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Co-occurrence of pliopithecoid and hominoid primates in the fossil record: An ecometric analysis

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ABSTRACT

Both pliopithecoid and hominoid primates were widely distributed throughout Eurasia during the Miocene but are known to have coexisted at only a few localities. It has been speculated that their different habitat preferences permitted only minimal overlap under special environmental conditions. Here we study the context for pliopithecoid and hominoid co-occurrence by assessing taxonomically-based palaeoecological diversity of associated fossil mammals and by direct ecometric analysis based on hypsodonty of mammalian herbivores. Our results show that pliopithecoids persistently inhabited more humid environments compared to the other primate groups studied, suggesting an inability to adapt to changing environmental conditions. The opportunity for hominoids and pliopithecoids to co-occur appears to have been restricted by niche conservatism in the latter group. Our study also indicates that direct ecometric analysis gives a better separation of the ecological preferences of these primate clades than do analyses of taxonomically-based community structure.

1. Introduction

Pliopithecoidea is an extinct and diverse superfamily of primitive catarrhine primates that ranged widely throughout Eurasia during the Miocene and were among the first fossil primates to be discovered and described (e.g., Lartet, 1837; Biedermann, 1863; Hofmann, 1893; Ginsburg and Mein, 1980; Ginsburg, 1986; Andrews et al., 1996; Harrison and Gu, 1999; Begun, 2002a; Alba et al., 2010; Harrison, 2013). Despite their wide distribution, pliopithecoids appear to have coexisted with the penecontemporaneous and equally broadly distributed hominoids at relatively few sites (e.g., Andrews et al., 1996; Harrison et al., 2002a; Alba et al., 2011; Almécija et al., 2012). In this study, we identify co-occurrence at only seven of 101 localities. Although inadequate sampling might be one explanation, many well-sampled and rich localities have yielded only one of the clades, while some poor localities have yielded both (Andrews et al., 1996). Another explanation is that differences in the habitat preferences of pliopithecoids and hominoids allowed only minimal overlap in their distribution (Andrews et al., 1996; Harrison et al., 2002b). This notion is supported by evidence from Rudabánya, where Armour-Chelu et al. (2005) noted the contemporaneity of *Anapithecus* and *Rudapithecus*. However, there were indications of ecological differences based on the relative abundance and age distribution of the two groups of primates at Rudabánya.

Here we study the ecological context of pliopithecoid and hominoid co-occurrence by assessing taxonomically-based palaeoecological diversity both with and without primates, and by direct ecometric analysis based on hypsodonty in mammalian herbivores. Ecological diversity analysis provides a means for comparing between the ecological features of fossil and extant communities across time and space (Andrews et al., 1979; Reed, 1997; Su and Harrison, 2007). This type of analysis was first applied to the fossil record by Andrews et al. (1979), who showed that ecological diversity patterns are comparable in similar habitats regardless of their species composition, and has been used in several palaeoecological studies of hominoid and hominin localities (e.g., Andrews, 1989; Reed, 1997, 1998, 2008; Su and Harrison, 2007). Mean hypsodonty, based on molar crown height of large herbivorous mammals, has been successfully used as a proxy for vegetation structure on an axis from closed to open (e.g., Fortelius et al., 2002, 2003, 2006; Eronen and Rook, 2004; Eronen, 2006; Eronen et al., 2010a, b), which in turn has been used as a proxy for past humidity and precipitation. Eronen and Rook (2004) investigated how

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primate localities differed from non-primate localities, but the current analysis examines the differences between different types of primate localities (specifically pliopithecoid, hominoid, and co-occurrence localities) and non-primate localities. Our goal is to examine whether there is a consistent difference between pliopithecoid and hominoid localities and hence infer whether the rarity of their co-occurrence may be due to environmental factors.

1.1. Localities with co-occurring pliopithecoids and hominoids

Seven localities with co-occurring pliopithecoids and hominoids in the same stratigraphic levels are recognized in this paper.

Děvínská Nová Ves, an MN 6 (middle Miocene) locality in Slovakia formerly known as Neudorf an der March, has yielded one of the earliest hominoids in Europe, *Griphopithecus suessi*, known from five isolated teeth (Abel, 1902; see also Andrews et al., 1996; Holec and Emry, 2003; Begun et al., 2006; Casanovas-Vilar et al., 2011). A single molar, a right M_3, of *Pliopithecus* cf. *antiquus* was found in association with *Griphopithecus* (Glaessner, 1931; Andrews et al., 1996; Begun et al., 2006).

Rudabánya, an MN 9 (early late Miocene) locality in Hungary has yielded a crouzeliine pliopithecoid, *Anapithecus hernyaki*, and a hominoid, *Rudapithecus hungaricus* (Kretzoi, 1984; Kordos and Begun, 2001a, b; Begun, 2002a, b, 2009; Begun et al., 2006, 2008, 2010; Kivell and Begun, 2009). Specimens discovered in 2009 conclusively demonstrate the temporal contemporaneity and spatial overlap of the two groups of primates at Rudabánya; *Rudapithecus* postcranial material was found only 10 cm apart from an *Anapithecus* cranium at the same elevation and in the same sedimentary horizon (Begun et al., 2010). The primates at this locality come from two sedimentary units, in which they are represented in different proportions. The grey marl layer is where most *Anapithecus* specimens are found, while the *Rudapithecus specimens* come primarily from the overlaying black mud layers (Kordos and Begun, 2001a; Andrews and Cameron, 2010). The higher proportion of *Anapithecus* juveniles compared to *Rudapithecus* in the grey marl suggests that the environment was more favourable for *Anapithecus* than for *Rudapithecus,* as a higher number of juveniles may indicate a core area for the species (Armour-Chelu et al., 2005). The proportion of juveniles in the black mud was equally low for both primates, implying that the area may have been more marginal for both species (Armour-Chelu et al., 2005; Andrews and Cameron, 2010). Based on the patterns of dimorphism, possible differences between home ranges of the two taxa have been hypothesised: monomorphic *Anapithecus* may have been more territorial with a small home range while the markedly dimorphic *Rudapithecus* may have had a larger home range (Begun et al., 2010).

Salmendingen in Germany is an MN10 (early late Miocene) locality with only three isolated teeth of primates. Of these, one is referred to *Anapithecus* cf. *hernyaki* (Begun, 1989), and the other two are attributed to the hominoid *Neopithecus brancoi* (Kordos and Begun, 2002; Begun et al., 2012). The type specimen of *N. brancoi* is an isolated M_3 resembling *R. hungaricus* from Rudabánya (Begun and Kordos, 1993). However, the attribution of the *Neopithecus* holotype has been much debated over the years (e.g., Schlosser, 1901, 1902; Abel, 1931; Hürzeler, 1954; Szalay and Delson, 1979; Begun, 2002b), with the consensus view being that the preserved anatomy is insufficient to allow a definitive taxonomic attribution (Begun, 2009; Moyà-Solà et al., 2009). However, Pickford (2012) argued that there is no evidence for the presence of *Anapithecus* at Salmendingen, and he instead contended that the primate teeth belong to *N. brancoi* and *Dryopithecus fontani*. Therefore, Salmendingen's status as a locality with the co-occurrence of a pliopithecoid and hominoid is uncertain.

Eppelsheim is an MN9 (early late Miocene) locality in Germany. The primate specimens comprise a femur and an upper canine. The femur is the holotype of *Paidopithex rhenanus*, often attributed to *Dryopithecus* based on its size (Begun, 1989, 1992; Andrews et al., 1996), but considered to be a pliopithecoid by Begun (1989, 1992, 2002b). The upper canine is comparable in size and morphology to pliopithecoid specimens from Rudabánya and Göriach (Begun, 1989), but since male pliopithecoid canines are morphologically similar, the affinity of the specimen is difficult to determine (Andrews et al., 1996). Köhler et al. (2002) compared the Eppelsheim femur with that of *Hispanopithecus laietanus* from Can Llobateres, Spain, and concluded that the former cannot be attributed to a dryopithecine as it differs both metrically and morphologically. Rejection of dryopithecine affinities does not necessarily imply that the femur belongs to a pliopithecoid, but this assumption is more parsimonious than invoking the presence of another group of primitive catarrhines in Europe (Köhler et al., 2002; Pickford, 2012). Eppelsheim's status as a locality of pliopithecoid and hominoid co-occurrence thus remains uncertain.

Castell de Barberà, an MN 7+8 (late middle Miocene) locality in Spain, has at least two primate species (Moyà-Solà et al., 1990; Andrews et al., 1996; Alba et al., 2011; Almécija et al., 2012). Hominoids are represented by a few postcranial specimens, including a partial humerus attributable to cf. *D. fontani* (Alba et al., 2011). In addition, a pliopithecoid, previously attributed to *Pliopithecus antiquus* (Andrews et al., 1996; Begun, 2002a) or *P.* cf. *antiquus* (Harrison et al., 2002b), was recently recognized as a new genus and species, *Barberapithecus huerzeleri*, by Alba and Moyà-Solà (2012). Sant Quirze, another MN 7+8 (late middle Miocene) locality in Spain, has co-occurrence of hominoids and pliopithecoids in the form of a fragmentary molar attributed to *H. laietanus* (Harrison, 1991; Golpe Posse, 1993) and an isolated upper molar of *Pliopithecus* sp. (Harrison et al., 2002a). However, the presence of hominoids at Sant Quirze is somewhat doubtful since the fragmentary molar may be incorrectly labelled and in fact may come from Can Vila (Golpe Posse, 1982; Alba, pers. comm.). Sant Quirze is therefore another locality with uncertain co-occurrence of pliopithecoids and hominoids.

Shihuiba, Lufeng is a rich MNEQ 12 (late Miocene) locality in southwest China with the crouzeliine pliopithecoid *Laccopithecus robustus* and the hominoid *Lufengpithecus lufengensis* (Pan, 1988; Qi, 1993; Harrison et al., 2002b). *Lufengpithecus* and *Laccopithecus* co-occur in Beds 2–6 in Section D at Shihuiba (Qi, 1993). In addition, pliopithecoids and hominoids are sometimes found at the same localities but in different stratigraphic levels. A few such examples are La Grive Saint-Alban in France, with *Pliopithecus antiquus* and *Plesiopliopithecus rhodanicus* together with *D. fontani* (Mein and Ginsburg, 2002; Pérez de los Rios et al., 2013), and Abocador de Can Mata in Spain (see Alba et al., 2012).

2. Materials and methods

2.1. Data

Palaeontological data were obtained from the Neogene of the Old World Database (NOW; Fortelius, 2010; http://www.helsinki.fi/science/now), the Paleobiology Database (PBDB; http://www.fossilworks.org), and from the literature if trophic or locomotor data were not available in NOW (Baudelot and Collier, 1978; Qi, 1979; Piller et al., 2000; Ye et al., 2000; Ginsburg, 2001; Moyà-Solà et al., 2001, 2009; Harrison et al., 2002b; Bernor et al., 2004; Xiang et al., 2004; Alba et al., 2006, 2010; Sun et al., 2007). The data from NOW included all mammal localities from 18 to 7 Ma, with the exception of singletons, i.e., localities where