SYSTEMATICS AND PHYLOGENY OF MIDDLE MIocene Cervidae (Mammalia) FROM Mae Moh Basin (Thailand) and a Paleoenvironmental Estimate Using Enamel Isotopy of Sympatric Herbivore Species

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INTRODUCTION

Today the family Cervidae is widely distributed in America, Eurasia, and North Africa. The possession of antlers in males is one of the main diagnostic features for this family. The first antlered cervids appeared in the early Miocene of Eurasia. Early to middle Miocene primitive cervids are classified within the subfamilies Procerulinae (Procerulus and Heteroprox), Lagomerycinae (Ligeromeryx, Lagomeryx, and Stephanocemas), and Dicrocerinae (Acteocemas and Dicrocerus) (Gentry, 1994; Gentry et al., 1999). Lagomerycines have been considered to be a separate family Lagomerycidae (Pilgrim, 1941) by some authors (e.g., Azanza and Ginsburg, 1997; Ginsburg and Chevrier, 2003). However, most authors (e.g., Gentry, 1994; Gentry et al., 1999; Groves, 2007; Wang et al., 2009; Rössner, 2010) regarded this group as a subfamily within the Cervidae (also in this paper).

Lagomeryx and Stephanocemas are distinctly characterized by their palmate antlers with a high number of branches. According to the phylogenetic relationships proposed by Azanza and Ginsburg (1997), the most primitive protoantler morphology among the Lagomerycinae is a forked construction with a prevalence of ramification by sprouting (e.g., Heterocemas). Derived protoantler morphologies among the lagomerycines are the multibranched construction defined by the presence of three or more branches (e.g., Ligeromeryx) and the palmation (e.g., Stephanocemas). Moreover, the multipointed construction of the European Lagomeryx is believed to derive from the multibranched construction according to the reduction of their protoantler sizes. However, the phylogenetic relationships of Lagomeryx have been poorly known since Roger’s (1904) initial recognition of this genus.

In Southeast Asia, the fossil record of the Lagomerycinae is scarce. Only Stephanocemas rucha was described by Ginsburg and Ukkakimapan (1983) from middle Miocene lacustrine deposits of Li Basin in northern Thailand (Fig. 1). This species represents the southernmost distribution of the genus Stephanocemas (Wang et al., 2009). Recent magnetostratigraphy (Benammi et al., 2002) and rodent biochronology studies (Chaimanee et al., 2007) suggest that the Li Basin strata are contemporaneous with those of Q and K coal layers of the Mae Moh Basin dated to the late middle Miocene, approximately 13 Ma. Unfortunately, the protoantler morphology of Stephanocemas rucha is poorly known, the holotype T Li 67 being fragmentary (palm portion bearing only one anterior tine). Additional protoantler fragments from the Li Basin were mentioned later by Mein and Ginsburg (1997) but were neither figured nor described.

During the numerous recent paleontological surveys in the middle Miocene sediments of the Mae Moh coal mine, northern Thailand (Fig. 1), new cervid fossils have been found in Q and K coal layers of the late middle Miocene age (about 13.4–13.2 Ma) (Coster et al., 2009) and are permanently stored at the University of Poitiers (France) in Paleontology collections of Mae Moh fossils (UPP MM). We identify these new cervid fossils as belonging to two distinct species of Lagomerycinae: Stephanocemas rucha and a new species of Lagomeryx. The latter genus is common in many Miocene localities of Europe (Azanza and Ginsburg, 1997;
Ginsburg and Chevrier, 2003; Rössner, 2010) and Asia (Young, 1964; Vislobokova, 1990; Wang et al., 2009).

Here we describe this new species of *Lagomeryx* and complete the description of *Stephanocemas rucha*. The relatively complete cranial appendages of the Mae Moh *Lagomeryx* give access to some morphological trends of this lineage. We thus take this opportunity to review all known species of *Lagomeryx*, and place them in the phylogenetic and zoogeographic frameworks. Finally, we propose an interpretation of the paleoenvironments of the Mae Moh locality by using the analysis of the isotopic composition of tooth enamel (\(\delta^{13}C\) and \(\delta^{18}O\)) of herbivores.

GEOLOGIC BACKGROUND

Northern Thailand comprises more than 40 Tertiary intermontane basins, tectonically interpreted as grabens or half grabens, including the Mae Moh Basin (Chaoadumrong, 1985). This basin, with maximum dimensions of 9 km in width and of 16 km in length, contains the largest coal deposits of Thailand and is located in the Mae Moh district, Lampang province. It follows a northeast–southwest general trend. Three formations were recognized by Corsiri and Crouch (1985) in the Mae Moh Group: the Huai King, Na Khaem, and Huai Luang formations. The lowermost part of the Mae Moh Group is the Huai King Formation. The Huai King Formation is overlain by the Na Khaem Formation, which comprises three main coal-bearing layers named Q, K, and J and two thin basal layers of coal, identified as R and S. Between the coal layers, the Na Khaem Formation contains lacustrine claystones, mudstones, minor sandstones (Ut-tamo, 2000), and one ash layer interbedded within the J coal layer. These facies indicate that sedimentation occurred under the alternation of freshwater lake and swamp/marsh in a calcium-rich lacustrine environment. The uppermost formation of the Mae Moh Group, the Huai Luang Formation, comprises the most recent coal layer of the Mae Moh Basin, lettered I (see Benammi et al., 2002; Coster et al., 2009, for more detailed sedimentology and stratigraphy).

Magnetostratigraphic studies have been used to define the age of this locality and to establish accurate stratigraphic correlations with the nearby Chiang Muan Basin (Fig. 1) (Coster et al., 2009). As a result, an age bracketed between 12.8 and 12.2 Ma has been assigned to the J coal layer. The main mammal-bearing coal layers (Q and K) have been dated between 13.4 and 13.2 Ma. The thickness of the Q and K coal layers can reach 80 m in some parts of the basin (massive coals of the central basin), but abundant mammalian fossils have only been collected from the northern margin of the basin, which displays thinner coals (20 m in thickness for both layers, interbedded with claystones).

In the central basin of the Q and K coal layers, mammalian fossils are poorly known, only some crocodiles and turtles having been found, due to a deeper water level of that area. However, the mammalian fossils collected from both coal layers represent a homogeneous fauna in terms of the taxonomy and paleoenvironments (see Suraprasit et al., 2011:table 3, for the mammalian fauna list).

CRANIAL APPENDAGE TERMINOLOGY FOR THE LAGOMERYCINES

Antlers are developed as an outgrowth of the frontal bone, a feature shared with all living cervids. The cranial appendages of lagomerycines presumably consist of two portions: a nondeciduous proximal part (pedicle) and a deciduous distal one (Bubenik, 1990; Azanza and Ginsburg, 1997). In *Lagomeryx* and *Stephanocemas*, this distal part is recognized as a ‘protoantler,’ due to the lack of a burr, and shows periodic shedding tines forming a palmate or crown-like antler. The term ‘protoburr,’ a weaker coarse surface surrounding the base of the antler than a modern burr, is properly used for early cervids. In this study, a ‘branch’ is termed as the ramification of protoantlers terminating with a single tine or a pair of tine bifurcations. Protoantler morphologies for the early cervids used here can be divided into three terms: forked, multibranched (numerous branches), and multi-pointed (numerous short tines or knobs without bifurcation) construction. The protoantler nomenclature of lagomerycines are given in Figure 2 for *Lagomeryx manai*, n. sp., and in Figure 4 for *Stephanocemas rucha*.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Family CERVIDAE Goldfuss, 1820
Subfamily LAGOMERYCINAE Pilgrim, 1941
Genus LAGOMERYX Roger, 1904
LAGOMERYX MANAI, sp. nov. (Figs. 2, 3)

**Holotype**—Partial right frontal with an appendage preserving from the base of the pedicle to a half of a protoantler with two complete tines, UPP MM-1 (Fig. 2A–D).

**Age and Locality**—Late middle Miocene (13.4–13.2 Ma, in Q and K lignite layers), Mae Moh coal mine, northern Thailand.

**Referred Specimens**—Half of a left protoantler with six preserved tines (UPP MM-2), a left fragmentary protoantler with two preserved tines (UPP MM-3), a right fragment of protoantler with three tines (UPP MM-4), a right mandibular fragment with one m1 and two m2 (UPP MM-5), and 13 isolated teeth: right P4 (UPP MM-6), left M1 (UPP MM-7), left M2 (UPP MM-8), right M3 (UPP MM-9 and UPP MM-10), left M3 (UPP MM-11), right m2 (UPP MM-12, UPP MM-13, and UPP MM-14), left m2 (UPP MM-15), and right m1 (UPP...
Etymology—In honor of Mr. Mana Rugbumrung who discovered many cervid fossils in Mae Moh coal mine.

Diagnosis—Large-sized Lagomeryx with a long pedicle. Protoanterior tine size is large relative to that of the pedicle. The base of the pedicle has a subtriangular cross-section, becoming oval in its middle part. The shaft of the pedicle curves anteriorly while bending posteriorly and outward (Fig. 2A–C), similar to those of Ligeromerxy. The construction pattern of the protoanterior is multibranched, instead of multipointed. The palmate antler consists of at least six tines, probably varying from 10 to 12 tines in adults (Fig. 2M), without a protoburr. The projecting tines display different orientations, varying from horizontal for the anterior medial tine (am1) and the posterior medial tine (pm) to nearly vertical for the anterior tine (a1). The anterior medial one and is also larger than it (Fig. 2E, F). The anterior medial tine projects in a nearly vertical plane (Fig. 2F). The trace of a posterior lateral tine (pl) can be detected at the posterior part of the palm portion. The posterior lateral tine is also upright, being distinctly smaller than the posterior medial tine (Fig. 2G). The anterior part of the palmate antler bends down following the margin of the missing pedicle, in a similar orientation of the holotype (Fig. 2H). These two specimens are probably assigned to juvenile individuals because of their smaller size.

Craniial Appendage and Dental Measurements—See Appendices 1–3.

Description of Craniial Appendages

The frontal bone of the holotype (UPP MM-1) is poorly preserved, only the medial part from the orbital margin probably to the sagittal suture remains. The supraorbital foramen is situated anteromedially to the appendage base, close to the anterior-most preserved part of the frontal bone (Fig. 2A). The shaft of the pedicle curves anteriorly in lateral and medial views (Fig. 2B, C). The pedicle is inserted posteriorly to the orbit and diverges outwardly from the sagittal plane (Fig. 2A). The cross-section of the pedicle is subtriangular at its base, oval in its middle portion, and bean-shaped with a mediolateral compression at the distal part (Fig. 2A). Based on the anterior curvature of the pedicle, the slope of the palmate antler lying on the pedicle falls from posterior to anterior (Fig. 2B). The central portion of the palmate antler is proportionally larger than that of most other species of Lagomerxy and Ligeromerxy, at least one side (half) of the palmate antler bearing approximately six tines.

Description of the Dentition of Lagomerxy manai, n. sp.

The teeth of Lagomerxy manai, n. sp., display rugose enamel. The tooth crowns are rather high for a cervid (Appendix 3). The dental nomenclature used here follows the dental terminology for ruminants, proposed by Bärmann and Rössner (2011).

Upper Dentition—P4: Labial styles are well developed. The mesolabial crista projects distinctly to the anterior part of the tooth. The lingual cone is also present with the bifurcated end, projecting posteriorly to the fossa. The anterolingual cingulum is distinctly shorter than the posterolingual cingulum (Fig. 3A).

Molars: All upper molars are relatively square in their outlines. Para-, meso-, and metastyles are well developed. The paracone rib projects anteriorly (Fig. 3B). The metacone rib is weaker than the paracone rib. An anterior cingulum is slightly developed and does not reach the labial side. The lingual cingulum is strongly expanded throughout the lingual part of the molar, and fused to the entostyle. The internal postprotocrista is also well developed, connecting to the premetacrista. The M2 is much larger than that of M1 (see Appendix 3). The posterior lobe of M3 is much narrower than the anterior lobe.

Lower Dentition—Lower molars have a rectangular outline in occlusal view. The external prototocristid (Palaeomeryx fold) and ectostylid (also called basal pillar) are distinct (Fig. 3C), the posterior ectostylid being present only on m3 between the hypoconid and the hypoconulid. However, the stylids are weaker than those of upper molars. The lingual wall is relatively flat. The anterior and posterior cingulids are often present. The internal postprotocristid is always fused with the preen- tocristid in all lower molars. The prehypocristid on m2 does not join the metastylid, at least in early wear stages or unworn teeth. The m3 displays a posteriorly extended back fossa between the hypoconulid and the pre- and posthypoconulid cristid. The posthypocristid is fused to the posthypoconulid cristid on the slightly worn m3.

Genus STEPHANOCEMAS Colbert, 1936

STEPHANOCEMAS RUCHA Ginsburg and Ukkakimapan, 1983

(Figs. 3, 4)
Type Specimen—A right side of an adult protoantler (T Li 67) from Li Basin, northern Thailand (13–12 Ma) (Fig. 4F).

Diagnosis—From Ginsburg and Ukakakimapan (1983:299) (translated into English): “Species of Stephanocemas close morphologically to the type species Stephanocemas thomsoni but distinctly smaller, with lateral tines closer to each other, anterior tine pointing more mediadly, and wider central palm portion especially in its posterior part.”

Referred Specimens—A complete left protoantler with a broken anterior tine and a few fragmentary parts of lateral and medial tines (UPP MM-19), an laterally branched fragment of a protoantler with two separated traces in left side (UPP MM-20), a right juvenile protoantler with four tines of (UPP MM-21) (Fig. 4), and seven isolated teeth: right M3 (UPP MM-22, UPP MM-23, and UPP MM-24), left p4 (UPP MM-25), left m2 (UPP MM-26 and UPP MM-27), and right m3 (UPP MM-28).

Age and Locality—Late middle Miocene of Li Basin and of Mae Moh Basin (Q and K lignite layers), northern Thailand.

Emended Diagnosis—Small-sized species of Stephanocemas without any posterior branch in the juvenile protoantlers. The anteroposterior extension of the palm portion is distinctly wider than its mediolateral extension. Most branches project in a nearly vertical plane. The palm portion consists of five main branches: one anterior (a), two medial (am and pm), and two lateral (al and pl) branches. Three branches are bifurcated: the anterior medial branch with am1 and am2 tines, the posterior medial branch with pm1 and pm2 tines, and the posterior lateral branch with pl1 and pl2 tines. Only the anterior lateral branch (al) is not bifurcated. It has a subcircular cross-section with a slightly concave dorsal surface and a convex ventral surface. However, judging from the condition of the medial branches, the line bifurcation does not extend far from the base of the split. All of medial branches are distinctly shorter than the lateral branches. They have a flattened cross-section. These medial tines bend almost 45° with a rather concave dorsal surface and a slightly convex ventral surface (Fig. 4B, C). The second posterior lateral branch (pl2) is the longest one and projects more horizontally than those of other branches (Fig. 4B). Contrary to the holotype, the base of the posterior lateral branch is preserved and indicates a more vertical orientation as the anterior lateral branch (Fig. 4F, G). The dorsal and ventral surfaces of posterior lateral branches are rather smooth and flattened. The palm portion is compressed mediolaterally. The central valley of the palm portion is moderately smooth without any trace of the longitudinal groove observed on the holotype (Fig. 4F).

Protoantler and Dental Measurements—see Appendices 1–3.

Description of Protoantlers

The additional palmate antler found in Mae Moh Basin (UPP MM-19) is more complete than the holotype. Some tines (anterior medial [am1 and am2], posterior medial [pm1 and pm2], and the second posterior lateral [pl2] tines) are completely preserved, but the anterior tine (a) is broken (Fig. 4A–C). The posterior branch is probably absent in Stephanocemas rucha, based on the observation of this specimen. The UPP MM-19 consists of four main branches, at least three of them being bifurcated: the anterior medial branch with am1 and am2 tines, the posterior medial branch with pm1 and pm2 tines, and the posterior lateral branch with pl1 and pl2 tines. Only the anterior lateral branch (al) is not bifurcated. It has a subcircular cross-section with a slightly concave dorsal surface and a convex ventral surface. However, judging from the condition of the medial branches, the line bifurcation does not extend far from the base of the split. All of medial branches are distinctly shorter than the lateral branches. They have a flattened cross-section. These medial tines bend almost 45° with a rather concave dorsal surface and a slightly convex ventral surface (Fig. 4B, C). The second posterior lateral branch (pl2) is the longest one and projects more horizontally than those of other branches (Fig. 4B). Contrary to the holotype, the base of the posterior lateral branch is preserved and indicates a more vertical orientation as the anterior lateral branch (Fig. 4F, G). The dorsal and ventral surfaces of posterior lateral branches are rather smooth and flattened. The palm portion is compressed mediolaterally. The central valley of the palm portion is moderately smooth without any trace of the longitudinal groove observed on the holotype (Fig. 4F).

One fragmentary palmate antler with a bifurcated branch (UPP MM-20) can be identified as a left posterior lateral branch of Stephanocemas rucha, based on its moderately long tines with flattened cross-sections (Fig. 4H). The posterior border of this
FIGURE 4. Palmate antler remains of *Stephanocemas rucha*. A left protoantler cast from Mae Moh Basin, UPP MM-19, in dorsal (A), lateral (B), and medial (C) views; the reconstruction of the UPP MM-19 specimen, in dorsal (D) and lateral (E) views; a cast of right protoantler from Li Basin (holotype), T Li 67, in dorsal view (F) and its reconstruction (G); a left fragmentary protoantler with two tines (Mae Moh Basin), UPP MM-20, in dorsal view (H); and a right juvenile protoantler from Mae Moh Basin, UPP MM-21, in dorsal (I) and lateral (J) views. Abbreviations: a, anterior; al, anterior lateral; am, anterior medial; m, medial; pm, posterior medial; p, posterior; pl, posterior lateral. Color area corresponds to the part that has been reconstructed.

The fragment is rather smooth and flattened. The two tines are unequal in size, the anterior one being distinctly larger.

Compared with the holotype, the orientation of palmate antlers is not always easily ascertained without attached frontal fragments or extensive ontogenetic series. Our identification of the additional specimen from the Mae Moh Basin (UPP MM-19) is based on comparison with a cast of the holotype. On the holotype, the anterior lateral branch (al) shows no bifurcation and projects in a nearly vertical plane (see reconstruction: Fig. 4F, G). Only one branch of the Mae Moh specimen (UPP MM-19) has characteristics that perfectly match the anterior lateral branch (al) and is thus used to orientate the specimen (Fig. 4D, E). An additional criterion or orientation is a scar below the palmate antler left by the separation between the palmate antler and the pedicle. This scar is observed on both the holotype (Ginsburg and Ukkakimapan, 1983) and UPP MM-19 but represents a mirrored image. Given these observations, we regard the Mae Moh specimen UPP MM-19 as a left protoantler of a juvenile or subadult individual, according to the smaller size of its palm portion and tines, a more horizontal posterior lateral branch, and the absence of a distinct central valley with longitudinal groove in comparison with the holotype.

One specimen found in Mae Moh Basin apparently belongs to a juvenile individual (UPP MM-21). The traces of four branches can be observed on this specimen: two medial branches (anterior medial and posterior medial branches) and two lateral branches (anterior lateral and posterior lateral branches). The anterior part is broken (Fig. 4I, J). Its size is clearly smaller than those of the specimens attributed to *Lagomeryx manai*, n. sp., and *Stephanocemas rucha*. The slope of the palm portion lying on the pedicle falls slightly from posterior to anterior. According to the protoantler ontogenetic series of *Ligeromeryx praestans*, the juvenile specimen UPP MM-21 probably corresponds to their early development, which produces an initial pattern of the protoantler growth starting with three or four branches (Azanza and Ginsburg, 1997:fig. 3E, morphotype A). But the palm portion lying on the pedicle is more horizontal for the UPP MM-21 specimen. Moreover, the protoantler ontogenetic growth of *Stephanocemas* has been well described by Colbert (1936) for *Stephanocemas thomsoni* and by Wang et al. (2009) for *Stephanocemas*...
palmatus and Stephanocemas sp. The UPP MM-21 specimen seems to fit well with juvenile forms of Stephanocemas sp. (Wang et al., 2009:fig.7), due to the position of its scar below the pallete antler and the horizontal orientation of its palm portion (Fig. 4I). This specimen therefore could represent a juvenile stage of Stephanocemas rucha.

**Remarks on the Teeth of Stephanocemas rucha**

Abundant isolated cervid teeth are represented in the Mae Moh collection (see Supplementary Data 1), although none are associated with protoantlers. Two dental types can be recognized and assigned to the two taxa (described above) based on their size. The dental size and morphology of Stephanocemas rucha from the Li Basin (Mein and Ginsburg, 1997) are similar to those of the small cervid samples from the Mae Moh locality. The molars of Stephanocemas rucha are rather similar morphologically to those of Lagomeryx manai, n. sp., but are of smaller sizes (Appendix 3).

Additional upper molars of Stephanocemas rucha were found in this locality, but most of them are heavily worn. These upper molars display some typical features of all early cervids such as the presence of internal and external postprotocristids, distinct lingual cingula, and extreme widths. The Mae Moh p4 (Fig. 3D), a slightly worn tooth, has a well-developed anterior conid and an anterior stylid that project to the lingual side of the tooth. The posterolabial conid is weak. The mesolabial conid is higher than that of the mesolingual conid. The mesolingual conid of p4 is separated into two flanges: anterior lingual cristid and posterolingual cristid. The latter does not reach the posterolingual conid. The posterior stylid projects lingually and does not fuse with the posterolingual conid at this wear stage. On lower molars, the postprotocristid is fused with the preentocristid on the m2 (Fig. 3E). The posthypocristid does not fuse with the posthypocristid cristid on the m3 (Fig. 3F).

These two dental characters of Stephanocemas rucha are different from those of Lagomeryx manai, n. sp., probably due to the wear stages. The hypoconulid on m3 of Stephanocemas rucha is well developed and consists of pre- and posthypocristid cristids posthypocristid cristids as in Lagomeryx manai, n. sp.

Most dental morphological similarities between Stephanocemas rucha and Lagomeryx manai, n. sp., support the conclusion that the dentition of Lagomerycinae is very conservative.

**Biogeographic Records and Comparisons of Lagomeryx**

**European Lagomeryx Records**—The earliest lagomerycines with pallete antlers appeared in Eurasia during the early Miocene (MN3, early Oleanrian of the Loire Basin in France), where they were represented by large (Ligeromeryx praestans) to very small forms (Lagomeryx parvulus, Lagomeryx palmilus, and Lagomeryx ruetimeyeri). Specimens of Ligeromeryx praestans were described for the first time by Stehlin (1937) who initially attributed them to the genus Ligeromeryx. Azanza and Ginsburg (1997) assigned them later to a new genus, Ligeromeryx, according to their larger size, their multibranched protoantler construction, and the absence of true pallete antler to the contrary of the other European species of Lagomeryx. The teeth and protoantlers of Lagomeryx manai, n. sp., seem to be similar in size to those of Ligeromeryx. But the true pallete antlers of the Thai specimens can distinguish them from Ligeromeryx. The European Lagomeryx fossil record is restricted to small-sized forms.

One species of the small-sized Lagomeryx, Lagomeryx palmilus, from Germany (early middle MN5 to early MN6, boundary early/middle Miocene to middle middle Miocene) belongs to the smallest representatives of Miocene European ruminants according to Rössner (2010). This species was initially represented only by the teeth (a right m3, holotype) (Roger, 1896). Additional specimens of Lagomeryx palmilus teeth were found especially from the fossil site Sandelzhausen, southern Germany, in a layer correlated with the biozone MN5 (Moser et al., 2009). The holotype, a right m3, displays an enlarged entoconulid forming a third lingual cusp (Roger, 1896). This character cannot be observed on the m3 of Thai specimens. However, the molars of Lagomeryx manai, n. sp., are apparently larger than those of Lagomeryx palmilus (Rössner, 2010:table 7).

**Lagomeryx parvulus** is a somewhat larger species compared with Lagomeryx palmilus, which was distributed widely in Europe during the early to middle Miocene (Rössner, 2010): it was recorded in France (MN3, late early Miocene) (Ginsburg, 2011), Austria (MN4 to early MN6, late early Miocene-middle middle Miocene) (Rössner, 1998), and Germany (MN4 to early MN6), (Rössner, 2006). Lagomeryx manai, n. sp., differs from this European species in having significantly larger teeth and protoantlers with an outward bending of the pedicle, longer tines (multibranched pattern), and probably a greater number of tines (total seven tines in Lagomeryx parvulus).

European material attributed to Lagomeryx ruetimeyeri, a slightly larger-sized species than Lagomeryx parvulus, was described from several localities of Germany and Austria (Ginsburg and Chevrier, 2003; Rössner, 2010), in the layers of MN4 and MN5 age (late early Miocene). Lagomeryx manai, n. sp., differs from Lagomeryx ruetimeyeri in having distinctly larger sizes, a larger pallete antler relative to the pedicle size, and a multi-branched construction (instead of the multipointed pattern in Lagomeryx ruetimeyeri).

**Asian Lagomeryx Records**—Several specimens of large-sized Lagomeryx were described from many Miocene Asian localities, especially in China. Ye (1989) described Lagomeryx sp and Stephanocemas aff. thomsoni from the lower portion of the middle Miocene Halamagai Formation, Xinjiang of China. According to this author, the recognition of a species of Lagomeryx in this locality relies on a cluster of smaller protoantlers containing specimens in which open shedding scars were observed. In addition, Lagomeryx sp. differs from Stephanocemas aff. thomsoni in having smaller lower molars with lower crowns, well-developed ectostylic and mesostylic, and undulating lingual walls. These specimens of Lagomeryx sp. can be distinguished from those of Lagomeryx manai, n. sp., by several characters: a smaller pedicle (less than 15 mm in diameter) with a circular cross-section and a fewer number of tines (four tines) on the pallete antlers. However, these two taxa share several characters on their lower molars such as the absence of a labial cingulum, well-developed ectostylic, metaconid ribs, and metastylic, and a posteriorly extended hypoconulid on m3.

From the middle Miocene Tung Gur Formation of Mongolia, two species of Stephanocemas have been described by the American Museum Asiatic Expedition team: Stephanocemas thomsoni and Stephanocemas triacuminatus (Colbert, 1936). Later on, Stephanocemas triacuminatus was transferred to the genus Lagomeryx due to its long pedicle (Colbert, 1940; Young, 1964). The cranial appendages of Lagomeryx manai, n. sp., differ from those of Lagomeryx triacuminatus in having a larger central palm portion, a higher number of tines, and a pedicle with an oval cross-section. However, the protoantler dimensions of the Thai specimen (holotype): the pedicle length and the transverse diameter of the pedicle base, are similar to those of Lagomeryx triacuminatus.

In addition, Lagomeryx colberti Young, 1937 has been described by Chow and Shih (1978) based on a relatively complete skull from the middle Miocene of Linchü in Shan tung, China. These authors also proposed to include three distinct taxa: Stephanocemas colberti, Lagomeryx simpsoni Young, 1937, and Lagomeryx teilhardi Young, 1964, as the junior synonym of Lagomeryx colberti. Lagomeryx manai, n. sp., can be distinguished clearly from Lagomeryx colberti by several characters:
an outward bending pedicle, a greater number of tines (four tines in *Lagomeryx colberti*), and higher tooth crowns.

Young (1964) erected the species *Lagomeryx complicidens* based on a protoantler from the late Miocene of Lantian, Shensi, in China. The holotype (V.2780) is a nearly complete right cranial appendage missing only the base with a part of the frontal. This species was found subsequently in the late middle Miocene of the Koujigou Formation at Lengshiguou, China (Qiu and Qiu, 1995). Various features of *Lagomeryx manai*, n. sp., are reminiscent of that species, for instance, the slope of the palm portion lying on the pedicle (higher in its posterior part), the size of the palmate antler related to the pedicle, the diameter and shape of the cross-section (oval) at the middle part of the pedicle, and the presence of the true palmate antler with numerous tines. However, *Lagomeryx manai*, n. sp., is clearly distinguishable from *Lagomeryx complicidens* by several characters such as an anterior curvature of the pedicle, a slightly smaller protoantler, and the presence of a larger number of tines (at least on a half palm portion).

Two least known species of *Lagomeryx*, *Lagomeryx tsaidamensis* (Bohlin, 1937) and *Lagomeryx primaevus* (Teilhard de Chardin, 1926), have been described respectively from the early late Miocene of the Tsaidam Basin (Qinghai Province, China) and late middle Miocene of Mongolia. Young (1964) mentioned that the size of *Lagomeryx tsaidamensis* is similar to that of *Heterocemas*, but the direction of the protoantler bending is quite different. However, this specimen is recognized by one single individual, only the main shaft being well preserved with a fragmentary palm portion. Wang et al. (2007) also reported that the Olongbuluk mammothian fauna (middle Miocene) from the upper part of the Lower Youshashan Formation is characterized by primitive deer such as *Lagomeryx tsaidamensis* and *Stephanoceras*. The Thai *Lagomeryx* is clearly different from *Lagomeryx tsaidamensis* in its oval cross-section at the middle part of the pedicle and its larger palmate antler relative to the pedicle. *Lagomeryx primaevus* had been initially attributed to the genus *Moschus* (Teilhard de Chardin, 1926), and later transferred to *Lagomeryx* by V.1slobokova (1983) based on dental characters (lower premolars and upper canines) and a few fragmentary postcranial bones. Comparison with this species is impossible because no lower premolars and upper canines of *Lagomeryx manai*, n. sp., and no protoantlers of *Lagomeryx primaevus* are known.

**Phylogenetic Position of Lagomeryx manai, n. sp.**

In order to reconstruct the phylogenetic position of *Lagomeryx manai*, n. sp., we performed a cladistic analysis based on the cranial appendages only. Eight fossil species of *Lagomeryx* have been sampled. Due to the lack of protoantler data, *Lagomeryx pumilio* and *Lagomeryx primaevus* have been eliminated. In addition, we have included in the analysis one species of *Ligeromeryx*, *Ligeromeryx praestans* Stehlin, 1937, two species of *Euprox*, *Euprox robustus* Dong et al. (2003) and *Euprox furcatus* (Hensel, 1859), and one species of *Procervulus*, *Procervulus praecucidus* (Obergfell, 1957). We selected one species of *Ligeromeryx praestans* as the ingroup according to several similarities of its cranial appendages shared with the Asian species of *Lagomeryx*, the basal cervid (*Procervulus praecucidus*) as a primary outgroup, and two species of muntiacines: *Euprox robustus* and *Euprox furcatus*, as additional outgroups. The plesiomorphic states of characters are coded as ‘0’. Sixteen cranial appendage characters have been selected to build the character data matrix (see Appendix 4). This matrix has been edited with NEXUS Data Editor (NDE) 0.4.8 (Page, 2000) and processed with PAUP 4.0 (Swofford, 2002). The characters were equally weighted and were defined as unordered with the exception of characters 1, 2, 3, 5, and 8. The most parsimonious topologies were obtained by a heuristic search (hsearch command) configured with the default options of PAUP. Heuristic search results were as follows: the length of tree is 32 steps, consistency index (CI) = 0.66, homoplasy index (HI) = 0.34, retention index (RI) = 0.77, and rescaled consistency index (RC) = 0.50, on the corresponding consensus tree (Fig. 5).

*Lagomeryx manai*, n. sp., is the sister group of *Lagomeryx complicidens*. These two species share four apomorphies involving the characters 3, 5, 8, and 14: a wide mediolateral extension of the pedicle, a greater number of tines (more than seven), well-developed lateral tines (two or three), and a pedicle with an oval cross-section. Considering the robustness of this clade, supported by a high Bremer index (4), it can be inferred that *Lagomeryx manai*, n. sp., has a close relationship with *Lagomeryx complicidens*. *Lagomeryx manai*, n. sp., and *Lagomeryx complicidens* are nested with a clade comprising all the sampled Asian representatives of *Lagomeryx* (node 6). This clade is supported by two apomorphies: the presence of bifurcated branches (character 7) and a curved pedicle posteriorly above the orbits (character 11). The relationships between the group *Ligeromeryx triacuminatus* and *Lagomeryx* sp. (Xinjiang) and the group *Lagomeryx manai*, n. sp., *Lagomeryx complicidens*, *Lagomeryx colberti*, and *Lagomeryx tsaidamensis* are not resolved. Moreover, the weak Bremer index of the Asian *Ligeromeryx* clade and some of its subclades (nodes 7 and 8) suggests that the phylogenetic reconstruction of the Asian species of *Lagomeryx* is still tenuous.

The European species of *Lagomeryx*, *Lagomeryx parvulus* and *Lagomeryx ruetimyieri*, form a robust clade (node 4) supported by a Bremer index of 3. This clade is reconstructed as the sister group of the clade comprising the Asian species of the genus.

As a result of the consensus tree, *Ligeromeryx praestans* is reconstituted as the sister group of *Lagomeryx*. *Ligeromeryx praestans* is autopomorphic in several traits, such as an anterior tine projecting in a nearly horizontal direction, an upright pedicle above the orbits, and the anterior bending of the palm portion. The *Ligeromeryx*-*Lagomeryx* clade (node 3) is supported by the following shared features: a multipointed construction, one or two developed lateral tines, and an anteriorly curved pedicle in its distal part. Originally placed in the genus *Lagomeryx*, the species

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**FIGURE 5.** Strict consensus of three shortest trees of the *Ligeromeryx-Lagomeryx* clade. Apomorphies support the monophyletic branches: node 3: 1(1), 8(1), 13(1); node 4: 1(2), 6(1), 8(2); node 5: 2(1), 3(1), 6(1), 15(1); node 6: 7(1), 11(1); node 7: 9(1), 16(1); node 8: 2(2), 15(0, reversed); node 9: 3(2), 5(2), 8(2), 14(1). Additive number (+) represents a Bremer index value supporting the robustness of each node.
praestans was transferred to Ligeromeryx by Azanza and Ginsburg (1997) on the basis of the absence of true palmate antlers, the multibranched construction of the protoantlers, the distinctly larger size of the pedicle compared with Lagomeryx, and the divergent pedicles. In fact, these authors took into account only the European species of Lagomeryx and considered them as a sister group of Stephanocemas in their phylogenetic relationships. The Asian Lagomeryx clade is therefore still unresolved. Another issue concerning some features of European Ligeromeryx praestans (only one species within this genus) is that it shares large-sized and multibranched protoantlers with some Asian species, Lagomeryx triacuminatus and Lagomeryx colberti, which may indicate possible relationships between these two groups. But this matter needs further study because these two Asian species display a more complex morphology of protoantlers and their dentition is more primitive based on the presence of p1 (Azanza and Ginsburg, 1997). From our phylogenetic analysis using cranial appendage characters, the genus Lagomeryx (including Asian and European taxa) still represents a monophyletic group that can be clearly separated from the genus Ligeromeryx.

Most characters of Lagomeryx are characterized by the peculiar pedicle morphologies (see Appendix 4). We admit that the scope of this study does not allow the resolution of the relationship between Lagomeryx and Stephanocemas because it is difficult to resolve them without access to the pedicle features that are lacking in all species of Stephanocemas with the exception of the type species, Stephanocemas thomsoni. Additionally, all early to middle Miocene cervids share dental and skeletal similarities with the other primitive antlerless ruminants. Within Lagomeryx, the symplesiomorphic dental morphology is difficult to distinguish even from that of the early cervids such as Procervus. Only a few plesiomorphic features, such as p1 being sometimes present, appears in the European Lagomeryx (Gentry et al., 1999). Cranial appendages are therefore a better basis for its species-level identification.

On the Distinction between Lagomeryx and Stephanocemas

According to Colbert (1940), the cervid Stephanocemas can be distinguished from Lagomeryx by a more complex palmate antler, characterized by a greater number of tines, and a shorter pedicle (defined by the type species Stephanocemas thomsoni). Despite the fact that the European species of Lagomeryx are clearly different from Stephanocemas by the presence of a multipointed construction, a long pedicle compared with the protoantler size, and a smaller size, some Asian species of Lagomeryx, such as Lagomeryx complicidens Young, 1964 and Lagomeryx manai, n. sp., share a well-developed protoantler construction (multibranched) with numerous tines (more than seven times) and a mediolateral extension of the palm portion with all species of Stephanocemas. Based on these protoantler characters, the distinction between these two genera is unclear. The large on- genetic series of Mae Moh cervid protoantlers support that tine number is useless to distinguish Lagomeryx from Stephanocemas, because an adult specimen of Lagomeryx manai, n. sp., has shown a greater number of tines (10–12 times) than the adult individual of Stephanocemas rucha. If our reconstruction of the protoantlers for both Mae Moh cervids is correct, then Lagomeryx manai, n. sp., can be distinguished from Stephanocemas rucha by having a more rounded cross-section of the medial tines, a greater number of tines, a weaker anteroposterior extension of the palm portion, a posterior branch of the palm portion in a juvenile form, and a larger size (indicated by the dental size). As observed on the protoantlers of all species of Lagomeryx and Stephanocemas, we propose to distinguish both genera on the basis of the anteroposterior extension of the palm portion (wider for Stephanocemas) and the pedicle length compared with the protoantler size. The presence of a long pedicle is a derived character shared between Lagomeryx and some extant representatives of Muntiacus.

 Zoogeographical Remarks on Lagomeryx

Based on our phylogenetic analysis above, Figure 6 shows the chronological ranges of the species of Lagomeryx and Ligeromeryx as well as their geographic locations. Lagomeryx parvulus from the late early Miocene (MN3) is the oldest palmatantlered cervid known in Europe. The small-sized species of Lagomeryx are restricted only to Europe and the large-sized species of Lagomeryx are known only in Asia. The genus Lagomeryx dispersed to Asia probably during early middle Miocene between 17 and 16 Ma. Then, its distribution extended widely to encompass the late middle Miocene of Southeast Asia. Evidence for this range extension is provided by the fossil record of Lagomeryx in northern Thailand, where it is represented by Lagomeryx manai, n. sp. Latitudinally, Lagomeryx is also widely distributed, spanning from Thailand to Mongolia, as wide as that of Stephanocemas (Wang et al., 2009). This biogeographic record supports an interpretation of a European origin of lagomerycines. A common ancestor of cervids probably originated from Asia, followed by a dispersal event to Europe (Gentry et al., 1999).

STABLE ISOTOPE ANALYSIS

We consider here carbon and oxygen isotopes extracted from the carbonate apatite of the enamel of mammalian teeth. Twenty four samples (proboscidean and rhinoceros are serial samples taken from the same tooth) corresponding to five mammalian taxa: cervids (Lagomeryx manai, n. sp.), indeterminate bovids, pigs (Conohys thailandicus), rhinoceros (Gaindatherium sp.), and proboscideans (Stegolophodon sp.) (Table 1) were collected from the Q and K coal layers of the Mae Moh coal mine. Similar pretreatment was used for all fossils and modern samples and the results for the enamel do not show any evidence of diagenetic contamination according to the same preparation of samples for the isotope analysis by Bocherens et al. (1996) and Pushkina et al. (2010).

Carbon Isotopic Results and Herbivore Diets and Habitats

Herbivore enamel samples from the Mae Moh locality display δ13C values ranging between −12.6% and −6.9% (Table 1 and Fig. 7A). Gaindatherium sp. has the most negative mean δ13C value.

| Taxa                | N  | Mean | SD  | Range          | Mean | SD  | Range          |
|---------------------|----|------|-----|----------------|------|-----|----------------|
| Lagomeryx manai n. sp. | 4  | −8.4 | 0.9 | −9.1 to −6.9   | −7.3 | 2.1 | −10.7 to −5.2  |
| Bovidae indet.      | 2  | −11.1| 0.4 | −11.5 to −10.7 | −3.4 | 1.8 | −5.3 to −1.7   |
| Conohys thailandicus| 2  | −9.7 | 0.2 | −9.9 to −9.5   | −8.6 | 1.8 | −10.5 to −6.8  |
| Stegolophodon sp.   | 4* | −9.5 | 0.1 | −9.6 to −9.3   | −7.8 | 0.3 | −8.1 to −7.4   |
| Gaindatherium sp.   | 12*| −12.0| 0.6 | −12.6 to −10.7 | −8.3 | 0.4 | −9.1 to −7.4   |

TABLE 1. Carbon and oxygen isotopic values of Mae Moh herbivores, per sample (N). *Correspond to the samples with serial sampling (not different individuals).
FIGURE 6. Biogeographic and chronological positions of the *Ligeromeryx*-Lagomeryx clade. Most of the species ranges are approximate. Phylogenetic relationships are based on strict consensus tree from our cladistic analysis.

FIGURE 7. Bivariate plot of mammalian isotopic data from Mae Moh Basin. (A) $\delta^{13}C$ versus $\delta^{18}O$ values for 24 tooth enamel samples; (B) $\delta^{13}C$ versus $\delta^{18}O$ values for 11 individual teeth.
of $-12\%$ ± 0.5\% (12 samples from two individual teeth). Another taxon displaying the subordinate negative $\delta^{13}C$ value is a bovid, which has a mean carbon isotope value of $-11.1\%$ ± 0.4\% (two individual samples). The two intermediate $\delta^{13}C$ values, suit (Conohyus thailandicus) and proboscidean (Stegolophodon sp.), display a mean of $-9.7\%$ ± 0.2\% (two individual molars) and $-9.5\%$ ± 0.1\% (four samples taken from one individual), respectively. Interestingly, the most positive carbon isotope values are observed in Lagomeryx manai, n. sp., representing a mean value of $-8.4\%$ ± 0.9\%.

As the age for Q and K coal layers of the Mae Moh locality recognized as being the late middle Miocene (around 13.4–13.2 Ma) (Coster et al., 2009), the ecosystem of this locality is naturally dominated only by C3 plants (Cerling et al., 1997; Zhang et al., 2009). Recent studies of carbon isotopes in pure C3-dominated environments explain the observed differences as a consequence of the different resource partitioning of herbivores (Bocherens, 2003; Cerling et al., 2004; Feranec and MacFadden, 2006; Tütken and Vennemann, 2009). Taxa feeding in more closed and mesic habitats are expected to have more negative carbon isotope values than those feeding in more open and/or arid environments (Cerling et al., 2004).

Compared with the mean $\delta^{13}C$ values ($-10.7\%$) observed among all taxa in this locality (Fig. 7B), the more positive $\delta^{13}C$ value for Lagomeryx manai, n. sp., may indicate occupation in a more open C3 habitat. The intermediate negative carbon isotope values observed in a pig and a proboscidean, Conohyus thailandicus and Stegolophodon sp., respectively, may suggest residence in more closed habitats than the cervid, and probably use of both open and forested habitats. The bovid has a rather negative $\delta^{13}C$ value compared with the other taxa, implying use of a more closed habitat, probably the ecotone between open grasslands and closed habitats that were very dense. Concerning the most negative $\delta^{13}C$ value measured for the rhinoceros (Gaindatherium sp.), it indicates a woodland or closed environments related to a canopy that was not very dense, according to the fact that the lowest $\delta^{13}C$ value is not very negative ($-12.6\%$) as compared with several other pure C3-dominated localities (MacFadden and Higgins, 2004; Feranec and MacFadden, 2006; Tütken and Vennemann, 2009). In addition, dentine $\delta^{13}C$ values of the rhinoceros and proboscideans are less negative than the enamel of the same individuals (see Appendix 5), indicating burial in an open environment as swamp deposits, as suggested by the sedimentology (Chaoedmrong, 1985).

**Oxygen Isotopic Results and Interpretations**

The range of $\delta^{18}O$ values among these taxa is much wider than the range observed for the $\delta^{13}C$ results (Table 1), varying from $-10.7\%$ to $-1.7\%$. The mean $\delta^{18}O$ of Lagomeryx manai, n. sp., is $-7.3\%$ ± 2.1\%. The bovid and rhinoceros display a mean $\delta^{18}O$ value at $-3.4\%$ ± 1.8\% and $-8.3\%$ ± 0.4\%. The pig (Conohyus thailandicus) has the most negative $\delta^{18}O$ value, with a mean at $-8.6\%$ ± 1.8\%. The proboscidean as Stegolophodon sp. has also a negative $\delta^{18}O$ value displaying a mean of $-7.8\%$ ± 0.3\%. Except for the bovid, all the other $\delta^{18}O$ values are somewhat similar, with about 1% total range for average values per taxon.

Generally, the animals that occupy open habitats would be expected to ingest more positive $\delta^{18}O$ as compared with taxa foraging in a cooler and moister forest habitat (Feranec and Mac-Fadden, 2006). The mammals drinking frequently display lower $\delta^{18}O$ enamel values, which are dependent on rainwater $\delta^{18}O$ values (Levin et al., 2006).

Pigs and proboscideans display rather similar $\delta^{13}C$ and $\delta^{18}O$ values, which suggest the same ecological niche (Fig. 7B). The pig, Conohyus thailandicus, which displays the lowest mean $\delta^{18}O$ value, was probably feeding in a more humid environment. Lagomeryx manai, n. sp., suggested as an open habitat animal in our study of its $\delta^{13}C$ values, displays a slightly higher $\delta^{18}O$ value than the other closed habitat taxa, except the bovid. The mean $\delta^{18}O$ value of this cervid indicates that it foraged predominantly in a more open environment or feeding on a somewhat more $^{18}O$-enriched diet. Two closed habitat taxa: an indeterminate bovid and a rhinoceros (Gaindatherium sp.), have mean enamel $\delta^{18}O$ values around $-5.3\%$ ± 1.8\% and $-8.3\%$ ± 0.4\%. The most positive $\delta^{18}O$ value of bovids suggests that it probably sometimes fed in an open habitat or was more water dependent species. The rhinoceros possibly foraged preferentially in a more humid environment related to its adaptation to moist or water-rich environments (Tütken and Vennemann, 2009). With their high ranges of mean $\delta^{18}O$ values, these taxa (Table 1) might have ingested water with variable $\delta^{18}O$ values. However, it is difficult to interpret absolutely the $\delta^{18}O$ values with a few samples of each taxon because the oxygen isotope composition in mammalian tooth enamel is dependent on several important factors, such as the isotopic composition of the ingested water, the consistent fractionation of oxygen isotopes between the body water and the tooth enamel, and the animal’s metabolism (Kohn, 1996; Kohn et al., 1996).

**Serial Isotope Analysis Results and Interpretations**

We also analyzed serial samples from three individuals of two large herbivorous taxa: upper and lower molars of the rhinoceros (Gaindatherium sp.) and one lower molar of the proboscidean (Stegolophodon sp.) (Fig. 8 and Appendix 5), which cover a longer time period than other groups analyzed (Feranec and Mac-Fadden, 2000; Passey and Cerling, 2002). The serial samples of Gaindatherium sp. have a potential to show seasonal variations, corresponding to more than one year (Goddard, 1970; Tafforeau et al., 2007). The Gaindatherium serial samples (N = 7 and 5) from two individuals (upper and lower molars) yield rather similar results of carbon and oxygen isotopes representing total $\delta^{13}C$ ranges of 1.9\% ($-12.6\%$ to $-10.7\%$ for upper molars) and 1.8\% ($-12.5\%$ to $-10.7\%$ for lower molars), with $\delta^{18}O$ ranges of 1.7\% ($-9.1\%$ to $-7.4\%$) and 0.9\% ($-8.5\%$ to $-7.6\%$), respectively. The serial sample of Stegolophodon sp. (N = 4) displays the $\delta^{13}C$ and $\delta^{18}O$ values ranging of 0.3\% ($-9.6\%$ to $-9.3\%$) and 0.7\% ($-8.1\%$ to $-7.4\%$), respectively.

As observed in the serial sample of some late Miocene/early Pliocene herbivores in eastern Tennessee, the carbon and oxygen isotope values, which display less than 1.5\% variation, indicate the lack of significant seasonal variation (DeSantis and Wallace, 2008). Moreover, the annual variation in carbon and oxygen isotope values can yield differences as great as 4\% in tooth enamel of taxa that lived in seasonally variable climates (Feranec and MacFadden, 2000).

As a result in the Mae Moh serial samples, there is little variation in the $\delta^{13}C$ and $\delta^{18}O$ values for the rhinoceros teeth (Fig. 8), indicating the lack of significant seasonal variation. A small fluctuation of $\delta^{13}C$ values is likely caused by the variation observed in the water stress of consumed C3 plants as seen in $\delta^{13}C$ data from Myanmar rhinoceros (late Miocene/early Pliocene) (Zin-Maung-Maung-Thein et al., 2011). The slightly lower $\delta^{18}O$ values observed on the base of the crown of the rhinoceros upper molar might be explained by the prebirth or/and preweaning water supply followed by the gradual reduction in the consumption of milk, related to the subsequent increase of $\delta^{18}O$ values. On the other hand, the variable range of the beginning $\delta^{18}O$ values is also based on the formation of molar, as demonstrated by Zazzo et al. (2002). Unfortunately, the molar sample of Stegolophodon sp. displays a relatively strong wear signature. The lack of seasonal variation might therefore be explained by the sampling design and sample series from the individual molar, being not long enough to encompass a full annual increment of molar growth. However, the lack of significant variation in both carbon and oxygen isotopes from the serial samples of these two herbivores
suggests minor differences in monthly precipitation and/or temperatures during the late middle Miocene of Thailand.

**DISCUSSION**

**Niche Partitioning between European and Thai Middle Miocene Cervids**

Based on mesowear data, the species of *Lagomeryx* from Europe were classified as pure browsers (Kaiser and Rössner, 2007). Rössner (2010) published the δ13C isotopic data from molar samples of two European species of *Lagomeryx*: *Lagomeryx parvulus* (−11.8‰) and *Lagomeryx pumilio* (−12.2‰) (Rössner, 2010:table 8). However, the highest δ13C value is found in the enamel of *Lagomeryx manai*, n. sp. (−8.4‰), which indicates a diet of C3 plants experiencing water stress. The δ13C values of the two European species of *Lagomeryx* are relatively lower than in those of *Lagomeryx manai*, n. sp., indicating the occupation of a more closed habitat for these two small-sized *Lagomeryx* from Europe. *Lagomeryx manai*, n. sp., was therefore probably not a closed-canopy browser as the European *Lagomeryx*. According to the isotopic study of the Mae Moh cervid tooth enamel, it appears that the late middle Miocene *Lagomeryx* foraged preferentially in an open-canopy environment at least in northern Thailand.

**Intratooth Variations and Mae Moh Climate**

Palynological data in the Mae Moh Basin indicate a forested environment with mixed vegetation associated with tropical and warm temperate elements, including deciduous, evergreen, and needle-leaved trees (Sepulchre et al., 2010). These data show that the vegetation cover and climate observed in Q and K layers (13.4–13.2 Ma) of the Mae Moh Basin were far from stable. In contrast to serial Mae Moh samples (Q and K layers), there are no carbon and oxygen isotopic shifts from the tooth enamel of large herbivore fossils. The serial δ13C and δ18O values of rhinoceros and proboscidean molars indicate the consumption of pure C3 plants throughout the course of a year with the absence of seasonal changes in meteoric water due to precipitation and/or temperature (Fig. 8). These serial sample values therefore provide an evidence for a more equable climate than today. However, the serial oxygen isotope analyses of mammalian teeth from the Irrawaddy sediments at Chaingzauk area of Myanmar show seasonal variations under the influence of the climatic changes during late Miocene/early Pliocene (Zin-Maung-Maung-Thein et al., 2011). It is probable that a seasonal pattern of the rainy season interrupted by a dry season might have occurred in the northern part of Thailand beginning at the latest Miocene/early Pliocene.

Compared with oxygen mammalian isotope data from Linxia Basin (middle Miocene (14–13 Ma) of northern China) (Wang and Deng, 2005), the range of δ18O values in Linxia (varying from −11‰ to −7‰) is more negative than the oxygen isotopic range of Mae Moh mammalian data from Q and K layers (−10.7‰ to −1.7‰) (Table 1), probably indicating cooler temperatures and/or less arid conditions than in lower latitudes. According to evidence from the uppermost coal layer (I) of the Mae Moh Basin, the extreme distribution of tropical castorids, as *Steneofiber*, extended widely from the northern continent (Europe and China) to northern Thailand (Suraprasit et al., 2011) and the occurrence of hominoids also supports the warmer climatic preference for late middle Miocene mammals in Southeast Asia, at least between 12.4 and 11.6 Ma.
Diets and Habitats of Thai Herbivores: Late Middle Miocene to Modern Day

The stable carbon isotope data observed from tooth enamel of terrestrial mammals during the late middle Pleistocene of the snake cave or Tham Wiman Nakin (northeastern Thailand) suggest that all bovids and the majority of cervids foraged in an open C4 habitat, whereas wild pigs were displaying mixed feeding habits (Pushkina et al., 2010). These authors also mentioned that the Tham Wiman Nakin and modern rhinoceros maintained their preferences for closed-canopy forests as well as modern elephants. Moreover, some extant cervids can be observed in both open habitats (the grassland and alluvial plain) and densely forested habitats of Thailand (Lekagul and McNeely, 1977). The Mae Moh isotopic data also suggest that the cervid and rhinoceros adaptations for residence in same habitat canopy (an open grassland for cervids and a forested habitat for rhinoceros) have occurred since the late middle Miocene in Thailand. However, the late middle Pleistocene and modern rhinoceros foraged preferentially in more closed habitats than those of Mae Moh rhinoceros. In contrast, the carbon isotopic results of Mae Moh bovids indicate occupation of different ecological niches at least since the late middle Pleistocene, but being similar to modern bovids. Additionally, the modern elephants occupy predominately more-closed environments than those of late middle Miocene proboscidea. The Mae Moh pigs, *Conohys thailandicus*, also seem to occupy mixed habitats (open and closed canopy), similar to those of Tham Wiman Nakin and modern wild pigs (Lekagul and McNeely, 1977; Pushkina et al., 2010).

Our results show that great differences occurred in habitat and species diets when compared with modern and late middle Pleistocene mammals in Thailand. Future analyses of better-dated samples and a larger number of samples are needed to study further the gap between late middle Miocene and late middle Pleistocene data.

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APPENDIX 1. Cranial appendage measurements (in millimeters) of two cervids, *Lagomeryx manai*, sp. nov. (holotype, UPP MM-1), and *Stephanocemas rucha* (UPP MM-19), from Mae Moh locality. The cross-section of tines has been taken from anteroposterior and mediolateral diameters.

|                      | Lagomeryx manai, n. sp. (holotype) | Stephanocemas rucha (UPP MM-19) |
|----------------------|-----------------------------------|----------------------------------|
| Pedicle height (posterior) | 110.67                           |                                  |
| Anteroposterior diameter of pedicle | 20.79 | 18.79 |
| Mediolateral diameter of pedicle | 19.32 | 14.25 |
| Anterior medial tine (am2) | 23.52 | 11.24 × 9.23 |
| Medial tine (m) | 15.27 | 7.55 × 6.83 |
| Posterior medial tine (pm) | 10.53 × 7.11 |                         |
| Posterior lateral tine (pl2) | 8.11 × 5.23 |                         |
| Anterior lateral tine (al) | 9.23 | 5.93 × 5.42 |
| Anterior medial tine (am2) | 9.98 × 9.04 |                         |
| Medial tine (m) | 10.42 × 8.47 |                         |
| Posterior tine (p) | 9.16 × 8.14 |                         |
| Anterior lateral tine (al) | 9.16 × 8.14 |                         |

APPENDIX 2. Protoantler measurements (in millimeters) of referred specimens of two cervids, *Lagomeryx manai*, n. sp., and *Stephanocemas rucha*. Length and cross-section diameter have been measured beginning at the point where the tine splits in dorsal view.

| Dimension               | Lagomeryx manai, n. sp. | Stephanocemas rucha |
|-------------------------|-------------------------|---------------------|
| UPP MM-2                |                         |                     |
| Maximum anteroposterior of palm | 47.43 |                     |
| Anterior tine (a2) | 7.31 × 6.69 |                     |
| Anterior medial tine (am1) | 7.37 × 7.24 |                     |
| Anterior medial tine (am2) | 9.64 × 8.52 |                     |
| Medial tine (m) | 9.98 × 9.04 |                     |
| Posterior medial tine (pm) | 10.42 × 8.47 |                     |
| Posterior tine (p) | 9.16 × 8.14 |                     |
| UPP MM-3                |                         |                     |
| Anterior medial tine (am2) | 21.71 |                     |
| Medial tine (m) | 10.25 × 7.82 |                     |
| UPP MM-4                |                         |                     |
| Anterior tine (a1) | 9.04 × 5.57 |                     |
| Anterior medial tine (pm) | 9.11 × 7.59 |                     |
| Posterior lateral tine (pl) | 6.81 × 5.87 |                     |
| Stephanocemas rucha     |                         |                     |
| T Li 67 (holotype)      |                         |                     |
| Maximum anteroposterior of palm | 49.47 |                     |
| Mediolateral palm | 27.57 |                         |
| Anterior tine (a) | 12.92 × 10.19 |                     |
| Anterior lateral tine (al) | 9.43 × 8.89 |                     |
| Posterior lateral branch (pl1 and pl2) | 14.09 × 8.95 |                     |
| UPP MM-20               |                         |                     |
| Posterior lateral tine (pl1) | 16.65 |                     |
| Posterior lateral tine (pl2) | 10.07 × 7.43 |                     |
| UPP MM-21               |                         |                     |
| Anterior medial tine (am) | 9.11 × 7.11 |                     |
| Posterior medial tine (pm) | 7.17 × 6.57 |                     |
| Posterior lateral tine (pl) | 8.88 × 7.19 |                     |
| Anterior lateral tine (al) | 6.25 × 5.36 |                     |

APPENDIX 3. Dental measurements, length, width, crown height, and hypsodont index ratio, of two cervids, *Lagomeryx manai*, sp. nov., and *Stephanocemas rucha* from Mae Moh Basin. The length (L) has been taken from the anterolabial to posterolabial border of upper teeth and from the anterolingual to posterolingual border of lower teeth. The width (W) has been measured at the anterior part of teeth. The crown height (H) has been measured at the labial side of upper teeth and at the lingual side of lower teeth, starting at the base of the crown.

| Specimen no. | Tooth | L | W | H | H/L |
|--------------|-------|---|---|---|-----|
| Lagomeryx manai, n. sp. | | | | | |
| UPP MM-5     | Right m1 | 14.75 | 9.62 | 11.39 | 0.77 |
|              | Right m2 | 17.35 | 10.39 | 11.36 | 0.65 |
|              | Right P4  | 10.16 | — | 10.28 | 1.01 |
| UPP MM-6     | Left M1  | 13.99 | 17.37 | 5.84 | 0.42 |
| UPP MM-7     | Left M2  | 16.32 | 18.99 | 11.32 | 0.69 |
| UPP MM-8     | Right M3 | 15.08 | 17.47 | 6.10 | 0.40 |
| UPP MM-9     | Right M3 | 14.59 | — | 11.03 | 0.76 |
| UPP MM-10    | Left M3  | 16.99 | 20.29 | 12.06 | 0.71 |
| UPP MM-11    | Left M2  | 16.66 | 11.75 | 10.46 | 0.63 |
| UPP MM-12    | Right m2 | 16.95 | 10.44 | 12.73 | 0.75 |
| UPP MM-13    | Right m2 | 17.40 | 11.78 | 12.19 | 0.70 |
| UPP MM-14    | Right m2 | 16.11 | 12.83 | 9.80 | 0.61 |
| UPP MM-15    | Left m2  | 15.08 | 12.03 | 9.83 | 0.65 |
| UPP MM-16    | Left m3  | 20.98 | 11.67 | 7.53 | 0.36 |
| UPP MM-17    | Left m3  | 21.98 | 11.69 | 13.64 | 0.62 |
| Stephanocemas rucha | | | | | |
| UPP MM-22    | Right M3 | 14.40 | 16.75 | 7.61 | 0.53 |
| UPP MM-23    | Right M3 | 13.28 | 15.64 | 6.81 | 0.51 |
| UPP MM-24    | Right M3 | — | — | 6.12 | — |
| UPP MM-25    | Left p4  | 11.98 | 6.81 | 9.52 | 0.79 |
| UPP MM-26    | Left m2  | 13.46 | 9.89 | 6.34 | 0.47 |
| UPP MM-27    | Left m2  | 13.41 | 9.10 | 7.58 | 0.57 |
| UPP MM-28    | Right m3 | 16.50 | 9.60 | 6.81 | 0.41 |
APPENDIX 4. Character matrix of the cladistic analysis with cranial appendage characters and states. ‘?’ indicates a missing character due to the incomplete material.

| Taxa                        | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|-----------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|
| Procervulus praelucidus     | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| Euprox robustus             | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0  | 0  | 0  | 1  | 0  | 0  | 0  |
| Euprox furcatus             | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0  | 0  | 0  | 1  | 0  | 0  | 0  |
| Ligeromeryx praestans       | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1  | 0  | 1  | 0  | 0  | 1  | 0  |
| Lagomeryx parvalus          | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1  | ?  | ?  | ?  | 1  | 0  | 1  |
| Lagomeryx ruetimeyeri       | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 1  | 0  | 0  | 1  | 0  |
| Lagomeryx triacuminatus     | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 1  | 0  | 0  | 0  | 1  | 0  | 0  |
| Lagomeryx sp. (Xinjiang)    | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | ? | ?  | ?  | ?  | 1  | 0  | 1  | 0  |
| Lagomeryx colberti          | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1  | 0  | 1  | 0  | 1  | 1  | 1  |
| Lagomeryx tsaidamensis      | 1 | 2 | 2 | 0 | 1 | 2 | 1 | 1 | 1 | 1  | 0  | 0  | 1  | 0  | 0  | 1  |
| Lagomeryx manai, n. sp.     | 1 | 2 | 2 | 0 | 2 | 0 | 1 | 2 | 1 | 1  | 1  | 1  | 1  | 1  | 0  | 1  |

1. Protoantler morphology: forked (0); multibranched (1); multipointed (2).
2. Palmate antler: absent (0); small (1); large (2).
3. Mediolateral extension of protoantler: absent or narrow (0); moderately wide (1); wide (2).
4. Proboscur: absent (0); present (1).
5. Total number of tines: 2 or 3 (0); 4–7 (1); more than 7 (2).
6. Tine-sizes represented within protoantler: unequal (0); equal (1).
7. Tine bifurcation: absent (0); present (1).
8. Lateral tines: absent or poorly developed (0); 1 or 2 (1); 2 or 3 (2) (Wang et al., 2009).

(9) Anterior tine orientation: vertical or nearly vertical (0); nearly horizontal (1).
10. Pedicle length: short (0); long (1).
11. Pedicle direction above orbits (lateral view): upright or slightly anterior (0); posterior (1).
12. Pedicle projecting above orbits (anterior view): straight or slightly inward (0); outward (1).
13. Pedicle shape: straight (0); curved at distal part (1).
14. Pedicle cross-section: circular (0); oval or ellipse (1).
15. Distal part of pedicle below protoantler: mediolaterally compressed (0); slightly or not compressed (1).
16. Protoantler slope lying on pedicle: horizontal (0); anterior bending (1).

APPENDIX 5. Stable carbon and oxygen isotopic values of Mae Moh mammalian teeth.

| Taxa                        | Distance from crown (mm) | CO₂ content (%CaCO₃) | δ¹³C (% VPDB) | δ¹⁸O (% VPDB) | δ¹⁸O (% SMOW) |
|-----------------------------|--------------------------|----------------------|---------------|---------------|---------------|
| Lagomeryx manai, n. sp.     | 4.0                      | −6.94                | −7.28         | 24.42         |
| Lagomeryx manai, n. sp.     | 3.2                      | −8.83                | −10.67        | 23.70         |
| Lagomeryx manai, n. sp.     | 4.9                      | −9.14                | −5.24         | 24.27         |
| Lagomeryx manai, n. sp.     | 5.6                      | −8.78                | −6.00         | 25.84         |
| Bovidae                     | 4.5                      | −11.53               | −5.31         | 23.11         |
| Bovidae                     | 4.6                      | −10.72               | −1.67         | 27.74         |
| Conohyus thailandicus      | 2.6                      | −9.91                | −10.45        | 27.97         |
| Conohyus thailandicus      | 3.5                      | −9.51                | −6.82         | 24.36         |
| Stegolophodon sp.           | 0                        | −9.28                | −8.07         | 24.48         |
| Stegolophodon sp.           | 4                        | −9.62                | −7.41         | 23.57         |
| Stegolophodon sp.           | 8                        | −9.58                | −8.04         | 23.69         |
| Stegolophodon sp.           | 12                       | −9.45                | −7.71         | 22.68         |
| Gaindatherium sp. upper molar | 5.2                     | −10.71               | −9.07         | 29.75         |
| Gaindatherium sp. upper molar | 4.3                     | −11.72               | −8.47         | 26.46         |
| Gaindatherium sp. upper molar | 3.3                     | −12.03               | −7.94         | 24.36         |
| Gaindatherium sp. upper molar | 12                      | −12.26               | −7.92         | 23.91         |
| Gaindatherium sp. upper molar | 16                      | −12.41               | −8.44         | 23.16         |
| Gaindatherium sp. upper molar | 20                      | −12.21               | −8.57         | 24.79         |
| Gaindatherium sp. upper molar | 24                      | −12.64               | −7.40         | 23.73         |
| Gaindatherium sp. lower molar | 0                        | −10.68               | −8.27         | 26.39         |
| Gaindatherium sp. lower molar | 4                        | −12.22               | −8.44         | 26.02         |
| Gaindatherium sp. lower molar | 8                        | −12.10               | −8.47         | 22.93         |
| Gaindatherium sp. lower molar | 12                      | −12.54               | −8.49         | 22.78         |
| Gaindatherium sp. lower molar | 16                      | −12.20               | −7.64         | 25.70         |
| Dentine of Stegolophodon sp. | 8.5                      | −6.04                | −9.33         | 28.43         |
| Dentine of Gaindatherium sp. | 6.4                      | −6.81                | −9.17         | 30.50         |
| Dentine of Gaindatherium sp. | 8.1                      | −6.28                | −9.25         | 26.31         |

The isotopic values of C and O were measured automatically with a Gasbench II system directly connected to a Finnigan Mat 252 mass spectrometer. The isotopic ratios of the samples are calibrated with NBS18 (δ¹³C = −5.00, δ¹⁸O = −22.96 Permille, relative to VPDB) and NBS19 (δ¹³C = 1.95, δ¹⁸O = −2.20 Permille, relative to VPDB). The external reproducibility is better than ±0.1 Permille for δ¹³C and ±0.1 Permille for δ¹⁸O measurements. The external reproducibility for the carbonate content is ±10%. The fractionation of the acid reaction was calculated for the calcite.