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THE OSTEOLOGY OF THE GIANT SNAKE *GIGANTOPHIS GARSTINI* FROM THE UPPER EOCENE OF NORTH AFRICA AND ITS BEARING ON THE PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHY OF MADTSOIIDAE

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ABSTRACT—Madtsoiidae is a speciose family of extinct snakes that achieved a wide Gondwanan and trans-Tethyan distribution by the Late Cretaceous, surviving until the late Pleistocene. *Gigantophis garstini*, the first and largest described madtsoiid, was recovered from the upper Eocene of Fayum, Egypt. The 20 vertebrae that constitute the syntype have only received brief description, hindering the referral of specimens to this taxon and our understanding of madtsoiid interrelationships in general. A detailed redescription of the syntype material demonstrates the validity of *Gigantophis*, based on two autapomorphies (including a strongly depressed neural canal in posterior trunk vertebrae) and a unique combination of characters. Referred material from the lower Paleocene of Pakistan differs significantly, and we restrict *Gigantophis* to the middle–late Eocene of North Africa. Using a model of morphological variation in extant snakes, we estimate that *Gigantophis* was 6.9 ± 0.3 m long. A phylogenetic analysis using the largest sample of putative madtsoiids (20 operational taxonomic units) and a revised and augmented matrix (148 characters) places *Gigantophis* as sister taxon to the latest Cretaceous Indian snake *Madtsoia pisdurensis*. Whereas our topology might suggest that a dispersal route was present between India and North Africa in the latest Cretaceous–early Paleogene, an evaluation of putative dispersal routes leads us to conclude that the paleobiogeography of Madtsoiidae is best explained by a poorly sampled, earlier widespread distribution in Africa, Indo-Madagascar, and South America. In contrast, latest Cretaceous madtsoiid occurrences in Europe might be explicable by trans-Tethyan dispersal from Africa across the Apulian Route.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Madtsoiidae is an extinct clade of snakes currently known from 23 species belonging to 14 genera. Their temporal range is the greatest of all snake groups, with a 100 million year (myr) history spanning the Cenomanian (100 Ma) to the late Pleistocene (Lawrence, 2000; LaDuke et al., 2010). Madtsoiid remains have most frequently been recovered from Gondwana (LaDuke et al., 2010; Fig. 1). During the Late Cretaceous, the group is known from deposits in Africa, Indo-Madagascar, and South America, with scarce finds from southern Europe (Rage, 1996; Sigé et al., 1997; Folie and Codrea, 2005; Vasile et al., 2013; Venczel et al., 2015). Their Cenozoic record is entirely Gondwanan, with the group first appearing in the Australian fossil record in the early Eocene

(Scanlon, 2005), and seemingly restricted to that continent by the Neogene (Scanlon, 2006).

The phylogenetic placement of Madtsoiidae within Ophidia remains enigmatic. Whereas some authors have recovered madtsoiids as alethinophidians (e.g., Wilson et al., 2010; Zaher and Scanferla, 2012; Vasile et al., 2013) or basal to Alethinophidia (e.g., Longrich et al., 2012; Hsiang et al., 2015), within crown group snakes (Serpentes), others have positioned them outside Serpentes (e.g., Scanlon and Lee, 2000, 2002; Scanlon, 2006; Caldwell et al., 2015; Martill et al., 2015). Part of this problem might stem from poor constraint of madtsoiid interrelationships, with only a single phylogenetic analysis (Vasile et al., 2013) including more than three putative madtsoiid species. This in turn might reflect the relatively incomplete nature of most madtsoiid skeletons, with only four skulls known, for example (Scanlon and Lee, 2000; Scanlon, 2006; LaDuke et al., 2010; Wilson et al., 2010). A lack of understanding of madtsoiid interrelationships also hinders our identification and recognition of the group's radiation, as well as biogeographic patterns. In particular, how and when Madtsoiidae achieved its wide Gondwanan and trans-Tethyan distribution is heavily debated (e.g., LaDuke et al., 2010; Mohabey et al., 2011; Vasile et al., 2013; Rage et al., 2014).

Gigantophis garstini was named by Andrews (1901), based on vertebral material collected from the upper Eocene Qasr-el-Sagha Formation of Fayum, Egypt. *Gigantophis* is regarded as the largest known madtsoiid and has been reconstructed as

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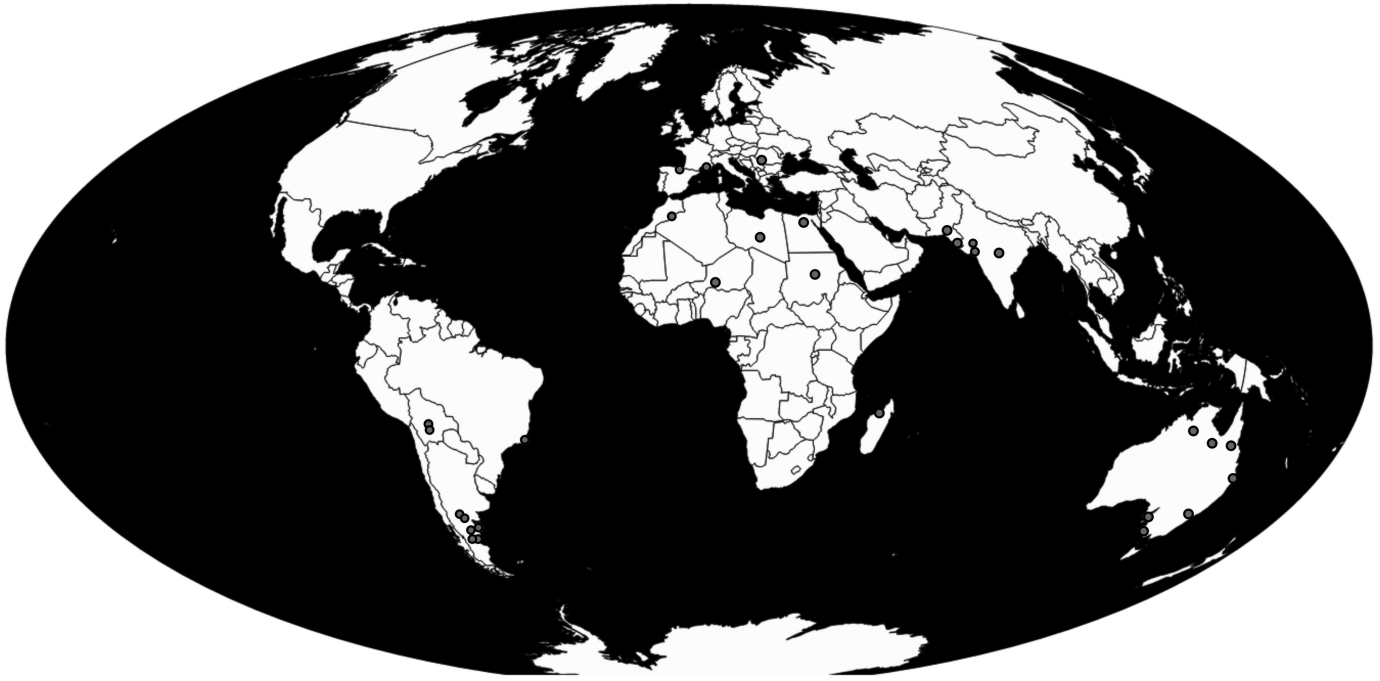


FIGURE 1. Geographic distribution of Madtsoiidae, plotted on a present-day map. The map and madtsoiid occurrences were produced using the Paleobiology Database Navigator on 16 January, 2017.

among the largest ophidians, second only to the boid *Titanoboa cerrejonensis* from the Paleocene of Colombia (Head et al., 2009). Although *Gigantophis* was the first described madtsoiid, the group was not formally recognized until the description of the Malagasy snake, *Madtsoia madagascariensis*, by Hoffstetter (1961a), who erected Madtsoiinae as a subfamily, later elevated to family status by McDowell (1987).

Over two publications, Andrews (1901, 1906) figured only four specimens of *Gigantophis garstini*, as well as the ramus of a referred lower jaw. He also provided only a small set of measurements from three vertebrae. Although the 20 vertebrae that constitute the syntype material are accessioned in the Egyptian Geological Museum, Cairo (CGM), nearly all subsequent comparative work has been based either on the limited information provided by Andrews (1901, 1906) or on first-hand observations of high-quality casts stored in the Natural History Museum, London (NHMUK), combined with information from referred specimens (e.g., Head et al., 2009; Rage et al., 2014; McCartney and Seiffert, 2016). In particular, one referred specimen (NHMUK R3188), figured by Andrews (1906:pl. XXVI, fig. 2), has come to epitomize our knowledge of *Gigantophis* over the last century. As such, the published record of *Gigantophis* is extremely brief and insufficiently characterizes the genus. Consequently, the referral of other materials to *Gigantophis* (e.g., from the Paleocene of Pakistan; Rage et al., 2014), and its character scoring in the only phylogenetic analysis to include it (Vasile et al., 2013), should be treated with caution, as should biogeographic hypotheses based on these studies.

Gigantophis garstini was last described over 100 years ago (Andrews, 1906). Here we provide a detailed redescription and revised diagnosis of the type material of *Gigantophis garstini*, based on the casts at the NHMUK, along with a reevaluation of referred material from North Africa and Pakistan. We also constrain the phylogenetic affinities of *Gigantophis* and other madtsoiids via the largest and most comprehensive data matrix to date. Finally, combined with the spatiotemporal fossil record of

the group, we utilize our revised phylogenetic topology to provide a reexamination of the paleobiogeography of Madtsoiidae.

Institutional Abbreviations—CGM, Egyptian Geological Museum, Cairo, Egypt; CPAG, Centre of Pure and Applied Geology, University of Sindh, Jamshoro, Pakistan; DPC, Duke Lemur Center, Durham, North Carolina, U.S.A; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, The Natural History Museum, London, U.K.

Anatomical Abbreviations—MTV, mid-trunk vertebrae; PPTV, posterior part of the posterior trunk vertebrae; PTV, posterior trunk vertebrae.

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811

OPHIDIA Brongniart, 1800

MADTSOIIDAE (Hoffstetter 1961a) McDowell, 1987

GIGANTOPHIS GARSTINI Andrews, 1901

(Figs. 2–6)

Syntype—CGM C.10022, six mid-trunk and 14 posterior trunk vertebrae, as well as portions of two ribs (Andrews, 1901, 1906), nominated as syntypes by Rage (1984). Eight of these vertebrae are disarticulated, whereas the remaining 12 vertebrae form four articulated sequences. As a result, the vertebrae of CGM C.10022 are preserved as 12 specimens, to which we assign the letters A–L (Figs. 2–6). NHMUK R8344 represents high-quality casts of the syntype vertebrae.

Emended Diagnosis—Madtsoiid snake with the following unique combination of characters (characters apply to the whole column unless otherwise stated and autapomorphies are denoted by an asterisk): (1*) exceptionally large vertebrae (Mohabey et al., 2011; McCartney and Seiffert, 2016) with postzygapophyseal width over 60 mm and centrum length >35 mm in MTV; (2) broad hemal keel narrowing posteriorly with a rhombic termination in MTV; (3) subcentral ridges weakly developed; (4) strongly posteroventrally pointing centrum in PPTV; (5*) neural

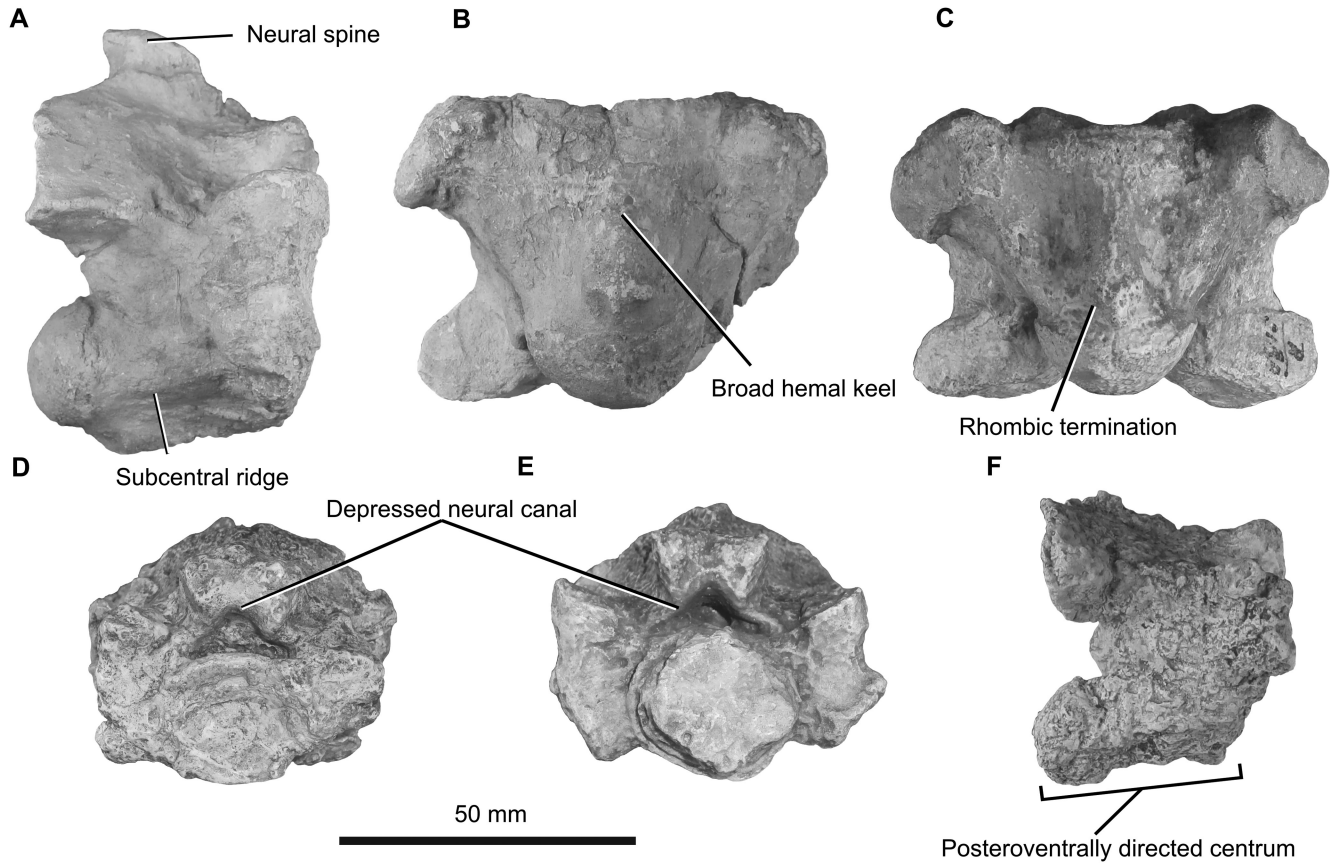


FIGURE 2. Diagnostic features in selected vertebrae of *Gigantophis garstini*. **A**, **B**, vertebra from the mid-trunk region, NHMUK R8344 specimen A, in **(A)** right lateral and **(B)** ventral views; **C**, vertebra from the mid-trunk region, NHMUK R3188, in ventral view; **D**, vertebra from the middle part of the posterior trunk, NHMUK R8344 specimen I, in anterior view; **E**, vertebra from the middle part of the posterior trunk, NHMUK R8344 specimen L, in anterior view; **F**, vertebra from the posterior part of the posterior trunk region, NHMUK R8344 specimen H, in right lateral view.

canal dorsoventrally depressed in PTV; and (6) low neural spine between 15% and 30% of total vertebral height.

Type Locality and Horizon—An unspecified locality north of Birket Qarun, Fayum, Egypt; Qasr-el-Sagha Formation, Priabonian, late Eocene, 37–35 Ma (Seiffert et al., 2005).

Referred Specimens—One unnumbered MTV from the Bartonian (late middle Eocene) Idam Unit of Dur-At-Talha, Libya (Hoffstetter, 1961b) reposit in the MNHN; NHMUK R3188 (one MTV) from the upper Eocene of Fayum, Egypt; NHMUK R3010 (three slightly crushed MTV) “presented by the Egyptian Government” (Andrews, 1906:309) from the upper Eocene of Egypt; DPC 25616 (one MTV) and DPC 25641 (one juvenile MTV) from the lowermost Priabonian (upper Eocene) Birket Qarun Formation, Fayum, Egypt (McCartney and Seiffert, 2016).

DESCRIPTION AND COMPARISONS

The following description is based on the detailed casts of the 20 vertebrae that form the syntype of *Gigantophis garstini* (Andrews, 1901; Figs. 2–6). Measurements are provided in Table 1. Based on consistency of preservation and size, there is no evidence to suggest that the vertebrae belong to more than one individual, and several vertebrae are in articulation.

The vertebrae are derived from the precloacal region, evident from the absence of pleurapophyses, lymphapophyses, and hemapophyses (LaDuke, 1991). They are divided into two regions, comprising six mid-trunk vertebrae (MTV) and 14 posterior trunk vertebrae (PTV), although subtle serial variation allows further differentiation of the latter into the middle PTV (MPTV) and the posterior end of the PTV (PPTV).

Comparisons are made with the following madtsoiid taxa: *Adinophis fisaka* (Pritchard et al., 2014); *Alamitophis argentinus* (Albino, 1986); *Alamitophis elongatus* (Albino, 1994); *Alamitophis tingamarra* (Scanlon, 2005); *Herensugea caristiorum* (Rage, 1996); *Madtsoia bai* (Simpson, 1933); *Madtsoia camposi* (Rage, 1998); *Madtsoia madagascariensis* (LaDuke et al., 2010); *Madtsoia pisduensis* (Mohabey et al., 2011); *Menarana laurasiae* (Rage, 1996); *Menarana nosymena* (LaDuke et al., 2010); *Nanowana godthelpi* (Scanlon, 1997); *Nanowana schrenki* (Scanlon, 1997); *Nidophis insularis* (Vasile et al., 2013); *Patagoniophis australiensis* (Scanlon, 2005); *Patagoniophis parvus* (Albino, 1986); *Sanajeh indicus* (Wilson et al., 2010); *Wonambi naracoortensis* (Smith, 1976); and *Yurlunggur camfieldensis* (Scanlon, 1992).

The vertebrae of *Gigantophis* are exceptionally large in absolute length and width (Table 1) compared with any other madtsoiid, and we consider this an autapomorphy of the taxon. *Gigantophis* has anteroposteriorly short vertebrae relative to

TABLE 1. Measurements (in mm) of *Gigantophis garsini*, NHMUK R8344—casts of the syntype CGM C.10022—and referred vertebrae NHMUK R3188 and NHMUK R3010.

Specimen	Dimension	CL	NAW	PRW	POW	IZW	COW	COH	CNW	CNH	NSH	ZW	ZT	ZTW	NCH	NCW	NN	ZC	TVH
R8344																			
A	MTV	38.3	44.8	66*	64*	40.8	29.3	22.6	24.5	18.7	9*	23.6	11.8	24*	8	18	7.1	0	60
B	MTV	38.7	—	60*	60*	—	24*	21*	23*	18*	—	—	—	—	—	—	—	—	—
C	MTV	37.2	—	—	—	—	28*	22*	23.5	18.3	—	—	—	—	—	—	—	—	—
D	MTV	38	42.5	58.7	58.1	42.9	28	23.3	23.4	19.1	—	22.3	11.6	32.4	7	16	12.3	1.6	—
E	MTV	34.3	43.5	60.1	50*	42.1	28.7	36.1	24.3	16.7	—	22.5	10.4	24.7	8.6	19.5	—	2	—
F	MTV	35.6	38.6	55.5	50*	42	25.1	21.1	23.5	19.2	—	21.7	9.3	24.4	6.8	16	11	1.4	—
G	MPTV	—	36.1	55*	—	—	25	21.2	—	—	—	22*	9*	24.3	6.2	18.2	8.4	—	—
J(1)	MPTV	41*	35.5	56.3	50.5	37.2	24.4	20.5	—	—	—	23*	8.9	—	—	—	9.6	—	50*
J(2)	MPTV	37*	35.4	53.7	50.5	39.2	26*	—	—	—	12*	22.6	—	—	—	—	11.7	—	—
J(3)	MPTV	35*	35.8	53.7	51	39.6	27*	—	—	—	—	20	—	20.9	—	—	11.7	—	—
J(4)	MPTV	—	34.4	52.6	47*	37	27*	—	—	—	—	20.1	—	—	—	—	11.7	—	—
I(1)	MPTV	38*	36	47*	50*	35.1	24.1	20.2	—	—	10*	20*	6.9	—	6.5	18	9.5	—	47.3
I(2)	MPTV	38*	38.1	56.4	50*	39.2	26.5	—	—	—	—	23.05	—	—	—	—	9	—	—
I(3)	MPTV	—	38.2	54.5	54*	39.3	27.2	—	—	—	—	23	—	23.7	—	—	10	—	—
K(1)	MPTV	36*	33.6	44*	50.5	36.2	24*	21.2	—	—	—	17.8	9.9	—	4.8	17	9.7	2.2	—
K(2)	MPTV	38*	34.3	52	48.9	38.8	24*	—	—	—	—	21	—	—	—	—	9.7	2.2	—
K(3)	MPTV	—	34.2	53.1	46	36.2	24*	—	—	—	—	22	—	24*	—	—	9.7	2.2	—
L(1)	MPTV	37*	32.7	49.6	47.8	38.3	27*	—	—	—	—	18.7	8.1	—	6	19.2	7.7	2.4	—
L(2)	MPTV	—	31.6	49.8	47.4	37.4	25*	24	—	—	—	20.4	—	20.9	—	—	8.4	—	—
H	PPTV	28.9	32.5	48*	42*	35.5	18.7	16.9	14.6	14.4	—	17*	9*	21	—	7.3	17.4	—	—
R3188	MTV	34.1	48.5	63	61.8	36.6	24.5	21.1	22.5	20	12*	28.8	13.7	27.4	8.4	16.2	8.8	1.2	57
R3010A	MTV	38.4	52.2	65.7	68	40.3	21.4	17.1	24.1	17	—	30.5	13.9	29.8	9.2	18.9	13	1	—
R3010B	MTV	32.8	47.2	61.6	59*	44.4	25*	20*	24.7	18.6	10*	25.2	13	25*	7.4	18.1	—	2*	53
R3010C	MTV	37.7	43	65.5	58*	41	31.5	20	23.4	16	—	25.4	9.2	27.6	7	14	10	0.8	—

Abbreviations: CL, Centrum Length; CNH, Condyle height; CNW, Condyle width; COH, Cotyle height; COW, Cotyle width; IZW, Interzygapophyseal width; NAW, Neural arch width; NCH, Neural canal height; NCW, Neural canal width; NN, Neural arch notch depth; NSH, Neural spine height; POW, Postzygapophyseal width; PRW, Prezygapophyseal width; TVH, Total vertebral height; ZC, Zygosphenic concavity; ZT, Zygosphenic thickness; ZTW, Maximum zygantrum width; ZW, Zygosphenic width.

*Estimated where broken, eroded, or hidden due to articulation.

neural arch width in MTV. This is common to the large madtsoiids, i.e., *Madtsoia* (Simpson, 1933; Rage, 1998; LaDuke et al., 2010), *Yurlunggur* (Scanlon, 1992), and *Wonambi* (Smith, 1976). In PTV, the vertebrae become anteroposteriorly longer, typically with a greater centrum length to neural arch width ratio (Table 1).

In ventral view, the procoelous centrum is triangular, broadening anteriorly (Fig. 3A). Its ventral surface is transversely convex, with a broad, poorly defined hemal keel that narrows posteriorly. This contrasts with the sharp hemal keel seen in *Nanowana* (Scanlon, 1997) and *Alamitophis* (Albino, 1986, 1994; Scanlon, 1993, 2005) and more closely resembles the condition in *Madtsoia* (LaDuke et al., 2010; Mohabey et al., 2011) and *Yurlunggur* (Scanlon, 1992). In one specimen (Fig. 3A), the posterior margin of the slightly eroded hemal keel has an arrow-shaped process, possibly analogous to the “rhombic area” described by Rage (1998:118) in the MTV of *Madtsoia camposi*. This process clearly contrasts with the two blunt protuberances that unite *Madtsoia madagascariensis* and *Madtsoia bai* (Simpson, 1933; LaDuke et al., 2010), as well as the unusual triangular process in *Madtsoia pisdurensis* (Mohabey et al., 2011). In lateral view, the profile of the ventral margin of the centrum is slightly concave (Figs. 3D, 4A).

Subcentral fossae are extremely shallow in *Gigantophis* (Figs. 3A, 4A) and appear to lack foramina; however, it is possible that these small foramina have become obscured during fossilization. The subcentral fossae begin posteriorly at the precondylar constriction and extend anteriorly as far as the ventrolateral edges of the cotyle. Here they define two shallow paracotylar notches (Fig. 3A). In specimens B (Fig. 3B), D (Fig. 3D), and E (Fig. 4A), these notches are poorly developed as a result of the limited ventral projection of the parapophyses. In the MPTV, the anterior widening of the centrum is more gradual, and the maximum centrum width is lower (Fig. 5F). Subcentral fossae are deeper in the MPTV, and the ventral margin of the centrum is more convex, with a more prominent hemal keel (Fig. 5H). In the PPTV, the centrum is strongly cylindrical and defined by paralympathic subcentral fossae (Fig. 4D), sensu LaDuke (1991).

In MTV, the hypapophysis occurs as a posterior swelling anterior to the precondylar constriction (Figs. 3A, D; 4A). An insufficient sample of vertebrae restricts comment on the pervasiveness of the hypapophysis throughout the vertebral column, but provisionally it appears to be restricted to a swelling in the MTV and is absent in PTV, as is also the case in *Madtsoia camposi* (Rage, 1998), *Madtsoia madagascariensis* (LaDuke et al., 2010), and *Yurlunggur* (Scanlon, 1992), as well as the smaller madtsoiids *Patagoniophis australiensis* (Scanlon, 2005) and *Nanowana godthelpi* (Scanlon, 1997).

In anterior view, the cotyle in MTV is oval, as in *Madtsoia*, *Wonambi*, and *Yurlunggur*. The roof of the cotyle is flat (Figs. 3A, 4A) to convex (Fig. 3D), and the dorsal cotylar lip projects strongly anteriorly. In MPTV, the cotyle is subcircular with a convex roof. Additionally, the ventral cotylar lip is recessed, resulting in an anteroventrally directed cotyle. In PPTV, this condition is more pronounced, with the cotyle directed even more ventrally (Fig. 4D).

The condyle projects posteriorly and is slightly dorsoventrally flattened, with a moderate precondylar constriction, contrasting with *Wonambi naracoortensis* (Smith, 1976) and *Yurlunggur*, in which the condyles point more dorsally and have strong precondylar constrictions. In PPTV, the centrum has a strong precondylar constriction and is directed posteroventrally (Fig. 4D). Subcentral ridges are moderately developed. They are straight to dorsally convex in lateral view and extend from the base of the synapophyses to the dorsoventral midpoint of the condyle.

The synapophyses are poorly preserved in MTV but are noticeably large. Their articular facets are oval to reniform in shape. A small constriction at their dorsoventral midpoint

divides the synapophysis into a diapophysis and parapophysis (Fig. 3D). This constriction is considerably less prominent than in *Madtsoia camposi* (Rage, 1998), *Yurlunggur* (Scanlon, 1992), or *Wonambi* (Smith, 1976) but resembles *Madtsoia madagascariensis* (LaDuke et al., 2010), and *Madtsoia pisdurensis* (Mohabey et al., 2011). The position of the synapophyses varies among the vertebrae. In MTV, the ventral margin of the parapophyses aligns approximately with the ventral cotylar lip (Fig. 3A), whereas the synapophysis is dorsally shifted in MPTV, such that the base of the parapophysis is well above the ventral cotylar lip (Fig. 4B). Progressively dorsally shifted synapophyses are also observed in *Madtsoia madagascariensis* (LaDuke et al., 2010), *Yurlunggur* (Scanlon, 1992), and *Patagoniophis* (Scanlon, 2005).

Laterally, the synapophyses of the MTV extend as far as, if not marginally beyond, the prezygapophyses. In lateral view, the long axis of the synapophysis is rotated 30° from vertical. In anterior view, the facets are inclined 45° ventromedially and slightly posteriorly.

The synapophyses are better preserved in MPTV. They are massive and project further than the prezygapophyses (Fig. 6C). This increase in lateral extent of the synapophyses towards PTV is also observed in *Adinophis* (Pritchard et al., 2014), *Madtsoia madagascariensis* (LaDuke et al., 2010), and prominently in *Madtsoia camposi* (Rage, 1998). The dorsal margin of the diapophysis in *Gigantophis* is situated at a level between the dorsoventral midpoint of the cotyle and the floor of the neural canal, as in *Yurlunggur* (Scanlon, 1992), *Nidophis* (Vasile et al., 2013), and *Madtsoia pisdurensis* (Mohabey et al., 2011), in contrast with the elevated diapophyses present in *Madtsoia madagascariensis* (LaDuke et al., 2010), *Madtsoia camposi* (Rage, 1998), and especially *Adinophis* (Pritchard et al., 2014).

The paracotylar fossae are shallow and broad in MTV (Fig. 4A). Their dorsal margins are each defined by a small strut extending between the anteromedial margin of the prezygapophyseal facet and the dorsolateral margin of the cotyle. This separates each paracotylar fossa from the neural canal. The fossae are deepest at the dorsolateral margin of the cotyle, whereas the lateral margin is poorly defined and the fossae fade out within the prezygapophyseal buttress. There is no ventral boundary, and thus the fossae merge with the paracotylar notches. Paracotylar foramina are inconsistently found in MTV. One large foramen (diameter = 1 mm) is observed in the left paracotylar fossa of specimens A and E, located on the dorsolateral corner of the cotyle. In MPTV, the paracotylar fossae are deeper and smaller in diameter (Fig. 4C) and paracotylar foramina are consistently present. One large foramen (1.5 mm in diameter) opens on the dorsolateral margin of the cotyle within each fossa.

The neural canal is strongly trifoliate, equidimensional, and inclined posteroventrally, walled by thick neural arch pedicles. Its cross-sectional area is less than half that of the cotyle. Trifoliate neural canals are only observed in *Madtsoia* (Rage, 1998; LaDuke et al., 2010; Mohabey et al., 2011) and *Menarana lauraisiae* (Rage, 1996). Unlike any other madtsoiid, the neural canal becomes dorsoventrally depressed in the PTV of *Gigantophis*. We do not consider this a result of deformation because other anatomical features are not distorted; as such, we regard this as an autapomorphy of *Gigantophis* (Figs. 4C, 6C).

Each prezygapophyseal buttress is massive and lacks prezygapophyseal accessory processes. In anterior view, the lateral margin of the prezygapophysis has a large constriction aligned with the dorsal margin of the cotyle, separating it from the synapophysis (Fig. 3D). The prezygapophyseal articular facets are oval to subcircular. They are inclined ~20° ventromedially, and the orientation of their long axes is ~70° to the sagittal plane. In MPTV (specimens I–L), the prezygapophyseal facets become smaller and rounded and are orientated obliquely to the sagittal plane (~50°). Increasingly oblique prezygapophyseal facets in more posterior trunk vertebrae have also been recognized in

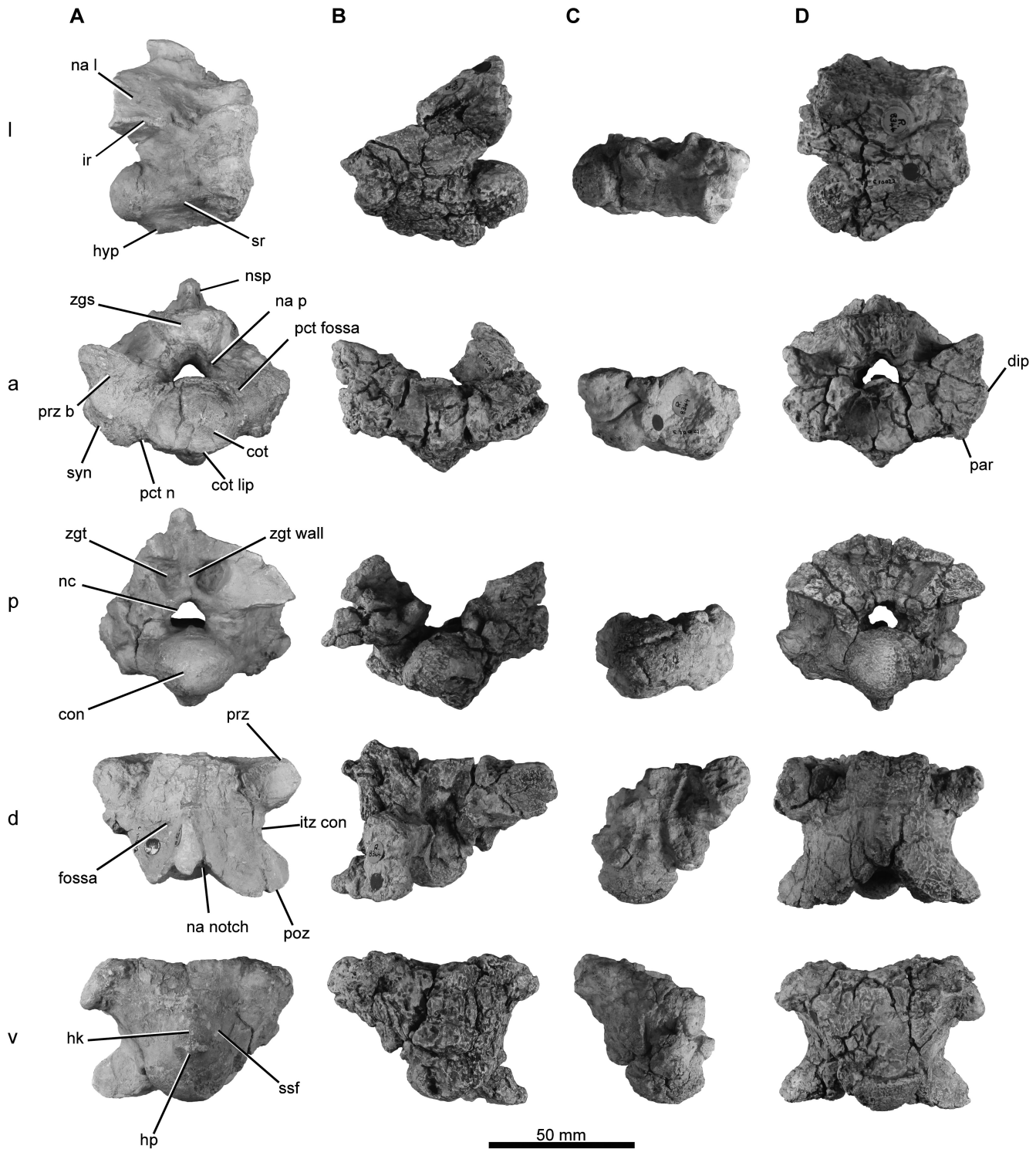


FIGURE 3. Precloacal vertebrae of *Gigantophis garstini*, NHMUK R8344 (casts of the syntype CGM C.10022) in l, lateral; a, anterior; p, posterior; d, dorsal; and v, ventral views. A, vertebra from the mid-trunk region, specimen A; B, vertebra from the mid-trunk region, specimen B; C, vertebra possibly from the mid-trunk region, specimen C; D, vertebra from the mid-trunk region, specimen D. **Abbreviations:** con, condyle; cot, cotyle; cot lip, cotylar lip; dip, diapophysis; hk, hemal keel; hp, hemal keel process; hyp, hypapophysis; itz con, interzygapophyseal constriction; ir, interzygapophyseal ridge; na l, neural arch lamina; na n, neural arch notch; na p, neural arch pedicle; nc, neural canal; nsp, neural spine; par, parapophysis; pct fo, paracotylar fossa; pct n, paracotylar notch; poz, postzygapophysis; prz, prezygapophysis; prz b, prezygapophyseal buttress; sr, subcentral ridge; ssf, subcentral fossae; syn, synapophysis; zgs, zygosphenes; zgt, zygantrum; zgt wall, zygantral wall.

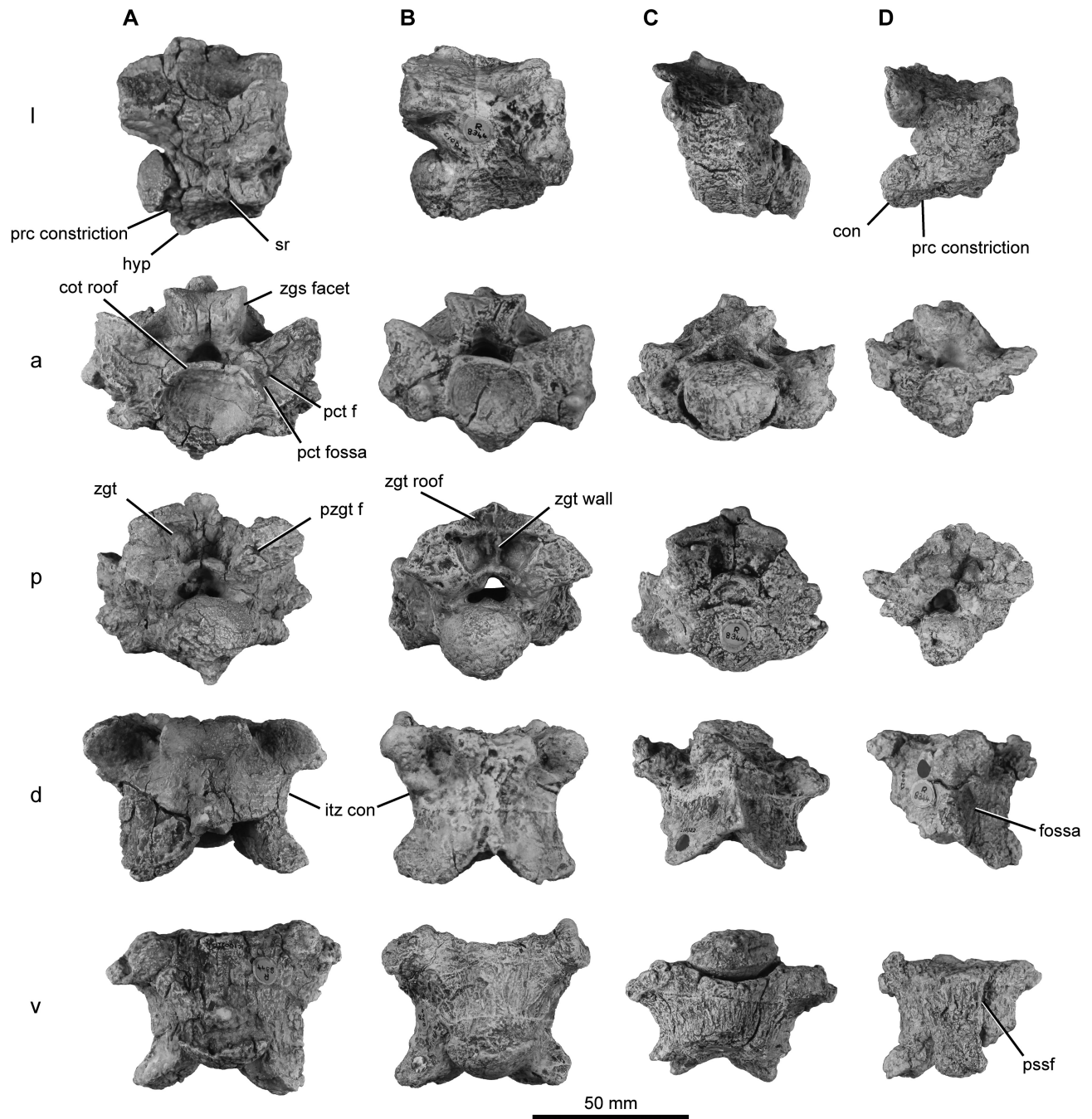


FIGURE 4. Precloacal vertebrae of *Gigantophis garstini*, NHMUK R8344 (casts of the syntype CGM C.10022) in **l**, lateral; **a**, anterior; **p**, posterior; **d**, dorsal; and **v**, ventral views. **A**, vertebra from the mid-trunk region, specimen E; **B**, vertebra from the mid-trunk region, specimen F; **C**, vertebra from the middle part of the posterior trunk region, specimen G; **D**, vertebra from the posterior part of the posterior trunk region, specimen H. **Abbreviations:** **cot roof**, cotyle roof; **hyp**, hypapophysis; **itz con**, interzygapophyseal constriction; **prc constriction**, precondylar constriction; **pct f**, paracotylar foramen; **pssf**, paracotylar subcentral fossa; **pzgt f**, parazygantral foramen; **sr**, subcentral ridge; **zgs facet**, zygosphenal facet; **zgt roof**, zygantral roof.

Madtsoia bai (Simpson, 1933:16, fig. 6). Other species, such as *Madtsoia madagascariensis* (LaDuke et al., 2010) and *Yurlunggur* (Scanlon, 1992), possess prezygapophyses with a consistent lateral orientation of the long axis, whereas *Patagoniophis*, *Alamitophis* (Scanlon, 2005), and *Nanowana* (Scanlon, 1997) have anterolaterally orientated prezygapophyses. The postzygapophyseal articular facets in *Gigantophis* are oval but narrower than those of the prezygapophyses, and their long axes are orientated

posterolaterally. The interzygapophyseal constriction is deep and arcuate, as in *Madtsoia* (Simpson, 1933; Rage, 1998; LaDuke et al., 2010; Mohabey et al., 2011), *Sanajeh* (Wilson et al., 2010), *Yurlunggur* (Scanlon, 1992), and *Wonambi* (Smith, 1976). In large MTV such as specimen A, the constriction is ‘C’-shaped but becomes more open and arcuate in subsequent vertebrae (specimens D–F and J). The interzygapophyseal ridge is fairly prominent in *Gigantophis* and lateral foramina appear to be

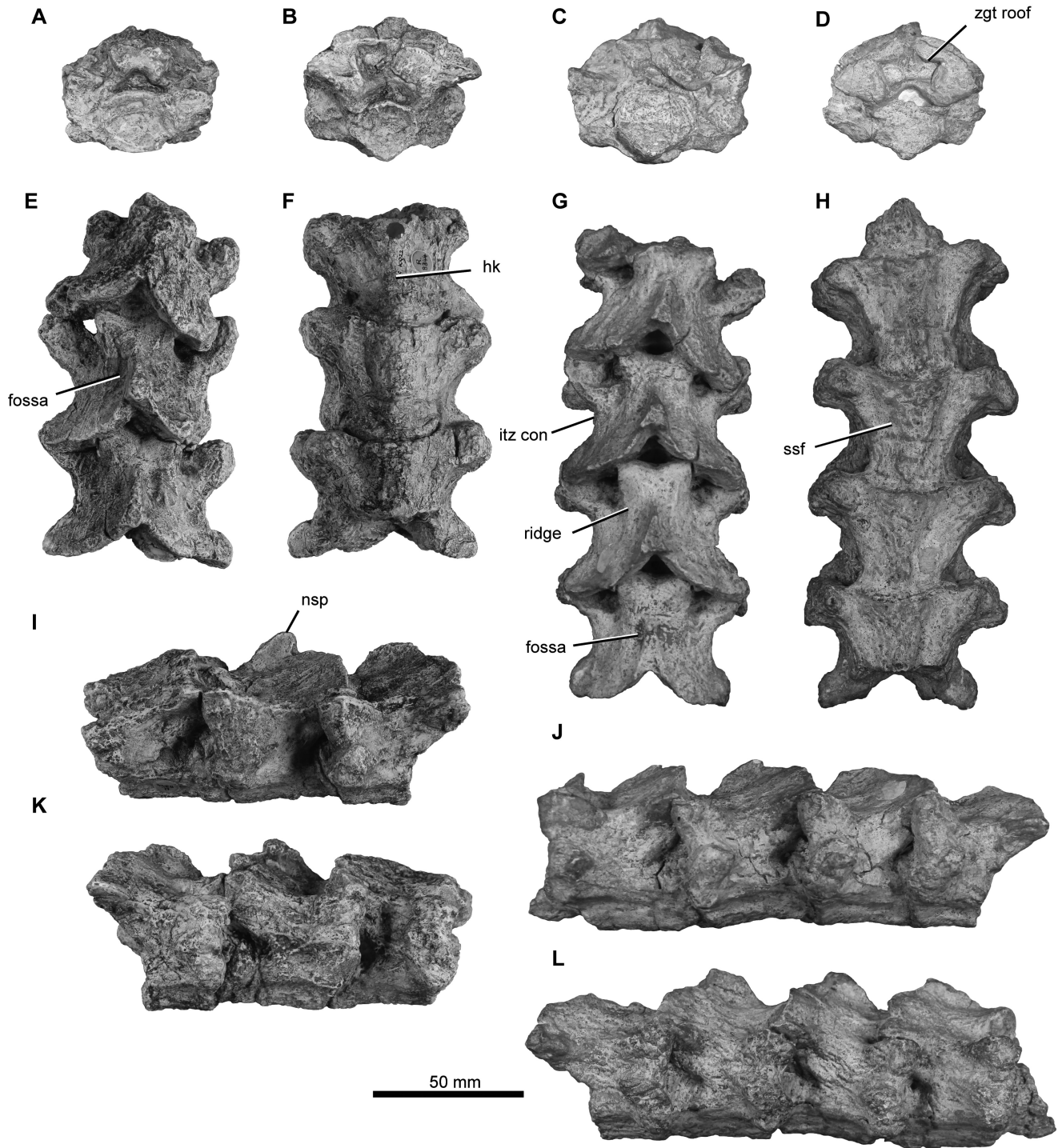


FIGURE 5. Articulated precloacal vertebrae of *Gigantophis garstini*, NHMUK R8344 (casts of the syntype CGM C.10022). Vertebra from the middle part of the posterior trunk, specimen I, in **A**, anterior; **B**, posterior; **E**, dorsal; **F**, ventral; **I**, right lateral; and **K**, right lateral views. Vertebra from the middle part of the posterior trunk, specimen J, in **C**, anterior; **D**, posterior; **G**, dorsal; **H**, ventral; **J**, right lateral; and **L**, right lateral views. Abbreviations: **hk** = hemal keel; **itz con** = interzygapophyseal constriction; **nsp** = neural spine; **ssf** = subcentral fossa; **zgt roof** = zygantral roof.

absent. However, as with subcentral foramina, these might have been obscured during fossilization.

The zygosphenes are massive and trapezoidal. Their roof is flat to concave (Figs. 3A, D; 4E), with a slightly concave anterior edge in dorsal view. The zygosphenes are dorsoventrally thick (up to

12 mm), and slightly narrower than the cotyle, a morphology it shares with *Madtsoia* (Simpson, 1933; Rage, 1998; LaDuke et al., 2010; Mohabey et al., 2011). This contrasts with the dorsoventrally thin and wide zygosphenes of *Nidophis* (Vasile et al., 2013) and *Herensugea* (Rage, 1996). The zygosphenal articular

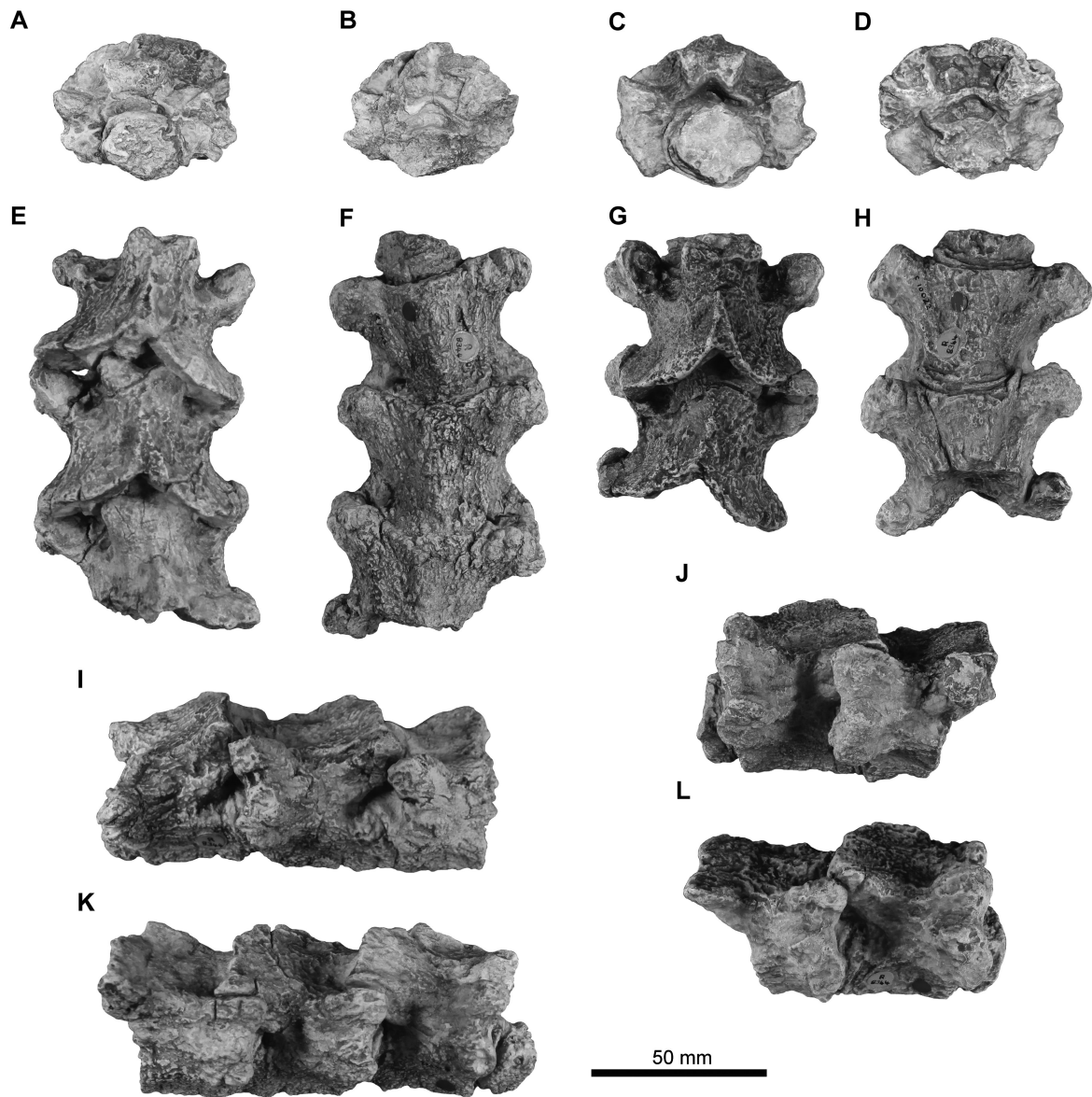


FIGURE 6. Articulated precloacal vertebrae of *Gigantophis garstini*, NHMUK R8344 (casts of the syntype CGM C.10022). Vertebra from the middle part of the posterior trunk region, specimen K, in **A**, anterior; **B**, posterior; **E**, dorsal; **F**, ventral; **I**, left lateral; and **K**, right lateral views. Vertebra from the middle part of the posterior trunk region, specimen L, in **C**, anterior; **D**, posterior; **G**, dorsal; **H**, ventral; **J**, left lateral; and **L**, right lateral views.

facets in *Gigantophis* are steeply inclined ($25\text{--}30^\circ$ from the vertical) and oval-shaped. Laterally, the zygosphenes do not extend as far as the prezygapophyseal articular facets. In MPTV, the zygosphenal width and thickness decrease and the anterior concavity is deeper.

The deep zygantrum is wider than tall, with oval facets steeply inclined at 50° from the horizontal. The internal architecture is poorly preserved. However, in some vertebrae (Figs. 3A, D; 4A, B), a prominent, 5 mm wide ridge divides the zygantrum into two chambers. In specimen F (Fig. 4B), this medial wall is itself divided into two ridges that are separated by a central cavity. This is weakly developed in specimen A, whereas the other specimens appear damaged in this region. The two ridges are more prominent than the more laterally positioned “fine subvertical ridges” that descend only a third the length of the zygantrum

in the MTV of *Madtsoia madagascariensis* (LaDuke et al., 2010:115) but resemble the condition in *Wonambi naracoortensis* (Smith, 1976) and *Yurlunggur* (Scanlon, 1992). In PPTV of *Gigantophis*, the zygantrum becomes dorsoventrally shorter and laterally wider (Fig. 4D).

The zygantral roof is horizontal and varies laterally in thickness in MTV. It is thickest at its midpoint, where the neural spine ascends, and thins laterally, giving the roof a triangular outline in posterior view (Fig. 4B), resembling the MTV of *Alamitophis* (Scanlon, 2005) and *Yurlunggur* (Scanlon, 1992). This morphology contrasts with the concave zygantral roof in *Menarana* (Rage, 1996; LaDuke et al., 2010), *Madtsoia madagascariensis* (LaDuke et al., 2010), and *Madtsoia bai* (Simpson, 1933), and with the convex roof of *Wonambi* (Smith, 1976), *Madtsoia camposi* (Rage, 1998), and *Patagoniophis* (Scanlon, 2005). A

large parazygantral foramen (diameter = 1 mm) opens in both parazygantral fossae, either side of the zygantrum. These foramina align with the dorsoventral midpoint of the zygantral facets (Fig. 4A). An endozygantral foramen pierces each zygantral wall above the anteroventral corners of the zygantral facets. In MPTV, no endozygantral foramina are apparent, although the zygantrum is poorly preserved here. Additionally, in posterior view, the zygantral roof becomes concave over each half of the zygantral cavity (Fig. 5D), as in the PTV of *Madtsoia camposi* (Rage, 1998) and *Madtsoia pisdurensis* (Mohabey et al., 2011).

In lateral view, the neural arch laminae rise medially and posteriorly to buttress the base of the neural spine. Posteriorly, the laminae are strongly arched (Fig. 3A) and terminate abruptly, giving a vertical face to the posterior margin of the postzygapophyses.

The neural spine is poorly preserved except in two vertebrae (Figs. 3A, 5I). It is very low relative to total vertebral height (Table 1). This contrasts with most large madtsoiids, such as *Wonambi* (Smith, 1976) and *Madtsoia madagascariensis* (LaDuke et al., 2010), although it closely resembles *Yurlunggur* (Scanlon, 1992) and the small madtsoiids *Patagoniophis* (Scanlon, 2005), *Adinophis* (Pritchard et al., 2014), and *Nidophis* (Vasile et al., 2013). The neural spine in *Gigantophis* emerges from the zygosphenes, with a maximum basal width of 10 mm. It gradually rises posteriorly at an angle of 30° up to the anteroposterior midpoint of the neural arch, where it sharply curves upwards, resulting in a dorsally concave outline in lateral view. Posteriorly, the spine flattens, similar to the condition in *Adinophis* (Pritchard et al., 2014), but differing from *Patagoniophis* (Scanlon, 2005) and *Nanowana* (Scanlon, 1997), which have dorsally convex spines that rise very gradually.

In dorsal view, two shallow fossae run parallel to the base of the neural spine. They begin posterior to the zygosphenes and fade out before reaching the neural arch laminae (Fig. 3A). These fossae are better defined in MPTV and PPTV, wherein ridges extend posteriorly from the lateral margins of the zygosphenes (Figs. 4D; 5E, G). Such fossae are also observed in the Cretaceous Indian species *Sanajeh* (Wilson et al., 2010) and *Madtsoia pisdurensis* (Mohabey et al., 2011); however, they are deeper and more strongly elliptical in those taxa. The neural arch notch is very deep relative to the width of the postzygapophyses in *Gigantophis*, similar to the condition in *Madtsoia madagascariensis* (LaDuke et al., 2010) and *Sanajeh* (Wilson et al., 2010). Where broken, the neural spine reveals a triangular cross-section that narrows anteriorly, lacking a posterior tubercle.

Posteriorly, the neural spine overhangs the zygantrum. The outline of the posterior margin is concave in lateral view. In MPTV (Fig. 5I), the neural spine has a smaller basal width of 5 mm and rises continuously at an angle of 45° from horizontal. The spine emerges anteriorly from the midline concavity of the zygosphenes and slightly overhangs the zygantrum posteriorly.

Taxonomic Status of Previously Referred Material

There have been several referrals to *Gigantophis* since the discovery of the genus. These comprise occurrences from the middle–upper Eocene of North Africa, with additional materials from other localities in Fayum, Egypt (Andrews, 1906; McCartney and Seiffert, 2016), as well as from Libya (Hoffstetter, 1961b), and material from the lower Paleocene of Pakistan (Rage et al., 2014). Below we provide a critical reassessment of these referrals, based on our revised view of the *Gigantophis garstini* type material.

Late Middle Eocene of Libya

Hoffstetter (1961b) described one MTV (unnumbered specimen) from the Bartonian (late middle Eocene) Idam Unit of

Dur-At-Talha, Libya (Jaeger et al., 2010). This specimen shares several features with the syntype of *Gigantophis*, including (1) a single, large parazygantral foramen (described but not figured by Hoffstetter [1961b:330]); (2) the absence of lateral foramina (although this may be an artifact of preservation); (3) a dorsoventrally thick zygosphenes; and (4) a broad hemal keel with a rhombic termination. The main differences from the syntype are the paired paracotylar foramina found in the Libyan specimen and the anteroposteriorly short neural spine not reaching the zygosphenes. However, these features might be attributable to intracolumnar variation, and so we support Hoffstetter (1961b) in referring the Libyan specimen to *Gigantophis garstini*.

Late Eocene of Egypt

NHMUK R3188—A mid-trunk vertebra (NHMUK R3188; Fig. 7A) was one of the few vertebrae figured by Andrews (1906). Consequently, it has persistently been used to characterize *Gigantophis* in the literature (e.g., Simpson, 1933; Hoffstetter, 1961b; LaDuke et al., 2010; Rage et al., 2014). The referral of NHMUK R3188 to *Gigantophis* is supported by the following features (features considered diagnostic marked with an asterisk): (1*) the very large size (postzygapophyseal width = 62 mm); (2*) low neural spine; (3) anteroposteriorly short neural spine reaching the zygosphenes; (4*) presence of a rhombic termination on the posterior hemal keel; and (5) absence of subcentral and lateral foramina. Overall, the general morphology of NHMUK R3188 is very similar to MTV of the type series, and the vertebra bears features regarded as autapomorphic of *Gigantophis garstini*. However, a number of subtle differences are observed in NHMUK R3188 in comparison with the type material: (1) considerably thicker neural arch laminae (LaDuke et al., 2010); (2) steeper postzygapophyseal facets (and resultantly, more arched neural arch laminae [LaDuke et al., 2010]); (3) posteriorly rising subcentral ridges; (4) zygosphenes wider than the cotyle; (5) steeply inclined synapophyses; (6) circular cotyle and condyle; (7) thick cotylar lip; (8) dorsoventrally lower parapophyses; (9) anterior face of the zygosphenes deeply concave in dorsal view; (10) strong precondylar constriction; (11) prominent subcentral ridges; (12) deeper subcentral fossae; and (13) a pronounced hemal keel. Several authors have used the presence of a pronounced hemal keel to differentiate *Gigantophis* from other large madtsoiids, including *Madtsoia*, which have blunt keels (Hoffstetter, 1961b; LaDuke et al., 2010; Rage et al., 2014; McCartney and Seiffert, 2016). However, the presence of a truly pronounced keel can only be documented in NHMUK R3188, and even here it is still rather broad and closely resembles that of *Madtsoia madagascariensis* (LaDuke et al., 2010). All MTV of the syntype have broad, poorly defined hemal keels; therefore, a pronounced hemal keel alone cannot currently be used to diagnose *Gigantophis*.

The most striking difference from the syntype is the robustness of NHMUK R3188, which was also noted by LaDuke et al. (2010). The neural arch laminae, neural arch pedicles, and cotylar lip are all extremely thick; the zygosphenes is massive; and the zygantrum is tall and spacious. Rage et al. (2014) suggested that some of these features are indicative of older individuals and thus NHMUK R3188 might be an ontogenetically more mature specimen of *Gigantophis*. We tentatively agree with this hypothesis but also suggest that NHMUK R3188 might come from a slightly more anterior position within the mid-trunk vertebrae than the syntype. We preliminarily retain NHMUK R3188 as referable to *Gigantophis garstini* pending the discovery of new, overlapping materials.

NHMUK R3010—Three vertebrae (NHMUK R3010; Fig. 7B, C, D) were referred to *Gigantophis* by Andrews (1906), although never figured. They were described as “three similar vertebrae”

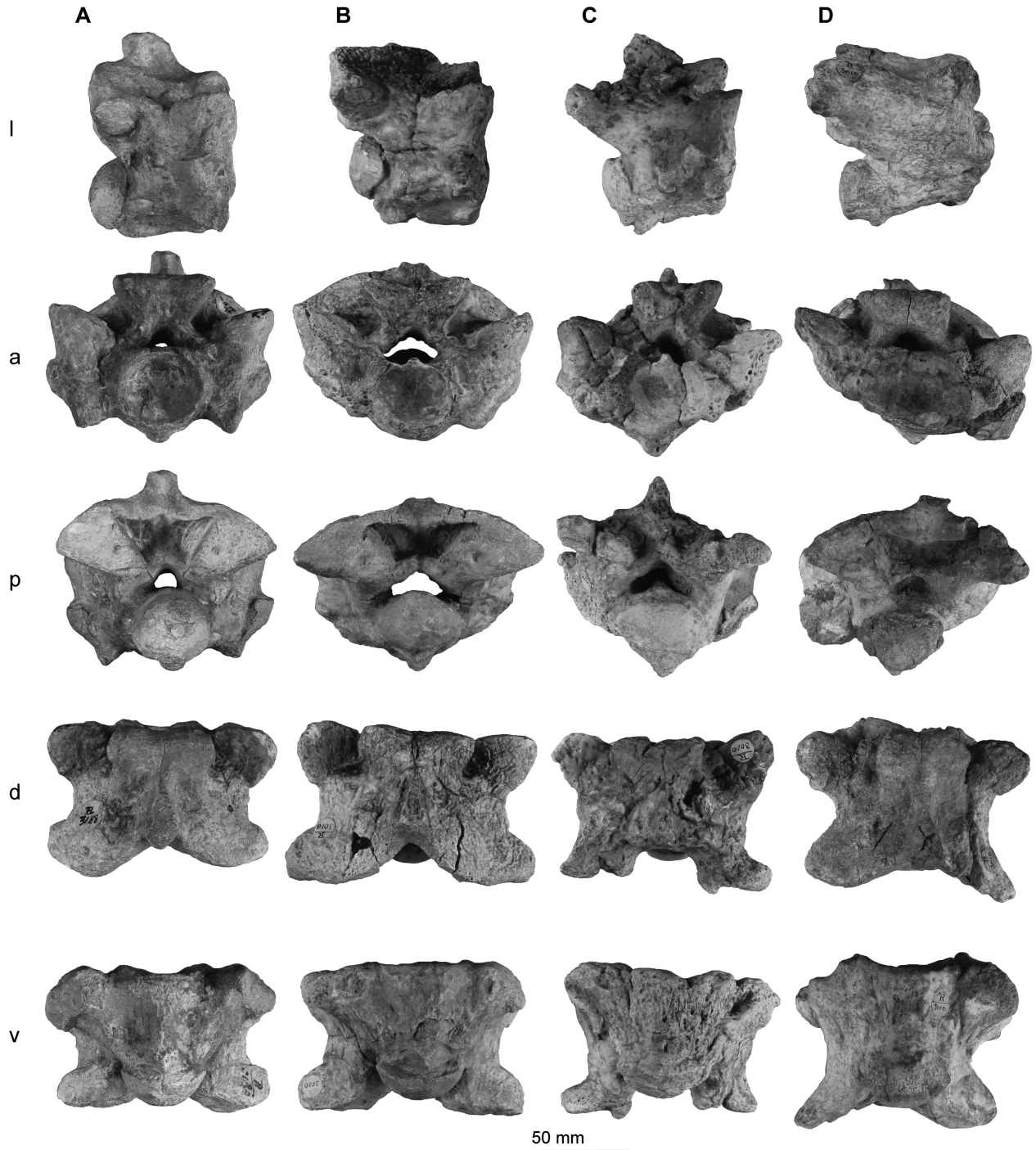


FIGURE 7. Preloacal vertebrae referred to *Gigantophis garstini* by Andrews (1906) in **l**, lateral; **a**, anterior; **p**, posterior; **d**, dorsal; and **v**, ventral views. **A**, vertebra from the mid-trunk region, NHMUK R3188; **B**, vertebra from the mid-trunk region, NHMUK R3010; **C**, vertebra from the mid-trunk region, NHMUK R3010; **D**, vertebra from the posterior trunk region, NHMUK R3010.

that were “presented by the Egyptian Government” in 1903 (Andrews, 1906:309). All three vertebrae are very large, some even larger than the syntype. Additionally, they all share the similarly robust aspect seen in NHMUK R3188. These three vertebrae are assigned the letters A, B, and C for convenience.

Specimen A differs from the syntype in having an exceptionally wide neural arch in posterior view (Fig. 7B), although this can be attributed to dorsoventral compression.

One major difference from the syntype that cannot be explained by deformation is the shape of the zygosphenic roof, which is extremely concave with pointed dorsolateral margins. Specimen B has been deformed obliquely, giving it an asymmetrical morphology (Fig. 7C). It differs from the syntype in possessing narrower, pointed postzygapophyses and a considerably taller zygosphenic. However, specimens A and B share diagnostic features of *Gigantophis*, including its

large size and a broad hemal keel with a rhombic termination.

Specimen C (Fig. 7D), although dorsoventrally compressed, more closely resembles the syntype, with its oval-shaped cotyle and dorsoventrally short zygosphenes. Unlike the other referred vertebrae (NHMUK R3188, R3010 specimens A and B), specimen C has a very cylindrical centrum, with a distinct notch in lateral view that separates it from the neural arch. This is observed in the PTV of many madtsoiids, e.g., *Yurlunggur* (Scanlon, 1992), *Madtsoia madagascariensis* (LaDuke et al., 2010), and *Madtsoia camposi* (Rage, 1998), suggesting that it also derives from the posterior trunk region. The posteroventral projection of the centrum in specimen C closely resembles the condition in the PPTV of the syntype of *Gigantophis* (Fig. 4D). Interestingly, this PTV (possibly PPTV) is larger than most MTV of the syntype (Table 1), suggesting that it belonged to a larger and probably older individual. This might support the hypothesis that some of the variation observed in the vertebrae from Fayum (NHMUK R3188 and R3010) is ontogenetic. In summary, we support the view that the three specimens comprising NHMUK R3010 are referable to *Gigantophis garstini*.

NHMUK R8343—A jaw fragment (angular and articular) from an uncertain locality was referred to *Gigantophis* by Andrews (1906). The referral of this jaw fragment to *Gigantophis* cannot be demonstrated because of a lack of overlapping material, and we regard it as an indeterminate snake.

DPC 25616 and DPC 25641—An adult MTV (DPC 25616) and a juvenile MTV (DPC 25641) from the same locality in the Priabonian Birket Qarun Formation were referred to *Gigantophis* by McCartney and Seiffert (2016). The referral of the adult specimen is supported by its large size, low neural spine, and the posterior position of the latter on the neural arch. Additionally, the hemal keel, although somewhat more pronounced, bears a rhombic termination. One large parazygantral foramen occurs at the dorsoventral midpoint of the zygantral facet, as in the syntype. Small fossae excavate each side of the neural spine; however, unlike the syntype, these are pierced by numerous foramina. Similarly, subcentral foramina are not observed in the syntype but occur in DPC 25616. However, because foramina can be inconsistently found across the vertebral column in madtsoiids (see *Madtsoia madagascariensis*; LaDuke et al., 2010) and may be obturated as a result of fossilization, the presence of foramina in DPC 25616 is insufficient cause to reject the referral.

Specimen DPC 25641 appears to share the rhombic termination of the keel. Although differing in some aspects, its shared provenance with DPC 25616 supports its referral to the same taxon, and we regard these differences as ontogenetic variation. Consequently, we follow McCartney and Seiffert (2016) in referring these two specimens to *Gigantophis garstini*.

Early Paleocene of Pakistan

CPAG-RANKT-V-1 and CPAG-RANKT-V-2—Rage et al. (2014) referred two vertebrae from the lower Paleocene Khadro Formation of Pakistan (Fig. 8) to *Gigantophis*: one MTV (CPAG-RANKT-V-1) and one PTV (CPAG-RANKT-V-2). Their referral was based on (1) the large vertebral size; (2) the narrow nature of the hemal keel; and (3) the obliquely orientated prezygapophyseal articular facets in dorsal view. Further similarities with the syntype also include the large zygosphenes relative to the prezygapophyseal width. Additionally, the zygosphenal width to thickness resembles *Gigantophis*, as does the zygosphenal width relative to the cotyle. Furthermore, the neural spine (although broken) is low relative to total vertebral height. Finally, subcentral and lateral foramina are absent.

Despite these similarities, there are significant differences in these vertebrae that are uncharacteristic of the syntype (features

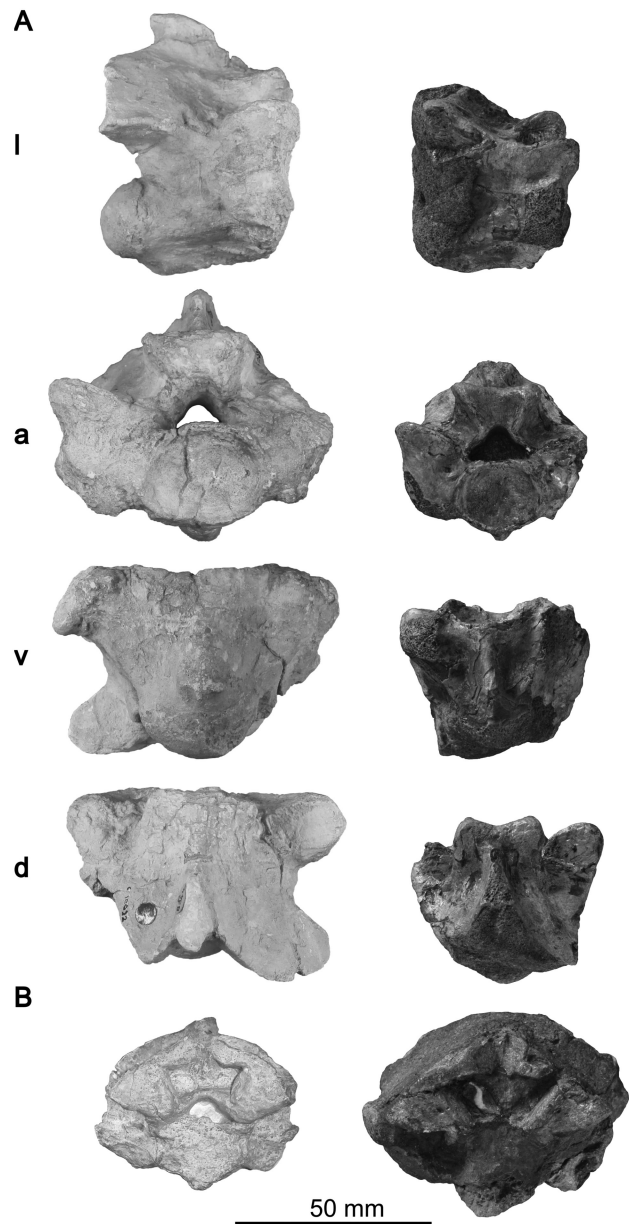


FIGURE 8. Comparison between the vertebrae of *Gigantophis garstini* (NHMUK R8344) and vertebra referred to *Gigantophis* sp. from Pakistan (Rage et al., 2014). **A**, mid-trunk vertebra of *Gigantophis garstini*, specimen A (left), compared with the referred mid-trunk vertebra CPAG-RANKT-V-1 (right) in **l**, lateral; **a**, anterior; **v**, ventral; and **d**, dorsal views. **B**, posterior trunk vertebra of *Gigantophis garstini*, specimen J (left), compared with referred posterior trunk vertebra CPAG-RANKT-V-2 (right) in posterior view. Photographs of the Pakistan specimen courtesy of J.-C. Rage.

conflicting with the diagnosis of *Gigantophis* marked with an asterisk): (1*) a sharp, narrow hemal keel; (2*) prominent subcentral ridges; and (3) a strongly concave anterior zygosphenal margin. Several other differences are also recognized, including (1) a posteriorly rising interzygapophyseal ridge; (2) rounded dorsal margin of zygosphenes in lateral view; (3) large neural canal in MTV, approximately as wide as the cotyle; (4)

zygosphene with a pronounced border in anterior view; (5) thin neural arch pedicles; (6) paired paracotylar foramina within deep fossa; (7) deep subcentral fossae in MTV; (8) strongly anterolaterally orientated prezygapophyseal articular facets in MTV; and (9) convex zygantral roof in PTV. As for the size of the specimen, although it ranks among the larger madtsoiids, and ontogenetic variation should be considered, CPAG-RANKT-V-1 is consistently smaller in all measurements compared with an MTV of *Gigantophis*.

In summary, we contend that there are significant differences between the Pakistan specimen and *Gigantophis*, but we test this further through its incorporation into a phylogenetic analysis (see below).

DISCUSSION

Body Length Estimation

Head et al. (2009) estimated the body length of the giant extinct bovid, *Titanoboa*. They created a model of morphological variation in the vertebral column of extant bovine species and then determined the likelihood of *Titanoboa* vertebrae coming from different positions along this column. They found that vertebral landmarks in *Titanoboa* specimens match a position 60–65% posteriorly along the column (i.e., MTV). Total body length (TBL) was regressed on postzygapophyseal width (POW) in extant bovine species (Supplemental Data) at this position, to calculate a linear equation that described the relationship between POW and TBL (Fig. 9).

Using this model and the postzygapophyseal width of a MTV in *Gigantophis* (specimen A of the syntype; Table 1), a total body length of 6.9 ± 0.3 m was estimated. However, it cannot be known whether the vertebrae of *Gigantophis* came precisely from the same body region without a model of intracolumnar variation tailored to Madtsoiidae. The latter is not currently available because of the paucity of madtsoiid remains preserving articulated vertebral columns. Furthermore, the relationship between body size and postzygapophyseal width may differ between *Gigantophis* and extant bovine species. As such, our estimate of 6.9 ± 0.3 m should be treated with caution.

Phylogenetic Interrelationships of Madtsoiidae

A phylogenetic analysis was conducted based on the character-taxon matrix (CTM) of Vasile et al. (2013). Four putative madtsoiid taxa were added to this CTM: *Adinophis fisaka* (Pritchard et al., 2014), *Madtsoia pisdurensis* (Mohabey et al., 2011), *Platyspondylophis tadkeshwarensis* (Smith et al., 2016),

and the material referred to *Gigantophis* from Pakistan (Rage et al., 2014). Six new characters were also added to the CTM, based on personal observations (J.P.R.) and a review of the literature, and 81 changes were made to existing character scores of seven taxa. Our revised CTM comprises 148 characters scored for 20 putative madtsoiids. The revised character list, along with all changes to character scores, is provided in Supplemental Data.

A parsimony analysis was conducted using TNT 1.1 (Goloboff et al., 2008). Characters 111, 117, 125, 126, 127, 128, 132, 133, 139, 140, and 145 were ordered. The data were analyzed using the ‘New Technology Search’ with Sectorial Search, Ratchet, Drift, and Tree fusing activated, with the consensus stabilized five times. The starting trees obtained from this analysis were then used to run a ‘Traditional search’ using tree bisection reconnection. The analysis recovered seven most parsimonious trees (MPTs) with a length of 190 steps. Bremer support is low, with all internal nodes collapsing in trees more than one to two steps longer than the MPTs; however, support is generally higher than in the analysis of Vasile et al. (2013), and there are a number of topological differences (compare Fig. 10A [strict consensus of Vasile et al., 2013] with Fig. 10B [strict consensus: this study]).

A monophyletic Madtsoiidae (Bremer support = 3) is supported by three vertebral and six cranial synapomorphies. A basal division into two monophyletic groups occurs in Madtsoiidae. Unlike the topology presented by Vasile et al. (2013), these two clades do not reflect a strict dichotomy in body size. In our results, one clade forms a large polytomy consisting predominantly of large madtsoiids (*Madtsoia*, *Gigantophis*, *Platyspondylophis*, plus the ‘medium-sized’ *Menarana laurasiae* and *Sanajeh*). Within this clade, *M. madagascariensis* and *Madtsoia bai* are sister taxa and *Platyspondylophis* + *Menarana laurasiae* + *Sanajeh* form a polytomy.

The second madtsoiid clade is composed of a group comprising the large Australian madtsoiids (*Wonambi* + *Yurlunggur*) + the Malagasy *Menarana nosymena*, which is the sister taxon of a clade of small madtsoiids (*Adinophis*, *Alamitophis*, *Herensugea*, *Nanowana*, *Nidophis*, and *Patagoniophis*). *Adinophis* and *Nanowana godthelpi* are successively more nested taxa that lie outside of a polytomy composed of *Herensugea* + *Nidophis*, *Nanowana schrenki*, *Patagoniophis*, and the two *Alamitophis* species. Our topology conforms to most previous studies that have recovered *Wonambi* and *Yurlunggur* as sister taxa (Scanlon, 2006; Wilson et al., 2010; Longrich et al., 2012; Zaher and Scanferla, 2012), but it differs most significantly from that of Vasile et al. (2013) in placing these taxa outside of the clade that includes *Gigantophis* and *Madtsoia*.

The Pruned Trees option in TNT identified the Pakistan *Gigantophis* sp. operational taxonomic unit (OTU) as the most unstable taxon. A second analysis was conducted following the same procedure described above, but excluding this OTU a priori. One fully resolved tree was found with a total length of 186 steps (Fig. 11). Bremer support is slightly higher, with all internal nodes collapsing in trees more than one or three steps longer than the MPT. The general topology of the tree is the same as in the first analysis; however, the two subclades of Madtsoiidae are now fully resolved. In the first clade, *Gigantophis garstini* is recovered as the sister taxon to the latest Cretaceous Indian species, *Madtsoia pisdurensis*. This differs markedly from the results of Vasile et al. (2013), which placed *Gigantophis* as the sister taxon to the Neogene Australian taxon *Yurlunggur*. This previously recovered relationship appears to have been driven by both taxa having low neural spines, which is instead here regarded as convergent. *Madtsoia pisdurensis* + *Gigantophis garstini* is the sister group to *Madtsoia bai* + *Madtsoia madagascariensis*, with *Madtsoia camposi* at the base of this clade. *Menarana laurasiae* forms a clade with the Indian snakes *Sanajeh* + *Platyspondylophis* (from the latest

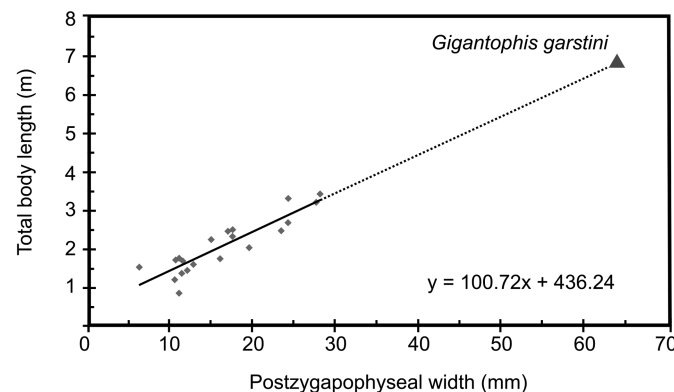


FIGURE 9. Regression of total body length on postzygapophyseal width in extant bovine species from vertebrae 60% posteriorly along the vertebral column. Measurements of extant bovine species (red diamonds) taken from Head et al. (2009) (Supplemental data). Estimated body length for *Gigantophis* shown as a green triangle.

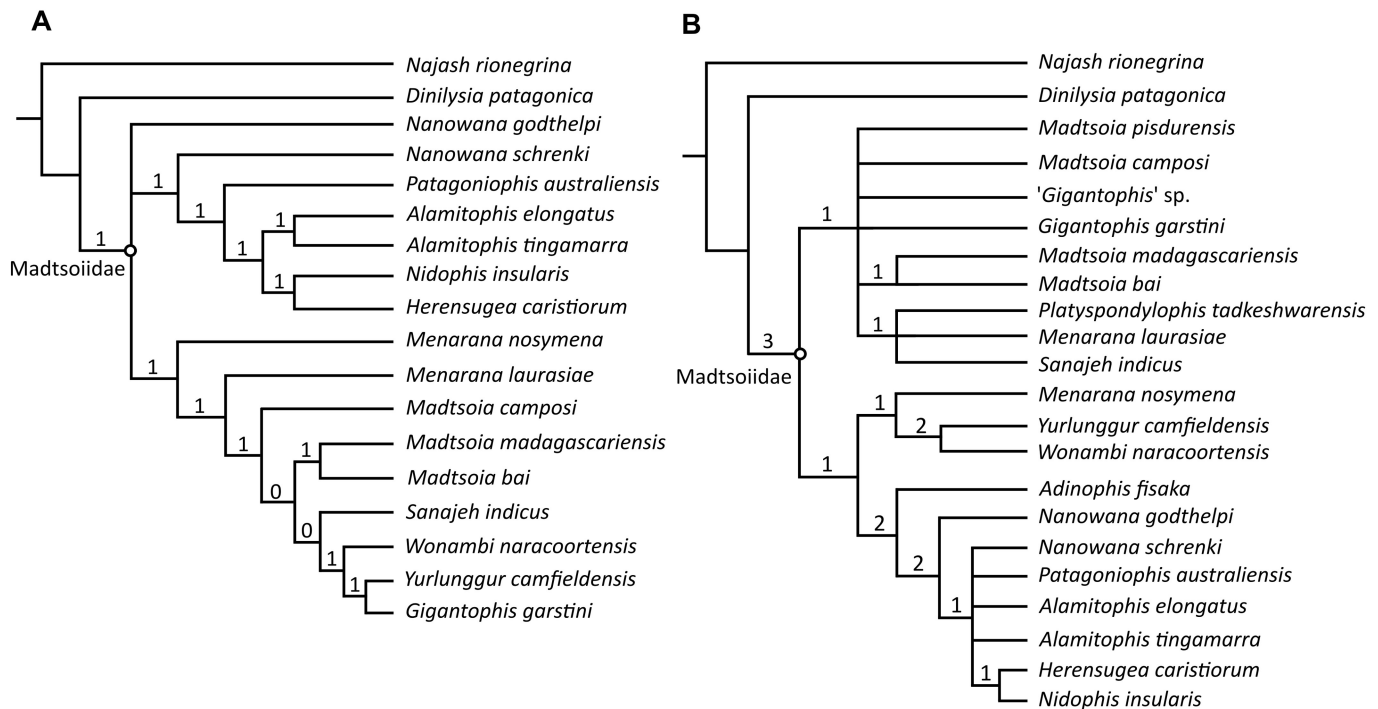


FIGURE 10. Results of the phylogenetic analysis and comparisons with the phylogeny of Vasile et al. (2013). Bremer support indicated above branches. **A**, strict consensus tree of two MPTs from Vasile et al. (2013) analysis of 16 madtsoiids, *Dinilyisia patagonica*, and *Najash rionegrina* (outgroups), using a CTM of 143 characters; **B**, strict consensus tree of seven MPTs from this study of 20 putative madtsoiids, *Dinilyisia patagonica*, and *Najash rionegrina* (outgroups), using a CTM of 148 characters. Bremer support indicated above branches.

Cretaceous and early Eocene, respectively), which in turn is the sister taxon to the *Madtsoia* + *Gigantophis* clade.

The topology of the second clade now recovers *Adinophis*, *Nanowana godthelpi*, *Nanowana schrenki*, and *Patagoniophis australiensis* as successively nested taxa that are basal to a clade composed of (*Alamitophis tingamarra* + *Alamitophis elongatus*) + (*Herensugea caristiorum* + *Nidophis insularis*) (Fig. 11).

A third analysis was conducted to determine the relationship of the Pakistan material referred to *Gigantophis* by Rage et al. (2014). An examination of the trees from our first analysis demonstrated that *Madtsoia camposi* was also an unstable taxon. Following a priori exclusion of this OTU, an identical tree topology to that of the second analysis was recovered, with *Gigantophis* sp. in the place of *Madtsoia camposi*. The Pakistan specimen does not cluster with *Gigantophis garstini*, supporting our view (see above) that it is not referable to the North African taxon, and we regard it as an indeterminate madtsoiid.

Our analyses suggest that a number of species are probably incorrectly attributed to genera, with neither *Menarana laurasiae* nor *Nanowana schrenki* clustering with the type species of those genera. Additionally, *Gigantophis garstini* is nested within a clade of species referred to the genus *Madtsoia*, 'interrupting' the monophyly of that genus. Our topology presents us with two options. Firstly, if all of the *Madtsoia* species belong to one genus, then *Madtsoia* would have to be considered a junior synonym of *Gigantophis*, which has nomenclatural priority. Several authors have commented on the similarity of *Gigantophis* and *Madtsoia*, although all studies have concluded that they represent distinct taxa (e.g., Simpson, 1933; Hoffstetter, 1961a, 1961b; LaDuke et al., 2010; Mohabey et al., 2011; Rage et al., 2014; Smith et al., 2016), a view supported by the autapomorphies and unique combination of characters described in this study. Given these anatomical differences, and the fact that *Madtsoia* is the

type genus for Madtsoiidae, synonymization of *Madtsoia* with *Gigantophis* appears to be a poor solution. The second option would be to restrict *Madtsoia* to *M. bai* (the type species) and *M. madagascariensis*, with *M. camposi* and *M. pisdurensis* given new genus names (or the latter species is referred to *Gigantophis*). Although we consider this second option as most appropriate, we refrain from making new taxonomic assignments because support for most of our topology is low.

Paleobiogeographic Implications

Madtsoiidae had a predominantly Gondwanan distribution, with specimens found on every southern continent except Antarctica (Fig. 1). Laurasian madtsoiids have been recovered, but finds are restricted to the upper Campanian–Maastrichtian of southern Europe. Explanations for the group's distribution commonly fall under two main, but not mutually exclusive, hypotheses (LaDuke et al., 2010; Mohabey et al., 2011; Vasile et al., 2013): (1) a series of dispersal routes connecting Gondwanan landmasses to one another and to southern Europe, and/or sweepstakes dispersal across oceanic barriers; or (2) a widespread but unsampled distribution in the Early Cretaceous of Gondwana, followed by vicariance and/or regional extinctions to leave relictual populations, with a Cretaceous dispersal to Europe.

With the exclusion of the early Paleocene Pakistan specimens from *Gigantophis*, this genus is restricted to the middle–late Eocene of North Africa. However, links to Indo-Pakistan remain in that *Gigantophis* is recovered as the sister taxon to the Maastrichtian Indian species *Madtsoia pisdurensis*. These distributional data might suggest that biotic links existed between Africa and India in the Late Cretaceous–early Paleogene. However, geological and geophysical data indicate that Indo-Madagascar

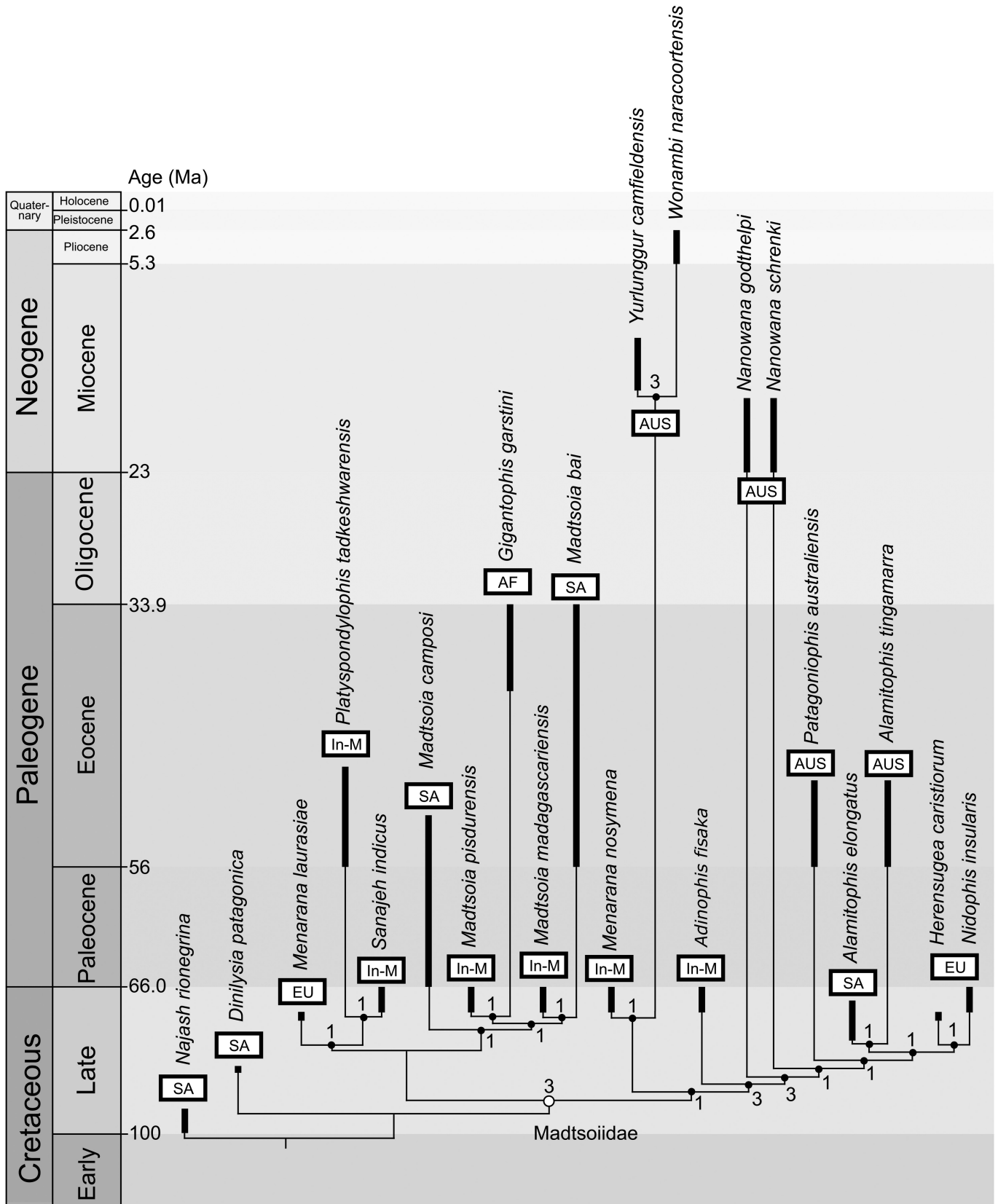


FIGURE 11. Time-calibrated, single most parsimonious tree from the analysis of 19 putative madtsoiids after pruning the least stable taxon, *Gigantophis* sp. (Rage et al., 2014). Bremer support indicated near branches. Age ranges (including stratigraphic uncertainty) based on the published literature and the Paleobiology Database. Time scale modified from the Geological Society of America Geological Time Scale (Walker et al., 2012). Geographic distribution of taxa given beneath taxon names. **Abbreviations:** AF, Africa; AUS, Australia; EU, Europe; In-M, Indo-Madagascar; SA, South America.

and Africa were last connected over 150 Ma (Jokat et al., 2003; Blakey, 2008), and that the two landmasses were separated by approximately 400 km of ocean (the Mozambique Channel) by ~130–120 Ma (Ali and Krause, 2011), with indirect connections via Antarctica and South America remaining until ~120–110 Ma at the latest (Smith et al., 1994; Ali and Krause, 2011; Wilf et al., 2013).

One possibility is that the sister-taxon relationship of *Gigantophis* and *Madtsoia pisdurensis* could be explained by sweepstakes dispersal between India and Africa across the Mozambique Channel. Most snakes have a capacity for marine locomotion (Parker and Grandison, 1977), and we cannot be certain that madtsoiids were obligate terrestrial snakes. Indeed, Rage et al. (2014) noted that *Gigantophis* has been recovered only from coastal deposits (Fayum and Durrat-Talha). Although a semiaquatic lifestyle may be undetectable in the skeletal morphology of snakes, neither *Gigantophis* nor any other madtsoiid has obvious skeletal features indicating a highly aquatic lifestyle. Given the distance involved (~400 km), the lack of evidence for aquatic adaptations in madtsoiids, and the reduced likelihood of large vertebrates dispersing across ocean barriers (Ali and Krause, 2011), we regard sweepstakes dispersal as an unlikely mechanism for explaining madtsoiid distributions. Furthermore, given the prevalent affinities of most terrestrial Maastrichtian Indian taxa (e.g., notosuchian crocodylomorphs, titanosaurian sauropods, abelisaurid theropods, and gondwanatherian mammals) with the rest of Gondwana (e.g., Krause et al., 1997; Wilson et al., 2001, 2003, 2007, 2009; Ali and Krause, 2011), a stable land route appears to have been a prerequisite, rather than multiple random sweepstakes dispersal events (Mohabey et al., 2011).

Several possible dispersal routes between Indo-Madagascar and Africa have been proposed during the latest Cretaceous–early Paleogene (Fig. 12). A number of convoluted routes for the dispersals of terrestrial taxa have been suggested, most notably involving the Kerguelen Plateau (Krause et al., 1997; Hay et al., 1999) and Gunnerus Ridge (Case, 2002) ~85–80 Ma (Fig. 12). These have been proposed to have connected Indo-Madagascar to Antarctica, which in turn was likely in contact with South America at the time (Wilf et al., 2013), with taxa then dispersing from South America to Africa. However, there are several problems with this proposed route. Firstly, Ali and Aitchison (2008) argued that the subsidence of the Kerguelen Plateau in the Campanian formed a 1000 km ocean barrier between Antarctica and India. Secondly, geological and geophysical evidence suggests that the Gunnerus Ridge never formed a viable route to Madagascar (Ali and Krause, 2011). Lastly, even if such connections between Indo-Madagascar and Antarctica did exist, there might have been a 100 km marine barrier between South America and Africa by 85 Ma (Granot and Dymant, 2015), with no evidence for a land bridge (Gheerbrant and Rage, 2006). One further convoluted dispersal route exists: following the collision of India with Asia in the late Paleocene–early Eocene (Chatterjee et al., 2013; Hu et al., 2016), taxa might have been able to disperse from India to North Africa via Eurasia, with intermittent terrestrial connections between southwestern Europe and North Africa during low sea levels proposed in the Eocene (Gheerbrant and Rage, 2006). However, the total absence of madtsoiids from the Cenozoic of Laurasia suggests that this route was unlikely, at least for this group.

Direct links have also been proposed, involving dispersal via Greater Somalia (Chatterjee and Scotese, 1999) or the Oman-Kohistan-Ladakh (or Oman-Kohistan-Dras) Island Arc, that

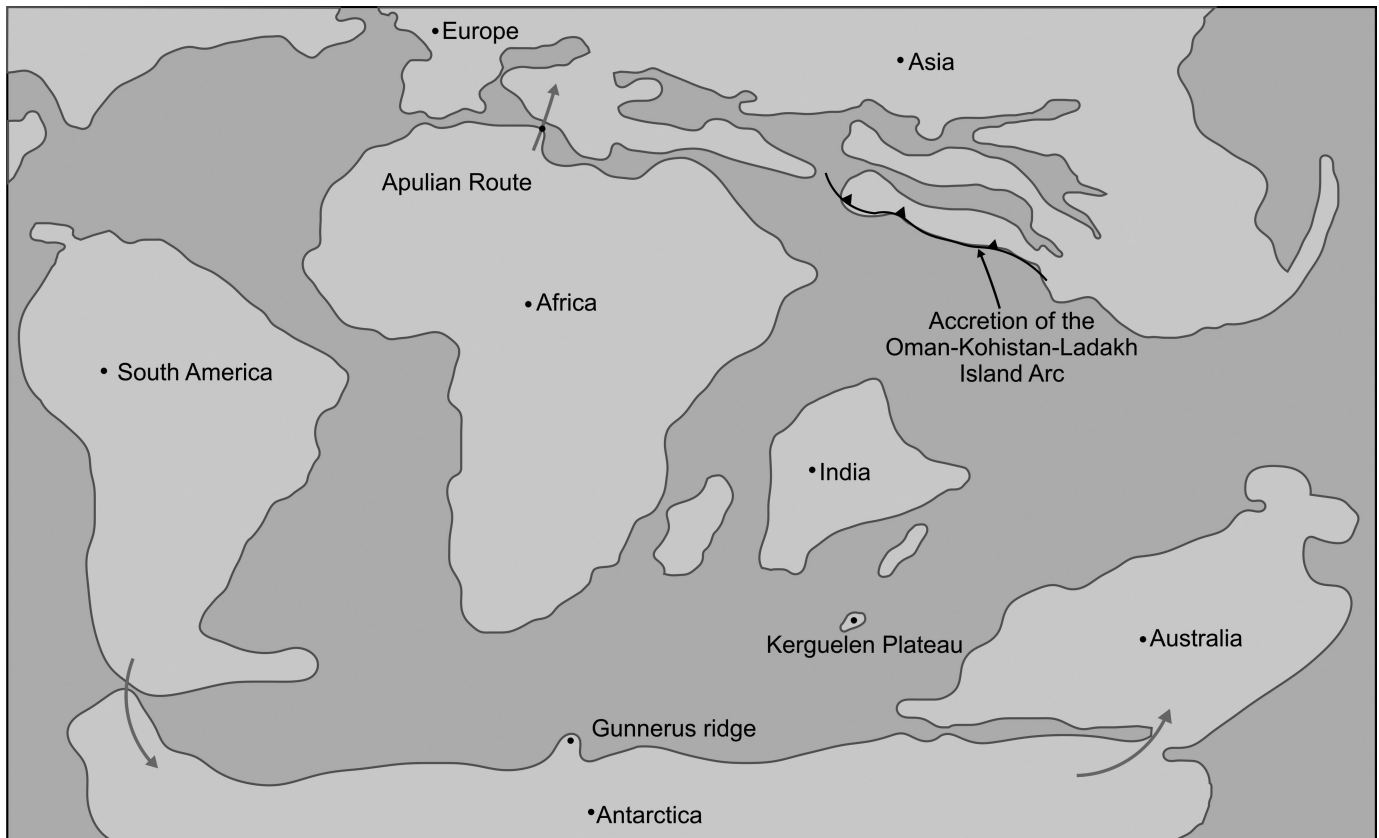


FIGURE 12. Possible dispersal routes to explain madtsoiid paleobiogeography superimposed on a paleogeographic map from the latest Cretaceous (70 Ma). Paleogeographic map downloaded using software available from Fossilworks (Alroy, 2013) and modified.

would purportedly have linked northeast Africa with India during the K/Pg transition (Chatterjee and Scotese, 2010; Chatterjee et al., 2013; Fig. 12). This latter route has also been considered as a possible explanation for the presence of several Laurasian groups during the latest Cretaceous–early Paleogene of India, with taxa able to disperse between Europe and North Africa intermittently (see below). In particular, the Maastrichtian Indian mammal *Deccanolestes* has been allied with adapisoriculid eutherian mammals from the Paleocene of North Africa and Europe (Prasad et al., 2010; Smith et al., 2010; Goswami et al., 2011), and other Maastrichtian Indian occurrences (including putative pelobatid and discoglossid frogs [Prasad and Rage, 1991, 1995], as well as a possible troodontid theropod [Goswami et al., 2013]) also appear to be nested within Laurasian clades. This route might also explain our recovery of the late Campanian European taxon *Menarana laurasiae* as the sister taxon to the Indian clade of *Sanajeh* (Maastrichtian) + *Platyspondylophis* (early Eocene), and Smith et al. (2016) considered this dispersal corridor as a likely explanation for the mixed Gondwanan and Laurasian fauna present in the early Eocene of India. Although there is geological and geophysical evidence for this island arc system (Chatterjee et al., 2013), recent dating of post-collisional molasse deposits indicates that the Oman-Kohistan-Ladakh Island Arc accreted to the southern margin of Asia between 92 and 85 Ma (Borneman et al., 2015). India therefore did not come into contact with the Oman-Kohistan-Ladakh Island Arc until its collision with Asia in the late Paleocene–early Eocene, and thus this arc could not have constituted a land bridge between India and North Africa in the latest Cretaceous–early Paleocene.

Rifting between India and Madagascar initiated approximately 88–87 Ma, and the two landmasses were likely to have been fully separated by the Campanian (~83 Ma) (Seton et al., 2012; Reeves, 2014). Given the lack of evidence for dispersal routes via Antarctica (see above), it is difficult to conceive latest Cretaceous–Paleogene biogeographic pathways (direct or indirect) that can explain sister-taxon relationships between Maastrichtian Malagasy and Cenozoic South American or Australian taxa, e.g., *Madtsoia madagascariensis* (Madagascar) + *Madtsoia bai* (Eocene of Argentina) and *Menarana nosymena* (Madagascar) + (*Wonambi* + *Yurlunggur*) (Neogene–Pleistocene of Australia).

The presence of madtsoiids in Australia is first documented in the early Eocene, with two species referred to genera otherwise known from the uppermost Cretaceous of Argentina (*Alamitophis* and *Patagoniophis*) (Scanlon, 2005). *Alamitophis* is here recovered as the sister taxon to the latest Cretaceous European clade *Herensugea* + *Nidophis*, with *Patagoniophis* outside of this grouping (see also Vasile et al., 2013). Two early Miocene Australian species of *Nanowana* (Scanlon, 1997) are outside of this clade, with the Maastrichtian Malagasy genus *Adinophis* positioned as the basal-most taxon. This clade in turn forms the sister taxon to *Menarana nosymena* + (*Wonambi* + *Yurlunggur*) (see above). After its separation from Indo-Madagascar by ~110 Ma, Australia + Antarctica retained a connection with South America until the late early Eocene (Wilf et al., 2013). Thus, a South America to Australia route, via Antarctica, is the only available biogeographic pathway to explain latest Cretaceous–early Paleogene dispersal, with all lineages leading to Australian madtsoiids having dispersed from South America by the late early Eocene.

Although most dispersal routes between Gondwanan continents remain controversial, trans-Tethyan dispersal from North Africa appears to be the simplest explanation for the presence of madtsoiids in Europe during the late Campanian–Maastrichtian. During the Berriasian–Barremian (early Early Cretaceous), there is some paleogeographic support for a land connection between Africa and Europe, known as the Apulian Route (Fig. 12). This would have allowed dispersal between these

continents during low sea levels, which has been used to explain faunal similarities of a diverse range of ‘Eurogondwanan’ terrestrial taxa (Gheerbrant and Rage, 2006; Pereda-Suberbiola, 2009; Csiki-Sava et al., 2015). Although this land connection appears to have been severed by approximately the Aptian (Ezcurra and Agnolín, 2012 [and references therein]), dispersal might have been possible again during the Campanian–Maastrichtian via a reemergent Apulian Route (Ezcurra and Agnolín, 2012; see also Rabi and Sebök [2015], who have argued for a more continuous connection based on biotic evidence).

The remaining hypothesis is that Madtsoiidae had a widespread but largely unsampled Gondwanan distribution in the Early to mid-Cretaceous. An early widespread distribution requires a 50–90 myr unsampled history of the lineage leading to *Gigantophis* + *Madtsoia pisdurensis* in Africa and Indo-Madagascar. However, support for such a poorly sampled early African history of Madtsoiidae is evidenced by indeterminate madtsoiids from the Cenomanian of Morocco (Rage and Dutheil, 2008), the occurrence of ‘? *Madtsoia* sp.’ from the Coniacian–Santonian of Niger (Rage, 1981; LaDuke et al., 2010), as well as indeterminate madtsoiids from Sudan (Rage and Werner, 1999), originally considered to be Cenomanian but now thought to be Campanian–Maastrichtian in age (Klein et al., 2016, and references therein). Poor sampling of the Late Cretaceous African terrestrial fossil record in general, coupled with the almost nonexistent pre-Maastrichtian Indo-Madagascan Late Cretaceous record (Mohabey et al., 2011), also supports the view that long ghost lineages should not be unexpected (Ali and Krause, 2011). Close relationships between Maastrichtian Malagasy and early Paleogene South American taxa also imply a relatively long, unsampled ghost lineage, given Madagascar’s isolation by ~83 Ma (Reeves, 2014). Similarly, a clade comprising latest Cretaceous European, South American, and Malagasy taxa, and several Cenozoic Australian lineages, appears to require an earlier, widespread distribution. Given the poor to nonexistent sampling of Australian terrestrial sediments from approximately 90 Ma until the early Eocene, dispersal from South America to Australia could have occurred at any time during this interval. The Neogene species must therefore imply long, unsampled ghost lineages, which is in keeping with the poor Cenozoic record of the Australian continent until the Oligocene–Miocene boundary (the early Eocene record is largely limited to a single fauna). Lastly, Vasile et al. (2013) suggested that madtsoiids might have reached Europe by the late Early Cretaceous; if correct, this would mean that the absence of madtsoiids from the European fossil record until the late Campanian should be interpreted as a sampling bias, and the dispersal would have happened prior to the Aptian severance of the Apulian Route.

In summary, there is a lack of evidence for the existence of dispersal routes connecting India and Africa during the latest Cretaceous–early Paleogene. One potential direct link between Africa and India, the Oman-Kohistan-Ladakh Island Arc (Chatterjee and Scotese, 2010; Prasad et al., 2010; Chatterjee et al., 2013), is herein rejected given new geological information demonstrating the later timing (late Paleocene–early Eocene) of its contact with Africa. An earlier widespread distribution, accounted for by poor sampling and long ghost lineages, appears to be the only explanation for biotic links between Indo-Madagascar and Africa and the close relationships between madtsoiids from the Maastrichtian of Madagascar and elsewhere (South America, Australia, Europe). In contrast, a trans-Tethyan dispersal between Africa and Europe via an emergent land bridge appears likely, but it remains uncertain whether this happened in the late Early Cretaceous or latest Cretaceous. Madtsoiids most likely reached Australia from South America via Antarctica, although the timing of the dispersal can only be constrained from approximately 90–50 Ma.


CONCLUSIONS

A redescription of the syntype of the ~7 m long fossil snake *Gigantophis garstini* reveals this taxon as distinct from all known madtsoiids, diagnosable by two autapomorphies and a unique combination of characters. Reassessment of referred specimens restricts *Gigantophis* to the middle–upper Eocene of North Africa. A near-comprehensive phylogenetic analysis of madtsoiid interrelationships groups *Gigantophis* with the latest Cretaceous Indian species *Madtsoia pisdurensis*. An evaluation of several putative Gondwanan dispersal routes leads us to conclude that an earlier widespread distribution of Madtsoiidae across Africa, Indo-Madagascar, and South America is the only feasible explanation, with poor sampling accounting for their absence in much of the fossil record. Their presence in Africa during the Late Cretaceous leads us to suggest that trans-Tethyan dispersal was responsible for the appearance of madtsoiids in Europe during the Campanian–Maastrichtian, possibly via the reemergence of the Apulian Route. Clarifying the paleobiogeographic history of Madtsoiidae will ultimately require better sampling of the Gondwanan fossil record in the Early to mid-Cretaceous and further geophysical and geological studies on the existence of putative Gondwanan land bridges in the latest Cretaceous–early Paleogene.

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