

# An enigmatic plant-eating theropod from the Late Jurassic period of Chile

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**Theropod dinosaurs were the dominant predators in most Mesozoic era terrestrial ecosystems<sup>1</sup>. Early theropod evolution is currently interpreted as the diversification of various carnivorous and cursorial taxa, whereas the acquisition of herbivorism, together with the secondary loss of cursorial adaptations, occurred much later among advanced coelurosaurian theropods<sup>1,2</sup>. A new, bizarre herbivorous basal tetanuran from the Upper Jurassic of Chile challenges this conception. The new dinosaur was discovered at Aysén, a fossil locality in the Upper Jurassic Toqui Formation of southern Chile (General Carrera Lake)<sup>3,4</sup>. The site yielded abundant and exquisitely preserved three-dimensional skeletons of small archosaurs. Several articulated individuals of *Chilesaurus* at different ontogenetic stages have been collected, as well as less abundant basal crocodyliforms, and fragmentary remains of sauropod dinosaurs (diplodocids and titanosaurs).**

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

*Chilesaurus diegosuarezi* gen. et sp. nov.

**Etymology.** In reference to Chile, and honoring Diego Suárez, who at the age of 7, discovered the first bone remains in the Toqui Formation. **Holotype.** Servicio Nacional de Geología y Minería, Chile (SNGM)-1935 consists of a nearly complete, articulated skeleton, approximately 1.6 m long (Fig. 1, Supplementary Information and Extended Data Fig. 1). Holotype specimen was skeletally immature at the time of its death, as evidenced by the incomplete fusion of neurocentral sutures. This ontogenetic inference agrees with the size of the holotype, which represents 50% the length of the larger specimen SNGM-1888 (ref. 3). **Paratypes.** Postcranial skeletons of four individuals, corresponding to different ontogenetic stages, ranging approximately from 1.2 to 3.2 m in total length (Extended Data Table 1). Several specimens referred to as indeterminate theropods and tetanurans previously<sup>3</sup> are here referred to as *Chilesaurus diegosuarezi*.

**Locality and horizon.** Central Patagonian Cordillera, Aysén (Chile; approximately 46° S); Toqui Formation<sup>3,4</sup>, Tithonian, latest Jurassic.

**Diagnosis.** *Chilesaurus* differs from other dinosaurs in the following combination of autapomorphies: premaxilla short and deep, with prominent plate-like postnasal process; teeth leaf-shaped, being finely denticulate only on the crown apex of erupting teeth; coracoid subquadrangular in side view and with transversely thick margins; manual digit II with short pre-ungual phalanges; manual digit III atrophied; iliac blade with posterodorsal prominence; ischiadic peduncle of ilium robust; supracetabular crest absent; pubis fully retroverted; pubic shaft rod-like and distally unexpanded; femoral mediobasal crest absent; tibia without fibular crest. In addition, *Chilesaurus* shows the

following unique combination of characters: dentary deeper anteriorly than posteriorly; cervicals with septate and paired pleurocoels; pubic apron transversely narrow; ischia connected through a proximodistally extended medial lamina ('ischial apron'); femoral greater trochanter anteroposteriorly expanded, astragalar ascending process lower than astragalar body; calcaneum subtriangular in distal view; metatarsal I robust, elongate, and proximally compressed transversely; metatarsal II transversely wider than the other metatarsals; pedal digit I large.

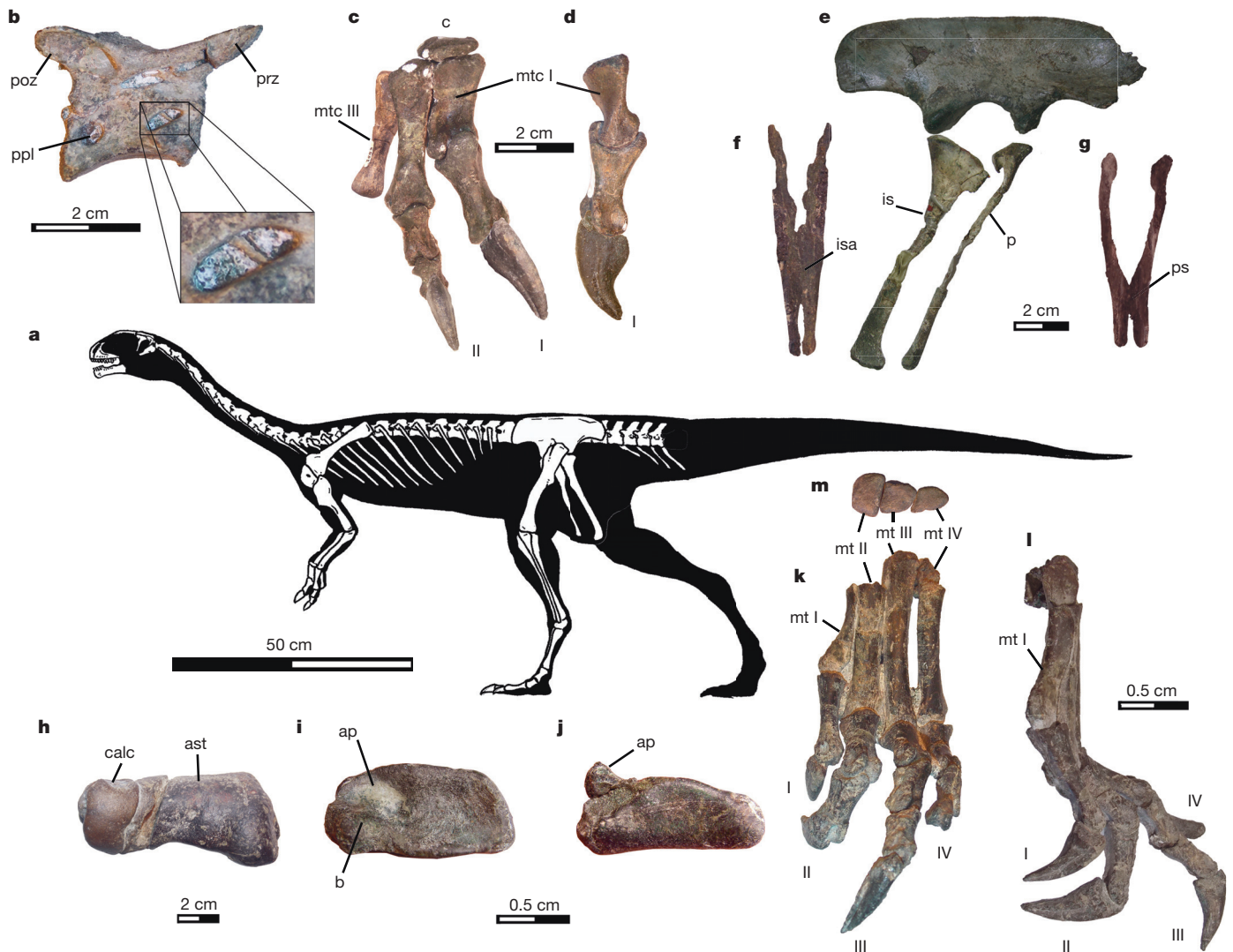
Isolated skull material (including premaxilla, maxillae, frontals, postorbital, squamosal, basicranium, ectopterygoid and dentary; Extended Data Fig. 2), suggests a proportionally small head for *Chilesaurus*. The premaxilla is short and deep, with a rugose rostral margin that suggests a ramphotheca (Fig. 2). Frontals are elongate and narrow and participate extensively in the orbital margin. The basi-sphenoidal recess is deep. The dentary is short and deep, with a downturned symphyseal region but a straight alveolar margin. Dentary teeth are tall, leaf-shaped, and procumbent, with small serrations restricted to the crown apex (Fig. 2).

Cervical vertebrae are long and low, forming a slender neck. Cervical and anterior dorsal vertebrae possess a pair of septate pleurocoels, which are absent posterior to the pectoral region (Fig. 1g). 'Pectoral' vertebrae bear prominent hypapophyses.

The scapular blade (Extended Data Fig. 3) is elongate and slightly anteroposteriorly expanded distally, as in basal averostrans<sup>5</sup>. The coracoid is subquadrangular and lacks theropod characteristics such as the posteroventral process and biceps tuberosity<sup>1</sup>. It is notably thick transversely, contrasting with the delicate anterodorsal and dorsal margins of most dinosaurs. The limb bones are stout, as in sauropodomorphs, and forelimb length is 56% that of hind limbs. The humerus is proximodistally short and transversely wide (Extended Data Fig. 3). The single proximal carpal is large, with a transversely convex proximal articular surface. Metacarpals I–III are present, but only manual digits I and II are well developed (Fig. 1d–f). Metacarpal I is stout, and phalanx 1-I is short and strongly twisted along its main axis, as in basal sauropodomorphs<sup>6</sup>. The ungual of digit I is shorter than metacarpal II and less curved than most basal tetanurans<sup>5,7</sup>. Metacarpal II is the longest, and its digit presents strongly shortened pre-ungual phalanges, as in some ceratosaurians<sup>8</sup>. Metacarpal III is much more slender than in basal theropods, and its digit comprises a single minute phalanx.

The ilium is dolichoiliac, typical for Theropoda<sup>1</sup> (Fig. 1b). The pubic pedicle is elongate (as in sauropods, ornithischians and therizinosaurs<sup>2,9</sup>), and the ischiadic peduncle is bulbous, as in ornithischians and alvarezsaurid coelurosaurs<sup>10</sup>. A prominent supratrochanteric process is present on the posterodorsal corner of the ilium, similar to those of sauropods, therizinosaurs, paravians, and some ornithischians<sup>11–13</sup>. The acetabular roof is transversely narrow and a supracetabular crest

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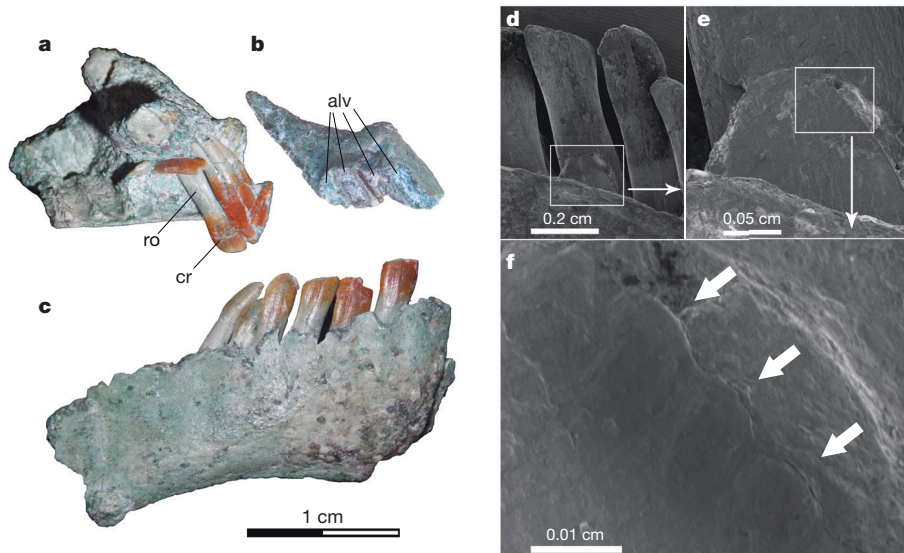


**Figure 1 | Skeletal anatomy of *Chilesaurus diegosuarezi* gen. et sp. nov.** **a**, Reconstructed skeleton (SNGM-1935). **b**, Fourth cervical vertebra (SNGM-1935) in right lateral view, with a close-up of tabicated anterior pleurocoel. **c**, **d**, Composite reconstruction of right hand (carpals, metacarpals, and non-ungual phalanges of digits I and II) are from specimen SNGM-1935; ungual phalanges I and II are from specimen SNGM-1887; metacarpal III is from specimen SNGM-1887 in dorsal (**c**) and medial (**d**) views. **e**, Pelvic girdle (SNGM-1936) in right lateral view. **f**, Articulated ischia (SNGM-1936) in

is absent, as occurs in derived coelurosaur and ornithomorphs<sup>1,11,13</sup>. The pubis (Fig. 1b, c) closely resembles that of basal ornithomorphs, therizinosaurs and dromaeosaurid paravians in being fully retroverted, with a reduced proximal end bearing a posteriorly open obturator notch<sup>1,2</sup>. The pubic apron is transversely narrow and the pubis has a rod-like shaft. It is distally unexpanded with a rounded contour, sharply contrasting with the prominent distal 'foot' of other theropods<sup>1</sup>. The ischium (Fig. 1a, b) is proximally expanded and lacks an obturator process. Notably, both ischia are connected through a proximodistally extended medial lamina (ischial apron), a feature reported in some megalosauroids<sup>14</sup>.

The femur is robust (Extended Data Fig. 4). The greater trochanter is anteroposteriorly expanded, similar to coelurosaur. The anterior trochanter is wing-like and proximally projected, and the fourth trochanter is semicircular. The distal third of the femur resembles sauropodomorphs in that it lacks distinctive theropod features, such as an anteromedial elliptical muscle scar, a mediolateral crest and its associated medial adductor fossa. The cnemial crest of tibia (Extended Data Fig. 4) is rounded in lateral view, as in basal sauropodomorphs and

basal ornithomorphs, and differs from the subtriangular crest present in most basal theropods<sup>1,15</sup>. As in sauropodomorphs, and unlike most theropods, the proximal end of the tibia lacks a fibular crest<sup>1</sup>. Like theropods, the distal end of the tibia is anteroposteriorly compressed with a laterally extending malleolus, more transversely expanded than in coelophysoids, but less than in tetanurans<sup>1</sup>. The fibula lacks a proximomedial pocket and iliofibular tubercle. The tarsus (Fig. 1k–m) resembles basal saurischians<sup>16</sup>. The astragalar ascending process is low and broad, unlike tetanurans, in which it is laminar, tall, and transversely wide<sup>1,6,17</sup>. The proximal astragalar surface possesses a deep, well-defined basin posterior to the ascending process, as in basal dinosaurs. As in early saurischians (for example, *Herrerasaurus*, basal sauropodomorphs), the calcaneum of *Chilesaurus* is transversely wide and subtriangular in distal view, rather than rectangular and disc-shaped as in theropods<sup>1,16,17</sup>. The foot is wide and proximodistally short (Fig. 1h–j). The proximal half of metatarsal I is transversely compressed but anteroposteriorly expanded, unlike most theropods, in which it tapers proximally. Metatarsal I of *Chilesaurus* represents more than 50% of the length of metatarsal II, in contrast with



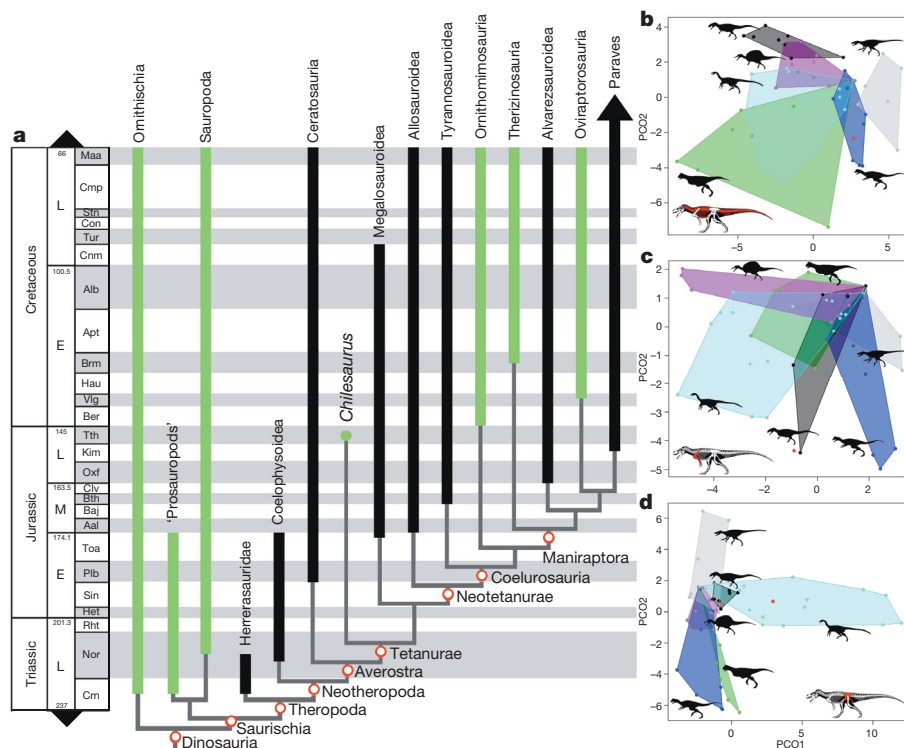
**Figure 2** | Selected cranial bones and teeth of *Chilesaurus diegosuarezi* gen. et sp. nov. (SNGM-1935). **a**, Partial right (?) maxilla in lateral view. **b**, Left premaxilla in medial view. **c**, Right dentary in lateral view. **d**, Details of dentary

teeth in lingual view. **e**, Crown of unerupted dentary tooth. **f**, Detail of the carina of an unerupted tooth (arrows indicate denticle positions). *alv*, alveoli; *cr*, crown tooth; *ro*, root tooth.

most other theropods (25–33%)<sup>1,17</sup>. Metatarsal III is the longest, but metatarsal II is the thickest, as in basal sauropodomorphs. Digit I is large, only slightly shorter than digit II, approaching the tetradactyl condition of early sauropodomorphs, ornithischians<sup>18</sup> and derived therizinosaur<sup>2</sup>.

The bizarre anatomy of *Chilesaurus* raises interesting questions about its phylogenetic relationships. We scored *Chilesaurus* into four

different integrative archosauriform, theropod and sauropodomorph data sets<sup>9,19–21</sup>. Remarkably, all these analyses placed *Chilesaurus* as a member of Theropoda, near the origin of tetanurans<sup>5</sup> (Fig. 3a), dismissing conceivable positions near Therizinosauria, Sauropodomorpha or Ornithischia. The theropodan position of *Chilesaurus* is supported by pleurocoels in cervical and anterior dorsal vertebrae; hypapophyses on ‘pectoral’ vertebrae; preacetabular process of ilium



**Figure 3** | Phylogenetic relationships of *Chilesaurus diegosuarezi* gen. et sp. nov. among main dinosaur clades and its plots in the theropod morphospaces. **a**, Time-calibrated simplified strict consensus tree, in which the green bars indicate herbivorous dinosaur lineages<sup>28</sup>. E, Early; L, Late; M, Middle. Aal, Aalenian; Alb, Albian; Apt, Aptian; Baj, Bajocian; Ber, Berriasian; Brm, Barremian; Bth, Bathonian; Clv, Callovian; Crn, Carnian; Cmp, Campanian; Cnm, Cenomanian; Con, Coniacian; Hau, Hauterivian; Het,

Hettangian; Kim, Kimmeridgian; Maa, Maastrichtian; Nor, Norian; Oxf, Oxfordian; Plb, Pliensbachian; Rh, Rhaetian; Sin, Sinemurian; Stn, Santonian; Tth, Tithonian; Toa, Toarcian; Tur, Turonian; Vlg, Valanginian. Numbers indicate millions of years ago. **b–d**, *Chilesaurus diegosuarezi* gen. et sp. nov. plotted in the theropod morphospace (principal coordinate (PCO)1 versus PCO2) based on axial skeleton (**b**); scapular girdle and forelimb (**c**); and pelvic girdle (**d**). Red dots in **b–d** indicate the position of *Chilesaurus*.

dorsoventrally expanded; femoral fourth trochanter semicircular; and tibia distally expanded and with lateral malleolus extending strongly laterally. Tetanuran affinities are supported by scapular blade elongate and strap-like; distal carpal semilunate; and manual digit III reduced (Supplementary Information). For a basal tetanuran, *Chilesaurus* possesses a number of surprisingly plesiomorphic traits on the hindlimbs, especially in the ankle and foot, which resemble basal sauropodomorphs<sup>7,9,12</sup>. These features are here considered as secondary reversals that might be related to a less-cursorial mode of locomotion. Furthermore, derived features of the dentary and teeth shared by *Chilesaurus*, sauropodomorphs and therizinosaurs are interpreted as homoplasies related to herbivorous habits<sup>22–25</sup>. In this context, pubic retroversion of *Chilesaurus* may be related to an increased gut capacity for processing plant material<sup>25</sup>.

The discovery of *Chilesaurus* lends support to the interpretation<sup>22,23</sup> that dietary diversification towards herbivory was more commonplace among basal theropods than previously thought. Independent evolution of herbivory has been recognized for several major coelurosaurian subclades<sup>23</sup>, but for just a single probable example outside Coelurosauria (that is, the toothless ceratosaurian *Limusaurus*<sup>26,27</sup>). *Chilesaurus* expands the list of non-coelurosaurian theropods that shifted their diet from carnivore to herbivore.

*Chilesaurus* represents an extreme case of mosaic evolution among dinosaurs, owing to the presence of dental, cranial and postcranial features that are homoplastic with multiple disparate groups. Using quantitative morphospace analysis, we explored morphospace occupation of different skeletal regions in *Chilesaurus* with respect to a variety of avian and non-avian theropods. This shows that *Chilesaurus* has a ceratosaur-like axial skeleton, a ‘basal tetanuran’ forelimb and scapular girdle, a coelurosaur-like pelvis, and a tetanuran-like hindlimb (Fig. 3b–d and Extended Data Fig. 5). General ankle and foot construction does not group with any theropod clade, probably as a result of the characters shared by *Chilesaurus*, sauropodomorphs and herrerasaurids.

*Chilesaurus* is the numerically dominant taxon in the Aysén tetrapod fossil assemblage, and represents an unusual case of a theropod having the palaeoecological role of a preeminent small-to-medium sized herbivore in a Jurassic ecosystem. This is in sharp contrast with other Late Jurassic dinosaur assemblages (for example, Tendaguru and Morrison formations<sup>11,27</sup>), in which ornithischian dinosaurs are the most abundant small-to-medium sized herbivores. Available evidence indicates that *Chilesaurus* is a unique dinosaur lineage known only from southern South America, suggesting an outstanding case of endemism among otherwise relatively cosmopolitan worldwide Jurassic dinosaur faunas<sup>28</sup>.

*Chilesaurus* illustrates how much relevant data on the early diversification of major dinosaur clades remain unknown. It also provides an important cautionary benchmark in our attempts to gain a reliable view of the overall evolutionary history of Dinosauria.

**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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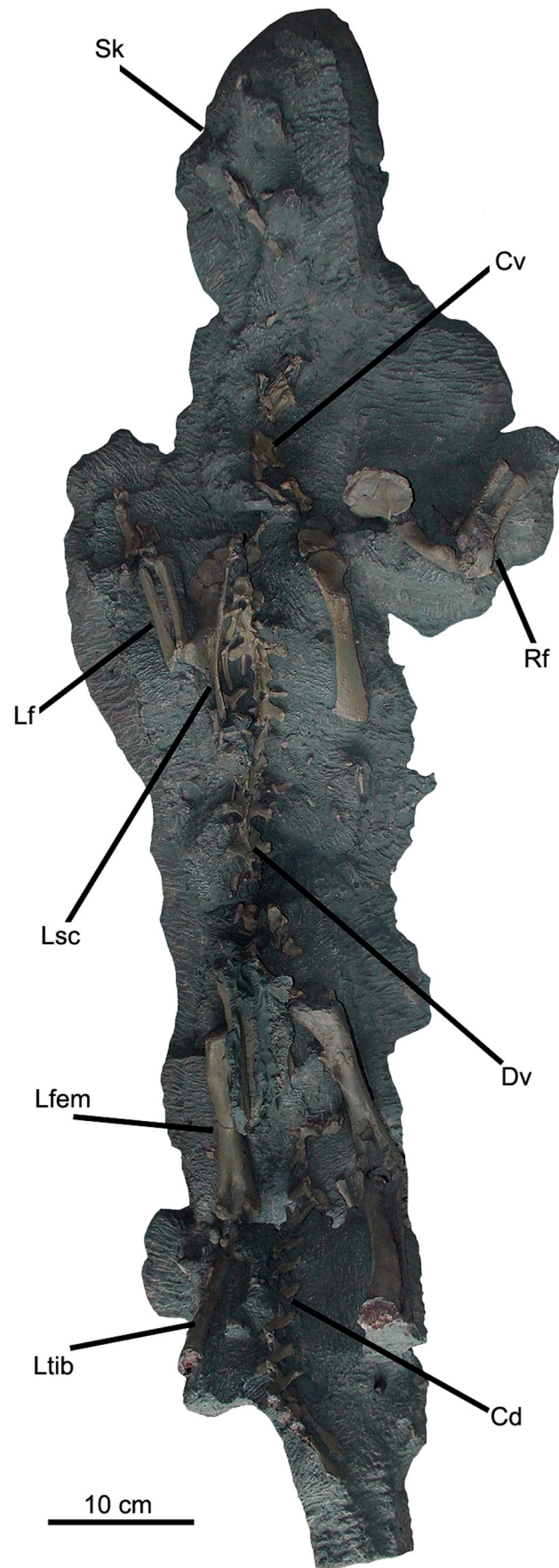
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**Supplementary Information** is available in the online version of the paper.

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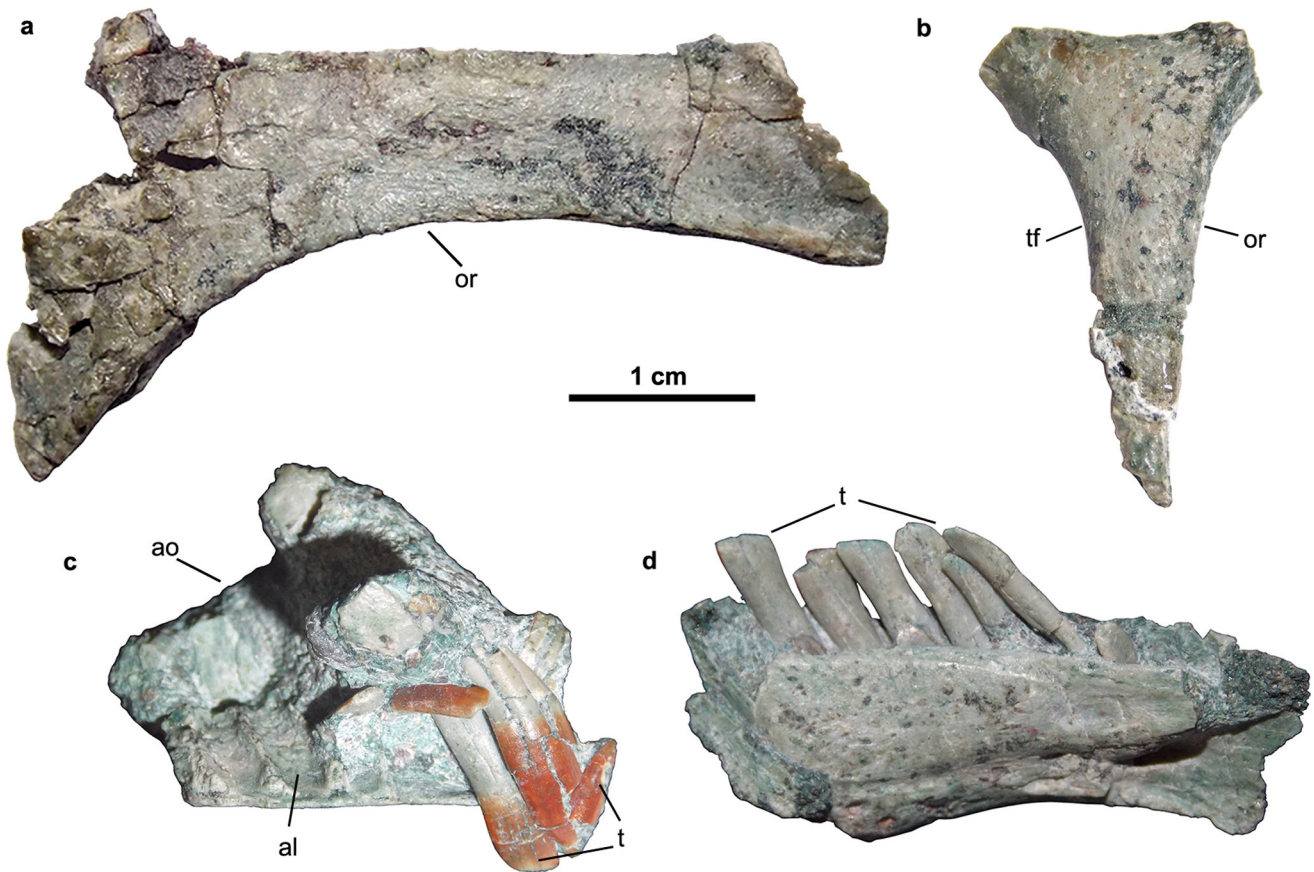
**Author Contributions** F.E.N., L.S., M.S., F.L.A., M.D.E., N.R.C., A.O.V. and D.R.-R. designed the study, collected data, performed the comparative and analytical work, and wrote the paper. R.d.l.C. and M.P.I. collected data and contributed to the writing and discussion.

**Author Information** Data have been deposited in ZooBank under Life Science Identifier (LSID) urn:lsid:zoobank.org:act:7B6DE8C7-C78D-48C0-B818-65C454AEFB58. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to F.E.N. (fernovas@yahoo.com.ar).



Extended Data Figure 1 | Holotype of *Chilesaurus diegosuarezi* gen. et sp. nov. (SNGM-1935) as it was found in the field. Cd, caudal vertebrae; Cv,

cervical vertebrae; Dv, dorsal vertebrae; Lf, left forelimb; Lfem, left femur; Lsc, left scapulocoracoid; Ltib, left tibia; Rf, right forelimb; Sk, skull.



Extended Data Figure 2 | Selected skull bones of *Chilesaurus diegosuarezi* gen. et sp. nov. (SNGM-1935; holotype). a, Right frontal in dorsal view; b, right postorbital in lateral view; c, incomplete right (?) maxilla in lateral view;

d, right dentary in medial view. al, alveolus; ao, antorbital opening; or, orbital rim; t, teeth; tf, lower temporal fossa rim.



**Extended Data Figure 3 | Scapular girdle and selected forelimb bones of *Chilesaurus diegosuarezi* gen. et sp. nov.** a, b, Left scapula and coracoid (SNGM-1938) in lateral (a) and posterior (b) views. c, Left humerus (SNGM-

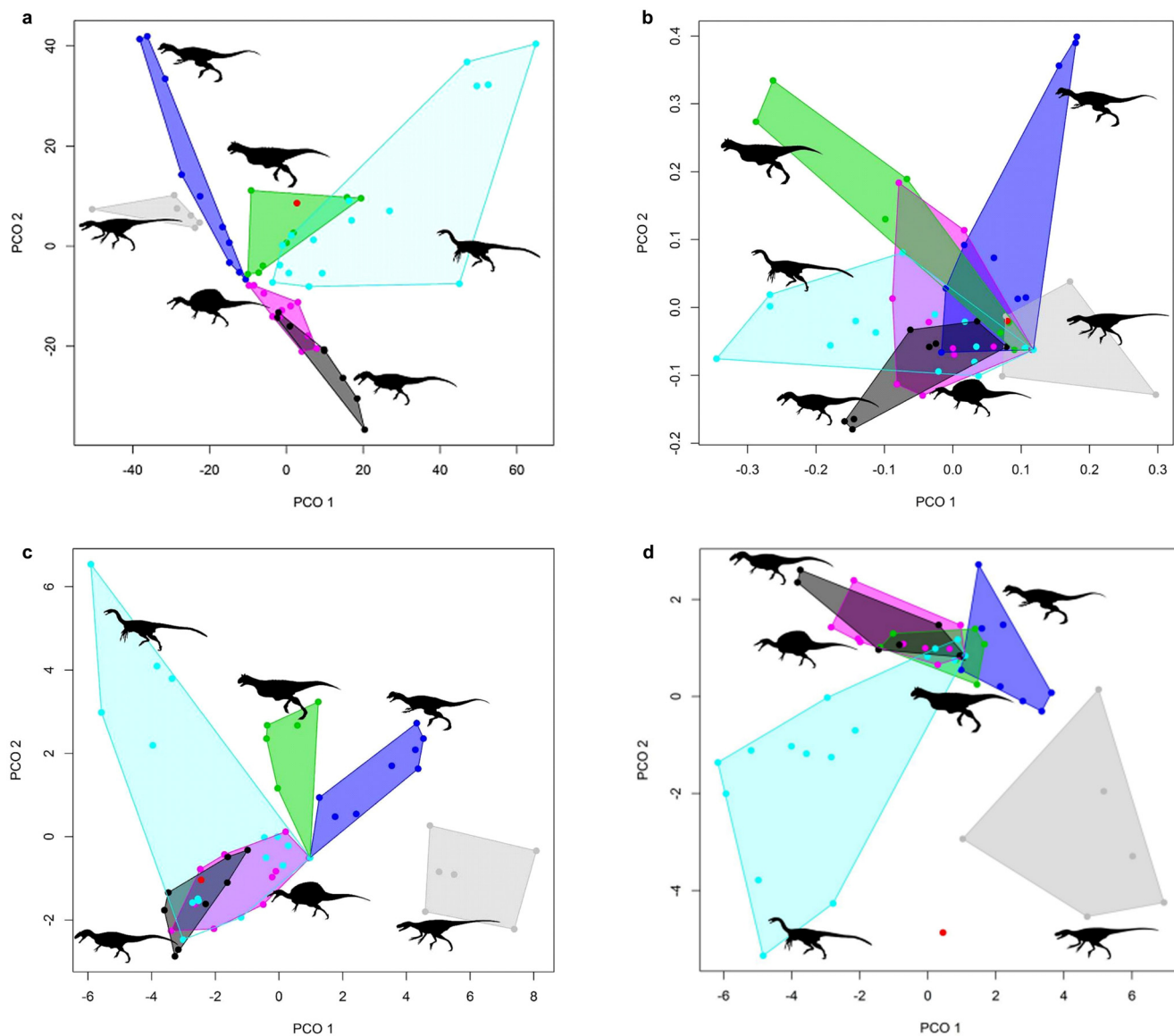
1938) in anterior view; d, left radius (SNGM-1935, holotype) in lateral view; and e, left ulna (SNGM-1935, holotype) in lateral view. cf, coracoid foramen; dp, deltopectoral crest; gl, glenoid cavity; ol, olecranon process.



**Extended Data Figure 4** | Selected hindlimb elements of *Chilesaurus diegosuarezi* gen. et sp. nov. **a, b**, Right femur (SNGM-1935) in anterior (a) and lateral (b) views. **c–e**, Articulated right tibia and fibula (SNGM-1935) in

posterior (c), medial (d) and proximal (e) views. at, anterior trochanter; cn, cnemial crest; f, fibula; fh, femoral head; 4t, fourth trochanter; gt, greater trochanter; ic, inner condyle; oc, outer condyle; t, tibia; tfc, tibiofibular crest.





**Extended Data Figure 5 | Bivariate plots showing the results of the morphospace occupation analysis of *Chilesaurus diegosuarezi* gen. et sp. nov. based on characters of different regions of the skeleton, taken from the modified data matrix and the first and second axes of the principal coordinate analysis. a–d, Bivariate plots using all the characters (a), cranial characters (b), hindlimb zeugopodium and stylopodium characters (c), and**

tarsal and pedal characters (d). The convex hulls represent different dinosauriform groups rather than statistically distinct clusters. Light grey polygon, non-neotheropod dinosauriforms; blue polygon, non-averostran neotheropods; green polygon, ceratosaurs; pink polygon, megalosauroids; dark grey polygon, allosauroids; light blue polygon, coelurosaur; red dot, *Chilesaurus*.

**Extended Data Table 1 | Selected postcranial measurements of three specimens of *Chilesaurus diegosuarezi* gen. et sp. nov.**

| Specimens<br>Bones | SNGM-1935 | SNGM-1937 | SNGM-1936 |
|--------------------|-----------|-----------|-----------|
| Scapula            | 116.3     | -         | -         |
| Radius             | 68.8      | 64.0      | -         |
| Humerus            | 97.8      | -         | -         |
| Metacarpal III     | 26.7      | 21.7      | -         |
| Iliac blade        | 116.9     | -         | -         |
| Pubis              | 95.7      | -         | 97.7      |
| Ischium            | 101.2     | -         | 101.6     |
| Femur              | 142.4     | -         | 114.6     |
| Tibia              | 144.4     | 114.6     | -         |
| Metatarsal I       | -         | 31.4      | -         |
| Metatarsal II      | -         | 50.9      | -         |
| Metatarsal III     | -         | 71.1      | -         |

Measurements are in mm. All the values represent maximum measurable lengths. Maximum deviation of the digital calliper equals 0.02 mm but measurements were rounded to the nearest 0.1 mm.