developed accessory laminae present in the next vertebra (see below). Consequently they are interpreted as weakly developed autapomorphic laminae, homologous to those present in following vertebrae. An accessory lamina, which is only present in this vertebra, runs parallel to the PPDL along its posterior course and is located dorsal to it and ventral to the PRDL (Fig. 5). This lamina originates within the posterior part of the infraprezygapophyseal fossa and meets the PCDL posteriorly, dorsal to the connection of this lamina with the PPDL. Anteriorly, the dorsal rim of the infraprezygapophyseal fossa runs in the anterior extension of this lamina. The infraprezygapophyseal fossa is much smaller than in D2 and D1 and is dorsally bordered by the accessory lamina only present in this vertebra and ventrally by the PPDL.

The neural spine is largely incomplete but seems to be similar to the neural spine of D6 (see below). Well-developed SPOL and SPDL are present on the postzygapophysis and the posterior end of the lateral side of the neural spine, respectively. These laminae enclose a depression that is larger than that of D1 and is subdivided in two distinct con-
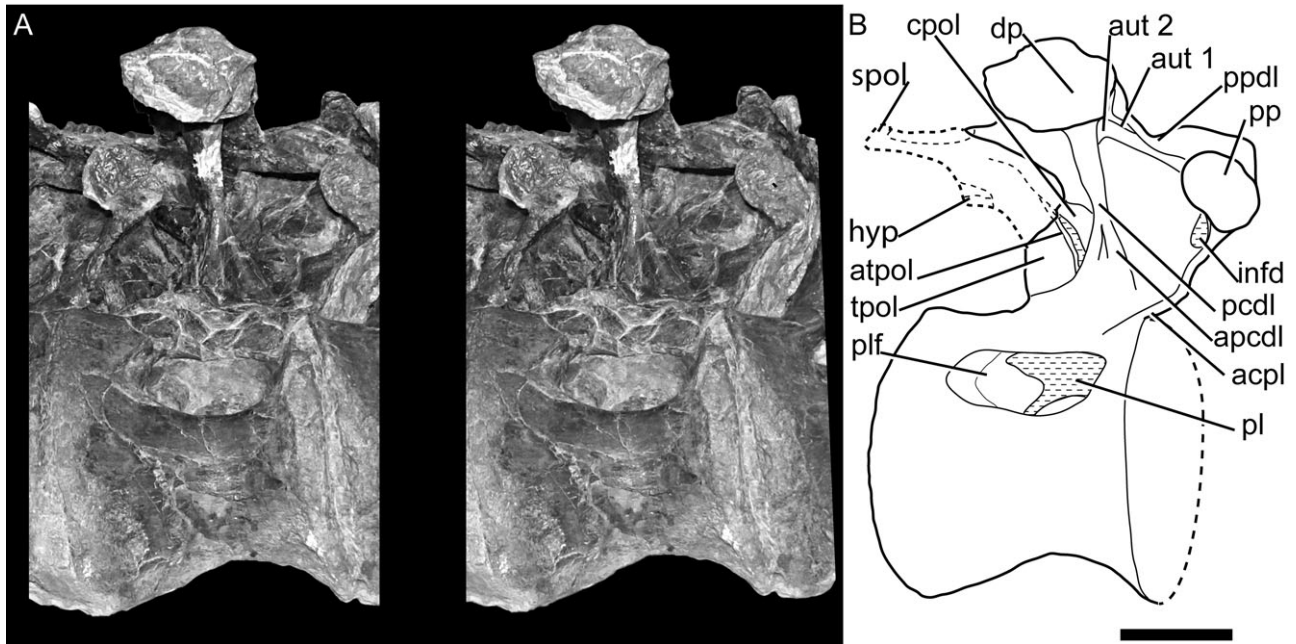
Figure 6. *Tehuelchesaurus benitezii*, ventrolateral view of the fourth preserved vertebra. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

cavities separated by a bony strut. The ventralmost depression is conical and deeper than the dorsal fossa. The SPRL are also present but nothing can be said about their development in detail due to poor preservation.

Dorsal 4 (Fig. 6)
The pleurocoel of this vertebra does not differ in shape or length from that of D3 and also bears a posterior fossa. This fossa is very similar both in shape and in length to that of D3, but differs from the fossa of subsequent vertebrae in the presence of an abrupt, step-like posterior border. From D4 to D9 (the last vertebra in which a small pleurocoel fossa is present) the pleurocoel fossa becomes progressively smaller. The parapophysis is more dorsally located on the neural arch than in D3 and is connected to the centrum by the ACPL, which is set at an angle of approximately 35° to the vertical, resembling the condition of subsequent dorsal vertebrae. The PPDL connects the parapophysis with the anterior margin of the diapophysis (Fig. 6), rather than with its ventral margin, as is the case in D3. The articular surface of the parapophysis is smaller than in D3 and is oval in outline (Fig. 6).

The lamination of the neural arch of this vertebra differs from that of D3 and remains more or less constant from this vertebra to D9, with only minor changes in the shape or orientation of some laminae. This is especially true for the two autapomorphic

laminae (named here as AUT 1 and AUT 2), which are better developed than in more anterior vertebrae. Two depressions are present just below these laminae. The larger depression is situated below AUT 1 and is rectangular in shape.

As in the anterior vertebra, the robust PCDL has an expanded and bifurcated ventral end, with a broad posterior branch and smaller anterior branch, enclosing an oval depression between them (Fig. 6). The PRDL is a very low strut and merges dorsolaterally with the PPDL.

A stout CPOL is present in this vertebra and in most of the following vertebrae. A lateromedially flattened and well-developed TPOL is present and clearly visible in lateral view, and bears an accessory lamina on its lateral surface that projects laterally and runs steeply posterodorsally, approximately parallel to the posterior margin of the TPOL. This accessory lamina, here defined as accessory TPOL (aTPOL), can be seen in all vertebrae where the TPOL is observed, and is interpreted as an autapomorphic lamina only present in *Tehuelchesaurus*. This lamina converges dorsally towards the CPOL (Fig. 6).

A trapezoidal infradiapophyseal fossa encloses two deeper depressions, as they are also present in D3. One of these depressions lies posteroventral to the parapophysis and is oval in outline and larger than that of the latter vertebra. This depression is here termed infraparapophyseal depression. The depression located below the AUT 1 is oval rather than
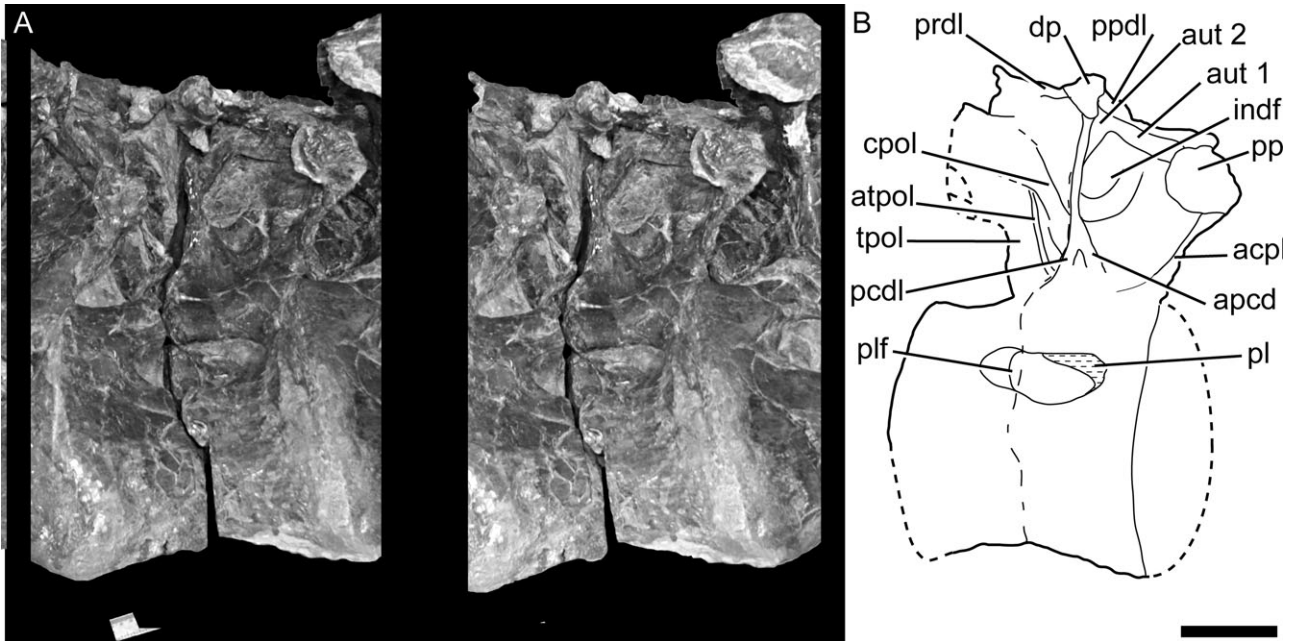
Figure 7. *Tehuelchesaurus benitezii*, lateral view of the fifth preserved vertebra. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

rectangular, as in D3. A bony strut separates this depression from the infraparapophyseal depression, and the AUT 1 runs posteriorly from this bony strut (Fig. 6). As in D3 this lamina joins with the laterally oriented AUT 2, which is smaller and less developed than the AUT 1 (Fig. 6). Due to the absence of homologous anchor points either at the beginning or at the end of these accessory laminae, no formal names in accordance with the nomenclature proposed by Wilson (1999) are proposed here, and they are simply referred to as autapomorphic lamina 1 and 2 (AUT 1 and AUT 2; Fig. 6). The more anterior lamina (AUT 1) runs posterodorsally from a small infraparapophyseal depression. The posterodorsal end of the AUT 1 joins with the lateral end of the AUT 2.

The anterior and posterior margins of the neural spine are formed by the paired SPOL and SPRL laminae, whereas the lateral surface of the spine bears a stout SPDL. The SPDL and SPOL run dorsally and are expanded laterally, whereas the SPRL projects anteriorly and it is not laterally expanded. A triangular depression is defined by the SPDL and SPOL. The rounded fossa present in D3 is also present in D4, although it is shallower than in the preceding vertebra.

Dorsal 5 (Fig. 7)
This vertebra is transversely broken close to the posterior margin of the pleurocoel (Fig. 7), slightly anterior to the level where D3 has been cut. The

pleurocoel is slightly shorter than that of the more anterior vertebrae and the posterior fossa behind the pleurocoel is small and shallows gradually posteriorly. As in D3 the pneumatic cavities of the centrum and neural arch can be seen in the exposed cross-section. The pleurocoel opens into camerae through its ventral and dorsal margins, especially in its anterior half where these fossae seem to be larger. As in the other vertebrae, the paired pneumatic cavities present in the centrum are true camerae (*sensu* Wedel *et al.*, 2000; Wedel, 2003a, b). The paired pneumatic cavities of the neural arch are supraneural camerae similar to those of some basal eusauropods and some basal neosauropods (e.g. *Barapasaurus*, *Patagosaurus*, *Camarasaurus*; Bonaparte, 1986b, 1999). The camerae of the centrum and supraneural camerae extend ventrally and dorsally from the pleurocoel, respectively. These pneumatic cavities are short and at least at this more posterior level, the centrum and the neural arch are only moderately pneumatized. Although the right infradiapophyseal fossa communicates with the right supraneural camera through a small opening, it cannot be determined whether this opening is natural. The opening bears numerous small fragments of thin, laminar bone, which may represent remains of thin bony septa that enclosed the supraneural camera laterally, as in *Camarasaurus* or *Diplodocus* (Upchurch *et al.*, 2004). As in D3 the reduced pneumaticity (compared with D1 or D9) is interpreted as a result of the posterior section at which the vertebra was cut.
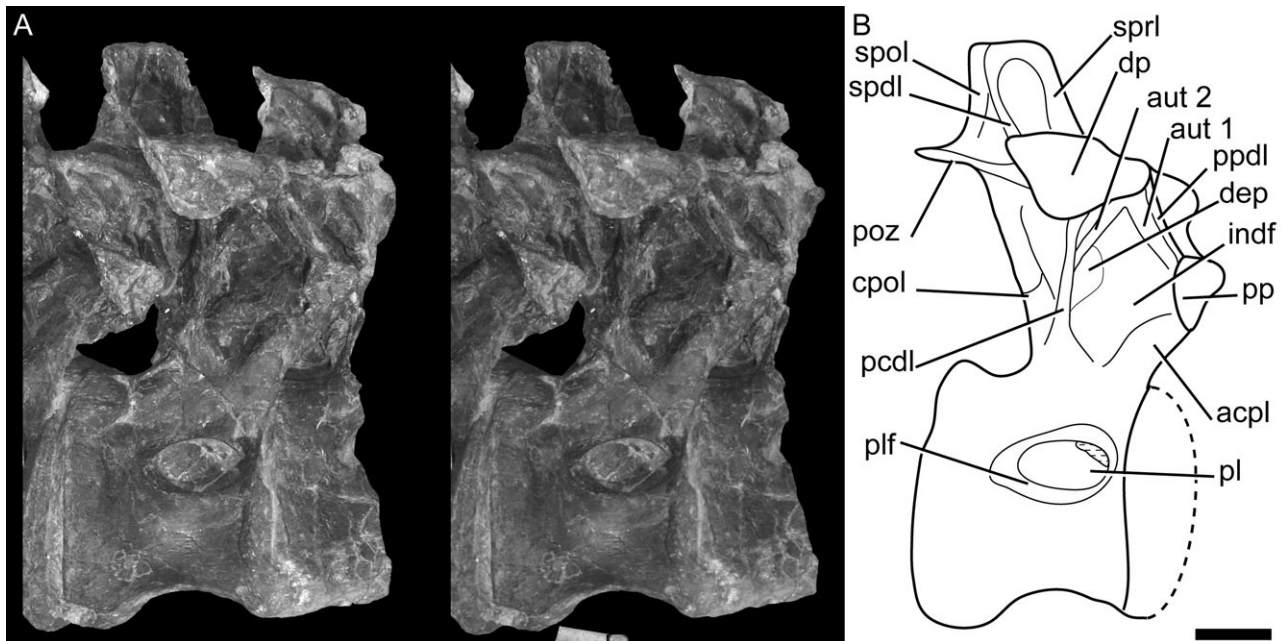
Figure 8. *Tehuelchesaurus benitezii*, lateral view of the sixth preserved vertebra. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

This vertebra was damaged laterally and the diapophysis and PODL are incomplete, but the general development of the laminae seems to be similar to that of D4. The expanded ventral margin of the PCDL is less developed than in D4, and especially its anterior branch is less robust. The length from the beginning of the bifurcation to the end of the anterior branch is half as that of the anterior vertebra. Although the PRDL is present as a weakly developed lamina in D4 and D6, this lamina seems to be completely absent in D5. Accessory autapomorphic laminae are better developed in this vertebra (and D6) than in any other element. In contrast to the situation observed in D3 and D4 AUT 1 and AUT 2 are equally developed and without a difference in length between them (Fig. 7). AUT 2 is not as laterally oriented as in D4 but is dorsoanteriorly oriented and meets the AUT 1 in an approximately right angle. AUT 1 extends posterodorsally and follows the course of the PPDL. Two deeper depressions are placed below these accessory laminae. As in D3 there is an almost rectangular depression below the AUT 1, and a depression with a small opening that seems to communicate with the right supraneural camera is situated just below the AUT 2. As in D4, a robust CPOL is present, but with a lateral position, in contrast to the more medial position that this lamina has in D4. The TPOL and its accessory lateral lamina are also present in this vertebra.

As in D4, the neural spine is formed by the paired SPOL, SPRL and SPDL. The principal difference between the neural spines of the former vertebra and D5 is that the SPOL of the latter is less laterally expanded and the SPDL is less developed.

Dorsal 6 (Fig. 8)
Due to erosion of the posterior end of D5, the anterior convex articular surface of this vertebra and the strongly concave posterior articular surface of D5 can be observed. The pleurocoel is very similar in size and shape to that present in the previous vertebra, but the fossa situated posterior to this structure is somewhat smaller.

The general features of the lamination of the neural arch do not differ notably from those of the preceding vertebra, except for the orientation and development of the two autapomorphic laminae (AUT 1 and AUT 2; see below). Although the PCDL does not have a marked accessory lamina (APCDL), it notably widens ventrally (Fig. 8), as also occurs in some titanosaurs. As in middle and posterior dorsal vertebrae in which this lamina is present, the CPOL of this vertebra is well developed. The TPOL is present in at least all vertebrae from D4 to D10, but in D6 this lamina is absent, and there are no signs of it, although there is a slightly convex ridge above the neural canal that does not seem to be broken. The PRDL, absent in D5, is present again in this vertebra showing a similar development and orientation to that observed and described in D3.

The infradiapophyseal fossa is slightly smaller than in D5. The strongly posteroventrally oriented ACPL
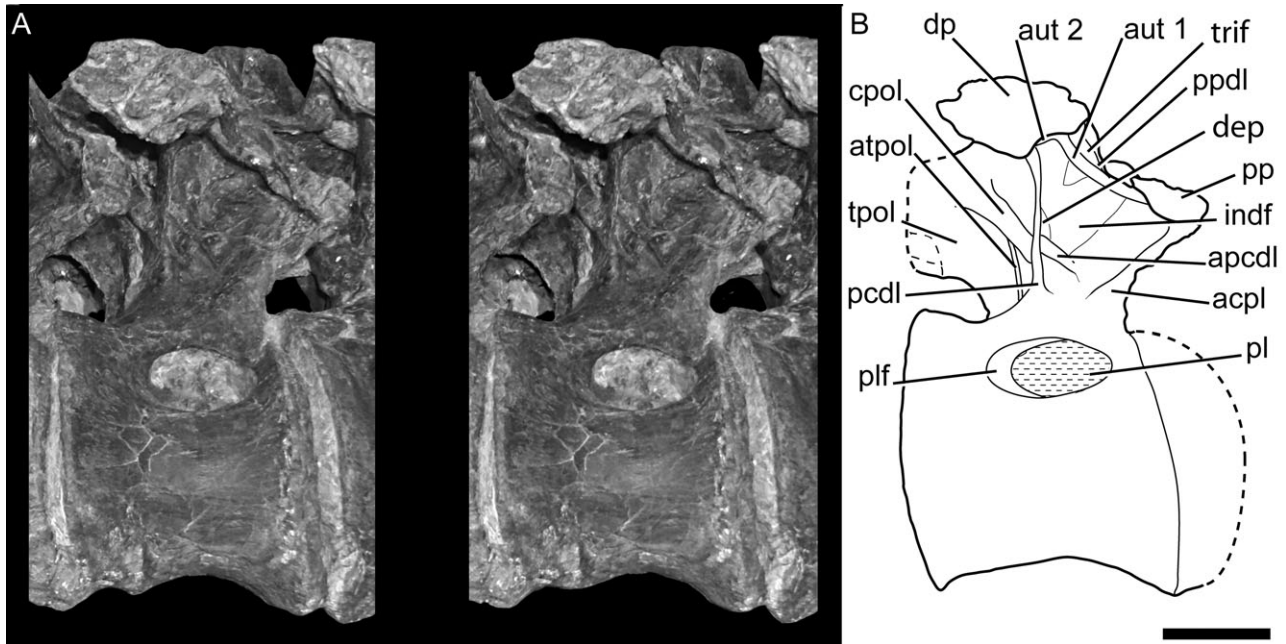
Figure 9. *Tehuelchesaurus benitezii*, lateral view of the seventh preserved vertebra. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

forms the ventral margin of this fossa. This fossa is further delimited by the PCDL and the strongly developed AUT 2 (posteriorly), PPDL (anterodorsally), and ACPL (anteroventrally). The two autapomorphic laminae (AUT 1 and AUT 2) show a different development and orientation than in D5. In D6 both laminae project laterally from the depth of the infradiapophyseal fossa, whereas they project more ventrally in D5. In contrast to D3 and D4, AUT 1 of this vertebra is less developed than AUT 2. The former extends from the dorsal end of the infraparapophyseal fossa to the anterodorsal end of AUT 2. The fossa below AUT 1 is rounded and larger than in anterior vertebrae. AUT 2 extends anterodorsally from the dorsoventral midpoint of the PCDL to its dorsal contact with the AUT 1 (Fig. 8). A small rounded depression is formed between AUT 1 and the PPDL. AUT 2 separates the infradiapophyseal fossa from a small triangular depression also delimited by the diapophysis (dorsally) and the PCDL (posteriorly).

The neural spine of this vertebra is the most complete, with its preserved height being 16 cm. The SPOL joins with the SPDL at its half-height and the resulting composite lamina extends dorsally where it meets the arched SPRL. As a result of this union there is an elongate depression on the lateral surface of the neural spine, as in many basal eusauropods, with the exception of the most basal forms. As this union is usually placed between half and two-thirds of the height of the neural spine, the mid-dorsal neural

spines in *Tehuelchesaurus* would have been 30–35 cm high at the most, and thus approximately as high as the neural arch (discounting the spine), or lower. The spine is very slightly inclined posteriorly in D6, and seemingly also in D5 and D7. Rich *et al.* (1999: 76) stated that it cannot be said whether the neural spines of *Tehuelchesaurus* were bifurcated; however, at least this spine does not show any signs of bifurcation, and the bases of the more anterior spines are also more consistent with un-bifurcated structures. This spine is unusual for a sauropod in that it is longer anteroposteriorly than wide transversely, probably at least partially as a result of the only weakly developed SPDL.

Dorsal 7 (Fig. 9)
The pleurocoel of this vertebra is slightly shorter than that present in D8 and is not oval as in the anterior vertebra, but more rounded. The posterior pleurocoel fossa is very weakly developed and this vertebra is the last element in which this fossa is clearly present (Fig. 9).

Unlike the situation observed in D6 and similar to that observed from D3 to D5 this vertebra has a ventrally bifurcated PCDL. The anterior branch of the ventrally bifurcated PCDL is continuous in direction with the CPOL (Fig. 9). As in the posterior dorsals of this taxon, the anterior branch of the PCDL might be an anterior continuation of the CPOL (and therefore not homologous to the APCDL of titano-
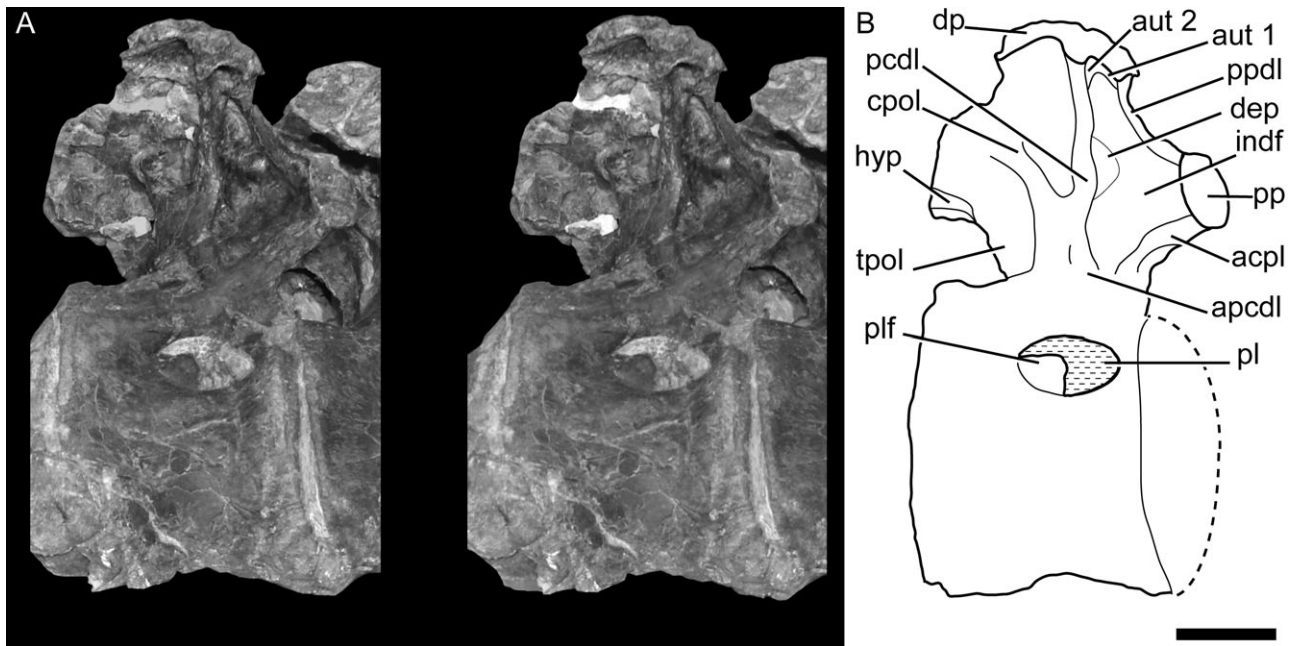
Figure 10. *Tehuelchesaurus benitezii*, lateral view of the eighth preserved vertebra. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

saurs). However, the different orientation of the anterior branch of the PCDL and the CPOL in more anterior vertebrae (see Figs 6, 7) argues against this interpretation. Thus, for the moment, we use the term APCDL for this structure.

A deep and triangular infradiapophyseal fossa is posteroventrally defined by the APCDL. Within this fossa, a smaller, deeper, triangular depression is present. A broad, rounded ridge that runs anterodorsally from its contact with the anterior projection of the PCDL delimits this deeper zone anteroventrally whereas the latter forms its posteroventral margin (Fig. 9). Two other anterior and posterior indentations are located within this triangular depression and might represent foramina that communicate with the supraneural camerae, but this area cannot be prepared and therefore the presence of such a communication cannot be confirmed. The anterior of these possible foraminae is located just above the anterodorsally oriented ridge whereas the posterior is at the level of the PCDL (above the anterior projection of the APCDL). Accessory autapomorphic laminae are also present but they are less developed than in D6 or D5. The AUT 1 runs posterodorsally from the midpoint of the PPDL and, together with the latter lamina, encloses a triangular fossa (Fig. 9). The AUT 2 is weakly developed and is partially broken. This lamina runs anterodorsally and meets the AUT 1 at the posterodorsal end of this lamina. A well-developed TPOL is present and has an accessory laterally expanded lamina (aTPOL), as in D4 and D5 (Fig. 9).

This accessory lamina is well developed and runs dorsally, disappearing at the level of the CPOL.

This vertebra presents a well-developed SPDL, which is vertical and does not contact the SPOL, as is the case in the preceding vertebra. The SPOL is well developed, but is not laterally expanded and is posteriorly oriented. A shallow ventral depression is present between this lamina and the anteroventrally expanded SPDL, and another rounded depression is present between the SPRL and the SPDL.

Dorsal 8 (Figs 10, 11)
As mentioned above, there is no fossa posterior to the pleurocoel in this vertebra, although a shallow concavity is present in this position. The length and shape of the pleurocoel are similar to that described for D7. The ACPL is a very robust lamina and its orientation does not differ from that in mid-dorsals. The PCDL and the CPOL merge at the base of the neural arch, forming a robust and dorsally oriented lamina. A small anterior branch runs from this lamina to the ventral end of the ACPL, and is interpreted as the APCDL. The prezygapophysis of the next vertebra (D9) was disarticulated and thus the contact between CPOL and the right postzygapophysis as well as the hyposphene ridge can be seen in D8 (Fig. 10). The TPOL is present but its accessory lamina seems to be absent in D8, although it is present in all other vertebrae in which the TPOL is present. In most sauropodomorphs the TPOL is absent in vertebrae that have a hyposphene, with the
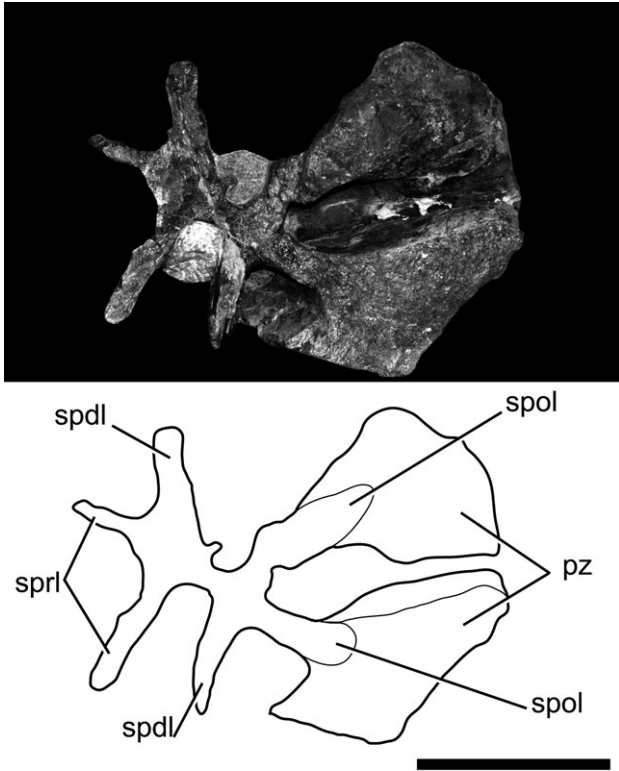
Figure 11. *Tehuelchesaurus benitezii*, horizontal cross-section through the base of the neural spine of the eighth dorsal vertebra. Scale bar = 10 cm. For abbreviations see text.

exception of diplodocids, in which this lamina supports the hyposphene from below (Wilson, 1999; Upchurch *et al.*, 2004; Apesteguía, 200s5). *Tehuelchesaurus* has a well-developed TPOL in almost all its mid to posterior dorsals and at least this vertebra shows a weakly developed hyposphene.

The infradiapophyseal fossa is ventrally defined by a low ridge, similar to that present in D7, in which this ridge forms the anteroventral margin of a deeper area. A rounded depression is located within the infradiapophyseal fossa, close to its posterior edge. This depression is more extensive than that in D7 and might be associated with a supraneural foramen, as in previous vertebrae, but preparation of this fossa is incomplete. The depression located at the anterior region of the infradiapophyseal fossa of D7 is absent in D8. This vertebra is the last element in which the AUT 1 and AUT 2 are present. The AUT 1 is very weakly developed as a low projection extending from the dorsal end of the PPDL (Fig. 10). The AUT 2 runs anterodorsally and meets the AUT 1 just below the diapophysis (Fig. 10).

The neural spine is eroded close to its base, exposing the dorsal view of a longitudinal section (Fig. 11).

No significant difference is observed between the neural spine of this vertebra and that of D6. The paired SPOL are posterolaterally projected, forming an angle of nearly 45° with respect to the sagittal plane, and the paired SPRL are craniolaterally oriented at a similar angle. The paired SPDL are laterally oriented, and probably suffered plastic deformation, given the asymmetric position and orientation of these laminae (Fig. 11).

Dorsal 9 (Figs 12, 13)
This vertebra is poorly preserved and the identification of its laminae is difficult, but no noticeable difference seems to be present in its general morphology compared with D8. Thus, the description is focused on its pneumatic features and not in the lamination. As is the case with D3 and D5, this vertebra was cut during the extraction of the specimen. The vertebra is cut along a transverse plane and the cross-section is relatively more anteriorly placed than those of D3 and D5, being just at the anterior margin of the pleurocoel. The exposed cross-section allows observation of the pneumatic features of this vertebra, both in the centrum and in the neural arch. The pleurocoel is round and slightly smaller than that of D10. The right pleurocoel was prepared and its ventral and dorsal communication with the right camera of the centrum can be observed (Fig. 12). The cut exposes this large communication (Fig. 12), which occupies the entire pleurocoel, except for its posterior border. A similar bony strut is located in the posterior region of the pleurocoels of other vertebrae. Paired camerae extend from the pleurocoel into the centrum, expanding both ventrally and dorsally (Fig. 12). The pneumatic spaces present in the centrum are true camerae (*sensu* Wedel *et al.*, 2000) and the neural arch bears large pneumatic spaces interpreted as supraneural camerae. The exact percentage of pneumatic space cannot be measured with confidence, given the strong lateromedial compression and deformation of the specimen, but, as preserved, at least half of the cross-section is occupied by the pneumatic spaces. The camerae of the centrum communicate with the supraneural camerae (exposed on the right side), but unfortunately the neural canal cannot be confidently identified. The left and right sides differ in the degree of pneumaticity (Fig. 12), but this difference seems to be product of the angle of the cross-section that is slightly oblique to the transverse plane of the vertebra (exposing a more posterior section on the left side).

Dorsal 10 (Fig. 13)
This vertebra resembles the first sacral more than any of the presacral vertebra. The centrum is stout and has a large, dorsally placed pleurocoel, without
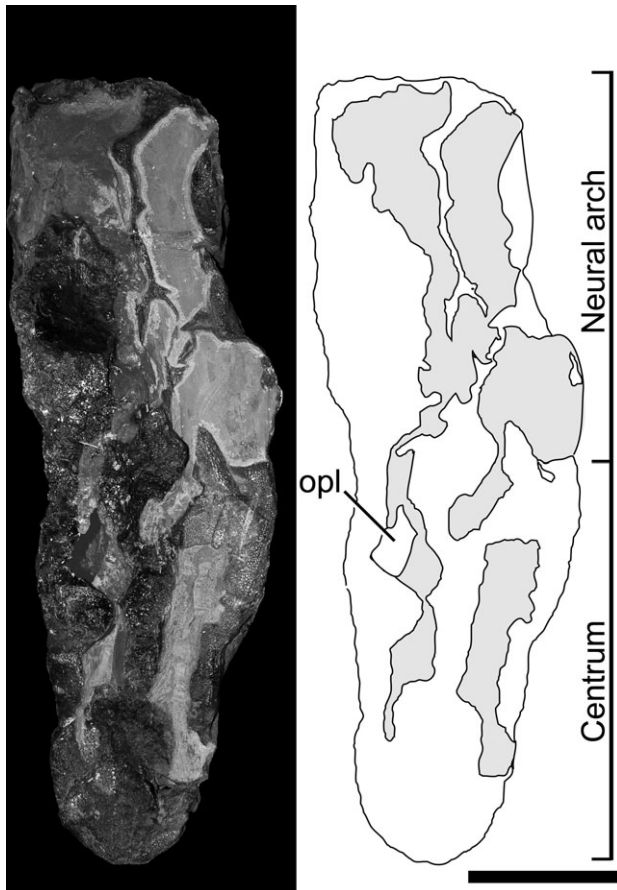
Figure 12. *Tehuelchesaurus benitezii*, transversal cut of the ninth preserved dorsal vertebra, showing the complex internal camerate system in grey. For position of cross-section see Figure 13. Scale bar = 10 cm. For abbreviations see text.

any posterior depression. In contrast to more anterior dorsals, the pleurocoel is more extended dorsally and almost as high as long.

The ACPL is not anterodorsally oriented, as in other presacral vertebrae, but the ventral half of this lamina runs dorsolaterally and the dorsal half is posterodorsally inclined (as a product of the deformation of the specimen; Fig. 13). The parapophysis is not preserved in this vertebra, and its former position cannot be determined with any certainty, given the deformation of the ACPL. The diapophysis is placed anterior to the end of the ACPL but this may also be a product of anteroposterior crushing of the specimen. In contrast to the condition of other presacral vertebrae, a well-developed prezygoparapophyseal lamina is present in this vertebra and in the first sacral (S1). The PCDL is absent and the paradiapophyseal lamina seems to be well developed, as in S1. The neural spine of this vertebra is mostly eroded and no laminae can be observed.

Sacrum (Fig. 13)

The pleurocoel in the first sacral vertebra is markedly smaller than those of the preceding dorsals. Of the sacrum, three complete and a fragment of a fourth centrum are preserved. All preserved sacrals are fused, but the first centrum is separated from the second by a strong posterior expansion, similar to the expanded articular ends in the dorsal vertebrae, whereas the second and third centra are fused without any visible suture and are separated only by a minor ventral swelling. The expansion between the third and the fourth sacral vertebra is again more pronounced than that between the second and the third. The ventral sides of the first three sacrals seem to have been broadly rounded ventrally, but are somewhat deformed. All the neural arches are damaged, more so in the posterior than in the anterior elements, and the neural spines are missing.

The first sacral has a dorsoventrally expanded parapophysis that spans the neurocentral suture (Fig. 13). Behind the parapophysis, a small pleurocoel is present in the dorsal part of the centrum. As in the last dorsal, a stout centropostzygapophyseal lamina extends anteriorly from the postzygapophysis up to the posterior edge of the parapophysis. A small, short lamina extends from the parapophysis posterodorsally. As in D10, no posterior centrodiapophyseal lamina is present. A stout sacral rib extends ventrally from the anteriorly directed transverse process, and spans from the neural arch to the mid-height of the centrum.

In the second sacral vertebra, the attachment for the sacral rib extends from the mid-height of the centrum to the top of the neural arch (Fig. 13). It expands further laterally and, apparently, formed part of the sacricoastal yoke. The lateral part of the sacri-coastal yoke is probably represented by a long, irregular bony plate that was found alongside the sacral vertebrae, but is too poorly preserved to correlate with the broken attachments of the sacral ribs. The attachment of the sacral rib consists of a thin vertical lamina and a stout, ventral antero-posterior expansion. At approximately the level of the neurocentral suture, a stout ridge expands from the posterodorsal part of the vertebral centrum and meets the sacral rib anterodorsally and laterally. A thin, strongly damaged lamina runs from the anterior part of this ridge dorsally, but its dorsal extent is uncertain, owing to the damage to the neural arch. No pleurocoel is present in the centrum, but a shallow depression is found on the posterior part of its lateral surface, between the ventral expansion of the attachment for the sacral rib and the posterodorsal ridge.

Only the centrum is preserved of the third sacral vertebra, including the ventral part of the attachment of the sacral rib, which is identical to that of the preceding vertebra.
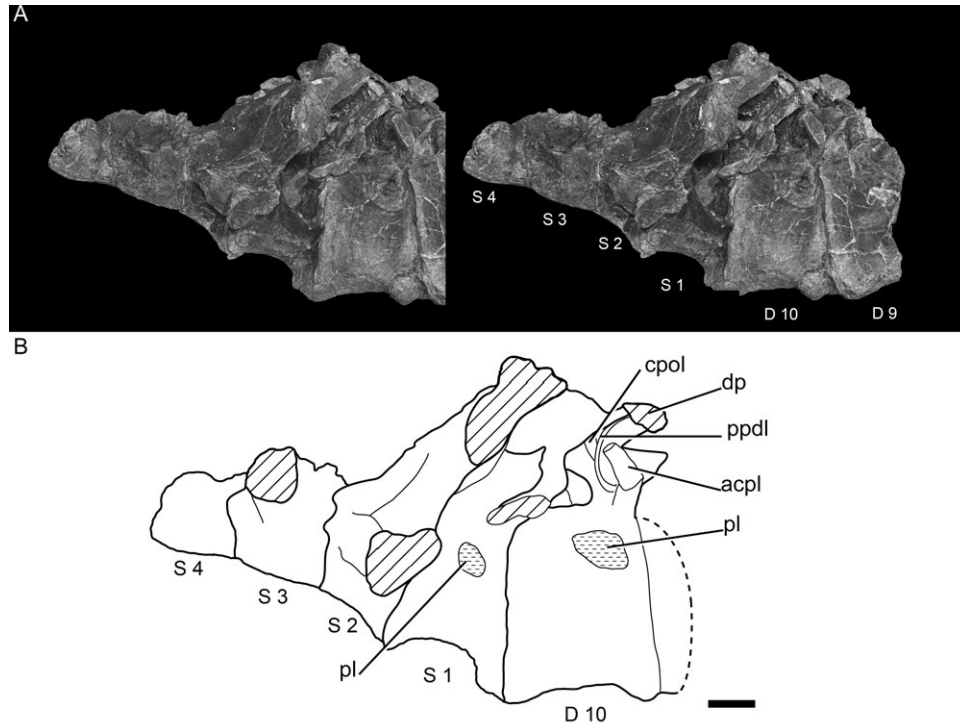
Figure 13. *Tehuelchesaurus benitezii*, lateral view of the posterior half of the ninth and tenth preserved dorsal vertebra and the four anterior sacral vertebrae. The cross-section in Figure 12 corresponds to the anterior end of the articulated series. Stereophotographs (A) and line drawing (B). Scale bar = 10 cm. For abbreviations see text.

The morphology of the vertebrae and their attachments to each other thus suggest that the sacrum of *Tehuelchesaurus* consisted of at least four vertebrae. Based on the presence of a pleurocoels and the neural arch lamination, the first sacral is interpreted as a dorsosacral, whereas the abrupt change in morphology in the next vertebra indicates that this and the subsequent element are the true sacrals. Thus, the fourth sacral would be a caudosacral. If one assumes that *Tehuelchesaurus* had five sacrals, as is the case in other neosauropods (Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002), the last sacral should therefore be a second caudosacral. This is in contrast to the model of formation of the sacrum in neosauropods proposed by Wilson & Sereno (1998), who reconstructed the incorporation of two dorsosacrals, and in accordance with the interpretation of McIntosh *et al.* (1996) for *Camarasaurus lewisi*.

Ribs
All of the ribs preserved with the type of *Tehuelchesaurus* are dorsal ribs and are fragmentary. They seem to have the typical morphology of the dorsal ribs of sauropods, with a double-headed proximal end, an L-shaped cross-section in the proximal shaft, and a rather massive, plate-like distal shaft. None of the fragments has any sign of pneumatization, and no pneumatic foramina or depressions are present in the few preserved parts of the proximal ends of the ribs. Although a few fragments of more slender ribs are present, the dissociation of ribs and vertebrae and the fragmentary nature of the rib material make it impossible to say whether there was a distinction of 'thoracic' (anterior) and 'lumbar' (posterior) ribs in this animal, as is present in other sauropods (Rauhut *et al.*, 2005).

SHOULDER GIRDLE AND FORELIMBS
Forelimb elements are represented by the complete right scapula and coracoid, which are preserved in articulation, but not fused (contrary to Rich *et al.*, 1999), the right humerus, and the left ulna and radius.

Scapulocoracoid (Fig. 14)
The right scapulocoracoid is completely preserved (Fig. 14). For convenience of description, and in accordance with the more upright position of the pectoral girdle argued for by Schwarz, Frey & Meyer (2007), the scapulocoracoid is treated as if it was oriented with its long axis vertical, so that the actual anterodorsal side is regarded as the anterior side here.
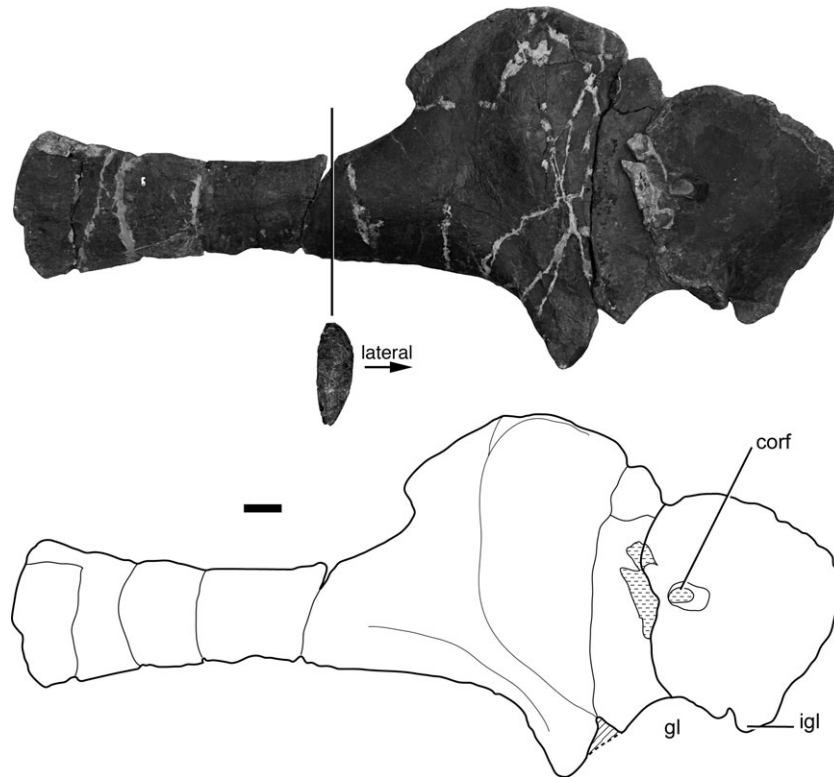
Figure 14. *Tehuelchesaurus benitezii,* right scapulocoracoid in lateral view, with cross-section of proximal shaft. Abbreviations: corf, coracoid foramen; gl, glenoid; igl, infraglenoid lip. Scale bar = 10 cm.

The shaft of the scapula is very slender. As noted by Rich *et al*. (1999), the distal shaft has only a slight, flattened, fan-shaped expansion, whereas the more proximal part of the shaft is anteroposteriorly convex laterally, and wing-like in cross-section, with a narrow posterior margin. Probably as a result of the slenderness of the shaft, the proximal expansion of the scapula is more pronounced than in most sauropods, with the greatest anteroposterior width of the acromion process over the glenoid (99 cm) being almost four times the minimal width of the shaft (25 cm), which probably represents a further autapomorphy of *Tehuelchesaurus*. The expanded acromial part accounts for 42% of the total length of the scapula (72 of 171 cm).

At the base of the acromion process, where the shaft meets the expansion, the lateral surface of the bone is flat again. As noted by Rich *et al*. (1999), the lateral acromial fossa is weakly developed and only anteriorly more sharply defined. The acromion process expands dorsally and overhangs the shaft so that there is a rounded incision between shaft and acromion process, as in mamenchisaurids and other neosauropods. The lateral surface of this dorsal process is depressed below the level of the acromion ridge.

The posterior margin of the scapula is strongly flexed posteriorly towards the glenoid. Whereas the bone is thin and plate-like in the acromion process, the glenoid part is strongly thickened. The articular surface of the glenoid is steeply ventroposteriorly inclined. Although it is slightly damaged, it can be seen that it is slightly flexed medially in its anteroventral part, as it is the case in somphospondyls (Wilson & Sereno, 1998).

The coracoid is significantly shorter anteroposteriorly than the acromial part of the scapula, its maximum length (68.5 cm) being less than 70% that of the scapula (Fig. 14). It is trapezoidal in shape, with the anterior margin being significantly longer than the posterior margin. The well-developed coracoid foramen is placed at approximately mid-height of the element and slightly offset from its dorsal margin. The anterior margin arises in a slight curve from the dorsal margin, resulting in a small incision between the articulated scapula and coracoid. The anterior margin is slightly convex over its entire length, and meets the ventral margin at a rounded angle of approximately 90°. The ventral margin is slightly posteroventrally directed. Posteroventrally, and slightly offset medially from the glenoid, a small, posteriorly directed, hook-like infraglenoid lip is

present. No biceps tubercle is present. The lateral surface of the coracoid is convex, with an almost flat anterodorsal part and a notable medial flexion along a line connecting the ventral end of the glenoid with the anteroventral corner of the coracoid. The articular facet of the glenoid on the coracoid is more posteriorly than dorsally directed, with its ventralmost third being flexed posteriorly. The length of the glenoid portion of the coracoid (15.5 cm) is only 55% of that of the scapula (28 cm). The facet is subdivided into a smaller ventrolateral part that is directed slightly laterally and a larger dorsomedial part that is directed slightly medially.

The suture between the coracoid and the scapula is slightly opened and filled with matrix, with the coracoid having been very slightly telescoped onto the scapula. The suture runs anteriorly and slightly dorsally from the glenoid, but flexes anteroventrally at about the level of the anterior rim of the coracoid foramen (Fig. 14).

Humerus (Fig. 15)
The right humerus is preserved, although this element was figured and described as left humerus by Rich *et al*. (1999). The element is rather short and stocky, with both ends strongly expanded and a slender mid-shaft (Fig. 15). The proximal end is more medially than laterally expanded, with a small, triangular, anteroposteriorly flattened internal tuberosity. The tuberosity is notably offset from the proximal articular facet and the posterior side of the humerus, but only slightly from the anterior side.

The proximal surface consists of a quadrangular articular surface medially and a slender, transversally longer lateral part that flexes anteriorly onto the proximal surface of the deltopectoral crest laterally. The posteromedial corner of the articular surface overhangs the posterior side of the proximal end of the humerus as a notable, small tubercle. The articular surface is notably convex medially, but becomes planar laterally.

Although the deltopectoral crest is clearly offset in posterior view, forming a rounded angle of approximately 90° with the posterior surface, it is low and only projects slightly anteriorly in anterior view. As noted by Rich *et al*. (1999), the deltopectoral crest extends over approximately half the length of the humerus (55 of 114 cm) and ends rather abruptly, with its anterolateral rim flexing posteriorly at an angle of almost 90°. Below the deltopectoral crest, the shaft is almost round in cross-section and only very slightly flattened anteroposteriorly.

The distal end of the humerus is both transversely and anteroposteriorly expanded and thus very massive, which might represent an autapomorphy of the taxon (Upchurch *et al*., 2004). The median part of

the anterior side is expanded and originally bore two small, anteriorly directed tubercles, as is typical for sauropod humeri, but only the medial tubercle is preserved. In posterior view, two distinct condyles of the distal end are discernible, separated by a wide but shallow extensor groove, as described by Rich *et al*. (1999).

Ulna (Fig. 16)
The left ulna is rather short and stocky (Fig. 16). The proximal end is strongly expanded both anteroposteriorly and transversely. As is usual in sauropods, the proximal end is triradiate, with a low olecranon process posteriorly, a longer, straight anterior process, and a shorter, distally anteriorly curved lateral process. The medial part of the proximal articular surface slopes anterodistally and is convex, whereas the lateral part is flat. The anterior and lateral processes define the large, anterolaterally directed radial fossa. In contrast to most other sauropods, the posterolateral egde that extends from the olecranon process distally forms a laterally overhanging shelf proximally, which defines a large posterolateral depression on the proximal end of the ulna.

The anterior process arises rather abruptly from the shaft, being restricted to approximately the proximal quarter of the length of the bone, whereas the posterior expansion extends to approximately half the length of the bone and the expansion of the lateral process even almost to the distal end. Distal to the anterior expansion, the shaft is broadly rounded transversely anteriorly. Distally, a large, subtriangular rugosity is present anterolaterally for the contact with the distal end of the radius. The distal end of the ulna is slightly flexed laterally, so the articular surface faces slightly latero-distally.

The distal articular end of the ulna is anteromedially–posterolaterally oriented and is slightly wider in its posterolateral part than in the anteromedial section. The articular surface is slightly convex, with a low, longitudinal ridge on the medial side.

Radius (Fig. 17)
A left radius is preserved (Fig. 17). The supposed medial view of the radius in Rich *et al*. (1999: figs 12.2, 12.4) is in fact the ulna in posterior view. Furthermore, Rich *et al*. (1999: 75 and figs 12.1, 12.3) mistook the proximal end for the distal end; thus, the proximal view figured by these authors (Rich *et al*., 1999: figs 13.3, 13.4) is indeed the distal view, and the distal view (figs 13.5, 13.6) the proximal view.

The radius is stout and both ends are expanded. The proximal end is flat and damaged anteriorly and posteriorly, more so on the anterior side, where the spongiosa is visible. As noted by Rich *et al*. (1999),
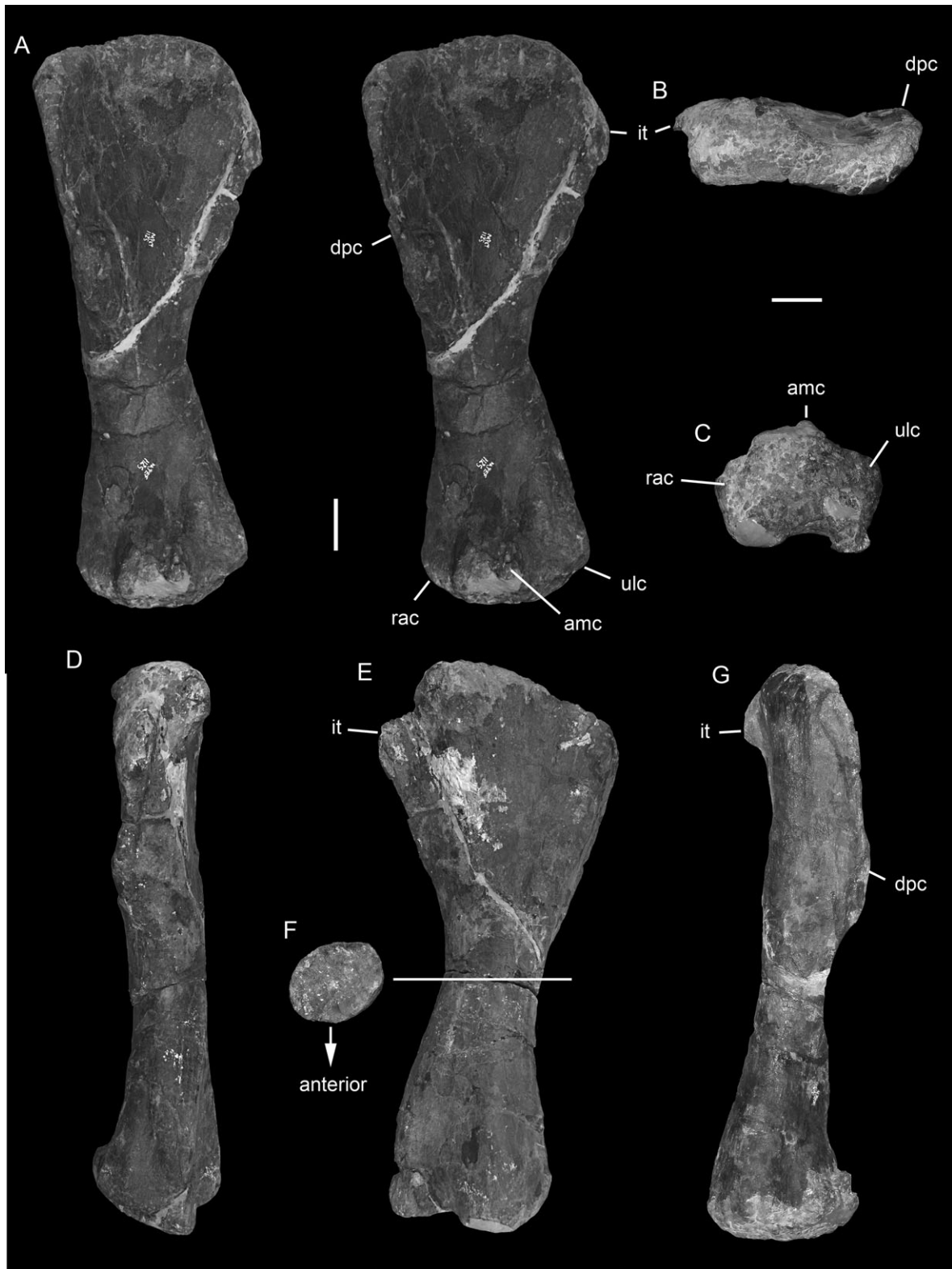
Figure 15. *Tehuelchesaurus benitezii*, right humerus. Anterior view, stereophotographs (A), proximal view (B), distal view (C), medial view (D), posterior view (E), cross-section at mid-shaft (F), and lateral view (G). Abbreviations: amc, anterior medial condyle; dpc, deltopectoral crest; it, internal tuberosity; rac, radial condlye; ulc, ulnar condyle. Scale bars = 10 cm.

Figure 16. *Tehuelchesaurus benitezii,* left ulna. Anterolateral view, stereophotographs (A), proximal view (B; anterior is to the left), distal view (C; anterior is to the left), lateral view, stereophotographs (D), and posterior view (E). Abbreviations: ap, anterior process; lp, lateral process; rr, rugosity for contact with radius. Scale bar = 10 cm.

Figure 17. *Tehuelchesaurus benitezii*, left radius. Medial view, stereophotographs (A), and anterior view (B). Abbreviations: d, depression; in, incision; ut, tubercle for contact with the ulna. Scale bar = 10 cm.

there is a deep, probably artificial incision in the posteromedial side of the articular end. From the anteromedial edge of the element, a broad, rounded ridge extends distally and gently turns onto the medial side of the bone towards its distal end, which is placed at approximately half-length of the bone. At the distal end of the bone, a large, rugose tubercle posteromedially marks the contact with the distal ulna. Below this tubercle, a small, anteromedially opening depression is present, as also seems to be the case in *Janenschia robusta* (Janensch, 1961: pl. 17, fig. 8). The distal end is posterolaterally–anteromedially oriented, with the wider part situated posterolaterally. Whereas the posterolateral part is slightly convex, the anteromedial part of the articular surface is almost flat and rises proximally anteriorly. The distal outline of the radius is subrectangular, with a flat posterior edge, in which the depression mentioned above forms a small incision. As is typical in sauropods, the articular ends are covered by irregular bumps and grooves.

PELVIC GIRDLE AND HIND LIMBS

Of the pelvic girdle, a small fragment of the right ilium, a complete right pubis, a fragment of the left pubis (mistakenly stated as 'left pubis, partial right pubis' by Rich *et al*., 1999: 63), the left ischium, and the shaft of the right ischium are preserved.

Ilium

Only the ventral part of the postacetabular blade of the right ilium is preserved in articulation with the lateral ends of two and a half sacral ribs. The ischial peduncle is low and transversely expanded. Posterior to the peduncle, the ventral margin of the postacetabular blade is thin, but rapidly expands posteriorly to form a notable, rounded tubercle at the distal end of the ventral margin of the postacetabular blade. Medially, a low medial shelf extends from the ischial peduncle posteriorly and marks the ventral margin of the attachment of the sacral ribs. The latter are expanded both anteroposteriorly and dorsoventrally and form a broad junction with the ilium, although the suture is clearly visible, so no fusion seems to be present. At the dorsal break, the iliac blade is thin.

The measurement for the ilium given by Rich *et al*. (1999: 80) most probably refers to the poorly preserved remains of the sacricostal yoke mentioned above and should thus be regarded as a minimal estimation of the length of the ilium.
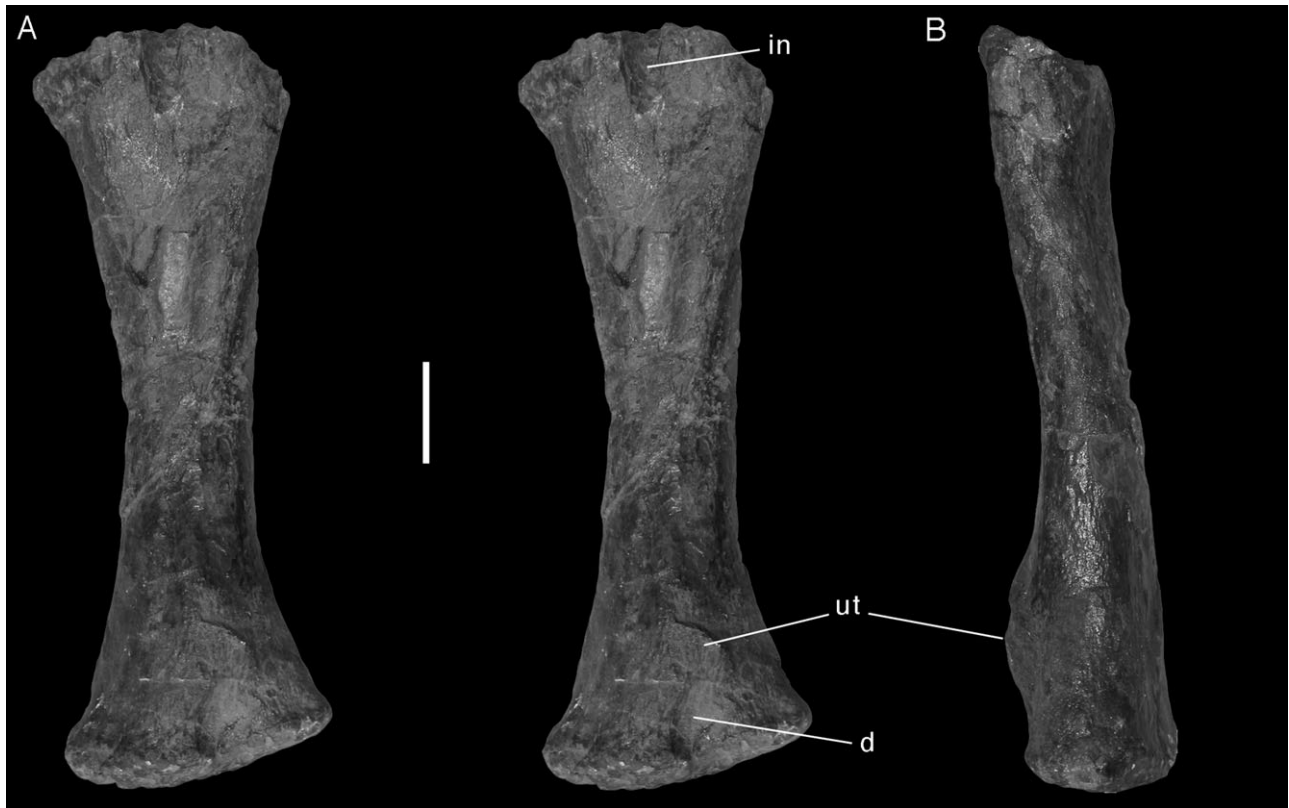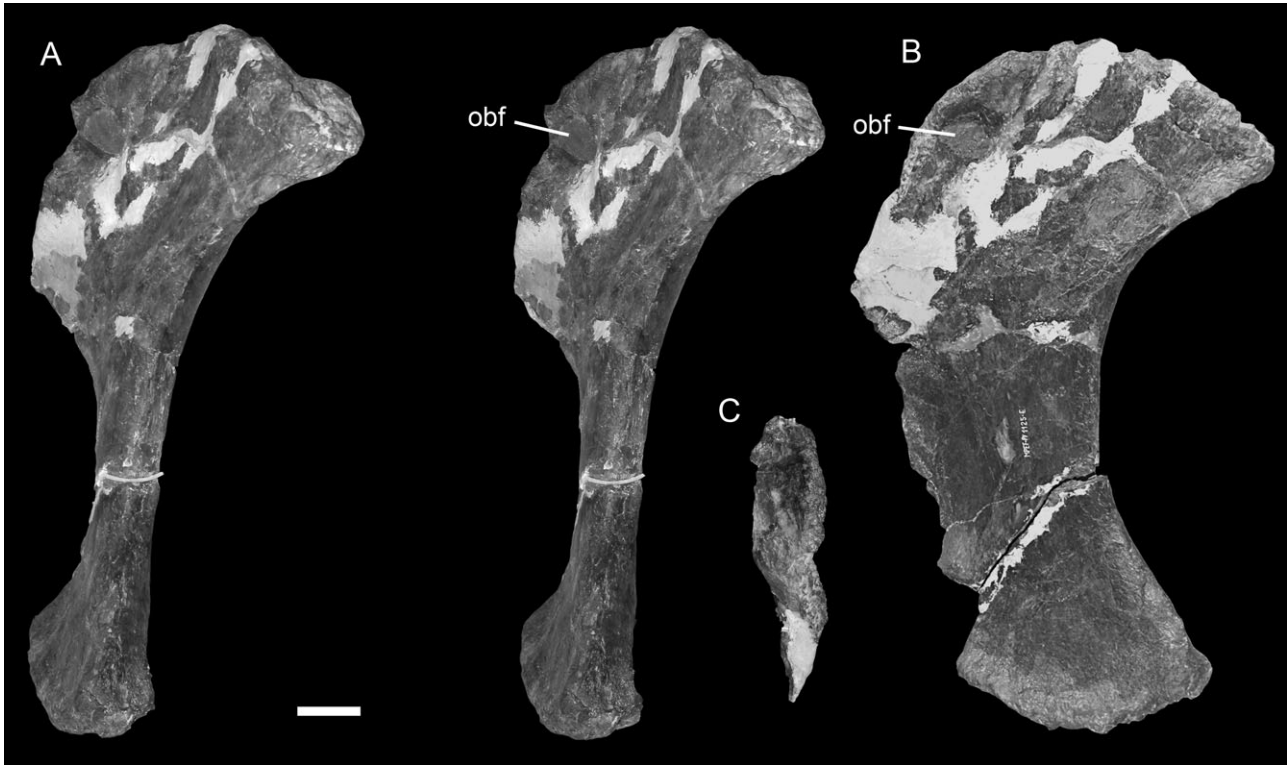
Figure 18. *Tehuelchesaurus benitezii*, rigth pubis. Lateral view, stereophotographs (A), posterolateral view (B), and outline of ischial peduncle (C). Abbreviation: obf, obturator foramen. Scale bar = 10 cm.

Pubis (Fig. 18)
As is usual for sauropods, the pubis shows only a weak and gradual torsion from the pubic apron to the proximal part (Fig. 18). In lateral view, the shaft of the pubis is notably flexed anteriorly, resulting in a concave anterior margin, as noted by Rich *et al*. (1999). The shaft is transversely wide and gradually fades into the apron medially. It is rather narrow anteroposteriorly, with a moderate distal expansion. The anterolateral margin of the pubis is rounded over most of its length, but becomes a sharp edge in its proximalmost one-fifth, towards the iliac peduncle. This sharp edge obviously corresponds to the ambiens process, which is not marked otherwise.

The iliac articulation of the pubis is broad anteriorly and narrows posteromedially. The acetabular margin of the pubis faces posterodorsally and is shorter than the iliac articulation. It is generally narrow but further narrows somewhat posteroventrally. The ischial articulation is considerably longer than both the iliac articulation and the acetabular margin; with a total length of *c*. 45 cm it is almost half the length of the entire pubis (94.5 cm). The facet is wide proximally and narrows ventrally, until its ventral end is represented by a thin lamina of bone, which might be slightly damaged distally. Proximally,

a large, oval, laterally opening pubic foramen is present directly adjacent to the ischial articulation.

Ischium (Fig. 19)
The ischium is slightly longer than the pubis, as in most sauropods, with the exception of titanosaurs. The slender shaft is only slightly inclined posteriorly in relation to the iliac peduncle (Fig. 19). It is most slender directly below the proximal expansion towards the peduncles and gradually expands distally. The distal end of the ischium is broad and plate-like. It is notably twisted in comparison with the proximal end, so that the long axis of its cross-section is anteromedially–posterolaterally oriented. The distal facet for the suture between the two ischia is well preserved in the fragmentary right element, being elongated and triangular and becoming gradually narrower proximally. It is placed on the medial side of the bone and ends at approximately one-third of the total length of the bone proximally; more proximally, the ischia obviously only contacted each other along their thin anteromedial edges. Thus, the articulated ischia had a rather restricted medial contact and would have formed a widely open V-shape in cross-section, unlike the extensive medial contact and narrow V-shape found in basal sauropods.
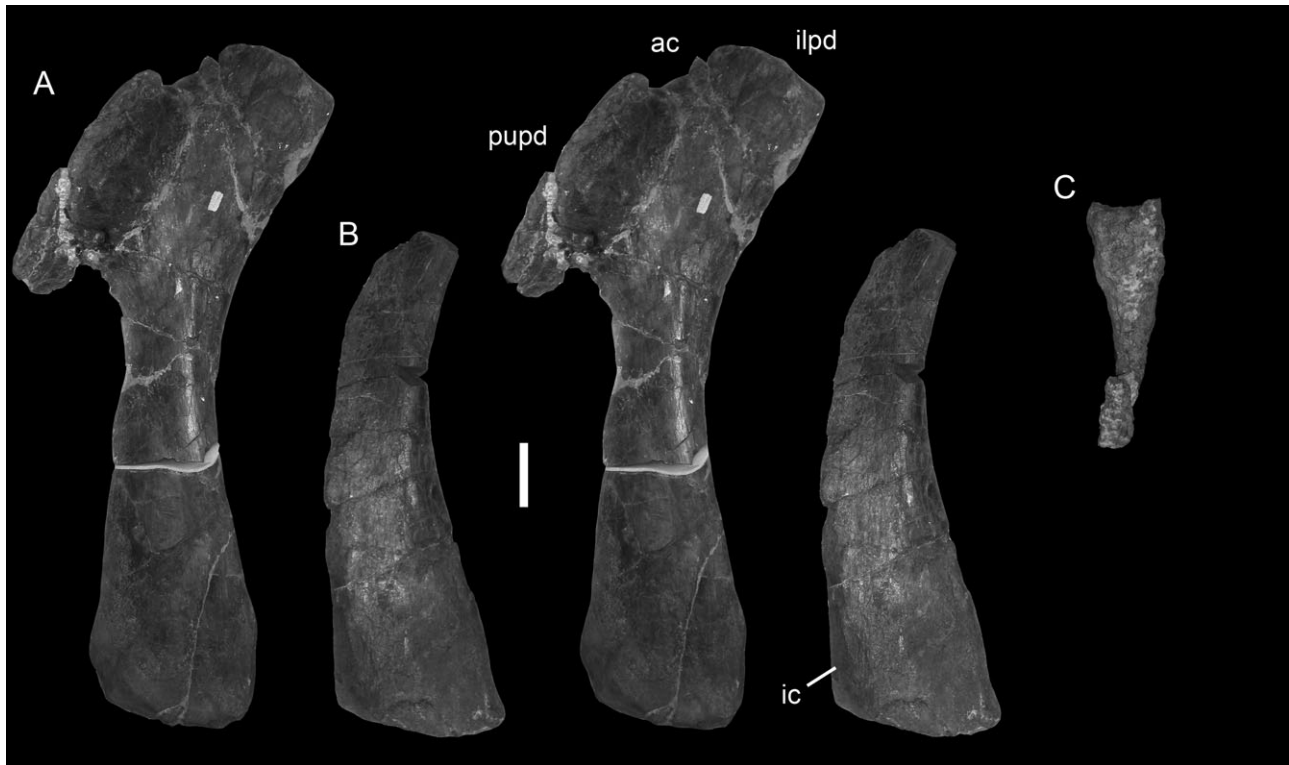
Figure 19. *Tehuelchesaurus benitezii*, ischium. Left ischium in anterolateral view, stereophotographs (A), right ischial shaft in posterior view, stereophotographs (B), and outline of pubic peduncle of left ischium (C). Abbreviations: ac, acetabular rim; ic, contact area between left and right ischium; ilpd, iliac peduncle; pupd, pubic peduncle. Scale bar = 10 cm.

In the proximal part of the ischium, the pubic peduncle is very short anteroposteriorly, but high dorsoventrally, accounting for approximately 37% of the total length of the bone. The articular facet for the pubis is broad dorsally, but rapidly narrows ventrally. A shallow, broad incision seems to have been present between the ischial shaft and the pubic articular surface distally, similar to the situation in *Dicraeosaurus* (Janensch, 1961) and at least some specimens of *Camarasaurus* (Ostrom & McIntosh, 1966: pl. 68; McIntosh *et al*., 1996). Although the margins of this incision are damaged, the thinness of the bone in this place indicates that it is not entirely an artifact.

The acetabular rim of the ischium is clearly offset from the articular surfaces of the peduncles. It is markedly concave, slightly laterally directed and of subequal width throughout its length. The iliac peduncle is short and its articular surface is of approximately the same length and width as the acetabular rim.

Femur (Fig. 20)
Both femora are preserved, but, as noted by Rich *et al*. (1999), both are deformed in quite different ways, making a detailed evaluation of their morphol-

ogy difficult (compare Fig. 20A, B with Fig. 20C, D). Whereas the left femur is compressed anteroposteriorly, the right femur has mainly suffered transverse deformation. However, the deformation of the left femur is less severe, so most of the characters stated below are based on this specimen, although many of the important traits can also be verified in the right femur.

The femoral head is well developed and medially directed. As in most sauropods, it is slightly elevated above the level of the greater trochanter, which is also well developed and approximately as broad as the head. A marked, lateral expansion is present in the proximal quarter of the bone, like the condition found in titanosauriforms (Salgado *et al*., 1997), although it is proximodistally slightly shorter than in the latter. This bulge is not obvious in the figures of this element by Rich *et al*. (1999: figs 5, 6), due to the transverse deformation of the right element and the angle in which the left femur was photographed. However, the bulge is clearly marked in the left femur (Fig. 20A) and its presence can also be verified in the right element, despite the transverse compression of this bone. The shaft seems to be anteroposteriorly flattened, as in almost all sauropods, but the exact

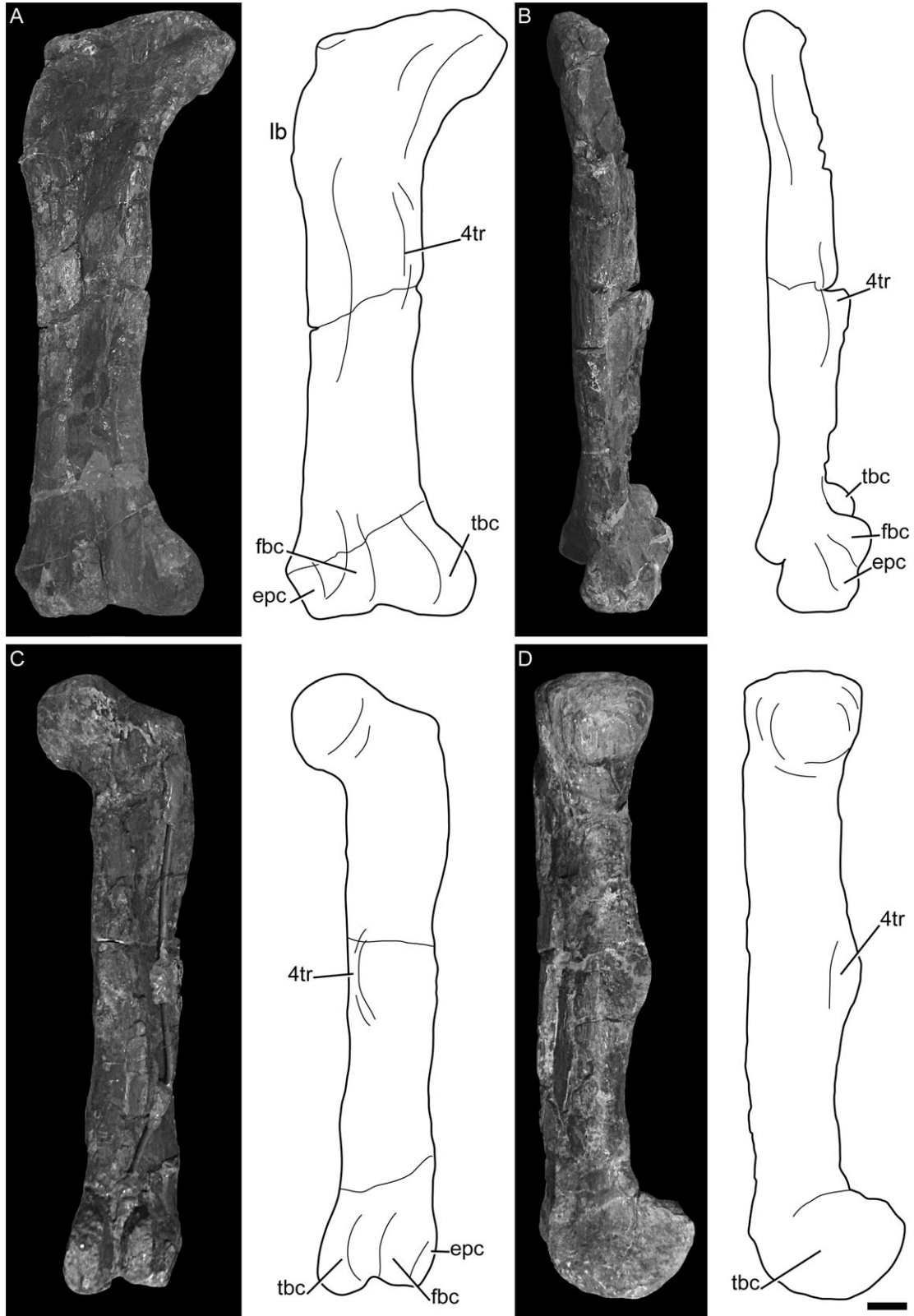**Figure 20.** *Tuelchesaurus benitezii*, right femur in posterior (A) and proximal views (B) and left femur in posterior (C), and medial views (D). Abbreviations: 4tr, fourth trochanter; epc, epicondyle; fbc, fibular condyle; lb, lateral bulge; tbc, tibial condyle. Scale bar = 10 cm.

degree of flattening cannot be ascertained due to deformation. As noted by Rich *et al.* (1999), the fourth trochanter is placed almost half way down the shaft on its posteromedial margin. It is developed as a low, stout ridge, with a marked depression medially. The distal condyles are well developed and semicircular in lateral or medial outline, extending well onto the anterior face of the bone. The lateral condyle is posteriorly narrow and slightly offset from the lateral margin of the bone. A low, distally slightly broadening ridge is present on the shelf between this condyle and the medial side of the shaft. The intercondylar groove is deep and broad.

PHYLOGENETIC ANALYSIS

The phylogenetic position of *Tehuelchesaurus* was tested in a cladistic analysis based on a data matrix of 249 characters and 45 taxa (see Appendix). Characters and taxa were mostly based on Carballido *et al.* (2011), which, subsequently, was based on an expansion of the dataset of Wilson (2002). Given that the two previous hypotheses on the phylogenetic placement of *Tehuelchesaurus* suggested either a close affinity with *Omeisaurus* (Rich *et al.*, 1999; Alifanov & Averianov, 2003; Upchurch *et al.*, 2004) or with Titanosauriformes (Rauhut *et al.*, 2005), the taxon sampling of the analysis was focused on advanced basal eusauropods and basal neosauropods, especially basal macronarians. Codings of the Chinese basal eusauropod taxa *Omeisaurus* and *Mamenchisaurus* were modified according to the newer literature (Tang *et al.*, 2001; Ouyang & Ye, 2002) and own observations on specimens in the IVPP, the CUM and the ZDM (by O.W.M.R.), and a few minor changes have been made in the codings of other taxa (see Appendix).

To better capture character polarity at the base of Eusauropoda, we added the non-sauropodan sauropodomorph *Plateosaurus* as a new outgroup (based mainly on our own observations on multiple specimens) and the basal, non-eusauropodan sauropod *Tazoudasaurus* (Allain & Aquesbi, 2008).

Because they were both of biogeographical and phylogenetic interest, we furthermore added *Tendaguria*, a taxon of uncertain systematic position, and the probable basal macronarian taxa *Janenschia* from the Late Jurassic of Tendaguru, Tanzania, to the matrix. In the most recent revision of *Janenschia* by Bonaparte, Heinrich & Wild (2000), these authors restricted this taxon to include only limb material, as the holotype is a partial hindlimb. Caudal vertebrae referred to *Janenschia* by Janensch (1929) were excluded from the genus by Bonaparte *et al.* (2000) due to lack of overlap with the type material. However, some caudal vertebrae were found in local-

ity P, which otherwise only included limb material that can be referred to *Janenschia* with certainty (Janensch, 1929; Heinrich, 1999; Bonaparte *et al.*, 2000), but were apparently lost in World War II. As the caudal vertebrae of *Janenschia* are distinct from those of all other Tendaguru sauropods, we accept Janensch's (1929) referral of caudal vertebrae from other localities to the same taxon and included information from these vertebrae in the cladistic analysis.

Phylogenetically uninformative characters were excluded from the matrix. Most characters were binary and multistate characters 66, 67, 83, 87, 98, 142, and 170 were treated as ordered. The complete data matrix is included in the Appendix, and an electronic version of the original Nexus file is available from the authors upon request.

An equally weighted parsimony analysis was performed using TNT v. 1.1 (Goloboff, Farris & Nixon, 2008a, b). Most-parsimonious trees (MPTs) were obtained performing a heuristic tree search consisting of 1000 replicates of Wagner trees (with random addition sequences) followed by TBR branch swapping (saving ten trees per replicate); the best score was reached in 80 of the 1000 replicates. The first 90 MPTs were subjected to a final round of TBR in order to find all the most-parsimonious trees. This analysis found 142 MPTs of 649 steps (CI = 0.41, RI = 0.67, RC = 0.28). The strict consensus tree of the most parsimonious trees is shown in Figure 21A. In the strict consensus tree, *Tehuelchesaurus* appears in a large polytomy at the base of Neosauropoda, which includes a plethora of close neosauropod outgroups and basal neosauropods, as well as two clades that correspond to the Diplodocoidea and Somphospondyli.

This large polytomy is caused by the alternative positions that three taxa have in the most-parsimonious topologies. Removal of these taxa from the MPTs posterior to the analysis resulted in a well-resolved reduced consensus tree (Fig. 21B). These taxa were *Tendaguria*, *Malarguesaurus*, and *Venenosaurus*. *Tendaguria* was found to be either a sister taxon to *Mamenchisaurus* or a basal, non-titanosauriform macronarian (in varying positions), whereas the other two had variable positions within Macronaria.

When the alternative positions for these taxa are ignored (Fig. 21B), *Tehuelchesaurus* was thus found to be a basal macronarian more derived than *Europasaurus*, but outside a clade formed by *Tastavinisaurus* and *Janenschia* and higher camarasauromorphs. It forms a clade with *Galvesaurus*.

The monophyly of *Tehuelchesaurus* and *Galvesaurus* is supported by two unambiguous synapomorphies. First, the neural spines of the dorsal vertebrae of *Tehuelchesaurus* and *Galvesaurus* are unusual for a macronarian sauropod. The neural spines of these
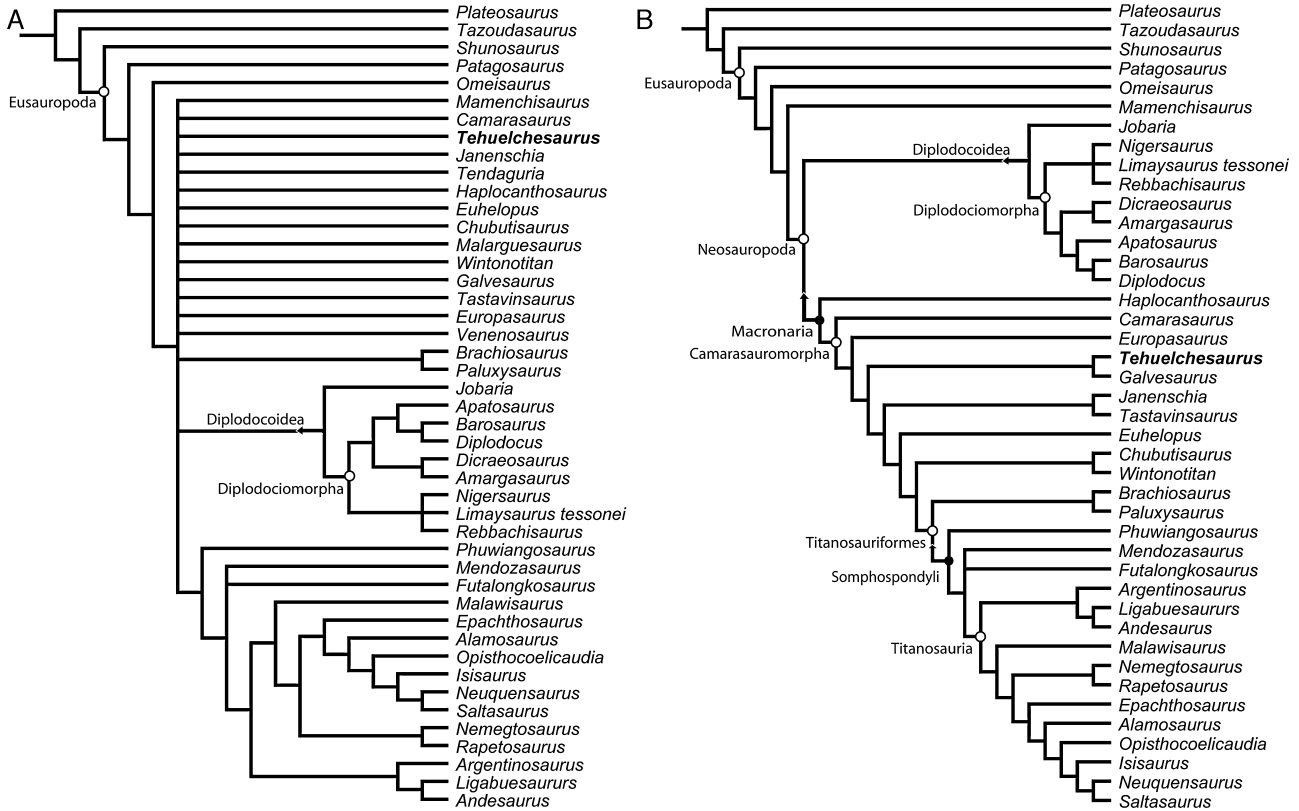
Figure 21. A, strict consensus of MPTs, showing the phylogenetic position of *Tehuelchesaurus*. B, reduced consensus tree of the MPTs after the exclusion of *Malarguesaurus*, *Tendaguria*, and *Venenosaurus*. Stem based groups are symbolized by arrows and node-based groups with open circles. Node definitions: Eusauropoda (Upchurch *et al.*, 2004); Neosauropoda (Wilson & Sereno, 1998); Diplodocoidea (Wilson & Sereno, 1998); Macronaria (Wilson & Sereno, 1998); Camarasauromorpha (Upchurch *et al.*, 2004); Titanosauriformes (Wilson & Sereno, 1998); Somphospondyli (Sereno, 2005); Titanosauria (Wilson & Upchurch, 2003).

taxa are lateromedially narrow and anteroposteriorly elongated, resembling the spines of non-sauropodan sauropodomorphs with respect to their proportions (see below). The second character shared by the two taxa is the undivided SPOL. As optimized in the present phylogeny, such an undivided SPOL was convergently acquired in somphospondyls.

The position of *Tehuelchesaurus* plus *Galvesaurus* as camarasauromorphs that are more derived than *Europasaurus* is supported by the following synapomorphic characters that are present in the former taxon: plank-like anterior dorsal ribs, and a lateral bulge on the proximal shaft of the femur. A further apomorphy at this node might be the presence of a pneumatic foramen or deep depression in the infradiapophyseal fossa, although the distribution of this character at the base of the Camarasauromorpha is ambiguous. Camarasauromorph synapomorphies of *Tehuelchesaurus* include an acromion process of the scapula that lies close to the midpoint of the scapular

body and a puboischial contact that reaches one-half of the length of the pubis. A possible synapomorphy of macronarians present in *Tehuelchesaurus* is the presence of posteriorly acute pleurocoels in the anterior dorsal vertebrae. This character is generally present in the clade containing *Euhelopus* and more derived camarasauromorphs, but its distribution among basal macronarians is problematic, as it is present in *Haplocanthosaurus* and *Europasaurus*, but absent in *Camarasaurus*, *Galvesaurus*, and *Tastavinisaurus*. A complete list of synapomorphies for all nodes is given in the Appendix.

Branch support of clades was evaluated using bootstrap and Bremer support. In an analysis of the complete data set, the very fragmentary and unstable taxa *Venenosaurus*, *Tendaguria*, and *Malarguesaurus* led to lack of support for the vast majority of clades, especially on the macronarian branch of the tree. The only clade within Macronaria holding up in the bootstrap analysis are the Saltasaurini, which have, however, only 59% support. Only Eusauropoda and

the Diplodocidae have a support over 80% in this bootstrap analysis.

Since the three very fragmentary taxa mentioned above may mask the true support for positioning *Tehuelchesaurus* within Macronaria, we tested a pruned matrix, removing these taxa from the analysis. The strict consensus tree of the nine most-parsimonious trees recovered from the pruned analysis was the same as the reduced consensus tree found in the analysis of the complete data matrix. Bootstrap analysis of the pruned matrix found significantly higher support for several clades, including eusauropods (99%), neosauropods (88%) and most clades within Diplodocoidea. However, support for the inter-relationships of all basal macronarians remained below 50%. Nevertheless, Bremer support for Macronaria is 2 for the pruned matrix, and the same value applies for the clade of *Camarasaurus* and more derived macronarians, and the *Tehuelchesaurus/Galvesaurus* clade and more derived camarasauromorphs. Furthermore, the clade formed by *Europasaurus* and more derived camarasauromorphs (which includes *Tehuelchesaurus*) has Bremer support of 3, indicating that at least the position of *Tehuelchesaurus* within Macronaria is moderately well supported (see also below).

DISCUSSION

Rich *et al*. (1999) classified *Tehuelchesaurus* as a cetiosaurid *sensu* McIntosh (1990), a paraphyletic assemblage of basal eusauropods (see Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002; Upchurch *et al*., 2004). Within 'cetiosaurids', they suggested a close relationship with *Omeisaurus*, a non-neosauropodan eusauropod from the Middle Jurassic of China. On the basis of this supposed relationship, and the perceived Middle Jurassic age of *Tehuelchesaurus*, Rich *et al*. (1999: 81) argued for a global exchange of dinosaur faunas in the Middle Jurassic, and thus rejected Russell's (1995) idea of a separation of Central Asian faunas from the rest of Pangea during the late Middle Jurassic. However, neither the 'cetiosaurid' (i.e. basal eusauropod) position nor the close affinities with *Omeisaurus* was supported with a formal phylogenetic analysis or by a set of specific derived characters by Rich *et al*. (1999). Wilson (2002) did not include *Tehuelchesaurus* in his cladistic analysis, but suggested *Tehuelchesaurus* was part of the group formed by *Patagosaurus* and more derived sauropods on the basis of a set of nested synapomorphies for basal sauropods resulting from his analysis, although only one of these synapomorphies (the presence of pleurocoels in the presacral vertebrae) was cited. Alifanov & Averianov (2003) used the matrix published by Upchurch (1998) with the addition of some taxa, including *Tehuelchesaurus*, to analyse the phylogenetic position of *Ferganasaurus*. On the basis of the published description, their analysis retrieved this taxon as part of the sister group to *Omeisaurus* [i.e. *Omeisaurus* + (*Tehuelchesaurus* + *Mamenchisaurus* + *Euhelopus*)], a similar position to that subsequently obtained by Upchurch *et al*. (2004). Other authors, however, have argued that *Tehuelchesaurus* is a more derived eusauropod, being nested within camarasauromorph neosauropods (Rauhut, 2002; Salgado & Bonaparte, 2007). This view was recently supported in a phylogenetic analysis that depicted *Tehuelchesaurus* in a polytomy with Titanosauriformes (Rauhut *et al*., 2005), although the main objective of this analysis was a resolution of the relationships of basal diplodocoids and therefore it had a limited taxon and character sampling of basal camarasauromorphs or non-neosauropod taxa. As mentioned above, the phylogenetic analysis presented here, with an expanded taxonomic and character sampling in both non-neosauropod eusauropods and macronarian neosauropods, recovered *Tehuelchesaurus* as a non-titanosauriform camarasauromorph (see Phylogenetic Analysis).

TESTING ALTERNATIVE POSITIONS FOR *TEHUELCHESAURUS*

Alternative positions for the phylogenetic position of *Tehuelchesaurus* were tested by moving the taxon within the reduced consensus tree in MacClace 4.06 (Maddison & Maddison, 2003). First, a position of *Tehuelchesaurus* as the sister taxon of *Omeisaurus*, as proposed by Rich *et al*. (1999), and retrieved in the phylogenetic analysis of Alifanov & Averianov (2003) and Upchurch *et al*. (2004), results in a tree that is nine steps longer than the MPTs, representing a considerably suboptimal topology. When this grouping (*Tehuelchesaurus* + *Omeisaurus*) is forced to be mono-phyletic, a single synapomorphy is retrieved for this clade. Character 224 (equally developed distal femoral condyles) is shared between these two taxa and represents a unique reversal of a eusauropod synapomorphy. Other characters noted by Rich *et al*. (1999) are interpreted either as plesiomorphies or synapomorphies within a larger clade under the present tree topology, such as the presence of opisthocoelous posterior dorsal vertebrae. The latter character is very conservative among camarasauromorphs and is recovered as a synapomorphy of the clade containing *Omeisaurus*, *Mamenchisaurus* and neo-sauropods, as it is present in the latter two taxa, and also in the basal macronarian *Haplocanthosaurus*, which has a weakly developed convexity in the anterior face of posterior dorsal centra (Hatcher, 1903: pl. II).

Moving *Tehuelchesaurus* into more or less derived positions within camarasauromorphs requires fewer steps. Only one additional step is needed to place this taxon in a position more derived than *Galvesaurus*, thus being more closely related to the *Janenschia/Tastavinsaurus* clade and more derived camarasauromorphs. Such a placement would be supported by the shared derived character of posterior dorsal vertebrae that are longer than wide, and, possibly, by the lateral bulge of the femoral shaft, as the latter character is unknown in *Galvesaurus*.

Placing *Tehuelchesaurus* as less derived than *Galvesaurus* results in a tree that is two steps longer than the MPTs. However, such a placement would only be supported by ambiguous synapomorphies of *Galvesaurus* with more derived camarasauromorphs, of which the character state is unknown in *Tehuelchesaurus*, such as ventrally transversely concave and extremely elongate cervical centra that are at least four times as long as they are high posteriorly and distoplatyan anterior caudal vertebrae. A further possible synapomorphy of *Galvesaurus* with more derived camarasauromorphs might be the presence of pneumatopores in the dorsal ribs. This character is also present in titanosauriforms, *Euhelopus* and *Chubutisaurus*, but absent in *Tastavinsaurus*.

Moving *Tehuelchesaurus* into a position more derived than the *Janenschia/Tastavinsaurus* clade also requires two additional steps. This placement would be supported by the tapering posterior margins of the anterior dorsal pleurocoels (which would here be optimized as synapomorphies at this node, being convergently developed in *Haplocanthosaurus* and *Europasaurus*).

Other positions within basal camarasauromorphs (in any position within the *Janenschia/Tastavinsaurus* clade, as sister taxon to *Europasaurus*, more basal than *Europasaurus*, and as sister taxon to *Camarasaurus*) and as a macronarian outside Camarasauromorpha, but more derived than *Haplocanthosaurus*, require three additional steps. Placing *Tehuelchesaurus* as sister taxon of *Haplocanthosaurus* results in a suboptimal tree four steps longer than the MPTs, and as the most basal macronarian needs even five additional steps. Even more steps are required to place this taxon in the Titanosauriformes (seven additional steps as a basal somphospondyl and eight additional steps as a basal brachiosaurid).

Any position outside Macronaria also results in considerably suboptimal tree lengths. Five additional steps are needed to make *Tehuelchesaurus* the most basal diplodocoid, but any position within higher diplodocoids results in trees that are at least ten steps longer than the MPTs. Likewise, placing *Tehuelchesaurus* outside Neosauropoda requires six additional

steps, and any placement among basal, non-neosauropodan taxa results in trees at least nine steps longer than the MPTs. Thus, the possibility of a Jurassic Patagonian clade of sauropods, including *Patagosaurus* and *Tehuelchesaurus*, can also be rejected, as it requires 12 additional steps.

To further test the robustness of the phylogenetic position of *Tehuelchesaurus* recovered here, a Templeton test for several of the alternative topologies was conducted. The positions tested were for *Tehuelchesaurus* as sister taxon to *Omeisaurus*, as originally proposed by Rich *et al*. (1999) and found by Alifanov & Averianov (2003) and Upchurch *et al*. (2004), for *Tehuelchesaurus* as immediate outgroup to neosauropods, as a non-camarasauromorph macronarian, and as a basal titanosauriform. The test was performed following the protocol recently summarized in Wilson (2002).

Slightly different values were obtained depending on the position of the problematic Tendaguru sauropod *Tendaguria* (see above). For all the positions tested the smaller *P*-values were always recovered when *Tendaguria* was placed within neosauropod dinosaurs. With *Tendaguria* in this position, the placement of *Tehuelchesaurus* as sister group to *Omeisaurus* can be rejected by the data with 95% confidence ($P = 0.029$, and thus < 0.05). Nevertheless, when *Tehuelchesaurus* is forced to be the sister group to Noesauropoda ($P = 0.057$) or a basal titanosauriform ($P = 0.052$) the *P*-values are close to the significance cut-off level (i.e. 0.05), so these positions seem very unlikely as well. In contrast, the only slightly suboptimal topologies retrieved when *Tehuelchesaurus* is placed as a non-camarasauromorph macronarian result in *P*-values of the Templeton test that are far from being significant ($P > 0.1$). If *Tendaguria* is placed as a non-neosauropod, only the *P*-value for a sister-group relationship with *Omeisaurus* is close to the cut-off level ($P = 0.059$).

In summary, the analysis presented here provides strong evidence against a placement of *Tehuelchesaurus* amongst basal eusauropods ('cetiosaurids' in the traditional sense), as was originally suggested by Rich *et al*. (1999), and later recovered by Alifanov & Averianov (2003) and Upchurch *et al*. (2004) in their analyses. In contrast, the results indicate that *Tehuelchesaurus* is a basal, non-titanosauriform macronarian. However, placement of taxa within basal macronarians is often poorly supported, indicating that there is still ample scope for research in this part of the phylogeny.

RELATIONSHIPS OF BASAL MACRONARIANS

Although the general topology of the reduced consensus tree (Fig. 21) is similar to that obtained in

other analyses (e.g. Wilson, 2002; Upchurch *et al.*, 2004), including recent publications (Barco, 2009; Wilson & Upchurch, 2009; Carballido *et al.*, 2011), there are differences in the position of some macronarian taxa. Some of these differences are most probably due to the fact that more basal macronarians were included here than in the vast majority of other analyses. Although a complete resolution of the problem of neosauropod origins and basal macronarian interrelationships is certainly beyond the scope of this paper, some comments are offered here.

Several taxa at the base of Neosauropoda have proved to be problematic in previous analyses. One of these taxa is *Haplocanthosaurus* from the Late Jurassic Morrison Formation of North America. This taxon was recovered as a basal diplodocoid by Calvo & Salgado (1995) and Wilson (2002), as a derived, non-neosauropodan eusauropod by Upchurch (1998) and Rauhut *et al.* (2005), as the most basal macronarian by Wilson & Sereno (1998) and Wilson & Upchurch (2009), and as a basal macronarian more derived than *Camarasaurus* by Upchurch *et al.* (2004). The current phylogenetic hypothesis supports the position of this taxon as the most basal macronarian, based on three unambiguous synapomorphies. These are the ventrally flat or transversely convex cervical vertebrae, the presence of a triangular aliform process on the neural spines of the dorsal vertebrae, and the absence of a proximal crus bridging the hemal canal in the chevrons. This taxon remains an interesting and potentially crucial taxon for our understanding of the origin of neosauropods, and a thorough revision of the available materials is needed.

A similarly interesting and problematic taxon at the base of Neosauropoda is *Jobaria* from the Middle Jurassic (Rauhut & López-Arbarello, 2009) or Early Cretaceous (Sereno *et al.*, 1999) of Niger. This taxon was recovered as a derived eusauropod outside Neosauropoda by Wilson (2002), Rauhut *et al.* (2005) and Wilson & Upchurch (2009), but as a basal macronarian by Upchurch *et al.* (2004; although see Wilson & Upchurch, 2009). Here it is recovered in a novel position as the most basal diplodocoid, thus mimicking the history of phylogenetic placements of *Haplocanthosaurus*. However, this placement is only supported by two unambiguous synapomorphies (see Appendix), the presence of a posterior centroparapophyseal lamina (also present in several more derived macronarians) and the absence of opisthocoelous posterior dorsal vertebrae (interpreted as a reversal to the plesiomorphic condition under the current tree topology). The latter character depends on the monophyly or non-monophyly of the clade consisting of *Omeisaurus* + *Mamenchisaurus* (Mamenchisauridae of several authors). Although three additional steps

are needed to make this group monophyletic, it must be noted that a test of the taxonomic composition of the Mamenchisauridae was not an objective of this work, and thus several potential synapomorphies of these animals might not have been included. Indeed, under the constraint of a monophyletic Mamenchisauridae, consisting of *Mamenchisaurus* and *Omeisaurus*, *Jobaria* falls outside Neosauropoda. Furthermore, other taxa that might be of importance to the question of the systematic position of *Jobaria*, such as *Atlasaurus* and *Abrosaurus* (Upchurch *et al.*, 2004), have not been included in the current analysis, as the published accounts of these materials are insufficient for coding characters and we have not seen the fossils ourselves.

The phylogenetic relationships among camarasauromorphs basal to the *Chubutisaurus/Wintonotitan* clade are moderately robust. Interestingly, creating a monophyletic Late Jurassic Gondwanan clade of *Tehuelchesaurus* and *Janenschia* and a monophyletic Iberian clade of *Tastavinsaurus* and *Galvesaurus* requires at least three additional steps, if all of these taxa are included in a monophyletic clade, or at least four steps, if they are treated as sequentuailly closer outgroups to Titanosauriformes.

The Asian taxon *Euhelopus*, regarded as a basal somphospondyl in recent analyses (Wilson, 2002; Wilson & Upchurch, 2009), is here depicted as a non-titanosauriform. A similar position was also obtained by Canudo, Royo-Torres & Cuenca-Bescos (2008) after expanding the character and taxon sampling of Wilson's (2002) matrix. Placement of *Euhelopus* is based on several plesiomorphic characters with respect to other titanosauriforms, such as the broad, chisel-like teeth, the flattened ventral surface of the dorsal vertebral centra, the only moderately posteroventrally directed postzygapophyses in the anterior to mid-dorsal vertebrae, the short posterior dorsal vertebrae, the relatively short pubic peduncle of the ischium, and the only moderately anteroposteriorly flattened femoral shaft. With the inclusion of more basal camarasauromorphs, some of the characters originally identified as titanosauriform or somphospondyl synapomorphies (see Wilson, 2002: 268) have been found to be more widely distributed among basal camarasauromorphs (e.g. camellate presacral vertebrae; strongly elongate cervical centra; pneumatic dorsal ribs; plank-like anterior dorsal ribs; angular proximolateral corner of the humerus; lateral bulge on the femur). However, several other possible synapomorphies of *Euhelopus* and Somphospondyli (or somphospondyls more derived than *Phuwiangosaurus*, as argued by Wilson & Upchurch, 2009) remain (six sacral vertebrae, scapular glenoid facet bevelled medially), and only two additional steps are needed to move this taxon within Somphospondyli.

In summary, although most recent phylogenetic analyses show a general agreement about the basal dichotomy within the Neosauropoda and most of the taxa that are included in either of the two branches, additional research is needed in several areas of the tree. One important question is the origin of neosauropods. Here, one of the problems might be the lack of detailed studies of several relevant taxa just outside or at the base of this clade (*Haplocanthosaurus*, *Jobaria*, *Atlasaurus*, *Ferganasaurus*, *Abrosaurus*), but also the rather great uncertainty of the relationships of basal eusauropods. This is especially the case for several Chinese taxa that might be close to neosauropods, such as *Mamenchisaurus* and *Omeisaurus*, even the taxonomy of which remains largely uncertain (see Upchurch *et al*., 2004).

Another area of uncertainty are the relationships of basal camarasauromorphs and thus the origin of the Titanosauriformes. The current study demonstrates that this part of the tree is very sensitive to the inclusion or exclusion of additional taxa, but one of the problems here might be the fragmentary nature of many relevant taxa (e.g. *Venenosaurus*, *Tendaguria*, *Pleurocoelus*, *Wintonotitan*). Again more rigorous and detailed studies of important taxa in this part of the tree might also help to obtain more robust hypotheses.

AUTAPOMORPHIC FEATURES OF *TEHUELCHESAURUS*

As noted in the description, *Tehuelchesaurus* shows several characters that are unique to this taxon. Most notably, the lamination of the dorsal vertebrae shows a series of accessory laminae. Two accessory laminae are located within the infradipapophyseal fossa, and a third lamina projects laterally from the lateral surface of the single TPOL. An additional unique autapomorphic feature of this taxon is that the greatest height of the acromion process of the scapula over the glenoid is almost four times the minimal height of the shaft. Furthermore, the anteroposteriorly expanded distal end of the humerus most probably represents another autapomorphy of *Tehuelchesaurus*, as noted by Upchurch *et al*. (2004). The notable deformation of other elements of this specimen (most notably the femora) leaves a slight possibility that this might be due to deformation, although the humerus seems otherwise undistorted.

Additionally, five characters were optimized as unambiguous autapomorphies and two as ambiguous autapomorphies of *Tehuelchesaurus* within the context of this analysis, but are not unique to this taxon. Two of the five unambiguous characters concern the morphology of the neural spine (characters 98 and 111) and the other three the neural arch lamination of the dorsal vertebrae of this taxon (char-

acters 91, 104, and 119). The ambiguous characters, for which the state is unknown in *Galvesaurus*, concern the morphology of the coracoid (character 177) and the femur (character 224). The distribution of these characters is discussed here.

The neural spines of the dorsal vertebrae of *Tehuelchesaurus* are unusual for a macronarian sauropod. The most striking character of this structure is its general proportions. In contrast to the vast majority of eusauropods, but resembling the spines of non-sauropodan sauropodomorphs and some of the most basal sauropods (Allain & Aquesbi, 2008), the spine is longer anteroposteriorly than broad transversely. Thus, in respect to its general proportions, the shape of the neural spine may be interpreted as a reversal to the ancestral sauropodomorph condition, although it should be noted that the spine shows these proportions despite having the typical spinal laminae of eusauropod dorsal neural spines. Within eusauropods, such proportions are only known in *Jobaria* (Sereno *et al*., 1999) and *Galvesaurus* (Barco, 2009), which also show a very similar pattern of lateral laminae on the neural spines. However, whereas the situation in *Jobaria* is here interpreted as a convergent development, the narrow dorsal neural spines are one of the shared derived characters that unite *Tehuelchesaurus* and *Galvesaurus* within the Macronaria. An autapomorphy of *Tehuelchesaurus* within camarasauromorphs is the absence of a postspinal lamina. The presence of this lamina is optimized as a synapomorphy of *Europasaurus* plus more derived camarasauromorphs, which is convergently present in diplodocoids under the current tree topology. Within higher camarasauromorphs it is only absent in *Phuwiangosaurus*. Likewise, the dorsal vertebrae of macronarians are characterized by the presence of a triangular aliform process, a lateral expansion of the neural spine in its distal part. This character is very strongly developed in *Galvesaurus* (Barco, 2009), but there is no sign of such an expansion in the best-preserved neural spine of *Tehuelchesaurus*. Although this spine is slightly incomplete distally, it seems unlikely that at least a well-developed process was present in this taxon, as the expansion of this process begins in an area of the neural spine in which the lateral laminae are still distinct in other taxa in which this structure is present (Janensch, 1950; Barco, 2009), whereas the laminae are already fused distally in the best preserved spine of *Tehuelchesaurus*, but no expansion is present. This feature is convergently lost in other macronarian taxa, such as *Isisaurus* and *Phuwiangosaurus*.

As mentioned above, the lamination of the neural arch in the dorsal vertebrae of *Tehuelchesaurus* also shows a unique combination of characters. First, this

taxon has a very well-developed single lamina above the neural canal that supports the hyposphene from below (a single TPOL). This single lamina, which is often present in posterior cervical vertebrae, is usually lost when the hyposphene–hypantrum system first appears in anterior dorsal vertebrae (Wilson, 2002; Apesteguía, 2005) but persists in basal forms (e.g. *Patagosaurus*, *Tazoudasaurus*) and in diplodocids. Thus, its presence in *Tehuelchesaurus* is interpreted as a convergence with the single TPOL of these taxa.

Second, the single lamina that links the prezygapophysis with the parapophysis (the prezygoparapophyseal lamina) seems to be absent in at least the middle and posterior dorsal vertebrae in *Tehuelchesaurus*. The presence of this lamina in middle and posterior dorsal vertebrae appears early in the evolution of sauropods, representing a synapomorphy of Gravisauria (see Allain & Aquesbi, 2008). Close inspection of the anterior part of the neural arch of *Tehuelchesaurus* indicates that the situation in this taxon rather represents a strong modification of this lamina than a reversal to the ancestral condition. This lamina is still present in the first preserved dorsal, but becomes 'inflated' in more posterior elements so that it fuses with the paradiapophyseal lamina and forms a broad, anterolaterodorsally directed surface. Thus, this unusual morphology can be understood as a true autapomorphy of *Tehuelchesaurus*.

Finally, the ventrally forked posterior centrodiapophyseal lamina, regarded as a titanosaurian synapomorphy by Salgado *et al*. (1997), is optimized in our analysis as convergently acquired in *Tehuelchesaurus*. However, as noted in the description, the anterior branch of the ventrally expanded PCDL of *Tehuelchesaurus* seems to be an anterior continuation of the CPOL. If this interpretation is correct, this would underline the hypothesis that the ventrally forked PCDL of this taxon is not homologous to the APCDL present in Titanosauria (Salgado *et al*., 1997), as indicated by the phylogenetic analysis. It might be noted that a similar orientation of laminae is present in some other sauropods (e.g. of the PCPL and PCDL in *Neuquensaurus*; Salgado *et al*., 2005), but the (probably biomechanical) reasons for the orientation of vertebral laminae in sauropods require further analyses.

Tehuelchesaurus shows a strongly developed infraglenoid lip on the coracoid, which is a character otherwise only found in derived titanosaurs (*Opisthocoelocaudia* and more derived taxa) amongst sauropods. In other sauropods, there is usually a small concave area in the posterior margin of the coracoid between the glenoid and the posteroventral corner of the bone, but no distinct process is present. This character is unknown for *Galvesaurus*. The same is true for the last potential autapomorphy of *Tehuelchesaurus*, the equally developed distal femoral condyles. This is a character found in *Plateosaurus* and several basal sauropods.

EVOLUTION OF VERTEBRAL PNEUMATICITY

The new phylogenetic hypothesis presented here, with an extended taxon sampling of basal macronarians, sheds some light on the evolution of vertebral pneumaticity in this group.

Despite the large amount of missing data in the character describing the pneumatization of presacral vertebrae, this feature seems to have a clear phylogenetic signal, even when the intermediate state (i.e. camerate vertebrae *sensu* Wedel *et al*., 2000) is added. Wedel (2003a, b) analysed the number of independent acquisitions of a camerate system based on the phylogenies of Wilson & Sereno (1998) and Upchurch (1998) and inferred that this feature had appeared twice (in Chinese sauropods and Neosauropoda) or three times (in Chinese sauropods, diplodocoids and macronarians) in the evolutionary history of Eusauropoda. The reduced consensus tree obtained in this analysis, in contrast, shows a simpler character optimization with a single acquisition of a camerate system in the node formed by sauropods more derived than *Barapasaurus*. The loss of pneumatic air spaces seems to be rare in the evolution of sauropods, and only *Haplocanthosaurus* shows a reversal to a procamerate system (*sensu* Wedel, 2003a, b) under the phylogenetic hypothesis presented here. In the present analysis this taxon was scored as 0 (no pneumatized vertebrae), although this taxon could also be scored with an uncertain scoring between states 0 (acamerate) and 1 (camerate) because of the intermediate development of its pneumatic structures. As noted by Wedel (2003a, b) the pneumatic structures become more complex in more derived macronarians. The presence of camellae has traditionally been linked with somphospondyl titanosauriforms (i.e. titanosauriforms more closely related to *Saltasaurus* than to *Brachiosaurus*). The basal position of *Euhelopus* retrieved here as well as that of *Chubutisaurus* and *Wintonotitan* shows that this system of small air spaces has a broader distribution and seems to have evolved in non-titanosauriform camarasauromorphs. In the most-parsimonious topologies obtained here the presence of camellae unambiguously diagnoses the clade formed by *Euhelopus* and more derived camarasauromorphs. Nevertheless, the camellate internal structure of the cervical vertebrae of *Galvesaurus* (with camerate dorsal vertebrae; Barco, Canudo & Cuenca-Bescos, 2006; Barco, 2009) indicates that this more derived system of pneumaticity
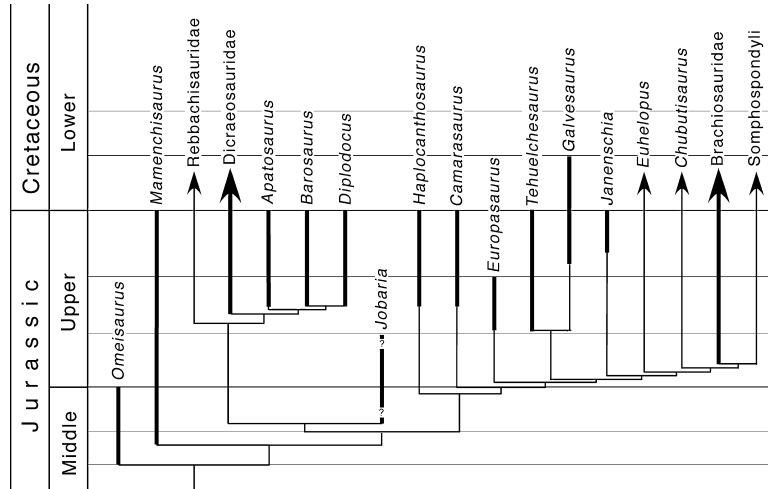
Figure 22. Simplified reduced consensus tree, showing the minimal implied stratigraphic gaps in the basal neosauropod radiation as predicted by the topology presented here. The stratigraphic position of *Jobaria* is based on Rauhut & López-Arbarello (2009).

probably started to appear earlier in camarasauromorphs, and its appearance was more gradual, probably beginning at the neck. The camellate condition is inferred to have independently evolved in *Mamenchisaurus*, and no reversal from a camellate to a camerate structure is observed among camarasauromorphs with camellate vertebrae.

IMPLICATIONS FOR THE EVOLUTION AND BIOGEOGRAPHY OF BASAL MACRONARIANS

Although some of the phylogenetic results seem to be moderately well supported (e.g. the macronarian affinities of *Tehuelchesaurus*), it must be noted that relationships at the base of Neosauropoda and within basal macronarians are still rather unstable, with bootstrap and Bremer support values being low for most nodes (see above). This result indicates the lack of a robust scheme for the relationships of this group within the context of this dataset. Therefore, evolutionary scenarios inferred for this group should be seen with caution. However, some observations and hypotheses on the pattern and timing of the neosauropod radiation (Fig. 22) on the basis of the available evidence (the results obtained here and from other analyses; e.g. Alifanov & Averianov, 2003; Upchurch *et al.*, 2004) will be offered.

First, with the reinterpretation of *Tehuelchesaurus* as a Late Jurassic macronarian sauropod, there is no evidence for a close biogeographical relationship between sauropod faunas in Patagonia and China in the Middle Jurassic, as proposed by Rich *et al.* (1999). On the contrary, the sauropods known from the Middle Jurassic Cañadón Asfalto Formation of

Patagonia represent rather basal forms, which were interpreted as a possible relictual fauna of an Early Jurassic sauropod radiation by Rauhut & López-Arbarello (2009), whereas close neosauropod outgroups or the oldest neosauropods are known from the late Middle Jurassic of northern Gondwana (*Atlasaurus*, probably *Jobaria*; Monbaron, Russell & Taquet, 1999; Sereno *et al.*, 1999; Rauhut & López-Arbarello, 2009), central Asia (*Ferganasaurus*; Alifanov & Averianov, 2003), and, probably, eastern Asia (*Bellusaurus*, *Abrosaurus*; Upchurch *et al.*, 2004). This might indicate a Middle Jurassic, central Pangean origin of the Neosauropoda, with subsequent dispersal of this group to southern Gondwana and, possibly, North America during Pangean times, in the latest Middle to earliest Late Jurassic.

However, it must be noted that this scenario is largely based on negative evidence. Middle Jurassic terrestrial archosaurs from North America are virtually unknown (Rauhut & López-Arbarello, 2008), so nothing can be said about pre-Late Jurassic sauropod faunas of this continent. Furthermore, there is increasing evidence that the Cañadón Asfalto Formation is older than the currently accepted Callovian age (Salani, 2007; Volkheimer *et al.*, 2008), so it is currently uncertain what its sauropod fauna might be able to tell us about late Middle Jurassic sauropod distribution and biogeography. Important materials from the Middle Jurassic of more southern Gondwanan areas, such as Madagascar (*Lapparentosaurus*; Bonaparte, 1986b) and Australia (*Rhoetosaurus*; Longman, 1926, 1927), have not been studied in detail yet. New discoveries and more detailed studies of Middle Jurassic sauropods are needed to elucidate
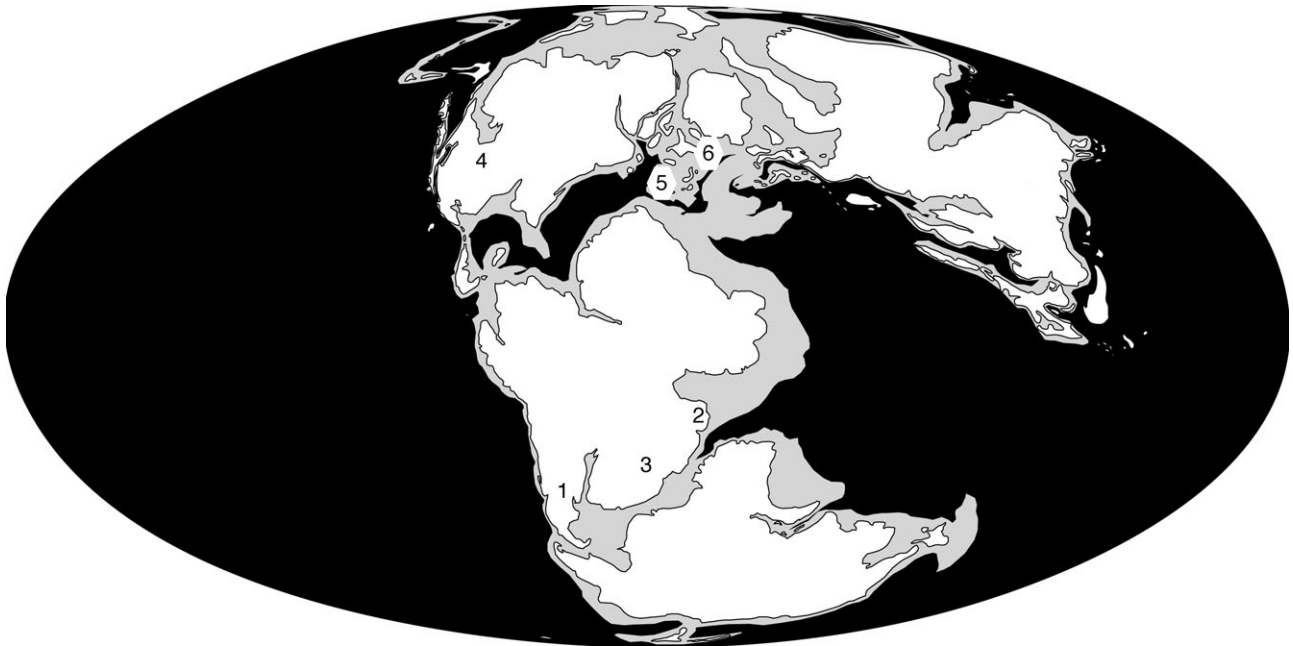
Figure 23. Occurrences of macronarians in the Late Jurassic. 1, Cañadón Calcáreo Formation (Tithonian–?Valangianian); *Tehuelchesaurus benitezii*, unidentified brachiosaurid. 2, Tendaguru Formation (Oxfordian–Tithonian); *Giraffatitan brancai, Janenschia robusta*. 3, Kadzi Formation (Late Jurassic); '*Brachiosaurus*' sp. (probably *Giraffatitan*), *Janenschia* sp., ?*Camarasaurus* sp. 4, Morrison Formation (Kimmeridgian–Tithonian); *Haplocanthosaurus* spp., *Camarasaurus* spp., *Brachiosaurus altithorax*. 5, Sobral Unit (Tithonian); *Lusotitan atalaiensis*; Villar de Arzobispo Formation (Tithonian-Berriasian); *Galvesaurus herreroi*. 6, unnamed carbonate unit at Oker (Kimmeridgian); *Europasaurus holgeri*; unnamed unit, Damparis (Oxfordian); 'French *Bothriospondylus*' (probable brachiosaurid).

the biogeographical history of the origin of the Neosauropoda.

Nevertheless, the identification of *Tehuelchesaurus* as a Late Jurassic macronarian underlines the wide distribution and taxonomic diversity of this clade already at that time (Fig. 23). In the Late Jurassic, macronarians are known from North America (*Camarasaurus, Brachiosaurus*; Foster, 2003; Taylor, 2009), Europe (*Europasaurus, Lusotitan, Galvesaurus*, French '*Bothriospondylus*'; Antunes & Mateus, 2003; Barco *et al.*, 2005; Sander *et al.*, 2006; Mannion, 2010), Africa (*Janenschia, Giraffatitan*, probably *Tendaguria*; Janensch, 1929; Bonaparte *et al.*, 2000; Taylor, 2009), and South America (*Tehuelchesaurus*, unnamed brachiosaur; Rauhut, 2006a; present study). The same is true for diplodocoid neosauropods, which have also been recorded from North America (e.g. *Diplodocus, Barosaurus, Apatosaurus, Suuwassea*; Foster, 2003; Harris, 2006), Europe (*Dinheirosaurus*; Bonaparte & Mateus, 1999), Africa (*Dicraeosaurus, Tornieria, Australodocus*; Janensch, 1929; Remes, 2006, 2007), and South America (*Brachytrachelopan*; Rauhut *et al.*, 2005). In contrast, if an Early Cretaceous age is accepted for *Euhelopus* (Wilson & Upchurch, 2009), neosauropods are conspicuously asbsent from the Late Jurassic of eastern Asia

(Weishampel *et al.*, 2004). Although we agree with Wilson & Upchurch (2009) that neosauropods probably diversified prior to the break-up of Pangea at the Middle–Late Jurassic boundary (but see below), this might indicate that at least the dispersal of the major clades over the supercontinent took place after eastern Asia had been separated from the rest of Pangea by the Turgai or Mongol-Okhotsk sea, probably in the Bathonian (see Russell, 1995; Upchurch *et al.*, 2002). In this case, more derived camarasauromorph macronarians would have invaded Asia after the closure of these epicontinental seas in the Cretaceous, probably from Europe (see Barrett *et al.*, 2002; Canudo *et al.*, 2002; Wilson & Upchurch, 2009). Even the possible presence of some of the basalmost macronarians in the late Middle Jurassic of China (Upchurch *et al.*, 2004) does not necessarily argue against this scenario. First of all, the phylogenetic position of *Bellusaurus* and *Abrosaurus* is far from certain (Upchurch *et al.*, 2004), but even if their macronarian relationships can be confirmed, they might simply represent a relic of the earliest macronarian radiation that originated and diversified prior to the origin of other major groups of neosauropods. A more severe problem for the hypothesis of a rapid diversification and dispersal of the major clades of

neosauropods after the separation of Asia might be the possible presence of a brachiosaurid in the latest Middle Jurassic of China (Hone *et al.*, 2009). However, the material is a single cervical vertebra, and no macronarian or brachiosaurid synapomorphies were identified by Hone *et al.* If the presence of such more derived neosauropod groups in the Jurassic of China can be confirmed by future studies, several possibilities might account for this.

First, it might be possible that derived neosauropods originated and dispersed over all of Pangea prior to the separation of Asia in the Bathonian. This interpretation would be consistent with the discovery of wide-gauge trackways in the late Middle Jurassic of England, which were interpreted to represent early titanosaurs (Day *et al.*, 2002, 2004; see also Wilson & Carrano, 1999). It should be noted, however, that other authors have argued that trackway morphology may be influenced by other aspects than systematic affinities of the trackmaker, such as body mass and substrate (Henderson, 2006; Wilson, Marsicano & Smith, 2009), and, thus, these sidentifications should be seen with caution. A more serious problem for the hypothesis of a pre-Bathonian origin and wide distribution of advanced, titanosauriform macronarians is the complete absence of any body fossils of this group prior to the Callovian (unless the Bathonian *Lapparentosaurus* really represents a brachiosaurid; see Upchurch *et al.*, 2004; Rauhut, 2006a; Rauhut & López-Arbarello, 2008), and the fact that neosauropods are generally absent in pre-Bathonian Middle Jurassic faunas and seem to be rare up to the Middle–Late Jurassic boundary, in stark contrast to their abundance in the Late Jurassic.

A second possibility might be that the separation of eastern Asia from the rest of Pangea occurred later, or that the separation by epicontinental seas was less strict than previously thought, and short-time changes in sea level might have allowed at least some selective faunal interchange between eastern Asia and the western parts of Pangea (or Laurasia, in the Late Jurassic). In this case, a few neosauropod taxa might have immigrated into eastern Asia after the Bathonian; if only a selective interchange was present, this might account for the apparent rarity of neosauropods in the Chinese Upper Jurassic. Support for this hypothesis might come from the probably close relationships between the late Middle Jurassic African taxa *Atlasaurus* and *Jobaria* and the roughly contemporaneous eastern Asian *Bellusaurus* (Upchurch *et al.*, 2004) and the placement of the late Middle to latest Jurassic European *Cetiosauriscus* and *Losillasaurus* in the Mamenchisauridae, together with the Asian *Omeisaurus* and *Mamenchisaurus* in the phylogenetic analysis of Rauhut *et al.* (2005). However, in both cases, the origin of the clades in

question reach back to at least the Bathonian, and the fact that the two African forms are more closely related to each other than either is to the Chinese taxon in the phylogenetic hypothesis of Upchurch *et al.* (2004) could also be taken as evidence of vicariance after the Bathonian separation. New fossil finds and more detailed studies of the taxa in question are necessary to evaluate these different hypotheses.

It is interesting to note that, with the identification of *Tehuelchesaurus* as a non-titanosauriform camarasauromorph, in all continents outside Asia brachiosaurid titanosauriforms occur in association with more basal macronarians. The results presented here indicate that non-titanosauriform macronarians were more diverse than previously thought, and distinct clades consisting of more than a single genus can be recognized within this array of taxa. Of special interest in this respect are the clades formed by Gondwanan and Iberian taxa. If confirmed by future finds and more detailed studies of the phylogeny of basal macronarians, these close relationships might indicate that some faunal interchange between Gondwana and the island that represented the Iberian peninsula in the Late Jurassic might still have been possible even after the final separation of the continents of the northern and southern hemispheres. Plate tectonic reconstructions show that Iberia retained close proximity to Africa through at least the Late Jurassic and Early Cretaceous (e.g. Ford & Golonka, 2003), so that brief sea-level changes might have made dispersal of taxa between the two land masses possible from time to time. Together with the close relationships between Late Jurassic taxa from Portugal with those of the Morrison Formation of the western USA (Mateus, 2006), this could indicate that the Iberian Peninsula might have been an important faunal turntable between Africa, Asia and North America (see also Gheerbrant & Rage, 2006).

Alternatively, if one accepts that no faunal interchange was possible between the continents of the northern and southern hemisphere in the Jurassic after the beginning of oceanic rifting between Central and South America, all macronarian lineages must reach back into at least the latest Middle Jurassic. In this case, a large number of basal macronarian taxa are still waiting to be discovered in sediments of the latest Middle to early Late Jurassic in both Gondwana and Laurasia.

CONCLUSIONS

A complete preparation and detailed study of *Tehuelchesaurus* provides a wealth of new information on the anatomy, diagnosis, and phylogenetic position of this taxon. *Tehuelchesaurus* can clearly be shown to represent a separate taxon by a rather high number

of autapomorphic characters, mainly in the lamination of the dorsal vertebrae. Furthermore, a phylogenetic analysis demonstrates that the taxon can securely be placed within camarasauromporph macronarians, but outside Titanosauriformes.

The large number of basal macronarian taxa described in recent years from the Late Jurassic or Early Cretaceous [e.g. *Galvesaurus* (Barco *et al*., 2005); *Europasaurus* (Sander *et al*., 2006); *Paluxisaurus* (Rose, 2007); *Tastavinsaurus* (Canudo *et al*., 2008)] adds a significant amount of new information that should be considered when evaluating hypotheses on the early evolution of this group. The inclusion of some of these taxa in the present analysis shows that non-titanosauriform camarasauromophs were a diverse assemblage of forms currently recorded in Late Jurassic and Early Cretaceous beds of both the Northern and Southern Hemisphere.

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APPENDICES

CHARACTER LIST

Description of characters used in phylogenetic analyses. Characters were mainly taken from Wilson (2002) with the addition of some other previously used (Salgado *et al.*, 1997; Upchurch, 1998; Upchurch *et al.*, 2004; Canudo *et al.*, 2008; Gonzáles Riga, Previtera & Pirrone, 2009), and some new characters. Most characters are binary and seven of the multistate characters (66, 67, 83, 87, 98, 142, 170) were treated as ordered

(1) Posterolateral processes of premaxilla and lateral processes of maxilla, shape: without midline contact (0); with midline contact forming marked narial depression, subnarial foramen not visible laterally (1). (Wilson, 2002)

(2) Premaxillary anterior margin shape: without step (0); with marked step, anterior portion of skull sharply demarcated (1). (Wilson, 2002)

(3) Preanteorbital fenestra: absent (0); present (1). (Wilson, 2002)

(4) Subnarial foramen and exterior maxillary foramen, position: well separated from one

another (0); separated by narrow bony isthmus (1). (Wilson, 2002)

(5) Antorbital fenestra: much shorter than (0); or subequal to orbital maximum diameter (1). (Wilson, 2002)

(6) External nares position: anterior to orbits (0); retracted to a position between orbits (1). (modified from Wilson, 2002)

(7) External nares, maximum diameter: shorter (0); or longer than orbital maximum diameter (1). (Wilson, 2002)

(8) Orbital ventral margin, anteroposterior length: broad, with subcircular orbital margin (0); reduced, with acute orbital margin (1). (Wilson, 2002)

(9) Lacrimal, anterior process: present (0); absent (1). (Wilson, 2002)

(10) Jugal–ectopterygoid contact: present (0); absent (1). (Wilson, 2002)

(11) Jugal, contribution to antorbital fenestra: very reduced or absent (0); large, bordering approximately one-third its perimeter (1). (Wilson, 2002)

(12) Prefrontal posterior process size: small, not projecting far posterior of frontal–nasal suture (0); elongate, approaching parietal (1). (Wilson, 2002)

(13) Prefrontal, posterior process shape: flat (0); hooked (1).

(14) Postorbital, ventral process shape: transversely narrow (0); broader transversely than anteroposteriorly (1). (Wilson, 2002)

(15) Postorbital, posterior process: present (0); absent (1). (Wilson, 2002)

(16) Frontal contribution to supratemporal fossa: present (0); absent (1). (Wilson, 2002)

(17) Frontals, midline contact (symphysis): sutured (0); or fused in adult individuals (1). (Wilson, 2002)

(18) Frontal, anteroposterior length: approximately twice (0); or less than minimum transverse breadth (1). (Wilson, 2002)

(19) Parietal occipital process, dorsoventral height: short, less than the diameter of the foramen magnum (0); deep, nearly twice the diameter of the foramen magnum (1). (Wilson, 2002)

(20) Parietal, contribution to post-temporal fenestra: present (0); absent (1). (Wilson, 2002)

(21) Postparietal foramen: absent (0); present (1). (Wilson, 2002)

(22) Parietal, distance separating supratemporal fenestrae: less than (0); or twice the long axis of supratemporal fenestra (1). (Wilson, 2002)

(23) Supratemporal fenestra: present (0); absent (1). (Wilson, 2002)

(24) Supratemporal fenestra, long axis orientation: anteroposterior (0); transverse (1). (Wilson, 2002)

(25) Supratemporal fenestra, maximum diameter: much longer than (0); or subequal to that of foramen magnum (1). (Wilson, 2002)

(26) Supratemporal fossa, lateral exposure: not visible laterally, obscured by temporal bar (0); visible laterally, temporal bar shifted ventrally (1). (Wilson, 2002)

(27) Squamosal–quadratojugal contact: present (0); absent (1). (Wilson, 2002)

(28) Quadratojugal, anterior process length: short, anterior process shorter than dorsal process (0); long, anterior process more than twice as long as dorsal process (1). (Wilson, 2002)

(29) Quadrate fossa: absent (0); present (1). (Wilson, 2002)

(30) Quadrate fossa, depth: shallow (0); deeply invaginated (1). (Wilson, 2002)

(31) Quadrate fossa, orientation: posterior (0); posterolateral (1). (Wilson, 2002)

(32) Palatobasal contact, shape: pterygoid with small facet (0); dorsomedially orientated hook (1); or rocker-like surface for basipterygoid articulation (2). (Wilson, 2002)

(33) Pterygoid, transverse flange (i.e. ectopterygoid process) position: posterior of orbit (0); between orbit and antorbital fenestra (1); anterior to antorbital fenestra (2). (Wilson, 2002)

(34) Pterygoid, quadrate flange size: large, palatobasal and quadrate articulations well separated (0); small, palatobasal and quadrate articulations approach (1). (Wilson, 2002)

(35) Pterygoid, palatine ramus shape: straight, at level of dorsal margin of quadrate ramus (0); stepped, raised above level of quadrate ramus (1). (Wilson, 2002)

(36) Epipterygoid: present (0); absent (1). (Wilson, 2002)

(37) Vomer, anterior articulation: maxilla (0); premaxilla (1). (Wilson, 2002)

(38) Supraoccipital, height: twice or subequal to (0); or less than height of foramen magnum (1). (Wilson, 2002)

(39) Paroccipital process, ventral non-articular process: absent (0); present (1). (Wilson, 2002)

(40) Crista prootica, size: rudimentary (0); expanded laterally into dorsolateral process (1). (Wilson, 2002)

(41) Basipterygoid processes, length: short, approximately twice (0); or elongate, at least four times basal diameter (1). (Wilson, 2002)

(42) Basipterygoid processes, angle of divergence: approximately 45° (0); less than 30° (1). (Wilson, 2002)

(43) Basal tubera, anteroposterior depth: approximately half dorsoventral height (0); sheet-like, 20% dorsoventral height (1). (Wilson, 2002)

(44) Basal tubera, breadth: much broader than (0); or narrower than occipital condyle (1). (Wilson, 2002)

(45) Basioccipital depression between foramen magnum and basal tubera: absent (0); present (1). (Wilson, 2002)

(46) Basisphenoid/basipterygoid recess: present (0); absent (1). (Wilson, 2002)

(47) Basisphenoid/quadrate contact: absent (0); present (1). (Wilson, 2002)

(48) Basipterygoid processes, orientation: perpendicular to (0); or angled approximately 45° to skull roof (1). (Wilson, 2002)

(49) Dentary, depth of anterior end of ramus: slightly less than that of dentary at mid-length (0); 150% minimum depth (1). (Wilson, 2002)

(50) Dentary, anteroventral margin shape: gently rounded (0); sharply projecting triangular process (1). (Wilson, 2002)

(51) Dentary symphysis, orientation: angled 15° or more anteriorly to (0); or perpendicular to axis of jaw ramus (1). (Wilson, 2002)

(52) External mandibular fenestra: present (0); absent (1). (Wilson, 2002)

(53) Surangular depth: less than twice (0); or more than two and one-half times maximum depth of the angular (1). (Wilson, 2002)

(54) Splenial posterior process, position: overlapping angular (0); separating anterior portions of prearticular and angular (1). (Wilson, 2002)

(55) Tooth rows, shape of anterior portions: V-shaped or U-shaped (0); rectangular, tooth-bearing portion of jaw perpendicular to jaw rami (1). (modified from Wilson, 2002)

(56) Tooth rows, length: extending posterior to subnarial foramen (0); restricted anterior to subnarial foramen (1). (Wilson, 2002)

(57) Dentary teeth, number: greater than 20 (0); 17 or fewer (1). (Wilson, 2002)

(58) Replacement teeth per alveolus, number: two or fewer (0); more than four (1). (Wilson, 2002)

(59) Teeth, orientation: perpendicular (0); or oriented anteriorly relative to jaw margin(1). (Wilson, 2002)

(60) Occlusal pattern: interlocking, V-shaped facets (0); high-angled planar facets (1); low-angled planar facets (2). (Wilson, 2002)

(61) Tooth crowns, orientation: aligned along jaw axis, crowns do not overlap (0); aligned slightly anterolingually, tooth crowns overlap (1). (Wilson, 2002)

(62) Tooth crowns, cross-sectional shape at mid-crown: elliptical or D-shaped (0); cylindrical (1). (modified from Wilson, 2002)

(63) Marginal tooth denticles: present (0); absent on posterior edge (1); absent on both anterior and posterior edges (2). (Wilson, 2002)

(64) Teeth, longitudinal grooves on lingual aspect: absent (0); present (1). (Wilson, 2002)

(65) Prominent groves near the mesial and distal margins of the labial surface of each tooth crown: absent (0); present (1). (Upchurch, 1998)

(66) SI values for tooth crowns: less than 3.0 (0); 3.0–4.0 (1); 4.0 or more (2). (modified from Upchurch *et al.*, 2004)

(67) Number of cervical vertebrae: 12 or fewer (0); 13 (1); 15 (2); 16 or more (3). [modified from Wilson (2002) and Upchurch *et al.* (2004)]

(68) Ventral surface of each cervical centrum: is flat or slightly convex transversely (0); transversely concave (1). (Upchurch *et al.*, 2004)

(69) Midline keels on the ventral surfaces of the cervical centra: prominent and plate-like (0); reduced to low ridges or absent (1). (Upchurch *et al.*, 2004)

(70) Pleurocoels on cervical centra: absent (0); present and undivided (1); present and divided by bony septa (2). (Wilson, 2002)

(71) Cervical neural arch lamination: Well developed, with well defined laminae and coels (0); rudimentary, diapophyseal laminae only feebly developed if present (1). (Wilson, 2002)

(72) Anterior cervical neural spines shape: single (0); bifid (1). (Wilson, 2002)

(73) Height: width ratio of anterior cervical centra: is 1.0 or less (0); is approximately 1.25 (1). (Wilson, 2002)

(74) Mid cervical centra, anteroposterior length/height of posterior face: less than 4 (0); more than 4 (1). (Wilson, 2002)

(75) Mid cervical neural arches, height: less than that of posterior centrum face (0); greater than that of posterior centrum face (1). (Wilson, 2002)

(76) Middle and posterior cervical neural arches, centroprezygapophyseal laminae (cprl), shape: single (0); divided (1). (Wilson, 2002)

(77) Posterior cervical and anterior dorsal neural spines shape: single (0); bifid (1). (Wilson, 2002)

(78) The lateral profile of neural spines on posterior cervical vertebrae: displays steeply sloping anterior and posterior faces(0); displays steeply sloping anterior face and noticeably less steep posterior margin (1). (Upchurch *et al.*, 2004)

(79) Middle and posterior cervical articular surfaces of prezygapophyses: are flat (0); are convex transversely (1). (Upchurch *et al.*, 2004)

(80) Posterior cervical and anterior dorsal bifid neural spines, median tubercle: absent (0); present (1). (Wilson, 2002)

(81) Posterior cervical neural spine, laterally expanded and wider than the centra: absent (0); present (1). (Gonzáles Riga *et al*., 2009)

(82) Distal shafts of longest cervical ribs: are elongate and form overlapping bundles (0); are short and do not project beyond the posterior end of the centrum to which they are attached (1). (Wilson, 2002)

(83) Number of dorsal vertebrae: 13 or more (0); 12 (1); 11 or fewer (2). (modified from Wilson, 2002)

(84) Pleurocoels in dorsal centra: absent (0); present (1). (Wilson, 2002)

(85) Pleurocoels in dorsal centra: are moderately deep but simple pits (0); deep excavations that ramify throughout the centrum and into the base of the neural arch, leaving only a thin septum on the midline of the centrum (1). (Upchurch *et al*., 2004)

(86) Pleurocoels in the dorsal centra: have margins that are flush with the lateral surface of the centrum (0); set within a larger depression on the lateral surface of the centrum (1). (Upchurch *et al*., 2004)

(87) Prescral centra pneumatic features: solid (0); camerate, large enclosed camerae with regular branching pattern (1); camellate (2). [modified from Wilson, 2002, adding new states following to Wedel (2003a, b)]

(88) Supraneural camera within some or all of the dorsal neural arches: absent (0); present (1). (modified from Upchurch, 1998)

(89) Infradiapophyseal pneumatic foramen: absent (0); present (1). (Upchurch, 1998)

(90) Hyposphene–hypantrum system: present (0); absent (1). (Wilson, 2002)

(91) Single midline lamina supporting the hyposphene from below in the dorsal vertebrae: absent (0); present (1). (Upchurch *et al*., 2004)

(92) Transverse processes: are directed laterally or slightly upwards (0); are directed strongly dorsolaterally (1). (Upchurch *et al*., 2004)

(93) Distal end of the transverse process in the dorsal vertebrae: curves smoothly into the dorsal surface of the process (0); is set off from the dorsal surface, the latter having a distinct, dorsally facing flattened area (1). (Upchurch *et al*., 2004)

(94) Ventral surface of the dorsal centra: convex transversely (0); flattened (1); have a sagital crest and ventrolaterally facing surfaces (2). (modified from Upchurch *et al*., 2004)

(95) Anterior face of dorsal neural arch: is flat or shallowly excavated (0); is deeply excavated, forming a large cavity above the neural canal (1). (Upchurch *et al*., 2004)

(96) Dorsal neural spines in anterior view: posses subparallel lateral margins (0); posses lateral margins which diverge steadily towards the summit (75%) (1). (Wilson, 2002)

(97) Dorsal neural spine height divided centrum length: approximately twice (0); four times (1). (Upchurch *et al*., 2004)

(98) Triangular aliform processes projecting laterally from the tops of the dorsal neural spines: absent (0); present but do not project far laterally (not as far as posterior zygapophyses) (1); present and project far laterally (as far as posterior zygapophyses) (2). [modified from Wilson (2002) and Upchurch *et al*. (2004)]

(99) Atlantal intercentrum, occipital facet shape: rectangular in lateral view, length of dorsal aspect subequal to that of ventral aspect (0); expanded anteroventrally in lateral view, anteroposterior length of dorsal aspect shorter tan that of ventral aspect (1). (Wilson, 2002)

(100) Anterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1). (Wilson, 2002)

(101) Pleurocoels in anterior dorsal centra: have rounded posterior margins (0); have tapering, acute posterior margins (1). (Upchurch *et al*., 2004)

(102) Middle and posterior dorsal neural arches, centropostzygapophyseal lamina (cpol), shape: simple (0); divided (1). (Wilson, 2002)

(103) Middle and posterior dorsal neural arches, anterior centroparapophyseal lamina (acpl): absent (0); present (1). (Wilson, 2002)

(104) Middle and posterior dorsal neural arches, prezygoparapophyseal lamina (prpl): absent (0); present (1). (Wilson, 2002)

(105) Middle and posterior dorsal neural arches, posterior centroparapophyseal lamina (pcpl): absent (0); present (1). (Wilson, 2002)

(106) Middle and posterior dorsal neural arches, spinopostzygapophyseal lamina (spol): single (0); divided (1). (Wilson, 2002)

(107) Accessory spinodiapophyseal lamina (spdl) on the dorsal vertebrae: absent (0); present (1). (Upchurch *et al*., 2004)

(108) Middle and posterior dorsal neural spines orientation: vertical (0); posterior neural spine summit approaches level of diapophyses (1). (Wilson, 2002)

(109) Centroprezygapophyseal lamina (cprl) on the middle and posterior dorsals: a single lamina

(0); bifurcates into medial and lateral portions toward its upper end (1). (Upchurch *et al.*, 2004)

(110) Prespinal lamina on the middle and posterior dorsal vertebrae: absent (0); present and bifurcates toward its ventral end (1); present and remains a single lamina throughout its length (2). (Upchurch *et al.*, 2004)

(111) Postspinal lamina on the middle and posterior dorsal vertebrae: absent (0); present (1). (Upchurch *et al.*, 2004)

(112) Spinodiapophyseal lamina (spdl) on middle and posterior dorsal neural arches: absent (0); present (1). (Upchurch *et al.*, 2004)

(113) Anterior to medial dorsal vertebrae, presygapophyseal articular facet: horizontal or slightly posteroventrally oriented (0); posteroventrally oriented (around 30°) (1); strongly posteroventrally oriented (more than 40) (2).

(114) Posterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1). (Wilson, 2002)

(115) Neural spines of posterior dorsal vertebrae: narrower transversely than anteroposteriorly (0); broader transversely than anteroposteriorly (1). (Wilson, 2002)

(116) Spinodiapophyseal lamina (spdl) on posterior dorsal vertebrae: absent (0); present (1). (Wilson, 2002)

(117) Posterior dorsal centra: subcircular in the transverse section (0); dorsoventrally compressed in the transverse section (1). (Upchurch *et al.*, 2004)

(118) Length/width ratio of posterior dorsal central: are less than 1.0 (0); greater than 1.0 (1). (Upchurch *et al.*, 2004)

(119) Posterior centrodiapophyseal lamina (pcdl) of the posterior dorsal vertebrae: has an unexpanded ventral tip (0); expands and may bifurcate toward its ventral tip (1). (Salgado *et al.*, 1997)

(120) Transverse processes of posterior dorsal vertebrae: lie posterior, or posterodorsal, to the parapophysis (0); lie vertically above the parapophysis (1). (Upchurch *et al.*, 2004)

(121) Dorsal ribs, proximal pneumatopores: absent (0); present (1). (Wilson, 2002)

(122) Anterior dorsal ribs, cross-sectional shape: subcircular (0); plank-like, anteroposterior breadth more than three times mediolateral breadth (1). (Wilson, 2002)

(123) Sacral vertebrae, number: 4 or fewer (0); 5 (1); 6 (2). (modified from Wilson, 2002)

(124) Sacrum, sacricostal yoke: absent (0); present (1). (Wilson, 2002)

(125) Sacral neural spines length: approximately twice length of centrum (0); approximately four times length of centrum (1). (Wilson, 2002)

(126) Sacral ribs, dorsoventral length: low, not projecting beyond dorsal margin of ilium (0); high extending beyond dorsal margin of ilium (1). (Wilson, 2002)

(127) Angle between the capitulum and tuberculum of the cervical ribs in anterior view: greater than 90°, so that the rib shaft lies close to the ventral edge of the centrum(0); less than 90°, so that the rib shaft lies below the ventral margin of the centrum (1).

(128) Pleurocoels in the lateral surfaces of sacral centra: absent (0); present (1). (Wilson, 2002)

(129) Ratio of the centrum length to centrum height for the proximal caudals: greater than 0.6 (0); less than 0.6 (1) (Upchurch *et al.*, 2004)

(130) Caudal bone texture: solid (0); spongy, with large internal cells (1). (Wilson, 2002)

(131) Ratio of centrum length to centrum height for the middle caudal centra: less than 2, usually 1.5 or less (0); 2 or higher (1). (Upchurch *et al.*, 2004)

(132) Ratio of length to height for the distal caudal centra: less than 5, usually 3 or less (0); 5 or higher (1). (Upchurch *et al.*, 2004)

(133) Ventral surfaces of the proximal caudal centra: convex transversely (0); concave transversely, with the resulting hollow bounded laterally by ventrolateral ridges (1). (Upchurch *et al.*, 2004)

(134) Ventrolateral ridges present on the anterior and middle caudal centra: absent (0); present (1). (Upchurch *et al.*, 2004)

(135) Location of the neural arches of the middle caudals: over the midpoint of the centrum with approximately subequal amounts of the centrum exposed at either end (0); on the anterior half of the centrum (1). (Upchurch *et al.*, 2004)

(136) Sharp ridge on the lateral surface of the middle caudals located at the junction of the neural arch and centrum: absent (0); present (1). (Upchurch *et al.*, 2004)

(137) Hyposphene ridge on the proximal caudals: absent (0); present (1). (Upchurch *et al.*, 2004)

(138) Caudal vertebrae, number: 35 or fewer (0); 40–55 (1); increased to 70–80 (2). (Wilson, 2002)

(139) Caudal transverse processes: persist through caudal 15 or more posteriorly (0); disappear by caudal 10 (1). (modified from Wilson, 2002)

(140) First caudal centrum, articular face shape: flat (0); procoelous (1); biconvex (2). (modified from Wilson, 2002)

(141) First caudal neural arch, coel on lateral aspect of neural spine: absent (0); present (1). (Wilson, 2002)

(142) Anterior caudal centra (excluding the first), articular face shape: amphiplatyan or amphicoelous (0); platycoelous/distoplatyan (1); procelous (2). (modified from Gonzáles Riga *et al*., 2009)

(143) Anterior caudal centra, pleurocoels: absent (0); present (1). (Wilson, 2002)

(144) Anterior caudal centra, length: approximately the same (0); or doubling over the first 20 vertebrae (1). (Wilson, 2002)

(145) Anterior caudal neural arches, spinoprezygapophyseal lamina (sprl): absent (0); present and extending onto lateral aspect of neural spine (1). (Wilson, 2002)

(146) Anterior caudal neural arches, spinoprezygapophyseal lamina (sprl)–spinopostzygapophyseal lamina (spol) contact: absent (0); present, forming a prominent lamina on lateral aspect of neural spine (1). (Wilson, 2002)

(147) Anterior caudal neural arches, prespinal lamina (prsl): absent (0); present (1). (Wilson, 2002)

(148) Anterior caudal neural arches, postspinal lamina (posl): absent (0); present (1). (Wilson, 2002)

(149) Anterior caudal neural arches, postspinal fossa: absent (0); present (1). (Wilson, 2002)

(150) Anterior caudal neural spines, transverse breadth: approximately 50% of (0); or greater than anteroposterior length (1). (Wilson, 2002)

(151) Anterior caudal transverse processes, shape: triangular, tapering distally (0); wing-like, not tapering distally (1). (Wilson, 2002)

(152) Anterior caudal transverse processes, diapophyseal laminae (acdl, pcdl, prdl, podl): absent (0); present (1). (Wilson, 2002)

(153) Anterior caudal transverse processes, anterior centrodiapophyseal lamina (acdl), shape: single (0); divided (1). (Wilson, 2002)

(154) Anterior and middle caudal centra, shape: cylindrical (0); quadrangular, flat ventrally and laterally (1). (Wilson, 2002)

(155) Anterior and middle caudal centra, ventral longitudinal hollow: absent (0); present (1). (Wilson, 2002)

(156) Middle caudal neural spines, orientation: angled posterodorsally (0); vertical (1). (Wilson, 2002)

(157) Middle caudal centra, articular face shape: amphiplatyan or amphicoelous (0); procoelous (1). (modified form Gonzáles Riga *et al*., 2009)

(158) Posterior caudal centra, articular face shape: (0) amphiplatyan or amphicoelous; (1) procoelous. (González Riga *et al*., 2009)

(159) Posterior caudal centra, shape: cylindrical (0); dorsoventrally flattened, breadth at least twice height (1). (Wilson, 2002)

(160) Distalmost caudal centra, articular face shape: platycoelous (0); biconvex (1). (Wilson, 2002)

(161) Distalmost biconvex caudal centra, length-to-height ratio: less than 4 (0); greater than 5 (1). (Wilson, 2002)

(162) Forked chevrons with anterior and posterior projections: absent (0); present (1). (Wilson, 2002)

(163) Forked chevrons, distribution: distal tail only (0); throughout middle and posterior caudal vertebrae (1). (Wilson, 2002)

(164) Chevrons, 'crus' bridging dorsal margin of haemal canal: present (0); absent (1).

(165) Chevron haemal canal, depth: short, approximately 25% (0); or long, approximately 50% chevron length (1). (Wilson, 2002)

(166) Chevrons: persisting throughout at least 80% of tail (0); disappearing by caudal 30 (1). (Wilson, 2002)

(167) Posterior chevrons, distal contact: fused (0); unfused (open) (1). (Wilson, 2002)

(168) Scapular acromion process, size: narrow (0); broad, width more than 150% minimum width of blade (1). (Wilson, 2002)

(169) Scapular blade, orientation respect to coracoid articulation: Perpendicular (0); forming a 45° angle (1). (Wilson, 2002)

(170) Scapular blade, shape: acromial edge not expanded (0); rounded expansion on acromial side (1); racquet-shaped (2). (Wilson, 2002)

(171) Scapular length/blade breadth is: less than 5.5 (0); 5.5 or higher (1).

(172) Scapular, acromial process position: lies close to glenoid level (0); lies close to the midpoint of the scapular body (1).

(173) Scapular glenoid orientation: relatively flat or laterally facing (0); strongly bevelled medially (1). (Wilson, 2002)

(174) Scapular blade, cross-sectional shape at base: flat or rectangular (0); D-shaped (1). (Wilson, 2002)

(175) Coracoid, proximodistal length: less than the length of scapular articulation (0); approximately twice the length of scapular articulation (1). (Wilson, 2002)

(176) Coracoid, anteroventral margin shape: rounded (0); rectangular (1). (Wilson, 2002)

(177) Coracoid, infraglenoid lip: small or absent (0); well developed (1). (Wilson, 2002)

(178) Sternal plate, shape: oval (0); crescentic (1). (Wilson, 2002)

(179) Dorsal margin of the coracoid in lateral view: reaches or surpasses the the level of the dorsal margin of the scapular expansion (0); lies below the level of the scapular proximal expansion and separated from the latter by a V-shaped notch (1). (Upchurch *et al*., 2004)

(180) Prominent posterolateral expansion of the sternal plate producing a kidney-shaped profile in dorsal view: absent (0); present (1). (Upchurch *et al*., 2004)

(181) Prominent parasagital oriented ridge on the dorsal surface of the sternal plate: absent (0); present (1). (Upchuch *et al*., 2004)

(182) Scapular with prominent and well developed ventromedial process: absent (0); present (1).

(183) Humeral proximolateral corner, shape: rounded (0); square (1). (Wilson, 2002)

(184) Humeral deltopectoral crest, shape: relatively narrow throughout length (0); markedly expanded distally (1). (Wilson, 2002)

(185) Humeral midshaft cross-section, shape: circular (0); elliptical, with long axis orientated transversely (1). (Wilson, 2002)

(186) Humeral distal condyles, articular surface shape: restricted to distal portion of humerus (0); exposed on anterior portion of humeral shaft (1). (Wilson, 2002)

(187) Humeral distal condyle, shape: divided (0); flat (1). (Wilson, 2002)

(188) Prominent rounded process on the lateral portion of the proximal end of the humerus: absent (0); present (1). (Upchurch *et al*., 2004)

(189) Humerus to femur ratio: less than 0.90 (0); greater than 0.90 (1). (Upchurch *et al*., 2004)

(190) Ratio of maximum length of sternal plate to the humerus length: less than 0.75, usually less than 0.65 (0); greater than 0.75 (1). (Upchurch *et al*., 2004)

(191) Ulnar proximal condylar processes, relative lengths: subequal (0); unequal, anterior arm longer (1). (Wilson, 2002)

(192) Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1). (Wilson, 2002)

(193) Ulna, length-to-proximal breadth ratio: gracile (0); stout (1). (Wilson, 2002)

(194) Radius, distal breadth: slightly larger than midshaft breadth (0); approximately twice midshaft breadth (1). (Wilson, 2002)

(195) Radius, distal condyle orientation: perpendicular to long axis of shaft (0); bevelled approximately 20° proximolaterally, relative to long axis of shaft (1). (Wilson, 2002)

(196) Carpal bones, number: 3 or more (0); 2 or fewer (1). (Wilson, 2002)

(197) Metacarpus, shape: spreading (0); bound, with subparallel shafts and articular surfaces that extend half their length (1). (Wilson, 2002)

(198) Metacarpals, shape of proximal surface in articulation: gently curving, forming a 90° arc (0); U-shaped, subtending a 270° arc (1). (Wilson, 2002)

(199) Longest metacarpal-to-radius ratio: close to 0.3 (0); 0.45 or more (1). (Wilson, 2002)

(200) Metacarpal I, length: shorter than metacarpal IV (0); longer than metacarpal IV (1). (Wilson, 2002) (Wilson, 2002)

(201) Metacarpal I, distal condyle shape: divided (0); undivided (1). (Wilson, 2002)

(202) Metacarpal I distal condyle, transverse axis orientation: bevelled approximately 20° in respect to axis of shaft (0); proximodistally or perpendicular with respect to axis of shaft (1). (Wilson, 2002)

(203) Phalanges in manual digits II and III: present (0); absent or unossified (1). (modified from Wilson, 2002)

(204) Manual phalanx I, shape: rectangular (0); wedge-shaped (1). (Wilson, 2002)

(205) Pelvis, anterior breadth: narrow, ilia longer anteroposteriorly than distance separating preacetabular processes (0); broad, distance between preacetabular processes exceeds anteroposterior length of ilia (1). (Wilson, 2002)

(206) Iliac preacetabular process, orientation: anterolateral to body axis (0); perpendicular to body axis (1). (Wilson, 2002)

(207) Iliac preacetabular process, shape: pointed, arching ventrally (0); semicircular, with posteroventral excursion of cartilage cap (1). (Wilson, 2002)

(208) Highest point on the dorsal margin of the ilium: lies caudal to the base of the pubic process (0); lies anterior to the base of the pubic process (1). (Upchurch *et al*., 2004)

(209) Pubis, ambiens process development: small, confluent with anterior margin of pubis prominent (0); projects anteriorly from anterior margin of pubis (1). (Wilson, 2002)

(210) Pubic apron, shape: flat (straight symphysis) (0); canted anteromedially (gentle S-shaped symphysis) (1). (Wilson, 2002)

(211) Puboischial contact, length: approximately one-third total length of pubis (0); one-half total length of pubis (1). (Wilson, 2002)

(212) Ischial blade, length: much shorter than pubic blade (0); longer than pubic blade (1). (Wilson, 2002)

(213) Ischial blade, shape: emarginate distal to pubic peduncle (0); no emargination distal to pubic peduncle (1). (Wilson, 2002)

(214) Ischia, pubic width length divided by total ischium length (from the acetabulum to the end of the blade): less than 0.5 (0); 0.5 or grater (1).

(215) Ischia pubic articulation: less or equal to the anteroposterior length of pubic pedicel (0); greater than the anteroposterior length of pubic pedicel (1). (Salgado *et al*., 1997)

(216) Ischial distal shaft, shape: triangular, depth of ischial shaft increases medially (0); bladelike, medial and lateral depths subequal (1). (Upchurch *et al*., 2004)

(217) Ischial distal shafts, cross-sectional shape: V-shaped, forming an angle of nearly 50° with each other (0); flat, nearly coplanar (1). (Wilson, 2002)

(218) Ischia, distal end: is only slightly expanded (0); is strongly expanded dorsoventrally (1). (Wilson, 2002)

(219) Pubis length respect to ischium length: shorter or subequal (0); significatively longer (1). (Salgado *et al*., 1997)

(220) Femoral head in anterior view: directed medially or ventromedially (0); directed dorsomedial (1). (Upchurch *et al*., 2004)

(221) Situation of the femoral fourth trochanter: on the posterior surface of the shaft, near the midline (0); on the posteromedial margin of the shaft (1). (Upchurch *et al*., 2004)

(222) Femoral midshaft, transverse diameter: subequal to anteroposterior diameter (0); 125–150% anteroposterior diameter (1); at least 185% anteroposterior diameter (2). (Wilson, 2002)

(223) Femoral shaft, lateral margin shape: directed dorsally (0); deflected dorsomedilly (1). (Wilson, 2002)

(224) Femoral distal condyles, relative transverse breadth: subequal (0); tibial much broader than fibular (1). (Wilson, 2002)

(225) Femoral distal condyles, orientation: perpendicular or slightly bevelled dorsolaterally (0); or bevelled dorsomedially approximately 10° relative to femoral shaft (1). (Wilson, 2002)

(226) Femoral distal condyles, articular surface shape: restricted to distal portion of femur (0); expanded onto anterior portion of femoral shaft (1). (Wilson, 2002)

(227) Tibial proximal condyle, shape: narrow, long axis anteroposterior (0); expanded transversely, condyle subcircular (1). (Wilson, 2002)

(228) Tibial cnemial crest, orientation: projecting anteriorly (0); or laterally (1). (Wilson, 2002)

(229) Tibia, distal breadth: approximately 125% (0); more than twice midshaft breadth (1). (Wilson, 2002)

(230) Tibial distal posteroventral process, size: broad transversely, covering posterior fossa of astragalus (0); shortened transversely, posterior fossa of astragalus visible posteriorly (1). (Wilson, 2002)

(231) Fibular distal condyle, size: subequal to shaft (0); expanded transversely, more than twice midshaft breadth (1). (Wilson, 2002)

(232) Astragalus, shape: rectangular (0); wedge-shaped, with reduced anteromedial corner (1). (Wilson, 2002)

(233) Distal end of tibia broader transversely than anteroposteriorly: absent (0); present (1). (Salgado *et al*., 1997)

(234) Astragalus, ascending process length: limited to anterior two-thirds of astragalus (0); extending to posterior margin of astragalus (1). (Wilson, 2002)

(235) Astragalus, posterior fossa shape: undivided (0); divided by vertical crest (1). (Wilson, 2002)

(236) Astragalus, transverse length: 50% more than (0); or subequal to proximodistal height (1). (Wilson, 2002)

(237) Calcaneum: present (0); absent or unossified (1). (Wilson, 2002)

(238) Metatarsus, posture: bound (0); spreading (1). (Wilson, 2002)

(239) Metatarsal I proximal condyle, transverse axis orientation: perpendicular to (0); angled ventromedially approximately 15° to axis of shaft (1). (Wilson, 2002)

(240) Metatarsal I distal condyle, posterolateral projection: absent (0); present (1). (Wilson, 2002)

(241) Metatarsal III length: more than 30% (0); or less than 25% that of tibia (1). (Upchurch *et al*., 2004)

(242) Metatarsals III and IV, minimum transverse shaft diameters: subequal to (0); or less than 65% that of metatarsals I or II (1). (Wilson, 2002)

(243) Metatarsal V, length: shorter than (0); or at least 70% length of metatarsal IV (1). (Wilson, 2002)

(244) Pedal nonungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1). (Wilson, 2002)

(245) Pedal digits II-IV, penultimate phalanges, development: subequal in size to more proximal phalanges (0); rudimentary or absent (1). (Wilson, 2002)

(246) Pedal unguals, orientation: aligned with (0); or deflected lateral to digit axis (1). (Wilson, 2002)

(247) Pedal digit I ungual, length relative to pedal-digit II ungual: subequal (0); 25% larger than that of digit II (1). (Wilson, 2002)

(248) Pedal digit I ungual, length: shorter (0);or longer than metatarsal I (1). (Wilson, 2002)

(249) Pedal ungual II-III, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1). (Wilson, 2002)

DATA MATRIX

Uncertain or polymorphic characters are indicated by symbols: P = 0/1; Q = 1/2.

	5	10	15	20	25	30
Plateosaurus	00000	00000	00000	00000	00000	0000-
Mamenchisaurus	110-0	01010	000?0	?0100	00010	10111
Omeisaurus	11000	00110	000?0	10110	00010	1?11?
Tazoudasaurus	?????	?????	??00	10???	??01?	???0-
Shunosaurus	01000	00110	00000	001??	00000	10110
Patagosaurus	1?00?	0????	????0	?????	?????	?????
Brachiosaurus	11100	01111	00010	10110	00010	11111
Camarasaurus	11100	01111	00010	10110	01010	10011
Tehuelchesaurus	?????	?????	?????	?????	?????	?????
Janenschia	?????	?????	?????	?????	?????	?????
Tendaguria	?????	?????	?????	?????	?????	?????
Haplocanthosaurus	?????	?????	????0	?????	?????	?????
Euhelopus	0110?	0??1?	??10	?????	??0??	??11
Jobaria	11100	01111	00010	10110	00010	10111
Malawisaurus	11???	0??1?	?????	?????	?????	?????
Alamosaurus	?????	?????	?????	?????	?????	?????
Nemegtosaurus	011-0	0?101	00010	10101	01010	00111
Neuquensaurus	?????	?????	?????	?????	?????	?????
Opisthocoelicaudia	?????	?????	?????	?????	?????	?????
Rapetosaurus	001?1	0?10?	000?0	00101	01010	00?11
Saltasaurus	?????	?????	?00??	101?0	0101?	?????
Isisaurus	?????	?????	?????	?????	?????	?????
Chubutisaurus	?????	?????	?????	?????	?????	?????
Malarguesaurus	?????	?????	?????	?????	?????	?????
Wintonotitan	?????	?????	?????	?????	?????	?????
Mendozasaurus	?????	?????	?????	?????	?????	?????
Futalongkosaurus	?????	?????	?????	?????	?????	?????
Ligabuesaururs	??0??	?????	?????	?????	?????	?????
Epachthosaurus	?????	?????	?????	?????	?????	?????
Andesaurus	?????	?????	?????	?????	?????	?????
Argentinosaurus	?????	?????	?????	?????	?????	?????
Phuwiangosaurus	?????	?????	?????	?????	?????	?????
Galvesaurus	?????	?????	?????	?????	?????	?????
Tastavinsaurus	?????	?????	?????	?????	?????	?????
Paluxysaurus	?????	0????	?????	?????	?????	?????
Europasaurus	111?0	011?1	00110	1?01?	10010	10111
Venenosaurus	?????	?????	?????	?????	?????	?????
Apatosaurus	00111	1011?	111?0	10111	?1010	11110
Barosaurus	?????	?????	?????	?????	?????	?????
Dicraeosaurus	0011?	???0?	?00?0	11111	11011	1????
Diplodocus	00111	10111	11110	10111	01010	11110
Amargasaurus	?????	???1?	?0010	1111?	11011	1????
Nigersaurus	0010?	000??	?0011	-001?	?-1--	-?111
Limaysaurus	?????	??01?	?0011	-0011	0-1--	10?11
Rebbachisaurus	?????	?????	?????	?????	?????	?????

DATA MATRIX *Continued*

	35	40	45	50	55	60
Plateosaurus	–0000	00000	00001	00000	00100	00000
Mamenchisaurus	0?0??	01?00	????0	?0?10	00000	00000
Omeisaurus	0?1??	1100?	0?0?0	?0010	000?0	01?00
Tazoudasaurus	–????	?????	?????	??00	000??	?0000
Shunosaurus	00100	10000	0000?	00010	00000	00?00
Patagosaurus	?????	?1???	?????	????0	????0	??00
Brachiosaurus	00101	11000	00001	10010	01110	01000
Camarasaurus	01101	11000	00000	10010	01110	01000
Tehuelchesaurus	?????	?????	?????	?????	?????	?????
Janenschia	?????	?????	?????	?????	?????	?????
Tendaguria	?????	?????	?????	?????	?????	?????
Haplocanthosaurus	?????	?????	???0?	?????	?????	?????
Euhelopus	???01	?????	?????	???10	01??0	01?10
Jobaria	0?10?	1?000	??000	?0000	0???0	00000
Malawisaurus	?????	?????	?????	???10	0???0	?10??
Alamosaurus	?????	?????	?????	?????	?????	?????
Nemegtosaurus	12111	1?110	00100	01010	11100	0100?
Neuquensaurus	?????	?????	?????	?????	?????	?????
Opisthocoelicaudia	?????	?????	?????	?????	?????	?????
Rapetosaurus	12111	??11?	0100?	11000	111?0	01001
Saltasaurus	?????	??010	00101	?????	?????	?????
Isisaurus	?????	?????	?????	?????	?????	?????
Chubutisaurus	?????	?????	?????	?????	?????	?????
Malarguesaurus	?????	?????	?????	?????	?????	?????
Wintonotitan	?????	?????	?????	?????	?????	?????
Mendozasaurus	?????	?????	?????	?????	?????	?????
Futalongkosaurus	?????	?????	?????	?????	?????	?????
Ligabuesaururs	?????	?????	?????	?????	?????	0??0?
Epachthosaurus	?????	?????	?????	?????	?????	?????
Andesaurus	?????	?????	?????	?????	?????	?????
Argentinosaurus	?????	?????	?????	?????	?????	?????
Phuwiangosaurus	?????	?????	?????	?????	?????	?????
Galvesaurus	?????	?????	?????	?????	?????	?????
Tastavinsaurus	?????	?????	?????	?????	?????	?????
Paluxysaurus	?????	?????	?????	?????	?????	1?000
Europasaurus	00101	??100	00001	10010	011?0	010?0
Venenosaurus	?????	?????	?????	?????	?????	?????
Apatosaurus	0020?	?0000	10000	001??	????1	11??2
Barosaurus	?????	?????	?????	?????	?????	?????
Dicraeosaurus	?1?0?	10001	11010	10111	0???1	11?02
Diplodocus	00201	10000	10000	10111	01001	11112
Amargasaurus	?????	??001	11011	?01??	?????	?????
Nigersaurus	0????	??000	1?00?	?0110	–10?1	10101
Limaysaurus	0??0?	??100	10101	101??	?????	?????
Rebbachisaurus	?????	?????	?????	?????	?????	?????

DATA MATRIX *Continued*

	65	70	75	80	85	90
Plateosaurus	00000	00010	10000	0000–	0000–	–0000
Mamenchisaurus	10101	03112	00110	11100	00110	0Q?00
Omeisaurus	10101	03112	00110	0010–	00110	01?00
Tazoudasaurus	0000?	??000	00?01	00?0–	0??0–	–0?00
Shunosaurus	10201	10000	00101	0010–	??000	–0?00
Patagosaurus	10001	0?000	00101	0010–	???10	0?110
Brachiosaurus	00201	11112	00011	0010–	00111	?Q?10
Camarasaurus	10201	00012	01001	01101	00111	01110
Tehuelchesaurus	?????	?????	?????	???0?	???11	01110
Janenschia	?????	?????	?????	?????	?????	?????
Tendaguria	?????	??112	0????	1000–	???1?	????0
Haplocanthosaurus	?????	?1012	00001	0010–	0?011	00000
Euhelopus	10201	03112	00111	01101	00010	02?1?
Jobaria	1000?	01??2	00001	0010–	0011?	?????
Malawisaurus	?0201	????0	10011	?010–	00?1?	12?01
Alamosaurus	????0	2???1	10000	?0??–	?1???	?2?0?
Nemegtosaurus	01201	2????	?????	?????	???0?	?????
Neuquensaurus	?????	????1	00001	?0??–	???11	?2?01
Opisthocoelicaudia	?????	?????	?????	01??0	0?21?	1??11
Rapetosaurus	0120?	????1	10011	?0??–	?????	?2?1?
Saltasaurus	?????	??012	00001	1010–	0??1?	12?01
Isisaurus	?????	????1	10001	0010–	0??10	???01
Chubutisaurus	?????	?????	?????	?????	?0?11	02–10
Malarguesaurus	?????	?????	?????	?????	?????	?????
Wintonotitan	?????	?????	?????	?????	???11	02???
Mendozasaurus	?????	??111	0??01	?010–	1??11	02??1
Futalongkosaurus	?????	????0	00001	?01??	1??11	02??1
Ligabuesaururs	00???	??111	00001	001?–	1??1?	?2000
Epachthosaurus	?????	?????	?????	?????	0???1	?2??0
Andesaurus	?????	?????	?????	?????	???1?	12??0
Argentinosaurus	?????	?????	?????	?????	???11	1??00
Phuwiangosaurus	?????	??002	01001	0110?	???1?	????1
Galvesaurus	?????	??102	0??11	0010–	01?11	0Q?10
Tastavinsaurus	?????	?????	?????	?????	???11	0Q110
Paluxysaurus	1120?	????2	01?1?	00???	???1?	?2?0?
Europasaurus	?011?	??012	00000	10??–	?1?11	1??00
Venenosaurus	?????	?????	?????	?????	?????	?????
Apatosaurus	012?1	22112	01001	11101	?1211	01?00
Barosaurus	?????	?2112	01?11	?1111	?121?	0??00
Dicraeosaurus	01201	20102	01001	01101	?1100	–??00
Diplodocus	01200	22112	01011	11111	?1211	01100
Amargasaurus	?????	?1??2	01001	01100	??200	–??0?
Nigersaurus	0121?	2???2	00001	?0??–	???11	?????
Limaysaurus	?121?	2???2	00001	0010–	???1?	0??01
Rebbachisaurus	?????	?????	?????	?0??–	?????	???0?

DATA MATRIX *Continued*

	95	100	105	110	115	120
Plateosaurus	0000–	00000	–0000	–0000	00000	00P00
Mamenchisaurus	0P001	00001	00110	10000	01111	10000
Omeisaurus	100?1	00001	00111	10010	01011	10000
Tazoudasaurus	10000	000?0	0011?	10000	01001	10000
Shunosaurus	?1000	00000	–00?0	–?000	?0001	00000
Patagosaurus	10001	000?1	00110	–0000	00001	00000
Brachiosaurus	00021	0020?	10111	10010	10?11	11100
Camarasaurus	00?01	00201	00110	10010	01111	10000
Tehuelchesaurus	10?01	000?1	1?100	000–0	01110	10110
Janenschia	?????	?????	?????	?????	?????	?????
Tendaguria	??1??	?0??1	0????	?????	?????	?????
Haplocanthosaurus	01101	001?1	10110	10010	001P1	1001?
Euhelopus	–1101	001?1	10111	10002	11111	110?0
Jobaria	?????	000?1	?0111	1?0??	?1?01	1???0
Malawisaurus	00??0	001?1	101?0	?0011	1?211	1???0
Alamosaurus	?0???	001?1	?0110	001??	???11	1????
Nemegtosaurus	?????	?????	?????	?????	?????	?????
Neuquensaurus	–1?20	00??1	??11	0?0?1	11211	11?11
Opisthocoelicaudia	000–1	001?1	10111	00102	1?211	11101
Rapetosaurus	?????	?01?1	?01?0	0????	???11	1????
Saltasaurus	–1111	001?1	101?1	00112	1?211	11111
Isisaurus	–0??1	000?1	10110	00?12	1?211	10??1
Chubutisaurus	00?01	0???1	10???	????1	11111	?110?
Malarguesaurus	?????	?????	?????	?????	?????	?????
Wintonotitan	?????	??Q??	1????	????1	11?11	1?1??
Mendozasaurus	?00?1	000?1	1????	?????	?????	???1?
Futalongkosaurus	?002?	000?1	1????	0???2	11?1?	11?1?
Ligabuesaururs	000?0	102?1	1?111	0?001	11111	11110
Epachthosaurus	000?0	001?1	1?110	0?0?1	11?11	11?10
Andesaurus	00???	00???	1?111	000?1	1?111	1?110
Argentinosaurus	00?10	002?1	1?1?1	?0??1	??211	?1110
Phuwiangosaurus	01?1?	000?1	10111	?00?0	0??11	?1100
Galvesaurus	00?20	002?1	00110	00000	1??10	10000
Tastavinsaurus	00???	001??	00110	1?0?0	11?11	10101
Paluxysaurus	01??0	00??1	10111	1?0??	?1211	????0
Europasaurus	?0?01	001?1	10110	1?0?0	11?11	10?0?
Venenosaurus	?????	?????	?????	?????	?????	?????
Apatosaurus	10001	00011	01111	11011	11101	1010?
Barosaurus	10??1	000?1	0?1?1	110?1	1?001	10???
Dicraeosaurus	01001	11011	–1100	11011	11101	10000
Diplodocus	10001	00011	01111	11011	11011	10000
Amargasaurus	010?1	11011	–?1??	?1P?1	11101	1010?
Nigersaurus	?????	?????	?????	?????	?????	?????
Limaysaurus	01001	110?1	001?1	110?1	11101	1010?
Rebbachisaurus	?????	11???	??111	1?0??	???01	1????

DATA MATRIX *Continued*

	125	130	135	140	145	150
Plateosaurus	00000	00000	00000	00100	00000	−0000
Mamenchisaurus	001?0	1101?	00010	01101	02000	−0000
Omeisaurus	0?110	1101?	00000	01100	00000	−0000
Tazoudasaurus	00???	???10	00000	01??0	000?0	−0000
Shunosaurus	00000	00010	00000	01100	00000	−0000
Patagosaurus	001?0	??01?	00000	01???	?00??	?????
Brachiosaurus	11110	11110	00001	01?00	00000	−1100
Camarasaurus	0?110	11110	00000	01100	00000	−1101
Tehuelchesaurus	01?1?	??1??	?????	?????	?????	?????
Janenschia	?????	???0?	00?00	00?0?	?2001	00001
Tendaguria	?????	?????	?????	?????	?????	?????
Haplocanthosaurus	00110	11110	0?000	11?00	00000	−1100
Euhelopus	112?0	11???	?????	?????	?????	?????
Jobaria	00110	11??0	0??0	??100	00000	−1100
Malawisaurus	1????	???0?	0?0?1	1??0?	?20?0	−1110
Alamosaurus	?????	???0?	10011	10012	12000	−1101
Nemegtosaurus	?????	?????	?????	?????	?????	?????
Neuquensaurus	??210	????1	?????	????2	020?0	−11?1
Opisthocoelicaudia	11210	??01?	00111	1101−	1−000	−1101
Rapetosaurus	??2??	?????	?????	?????	?2??0	?????
Saltasaurus	??210	1?001	10111	?????	?20?0	−1111
Isisaurus	?1210	?100?	0??11	10???	?2000	−1101
Chubutisaurus	11???	???10	00001	00?00	0100−	−??0
Malarguesaurus	?????	???00	00?01	00???	?100?	011?0
Wintonotitan	?????	???10	00111	??00?	?100?	011??
Mendozasaurus	?????	???10	0??1	00??1	?200?	111?0
Futalongkosaurus	??2?0	1?0?0	?????	????1	0????	?????
Ligabuesaururs	?1???	?????	?????	?????	?????	?????
Epachthosaurus	102??	?????	?????	?1?01	0200?	?11?1
Andesaurus	?????	????0	000?1	?000?	1200?	????0
Argentinosaurus	??Q??	?????	?????	?????	?????	?????
Phuwiangosaurus	??1??	??11?	00011	01???	?10?0	00??0
Galvesaurus	11110	?1010	0?0?1	?????	?100?	?????
Tastavinsaurus	0?110	1?1?0	0?001	??000	01000	00000
Paluxysaurus	1111?	?1??0	00??1	?0???	?0000	01101
Europasaurus	0011?	011?0	???01	??1?0	00000	01100
Venenosaurus	11???	???10	00001	00???	?1000	00100
Apatosaurus	00111	11110	11000	01201	00001	11101
Barosaurus	001??	?10?0	11110	01?01	02111	11101
Dicraeosaurus	00111	?1010	1?000	01?01	00001	01101
Diplodocus	00111	11110	11110	01201	02111	11101
Amargasaurus	?01?1	?????	?????	????0	??0??	?????
Nigersaurus	00???	?????	?????	?????	?????	?????
Limaysaurus	0????	???10	110?0	?0Q00	00000	−1101
Rebbachisaurus	?????	?????	?????	?????	?????	?????

DATA MATRIX *Continued*

	155	160	165	170	175	180
Plateosaurus	00–00	10000	–0–00	00001	10000	0000?
Mamenchisaurus	0000?	00?0?	?1100	?010?	????0	0?0??
Omeisaurus	0000?	00?0?	?1100	00100	?00?0	00000
Tazoudasaurus	00000	00000	?1100	??000	?????	00???
Shunosaurus	0000?	00?0–	–1110	10000	1?000	00010
Patagosaurus	???0?	00?0?	???00	??10?	100?0	00?1?
Brachiosaurus	00000	0000?	???10	??101	??010	00010
Camarasaurus	00000	00000	–1010	10101	11010	00010
Tehuelchesaurus	?????	?????	?????	??100	11010	01?1?
Janenschia	00001	10?0?	?????	?????	?????	?????
Tendaguria	?????	?????	?????	?????	?????	?????
Haplocanthosaurus	00000	000??	???10	??000	10010	00??0
Euhelopus	?????	?????	?????	??100	??100	00???
Jobaria	00000	0000?	?1?00	10101	??010	0000?
Malawisaurus	00001	0000?	?0–11	?????	????0	001?1
Alamosaurus	00001	0110?	?0–11	11110	00111	1?111
Nemegtosaurus	?????	?????	?????	?????	?????	?????
Neuquensaurus	00001	01111	0????	??110	00101	1110?
Opisthocoelicaudia	00001	01–01	00–11	11000	00111	11101
Rapetosaurus	?00??	?11??	?????	??110	????1	001??
Saltasaurus	00001	01111	0??11	?0110	00101	11101
Isisaurus	00001	0110?	?0–11	?0010	0010?	?????
Chubutisaurus	00?00	?000?	???10	??110	1101?	?????
Malarguesaurus	00?0?	0011?	?????	?????	?????	?????
Wintonotitan	??00	?000?	???10	??110	11?1?	?????
Mendozasaurus	00?0?	0110?	?????	??110	1011?	??1??
Futalongkosaurus	?????	?????	?????	?????	?????	??1??
Ligabuesaururs	?????	?????	?????	??110	11110	?????
Epachthosaurus	0??0?	0110?	?????	?????	?????	?????
Andesaurus	00?0?	000??	?????	?????	?????	?????
Argentinosaurus	?????	?????	?????	?????	?????	?????
Phuwiangosaurus	00–10	10000	–0–10	??100	101??	??1?1
Galvesaurus	0??00	?000?	?0–11	?????	?????	??0??
Tastavinsaurus	00000	1000?	?0010	111??	?????	?????
Paluxysaurus	00000	00000	???10	??101	??010	000??
Europasaurus	00000	00?00	?0010	?010?	11?00	00010
Venenosaurus	0??00	1000?	?????	??1?0	11???	?????
Apatosaurus	11100	00?01	11100	10100	10110	00010
Barosaurus	11111	10?01	11?00	?0???	?????	??01?
Dicraeosaurus	10000	00?01	11?00	??100	??010	00???
Diplodocus	11111	10?01	11100	10100	01010	00010
Amargasaurus	?????	?0???	?????	????0	???1?	?????
Nigersaurus	?????	?????	?????	??102	?–0?0	?????
Limaysaurus	00000	00?01	1??1?	??102	0–0?0	00111
Rebbachisaurus	?????	?????	?????	??102	?–01?	?????

DATA MATRIX *Continued*

	185	190	195	200	205	210
Plateosaurus	??000	0000?	–0001	00010	00000	00000
Mamenchisaurus	??001	01?0?	11000	101?0	000??	0000?
Omeisaurus	1?001	01000	01000	00000	00010	00001
Tazoudasaurus	?0001	010??	?100?	?00?0	01?00	??000
Shunosaurus	1?001	01?00	01000	00000	01000	00001
Patagosaurus	??001	11???	11000	?????	?????	00001
Brachiosaurus	0?101	01010	11000	11111	11001	01101
Camarasaurus	0?001	01000	11000	11111	00011	00001
Tehuelchesaurus	??001	0100?	11000	?????	?????	???01
Janenschia	??101	010??	1011?	111?1	0001?	?????
Tendaguria	?????	?????	?????	?????	?????	?????
Haplocanthosaurus	0????	?????	?????	?????	????1	00001
Euhelopus	??101	01???	?????	?????	????1	??101
Jobaria	??001	01?0?	11000	01100	00011	00001
Malawisaurus	0?101	01???	00000	?1??1	11???	?????
Alamosaurus	0?111	100?1	10011	–1111	111–?	?????
Nemegtosaurus	?????	?????	?????	?????	?????	?????
Neuquensaurus	?0111	10???	10111	?????	?????	11?01
Opisthocoelicaudia	0?111	10101	10111	–1111	111–1	11101
Rapetosaurus	??101	10???	?0010	???1?	1???1	01101
Saltasaurus	0?111	101??	10111	?????	????1	11101
Isisaurus	??101	11???	101??	?????	????1	11101
Chubutisaurus	?1101	0100?	??010	?1111	11???	?????
Malarguesaurus	?????	?????	?????	?????	?????	?????
Wintonotitan	?1?01	00???	??01?	?111?	?????	?????
Mendozasaurus	??10?	00???	??0??	?11??	?????	?????
Futalongkosaurus	?????	?????	?????	?????	?????	?????
Ligabuesaururs	?1101	00?1?	?????	?????	?????	?????
Epachthosaurus	?0111	00???	?0010	?????	????1	1??0?
Andesaurus	?0???	?????	?????	?????	?????	???0?
Argentinosaurus	?????	?????	?????	?????	????1	?????
Phuwiangosaurus	?000?	000??	10101	?????	?????	00101
Galvesaurus	??001	010??	?????	?????	?????	?????
Tastavinsaurus	?????	?????	?????	?????	????1	01101
Paluxysaurus	??001	01?1?	110?0	?1?1?	11??1	0??01
Europasaurus	??001	01???	11000	?11??	????1	011?1
Venenosaurus	?????	?????	?100?	???1?	?????	???0?
Apatosaurus	0?001	01?0?	01000	11100	00011	00011
Barosaurus	???0?	0????	?????	?????	?????	??011
Dicraeosaurus	??001	0100?	110??	?????	????1	00011
Diplodocus	0?001	01000	11000	?????	????1	00011
Amargasaurus	??001	0100?	01000	?????	?????	001??
Nigersaurus	?????	?????	?????	?????	?????	?????
Limaysaurus	??000	0100?	11000	?????	?????	???01
Rebbachisaurus	????0	?????	?????	?????	?????	?????

DATA MATRIX *Continued*

	215	220	225	230	235	240
Plateosaurus	00000	00010	10001	00000	10000	00001
Mamenchisaurus	?10??	10??1	01010	01101	10?11	0?1?0
Omeisaurus	0100?	10??1	01000	00101	?0?01	00111
Tazoudasaurus	0?000	10??0	00000	000?0	01001	00000
Shunosaurus	010??	?0??1	01010	01101	00?0?	00110
Patagosaurus	0100?	10?01	01010	00001	?????	??100
Brachiosaurus	11011	11001	12110	01101	11011	00110
Camarasaurus	11001	11001	11010	01101	01011	00110
Tehuelchesaurus	11?01	11001	11100	0????	?????	?????
Janenschia	?????	????1	11110	011P1	P1?11	0?110
Tendaguria	?????	?????	?????	?????	?????	?????
Haplocanthosaurus	01000	110?1	11010	0????	?????	?????
Euhelopus	??00?	110?1	01110	01101	01?1?	00110
Jobaria	010??	11??1	?1010	01101	01?11	00110
Malawisaurus	??111	110??	?11??	???11	0?1??	??1??
Alamosaurus	?0111	1101?	?????	?????	??1??	?????
Nemegtosaurus	?????	?????	?????	?????	?????	?????
Neuquensaurus	?0111	110??	?2111	11111	01?10	1?110
Opisthocoelicaudia	1011?	11011	12111	01111	01110	11110
Rapetosaurus	101??	11?1?	??110	1????	?????	?????
Saltasaurus	10111	11011	12111	11111	0?1??	?????
Isisaurus	10111	110??	???1?	?????	??1??	?????
Chubutisaurus	??011	110?1	12110	01101	??1??	?????
Malarguesaurus	?????	?????	?21??	?????	?????	?????
Wintonotitan	??011	?101?	?????	?????	?????	?????
Mendozasaurus	?????	?????	??1??	??10?	??1??	?????
Futalongkosaurus	?0001	1101?	?????	?????	?????	?????
Ligabuesaururs	?????	?????	?????	?????	?1???	?????
Epachthosaurus	??0??	??11	????0	0????	??1??	?????
Andesaurus	10111	??01?	1????	?????	?????	?????
Argentinosaurus	?????	?????	?????	???0?	?????	?????
Phuwiangosaurus	1011?	11011	12110	01111	0????	?????
Galvesaurus	?????	100??	?????	?????	?????	?????
Tastavinsaurus	11???	11011	11110	01101	0?1??	??111
Paluxysaurus	01001	110??	12110	00101	??1??	?????
Europasaurus	110??	1100?	?1010	01101	01?11	0?1??
Venenosaurus	00???	1?0??	?????	?????	?????	?????
Apatosaurus	010?1	00101	11010	01101	01?11	01111
Barosaurus	?????	??1?1	1????	?1???	?????	?????
Dicraeosaurus	010??	00101	11010	01101	01?11	0?111
Diplodocus	010?0	001?1	11010	11101	01?11	00111
Amargasaurus	?????	????1	110?0	0????	?????	?????
Nigersaurus	?????	????0	?????	?????	?????	?????
Limaysaurus	01000	110?1	110?0	0?10?	?1???	0?100
Rebbachisaurus	??0??	11???	?????	?????	?????	?????

DATA MATRIX *Continued*

	245	249
Plateosaurus	00000	0000
Mamenchisaurus	1?111	1???
Omeisaurus	11111	1111
Tazoudasaurus	?0?00	0100
Shunosaurus	10111	?111
Patagosaurus	?????	????
Brachiosaurus	1?11?	1??1
Camarasaurus	11111	1111
Tehuelchesaurus	?????	????
Janenschia	11011	?111
Tendaguria	?????	????
Haplocanthosaurus	?????	????
Euhelopus	11?1?	??1?
Jobaria	111??	????
Malawisaurus	?????	????
Alamosaurus	?????	????
Nemegtosaurus	?????	????
Neuquensaurus	???1?	????
Opisthocoelicaudia	11111	1011
Rapetosaurus	?????	????
Saltasaurus	?????	????
Isisaurus	?????	????
Chubutisaurus	1????	????
Malarguesaurus	?????	????
Wintonotitan	?????	????
Mendozasaurus	1????	????
Futalongkosaurus	?????	????
Ligabuesaururs	?????	????
Epachthosaurus	?????	????
Andesaurus	?????	????
Argentinosaurus	?????	????
Phuwiangosaurus	?????	????
Galvesaurus	?????	????
Tastavinsaurus	0111?	1001
Paluxysaurus	?????	????
Europasaurus	1??1?	1??1
Venenosaurus	?????	????
Apatosaurus	11?11	11?1
Barosaurus	?????	????
Dicraeosaurus	?11??	??1?
Diplodocus	11111	1?11
Amargasaurus	?????	????
Nigersaurus	?????	????
Limaysaurus	11???	????
Rebbachisaurus	?????	????

SYNAPOMORPHIES

Synapomorphies of nodes in the phylogenetic analysis (numbers in parentheses indicate character state at the node). An asterisk denotes ambiguous synapomorphies under accelerated transformation; ° indicates ambiguous synapomorphies under delayed transformation. For numbers of nodes see Figure 24.

Node 1, Eusauropoda: °2(1); °8(1); °9(1); °18(1); °26(1); °28(1); 29(1); °33(1); °36(1); 49(1); 61(1); °65(1); °179(1); °195(0); °199(0); 210(1); °212(1); 220(1); 221(1); 224(1); *228(1); 230(1); 238(1); *239(1); °241(1); *242(1); °243(1); 244(1); 245(1); *246(1); 248(1); 249(1)

Node 2: 1(1); *14(1); *35(1); 37(1); *46(1); *67(1); *83(1); 84(1); *87(1); °88(1); 95(1); 100(1); °103(1); 123(1); *124(1); *126(1); *127(1); 168(1); *174(1); *191(1); *202(1); *204(1); °242(1)

Node 3: °16(1); 63(1); 68(1); 69(1); 70(2); *74(1); *75(0); *83(1); °87(1); *109(1); 112(1); 114(1); 116(1); °124(1); °126(1); °127(1); °204(1); °228(1); °239(1)

Node 4: 4(1); 7(1); °30(1); 91(0); *92(1); 113(1); *181(1); °191(1); 196(1); 198(1); *205(1); 227(1); 234(1); °246(1)

Node 5, Neosauropoda: 3(1); 10(1); °14(1); °35(1); °46(1); 52(1); 63(2); °67(1); 73(0); *74(0); *75(1); 85(1); °109(1); *128(1); 147(1); 148(1); °166(1); °174(1); °181(1); 197(1); °205(1); 217(1); 221(1); 232(1)

Node 6, Diplodocoidea: *37(0); *41(1); *99(1); 105(1); *107(1); *110(1); *111(1); 114(0); *118(1); *132(1); *160(1); *170(1); *171(0)
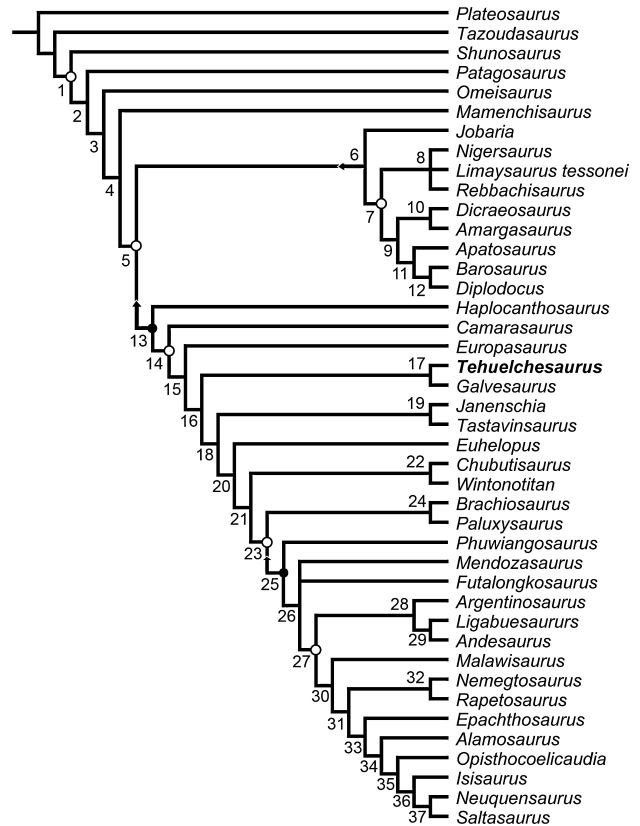

Figure 24. Phylogenetic hypothesis presented here, with internal nodes numbered for list of synapomorphies (see Appendix).

Node 7: 1(0); 2(0); *5(1); 7(0); *11(1); 20(1); *22(1); *33(2); °41(1); 48(1); 55(1); 56(1); 58(1); *60(1); 61(0); 62(1); 66(2); *82(1); *83(2); *96(1); *97(1); °107(1); °110(1); °111(1); *125(1); 131(1); °132(1); *138(2); 150(1); °160(1)

Node 8, Rebbachisauridae: *8(0); *15(1); *18(0); *23(1); *45(1); *64(1); *90(1); °96(1); °97(1); *137(1); *164(1); 170(2); *178(1); *180(1); *185(0); *239(0)

Node 9, Flagellicaudata: *6(1); °22(1); *27(1); *30(0); °37(0); 50(1); 57(1); °60(2); 72(1); 77(1); °82(1); °99(1); 102(1); °125(1); *140(1); 145(1); 151(1); 209(1); 216(0); 217(0); 218(1); 240(1)

Node 10, Dicraeosauridae: 17(1); 21(1); 25(1); *32(1); 40(1); 42(1); 44(1); *69(0); 84(0); 85(0); °96(1); °97(1); *104(0); *105(0)

Node 11, Diplodocidae: °5(1); °6(1); °11(1); 12(1); 13(1); °27(1); °30(0); *33(2); *59(1); 67(2); 76(1); °83(2); 91(1); *92(0); *96(0); *97(0); °138(2); °140(1); 146(1); 152(1); 153(1)

Node 12, Diplodocinae: *65(0); 74(1); 79(1); 113(0); 133(1); 134(1); 142(2); 143(1); 144(1); 154(1); 155(1); 156(1); *172(1); *226(1)

Node 13, Macronaria: *53(1); *54(1); *57(1); 68(0); *93(1); 98(1); *101(1); °128(1); *163(1); 164(1); *199(1); *200(1)

Node 14, Camarasauromorpha: °53(1); °57(1); *89(1); *92(0); °163(1); 172(1); °199(1); 200(1); 211(1); 215(1)

Node 15: 45(1); *82(1); *109(0); 111(1); *118(1); 135(1); *137(1); 162(0); 207(1); 208(1); *233(1)

Node 16: 68(1); 74(1); °89(1); 122(1); *138(0); 142(1); *167(1); 223(1)

Node 17: *69(0); 106(0); 115(0); *129(0); *165(1); *177(1); *224(0)

Node 18: *87(2); °137(0); °138(0); °167(1); 183(1); *192(0); *194(1); 219(1); °233(1)

Node 19: *120(1); *129(0); 147(0); 148(0); 156(1); *193(1)

Node 20: *82(0); *87(2); *88(0); °101(1); 105(1); 117(1); 121(1); °183(1); °201(1); *202(1); *204(0)

Node 21: *61(0); *66(1); °118(1); °201(1); °202(1); 214(1); 222(2)

Node 22: 110(1); 169(1); 182(1); °194(1)

Node 23, Titanosauriformes: °66(1); *89(0); *93(0); 113(2); *172(0); *189(1); *194(0)

Node 24, Brachiosauridae: *27(1); *98(2); *109(1); 170(1); °189(1); *192(1); *219(0); *231(1)

Node 25, Somphospondyli: *22(1); *26(0); *31(1); *32(2); *34(1); *39(1); *47(1); *60(1); *66(2); 74(0); *81(1); 90(1); *98(0); *106(0); 134(1); *140(1); 169(1); °172(0); 173(1); 178(1); 180(1); 187(0); *190(1); °192(0); *203(1); 212(0); *213(1); *235(0); *236(1); *237(1)

Node 26: 70(1); °106(0); 119(1); 123(2); 128(1); °140(1); 142(2); *146(1); *155(1); *160(1); *165(1)

Node 27: °61(0); 86(1); °89(1); 95(0); *98(1); 110(1); *129(0); *136(1); *141(1); °213(1)

Node 28: *3(0); 90(0); 98(2); *172(1)

Node 29: 113(1)

Node 30: *68(0); 71(1); *74(1); *81(0); 105(0); *109(1); °129(0); *130(1); °136(1); °155(1); °165(1); *171(0); 229(1)

Node 31: *1(0); *9(0); °22(1); °39(1); *51(1); *62(1); °66(2); *82(1); *150(1); 157(1); 158(1); 175(1); *186(1); 194(1)

Node 32: °1(0); °9(0); 20(1); °26(0); °31(1); °32(2); °34(1); 38(1); °47(1); °51(1); °62(1); *84(0); 89(1); *226(1)

Node 33: *65(0); *74(0); °150(1); *177(1); 184(1); 206(1)

Node 34: *95(1); 108(1); *110(2); *120(1); 139(1); 140(2); °171(0); *176(1); °186(1); °190(1); 195(1); °203(1); *225(1)

Node 35: °95(1); *105(1); °110(2); *120(1); 133(1); °160(1); *168(0); °176(1); °177(1); 179(0); 188(1); 193(1); °225(1); °235(0); °236(1)

Node 36: *93(1); 167(0); 174(0); *226(1)

Node 37: 71(0); *76(1); 92(1); °105(1); °130(1); *131(1); *149(1); 159(1); °168(1); °226(1)