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The last of the dinosaur titans: a new sauropod from Madagascar

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The Titanosauria, the last surviving group of the giant sauropod dinosaurs, attained a near-global distribution by the close of the Cretaceous period (65 Myr ago). With the exception of a few new discoveries in Argentina[1-3], most titanosaurs are known only from fragmentary postcranial skeletons and rare, isolated skull elements[4-9]. Here we describe the most complete titanosaur yet discovered. *Rapetosaurus krausei* gen. et sp. nov., from the Maevarano Formation of Madagascar, provides a view of titanosaur anatomy from head to tail. A total-evidence phylogenetic analysis supports a close relationship between brachiosaurids and titanosaurs (Titanosauriformes[10-13]). The inclusion of cranial data from *Rapetosaurus* also lays to rest questions concerning the phylogeny of the enigmatic Mongolian genera *Nemegtosaurus* and *Quaesitosaurus*[14,15]. In spite of their elongated, diplodocoid-like skulls, all three taxa are now firmly nested within Titanosauria.

Fragmentary titanosaur remains have been known from the Upper Cretaceous strata of Madagascar since Charles Depéret described '*Titanosaurus madagascariensis*' from two procoelous caudal vertebrae, a partial humeral diaphysis and a large osteoderm[16]. Currently we recognize two titanosaur taxa in the Maevarano Formation that are distinguished, in part, by their caudal vertebrae[17-19]. Depéret's *T. madagascariensis* syntype includes both caudal morphologies and is therefore considered a *nomen dubium*.

The disarticulated bones of the holotype skull of *Rapetosaurus krausei* were recovered from a single stratum over an area of ~1 m² at locality MAD 96-02. Holotype material shows no duplication of elements and exhibits exact sutural articulations. Additional skull material from at least two juvenile sauropods was recovered from locality MAD 93-18 (refs 18, 19). Most of these juvenile skull elements were found intimately associated with a nearly complete juvenile postcranial skeleton that also shows no duplication of elements. Several of the juvenile skull elements from MAD 93-18 share autapomorphies with the holotype adult skull, and thus are referred to *R. krausei*.

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Dinosauria Owen, 1842
Saurischia Seeley, 1888
Sauropoda Marsh, 1878
Titanosauria Bonaparte & Coria, 1993
Rapetosaurus krausei gen. et sp. nov.

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Etymology. *Rapeto* (ruh-PAY-tu, Malagasy), a mischievous giant of Malagasy folklore; *saurus* (Greek), lizard. Specific name for David W. Krause, in recognition of his contributions to palaeontology in Madagascar.

Holotype. Université d'Antananarivo UA 8698, adult skull including right maxilla with eight teeth, left maxilla, right lacrimal, left jugal, right and left nasals, right quadrate, right and left pterygoids, partial basioccipital, right paroccipital process, left dentary with 11 teeth, both angulars, right surangular, and five associated teeth (Figs 1 and 2).

Referred specimens. Field Museum of Natural History FMNH PR 2184-2192, 2194, 2196, 2197, 2209, 2210; right exoccipital, opisthotic, laterosphenoid, supraoccipital, associated right and left frontals,

two right prefrontals, left surangular, right parietal, left squamosal, right quadrate, right pterygoid, right angular, six associated teeth, fused basioccipital, basisphenoid, parasphenoid, associated juvenile skeleton, mid-caudal centrum, respectively; UCB (Université Claude Bernard) 92829, mid-caudal centrum (Figs 1–3).

Type locality and horizon. MAD 96-02, Mahajanga basin, northwestern Madagascar; Anembalemba Member, Maevarano Formation, Upper Cretaceous, Maastrichtian[20].

Diagnosis. *Rapetosaurus* is characterized by the following autapomorphies: expanded antorbital fenestra extends over tooth row; preantorbital fenestra positioned posterior to antorbital fenestra; subnarial foramen anteriorly positioned and dorsoventrally elongate; jugal process of maxilla posterodorsally elongate and narrow; frontals with median dome; quadrate with V-shaped quadratojugal articulation; supraoccipital with two anteriorly directed median parietal processes; pterygoid with extremely shallow basipterygoid articulation and dorsoventrally expanded anterior process; basipterygoid processes diverge only at distal extremes; dentary with 11 alveoli that extend two-thirds the length of the element; gracile cylindrical teeth with high-angle planar wear facets; 16 cervical vertebrae with constricted neural canals and continuous pre- and postspinal coels devoid of pre- or postspinal laminae; cervical neural spines with proximal bifurcation and three pneumatized coels bounded by discrete laminae; 11 dorsal vertebrae with deep lateral pleurocoels; dorsal neural spines with strong pre- and postspinal laminae in deeply excavated anterior and posterior coels; dorsals with median interpre- and interpostzygapophyseal laminae; middle and posterior dorsals with divided spinodiapophyseal lamina; six sacral centra with deep lateral pleurocoels; all caudal centra procoelous with convex ventral margin lacking
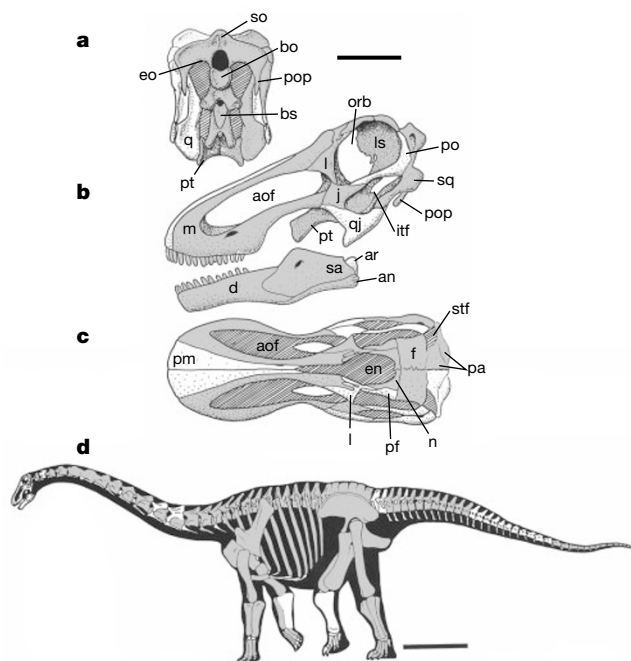

Figure 1 *Rapetosaurus krausei* from the Upper Cretaceous Maevarano Formation of Madagascar. The skull reconstruction is a composite based on holotype and referred specimens and shown in posteroventral (**a**), left lateral (**b**) and dorsal (**c**) views. The skeleton, in left lateral view (**d**), is based on a juvenile postcranial skeleton (FMNH PR 2209), which is ~75% complete. Scale bars are 10 cm (**a**–**c**) and 1 m (**d**). an, angular; aof, antorbital fenestra; ar, articular; bo, basioccipital; bs, basisphenoid; d, dentary; en, external nares; eo, exoccipital; f, frontal; itf, infratemporal fenestra; j, jugal; l, lacrimal; ls, laterosphenoid/orbitosphenoid; m, maxilla; n, nasal; orb, orbit; pa, parietal; pop, paraoccipital process; pf, prefrontal; pm, premaxilla; po, postorbital; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sq, squamosal; stf, supratemporal fenestra.

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excavation; anterior caudal centra broad transversely and antero-posteriorly compressed; middle–posterior caudal centra with constant length:width ratio; anterior–middle caudal neural spines with spinoprezygapophyseal, prespinal and postspinal laminae on rectangular and anteriorly positioned neural arches; chevrons throughout 80% of tail; iliac peduncle of ischium comprises one-quarter of acetabulum; ischial peduncle of ilium low and poorly developed; pubis more than twice as long as ischium; scapula and coracoid with equal glenoid contribution; scapular blade not distally expanded; humerus/femur length quotient 0.80; radius and ulna with oblique interosseus ridges (Figs 1–3).

The *Rapetosaurus* maxilla has a posterodorsally sloping dorsal ascending process with a long premaxillary articulation along its proximal two-thirds. The enlarged antorbital fenestra is unique among sauropods in that it extends anteriorly over the tooth row and is bound ventrally by an elongate, narrow jugal process (Figs 1a–c and 2a). Cylindrical teeth occupy the anterior two-thirds of the element, and have high-angled, lingually oriented wear facets (Fig. 2b) indicating precise tooth-to-tooth occlusion. This straight maxillary profile and the cylindrical teeth are more similar to diplodocoid skulls than they are to the 'stepped' snout profile of brachiosaurids. In contrast to diplodocoids, *Rapetosaurus* teeth occupy the anterior two-thirds of the maxilla. The external nares of *Rapetosaurus* are retracted to the level of the orbit and incompletely divided by medial nasal processes (Figs 1c and 2e) as in diplodocoids, thus confirming that the nostrils were located on the top of the skull. As in other titanosaurs, the supratemporal fenestrae are transversely oriented, and the quadrate is hollow, with a posteriorly facing excavation (Fig. 2f). *Rapetosaurus* has short basal tubera that diverge at 35° and project away from the skull. The basipterygoid processes are longer than those of any other titanosaur, and fit into shallow facets on the plate-like pterygoids, as in *Nemegtosaurus*.
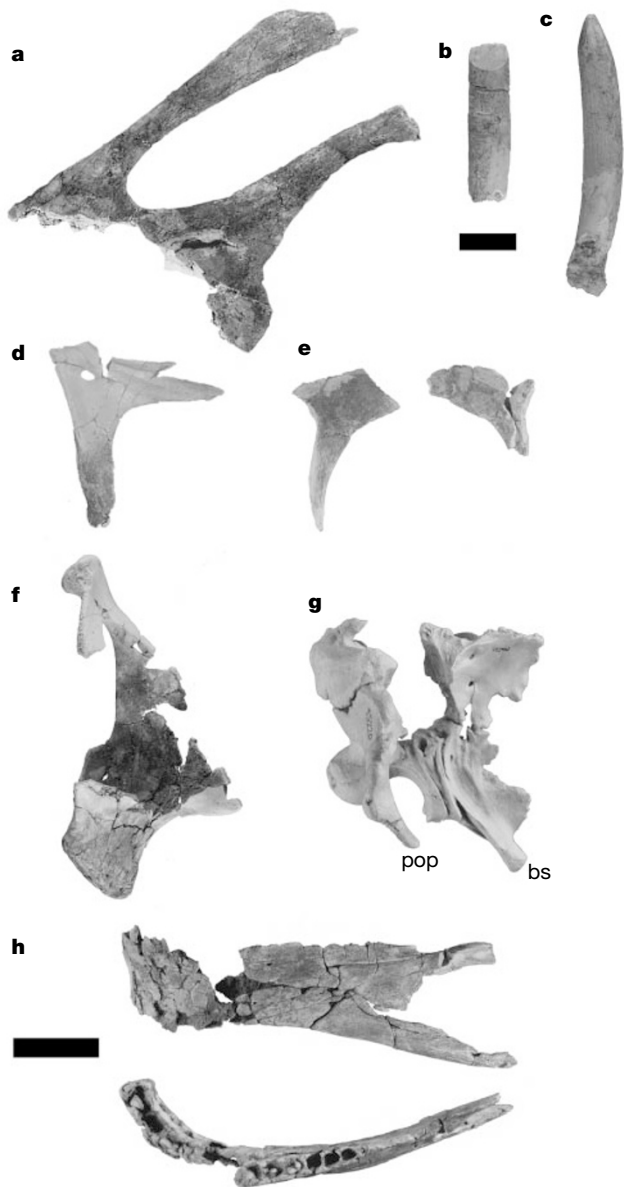
Figure 2 *Rapetosaurus krausei* cranial elements. **a**, Holotype (UA 8698) left maxilla in lateral view. **b**, UA 8698 worn maxillary tooth in lingual view showing high-angled wear facet. **c**, UA 8698 unworn maxillary tooth in mesial/distal view. **d**, UA 8698 right lacrimal in lateral view. **e**, UA 8698 right and left nasals in dorsal view. **f**, UA 8698 right quadrate in anterior view. **g**, FMNH-PR 2184, 2197, articulated supraoccipital, exoccipital/opisthotic, basioccipital, basipterygoid, basisphenoid and laterosphenoid in right lateral view. **h**, UA 8698 dentary in left lateral (top) and dorsal (bottom) views. Scale bars are 5 cm (**a, d–h**) and 1 cm (**b, c**). bs, basisphenoid; pop, paraoccipital process.
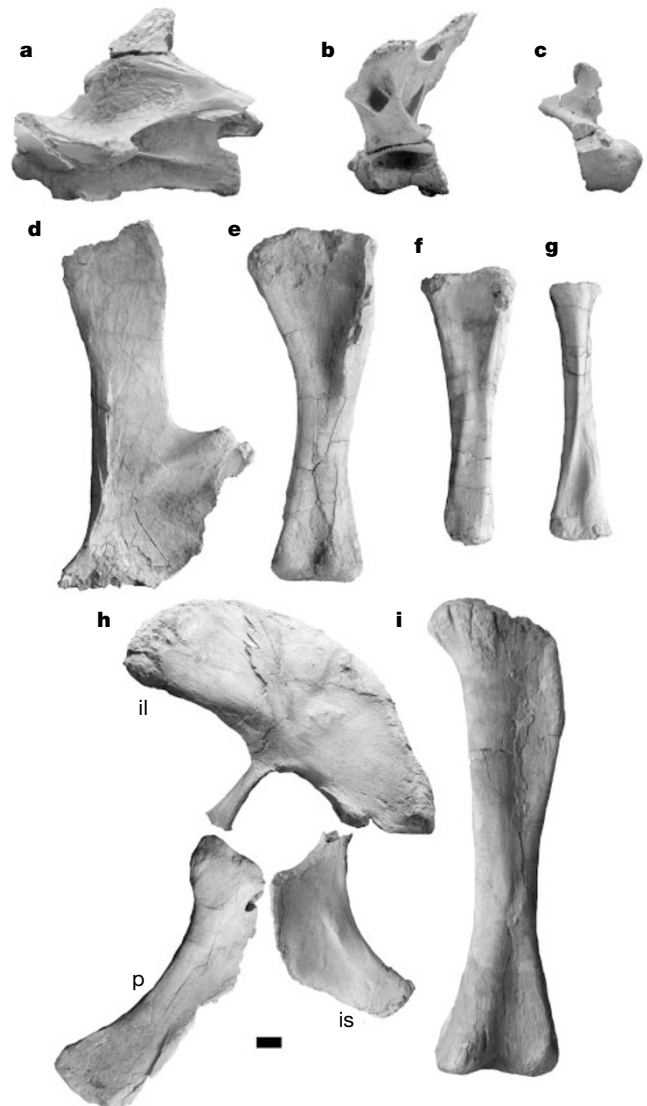
Figure 3 *Rapetosaurus krausei* postcranial elements, all from referred juvenile skeleton (FMNH PR 2209). **a**, Cervical vertebra 10 in left lateral view. **b**, Dorsal vertebra 4 in left lateral view. **c**, Anterior caudal vertebra in left lateral view. **d**, Left scapula in lateral view. **e**, Left humerus in anterior view. **f**, Left ulna in anterior view. **g**, Left radius in posterior view. **h**, Left pubis, ischium and ilium in lateral view. **i**, Left femur in anterior view. Scale bar is 3 cm. il, ilium; is, ischium; p, pubis.

Antarctosaurus, *Saltasaurus*, *Malawisaurus*[26] and *Rapetosaurus* share elongate, recurved paroccipital processes (Figs 1a, b and 2g). The lower jaw is similar to that of brachiosaurids in its broad U shape, the 11 alveoli occupying the anterior two-thirds of the dentary, and the surangular's prominent coronoid eminence (Figs 1c and 2h). Based on the associated elements of the lower jaw, the skull of an adult *Rapetosaurus* is ~40 cm long.

As in other titanosaurs, the cervical vertebrae (Fig. 3a) are elongate with shallow lateral pleurocoels. The cervical neural canal is narrow and constricted and the proximal neural spines are bifid. Cervical neural spines and pleurocoels are marked by large, polished areas indicating axial pneumaticity. Like *Alamosaurus* and *Titanosaurus colberti*, dorsal neural spines (Fig. 3b) are craniocaudally compressed and broad, tapering only at their distal extremes. Posterior dorsal transverse processes are positioned directly above the parapophysis. In contrast to most other titanosaurs, *Rapetosaurus* dorsals and sacrals have deep pleurocoels. All caudal vertebrae (Fig. 3c) are strongly procoelous, as in *T. colberti* and *Saltasaurus*. Unique among titanosaurs, *Rapetosaurus* bears a strongly developed spinoprezygapophyseal lamina on anterior caudal neural spines.

The appendicular skeleton of *Rapetosaurus* is characterized by many typical titanosaur features (Fig. 3d–i), including a lateral projection from the proximal end of the femur, elongated metacarpals, an extremely elongated pubis, an anterodorsally expanded and semicircular preacetabular process of the ilium, and an elevated olecranon process of the ulna. Like most saltasaurines, the scapular blade of *Rapetosaurus* forms a 45° angle with the coracoid. The distal condyles of the humerus and femur expand onto the anterior surface of the shaft in *Rapetosaurus*, *Neuquensaurus* and *Saltasaurus*.

Discussion. *Rapetosaurus krausei* exhibits a suite of features (Fig. 4) that confirm its status as a titanosaur[10–13]. Titanosaurs have historically been allied with diplodocoid sauropods[21–25], but recent studies suggest they share a closer relationship with brachiosaurids within Titanosauriformes[10–13]. Character support for Titanosauriformes has rested almost exclusively on postcranial data, primarily owing to the lack of titanosaur skulls. *Rapetosaurus* offers an opportunity to test the monophyly of Titanosauriformes with abundant, associated skull and skeletal data. *Rapetosaurus* also offers the best opportunity yet to resolve the phylogenetic position of two controversial Mongolian sauropods, *Nemegtosaurus* and *Quaesitosaurus*. These taxa are known only from skulls, and have been alternately placed within the Titanosauria[11,12] or the Diplodocoidea[5,13,15,24]. With regard to these Mongolian genera, *Rapetosaurus* is particularly illuminating because its elongated skull with retracted nares exhibits a general similarity to diplodocoids, whereas its skeleton shows striking commonalities with brachiosaurids and other titanosaurs.

We conducted a phylogenetic analysis with 228 characters (74 cranial and 154 postcranial; see Supplementary Information) and 16 in-group taxa (Fig. 4)[10–13,15,26]. Our analysis supports the higher-level grouping of Titanosauriformes (the most recent common ancestor of *Brachiosaurus* and *Saltasaurus*, and all of its descendents[10,12]), which are united by eleven characters including four unambiguous characters: 23, presence of a rod-like palatine–maxillary contact; 106, simple and undivided chevron blades; 152, proximal one-third of femur deflected medially; 219, blades of middle and caudal chevrons curve backward and downwards.
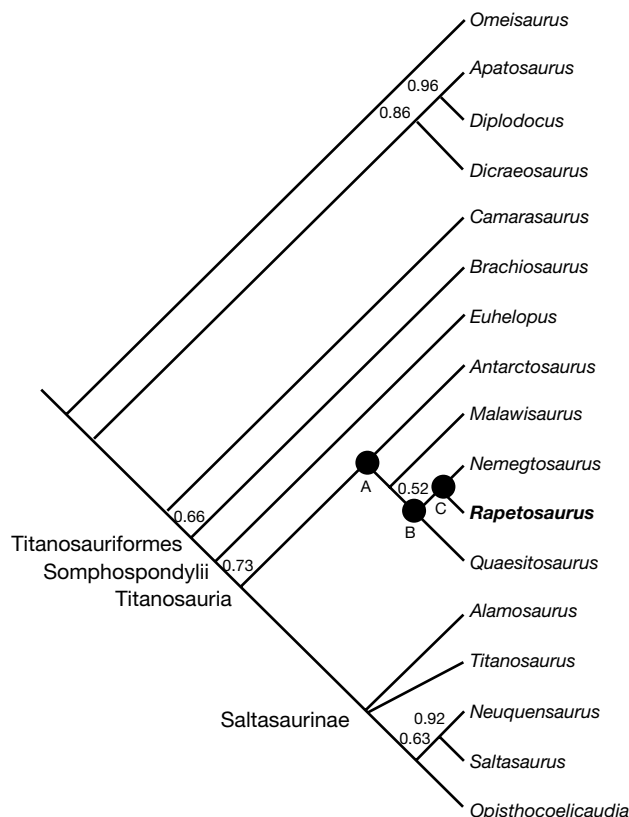
Figure 4 Cladogram showing phylogenetic position of *Rapetosaurus krausei* based on strict consensus of the two most parsimonious trees (447 steps; consistency index = 0.5481; rentention index = 0.6189) generated by a branch and bound search in PAUP* (v.4.0b2a)[31]. Trees were rooted with *Omeisaurus* as the outgroup and optimized with delayed transformations, and all characters were unordered. Characters were drawn from recent analyses of sauropod phylogeny[10–13,15,24,26]. *Titanosaurus* skull data is derived from *T. indicus*, postcranial data from *T. colberti*; *Antarctosaurus* refers to *A. septentrionalis*. Bootstrap values (300 replicates) are listed at nodes. Bremer support values for labelled nodes are as follows: Nodes A–C, 1; Titanosauria, 2; Titanosauriformes, 3. For character list and taxon/character matrix, see Supplementary Information.

Sixteen additional steps are required to move Titanosauria into its more traditional position as a sister group to diplodocoids. Titanosauria is united by 20 characters, including nine that are unambiguous: 71, hyposphene–hypantra articulations present on posterior dorsal neural arches; 77, spongy bone texture of caudals; 78, ≤35 caudal vertebrae; 108, haemal canal approximately half of chevron length; 118, crescentic sternal plates; 125, ulnar olecranon process prominent and projects above the proximal articulation; 128, distal breadth of radius twice midshaft breadth; 154, transverse axis of femoral distal condyles bevelled dorsomedially ~10°; 226, ischium/pubis quotient ≤0.90. Within Titanosauriformes, two clades of titanosaurs are distinguished: a group that includes *Rapetosaurus* (*Rapetosaurus* clade) and the Saltasaurinae[27] (Fig. 4). The Saltasaurinae is united by 16 characters including four that are unambiguous: 80, first caudal centrum with biconvex articular shape; 121, deltopectoral crest reduced to a low rounded crest or ridge; 138, manual digits II and III lack phalanges; 157, distal breadth of tibia more than twice its midshaft breadth.

Taxa in the *Rapetosaurus* clade are united by four ambiguous cranial synapomorphies (Fig. 4, Node A): 12, frontals with fused midline contact; 13, parietal does not contribute to post-temporal fenestra; 16, occipital region of skull anteroposteriorly deep with paroccipital processes oriented posterolaterally (reversal); 25, basipterygoid process at least four times that of basal diameter. All four of these characters are shared with one or more diplodocoids, and the addition of only one step collapses the node. Within the *Rapetosaurus* clade, *Malawisaurus* is the sister taxon of *Quaesitosaurus* (*Rapetosaurus* + *Nemegtosaurus*), a relationship supported by 10 ambiguous characters, including four postcranial features shared with one or more diplodocoids. *Nemegtosaurus*, *Quaesitosaurus*, and *Rapetosaurus* are further united by eleven synapomorphies, two of which are unambiguous (Fig. 4, Node B): 37, posterodorsal process of the splenial present; 195, angle between the long axis of mandibular symphysis and the long axis of mandible ~90°. *Rapetosaurus* and *Nemegtosaurus* are united by seven ambiguous cranial characters, five of which occur in one or more diplodocoids (Fig. 4, Node C): 5, external nares are retracted to a position between the eyes; 9, presence of an anterior prefrontal process; 11, frontal contributes to supratemporal fenestra; 172, external nares face dorsally or rostrodorsally; 174, absence of a 'stepped' snout profile; 190, ectopterygoid process of pterygoid lies ventral or caudoventral to lacrimal; 197, slenderness indices for teeth >5.0.

All five taxa in the *Rapetosaurus* clade, but only two saltasaurines (*Saltasaurus* and *Titanosaurus*), have cranial material. When only postcranial data are analysed (*Nemegtosaurus*, *Quaesitosaurus* and *Antarctosaurus* are eliminated owing to their lack of postcranial data), *Rapetosaurus* + *Malawisaurus* remains the sister taxon to Saltasaurinae. Whereas the current data seem to indicate a close relationship between *Rapetosaurus* and the two Mongolian taxa, missing data and the uneven distribution of cranial and postcranial materials among taxa lead us to advise caution when interpreting such relationships. For example, the two unambiguous characters that unite *Rapetosaurus*, *Nemegtosaurus* and *Quaesitosaurus* (Node B; characters 37 and 195) are coded as missing for all saltasaurines and *Antarctosaurus*. Even so, a rearrangement of *Rapetosaurus*, *Nemegtosaurus* and *Quaesitosaurus* to a sister-group relationship with diplodocoids results in the addition of 29 steps.

From a palaeobiogeographic perspective, a resolved phylogeny of the globally distributed Titanosauria offers an opportunity to explore Cretaceous vicariance. Our phylogenetic analysis suggests that the biogeographic history of *Rapetosaurus* may be most closely linked to Africa, Asia and India. This finding contrasts with the proposed biogeographic history of Maevarano Formation mammals, crocodyliforms and theropod dinosaurs, which make a strong case for extensive faunal interchange between South America, India and Madagascar[28]. However, missing data coupled with low Bremer support and bootstrap values for most nodes within Titanosauria, as well as the lack of a palaeogeographic model to explain the potential Asia–Madagascar connection, reduces our confidence in this arrangement. As such, the significance of these biogeograhic possibilities must be tested in the context of a more global analysis of titanosaur phylogeny and, we hope, with the addition of more cranial and postcranial data.

Finally, titanosaurs are unique among sauropod clades in that they evolved alongside large-bodied, herbivorous ornithischian dinosaurs, notably the horned ceratopsians, 'duck-billed' hadrosaurs and armoured ankylosaurs[27,29]. *Rapetosaurus*, in contrast, shares the Mahajanga basin with only one large-bodied herbivore, another titanosaur[17–19]. Small herbivores are also exceedingly rare in the Cretaceous of Madagascar, with only a single herbivorous/omnivorous crocodyliform[30] discovered in more than 100 years of collection. The occurrence of these co-existing titanosaurs in the apparent absence of ornithischian dinosaurs suggests a different herbivore community dynamic on Madagascar than is seen elsewhere in the Cretaceous. □

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Neanderthal cranial ontogeny and its implications for late hominid diversity

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Homo neanderthalensis* has a unique combination of craniofacial features that are distinct from fossil and extant 'anatomically modern' *Homo sapiens* (modern humans). Morphological evidence, direct isotopic dates[1] and fossil mitochondrial DNA from three Neanderthals[2,3] indicate that the Neanderthals were a separate evolutionary lineage for at least 500,000 yr. However, it is unknown when and how Neanderthal craniofacial autapomorphies (unique, derived characters) emerged during ontogeny. Here we use computerized fossil reconstruction[4] and geometric morphometrics[5,6] to show that characteristic differences in cranial and mandibular shape between Neanderthals and modern humans arose very early during development, possibly prenatally, and were maintained throughout postnatal ontogeny. Postnatal differences in cranial ontogeny between the two taxa are characterized primarily by heterochronic modifications of a common spatial pattern of development. Evidence for early ontogenetic divergence together with evolutionary stasis of taxon-specific patterns of ontogeny is consistent with separation of Neanderthals and modern humans at the species level.

Comparative analyses of immature crania indicate that diagnostic Neanderthal characters appeared early during ontogeny[7,8] and that the Neanderthal ontogenetic process was fast relative to that of the modern humans[7,9–11]. Here, we use a new methodological approach to study the comparative ontogeny of Neanderthal and modern human skulls. After computerized reconstruction of fragmentary fossil specimens[4,12–14], we applied geometric morphometric methods (GMM)[5] to identify and visualize complex patterns of morphological change during ontogeny (see Methods). In GMM the form of a specimen is described by the spatial configuration of a set of three-dimensional anatomical landmarks. Size-corrected variation in shape can then be computed in terms of between-specimen rearrangements of landmark positions. To capture large trends in shape variation in ontogenetic samples of Neanderthals and modern humans, we used relative warp analysis[5,6], which separates shape variability into statistically independent factors. Each relative warp thus captures an independent aspect of shape variation in the sample (Fig. 1) that can be plotted ontogenetically

as temporal (Fig. 2) and spatial (Figs 3 and 4) patterns of morphological change.

Our relative warp analyses are based on a large cross-sectional ontogenetic series of Neanderthal cranial and mandibular specimens that were reconstructed by computerized methods, and a comparative fossil/recent modern human sample. The Neanderthal sample mostly comprises individuals from dental stage 3 (3–6 yr) to adulthood, but includes an early postnatal mandible (Amud 7, about 0.5 yr[8]) and a cranium and mandible from dental stage 2 (Pech de l'Azé, about 2.5 yr); the modern human sample includes individuals from all ontogenetic stages—from perinatal through to adulthood (see Methods and Supplementary Information for sample details and landmark definitions). We computed the statistically independent relative warps for the combined craniomandibular landmark configurations (Fig. 1a) and for cranial and mandibular configurations in isolation (Fig. 1b, c), and plotted these against three additional factors: (1) individual age (dental
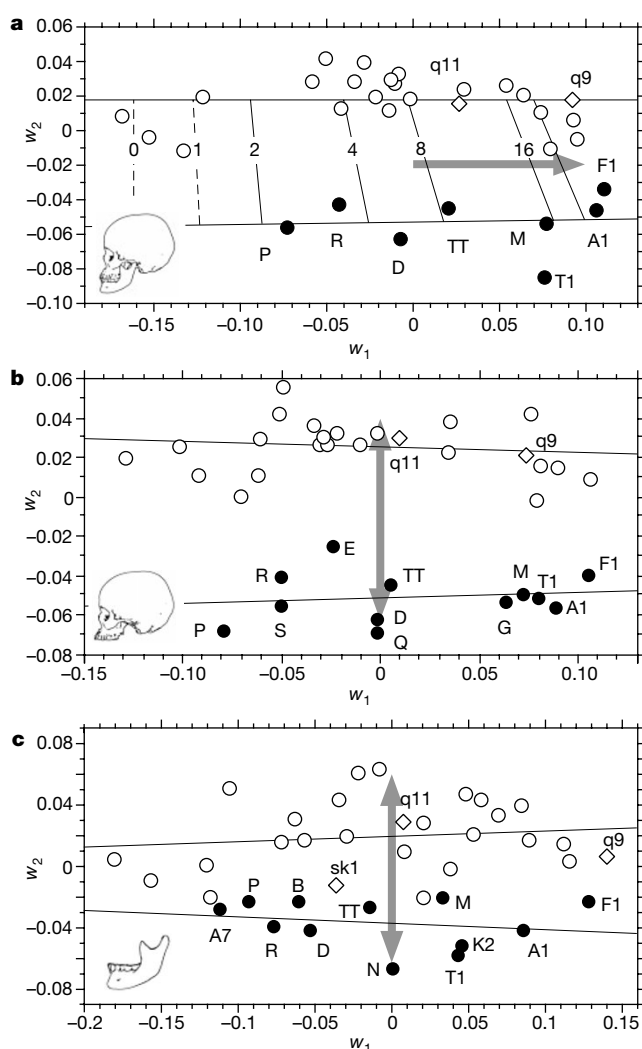
Figure 1 Shape variability in an ontogenetic series of Neanderthals (filled circles; see Methods for specimen labels) and modern humans (open circles/diamonds indicate extant/fossil specimens, respectively) for craniomandibular (**a**), cranial (**b**) and mandibular (**c**) landmark configurations. The labels w_1 and w_2 represent factors of shape variation resulting from relative warp analysis[5,6]. Neanderthals and modern humans follow ontogenetic trajectories that are approximately parallel (lines are principal axes of within-taxon correlation). The arrow in **a** characterizes the shared Neanderthal/modern human mode of development as shown in Fig. 3; taxon-specific trajectories are connected with lines at dental ages 0 (birth), 1, 2, 4, 8, 16 yr and adulthood. Arrows in **b** and **c** indicate differences in shape between Neanderthals and modern humans as shown in Fig. 4.