

# DOES THE JURASSIC *AGILODOCODON* (MAMMALIAFORMES, DOCODONTA) HAVE ANY EXUDATIVOROUS DENTAL FEATURES?

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Obligate exudativory, including active wounding of bark to acquire gum and/or sap, is rare among extant mammals and does not show a consistent dental signature. A recently described Middle Jurassic docodont *Agilodocodon* was reconstructed as an exudativore based on proposed similarities of its lower anterior dentition to some extant New World monkeys, specifically marmosets, spider monkeys, and howler monkeys. Oddly enough, of these, only marmosets are exudate-feeders. In our reinvestigation, we did not find any significant resemblance in the lower (and upper) anterior dentition between the Middle Jurassic fossil and these extant New World monkeys. The marmosets, the only obligate platyrrhine exudativores, have lower and upper incisors that are distinguished from *Agilodocodon* and other New World monkeys by having enamel restricted to the labial surface. Differential wear between the enamel and softer dentine maintains a chisel-like tooth that marmosets use in gouging bark. Additional comparisons of the anterior dentition of *Agilodocodon* and other extant mammals were conducted. The lower and upper anterior teeth of *Agilodocodon* were found to be most similar to some elephant shrews and South American marsupials, which have a primarily insectivorous diet. *Agilodocodon* does not show any dental adaptations found in extant mammals for exudativory.

Key words: Docodonta, *Agilodocodon*, marmosets, exudativory, incisors, gums.

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## INTRODUCTION

New discoveries in the Mesozoic record of mammals and their near relatives (Mammaliaformes) reveal ecomorphological specializations that unexpectedly include many niches occupied by extant mammals (Luo 2007). The extinct mammaliaform clade Docodonta is a fitting example. It comprises about 14 genera from the Middle Jurassic to Early Cretaceous of Laurasia (Luo and Martin 2007; Luo *et al.* 2015; Meng *et al.* 2015) and one putative taxon from the Middle Jurassic of India (Prasad and Manhas 2007; Meng *et al.* 2015). Although the taxonomic diversity of Docodonta is low, its ecomorphological diversity is high and includes the beaver-like *Castorocauda* (Ji *et al.* 2006), the desman mole-like *Haldanodon* (Martin 2005, 2006), the golden mole-like *Docofossor* (Luo *et al.* 2015), and the arboreal or scansorial *Agilodocodon* (Meng *et al.* 2015). The last is the subject of this contribution.

In announcing *Agilodocodon scansorius* from the Middle Jurassic of China, Meng *et al.* (2015, p. 764) suggested that it had “dental characters indicative of an omnivorous diet that included plant sap”. Specifically, it was said to have lower incisors similar to those of some extant New World monkeys, which use these teeth “to gnaw into the bark of trees to feed on exudates, such as gum and sap” (Meng *et al.* 2015, p. 765). They argued that the similarity of incisor morphology supported a similar dietary component for *Agilodocodon*, which makes this the oldest evidence for exudativory in mammaliaforms.

Among extant mammals, gum and sap feeders are either facultative (seasonal) or obligate (full-time), with the latter usually inflicting a wound through gouging to initiate exudate flow. It is not fully known how widespread the facultative type is, as appropriate field data are not available for many species; the occurrence of the obligate type is rare but includes members of Primates and Diprotodontia (Nash 1986; Nash and Burrows 2010). The vast majority of extant exudativores, both facultative and obligate, are found within the Order Primates, with at least 69 species having some level of exudativory (Smith 2010) out of a total of 376 species (Wilson and Reeder 2005). Among the New World monkeys, marmosets are the only obligate exudate-feeders whereas the closely related tamarins are facultative, feeding from exudate flows or semi-dried drops that are already present (Smith 2010). However, only the marmosets show any dental specializations for exudativory. Rosenberger (1978) described a loss of lingual enamel on the lower incisors of the marmosets *Callithrix jacchus*, *Cebuella pygmaea*, and *Mico argentatus* (*Callithrix argentata* therein), creating in effect a chisel-like, honed edge to these teeth used in gouging tree bark to open a wound. Additionally, marmosets are characterized as showing the “short-tusked” condition with the lower canine on the same occlusal plane as the lower incisors (Swindler 2002).

Here, we assess the claim by Meng *et al.* (2015) that the lower incisors of *Agilodocodon* resemble those of marmosets, spider monkeys (*Ateles*), and howler monkeys (*Alouatta*), which is an odd claim in that only the marmosets are exudate-feeders. Additionally, we assess the notion put forth by Meng *et al.* (2015) that this resemblance is consistent with those teeth being used by *Agilodocodon* to obtain exudates. We address whether there are other extant mammals not considered by Meng *et al.* (2015) with an anterior lower dentition similar to *Agilodocodon*. Finally, we review whether there are other craniodental features that might distinguish exudate-feeders.

**Institutional abbreviations.** — AMNH, Department of Mammalogy, American Museum of Natural History, New York, New York, USA; CM, Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.

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## MATERIAL

*Agilodocodon* was studied only from the literature (Meng *et al.* 2015 and associated supplementary files). We studied the following New World monkey specimens in the Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, PA. For dental terminology, we follow Hershkovitz (1977).

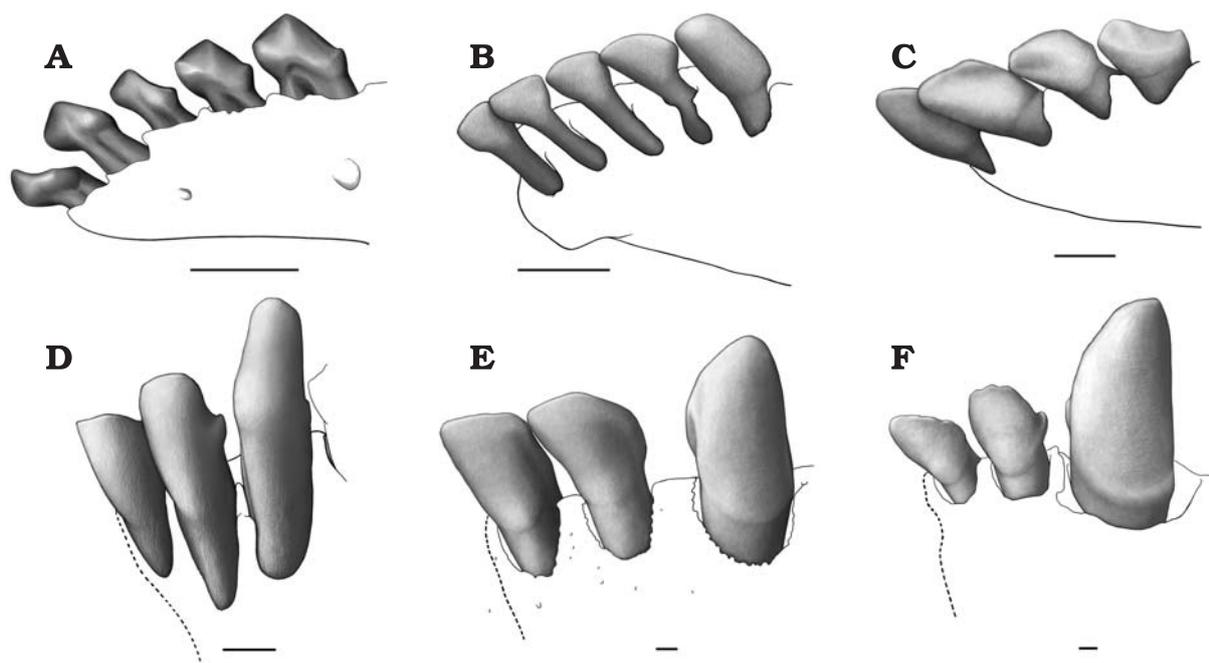


Fig. 1. Left lower anterior dentitions in labial view. **A.** *Agilodocodon* (reproduced with permission from Meng *et al.* 2015, fig. 2H), four incisors and canine. **B.** *Dromiciops australis* AMNH 92147 (male), four incisors and canine. **C.** *Elephantulus edwardii* CM 40801 (male), three incisors and canine. **D.** *Mico argentatus* CM 1964 (male), two incisors and canine. **E.** *Ateles paniscus* CM 68450 (female), two incisors and canine. **F.** *Alouatta seniculus* CM 2719 (female), two incisors and canine. Scale bars 1 mm.

*Callithrix jacchus* (common marmoset): female CM 12174; male CM 1720.

*Mico argentatus* (silvery marmoset): females CM 1964, 5011, 5013, 5016, 12187; males CM 1963, 1965, 1966, 4985, 5012.

*Ateles belzebuth* (white-fronted spider monkey): female CM 1559.

*Ateles fusciceps* (black-headed spider monkey): male CM 17455.

*Ateles geoffroyi* (Geoffroy's spider monkey): female CM 1576; male 1252.

*Ateles paniscus* (red-faced spider monkey): females CM 2772–2775, 68450, 76826; male CM 68451.

*Alouatta caraya* (black howler): female CM 61431; male CM 61430.

*Alouatta guariba* (brown howler): male CM 1719.

*Alouatta seniculus* (Venezuelan red howler): females CM 2712, 2719; males CM 2722, 68447, 68448.

## DESCRIPTIONS

Although Meng *et al.* (2015) reported that it is the lower anterior dentition (incisors and canines) of *Agilodocodon* that shows exudativorous adaptations, our descriptions are not limited to these teeth but include the upper anterior dentition as well.

**Anterior dentition of *Agilodocodon*.** — *Agilodocodon* has a dental formula in the upper and lower jaws of four incisors, one canine, six premolars, and four molars. Meng *et al.* (2015, supplementary materials, pp. 16–17) (Figs 1A, 2A, 3A) described the incisors as spatulate and spade-shaped with crowns that are bucco-lingually compressed and mesiodistally broad. They also described the crowns as being curved with a convex buccal surface and a concave lingual surface ornamented with a low median ridge and a lingual cingulid at the crown base. Most of the eight left and right lower incisors have incipiently divided roots or divided roots. The canine is also spade-shaped and has an incipiently divided root. Overall, the canine is similar to the incisors and is small.

Based on their illustrations (Meng *et al.* 2015, fig. 2A, G, H), we also note that the roots of the upper and lower anterior teeth are not uniform in girth but taper to their narrowest at the crown-root junction (Figs 1A, 2A, 3A). The four lower incisors and the lower canine show decreasing procumbency from anterior to pos-

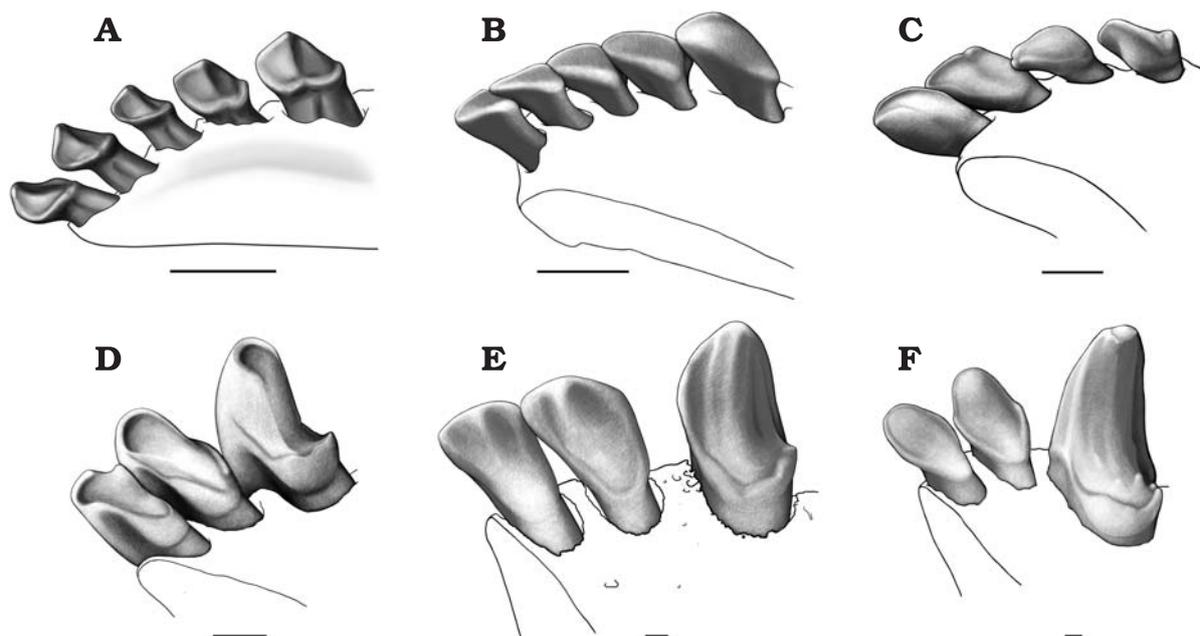


Fig. 2. Left lower anterior dentitions in lingual view. **A.** *Agilodocodon* (reproduced with permission from Meng *et al.* 2015, fig. 2G), four incisors and canine. **B.** *Dromiciops gliroides* AMNH 92147 (male), four incisors and canine. **C.** *Elephantulus edwardii* CM 40801 (male), three incisors and canine. **D.** *Mico argentatus* CM 1964 (male), two incisors and canine. **E.** *Ateles paniscus* CM 68450 (female), two incisors and canine. **F.** *Alouatta seniculus* CM 2719 (female), two incisors and canine. Scale bars 1 mm.

terior (Figs 1A, 2A). In contrast, the upper canine is vertical and the upper incisors have their tips directed posteriorly (Fig. 3A). The upper and lower anterior teeth are separated by small interdental spaces and none of the crowns come into contact (Figs 1A, 2A, 3A). The crowns of the lower anterior teeth are much broader than they are tall (Figs 1A, 2A). The first three lower incisors are triangular in shape and come to a blunt point at their apex. The upper incisors and canine have crowns as tall as wide and come to a blunt point except for the first, which is rounded (Fig. 3A).

Given that the mandible of *Agilodocodon* accommodates 15 teeth, it is long and low (Fig. 4A). It is of relatively uniform height under the postcanine teeth but shallowest under the anterior teeth, extremely so under the first incisor. What appears to be the surface of the symphysis is indicated by a shelf in Meng *et al.* (2015, fig. S3); it ends under the second premolar. In light of the long, low jaw, the symphysis must be narrow and horizontal. The preserved mandible is straight, which reconstructs as a V-shaped lower jaw (Fig. 4A).

**Anterior dentition of marmosets.** — We examined males and females of species from two of the three genera of marmosets (Garbino 2015): the common marmoset *Callithrix jacchus* and the silvery marmoset *Mico argentatus*. We found the anterior dentition (incisors and canine) to be relatively uniform across these two forms. The dental formula in the upper and lower jaws has two incisors, a canine, three premolars, and two molars.

The mandible is U-shaped and the two lower incisors are set anteroposteriorly in the bottom of the U (Fig. 4D). The second lower incisor is offset slightly posterior to the first and its root is set slightly obliquely compared to the sagittal placement of the first. The incisors are similar in their morphology, but the second is taller and anteroposteriorly broader than the first (Figs 1D, 2D). The lower incisors are tall, mediolaterally compressed with the anteroposterior dimension roughly twice the mediolateral, and only slightly procumbent with the first more so than the second. In labial view (Fig. 1D), the surface of the crown is strongly convex, much taller than wide, and only slightly wider than the root. Its apex is relatively flat. In lingual view (Fig. 2D), the apex of the tooth at the labial margin has a thick band of enamel with a very broad wear facet behind it in dentine that slopes posteroventrally and is relatively flat. This facet is flanked by mesial and distal ridges and ends posteriorly at a lingual cingulid. The medial and lateral faces of each incisor has a slight prominence (mesio- and distostylid), the latter being stronger; this is nearer the apex in the first incisor and halfway down the crown of the second. The incisors are tightly packed with little or no space between their crowns.

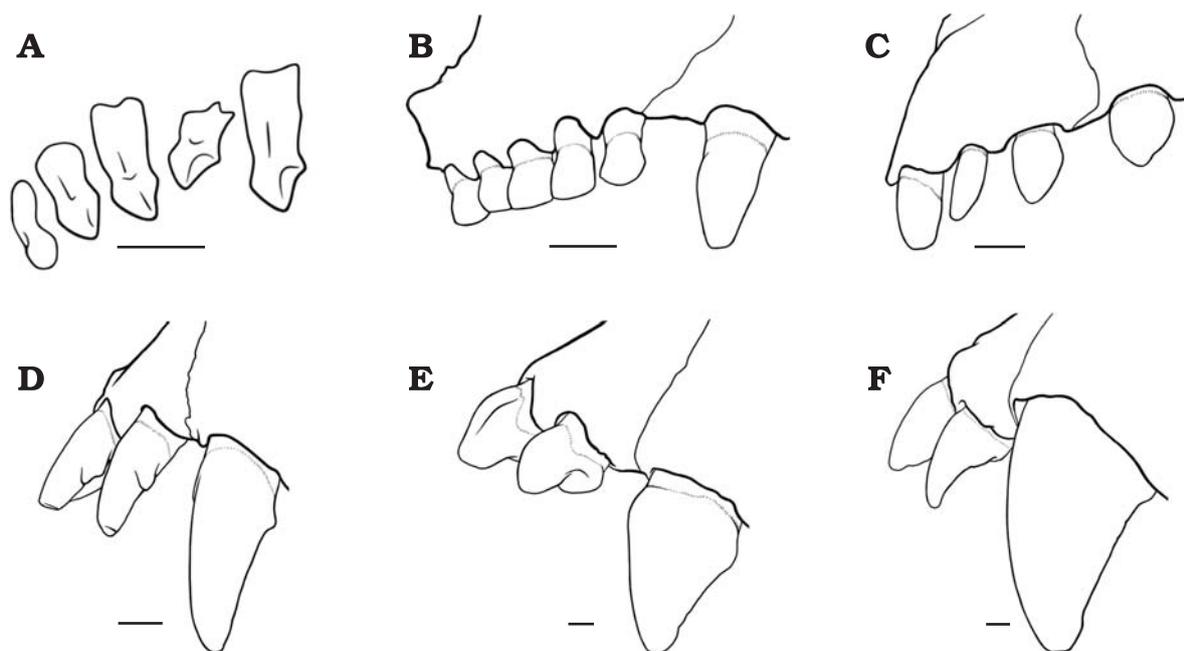


Fig. 3. Left upper anterior dentitions in lateral view. **A.** *Agilodocodon* (reproduced with permission from Meng *et al.* 2015, fig. 2A), four incisors and canine. **B.** *Dromiciops gliroides* AMNH 92147 (male), five incisors and canine. **C.** *Elephantulus edwardii* CM 40801 (male), three incisors and canine. **D.** *Mico argentatus* CM 1964 (male), two incisors and canine. **E.** *Ateles paniscus* CM 68450 (female), two incisors and canine. **F.** *Alouatta seniculus* CM 2719 (female), two incisors and canine. Scale bars 1 mm.

The absence of enamel on the lingual incisor face was reported by Rosenberger (1978) in these same two taxa studied here plus *Cebuella pygmaea*, the pygmy marmoset. “Differential wear of the softer dentine lingually serves to maintain a chisel-like edge to these teeth”, which is used in gouging tree bark (Rosenberger 1978, p. 208). Subsequently, Gantt (1980, p. 209) showed that *Cebuella* has “a covering of enamel a few micra thick which is rapidly worn away and is absent in adult animals”. Juveniles that could confirm this were not in our marmoset sample.

The lower canine is caniniform, taller and broader than the incisors with a sharper apex (Figs 1D, 2D). It is set posterolateral to the second incisor and separated from that tooth by only a narrow gap (Fig. 4D). As with the incisors, the canine is mediolaterally compressed. The surfaces of the crown are convex except for that facing the second incisor, which is flat. A distinct cingulid is present wrapping from the medial surface across the posterior surface onto the posterior one-third of the lateral surface (Fig. 2D). As with the incisors, the apex of the canine at the labial margin has a thick band of enamel with the surface posterior to it exposing dentine.

The mandible has a thick, fused symphysis that is obliquely oriented and extends to the level of the second premolar (Fig. 4D).

The two upper incisors are procumbent, subequal, and set anteroposteriorly, with the first more procumbent than the second (Fig. 3D). The first incisor is roughly mitten-shaped with the distostyle representing the “thumb”; however, the crown apex is flat and contacts the first incisor of the opposite side producing an expanded chisel-like surface. The second incisor is separated from the first by a narrow gap, has a mesio- and distostyle, and ends in a blunt point. Both the labial and lingual surfaces of the two incisors are convex. Additionally, the two incisors show the same restricted enamel reported by Rosenberger (1978) for the lowers.

The canine is a large caniniform tooth, projecting ventral to the incisors and separated from the second by a gap. The canine has a mesio- and distostyle, but these are not as well developed as on the second incisor.

**Anterior dentition of spider monkeys.** — We examined representatives of four of the seven species of *Ateles* (Groves 2005): *A. belzebuth*, *A. fusciceps*, *A. geoffroyi*, and *A. paniscus*. The anterior dentition was relatively uniform except for the moderate sexual dimorphism in canine size (Plavcan 2001). The dental formula in the upper and lower jaws has two incisors, a canine, three premolars, and three molars.

The shape of the mandible and position of the lower anterior dentition in the spider monkeys is reminiscent of that in the marmosets (Fig. 4E). The two lower incisors are similar to each other in their morphology, but the second is slightly larger in both mediolateral and anteroposterior dimensions (Figs 1E, 2E). The roots

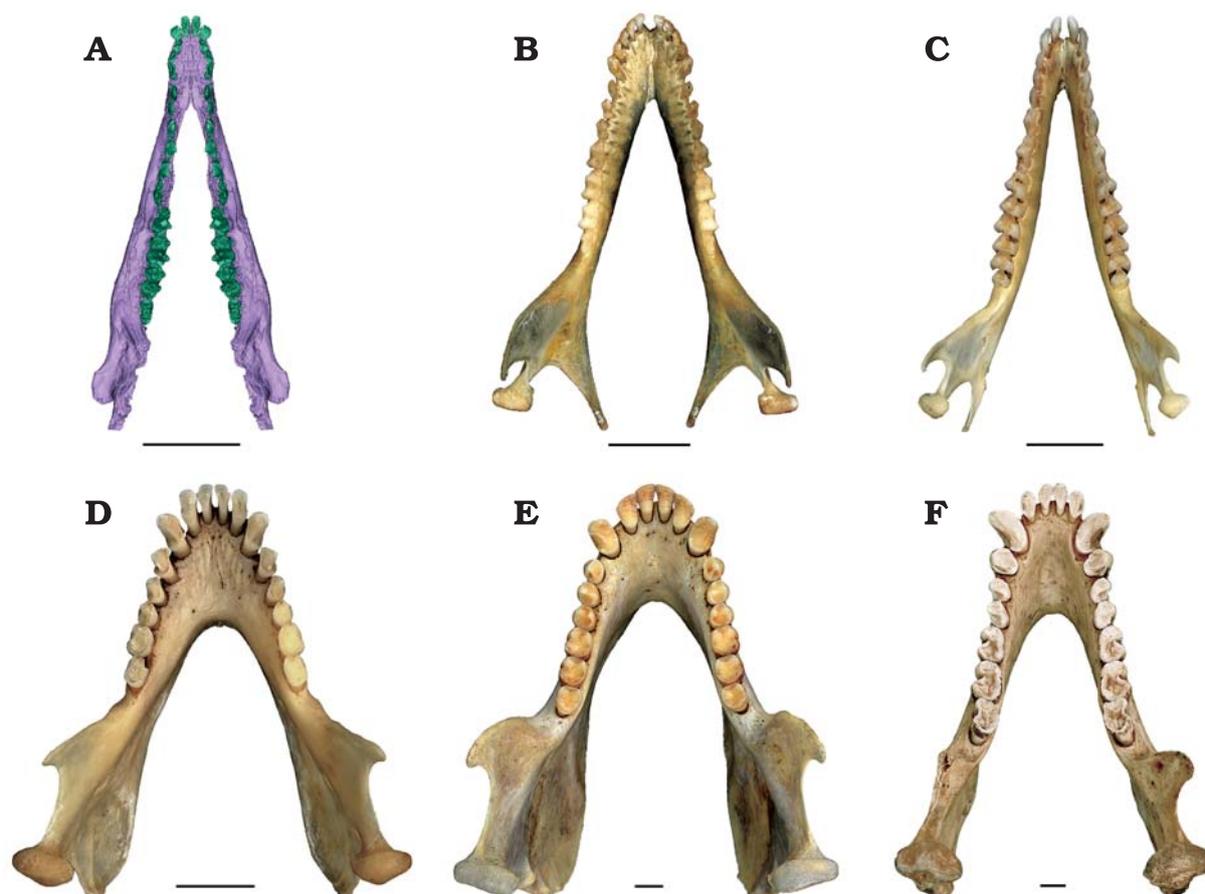


Fig. 4. Mandibles in occlusal view. **A.** *Agilodocodon* (modified from Meng *et al.* 2015, fig. S3B). **B.** *Dromiciops gliroides* CM 40621 (female). **C.** *Elephantulus edwardii* CM 40801 (male). **D.** *Mico argentatus* CM 1964 (male). **E.** *Ateles paniscus* CM 68450 (female). **F.** *Alouatta seniculus* CM 2719 (female). Scale bars 5 mm.

are mediolaterally compressed and of uniform girth. The base of the crown is of comparable girth to the root. The crown is triangular, taller than wide, with the widest part of the triangle at the crown apex. The apices of the two incisors are relatively flat, of similar height, and in contact. The greatest mediolateral and antero-posterior dimensions are subequal for each incisor. The labial surface of the crown is convex and vertical, whereas the lingual surface slopes posteroventrally and is relatively flat. The enamel is uniform.

The lower canine is caniniform, taller than the incisors with a sharper apex. The canine is mediolaterally compressed and separated from the second incisor by a small gap. The labial surface of the crown is convex; the lingual surface is relatively flat with a distinct cingulid.

The mandible has a thick, fused symphysis that is more vertical than that of the marmosets but also extends to the level between the first and second premolar (Fig. 4E).

In the uppers (Fig. 3E), the incisors are set anteroposteriorly with the first larger and more procumbent than the second. The first incisor has a flat apex and contacts the tooth of the opposite side at the midline. The second incisor is separated from the first by a narrow gap and its apex is more rounded. Both incisors are convex labially and have an extensive lingual heel; on the second this is a raised cingulum, but not on the first. Swindler (2002) reported the opposite distribution of the lingual cingulum in his sample. The canine is a stout caniniform tooth that projects well beyond the occlusal plane. It is separated from the second incisor by a wide gap. The enamel is uniform in the upper anterior teeth.

**Anterior dentition of howler monkeys.** — We examined representatives of three of the ten species of *Alouatta* (see Groves 2005): *A. caraya*, *A. guariba*, and *A. seniculus*. The anterior dentition was relatively uniform except for the strong sexual dimorphism in canine size (Plavcan 2001), lacking in the exudativorous marmosets. The dental formula in the upper and lower jaws has two incisors, a canine, three premolars, and three molars.

The shape of the mandible and position of the lower anterior dentition in the howler monkeys is reminis-

cent of that in the marmosets and spider monkeys (Fig. 4F). The shape of the two lower incisors is similar to each other, but the second is larger and taller than the first (Figs 1F, 2F). The roots are mediolaterally compressed and of uniform girth, with the base of the crown of comparable girth as the root. The crowns are taller than wide and roughly mitten-shaped in both labial and lingual views with the “thumb” eminence positioned laterally. In lingual view, the “thumb” eminence is a distostylid; a weaker mesiostylid is present on the second incisor. The incisors are much longer anteroposteriorly than they are mediolaterally wide. The labial surfaces are convex. The first incisor is slightly procumbent and has a narrow contact across the midline. The second incisor is more vertical and separated from its medial and lateral neighbors by narrow spaces. In lingual view (Fig. 2F), both incisors have a relatively flat surface that slopes posteroventrally from the apex, with the slope lower on the first incisor than the second. The second has a distinct ridge on the lateral margin, posterior to the distostylid. The enamel is uniform.

The lower canine is caniniform, much larger and taller than the incisors with a very sharp apex. The canine is subcircular in outline and has distinct medial and lateral ridges that delimit labial and lingual surfaces. The labial surface is strongly convex, whereas the lingual is mildly convex with a distinct cingulid.

The mandible has a thick, fused symphysis resembling that in the spider monkeys, but it extends to the level between the second and third premolar (Fig. 4F).

In the uppers (Fig. 3F), the anterior teeth are reminiscent of those in the spider monkeys with the following differences: both incisors come to a blunt point and have a lingual cingulum, and the canine is a more substantial caniniform tooth.

## COMPARISONS

As noted above, Meng *et al.* (2015) made two claims for *Agilodocodon*: (1) that its lower anterior dentition resembles that of marmosets, spider monkeys, and howler monkeys; and (2) the resemblances are of a sort occurring in exudativores. We address each of these claims separately below and also whether there are other extant mammals with a lower anterior dentition more similar to *Agilodocodon* and whether there are craniodental features of exudativores beyond those of the lower anterior dentition.

**Does the lower anterior dentition of *Agilodocodon* resemble that of marmosets, spider monkeys, and howler monkeys?** — The New World monkeys studied here have lower incisors built on a similar bauplan (Figs 1D–F, 2D–F) that includes mediolateral compression, crowns taller than wide, and relatively flat posteroventrally sloping lingual faces; differences concern overall shape, relative sizes, interdental spacing, and procumbency, and in the case of the marmosets the presence of enamel restricted to the labial surface and roots that are comparable in girth to the crowns. However, there is little similarity between the New World monkey bauplan and *Agilodocodon*. In *Agilodocodon* (Figs 1A, 2A), the incisors are labio-lingually compressed, the crowns are much wider than tall, and the lingual faces are concave with a median ridge. Additionally, the shape of the incisors in *Agilodococon* changes considerably through the series: cup-shaped at the front and quadrangular at the rear. The first and third show a strongly concave distal margin, whereas the second and fourth are straight. Finally, *Agilodocodon* has incisors with uniformly strong lingual cingulids; in the New World monkeys this is either weak or entirely absent.

The New World monkey lower canines do not show a uniform morphology, but all are caniniform (Figs 1D–F, 2D–F). In contrast, the canine in *Agilodocodon* repeats the morphology of the most proximate incisor and the difference is one of the slightly greater size of the canine (Figs 1A, 2A).

The arrangement of the anterior dentition in the mandible is also quite different between the New World monkeys and *Agilodocodon*. In the former (Fig. 4D–F), the mandible is U-shaped, with the incisors and canine closely packed at the bottom of the U; the shape and position of the incisors in the marmosets and spider monkeys, in particular, creates an effective cutting edge. Additionally, the mandibular symphysis is fused and thick. In *Agilodocodon* (Fig. 4A), the mandible is V-shaped with the incisors and canines separated by interdental spaces, which reduces the cutting edge available for gouging seen in the marmosets. The symphysis of *Agilodocodon* is thin and mobile.

The upper anterior dentition in the New World monkeys is also built on a similar bauplan (Fig. 3D–F), with the incisors procumbent (the mesial more so than the distal) and the canine caniniform and larger than

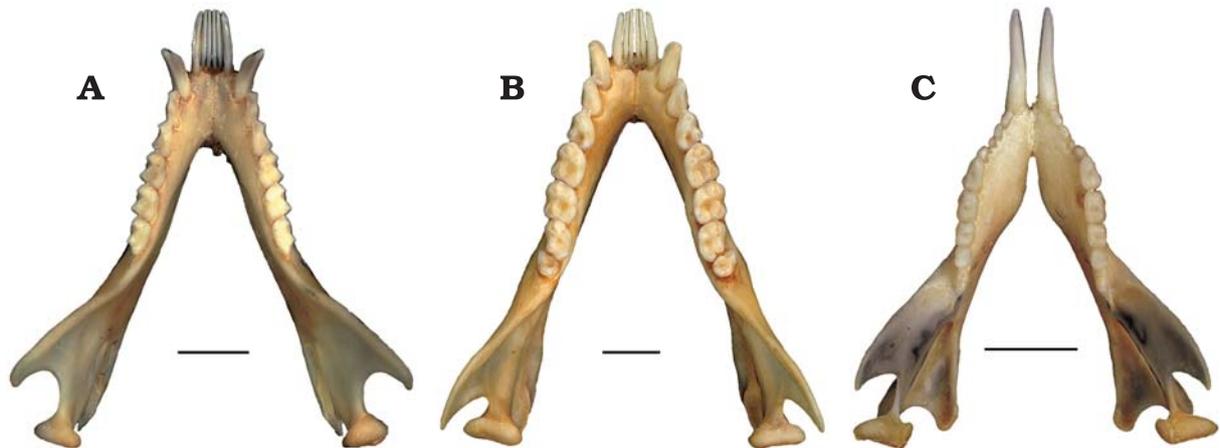


Fig. 5. Mandibles in occlusal view. **A.** *Euoticus elegantulus* CM 41122 (male). **B.** *Nycticebus coucang* CM 59519. **C.** *Petaurus breviceps* CM 116682 (male). Note in B, the small supernumerary tooth at the rear of the tooth row. Scale bars 5 mm.

the incisors. The marmosets differ in that their incisors have restricted enamel, the mesial incisors meet on the midline to form an effective cutting edge, and the size disparity between the incisors and canine is reduced. In contrast, in *Agilodocodon* (Fig. 3A), the incisors and canine are similar in morphology and size, are pointed (except the first incisor), are oriented posteriorly rather than procumbent, and separated by interdental spaces; this arrangement does not produce a cutting edge for gouging.

In light of the profound differences, we conclude that the anterior dentition of *Agilodocodon*, both lower and upper, has no resemblance to the anterior dentition of marmosets, spider monkeys, and howler monkeys.

**Are there features of the lower anterior dentition of *Agilodocodon* expected in obligate exudativores?** — Among New World monkeys, marmosets are the only obligate exudativores (Smith 2010). It has long been suggested that their ability to wound bark to procure exudates is a function of the restricted enamel on their lower incisors, which results in a chisel-like tooth (Rosenberger 1978; Swindler 2002). Restricted enamel is one dental characteristic that distinguishes marmosets from closely related tamarins (Rosenberger 1978), which are facultative exudativores, as well as other New World monkeys including spider monkeys and howler monkeys, which are not known to feed on exudates but are instead intensively frugivorous and folivorous, respectively (DiFiore *et al.* 2010). If restricted enamel on tightly packed incisors is indeed a mark of exudativory in marmosets, then *Agilodocodon* is not an exudativore of the marmoset type.

Other features of the lower anterior dentition of marmosets have been implicated in their ability to gouge trees. In a comparison between *Callithrix jacchus* and various species of the facultative exudativore *Saguinus*, the former has incisor features accommodating increased stresses linked to dissipating gouging forces, including root surface areas larger relative to symphyseal volume, labiolingually thicker crowns, and enamel with greater decussation (Hogg *et al.* 2011).

Of course, there are other obligate exudativores that have different morphological features of their lower anterior dentition. Beyond marmosets, the best known obligate exudate-feeders among Primates are certain strepsirhines, including the needle-clawed bushbaby *Euoticus elegantulus*, the greater bushbaby *Otolemur crassicaudatus*, and the slow loris *Nycticebus coucang*, all of which include exudates as at least 75% of their diet year round (Smith 2010; Starr and Nekaris 2013). The anterior lower dentition in these forms includes a procumbent toothcomb (Fig. 5A, B) composed of four incisors and two canines (Swindler 2002). *Euoticus elegantulus* and *O. crassicaudatus* do not gouge to acquire exudates. Instead, they scrape, twist, or flick away at semi-dried exudate drops or scoop flowing exudates with their anterior dentition (Charles-Dominique 1977; Nash 1986). In contrast, *N. coucang* is an active gouger (Wiens *et al.* 2006; Starr and Nekaris 2013). Although both *E. elegantulus* and *O. crassicaudatus* may use their toothcombs as scraping devices, they are characterized by robust posterior dentition (upper canines and upper and lower premolars) that may be more intensively used in exudate-feeding than the gracile and delicate teeth of the toothcomb, cracking away at dried exudate drops to re-stimulate flow (Burrows and Nash 2010). The toothcomb of the slow loris *N. coucang* (Fig. 5B) is short, robust, and well designed to resist increased forces that may be generated during gouging activities (Burrows *et al.* 2015).

Beyond Primates, the best known obligate exudativores are several petaurid marsupials, the sugar glider *Petaurus breviceps* (Smith 1982; Howard 1989), the yellow-bellied glider *Petaurus australis* (Goldingay 1987), and Leadbeater's possum *Gymnobelideus leadbeateri* (Smith 1984). As diprotodonts, these forms have a pair of curved, elongated, procumbent lower incisors (Fig. 5C), which are used to incise bark to acquire exudates (Smith 1982, 1984; Goldingay 1987; Howard 1989).

While there seems to be little in the way of a definitive dental signature for exudativory in the lower anterior dentition of extant mammals, *Agilodocodon* possesses none of the morphological characters seen in the dentition of extant exudate-feeders such as tightly packed incisors with reduced lingual enamel, curved, elongated lower incisors, or a short, robust toothcomb.

**Does the anterior lower dentition of *Agilodocodon* resemble that of any other extant mammals? —**

Not many extant mammals have a lower anterior dentition resembling that of *Agilodocodon*, with lower incisors that are labio-lingually compressed and an incisiform canine (Thenius 1989; Hillson 2005). One South American marsupial in particular, the monito del monte *Dromiciops gliroides* (for illustrations of the entire dentition see Reig *et al.* 1987, fig. 6), shows some remarkable similarities to *Agilodocodon*. Its four lower incisors (Figs 1B, 2B, 4B) are generally similarly shaped to those of *Agilodocodon*, show decreasing procumbency posteriorly, are labio-lingually compressed with the crown much broader than the root, and lingual cingulid developed, and the canine is similar to the last incisor but is larger. The upper anterior teeth of *Dromiciops* (Fig. 3B) also have some similarity in shape and orientation to those of *Agilodocodon* (Fig. 3A). The principal differences in both the upper and lower anterior teeth are that *Dromiciops* lacks interdental spaces (except for the upper canine) and the teeth form more of a cutting edge. According to Nowak (1991), *Dromiciops* has a natural diet consisting mainly of insects and other invertebrates. Many didelphid marsupials also have lower incisors (see Reig *et al.* 1987; Voss and Jansa 2009) that are reminiscent of *Agilodocodon*, such as the brown four-eyed opossum *Metachirus nudicaudatus*, which include a similar degree of decreasing procumbency, a pointed crown, and a low median ridge on the lingual surface (Fig. 6). The principal difference is the presence in *Metachirus* of a larger caniniform canine. *Metachirus* has a “diet that includes fruits, insects, mollusks, amphibians, reptiles, birds, eggs, and small mammals” (Nowak 1991, p. 19).

A placental group with resemblances to *Agilodocodon* in the anterior dentition is Macroscelidea (Thenius 1989; Hillson 2005), such as the Cape elephant shrew *Elephantulus edwardii*. Its three lower incisors (Figs 1C, 2C, 4C) are similar in shape to those of *Agilodocodon*, show decreasing procumbency posteriorly, are labio-lingually compressed with crowns that are much broader than the root, and its canine repeats the pattern of the last incisor. The principal difference is the lack of interdental spaces in *Elephantulus*. The upper anterior teeth of *E. edwardii* (Fig. 3C) are even more remarkable in their similarity to *Agilodocodon*; the upper incisors and canine are similarly shaped, oriented, and positioned with regard to one another with interdental spaces. The natural diet of *Elephantulus* is insects, especially ants and termites (Nowak 1991).

**Are there other craniodental features expected in obligate exudativores occurring in *Agilodocodon*? —**

Extant marmosets are known to gouge in part by producing a relatively wide jaw gape (Eng *et al.* 2009; Hogg *et al.* 2011). Mandibular features seen in these extant gougers include a short coronoid process and a low mandibular condyle (Vinyard *et al.* 2003; Forsythe and Ford 2011). *Agilodocodon* bears no evidence of either of these traits compared to the closely related docodont *Haldanodon*, which is reconstructed as an insect-feeder by Martin and Nowotny (2000). In fact, the condyle is positioned well above the occlusal surface in *Agilodocodon* (Meng *et al.* 2015, fig. 2E) but is even with it in *Haldanodon* (Martin and Nowotny 2000, figs 14.4, 14.5).

In Primates, molar differences have been noted between obligate exudativores and other

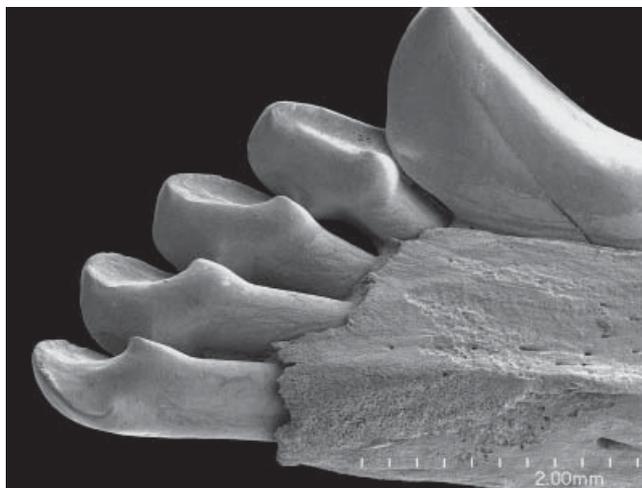


Fig. 6. *Metachirus nudicaudatus* AMNH 266452 (reproduced with permission from Voss and Jansa 2009, fig. 9), lingual view of lower incisors.

forms. In New World monkeys, taxa that consume large amounts of fibrous foods or chitinous insects have molars with well-developed shearing crests, whereas those feeding on tree gum or less fibrous foods have flatter molars with more rounded cusps (Kay *et al.* 2002). A shearing quotient developed to quantify these differences separates exudativorous marmosets from folivores (*e.g.*, *Alouatta*) and insectivores (*e.g.*, *Saimiri*) but not from frugivores (*e.g.*, *Ateles*) (Kay *et al.* 2002). In strepsirhines, exudate-specialist galagos have relatively smaller lower molars than non-specialists, possibly indicating less use of molars in processing sap and gum (Burrows and Nash 2010; Burrows *et al.* 2015). Docodonts as a group are defined in part on the unique morphology of their molars, possessing high shearing crests that would be useful in crushing functions (Averianov 2004; Kielan-Jawaworska *et al.* 2004) with diverse dietary adaptations, from insectivory to omnivory and even carnivory (Luo and Martin 2007). Meng *et al.* (2015, p. 765) described the upper molars in *Agilodocodon* as having crest patterns “analogous to those of galagid and some lorised primates that have a mixed diet of insects, other small animals, fruits, tree gums, and sap”. The images they provided of the *Agilodocodon* upper molars with relatively high crests (Meng *et al.* 2015, fig. 2A, C) are not particularly reminiscent of the more rounded cusps found in the exudate-specialists *Otolemur crassicaudatus*, *Euoticus elegantulus*, and *Nycticebus coucang* (Swindler 2002). Consequently, there is no evidence in the molars to support an obligate exudativorous lifestyle in *Agilodocodon* as seen in marmosets or any obligate exudate-feeding strepsirhine.

## CONCLUSIONS

We reviewed the claims by Meng *et al.* (2015) that the anterior lower dentition of the Middle Jurassic docodont *Agilodocodon* resembles that of some extant New World monkeys and that the resemblance is indicative of an exudativorous component in its diet. We found no particular resemblance in the lower anterior dentition of *Agilodocodon* on the one hand and marmosets, spider monkeys, and howler monkeys on the other. Moreover, the marmosets, the only obligate exudativores in the New World monkey sample, are distinguished by having lower (and upper) incisors with enamel restricted labially, lower incisors with root girth comparable to crown girth, and a “short-tusked” canine. Differential wear between the enamel and softer dentine on the tightly packed incisors maintains a chisel-like cutting edge and the broad incisor root dissipates stress produced in tree gouging. *Agilodocodon* does not share these features. Comparisons with other exudate- and nonexudate-feeding mammals reveal that the lower (and upper) anterior dentition of *Agilodocodon* has more similarities with some South American marsupials and placental elephant shrews, both of which have primarily insectivorous diets. Ultimately, we are unsure what *Agilodocodon* ate, but it was not an obligate exudativore of a type found among extant mammals.

## REFERENCES

- Averianov, A.O. 2004. Interpretation of the Early Cretaceous mammal *Peraiocynodon* (Docodonta) and taxonomy of some British Mesozoic docodonts. *Russian Journal of Theriology* **3**, 1–4.
- Burrows, A.M. and Nash, L.T. 2010. Searching for dental signals of exudativory in galagos. In: A.M. Burrows and L.T. Nash (eds.) *The Evolution of Exudativory in Primates*, 211–233. Springer, New York.
- Burrows, A.M., Hartstone-Rose, A., and Nash, L.T. 2015. Lorid exudativory—it’s the toothcomb that counts. *American Journal of Physical Anthropology* **158**, 663–672.
- Charles-Dominique, P. 1977. *Ecology and Behaviour of Nocturnal Primates: Prosimians of Equatorial West Africa*. 277 pp. Columbia University Press, New York.
- Di Fiore, A., Link, A., and Campbell, C.J. 2010. The atelines: behavioral and socioecological diversity in a New World radiation. In: C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger, and S.K. Bader (eds), *Primates in Perspective, Second Edition*, 155–188. Oxford University Press, Oxford.
- Eng, C.M., Ward, S.R., Vinyard, C.J., and Taylor, A.B. 2009. The morphology of the masticatory apparatus facilitates muscle force production at wide jaw gapes in tree-gouging common marmosets (*Callithrix jacchus*). *Journal of Experimental Biology* **212**, 4040–4055.
- Forsythe, E.C. and Ford, S.M. 2011. Craniofacial adaptations to tree-gouging among marmosets. *Anatomical Record* **294**, 2131–2139.

- Gantt, D.G. 1980. Implications of enamel prism patterns for the origin of the New World monkeys. In: R.L. Ciochon and A.B. Chiarelli (eds), *Evolutionary Biology of the New World Monkeys and Continental Drift*, 201–217. Plenum Press, New York.
- Garbino, G.S.T. 2015. How many marmoset (Primates: Cebidae: Callithricinae) genera are there? A phylogenetic analysis based on multiple morphological systems. *Cladistics* **31**, 652–678.
- Goldingay, R.L. 1987. Sap feeding by the marsupial *Petaurus australis*: an enigmatic behavior? *Oecologia* **73**, 154–158.
- Groves, C.P. 2005. Order Primates. In: D.E. Wilson and D.M. Reeder (eds.) *Mammal Species of the World: A Taxonomic and Geographic Reference, Vol. 1, Third Edition*, 111–184. The Johns Hopkins University Press, Baltimore.
- Hershkovitz, P. 1977. *Living New World Monkeys (Platyrrhini)*. The University of Chicago Press, Chicago.
- Hillson, S. 2005. *Teeth, Second Edition*. 388 pp. Cambridge University Press, Cambridge.
- Hogg, R., Ravosa, M.J., Ryan, T.M. and Vinyard, C.J. 2011. The functional morphology of the anterior masticatory apparatus in tree-gouging marmosets (Cebidae, Primates). *Journal of Morphology* **272**, 833–849.
- Howard, J. 1989. Diet of *Petaurus breviceps* (Marsupialia: Petauridae) in a mosaic of coastal woodland and heath. *Australian Mammalogy* **12**, 15–21.
- Ji, Q., Luo, Z.-X., Yuan, C.-X., and Tabrum, A.R. 2006. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. *Science* **311**, 1123–1127.
- Kay, R.F., Williams, B.A., and Anaya, F. 2002. The adaptations of *Branisella boliviana*, the earliest South American monkey. In: J.M. Plavcan, C. van Schaik, R.F. Kay, and W.L. Jungers (eds.) *Reconstructing Behavior in the Primate Fossil Record*, 339–370. Kluwer Academic/Plenum Publishers, New York.
- Luo, Z.-X. 2007. Transformation and diversification in early mammal evolution. *Nature* **450**, 1011–1019.
- Luo, Z.-X. and Martin, T. 2007. Analysis of molar structure and phylogeny of docodont genera. In: K.C. Beard and Z.-X. Luo (eds), *Mammalian Paleontology on a Global Stage: Papers in Honor of Mary R. Dawson. Bulletin of Carnegie Museum of Natural History* **39**, 27–47.
- Luo, Z.-X., Meng, Q.-J., Ji, Q., Liu, D., Zhang, Y.-G., and Neander, A.I. 2015. Evolutionary development in basal mammaliaforms as revealed by a docodontan. *Science* **347**, 760–764.
- Martin, T. 2005. Postcranial anatomy of *Haldanodon expectatus* (Mammalia, Docodonta) from the Late Jurassic (Kimmeridgian) of Portugal and its bearing for mammalian evolution. *Zoological Journal of the Linnean Society* **145**, 219–248.
- Martin, T. 2006. Paleontology: early mammalian evolutionary experiments. *Science* **311**, 1109–1110.
- Martin, T. and Nowotny, M. 2000. The docodont *Haldanodon* from the Guimarota mine. In: T. Martin and B. Krebs (eds), *Guimarota: A Jurassic Ecosystem*, 91–96. Verlag Dr. Frierich Pfeil, Munich.
- Meng, Q.-J., Ji, Q., Zhang, Y.-G., Liu, D., Grossnickle, D.M., and Luo, Z.-X. 2015. An arboreal docodont from the Jurassic and mammaliaform ecological diversification. *Science* **347**, 764–768.
- Nash, L.T. 1986. Dietary, behavioral, and morphological aspects of gummivory in primates. *Yearbook of Physical Anthropology* **29**, 113–137.
- Nash, L.T. and Burrows, A.M. 2010. Introduction: advances and remaining sticky issues in the understanding of exudativory in primates. In: A.M. Burrows and L.T. Nash (eds), *The Evolution of Exudativory in Primates*, 1–23. Springer, New York.
- Nowak, R.M. 1991. *Walker's Mammals of the World, Fifth Edition, Vol. 1*. 642 pp. The Johns Hopkins University Press, Baltimore.
- Plavcan, J.M. 2001. Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology* **44**, 25–53.
- Prasad, G.V.R. and Manhas, B.K. 2007. A new docodont mammal from the Jurassic Kota Formation of India. *Palaeontologia Electronica* **10** (2), 1–11.
- Reig, O.A., Kirsch, J.A.W., and Marshall, L.G. 1987. Systematic relationships of the living and Neocenozoic American “opossum-like” marsupials (suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. In: M.A. Archer (ed.), *Possums and Opossums: Studies in Evolution, Vol. 1*, 1–89. Surrey Beatty & Sons Pty Limited, Chipping Norton, New South Wales.
- Rosenberger, A.L. 1978. Loss of incisor enamel in marmosets. *Journal of Mammalogy* **59**, 207–208.
- Smith, A.C. 2010. Influences on gum feeding in primates. In: A.M. Burrows and L.T. Nash (eds), *The Evolution of Exudativory in Primates*, 109–121. Springer, New York.
- Smith, A.P. 1982. Diet and feeding strategies of the marsupial sugar glider in temperate Australia. *Journal of Animal Ecology* **51**, 149–166.
- Smith, A.P. 1984. Diet of Leadbeaters possum, *Gymnobelideus leadbeateri* (Marsupialia). *Wildlife Research* **11**, 265–273.
- Starr, C., and Nekaris, K.A.I. 2013. Obligate exudativory characterizes the diet of the pygmy slow loris *Nycticebus pygmaeus*. *American Journal of Primatology* **75** (10), 1054–1061.
- Swindler, D.R. 2002. *Primate Dentition: An Introduction to the Teeth of Nonhuman Primates*. 296 pp. Cambridge University Press, Cambridge.
- Thenius, E. 1989. Zähne und Gebiß der Saugetiere. In: J. Niethammer, H. Schliemann, and D. Starck (eds), *Handbook of Zoology, Vol. 8 Mammalia, Part 56*, 1–513. Walter de Gruyter, Berlin.
- Vinyard, C.J., Wall, S.E., Williams, S.H., and Hylander, W.L. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. *American Journal of Physical Anthropology* **120**, 153–170.
- Voss, R.S. and Jansa, S.A. 2009. Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. *Bulletin of the American Museum of Natural History* **322**, 1–177.
- Wiens, F., Zitzmann, A., and Hussein, N.A. 2006. Fast food for slow lorises: is low metabolism related to secondary compounds in high-energy plant diet? *Journal of Mammalogy* **87**, 790–798.