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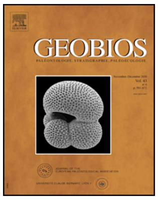

Original article

First report of the giant snake *Gigantophis* (Madtsoiidae) from the Paleocene of Pakistan: Paleobiogeographic implications[☆]

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ABSTRACT

We report here the discovery of madtsoiid snake remains from the early Paleocene Khadro Formation (Ranikot Group, Sindh, Southern Pakistan). These specimens consist of vertebrae and are referred to *Gigantophis*. This is the first report of *Gigantophis* from outside of Africa. The problem of the generic distinction between *Gigantophis* and *Madtsoia* is stressed. The specimens from Pakistan slightly differ from the single species (*G. garstini*) referred to the genus *Gigantophis*, but the available material does not allow further considerations and the fossil is referred to as *Gigantophis* sp. However, *Gigantophis* sp. from the Khadro Formation is more closely related to *G. garstini*, that is known only from the middle and late Eocene of northern Africa, than to any other species, thus suggesting dispersal between these two areas during the Paleocene or earlier. These results are consistent with the hypothesis of intermittent dispersals between the Indo-Pakistan Plate and Africa suggested by other fossil evidences.

1. Introduction

The Madtsoiidae is a presumed monophyletic assemblage of snakes that primarily inhabited Gondwanan continents. They are known from the Late Cretaceous to the Eocene of South America and Africa (Andrews, 1901; Simpson, 1933; Hoffstetter, 1959, 1961a; Albino, 1986, 1994, 2000; Rage, 1998, 2011; Rage and Dutheil, 2008). In Madagascar, they are known from the Late Cretaceous (Hoffstetter, 1961b; LaDuke et al., 2010). Madtsoiids were also reported from the latest Cretaceous to the Eocene of the Indo-Pakistan Plate (Rage et al., 2004, 2008; Wilson et al., 2010; Mohabey et al., 2011). They were recovered in Australia from the Eocene to the Pleistocene (Scanlon, 2005a, 2005b). Aside from Gondwanan areas, a few remains were found in the latest Cretaceous of southern Europe (Rage, 1999; Folie and Codrea, 2005; Vasile et al., 2013).

With a few exceptions, Madtsoiidae are represented only by vertebrae and, sometimes, ribs. The diagnoses of most species rest only on vertebral characters. Consequently, interrelationships cannot be analyzed confidently and even the monophyly of the group was more or less questioned (Mohabey et al., 2011). However, Scanlon (2005a) proposed a diagnosis of the Madtsoiidae based only on vertebral features. This diagnosis is a combination of derived and plesiomorphic characters and features of doubtful polarization which is unique to the group. Among these characters, Mohabey et al. (2011) recognized that the long-used "presence of a large parazygantral foramen located within a fossa" is a unique feature; however, they regarded this character as restricted to the Cretaceous-Paleogene large "taxa *Madtsoia* and *Gigantophis*, and possibly *Wonambi* and *Yurlunggur*". Surprisingly, they do not acknowledge the presence of this character in other, smaller snakes assigned to madtsoiids, in which this feature occurs. Be that what it may, Mohabey et al. (2011) suggest that large Madtsoiidae that have parazygantral foramina in fossae form a clade, implicitly regarding large size as a derived and phylogenetically significant character. As they express their opinion, within large madtsoiids, *Madtsoia* Simpson, 1933 and *Gigantophis* Andrews, 1901 are more closely related to each other than to any other taxon. The fact that *Madtsoia* and *Gigantophis* are closely related is not surprising if the taxonomic history of madtsoiids is taken into account.

In the frame of a joint project dedicated to the Ranikot Series, Sindh Province, Southern Pakistan, the different lithological units of the Ranikot group were surveyed for stratigraphic and

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paleontological purposes. During the early Paleocene, this area was part of the western edge of the Indo-Pakistan plate (IPP), prior to the collision with Asia (Tibet's southern margin; Chatterjee et al., 2013). This interval is interesting because it postdates the collision of the IPP with the Kohistan-Ladakh Arc during the late Cretaceous (~85Ma; Chatterjee et al., 2013), and predates the IPP-Asia collision during the early Eocene (Copley et al., 2010). Ranikot beds have yielded rare remains of often unidentified reptile bones (Gingerich et al., 1979), and fragments of a vertebral column of a dyrosaurid crocodile were reported by Storrs (1986). It is worth noting that Storrs (1986) mentioned that the dyrosaurid specimen was found from the Bahri Nala, near Rahman Doro, and he stated that the fossil locality is unquestionably from the Lakhra Formation, the uppermost and marine unit of the Group (Shah, 2009). However, according to the photos of the dyrosaurid locality figured in Storrs (1986), we strongly suspect that this specimen was actually recovered from the Khadro or the overlying Bara Formation, because the Lakhra Formation is almost not exposed in that area, and dark sediments of the fossiliferous locality do not match the typical facies of the Lakhra Formation. Here we report new fossil material of the madtsoiid snake *Gigantophis* from the early Paleocene Khadro Formation, and provide new insights into the historical biogeography of this fossil taxon.

2. Systematic history of *Gigantophis* and *Madtsoia*

The first named madtsoiid was *Gigantophis garstini* (a monospecific genus) from the late Eocene of Egypt. It was described by Andrews (1901) who noted resemblance with the extant *Python*, but did not assign the taxon to a family. Subsequently, Andrews (1906) referred *Gigantophis* to the Boidae (at that time, the concept of the Boidae was broad). Simpson (1933) erected the second madtsoiid taxon, *Madtsoia bai*, based on a specimen from the middle-late Eocene of Argentina. He noted that *Madtsoia* and *Gigantophis* shared similar features. However, apparently influenced by the geographic ranges, he stressed the differences between the African and South American fossils and regarded them as two distinct genera. Among the differences noted by Simpson, only the degree of lateral projection of the paradiapophyses may be regarded as significant (but it is now established that it varies within *Madtsoia*). In 1961, Hoffstetter both reevaluated the distinction between the two genera (Hoffstetter, 1961a) and recognized that they belong to a clade of their own (Hoffstetter, 1961b). He also reported new specimens of *Gigantophis garstini* from the middle Eocene of Libya (1961a) and described the second species of *Madtsoia*, *M. madagascariensis*, from the latest Cretaceous of Madagascar (Hoffstetter, 1961b). In these two articles, he compared *Madtsoia* to *Gigantophis*. Only one character permitted him to distinguish the two genera: in *Gigantophis*, the hemal keel is well marked off from the centrum, its ventral edge is rather sharp and, posteriorly, the keel ends as a shallow salient; in *Madtsoia*, the hemal keel is less distinct and, posteriorly, it bears a pair of small and blunt tubercles. In order to express the close relationships between *Madtsoia* and *Gigantophis*, Hoffstetter (1961b) erected the Madtsoiinae, subfamily included in the Boidae. The Madtsoiinae were raised to family level by McDowell (1987), a family whose relationships remain debated (Wilson et al., 2010; Palci et al., 2013; Vasile et al., 2013), but this issue is beyond the scope of the present study.

Subsequently, three additional species of *Madtsoia* were described: *M. laurasiae* from the latest Cretaceous of southern Europe (Rage, 1996, 1999), *M. camposi* from the Paleocene or Eocene of Brazil (Rage, 1998), and *M. pisdurensis* from the latest Cretaceous of India (Mohabey et al., 2011). LaDuke et al. (2010) removed the European species from *Madtsoia* and assigned it to their new genus *Menarana*, along with a species from the latest Cretaceous of Madagascar. Therefore, as presently defined, *Madtsoia* comprises four species (*M. madagascariensis*, *M. pisdurensis*, *M. camposi*, and *M. bai*), whereas *Gigantophis* still includes a single species (*G. garstini*). The addition of *M. camposi* and *M. pisdurensis* led to discard the presence of a posterior pair of tubercles on the hemal keel from the differences between *Madtsoia* and *Gigantophis*, thus weakening even more the distinction between the two genera. LaDuke et al. (2010) proposed a diagnosis of *Madtsoia* in which only the more or less distinct condition of the hemal keel distinguishes this genus from *Gigantophis*. Based on specimens described by Andrews (1906), LaDuke et al. (2010) also suggested, off-diagnosis, two features that might discriminate between the two genera: in *Gigantophis* the laminae of the neural arch would be thickened and strongly arched and the zygosphene hypertrophied. However, these features (even arching of the neural arch that depends on the thickness of the zygosphene, i.e. height of the zygantrum) appear to be typical of old, overgrown individuals. The smaller specimens of *Gigantophis* from Libya do not show these characters. Therefore, the morphological distinction between *Gigantophis* and *Madtsoia* is weak, but the two taxa are distinct as acknowledged by LaDuke et al. (2010) and Mohabey et al. (2011).

3. Geological Setting

In the lower Indus basin, the term "Ranikot series" or "infra-Nummulitic", first introduced by Blanford (1876), designates different lithological units sandwiched between the late Cretaceous Pab Sandstone and the early Eocene limestone and shales of the Laki series ("Kirthar or lower nummulitic group" of Blanford). Thus, the "Ranikot" is classically considered as Paleocene in age, but the upper and lower boundaries of the Ranikot Group, as those of its three constituent units (in ascending order: Khadro, Bara, and Lakhra), remain poorly constrained chronostratigraphically. The main exposures of the Ranikot Group are in the North-South anticlinal structures forming the Laki Range, and extending between Thano Bula Khan to the South and Sehwan Sharif to the North (Fig. 1). Blanford (1876, 1879) distinguished in ascending order the *Cardita beaumonti* beds, clastics of the Lower Ranikot, and foraminiferal limestone and sandstone of the Upper Ranikot. The *Cardita beaumonti* beds is a lithological unit of variable thickness, characterized by a high concentration of the bivalve *Cardita beaumonti*, and these beds have been reported from various spots of the eastern Tethys (Douvillé, 1928). Williams (1959) substituted the term Khadro Formation for the *Cardita beaumonti* beds of Blanford (1879) as the lowermost unit of the Ranikot Group and proposed a type section at Bara Nai (~20 km north from locality K18-12), but the unit has not been properly defined. In the Ranikot area, the Khadro Formation consists of olive, reddish to brown sandstone and shale resting uncomformably on the Khaskheli altered basalts (Shah, 2009; Agheem et al., 2011), themselves overlying the Campano-Maastrichtian Pab Formation.

Deposition of the Khadro Formation is interpreted to have occurred along the approximately North-South trending passive margin of eastern Tethys, and the lithology and fossil content suggest estuarine-coastal to inner shallow Platform environments. Uplift and compression have been episodic since the Paleocene, but the main phase of compression, folding and uplift was during the Pliocene to the present (Schelling, 1999).

The fossil specimens were collected on the surface of a large platform of indurate sandstone (locality K18-12), which has also yielded crocodile and turtle remains, oysters, bivalves (?*Crassatella* sp.), and gastropods (*Turritella* sp.), suggesting a coastal depositional environment. The stratigraphic position of the