

# Theropod tooth assemblages from the Late Cretaceous Maevarano Formation and the possible presence of dromaeosaurids in Madagascar

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The latest Cretaceous (Campanian?–Maastrichtian) Maevarano Formation of the Mahajanga Basin, Madagascar, preserves one of the most diverse fossil vertebrate faunas of the Gondwanan landmasses. Over 180 isolated theropod teeth recovered from that formation were studied in order to document theropod diversity in the Madagascar insular setting. Tooth morphology and characteristics of the Maevarano teeth were compared to those of known theropod teeth for identification, including the Malagasy non-avian theropods *Majungatholus atopus* and *Masiakasaurus knopfleri*. Tooth and denticle morphologies permit the recognition of five tooth morphotypes: three morphotypes are referable to *Majungatholus atopus* based on variation in tooth morphology observed in teeth preserved *in situ* in the jaws of two specimens, and one morphotype is ascribable to *Masiakasaurus knopfleri*. Teeth pertaining to the fifth morphotype differ from other morphotypes in the size and orientation of the denticles, shape and orientation of blood grooves, and in general tooth morphology. Statistical analyses reveal that the fifth Maevarano tooth morphotype is similar to dromaeosaurid teeth, suggesting that a yet unknown theropod taxon inhabited Madagascar during the latest Cretaceous. This morphotype represents the first evidence of the possible presence of a dromaeosaurid in Madagascar and supports the theory that dromaeosaurids were present throughout Pangaea before the break-up of the supercontinent during the Late Jurassic and had colonized Madagascar before its separation from Africa during the Early Cretaceous.

**Key words:** Dinosauria, Dromaeosauridae, Abelisauridae, theropod diversity, paleobiogeography, Campanian, Maastrichtian, Gondwana.

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## Introduction

Upper Cretaceous (Campanian?–Maastrichtian) terrestrial deposits of the Maevarano Formation, Mahajanga Basin, north-western Madagascar (Fig. 1), yield abundant and exceptionally well preserved fossil vertebrates (Depéret 1896; Besairie 1936, 1972). To date, over 30 species of terrestrial and freshwater vertebrates have been recognized on the basis of articulated and isolated elements, including avian and non-avian dinosaurs, crocodylians, fishes, and mammals, found in several multi-individual and multi-specific bone beds within a small geographic area (Forster et al. 1996; Krause and Hartman 1996; Sampson et al. 1998; Krause et al. 1999; Buckley et al. 2000; Curry-Rogers and Forster 2001; Rogers 2005, see also Krause et al. 2006 for review).

Isolated theropod teeth are common in the Maevarano Formation, especially in the Berivotra area where isolated teeth litter the surface of outcrops. Despite continued collection of isolated theropod teeth over the years, research has emphasized the study of bonebeds and articulated skeletons. Consequently, the isolated theropod teeth from the Maeva-

rano Formation have not been well-studied. Because tooth assemblages give insight into faunal constituents often poorly represented by skeletal remains (e.g., Baszio 1997a, b; Csiki and Grigorescu 1998; Sankey 2001; Codrea et al. 2002; Sankey et al. 2002, 2005), the study of isolated theropod teeth offers the unique opportunity to compare the theropod tooth diversity of Madagascar with its currently known theropod diversity based on skeletal material. This study presents evidence for the occurrence of a possible dromaeosaurid taxon in the Maevarano Formation, previously unknown from skeletal material, representing the first occurrence of an animal of this lineage in Madagascar. As such, the results of this research improve our understanding of the Late Cretaceous Malagasy ecosystems and have important implications for Gondwanan paleobiogeography.

*Institutional abbreviations.*—AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; MSNM, Museo Civico di Storia Naturale di Milano, Milan, Italy; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

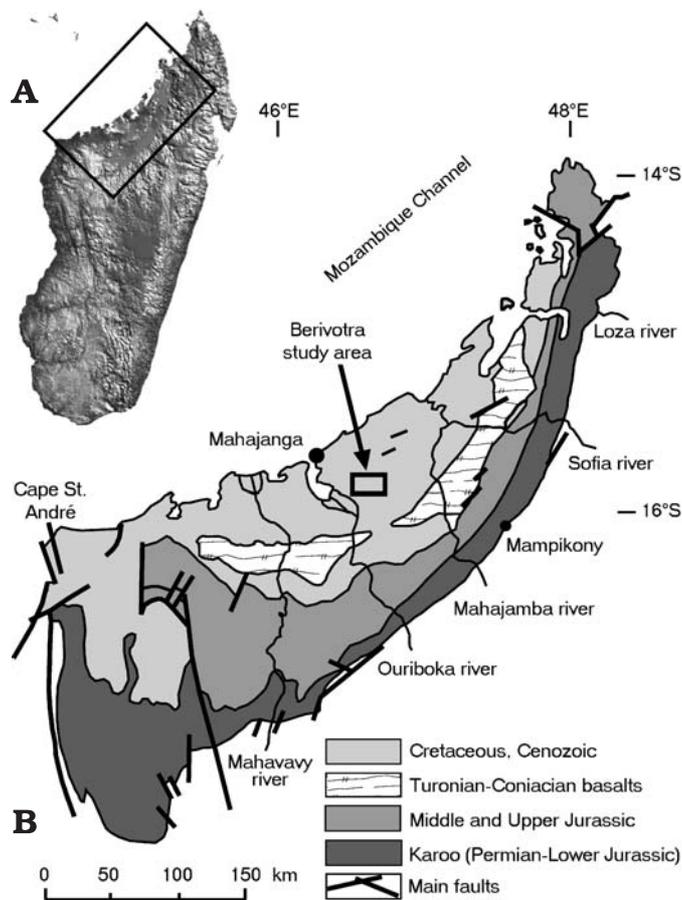


Fig. 1. A. Map of Madagascar showing the position of the Mahajanga Basin. B. Geologic map of the Mahajanga Basin with location of Berivotra study area.

*Other abbreviations.*—BW, tooth basal width; DSDI, denticle size difference index; FABL, fore-aft basal length; FABL/BW, basal compression ratio; FABL/TCH, elongation ratio; NDPMa, number of denticles per millimetre on anterior carina (measured at mid-crown); NDPMp, number of denticles per millimetre on posterior carinae (measured at mid-crown); TCH, tooth crown height.

## Geological setting

Recent stratigraphic studies revealed that the strata exposed near Berivotra include the terrestrial Maevrano Formation (Campanian?–Maastrichtian) and the marine Berivotra Formation (latest Maastrichtian) (Rogers et al. 2000, 2001; Abramovich et al. 2002; Rogers 2005). All bonebeds and the majority of skeletal remains occur within the Maevrano Formation (Fig. 2), predominantly from the sandstone-dominated Anembalemba Member (Rogers et al. 2000; Rogers 2005). The teeth studied in this research were collected in the Anembalemba Member.

Based on the association of particular fossil assemblages with specific facies, three different Late Cretaceous subtropical ecosystems were identified on the western coast of Mad-

agascar: (1) an alluvial plain ecosystem, dominated by the large theropod *Majungatholus atopus* Sues and Taquet, 1979 and the titanosaur *Rapetosaurus krausei* Curry Rogers and Forster, 2001; (2) a fluvio-lacustrine ecosystem, representing the ideal habitat for a variety of crocodyliforms, and; (3) a marine coral reef ecosystem, populated by several marine vertebrates, bounding the coast of the Mahajanga Basin (Beltan 1996; Gottfried and Krause 1998; Gottfried et al. 2001; Fanti, 2005).

Although the geology and stratigraphy of the Mahajanga Basin are well documented, the paleogeographical history of the island of Madagascar is poorly understood. Although it is agreed that Madagascar became separated from Africa during the Early Cretaceous (approximately 135 Ma; Marks and Tikku 2001; Tikku et al. 2002; Frey et al. 2003; Mette, 2004; Winberry and Anandakrishnan 2004), relatively little is known about the faunal composition of these landmasses at that time. This gap in knowledge complicates the formulation of paleobiogeographic hypotheses linking dinosaurs and other taxa to the evolution of the island and hinders the development of a convincing faunal dispersal model through Gondwana during the middle and Late Cretaceous.

## Material and methods

Isolated teeth can be used to identify theropod taxa to the genus level with accuracy despite the presence of intraspecific variation (associated with tooth position along the jaws) (Currie et al. 1990; Farlow et al. 1991; Abler 1992; Fiorillo and Currie 1994; Rauhut and Werner 1995; Baszio, 1997; Holtz et al. 1998; Vickers-Rich et al. 1999; Fiorillo and Gangloff 2000; Park et al. 2000; Sankey 2001; Candeiro 2002, 2004; Torices 2002; Sankey et al. 2002; Maganuco et al. 2005; Samman et al. 2005; Smith et al. 2005). Maxillary (i.e., lateral) and premaxillary (i.e., anterior) teeth are usually easily distinguishable in theropod dinosaurs (Currie et al. 1990; Candeiro 2002; Smith and Dodson 2003). The large number of specimens studied in this research permits the recognition of a gradual transition between maxillary and premaxillary teeth.

A total of 189 isolated theropod teeth were studied. These teeth were surface collected during several joint expeditions conducted by paleontologists from the Museo Civico di Storia Naturale (Milano, Italy) and the Museo Civico dei Fossili (Besano, Italy), in collaboration with the Ministère de l'Énergie et des Mines and the Direction des Mines et de la Géologie de Madagascar. Teeth are categorized into five distinct morphotypes on the basis of the following parameters: tooth crown height (TCH), fore-aft basal length (FABL), tooth basal width (BW), basal compression ratio (FABL/BW), elongation ratio (FABL/TCH), number of denticles per millimetre on both anterior (NDPMa) and posterior carinae (NDPMp) (both measured at mid-crown), and denticle size difference index (DSDI) (Fig. 3, Appendix 1; all Appendices are available on the APP website at <http://app.pan.pl/acta52/app52-199A.htm>). Despite the fact that blood grooves have not been formally described in the literature, they were considered as a relevant and

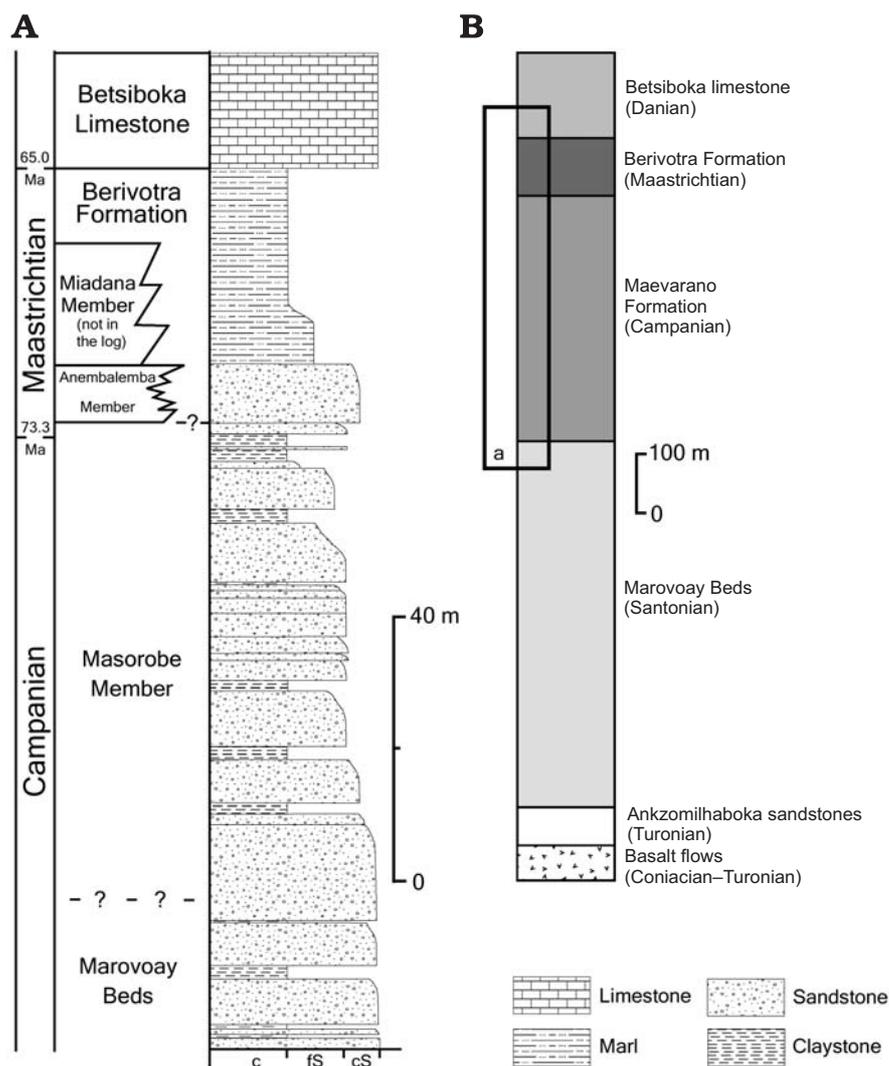


Fig. 2. **A.** Stratigraphic section of the Late Cretaceous succession exposed near the village of Berivotra (based on Papini and Benvenuti 1998 and Rogers et al. 2000). **B.** Stratigraphic succession of Coniacian–Danian sedimentary units in the central Mahajanga Basin (based on Papini and Benvenuti 1998 and Razafindrazaka et al. 1999).

diagnostic parameter for taxonomic identification in the light of the peculiar characteristics of the Malagasy specimens (Fig. 3). The parameter terminology follows Currie et al. (1990), Farlow et al. (1991), Rauhut and Werner (1995), and Baszio (1997b). Measurements were made with digital callipers with a precision to the nearest mm.

To identify the isolated teeth studied, the tooth morphotypes were compared to the dentition of the two Maevarano abelisauroid theropods known from skeletal material: the abelisaurid *Majungatholus atopus* Sues and Taquet, 1979 and the noasaurid *Masiakasaurus knopfleri* Sampson, Carrano, and Forster, 2001. Individual (relative to the position along the tooth row) and intraspecific (age- or size-related) tooth variability was documented in the latter taxa to determine if different tooth morphotypes pertained to the same taxon. Available specimens of *Majungatholus atopus* (FMNH PR 2100 and FMNH PR 2278) show tooth variability along the tooth row and between similar-sized individuals, but cannot be used to reveal ontogenetic differences in tooth morphology (Appendix 2). When the tooth at a specific alveolus was not preserved, the shape of the alveoli provided

useful information on tooth morphology, such as diameters and symmetry of the basal cross-section. For *Masiakasaurus knopfleri*, tooth characteristics and morphology were compared to published descriptions (see Sampson et al. 2001; Carrano et al. 2002; Smith et al. 2005).

Morphometric parameters of isolated teeth were compared statistically to those of Madagascar theropods and of well-known theropod taxa from other continents, principally North America. Tooth parameters for *Richardoestesia gilmorei* Currie, Rigby, and Sloan, 1990, *Saurornitholestes langstoni* Sues, 1978, *Dromaeosaurus albertensis* Matthew and Brown, 1922, *Albertosaurus sarcophagus* Osborn, 1905, *Gorgosaurus libratus* Lambe, 1914, *Daspletosaurus torosus* Russell, 1970, and unidentified Campanian tyrannosaurids were measured by the senior author on specimens curated at the Royal Tyrrell Museum of Palaeontology (Appendix 3). To expand the comparative database, parameters from isolated and *in situ* teeth for *Masiakasaurus knopfleri*, *Deinonychus antirrhopus* Ostrom, 1969, *Velociraptor mongoliensis* Osborn, 1924, *Majungatholus atopus*, and *Indosuchus raptorius* Huene and Matley, 1933 were gathered from pub-

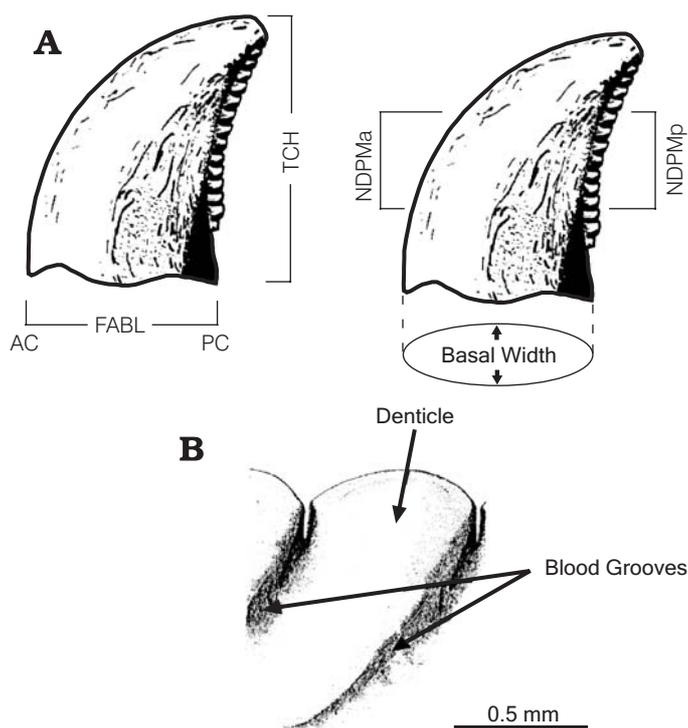


Fig. 3. **A.** Tooth parameters considered in this study. FABL, fore-aft basal length, excluding denticles; TCH, tooth crown height; AC, anterior carina; PC, posterior carina; NDPMa, number of denticles per millimetre on the anterior carina, determined at mid-crown; NDPMp, number of denticles per millimetre on the posterior carina, determined at mid-crown. **B.** Detailed representation of denticles and blood grooves as described in the text (modified after Currie et al. 1990).

lished reports (Carrano et al. 2002; Smith et al. 2005) and from unpublished data (A. Torices Hernández, personal communication 2004). Statistical comparison of the various teeth was conducted with the software SPSS 8.0 for the cluster analysis and R 2.2.0 for the quadratic discriminant analysis.

## Results

The Maevarano theropod teeth can be classified into five morphotypes (Table 1).

**Morphotype 1** (Fig. 4).—Teeth pertaining to Morphotype 1 are uncommon (9.5% of tooth sample) but distinctive. Although the preservation quality of the crown and denticles is good, all represent shed teeth as the root is never preserved. These primarily lateral teeth: (1) are generally small (TCH 8–15 mm); (2) are laterally compressed (FABL as much as double BW); (3) have a nearly symmetrical, teardrop-shaped basal cross-section; (4) display a slightly curved posterior carina, and; (5) possess 3–3.5 denticles/mm along the posterior carina and 3 to 5.5 denticles/mm along the anterior one. The denticles are generally low, their height being approximately half of their length. The distal extremity of the denticles is slightly pointed toward the apex of the crown (Fig. 4). The

overall denticle morphology appears to be intermediate between the chisel-shape denticles of *Dromaeosaurus* and the hook-like denticles of *Saurornitholestes* (see Currie et al. 1990). On the posterior carina, denticles are almost as long as they are wide and are oriented perpendicular to the edge of the tooth. In contrast, denticles on the anterior carina are small, usually near half the length and basal width of the posterior ones, and inclined toward the apex of the crown. On both carinae, denticle size decreases toward the basal and apical ends of the carinae. Blood grooves are generally shallow and poorly defined; however in a few instances, blood grooves can be observed close to the base of the denticles where they are oriented perpendicular to the longitudinal axis of the tooth (Fig. 4). In labial view, some teeth show a distinct inflection point where the curvature of both the tooth and carina becomes more pronounced.

Although Morphotype 1 generally applies to lateral teeth, some specimens (e.g., MSNM V5365, V5372, V5394, and V5590; see Appendix 1) presumably represent premaxillary teeth. The basal cross-section is asymmetrical and strongly convex on the labial side. The denticles are inclined slightly toward the apex of the crown. The number of denticles per mm on the anterior and posterior carinae varies between 2.5–3 and 2–2.5 respectively. Both carinae are located on the lingual side of the crown, with the anterior carina strongly twisted toward the apex of the tooth. These presumed premaxillary teeth of Morphotype 1 are smaller than premaxillary teeth ascribed to Morphotype 5 (see Table 1).

**Morphotype 2** (Fig. 5).—The characteristics of MSNM V5378 are unique among the Maevarano theropod teeth studied and justify its placement within a distinct morphotype. Although the tooth is similar in size to Morphotype 1 (TCH 13 mm), it is more elongate and strongly recurved. Denticles are smaller than in Morphotype 1, with 4 denticles per millimetre being found on the anterior carina, and 3 denticles per millimetre occurring on the posterior carina.

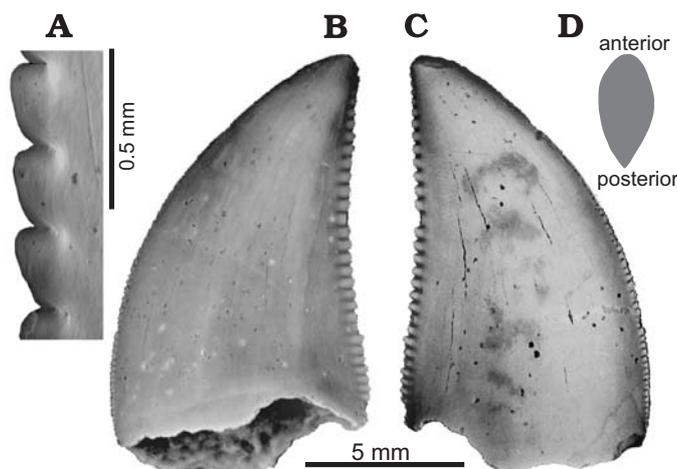


Fig. 4. Morphotype 1, specimen MSNM V5373. Berivotra, Mahajanga Basin, northern Madagascar; Anembalemba Member, Maevarano Formation (Campanian?–Maastrichtian). **A.** Mesial denticles from the posterior carina. **B.** Labial view. **C.** Lingual view. **D.** Basal cross-section.

Table 1. Maevarano theropod tooth morphotypes. NDPMa, number of denticles per millimetre on anterior carina (measured at mid-crown); NDPMp, number of denticles per millimetre on posterior carinae (measured at mid-crown).

	Number of specimens	NDPMa	NDPMp	Blood grooves	Position along the dental series	Taxonomic identity
Morphotype 1	18	3–5.5	3–3.5	Absent or close to the base of the denticle. Perpendicular to the longitudinal axis of the tooth.	premaxillary and lateral teeth	indeterminate dromaeosaurid
Morphotype 2	1	4	3	Absent or close to the base of the denticle. Perpendicular to the longitudinal axis of the tooth.	lateral teeth	<i>Masiakasaurus knopfleri</i>
Morphotype 3	124	2–3.5	1.5–3	Well-developed and strongly inclined toward the proximal end of the tooth.	lateral teeth (M2-17 and D8-17)	<i>Majungatholus atopus</i>
Morphotype 4	25	2–2.5	1.5–2.5	Well-developed and strongly inclined toward the proximal end of the tooth.	lateral teeth (intermediate) (P4, M1, and D1-6)	<i>Majungatholus atopus</i>
Morphotype 5	20	1.5–2.5	1.5–2.5	Well-developed and strongly inclined toward the proximal end of the tooth.	premaxillary teeth (P1-3)	<i>Majungatholus atopus</i>

Denticles are as long as they are high. The denticles of Morphotype 2 are very similar to the chisel-shaped denticles of *Dromaeosaurus* (Currie et al. 1990), but the distal curvature toward the apex of the crown is slightly more accentuated in the Madagascar morphotype (Fig. 5). The height of the denticles differs significantly on the two carinae: the posterior denticles are three to four times taller than the anterior ones (Fig. 5). Blood grooves are either absent or restricted to the base of denticles. Both anterior and posterior carinae are on the lingual side of the tooth although the anterior carina is strongly twisted toward the base of the tooth. In cross-section, the labial surface is remarkably convex close to the anterior carina, while the lingual surface is flat. The basal cross-section is laterally compressed—such that FABL is double BW—and slightly asymmetrical (Fig. 5).

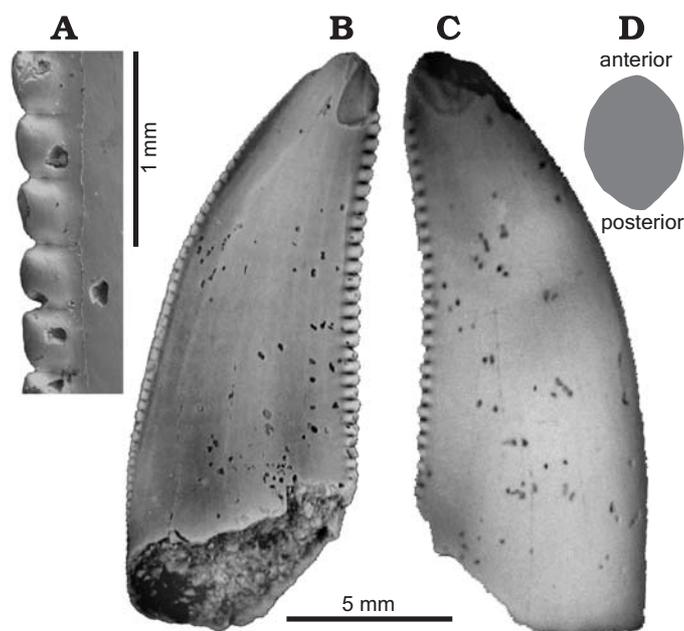
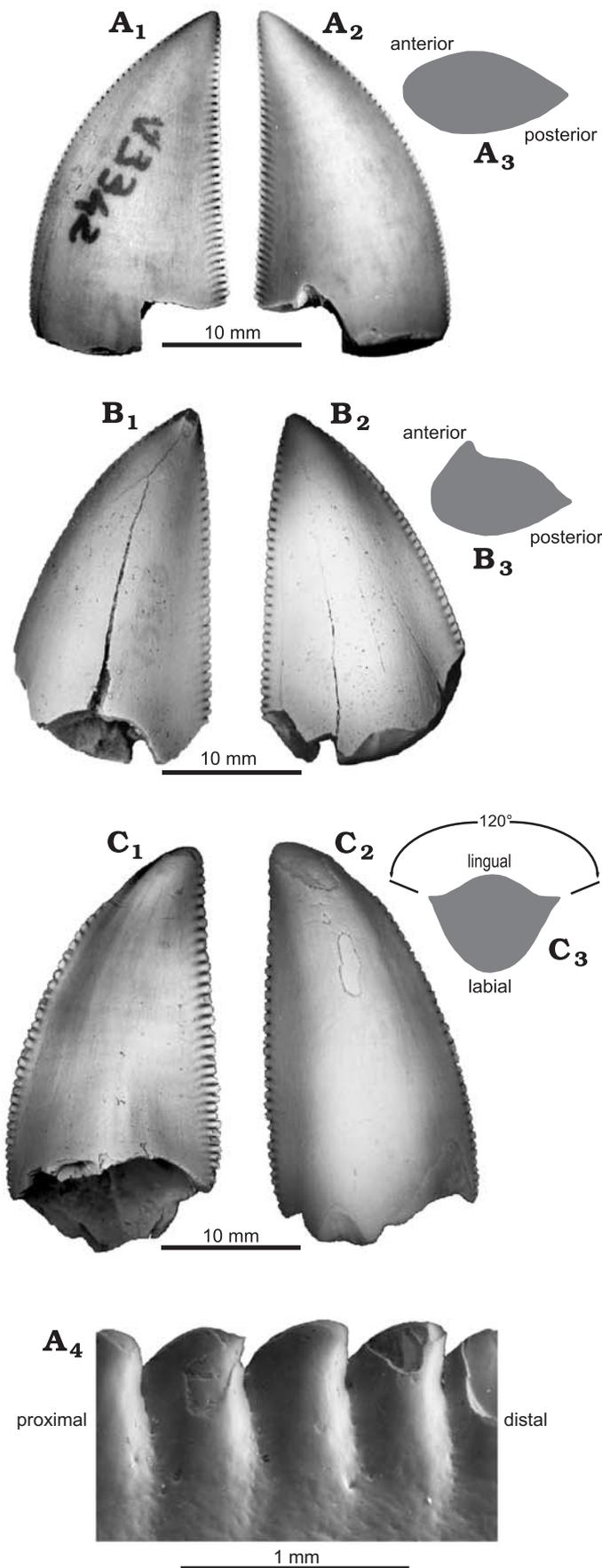


Fig. 5. Morphotype 2, specimen MSMN V5378. Berivotra, Mahajanga Basin, northern Madagascar; Anembalemba Member, Maevarano Formation (Campanian?–Maastrichtian). A. Mesial denticles from the posterior carina. B. Labial view. C. Lingual view. D. Basal cross section.

**Morphotype 3** (Fig. 6A).—A large number of specimens pertain to Morphotype 3 (65.6% of tooth sample), which permits a detailed documentation of individual and ontogenetic variability in tooth morphology. Morphotype 3 includes teeth of different sizes, presumably representing young and old individuals, and quality of preservation. Many of the specimens are incomplete and the roots are almost never preserved. Nevertheless, it is still possible to study the shape and size of the denticles, and the characteristics of the carinae. These lateral teeth demonstrate a large size variability, but are generally larger than Morphotypes 1 and 2 (FABL >50%, TCH >60%, BW >35% in average). The basal cross-section is laterally compressed (FABL never more than double BW), teardrop-shaped, and usually symmetrical (Fig. 6A). The denticles are strongly recurved toward the apex of the crown, similar in shape to a shark dorsal fin. These denticles are very similar to the hook-like denticles of *Saurornitholestes* (see Currie et al. 1990) (Fig. 6D). Denticles are smaller and shorter (2.5–3 denticles per mm) on the anterior carina than on the posterior carina (2–3 denticles per mm). The size of the denticles decreases toward the basal and apical ends of both carinae. Blood grooves are clearly visible to the naked eye, regardless of tooth size, and are strongly inclined toward the basal end of the tooth relative to the denticles (Fig. 6A, D). In many specimens, the posterior carina is slightly curved toward the lingual surface of the tooth while the anterior carina is straight. Finally, teeth of Morphotype 3—especially “medium sized” teeth (averaging FABL 11.68 mm, TCH 20.64 mm, BW 5.76 mm)—display an inflection point where the curvature of the posterior carina becomes more pronounced lingually, as also observed in *Carnotaurus sastrei* (Fanti, personal observations).

**Morphotype 4** (Fig. 6B).—Teeth pertaining to Morphotype 4 (13.2% of tooth assemblage) display a shape intermediate between that of premaxillary and maxillary teeth. The specimens are often broken, but have well-preserved denticles and carinae. The teeth are large (TCH 16–35 mm) and stocky, with strongly asymmetrical basal cross-sections. Denticles are similar in shape and number per mm to those described



for Morphotype 3 (NDPMa close to 2.5 and NDPMp close to 2). The asymmetry of the basal cross-section is reflects the convexity of the labial surface of the tooth (Fig. 6B). The carinae exhibit a unique sigmoidal shape when viewed from the apical end of the tooth. Finally, a small but clear concavity is observed close to the anterior carina on the lingual side of the tooth (particularly well-developed in MSNM V3360, V3363, V3368, and V5518) due to the presence of a faint ridge (Fig. 6B). This ridge is missing in Morphotype 3, is slightly pronounced in Morphotype 4, but is clearly observable in all teeth ascribed to Morphotype 5 (Fig. 6).

**Morphotype 5** (Fig. 6C).—Morphotype 5 consists of well-preserved premaxillary teeth (10.6% of tooth sample, TCH 15–30 mm). These teeth are easily distinguishable by their symmetrical, wide D-shaped basal cross-section, their identical number of denticles on both carinae, and by the wide, flat lingual surface separating the carinae. Denticles are less recurved and larger than in the four previous morphotypes (NDPMa and NADPMp range from 1.5 to 2.5), and are inclined toward the apex of the crown. The size of the denticles decreases toward the apical and basal portions of the carinae but not to the extent observed in all previous morphotypes. Blood grooves are clearly visible and are strongly inclined toward the base of the tooth (Fig. 6C). In addition, the basal cross-section of Morphotype 5 is strongly labiolingually compressed (Fig. 6C), more so than in teeth of large theropods of equivalent size, such as *Daspletosaurus torosus* and *Albertosaurus sarcophagus*. A marked but low longitudinal ridge is present on the lingual surface of the tooth. In contrast, the labial surface is strongly convex and smooth.

## Discussion

**Variability in tooth morphology among Malagasy theropods and identification of the Maevarano tooth morphotypes.**—To infer the taxonomic identity of the Maevarano tooth morphotypes, it is essential to understand the variability in dentition in known Malagasy theropods, *Majungatholus atopus* and *Masiakasaurus knopfleri*.

Tooth morphology varies greatly along the tooth row in *Majungatholus atopus*. Study of teeth preserved *in situ* in jaws revealed three distinct features: (1) maxillary teeth are bigger (usually 20–30%) than similarly positioned teeth on the dentary; (2) tooth size varies greatly along the tooth row, especially along the dentary, and; (3) there is a gradual transition in tooth symmetry and tooth basal cross-sectional shape along the dentary and maxilla (Appendix 2).

Fig. 6. Theropod teeth from Berivotra, Mahajanga Basin, northern Madagascar; Anembalemba Member, Maevarano Formation (Campanian?–Maastrichtian). **A.** Morphotype 3 (MSMN V3342) in labial (A<sub>1</sub>) and lingual (A<sub>2</sub>) views; A<sub>3</sub>, basal cross section; A<sub>4</sub>, mesial denticles. **B.** Morphotype 4 (MSMN V5518) in labial (B<sub>1</sub>) and lingual (B<sub>2</sub>) views; B<sub>3</sub>, basal cross section. **C.** Morphotype 5 (MSMN V5368) in labial (C<sub>1</sub>) and lingual (C<sub>2</sub>) views; C<sub>3</sub>, basal cross section.

The premaxilla of *Majungatholus* bears four teeth (Fig. 7). The posterior-most tooth is slightly asymmetric in cross-section and is convex labially, as for teeth ascribed to Morphotype 4. All other premaxillary teeth (alveoli 1, 2, and 3) are strongly flattened on the lingual side and display a wide, symmetrical cross-section. Denticles are equal in number on both carinae (NDPM is usually 1.5) and blood grooves are inclined toward the base of the tooth. A ridge on the lingual side is also clearly visible. Such characteristics clearly allow referral of teeth ascribed to Morphotype 5 to the first three premaxillary teeth of *Majungatholus*.

The maxilla of *Majungatholus* bears 17 teeth (Fig. 8). The first maxillary tooth is slightly convex labially and is comparable to the fourth premaxillary tooth and to teeth ascribed to Morphotype 4. The second through the seventeenth maxillary teeth have symmetrical, teardrop-shaped basal cross-sections and are larger than teeth occupying similar positions in the dentary. These teeth exhibit all the features characteristic of Morphotype 3. The seventeenth maxillary tooth is particularly interesting in the context of identifying isolated teeth. Although this tooth is significantly smaller than all other maxillary teeth, the number of denticles per mm on the anterior or posterior carinae (NDPM a/p) is identical to that of maxillary and dentary teeth. In addition, denticles are elongated and inclined toward the distal end of the tooth, and the blood grooves are clearly visible. Thus, this observation implies that even teeth of small size can be recognized as pertaining to *Majungatholus* based on the dental parameters investigated in this research.

Like the maxilla, the dentary of *Majungatholus* bears 17 teeth (Fig. 9). The first six teeth have remarkably asymmetrical cross-sections and are strongly convex labially. On the lingual side of some teeth, a peculiar concavity close to the anterior carina is clearly visible. The first six dentary teeth display the characteristics of Morphotype 4. The basal cross-section of the seventh tooth is transitional between the asymmetric cross-section of more anterior teeth and the symmetric cross-section of more posterior teeth. The eighth through seventeenth teeth are large with a symmetrical teardrop-shaped basal cross-section. As such, posterior dentary teeth correspond to Morphotype 3.

The highly specialized dentition of *Masiakasaurus knopfleri* is known only from fragmentary material: only four teeth are preserved in situ in the dentary of the holotype (Sampson et al. 2001; Carrano et al. 2002) and 10 isolated teeth have been formally referred to this taxon (Smith et al. 2005). Nevertheless, the characteristics of the known teeth, combined with the shape of the alveoli in the holotype (Carrano et al. 2002), permit the recognition of diagnostic features useful for the identification of isolated teeth. As observed in the holotype, the anterior carina is not located on the edge of the tooth but in a more "lateral" position, and both carinae converge on the posteriorly-inclined tooth apex (see Sampson et al. 2001; Carrano et al. 2002). Bivariate plots of FABL-TCH and BW-TCH (Fig. 10) show that Morphotype 2 (MSNM V5378) is very similar to teeth of *Masiakasaurus knopfleri*.

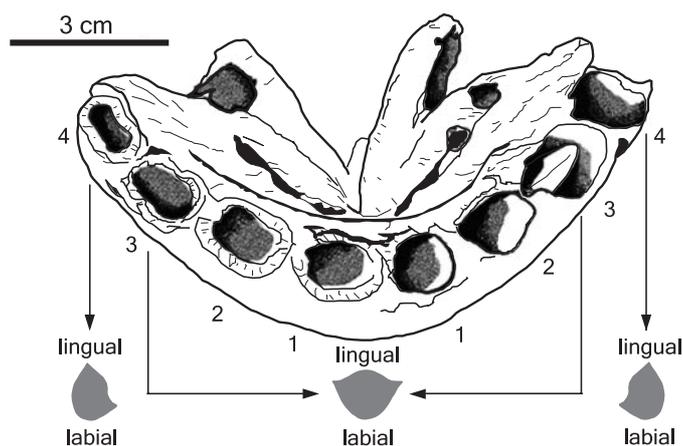


Fig. 7. Premaxilla of *Majungatholus atopus* Sues and Taquet, 1979 (FMNH PR 2100) in ventral view showing alveoli and associated tooth basal cross-section.

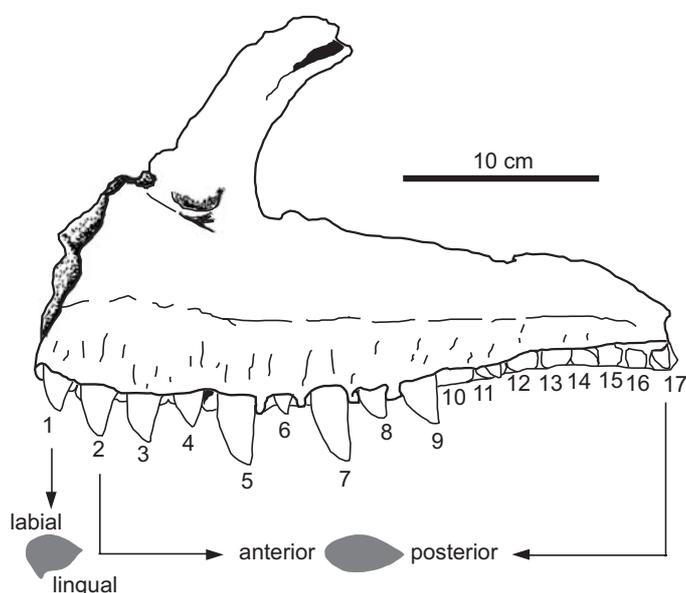


Fig. 8. Right maxilla of *Majungatholus atopus* Sues and Taquet, 1979 (FMNH PR 2100) in medial view showing alveoli and associated tooth basal cross-section.

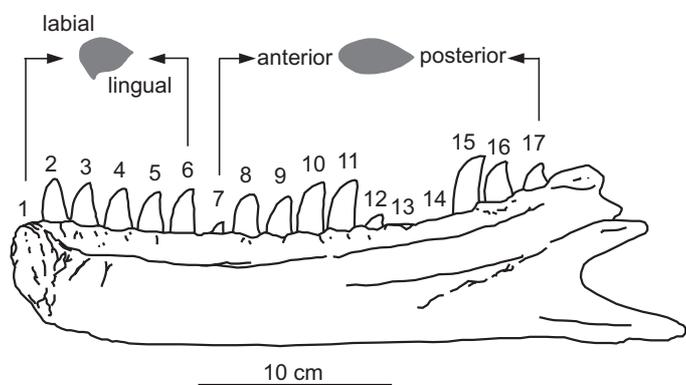


Fig. 9. Right dentary of *Majungatholus atopus* Sues and Taquet, 1979 (FMNH PR 2100) in lingual view showing alveoli and associated tooth basal cross-section.

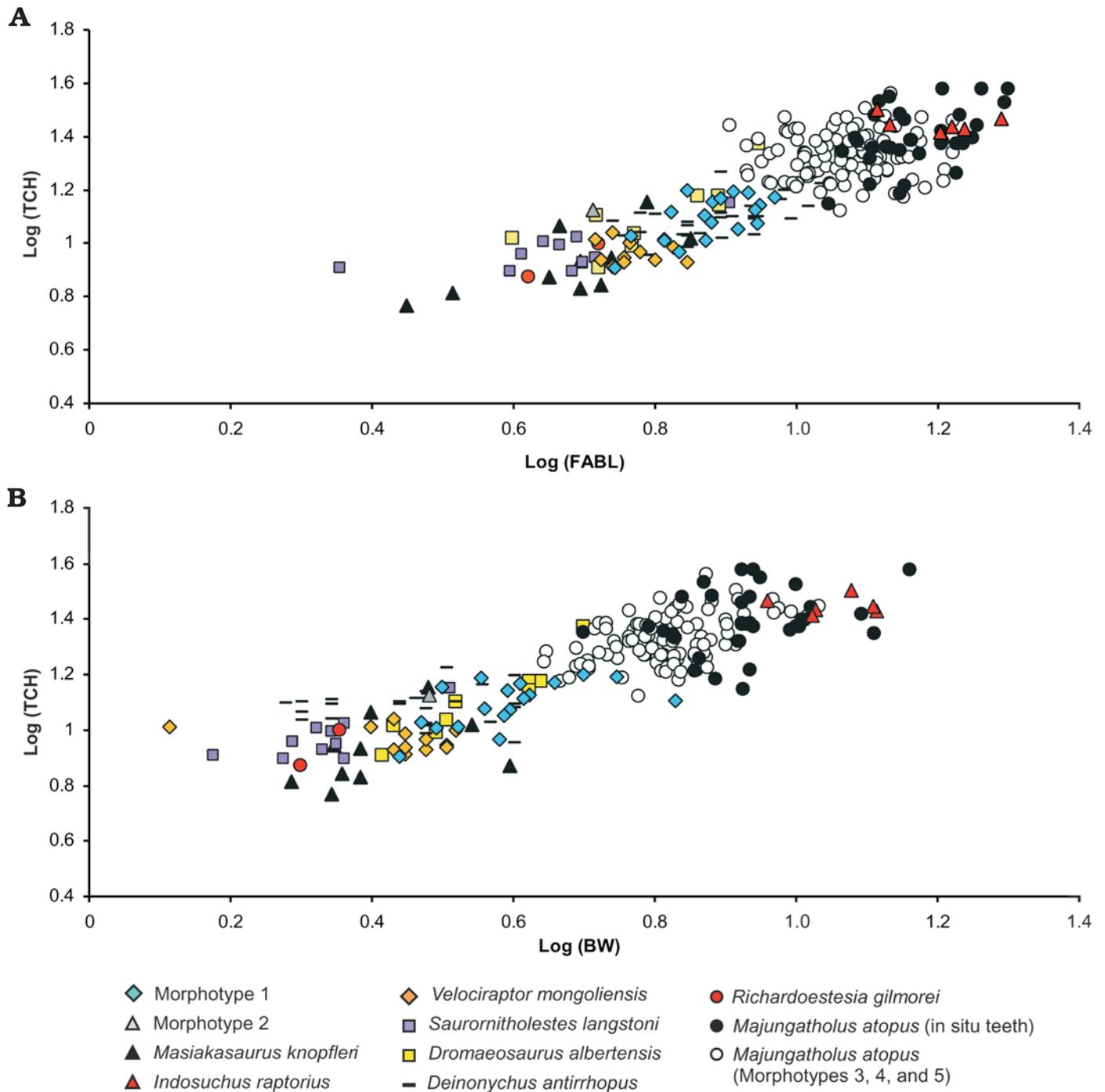


Fig. 10. Bivariate plots of tooth parameters. **A.** Tooth Crown Height versus Basal Width. **B.** Tooth Crown Height versus Basal Width. Teeth pertaining to Morphotype 1 falls closer to dromaeosaurids than to *Majungatholus atopus* teeth. Morphotype 2 falls close to *Masiakasaurus knopfleri* teeth.

Particularly diagnostic is the nearly circular basal cross-section (FABL/BW ratio = 1.14) of MSNM V5378, which corresponds closely with the 4<sup>th</sup> alveolus of the dentary (Sampson et al. 2001: fig. 2-f) and allows us to refer this specimen to the 4<sup>th</sup> or 5<sup>th</sup> alveolus of the dentary of *Masiakasaurus knopfleri*.

**Problematic identity of Morphotype 1.**—Although Morphotypes 2 through 5 can be referred to *Majungatholus*

*atopus* and *Masiakasaurus knopfleri*, the small teeth ascribed to Morphotype 1 cannot be unequivocally attributed to either of the known Malagasy non-avian theropods. Comparison between lateral teeth of Morphotypes 1 and 3 reveals that similarities between these two groups are restricted to the shape of the basal cross-section and the presence of hook-like denticles oriented towards the apex of each tooth.

Numerous parameters distinguish Morphotype 1 from teeth referred to *Majungatholus atopus* (Morphotypes 3, 4,

and 5), including: (1) the number and shape of denticles; (2) the presence of blood grooves; and (3) the shape and size of the teeth. The number of denticles per mm in Morphotype 1 is greater than on *Majungatholus* teeth. The denticles observed on in situ and isolated *Majungatholus atopus* teeth are remarkably elongate, particularly on the posterior carina, where the denticle height is three times its width. In contrast, denticles on the posterior carina of all teeth included in Morphotype 1 are equally large and tall. In addition, while denticles are inclined toward the apex of the tooth in *Majungatholus*, they are oriented perpendicular to the edge of the tooth in Morphotype 1. Blood grooves prove to be one of the most distinctive features of *Majungatholus atopus* teeth. Isolated teeth referred to *Majungatholus* display clearly blood grooves that are strongly inclined toward the base of the tooth on the posterior carina. In contrast, teeth pertaining to Morphotype 1 either lack blood grooves entirely or their presence is restricted to the base of the denticles. Finally, Morphotype 1 teeth are smaller and less elongate than the smallest tooth referred to *Majungatholus* (Appendices 1, 2).

The differences observed between teeth ascribed to Morphotype 1 and *Majungatholus* teeth cannot be explained by variation in tooth morphology along the tooth row observed in the latter taxon. Two possibilities can explain the identity of Morphotype 1: (1) the morphotype represents the dentition of juvenile *Majungatholus atopus*; or (2) the morphotype represents a new species of small theropod. It has been shown that the number of denticles per millimetre on a tooth varies within a single individual and, most importantly, through ontogeny within a given species (Farlow et al. 1991). However, the orientation of the denticles and the scarcity of blood grooves in Morphotype 1 suggest that the differences with *Majungatholus* teeth cannot be explained by ontogenetic changes in tooth morphology. The fact that some teeth pertaining to Morphotypes 3, 4, and 5 can be confidently identified as belonging to juvenile *Majungatholus* individuals further supports this interpretation. Therefore, we conclude that Morphotype 1 represents a yet unknown small-bodied theropod taxon.

Morphometric and statistical techniques were used to clarify the systematic affinity of Morphotype 1. Because previous studies of theropod teeth demonstrated a linear (or nearly linear) relation between BW, FABL, and TCH (Farlow et al. 1991; Baszio 1997b; Holtz et al. 1998; Sankey et al. 2002), teeth pertaining to the Malagasy theropods (Morphotypes 1 through 5), the abelisaurid *Indosuchus raptorius*, *Richardoestesia gilmorei*, and dromaeosaurids were compared on the basis of their linear dimensions. Bivariate plots reveal that teeth of Morphotype 1 are clearly more similar to the teeth of dromaeosaurids than to those of other theropod taxa studied (Fig. 10).

To test the hypothesis that Morphotype 1 pertains to a dromaeosaurid, seven different tooth parameters (FABL, TCH, BW, NDPMa, NDPMp, FABL/TCH, FABL/BW) were tabulated from personal observations, personal communications, and published literature (see "Materials and methods"), and compared among various theropod taxa. Based on the data

considered, an ANOVA reveals that each parameter can be used to statistically and significantly differentiate each group ( $p < 0.08$ ). Subsequently, a quadratic discriminant analysis (QDA) was conducted on teeth grouped at the family level (i.e., tyrannosaurids, dromaeosaurids, abelisaurids including Morphotypes 3–5, and *Masiakasaurus*) to determine if individual teeth can be ascribed to the appropriate taxonomic group on the basis of the seven morphometric parameters; note that *Richardoestesia* was not considered in this analysis due to the limited number of specimens.

The results of the QDA reveal that teeth can be accurately recognized as members of a specific taxonomic group on the basis of the studied parameters with an accuracy of 96%. Interestingly, eight dromaeosaurid teeth were mistakenly identified as *Masiakasaurus* teeth by the QDA, which suggests that the teeth of these taxa are similar (Table 2). Finally, a cluster analysis, a useful approach for comparing new fossil material to that of established taxa, was conducted to sort the studied teeth into clusters based on similar parameters. The results of the cluster analysis (Fig. 11, Table 3) reveal that Morphotype 1 is most similar to teeth of *Deinonychus antirrhopus* and *Dromaeosaurus albertensis* than to any other theropod studied. In turn, the cluster analysis demonstrates that *Masiakasaurus* teeth are more similar to the teeth of *Velociraptor mongoliensis*, *Saurornitholestes langstoni*, and *Richardoestesia gilmorei* than any other theropods. Finally, teeth pertaining to Morphotypes 1 and 2, dromaeosaurids, and *Richardoestesia* are more similar to each other than any are to *Majungatholus* teeth. Thus, the results of morphometric and statistical analyses strongly support a dromaeosaurid affinity for Morphotype 1 rather than an affinity with the previously-known Maevarano theropods *Majungatholus* and *Masiakasaurus*. However, it must be noted that *Masiakasaurus* teeth also plot with dromaeosaurid teeth (Fig. 11) and that some South American noosaurids display dental features reminiscent of dromaeosaurids, such as comparable tooth dimension and equal number of denticles per mm (Roberto Candei, personal communication 2004; Fernando Novas, personal communication 2004). Although Morphotypes 1 and 2 represent clearly distinct animals and differ significantly from *Majungatholus*, the similarities between noa-

Table 2. Results of the quadratic discriminant analysis conducted at the family level. Eight dromaeosaurid teeth were erroneously predicted to be *Masiakasaurus knopfleri* teeth in light of dental parameters, suggesting that teeth pertaining to these taxa are similar.

		Taxon predicted by discriminant analysis			
		<i>M. knopfleri</i>	Dromaeosauridae	Abelisauridae	Tyrannosauridae
Taxon to which teeth pertain	<i>M. knopfleri</i>	10	0	0	0
	Dromaeosauridae	8	51	1	0
	Abelisauridae	0	1	137	0
	Tyrannosauridae	0	0	0	17

Table 3. Agglomeration schedule of the cluster analysis showing the progressive regrouping of the different taxa (clusters).

Stage	Cluster 1	Cluster 2	Coefficients
1	Morphotype 1	<i>Dromaeosaurus albertensis</i>	1.292
2	<i>Saurornitholestes langstoni</i>	<i>Richardoestesia glimorei</i>	1.301
3	<i>Velociraptor mongoliensis</i>	<i>Saurornitholestes langstoni</i>	1.677
4	<i>Masiakasaurus knopfleri</i>	<i>Velociraptor mongoliensis</i>	1.835
5	Morphotype 1	<i>Deinonychus antirrhopus</i>	2.900
6	<i>Majungatholus atopus</i>	<i>Indosuchus raptorius</i>	4.370
7	Morphotype 1	<i>Masiakasaurus knopfleri</i>	5.026
8	<i>Majungatholus atopus</i> (Morphotypes 3, 4, and 5)	<i>Majungatholus atopus</i>	7.410
9	<i>Daspletosaurus torosus</i>	indeterminate tyrannosaurid	7.649
10	<i>Albertosaurus sarcophagus</i>	<i>Daspletosaurus torosus</i>	15.163
11	Morphotype 1	<i>Majungatholus atopus</i> (Morphotypes 3, 4, and 5)	18.090
12	Morphotype 1	<i>Albertosaurus sarcophagus</i>	45.285

saurid and dromaeosaurid teeth do not allow us to rule out undeniably the possibility that Morphotype 1 may pertain to a noosaurid. Unfortunately, the paucity of published descriptions of noosaurid teeth prevents us from testing this hypothesis. All that can be said at the moment is that Morphotype 1 could potentially pertain to a dromaeosaurid. Nevertheless, the discovery of more complete and diagnostic material from the Maevarano Formation is needed to confirm the dromaeosaurids affinity of Morphotype 1 and permit the assignment of a name to this new taxon.

**Paleobiogeographical implications of the possible presence of dromaeosaurids in Madagascar.**—Recent reports of maniraptoran dinosaurs from Gondwana have greatly improved our knowledge of the geographic and temporal distribution of this lineage previously thought to be exclusively Laurasian (Rauhut and Werner 1995; Forster et al. 1996, 1998; Krause et al. 1999; Novas and Agnolin 2004; Makovicky et al. 2005). This study presents the first tentative evidence that dromaeosaurid theropods inhabited north-western Madagascar during the Late Cretaceous. This conclusion supports the previous claims that the Gondwanan distribution of maniraptorans started before the separation of Laurasia and Gondwana during the Late Jurassic (Rauhut and Werner 1995; Makovicky et al. 2005). Knowledge of the complex geographic evolution of Madagascar can be used to temporally constrain the dispersal of maniraptorans onto the island. Madagascar, along with the Indian subcontinent, separated from continental Africa during the Early Cretaceous, around 135 Ma (Marks and Tikku 2001; Tikku et al. 2002; Frey et al. 2003; Mette, 2004; Winberry and Anandkrishnan 2004). Consequently, colonization of south-eastern Africa and Madagascar by possible dromaeosaurids and abelisauroids (the ancestors of the abelisaurid *Majungatholus* and the noosaurid *Masiakasaurus*) had to occur no later than during the Late Jurassic–Early Cretaceous, before Madagascar became totally isolated from Africa. Following the separation of Africa and Madagascar, Malagasy theropods evolved independently from their African relatives into endemic faunal assemblages. The Late Jurassic separation of Gondwana and Laurasia followed by the Early Cretaceous separation of Africa and Madagascar impose significant temporal constraints on the migration of dromaeosaurids into Madagascar. As such, the presence of dromaeosaurids in the latest Cretaceous (Campanian?–Maastrichtian) Maevarano Formation of Madagascar can only be explained through vicariance, the survival of a taxon long after geographic separation from the original “population,” rather than through the late immigration of dromaeosaurids into Madagascar (also see Makovicky et al. 2005; Novas and Pol 2005).

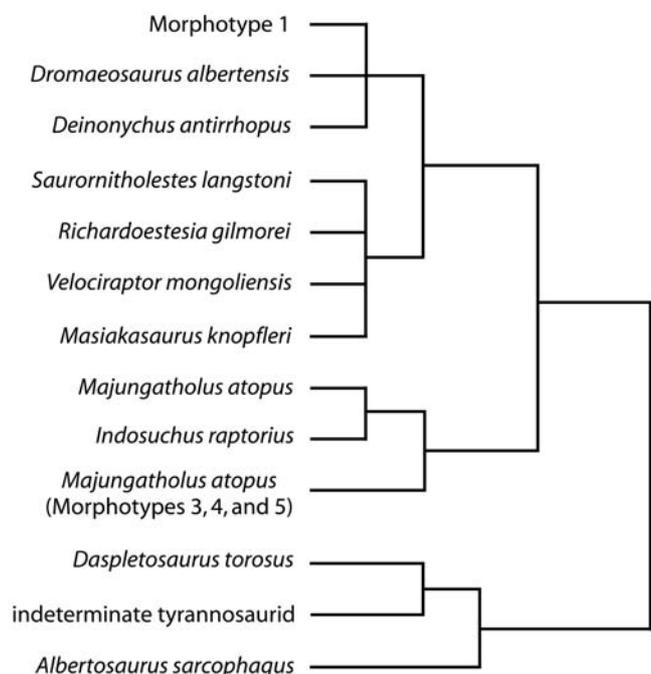


Fig. 11. Dendrogram drawn from the results of the cluster analysis. Statistical level of confidence for a node decreases toward the right (i.e., similarities between taxa increase toward the left). The results of the cluster analysis reveal that Morphotype 1 is very similar to *Dromaeosaurus albertensis* and *Deinonychus antirrhopus* while *Masiakasaurus knopfleri* (including Morphotype 2) is more similar to *Saurornitholestes langstoni*, *Velociraptor mongoliensis*, and *Richardoestesia glimorei*. Morphotypes 1 and 2 are clearly different from *Majungatholus atopus*.

## Conclusion

Isolated theropod teeth from the latest Cretaceous (Campanian?–Maastrichtian) Maevarano Formation of Madagascar can be classified into five distinct morphotypes. Detailed study of the teeth revealed that four of the five morphotypes can be referred to known Maevarano non-avian theropods: three morphotypes belong to *Majungatholus atopus* (Morphotypes 3, 4, and 5) and one morphotype belongs to *Masiakasaurus knopfleri* (Morphotype 2). However, Morphotype 1 is characterized by features that cannot be explained simply in the light of ontogenetic or individual variability among known Maevarano non-avian theropods. Morphometric and statistical analyses suggest that Morphotype 1 pertains to a yet-unknown taxon closely related to dromaeosaurids, although a noasaurid affinity cannot be excluded at this time. These results support earlier theories for a Gondwanan distribution of dromaeosaurids prior to the complete separation of Laurasia and Gondwana and the break-up of southern landmasses. Particularly, ancestors of the Late Cretaceous Malagasy theropods (abelisauroids and dromaeosaurids) must have reached the Indo-Madagascar landmass before its separation from continental Africa around 135 Ma. Following the separation of Africa and Madagascar, theropods evolved in isolation on the island into a highly endemic faunal assemblage. The presence of dromaeosaurids in Madagascar results from the survival of this lineage long after their isolation from mainland rather than from a late immigration event. The results of this research shed new light on the Late Cretaceous theropod diversity of Madagascar and on the evolution and dispersal of maniraptorans in Gondwana.

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