

Kermadec slab morphology, with a significant change in slab dip near 25° (ref. 32). We note that it is from this region that we observe the smallest amounts of splitting.

Although the precise origin of the anisotropy is not clear at present, our observations and linked modelling show evidence for anisotropy in the uppermost lower mantle beneath the eastern part of the Australian plate. The anisotropy is probably inhomogeneous, as there appears to be an appreciable north–south variability in its magnitude. There must be large strains in this region, which are probably related to slab interaction with the sharp increase in viscosity at this boundary. Figure 3 summarizes the potential mechanisms that we propose. Our results may help describe to what extent there is an impediment of flow at this boundary between the upper and lower mantle. □

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A basal troodontid from the Early Cretaceous of China

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Troodontid dinosaurs form one of the most avian-like dinosaur groups^{1–5}. Their phylogenetic position is hotly debated, and they have been allied with almost all principal coelurosaurian lineages^{6–13}. Here we report a basal troodontid dinosaur, *Sinovenator changii* gen. et sp. nov., from the lower Yixian Formation of China. This taxon has several features that are not found in more derived troodontids, but that occur in dromaeosaurids and avialans. The discovery of *Sinovenator* and the examination of character distributions along the maniraptoran lineage indicate that principal structural modifications toward avians were acquired in the early stages of maniraptoran evolution.

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Troodontidae Gilmore, 1924

Sinovenator changii gen. et sp. nov.

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V 12615, a disarticulated partial skull and skeleton.

Referred specimen. IVPP V12583, an incomplete, articulated postcranial skeleton.

Etymology. ‘*Sinae*’, Latin referring to China, plus ‘*Venator*’, Latin for hunter. The specific name honours Meeman Chang of the IVPP for her significant role in the study of the Jehol fauna.

Locality and horizon. Lujiatun and Yanzigou, Shanyuan, western Liaoning, China; lowest part of Yixian Formation, older than 128 Myr (ref. 14; Hauterivian?); associated vertebrate fossils include the ceratopsian *Psittacosaurus*, the primitive ornithischian *Jeholosaurus*¹⁵, and the primitive mammal *Repenomamus*¹⁶.

Diagnosis. A troodontid with the following derived characters: straight and vertical anterior margin of antorbital fenestra; frontal with a vertical lamina bordering the lacrimal; surangular T-shaped

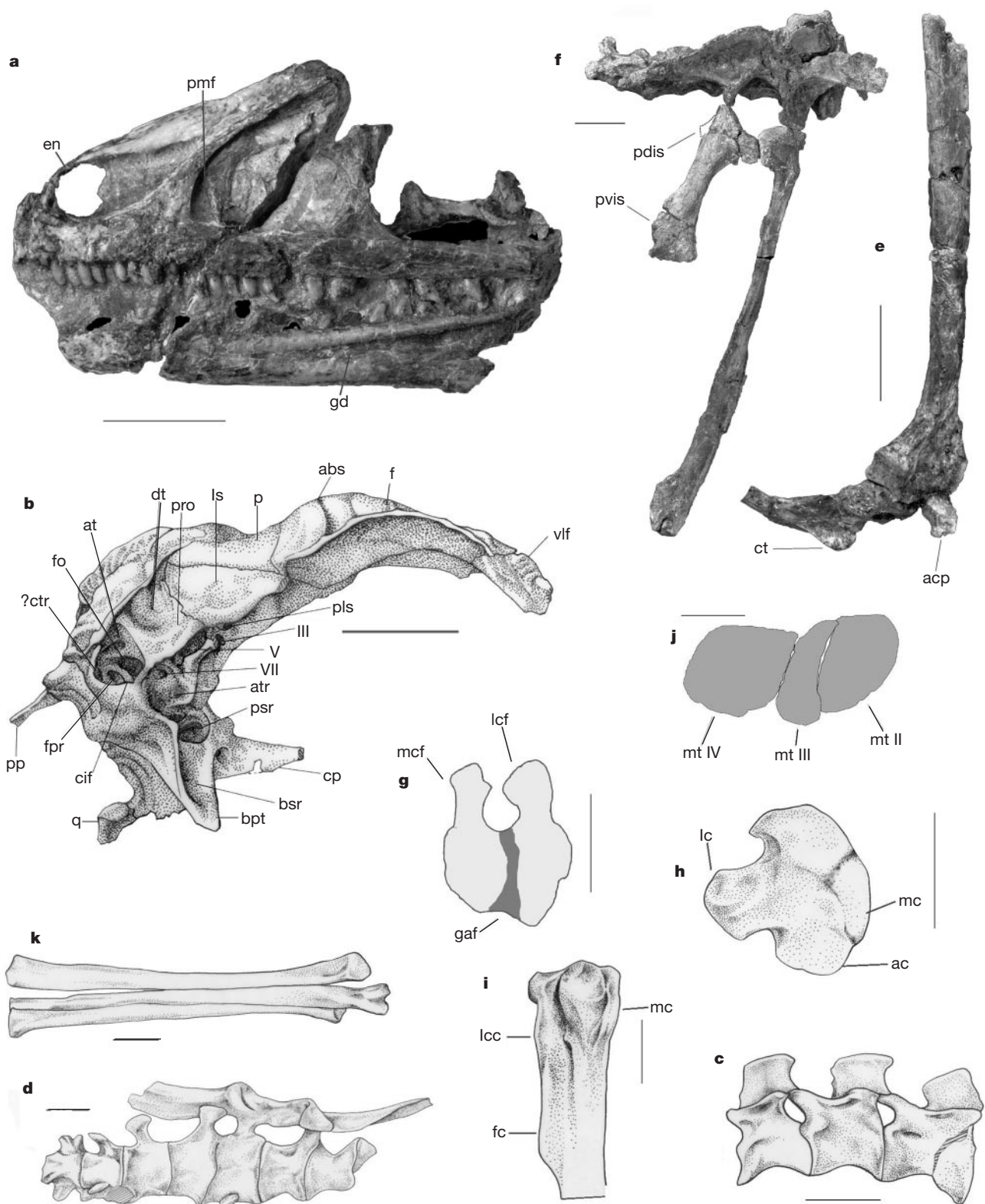


Figure 1 Select elements of *Sinovenator changii*. **a**, Right lateral view of the rostrum (IVPP V 12615). **b**, Right lateral view of the braincase (IVPP V 12615). **c**, Three anterior dorsals in lateral view (IVPP V 12615); **d**, sacrum in ventral view (IVPP V 12615). **e**, Right scapula and coracoid in lateral view (IVPP V 12615). **f**, Right pelvis in lateral view (IVPP V 12615); the presence of posterodorsal and posteroventral processes of the ischium is based on IVPP V 12583. **g**, Right femur in distal view (IVPP V 12615). **h**, **i**, Right tibia in proximal (**h**) and anterior (**i**) views (IVPP V 12583). **j**, **k**, Left metatarsus in proximal (**j**) and anterior (**k**) views (IVPP V 12583). abs, anterior boundary of the supratemporal fossa; ac, anterior condyle; acp, acromion process; at, accessory tympanic recess; atr, anterior tympanic recess; bpt, basiptyergoid process; bsr, basiptyergoid pneumatic recess; cif, crista

interfenestralis; ct, coracoid tubercle; ctr, caudal tympanic recess; cp, cultriform process; dt, dorsal tympanic recess; en, external naris; f, frontal; fc, fibular crest; fo, fenestra ovalis; fpr, fenestra pseudorotundum; gaf, extensor groove on femur; gd, groove on dentary; III, the third cranial nerve; lc, lateral condyle; lcc, lateral cnemial crest; lcf, lateral condyle of femur; ls, laterosphenoid; mc, medial condyle; mcf, medial condyle of femur; mt II–IV, metatarsal II–IV; pdis, posterodorsal process of ischium; pls, pit on laterosphenoid; pmf, promaxillary fenestra; p, parietal; pp, paroccipital process; pro, prootic; psr, parasphenoid pneumatic recess; pvis, posteroventral process of ischium; q, quadrate; V, fifth cranial nerve exit; VII, seventh cranial nerve exit; vlf, vertical laminae of frontal.

in cross-section; and a prominent lateral cnemial crest continuous with the fibular crest.

Description and comparison. *Sinovenator* is a small theropod, with an estimated length of less than 1 m. The skull is triangular in lateral view, with a shallow snout and a deep dorsally convex postorbital region. The supratemporal fenestra is reduced in dorsal view. The exposed endocast of *Sinovenator* is similar to the one reconstructed for *Archaeopteryx*¹⁷.

The external naris is significantly larger than the premaxilla as in other troodontids (Fig. 1a). As in dromaeosaurids¹⁸ and most theropods, but not other troodontids¹⁹, there is a long and slender posterior process of the premaxilla, which excludes the maxilla from the external naris. The sharp-rimmed antorbital fossa contains an antorbital fenestra, a maxillary fenestra and a promaxillary fenestra (Fig. 1a), the last one of which is not present in other troodontids. Unusually, the lateral edge of the nasal is deflected and faces dorsally rather than laterally as in most other theropods. It forms a small shelf adjacent to the nasomaxillary suture. The jugal is similar to that of dromaeosaurids in that the postorbital process is long, slender and oriented posteriorly. A pneumatic fossa is present on the posterior surface of the quadrate shaft, as in some other troodontid taxa²⁰.

The braincase shows many troodontid features including an oval foramen magnum, which is taller than it is wide, a shallow, 'V'-shaped incisure between the basal tubera, absence of a basisphenoid recess, and a pit on the ventral surface of the laterosphenoid

(Fig. 1b). Periotic pneumatic systems present in *Sinovenator* include the anterior tympanic recess, an accessory tympanic recess dorsal to the crista interfenestralis as in *Archaeopteryx*, a dorsal tympanic recess on the prootic, and a small caudal tympanic recess (Fig. 1b) that opens into the columellar recess, closely resembling those of *Archaeopteryx*^{21,22} and *Shuuuuvia*²³. *Sinovenator* lacks the well-developed subotic recess seen in other troodontids.

The basiptyergoid processes taper distally and bear prominent basiptyergoid recesses on their anterodorsal surfaces. A large fossa is adjacent to the base of the cultriform process (the parasphenoid recess) and is also observed in the basal dromaeosaurid *Sinornithosaurus*¹¹. This fossa is continuous with the anterior tympanic recess owing to the lack of a prominent otosphenoidal crest that delimits the 'lateral depression' of most other troodontids^{1,24}. In *Sinovenator* the parabasisphenoid rostrum is not bulbous. *Sinovenator* possesses several characters that are unique among troodontids including an accessory rod-like ventral process on the posterior pterygoid, a deep posterior end of the surangular, and a foramen magnum that is much larger than the occipital condyle.

As in other troodontids, a row of foramina is located in a groove posteriorly on the subtriangular labial surface of the dentary (Fig. 1a). The surangular is 'T'-shaped in cross-section, and the medial edge of the dorsal margin is significantly lower than the lateral edge and roofs over the internal mandibular fossa. The surangular is 'L'-shaped in cross-section in most other theropods.

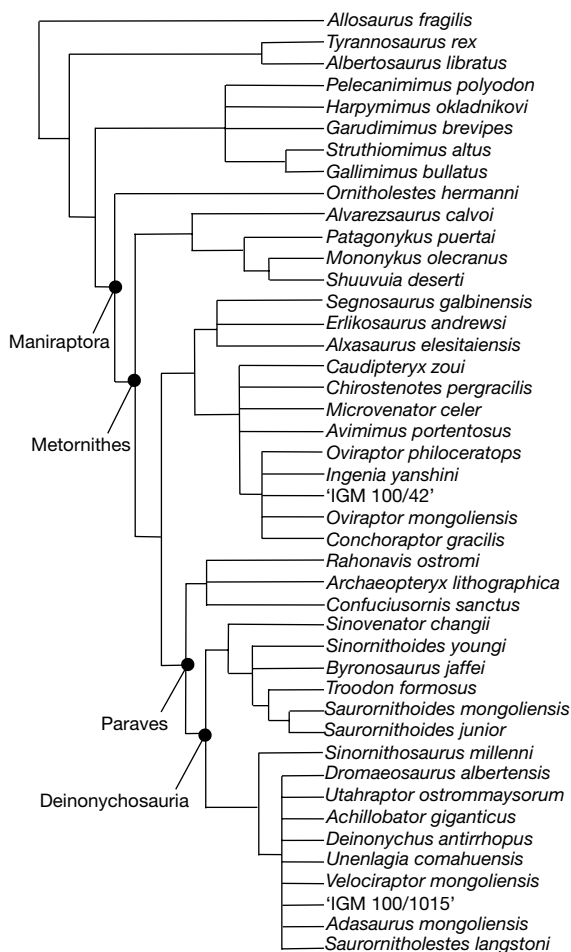


Figure 2 A proposed coelurosaurian phylogeny that is based on the strict consensus of the 336 equally most parsimonious trees (tree length, 576; consistency index, 0.43; retention index, 0.70). Examining the character distributions along the maniraptoran lineage indicates that some major character transformations, such as basally constricted

teeth, an 'L' shaped shoulder girdle and an opisthopubic pelvis, are characteristic of more inclusive maniraptoran clades and did not evolve at the base of or within the avialan clade.

The dentary teeth are closely packed rostrally as in other troodontids¹⁹, but the posterior maxillary teeth are slightly inset medially—an unusual condition in theropods. Denticles seem to be absent on the anterior teeth, and are small on the maxillary teeth as in dromaeosaurids.

The dorsals have moderately tall, fan-shaped neural spines; weakly developed hypapophyses are present on the anterior dorsal centra (Fig. 1c). Unlike other troodontids, which possess six sacrals, *Sinovenator* has five sacrals (Fig. 1d). The middle sacrals are wider than the anterior and posterior ones, as in the basal dromaeosaurid *Microraptor*²⁵ and avians (Fig. 1d).

The scapula and coracoid are very similar to those in dromaeosaurids and other derived maniraptorans^{11,26} in that the glenoid fossa faces laterally and the scapula and coracoid form an angle of less than 90° in lateral view (Fig. 1e). The ilium is small, being less than 60% the femoral length as in *Archaeopteryx* and the basal dromaeosaurid *Sinornithosaurus*. The pubic peduncle is deep and wide, and slightly posteriorly oriented as in *Archaeopteryx* and some dromaeosaurids. Unlike other troodontids^{4–6}, the pubis is posteriorly oriented. The ischium is similar to some advanced maniraptorans, including basal birds, in its small size, the distally positioned obturator process, and the presence of posterodorsal and posteroventral processes (Fig. 1f).

The femur has a derived distal end with a shallow extensor groove on the anterior surface, and a deep popliteal fossa that is constricted between the expanded distal ends of the medial and lateral condyles (Fig. 1g). The tibia is avian-like with an anteroposteriorly elongate proximal end, an incipient development of a medial cnemial crest (Fig. 1h), and a subrectangular distal end instead of the subtriangular one that is seen in most other theropods. Unusually, a prominent lateral cnemial crest continues onto the fibular crest (Fig. 1i). The metatarsus is very similar to the basal dromaeosaurids *Sinornithosaurus* and *Microraptor* except that the metatarsal II is markedly short and slender as in other troodontids^{25,27} (Fig. 1k). The proximal end of metatarsal III is visible anteriorly (Fig. 1j, k); however, the foot resembles more closely the subarctometatarsalian condition seen in the basal dromaeosaurid *Sinornithosaurus* than the non-arctometatarsalian condition.

Discussion. *Sinovenator* is from the lowermost, fluvial deposits of the Yixian Formation, and predates other known coelurosaurs with preserved feather-like integumentary structures from the lacustrine beds that occur higher within the formation. The facies that yielded the specimens of *Sinovenator* do not preserve soft tissue. At present, it is the oldest known taxon that can be referred confidently to the Troodontidae.

A comprehensive phylogenetic analysis (Supplementary Information) shows that *Sinovenator* is the most basal troodontid found so far, and that Troodontidae is the sister group to Dromaeosauridae within a monophyletic Deinonychosauria, which in turn is the sister group of Avialae (Fig. 2), as proposed in some previous studies^{6,10,12}.

The discovery of *Sinovenator* is significant in that, as the most primitive member of the Troodontidae, it resets character polarities at the base of this clade. The absence of a bulbous parasphenoid capsule in *Sinovenator* removes much of the support for a monophyletic Ornithomimosaur–Troodontid clade, Bullatosauria^{1,8,28,29}, and our phylogenetic analysis indicates that this character evolved independently in the two lineages. Exclusion of *Sinovenator* from the phylogenetic analysis posits troodontids as the sister taxon to an Oviraptorosaur–Therizinosaur clade¹³, mainly owing to the numerous teeth with large denticles, hollow basipterygoid processes, and absence of a tertiary antorbital opening shared by higher troodontids and therizinosaurs. Again, the absence of these derived characters in *Sinovenator* indicates that these similarities were acquired convergently, and underscores the pivotal role of *Sinovenator* in reconstructing maniraptoriform phylogeny. Gaining a full understanding of character evolution within Coelurosauria may not be possible if taxon sampling is carried out at higher taxonomic levels,

and the benefits of sampling species outweighs the problems caused by missing data in some fragmentary taxa.

The discovery of *Sinovenator changii* improves our understanding of the transition of several salient osteological characters to birds, notably, the laterally projected glenoid of the scapulacoracoid and the opisthopubic pelvis. In maniraptorans, a laterally projected glenoid of the scapulacoracoid can now be considered as diagnostic of the Deinonychosaur–Avialan clade (Paraves), and the opisthopubic pelvis as diagnostic of an even more inclusive clade (Metornithes) rather than as homoplastic in dromaeosaurids and avialans as suggested previously^{6,9,10,12}. Notably, small body size seems to be primitive for Paraves, and the trend toward miniaturization in early bird evolution¹² is a continuation of the paravian trend²⁵. Unexpectedly, this trend is reversed independently in dromaeosaurids and troodontids toward an increasing body size, and this is accompanied by homoplastic reversals in some key characters, such as the propubic or near-propubic pelvis of derived troodontids and the bizarre dromaeosaurid *Achillobatar*³⁰. Convergent evolution of other features that have caused confusion about the phylogenetic position of troodontids, such as the large denticles and pneumatic bullae, also occurred late in the evolution of this group in a subclade of larger-bodied troodontid taxa. □

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Chameleon radiation by oceanic dispersal

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Historical biogeography is dominated by vicariance methods that search for a congruent pattern of fragmentation of ancestral distributions produced by shared Earth history^{1–3}. A focus of vicariant studies has been austral area relationships and the break-up of the supercontinent Gondwana^{3–5}. Chameleons are one of the few extant terrestrial vertebrates thought to have biogeographic patterns that are congruent with the Gondwanan break-up of Madagascar and Africa^{6,7}. Here we show, using molecular and morphological evidence for 52 chameleon taxa, support for a phylogeny and area cladogram that does not fit a simple vicariant history. Oceanic dispersal—not Gondwanan break-up—facilitated species radiation, and the most parsimonious biogeographic hypothesis supports a Madagascan origin for chameleons, with multiple ‘out-of-Madagascar’ dispersal events to Africa, the Seychelles, the Comoros archipelago, and possibly Reunion Island. Although dispersal is evident in other Indian Ocean terrestrial animal groups^{8–16}, our study finds substantial out-of-Madagascar species radiation, and further highlights the importance of oceanic dispersal as a potential precursor for speciation.

The break-up of Gondwana provides one of the most obvious test cases for vicariance biogeography, with the separation of Africa, Madagascar, the Seychelles and India providing a well documented geologic history⁴. Magnetic anomaly data and Mesozoic timescales reveal that Madagascar and Greater India first broke away from Africa 165 Myr ago, with movement ending by 121 Myr ago¹⁷; Greater India and Madagascar separated approximately 88 Myr ago based on dating of Marion hot-spot-related volcanism¹⁸, and the

Seychelles granitic archipelago split from India during formation of the Deccan basalt province between 69 and 65 Myr ago¹⁹. The main source of current controversy concerns the sequence and timing of separation of Antarctica with India, South America and Australia between 80–100 Myr ago^{18,20}.

Gondwanan origins have been proposed for extant terrestrial vertebrates in Madagascar⁸; however, no modern systematic evidence congruent with a Gondwanan break-up vicariant pattern has been reported to date. Chameleons (family Chamaeleonidae: subfamily Chamaeleoninae²¹) are claimed to be an ancient Gondwanan group, on the basis of limited immunological distances and a calibrated albumin molecular clock⁷. Previous cladistic studies, using 11–24 morphological characters, supported conflicting biogeographic hypotheses that are partly congruent with Gondwanan break-up^{6,22}, or that suggest a post-Gondwanan, Madagascan origin for chameleons²³.

To test the Gondwanan vicariance hypothesis, we conducted a phylogenetic analysis that included 52 chameleon taxa (approximately 40% of all chameleon species). These taxa represent all Chamaeleoninae genera and subgenera, and include species found in each continental region (including the granitic Seychelles), and the Comoros archipelago and Reunion Island (both of volcanic origin). To test the monophyly of chameleons, the two other Chamaeleonidae subfamilies (Leiolepidinae and Agaminae) were also included. Molecular characters (mitochondrial DNA (mtDNA), NADH subunit 4 and adjacent transfer RNA sequences), morphological characters, and behavioural/life-history characters were used to produce a combined data set of 644 potentially parsimony-informative characters.

Three equally parsimonious trees were found for the combined equally weighted data set. These results (Fig. 1) support the monophyly of chameleons, with the two most basal clades representing dwarf chameleons (*Brookesia*), which are endemic to Madagascar. Basal to the crown clade of ‘typical’ chameleons (*Furcifer*, *Calumma* and *Chamaeleo*) are the endemic African genera, *Rhampholeon* and *Bradypodion*. The resulting area cladogram (Fig. 1) has the following features: (1) The two most basal lineages are distributed in Madagascar; (2) The more derived lineages occur in Madagascar, Africa, the Seychelles and India, with the two most basal lineages of this clade occurring in Africa; (3) the India lineage is sister to an African clade; (4) the Seychelles lineage is sister to a Madagascan clade; and (5) the Comoros lineage is sister to a Madagascan clade.

The corresponding chameleon continental area cladogram (Fig. 2a) cannot be reconciled²⁴ with proposed Gondwanan break-up

Table 1 Chameleon area cladogram reconciled with origin hypotheses

Biogeographic hypothesis	Minimum assumption*		
	Extinction†	Dispersal	Total
Gondwanan origin 1‡			
Vicariance only	38	0	38
Vicariance and dispersal	3	5	8
Gondwanan origin 2§			
Vicariance only	25	0	25
Vicariance and dispersal	1	5	6
Partial Gondwanan origin			
Madagascar + Seychelles + India	0	12	12
Madagascar + Seychelles + India	1	11	12
Seychelles + India	0	14	14
Post-Gondwanan origin			
Madagascar	0	5	5
Africa	0	6	6
Seychelles	0	12	12
India	0	11	11

* Minimum number of assumption events to reconcile area cladogram with biogeographic hypothesis.

† Minimum number of losses²⁴. Inclusion of all missing nodes (items of error⁷) would add additional extinction events.

‡ Conventional hypothesis.

§ Hypothesis of ref. 20.