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A new Late Cretaceous iguanomorph from North America and the origin of New World Pleurodonta (Squamata, Iguania)

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Iguanomorpha (stem + crown Iguania) is a diverse squamate clade with members that predominate many modern American lizard ecosystems. However, the temporal and palaeobiogeographic origins of its constituent crown clades (e.g. Pleurodonta (basilisks, iguanas, and their relatives)) are poorly constrained, mainly due to a meagre Mesozoic-age fossil record. Here, we report on two nearly complete skeletons from the Late Cretaceous (Campanian) of North America that represent a new and relatively large-bodied and possibly herbivorous iguanomorph that inhabited a semi-arid environment. The new taxon exhibits a mosaic of anatomical features traditionally used in diagnosing Iguania and non-iguanian squamates (i.e. Scleroglossa; e.g. parietal foramen at the frontoparietal suture, astragalocalcaneal notch in the tibia, respectively). Our cladistic analysis of Squamata revealed a phylogenetic link between Campanian-age North American and East Asian stem iguanomorphs (i.e. the new taxon + Temujiniidae). These results and our evaluation of the squamate fossil record suggest that crown pleurodontans were restricted to the low-latitude Neotropics prior to their early Palaeogene first appearances in the mid-latitudes of North America.

1. Introduction

Iguanomorpha (*sensu* [1]) is a stem-based clade of lizards that includes chamaeleons, agamas, iguanas, and their extinct relatives and has modern occurrences on every continent except Antarctica [2,3]. The two major crown groups of Iguanomorpha that constitute Iguania (*sensu* [1]), Old World Acrodonta (chamaeleons and agamas), and the primarily New World Pleurodonta (i.e. Iguanidae *sensu* [4]), are highly diverse in morphology and ecology, and have been the focus of numerous evolutionary studies (e.g. phylogenetics, adaptive radiations, ecophysiology, species delimitation, phylogeography [5–9]). Pleurodontans dominate many modern lizard faunas in North and South America; for example, horned, spiny, and collared lizards and desert iguanas in the Sonoran Desert of the USA and Mexico; anoles in The Bahamas and Greater Antilles; and liolaemids in Argentina [3,7,10]. Studies based on molecular and fossil data have presented conflicting views on the temporal and palaeobiogeographic origins of Pleurodonta. Pleurodontan biogeography [2] combined with molecular divergence estimates [8,11–13] imply that the crown clade originated in North America before the Cretaceous–Palaeogene (K-Pg) boundary (*ca* 66 Ma). The fossil data are more equivocal. Whereas the latest Cretaceous (Maastrichtian) taxon *Pristiguana brasiliensis* from Brazil was considered the oldest member of Pleurodonta [14–16], recent phylogenetic analyses have removed it from Pleurodonta as well as from Iguanomorpha [17].

Recent fossil discoveries of Late Cretaceous (Campanian) East Asian stem pleurodontans are consistent with but do not exclusively support a Northern Hemisphere origin for the crown group (e.g. [18,19]); those Asian stem taxa might have dispersed to North America during the Late Cretaceous where they later evolved into crown lineages during the Palaeogene [20,21]. Until now the Mesozoic fossil record of North American iguanomorphs, which comprises less than a dozen isolated and fragmentary jaws of uncertain phylogenetic position [22–25], could not adequately address these conflicting hypotheses for the origin of Pleurodonta. Here, we describe two nearly complete skeletons of a new North American Cretaceous iguanomorph and conduct a series of cladistic analyses that sheds light on the temporal and palaeobiogeographic origin of Pleurodonta.

2. Systematic palaeontology

Squamata Oppel 1811

Iguanomorpha Sukhanov 1961 *sensu* [1]

Magnuviator ovimonsensis gen. et sp. nov.

(a) Etymology

'*Magnus*' (Latin) mighty; '*viātor*' (Latin) traveller; *ovi-* (Latin) egg; *mons* (Latin) mountain; *-ēnsis* (Latin) suffix meaning 'from.' The genus name refers to the body size and biogeographic history of the animal as implied by its sister-group relationships; the species name refers to its type locality (Egg Mountain, Teton County, MT, USA).

(b) Holotype

MOR 6627 (Museum of the Rockies), a nearly complete and mostly articulated skeleton (figure 1*a*,*b*; electronic supplementary material, file S1 and figures S1–S6).

(c) Referred specimen

MOR 7042, a nearly complete and mostly articulated skeleton (figure 1*c*–*e*; electronic supplementary material, file S1, figures S7–S9 and videos 1–9).

(d) Locality and horizon

Egg Mountain locality, Upper Cretaceous (Campanian; *ca* 75.5 ± 0.40 Ma [26]) Two Medicine Formation, Teton County, northwestern Montana, USA (approx. 48° N palaeolatitude [27]). See the electronic supplementary material, file S1 for palaeoenvironmental interpretation of this locality.

(e) Diagnosis

The new taxon is a member of Iguanomorpha based on the presence of three unambiguous synapomorphies: (i) parietal foramen at the frontoparietal suture, (ii) prefrontal boss, and (iii) prearticular angular process. *Magnuviator* possesses the following unique combination of character states: presence of a palatine foramen that enters the palatine dorsally towards its anterior end to pass anteroventrally into the infraorbital canal; anterior extent of splenial reaches about two-thirds the length of the dentary tooth row; splenial anterior inferior alveolar foramen (aiaf) positioned posterodorsal to the anterior mylohyoid foramen; and vertebral zygosphene is a separate facet set on a distinct ventrolaterally facing pedicle. *Magnuviator* is united with Temujiniidae in possessing a splenial aiaf that is shared between the splenial and the dentary and a thin symphyseal process of the pubis. It differs from Temujiniidae in possessing an ascending process of the squamosal. It differs from stem + crown Pleurodonta in possessing an unrestricted and open Meckelian canal of the dentary and from Chamaeleontiformes (stem + crown Acrodonta) in lacking enlarged 'fang-like' maxillary teeth and V-shaped wear facets of maxillary teeth that are incised on the lateral face of the dentary between the dentary teeth. It further differs from Chamaeleontiformes in possessing a greater number of dentary teeth. *Magnuviator* differs from all iguanomorphs in possessing an astragalocalcaneal notch in the tibia.

(f) Description

Magnuviator ovimonsensis gen. et sp. nov. is a large-bodied iguanomorph with an estimated snout–vent length (SVL) of up to 216 mm (holotype). Nearly all skull bones, including portions of the hyoid and sclerotic ring, are preserved between the holotype and referred specimen. The azygous frontal is moderately rugose dorsally and has a narrow interorbital region and a transversely oriented posterior margin at the frontoparietal suture (figure 1*c*,*d*; electronic supplementary material, file S1 and figure S3). The presence of an ascending process of the squamosal is typical of Iguanomorpha, except in Temujiniidae [1,21,28]. The presence of a 'semilunate' postfrontal that clasps the frontoparietal suture, which once was considered a diagnostic feature of Scleroglossa but now known to be present in stem iguanians (e.g. Temujiniidae), could not be determined with certainty due to poor preservation or lack thereof in *Magnuviator* (see figure 1*d* and electronic supplementary material, file S1 for details). The braincase lacks a prominent prootic alar process (electronic supplementary material, videos S4–S6).

The elongate dentary (figure 1*e*) possesses an open and unrestricted Meckel's canal, as in the stem-based acrodontan clade Chamaeleontiformes (*sensu* [1]), but in contrast to the derived conditions in *Temujinia ellisoni*, *Pariguana lancensis*, and basal and most extant pleurodontans [18,21,23]. Maxillary and dentary teeth are pleurodont, closely spaced, non-striated, sub-equal in height and columnar (figure 1*e*; electronic supplementary material, file S1 and figure S4). Teeth in the mesial quarter of the maxilla transition in form mesiodistally, from monocuspid to bicuspid to tricuspid. The bicuspid teeth possess a short primary central cusp and a small distal cusp; tricuspid teeth possess an additional small mesial cusp. Maxillary tooth counts, including vacant tooth spaces in the holotype and referred specimen, range from 22 to 24. Thirty dentary tooth positions are present in MOR 7042.

The pectoral and pelvic girdles and most limb elements are preserved. The clavicle is expanded and notched medially. The interclavicle possesses an anterior process (electronic supplementary material, file S1 and figure S5). *Magnuviator* possesses a scapulocoracoid and primary coracoid fenestra of the scapulocoracoid; it lacks the secondary coracoid fenestra present in *Saichangurvel davidsoni* [28]. The presence of a scapular fenestra could not be determined. The ilium, pubis, and ischium of the holotype and referred specimen are fused at the acetabulum, indicating that they likely represent adult individuals. The tibia is notched distally for articulation with a ridge on the fused astragalocalcaneum (electronic supplementary material, file S1 and

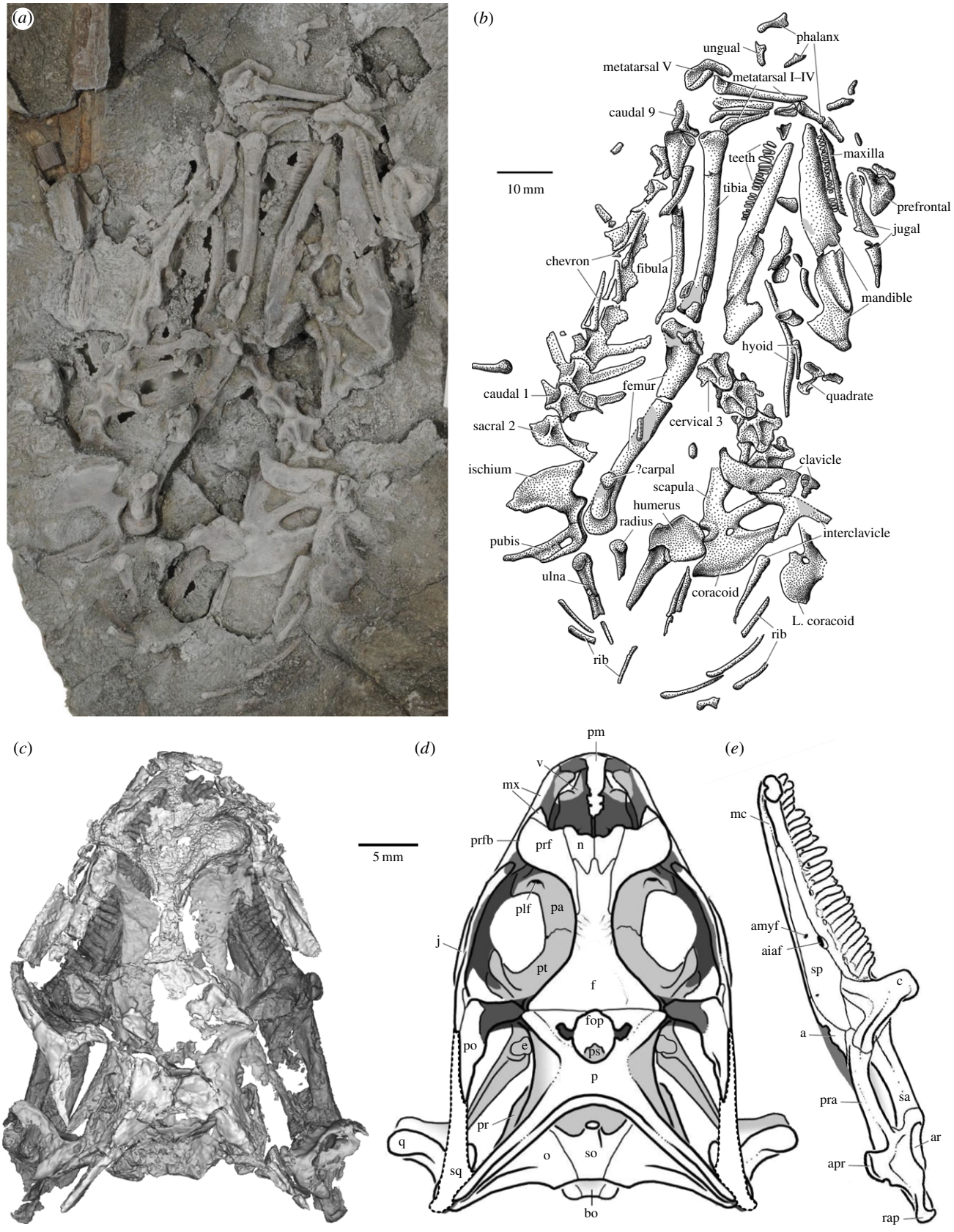

Figure 1. Holotype (MOR 6627) and referred (MOR 7042) specimens of *Magnuviator ovimonsensis* gen. et sp. nov. (*a*,*b*) Holotype nearly complete skeleton in ventral view. Photograph (*a*) and corresponding labelled illustration (*b*). (*c*–*e*) Referred specimen skull and mandibles. Virtual two-dimensional rendering of skull and mandibles (*c*) in dorsal view derived from computed and micro-computed tomography (CT and μCT, respectively) data. Labelled reconstructions of skull (*d*) and right mandible (*e*) in dorsal and lingual views, respectively. Squamosal shape (dashed lines in *d*) is based on MOR 6627. Dark transparent grey shading represents missing bones such as the postfrontal (see the electronic supplementary material, file S1 for details). Anatomical abbreviations: a, angular; aiaf, anterior inferior alveolar foramen; amyf, anterior mylohyoid foramen; apr, angular process; ar, articular; c, coronoid; e, epipterygoid; f, frontal; fop, parietal foramen; j, jugal; L., left; mc, Meckel's canal; mx, maxilla; n, nasal; o, otooccipital; p, parietal; pa, palatine; plf, palatine foramen; pm, premaxilla; po, postorbital; pr, prootic; pra, prearticular; prf, prefrontal; prfb, prefrontal boss; ps, parasphenoid; q, quadrate; rap, retroarticular process; sa, surangular; so, supraoccipital; sp, splenial; sq, squamosal; v, vomer. Scale bars, 10 mm (*a*,*b*) and 5 mm (*c*–*e*).

figure S6), a purported non-iguanian (scleroglossan) squamate synapomorphy [21,29].

3. Material and methods

(a) Computed tomography

Three-dimensional volumetric renderings derived from computed and micro-computed tomography (CT and μCT, respectively) of MOR 6627 and 7042 augmented our descriptions and character scorings for cladistic analysis. CT and μCT data were processed, segmented, and visualized using the software programs Fiji [30], DataViewer (v. 1.5.1.2, Bruker microCT, Belgium), and Mimics (v. 17, Materialise, Belgium). See the electronic supplementary material, file S1 for details.

(b) Phylogenetic analysis

To assess the phylogenetic relationships of *Magnuviator ovimonsensis*, we conducted cladistic analyses using the character/taxon data matrix assembled by Gauthier *et al*. [21] (original dataset contains 610 morphological characters and 189 squamates and three rhynchocephalians). We assembled the data matrix in Mesquite v. 3.02 [31]. Character scores of *M. ovimonsensis* and *Pariguana lancensis* (see below) are provided in the electronic supplementary material, file S1. We performed cladistic analyses in TNT v. 1.1 [32]. We used the New Technology search (sectorial, ratchet, drift, and tree fusing options activated) to search for 500 minimum tree length recoveries. We treated 149 characters as ordered per [21]. We ran a secondary cladistic analysis to further test the pleurodontan affinities of *P. lancensis*, a tentative hoplocercid from the Maastrichtian of Wyoming [23], and the hypothesis that Pleurodonta originated during the Cretaceous of North America. Strict consensus trees were constructed in PAUP* 4.0b10 [33] and visualized in FigTree v. 1.3.1. Bremer (BS) and bootstrap (BP) results are provided below (see the electronic supplementary material, file S1 for details). A synapomorphy list including unambiguous character-state optimizations for the strict consensus tree was created in PAUP* 4.0b10 (electronic supplementary material, file S1). Because molecular-based phylogenies of Squamata radically differ from those based on morphology, particularly for Iguania (see [21] for a review), we ran additional cladistic analyses using a molecular-only and a combined morphological-and-molecular constraint tree based on the higher level phylogenetic relationships presented in [34,35], respectively. See the electronic supplementary material, file S1 for details.

4. Results and discussion

Cladistic analysis recovered *Magnuviator ovimonsensis* as the sister taxon to Temujiniidae (*Temujinia ellisoni* + *Saichangurvel davidsoni*). Support for that relationship is moderate (BS = 3; BP = 0). The *Magnuviator*-temujiniid clade is in a polytomy with Chamaeleontiformes and stem and crown Pleurodonta (figure 2*a*). Among our 16 most parsimonious trees, the *Magnuviator*-temujiniid clade equally occurs as either the basalmost stem pleurodontan or as a stem iguanomorph sister to Chamaeleontiformes + stem and crown Pleurodonta (electronic supplementary material, file S1 and figure S10). Results of our constrained analysis per [35] support the stem pleurodontan relationships of *Magnuviator* and Temujiniidae (electronic supplementary material, file S1 and figure S13). Our molecular-only constrained analysis recovered those taxa within a poorly resolved Iguanomorpha (electronic supplementary material, file S1 and figure S14).

The *Magnuviator*-temujiniid clade provides the first, and earliest known, phylogenetic link between Asian and North American iguanomorphs. Among Late Cretaceous reptiles, terrestrial interchange between those landmasses has mainly been reported for larger bodied forms (e.g. [43–45]). Hypothesized phylogenetic relationships among squamates, for example, imply Asian–North American interchange occurred among Late Cretaceous polyglyphanodontians (e.g. *Gilmoreteius*, *Polyglyphanodon* [1,21]) and platynotans (e.g. *Estesia*, *Palaeosaniwa* [46]), all of which are relatively large in body size ([23,47]; electronic supplementary material, file S2). Similarly, *Magnuviator* is larger in body size than members of its sister taxon Temujiniidae (e.g. SVL = ∼216 mm versus ∼117 mm in *Saichangurvel davidsoni*) and most Late Cretaceous iguanomorphs from East Asia (electronic supplementary material, file S2). The absence of this pattern in the smaller-bodied squamates might reflect their relatively poor fossil-preservation potential, uncertainties in their phylogenetic relationships, or both. Another possibility is that size-dependent physiological tolerances limited smaller-bodied ectotherms from traversing the cooler climates of the high-latitude Beringian crossing (e.g. [48]) between Asia and North America during the Late Cretaceous.

Magnuviator is the oldest unequivocal iguanomorph from North America and predates the occurrence of Pleurodonta by nearly 20 Ma. Previously proposed pleurodontans from the Late Cretaceous of Canada (e.g. *Cnephasaurus locustivorus* [22]) and the Palaeocene of Wyoming, USA (*Swainiguanoides milleri* [39]) are based on isolated and fragmentary jaws that either lack synapomorphies of Pleurodonta or have now been referred to non-iguanian clades (e.g. Chamopsiidae [23–25]). Similarly, our analysis does not find the Maastrichtian-age *Pariguana lancensis* [23] to be a pleurodontan, although it likely is an iguanomorph (electronic supplementary material, file S1 and figure S11). The oldest definitive crown pleurodontans are the early Eocene *Afairiguana avius* (Polychrotidae *sensu lato* [42]) and *Anolbanolis banalis* [41], both from Wyoming, USA. Additional representatives of pleurodontan crown clades, such as the corytophanids *Babibasiliscus alxi* and *Geiseltaliellus maarius* from Wyoming, USA and Germany, respectively, occur in the middle Eocene ([20,49]; see [41,50,51] for additional North American records). The presence of Cretaceous and Palaeogene pleurodontans in South America is also equivocal. Relevant South American taxa (e.g. *Pristiguana brasiliensis*) are based on fragmentary remains that possess features common to both stem and crown Pleurodonta (see the electronic supplementary material, file S1 and references therein). The oldest unequivocal South American pleurodontans are from the early Miocene of Argentina [52,53].

The lack of fossil evidence for Cretaceous-age pleurodontans contrasts with molecular-based time estimates that indicate a Late Cretaceous origin for Pleurodonta and its primary subclades [8,11–13] (figure 2*a*). The Late Cretaceous iguanian fossil record from the mid- to high-latitudes of Asia and North America consists exclusively of stem taxa [20,21], including *Magnuviator*, and the oldest fossil crown pleurodontans are early Eocene in age [41,42,50,51]. The absence of crown taxa from the comparatively well-sampled regions of Asia and North America [19,24], combined with the high diversity and/or endemism of many extant pleurodontan clades in the Neotropics [2,3] is consistent with an origin or initial diversification of crown Pleurodonta in the

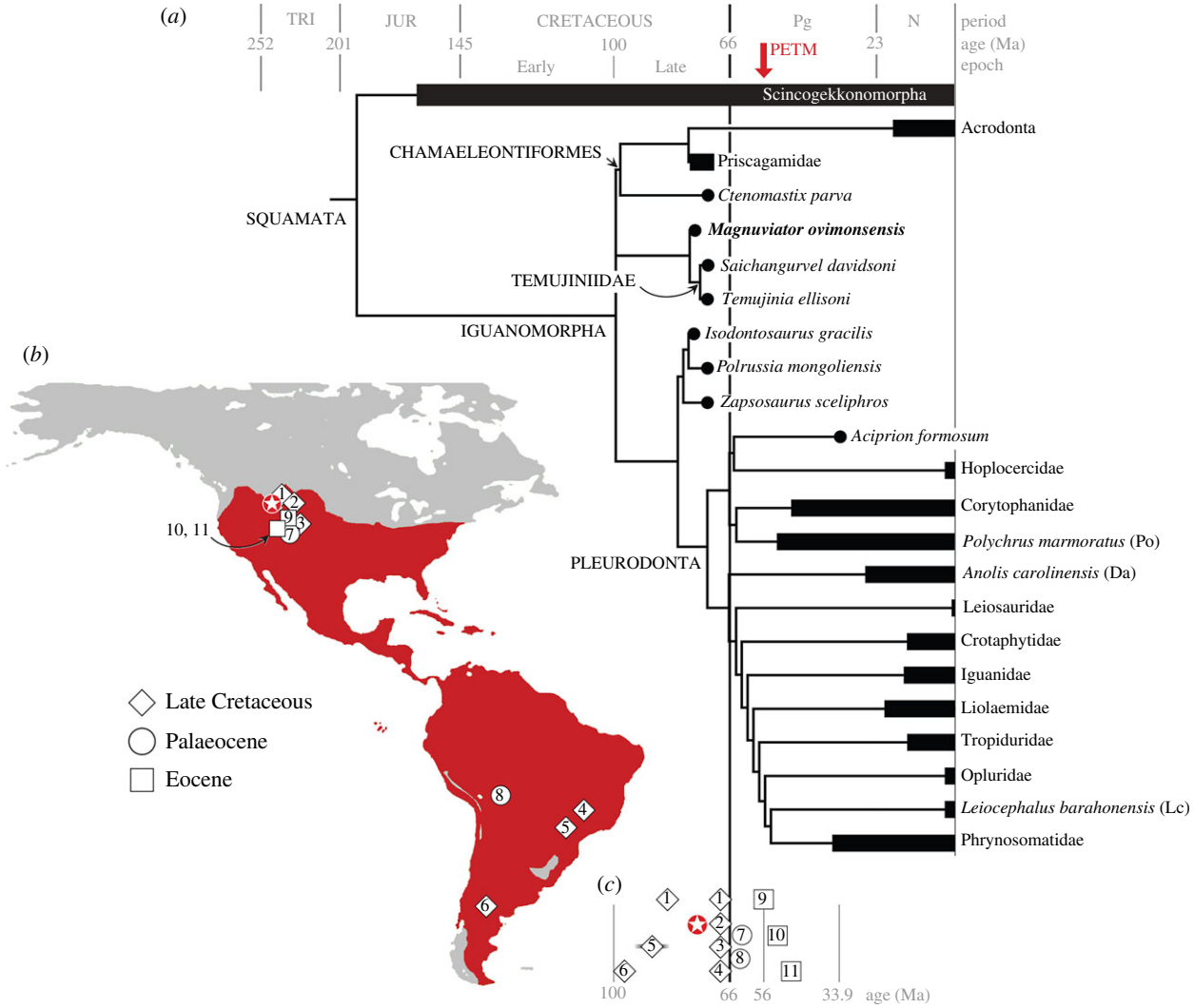

Figure 2. Time-calibrated phylogenetic interrelationships of *Magnuviator ovimonsensis* gen. et sp. nov. and the geographic distributions of fossil iguanomorphs and extant and extinct pleurodontans. (*a*) Strict consensus of 16 most parsimonious trees. Taxon temporal ranges and occurrences are indicated by the horizontal black bars and circles, respectively. Node ages for Squamata (193 Ma) and Chamaeleontiformes (99 Ma) per [11] and [36], respectively. Pleurodontan divergences constrained per [8]. The Palaeocene-Eocene Thermal Maximum (PETM) is marked by the red arrow at the top of the figure. Da, Dactyloidae *sensu* [8]; JUR, Jurassic; Lc, Leiocephalidae; N, Neogene; Pg, Palaeogene; Po, Polychrotidae; TRI, Triassic. (*b*) New World geographic distributions of Late Cretaceous and early Palaeogene iguanomorphs and fossil and extant pleurodontans. Modern New World pleurodontan distributions shown in red. Fossil taxa are represented by the numbered symbols: star, *Magnuviator ovimonsensis*; 1, *Cnephasaurus locustivorus* and unnamed 'iguanids' [22]; 2, non-acrodontan iguanomorph [25]; 3, *Pariguana lancensis* [23]; 4, *Pristiguana brasiliensis* [14]; 5, *Brasiliguana prudentis* [37]; 6, ?Iguanidae [38]; 7, *Swainiguanoides milleri* [39]; 8, ?Iguanidae [40]; 9, *Anolbanolis banalis* [41]; 10, *Afairiguana avius* [42]; 11, *Babibasiliscus alxi* [20]. (*c*) Temporal distributions of fossil taxa. Numbered symbols (1–11) correspond to those on the map at (*b*) and are the approximate age. The shaded horizontal bar behind 5 denotes age uncertainty [37]. 'The left diamond labelled with a 1 represents the age of *Cnephasaurus locustivorus* as well as some unnamed 'iguanids'; the right diamond labelled with a 1 represents the other unnamed 'iguanids' [22].

low-latitude Neotropics during the Late Cretaceous. The oldest crown pleurodontans are members of extant Neotropical clades (Corytophanidae, Polychrotidae), and they first appeared in the northern mid-latitudes of North America shortly after the Palaeocene-Eocene Thermal Maximum (PETM). These records are consistent with a Neotropical origin and dispersal from the low latitudes of the Americas in response to a northward expansion of megathermal climates [41], a pattern seen in other components of North American Palaeogene herpetofaunas [54]. The occurrence of *Magnuviator* in the North American Late Cretaceous indicates the likelihood of an earlier transcontinental distribution of stem pleurodontans across Laurasia prior to the radiation and dispersal of the pleurodontan crown than previously considered ([21]; but see [23]).

Tooth crown morphology and body size of *Magnuviator* imply a faunivorous and possibly herbivorous diet. Whereas multi-cusped teeth occur in both insectivorous and herbivorous extant iguanians, the herbivorous taxa tend to possess more mesiodistally expanded, labiolingually compressed, and blade-like teeth that are adorned with more numerous and typically well-defined cusps (e.g. *Ctenosaura* [55–57]). *Magnuviator* exhibits tooth-crown morphology intermediate between extant insect specialists (e.g. blunt, non-cuspate, and peg-like teeth in *Phrynosoma*) and principally herbivorous taxa (e.g. 'serrate' teeth in *Iguana iguana* in addition to those features noted above); its dentition is most like that of some extant phrynosomatids such as *Callisaurus* and *Urosaurus* (e.g. slender, cylindrical, and weakly cuspate [55]). Some species of *Callisaurus* and *Urosaurus* feed heavily on wasps and bees [55]. Indeed, fossilized hymenopteran pupae cases are abundant at the Egg Mountain locality [58] and are morphologically identical to those that have been attributed to wasps and found at a nearby locality in the Two Medicine

Formation [59]. On the basis of its relatively large body size, we infer that *Magnuviator* also might have been capable of digesting plant matter. Owing to energetic constraints, herbivory is restricted to large-bodied forms in extant and presumably extinct lizards (more than 100 mm SVL; except Liolaemidae), occurring mostly within Iguania [5,60]; *Magnuviator* falls within this body-size range (electronic supplementary material, file S1 and figure S12).

Taken together, our study expands our understanding of the morphological evolution of Iguanomorpha and more broadly Squamata. Some features, such as the distal tibial notch, that were previously restricted to non-iguanian squamates (Scincogekkonomorpha *sensu* [1]) are now known to be more broadly distributed within Squamata (present in *Magnuviator*). The revised character polarizations resulting from these findings could prove important in (i) resolving the conflict between morphology-based and genetics-based phylogenetic hypotheses [1,21,34,35], (ii) determining which fossil taxa fall within crown-group Pleurodonta, and (iii) identifying which fossils should be used to temporally calibrate molecular divergence estimates of the clade.

Data accessibility. The electronic supplementary material including the supplementary text, tables, figures, videos, and phylogenetic data are available at DeMar D, Conrad J, Head J, Varricchio D, Wilson G. 2016 Data from: A new Late Cretaceous iguanomorph from North America and the origin of New World Pleurodonta (Squamata, Iguania). Dryad Digital Repository. doi:10.5061/dryad.tp802.

Authors' contributions. D.J.V. collected the specimens. D.G.D. and J.L.C. described the specimens and conducted the cladistics analyses, created the figures, and acquired the CT and μCT data. D.G.D. processed the CT and μCT data and created the virtual 3D reconstructions. All authors revised and commented on drafts of the manuscript by D.G.D.

Competing interests. We have no competing interests.

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