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Dietary reconstruction of the Amphipithecidae (Primates, Anthropoidea) from the Paleogene of South Asia and paleoecological implications

Anusha Ramdarshan [a,*], Gildas Merceron [b], Paul Tafforeau [c], Laurent Marivaux [a]

[a] *Laboratoire de Paléontologie, Institut des Sciences de l'Evolution de Montpellier (ISE-M, UMR-CNRS 5554), c.c. 64, Université Montpellier 2, Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France*
[b] *PaléoEnvironnements et PaléobioSphère (PEPS, UMR-CNRS 5125) Université Lyon 1, Campus de la Doua, 2 Rue Raphaël Dubois, F-69622 Villeurbanne, France*
[c] *European Synchrotron Radiation Facility, BP220, 6 rue Jules Horowitz, F-38043 Grenoble Cedex, France*

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ABSTRACT

The primate family, Amphipithecidae, lived during the early Cenozoic in South Asia. In this study, the diet of late middle Eocene amphipithecids from the Pondaung Formation (Central Myanmar) is characterized using three different approaches: body mass estimation, shearing quotient quantification and dental microwear analysis. Our results are compared with other Paleogene amphipithecids from Thailand and Pakistan, and to the other members of the primate community from the Pondaung Formation. Our results indicate a majority of frugivores within this primate community. *Pondaungia* and "*Amphipithecus*" included hard objects, such as seeds and nuts, in their diet. Folivory is secondary for these taxa. *Myanmarpithecus* probably had a mixed diet based on fruit and leaves. Contrasting results and a unique dental morphology distinguish *Ganlea* from other amphipithecids. These render interpretation difficult but nevertheless indicate a diet tending towards leaves and fruit. However, the anterior dentition of *Ganlea* suggests that this taxon engaged in seed predation, using its protruding canine as a tool to husk hard fruits and obtain the soft seeds inside. *Bahinia* and *Paukkaungia*, two other Pondaung primates, are small (<500 g) and therefore would have depended on insects as their source of protein. As such, they occupied a very different ecological niche from Pondaung amphipithecids. This primate community is then compared with the Eocene-Oligocene primate communities of the Fayum from North Africa. Similarities between the late middle Eocene Pondaung primate community and extant equatorial and tropical South American primate communities are noted.

Introduction

The primate family, Amphipithecidae, lived during the early Cenozoic in South Asia. They were first identified from the late middle Eocene Pondaung Formation of Myanmar (Pilgrim, 1927; Colbert, 1937) in the early part of the twentieth century. Amphipithecids have also been described from the latest Eocene of Peninsular Thailand (Chaimanee et al., 1997, ; Ducrocq, 1999; Chaimanee et al., 2000a) and the early Oligocene of central Pakistan (Marivaux et al., 2005; Marivaux, 2006). They are primarily known from isolated teeth, jaws and a few bony elements. As their fossil record is so fragmentary, the debate over their phylogenetic affinities has been ongoing since their discovery (anthropoid *versus* adapiform affinities; e.g. Ciochon and Holroyd, 1994; Ciochon and Gunnell, 2002, 2004; Gunnell et al., 2002; Takai et al., 2003; Kay et al., 2004b). However, continuing field expeditions to the Pondaung Formation have allowed for a significant improvement of this family's fossil record, substantiating their anthropoid status (Jaeger et al., 1998, 2004; Chaimanee et al., 2000b; Marivaux et al., 2003; Beard et al., 2009). As such, the Amphipithecidae have been central to discussions on anthropoid origins.

While many studies are focused on the phylogenetic aspects of this Asian primate family, few thus far have been conducted on paleoecological aspects, such as body mass or diet (Ciochon and Gunnell, 2002; Egi et al., 2004; Kay et al., 2004a; Kay, 2005). Diet is the parameter that holds the most influence with primates on an ecological and behavioral level, as the quest for food takes up a large portion of their daily activities (Fleagle, 1999). While the diet of modern species is easily observable, it is sometimes hard to quantify this aspect of the paleoecology of fossil taxa.

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[*] Corresponding author. Tel.: +33 (0) 4 67 14 93 70(Office); fax: +33 (0) 4 67 14 36 22(Lab).

E-mail addresses: Anusha.Ramdarshan@univ-montp2.fr (A. Ramdarshan), Gildas.Merceron@adm.univ-lyon1.fr (G. Merceron), paul.tafforeau@esrf.fr (P. Tafforeau), Laurent.Marivaux@univ-montp2.fr (L. Marivaux).

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Different methods can be used to assess the diet of extinct species. This study focuses on body mass estimation, shearing quotient quantification and microwear analysis.

Body mass is useful in predicting species adaptations as it correlates closely to many aspects of life history, behavior patterns and ecology (e.g., trophic specialization, diet). In fact, body mass can be used as a first step towards determining diet by helping to rule out certain possibilities (Kay and Covert, 1984). Unfortunately, as overlap occurs among the different dietary categories (Kirk and Simons, 2001), body mass cannot be used as an exclusive method of dietary reconstruction, but it nevertheless provides a useful way of determining a fossil primate's probable primary source of protein.

In modern primates, the smaller sized forms (under 350 g) are mainly insectivores, while the larger forms (above 600 g) are generally plant eaters. Thus, for fossil species, Kay's threshold of 500 g is used to distinguish between insect and plant eaters (Gingerich, 1980; Kay and Covert, 1984). Frugivores cover a wide weight spectrum that does not help to characterize their dietary habits. However, given that fruit contains only small amounts of protein, frugivorous primates, depending on their size, supplement their diet with leaves or insects (Kay and Simons, 1980). Even though sizes overlap, it is still possible to characterize certain dietary habits. Frugivorous primates that rely on insects as their secondary source of protein tend to be under 1600 g, while those that rely on leaves tend to be over 1000 g. The overlap between 1000 g and 1600 g is therefore an interval in which one cannot assess the likely source of protein. These correlations have been explained in previous studies, notably Kirk and Simons (2001).

Shearing quotients (SQ) quantify diet-related dental morphological adaptations. Incisors and canines can fulfill different functions (e.g., ingestion, grooming, fighting), while the cheek teeth (premolars and molars) have more specific roles in the mechanical reduction of whatever is consumed. These cheek teeth reflect the physical and structural properties of food (Strait, 1997). The SQ, a relative measurement of molar shearing development, strongly correlates to diet (e.g., Kay, 1975, 1977, 1981; Kay and Simons, 1980; Kay and Covert, 1984; Anthony and Kay, 1993; Kirk and Simons, 2001). However, while tooth morphology reflects to some extent adaptation to diet, it also includes a phylogenetic component (Butler, 2000). The shearing crests of the molars are more or less developed depending on the nature of the alimentary bolus. Insects and leaves are composed of chitin and cellulose, respectively, both of which are more resistant to digestion than fruit. Extant primates that eat them have long, sharp crests so as to be able to cut leaves and perforate chitinous exoskeletons. Conversely, extant frugivores have shorter crests and shallower basins so as to squash the fruits.

Examining dental microwear is another useful method for dietary reconstruction. Ingested food often leaves traces on the surface of dental enamel. This abrasion carries a specific signature depending on the physical nature of the food consumed. The analysis of such microwear thus helps to predict the diet of fossil taxa by analogy with modern fauna. Several studies have focused on the analysis of this microwear to predict the diet of fossil taxa, particularly primates (e.g., Teaford and Walker, 1984; Grine and Kay, 1988; Ungar, 1996; King et al., 1999; Merceron et al., 2005, 2009). However, it should be noted that dental microwear only imprints the last weeks or even days in the life of the animal, depending on the nature of its diet (Teaford and Oyen, 1989). Thus, dental microwear patterns are, at best, a direct record of the last meals before death and not necessarily an indication of the overall diet of the animal. For example, seasonal variations of their environment can affect diet, although Teaford and Robinson (1989) have shown that these variations are not great enough to mask interspecific differences. Be that as it may, these elements do highlight the importance of having a sufficient sample size, which is rarely the case in fossil samples.

This paper will focus on providing, through the three previously described methods, an assessment of the diet of the amphipithecids of Myanmar (*Pondaungia*, "*Amphipithecus*," *Myanmarpithecus* and *Ganlea*). Although not the main focus of this study, it should be noted that ambiguity remains as to the number of valid taxa within the Amphipithecidae of Myanmar. The genera, *Pondaungia* and "*Amphipithecus*," are considered by some authors to be synonymous (Jaeger et al., 2004) (for the opposing opinion, see Gunnell et al., 2002). Questions regarding the number of valid species of *Pondaungia* are also complicated by the possibility of a high level of sexual dimorphism in this group.

Amphipithecids are mainly documented from the late middle Eocene Pondaung Formation, where they form the majority of the primate fossil sample. However, this study will also consider amphipithecids in relation to the other primate taxa of the Pondaung Formation [i.e., *Bahinia* (Jaeger et al., 1999) and *Paukkaungia* (Beard et al., 2007)], in order to understand how dietary niches were partitioned within this primate community. Comparisons will further be made between Pondaung amphipithecids and other representatives of this family from Thailand (*Siamopithecus*; Chaimanee et al., 1997) and Pakistan (*Bugtipithecus*; Marivaux et al., 2005).

Geological setting

The late middle Eocene Pondaung Formation in Central Myanmar consists of a succession of sandstones and clays with facies associations that characterize a river delta environment (Soe et al., 2002). The Pondaung Formation is divided into two lithological units. The lower member is composed of a conglomerate deposit with no fossils. The upper member, which consists of alternating sandstones and clays, was deposited in a sedimentologically lower energy environment. This is where most of the fossils were found, including both micro and macro remains of vertebrates and plants. Most of the primate remains were found in swale-fill sediments, sometimes contained in carbonate nodules of pedogenetic origin (i.e., poorly developed paleosoils) (Soe et al., 2002). These concretions develop by leaching processes, which could indicate the seasonality of climates (Soe et al., 2002; Jaeger et al., 2004).

The primates

The sites of the Pondaung Formation have a large primate presence, composed of anthropoids and adapiforms (Beard et al., 2007). A paleontological site only represents a snapshot at a given time. As such, it does not necessarily record the whole diversity of an ecosystem. Different taxa occur at different localities in the Pondaung Formation and in these conditions, it seems difficult to discuss a primate community as such. However, Pondaung primates are found in nearly every locality. For example, *Bahinia*, *Myanmarpithecus*, "*Amphipithecus*" and *Pondaungia* can be found together at Yarshe, indicating a possible sympatry for these species. Similarly, *Pondaungia*, "*Amphipithecus*" and a large sivaladapid (NMMP 20) can be found together at Saba Pondaung (Paukkaung Kyitchaung 1). Nearly all of the Pondaung primates are found at Paukkaung Kyitchaung 2 including *Bahinia*, "*Amphipithecus*", *Pondaungia*, *Myanmarpithecus*, *Ganlea*, *Paukkaugia*, *Kyitchaungia*, and the new undescribed tarsiid. So, although we cannot categorically prove these primates were sympatric, it seems reasonable to propose the hypothesis of a Pondaung primate community, which will be discussed further on.