

Systematics and palaeoecology of Ruminantia (Artiodactyla, Mammalia) from the Miocene of Sandelzhausen (southern Germany, Northern Alpine Foreland Basin)

Gertrud E. Rössner

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Abstract In more than 20 years of excavation at the fossil lagerstätte Sandelzhausen (Early/Middle Miocene boundary, Burdigalian/Langhian boundary, early middle MN5) a substantial amount of fossil remains of ruminants have been recovered. Currently, it is the largest recorded assemblage of ruminants from the Miocene Northern Alpine Foreland Basin. More than 1,000 teeth, almost 70 antler remains and one skull enable the identification of five ruminants, namely the tragulid *Dorcatherium crassum*, the palaeomerycid *Germanomeryx* n. g. *fahlbuschi* n. sp., and the cervids *Lagomeryx parvulus*, *Lagomeryx pumilio*, and *Heteroprox eggeri* n. sp. *Lagomeryx parvulus* and *L. pumilio* have the most extensive record yet known for these species, opening up a much more complete view of them 120 years after the discovery of the type materials. The newly established *G.* n. g. *fahlbuschi* n. sp. and *H. eggeri* n. sp. enlarge our knowledge on the taxonomic composition of Miocene European Ruminantia. Because of the exceptionally large number of specimens, nearly all tooth positions of all five species are documented, thereby completing hitherto partially known character sets. The investigation comprises extensive taxonomic descriptions of all species represented and an interpretation of the palaeoecology based on an analysis of the community structure. This clearly suggests a humid closed canopy forest interspersed with temporary and perennial waters and accompanying open areas. Moreover, a comparison

with other, stratigraphically close Molasse Basin communities emphasizes the various peculiarities of the Sandelzhausen community (low species number, cervid-dominance, dominance of *L. pumilio* over *L. parvulus*, non-dominance of very small-sized ruminants, comparably high portion of palaeomerycids, all species being browsers, no *Eotragus* and no *Amphimoschus*). The investigation also clarifies the similarity with the communities from Undorf and Viehhausen (Germany, MN5). The deduced dynamics in community structure of the late Early and early Middle Miocene Northern Alpine Foreland Basin provides further support for the current hypothesis of a vast wetland environment under the strong influence of alternating dry and flood seasons.

Keywords Tragulidae · Cervidae · Palaeomerycidae · Phylogeny · Palaeoecology · Biostratigraphy

Kurzfassung In mehr als 20 Jahren Grabung an der Fossilagerstätte Sandelzhausen (Grenze Unter-/Mittelmiozän, Grenze Burdigalium/Langhium, frühes mittleres MN5) wurde eine beachtliche Menge an fossilen Resten von Wiederkäuern geborgen. Gegenwärtig ist das die umfangreichste überlieferte Ansammlung von Wiederkäuern aus dem miozänen nordalpinen Molassebecken. Mehr als 1000 Zähne, fast 70 Geweihreste und ein Schädel erlauben die Identifizierung bzw. die Aufstellung des Traguliden *Dorcatherium crassum*, des Palaeomeryciden *Germanomeryx* n. g. *fahlbuschi* n. sp., sowie der Cerviden *Lagomeryx parvulus*, *Lagomeryx pumilio* und *Heteroprox eggeri* n. sp. *L. parvulus* und *L. pumilio* sind mit dem bei weitem umfangreichsten Material dieser Arten überliefert, was endlich eine wesentlich vollständigere Kenntnis 120 Jahre nach der Entdeckung des Typusmaterials möglich macht. Die neu aufgestellten Arten *G.* n. g. *fahlbuschi* n. sp. und

G. E. Rössner (✉)
Bayerische Staatssammlung für Paläontologie
und Geologie München, Paläontologie und Geobiologie
des Departments für Geo- und Umweltwissenschaften
and Geobio-Center of the Ludwig-Maximilians-Universität
München, Richard-Wagner-Str. 10, 80333 Munich, Germany
e-mail: g.roessner@lrz.uni-muenchen.de

H. eggeri n. sp. ergänzen das Wissen über die taxonomische Zusammensetzung der miozänen Ruminantia Europas. Dank der aussergewöhnlich hohen Zahl an fossilen Resten sind beinahe alle Zahnpositionen aller fünf Arten dokumentiert, welche die bisher bekannten Merkmalsreihen wesentlich vervollständigen. Die Studie umfasst umfangreiche taxonomische Beschreibungen aller repräsentierten Arten sowie eine Interpretation verschiedener Aspekte der Paläoökologie. Letztere baut auf einer Analyse der Struktur der Lebensgemeinschaft auf und lässt auf einen humiden dichten Wald mit geschlossenem Blätterdach durchsetzt von temporären sowie perennierenden Gewässern und begleitenden offenen Bereichen als Lebensraum schließen. Des Weiteren hebt ein Vergleich mit anderen stratigraphisch nahen Vergesellschaftungen des Nordalpinen Vorlandbeckens die Besonderheiten der Vergesellschaftung von Sandelzhausen hervor (niedrige Artenzahl, Cerviden-Dominanz, Dominanz von *L. pumilio* über *L. parvulus*, fehlende Dominanz der sehr kleinen bis kleinen Wiederkäuer, vergleichsweise hoher Anteil der Palaeomeryciden, ausschließlich *Browser*, kein *Eotragus* und kein *Amphimoschus*). Gleichzeitig wird damit aber auch die Ähnlichkeit zu den Vergesellschaftungen von Undorf und Viehhausen (MN5, Deutschland) deutlich. Die abgeleitete Dynamik in den Strukturen dieser Wiederkäuergemeinschaften des späten Früh- und des frühen Mittelmiozän liefert Argumente für die aktuelle Hypothese eines weit ausgedehnten Süßwasserfeuchtgebietes unter dem Einfluß jahreszeitlich wechselnder Trocken- und Hochwasserphasen.

Schlüsselwörter Tragulidae · Cervidae · Palaeomerycidae · Phylogenie · Paläoökologie · Biostratigraphie

Introduction

Since the beginning of palaeontological investigations in Miocene sediments of the German Northern Alpine Foreland Basin (NAFB) the revealed ruminant fossil remains have been studied only intermittently (von Meyer 1846; Rüttimeyer 1881; Roger 1885, 1896, 1898, 1900, 1904; Schlosser 1886; Stehlin 1937; Dehm 1944; Rinnert 1956; Fahlbusch 1977, 1985; Rössner 2004, 2006). They represent a continuous component of the numerous large mammal faunal assemblages, reflect a colonisation of the wetland environment emerging from the regression of the Paratethys, and a successful diversification with a peak in species numbers in the lower Serravalian (MN6) (upper Badenian) (Eronen and Rössner 2007).

The assemblage of ruminant remains from Sandelzhausen is the largest known from the Miocene NAFB. Because of its early middle MN5-age at the Early/Middle Miocene boundary (Moser, Rössner et al. 2009) it

documents a ruminant composition qualitatively and quantitatively unknown within the Miocene Molasse Basin.

Although, several vertebrate groups found at Sandelzhausen have already been described (Moser, Rössner et al. 2009), the Ruminantia from Sandelzhausen have appeared only in faunal lists (Fahlbusch and Gall 1970; Fahlbusch et al. 1974; Rössner 1997, 2004; Fahlbusch 2003; Eronen and Rössner 2007; Kaiser and Rössner 2007) with the exception of the description of a very well preserved antler specimen of the tiny cervid *Lagomeryx* (Fahlbusch 1977). In this paper I give a detailed and comprehensive description of teeth, skull remains, and cranial appendages, and palaeobiological interpretations of the five ruminant taxa represented in Sandelzhausen.

Generally, the material is outstanding in specimen number. It includes the richest known record of the cervids *Lagomeryx pumilio* and *L. parvulus*, hitherto only rarely documented but widely distributed in Central and Western Europe. The tragulid *Dorcatherium crassum* was common in the Early and Middle Miocene of Central, Western and Southwestern Europe, but Sandelzhausen yielded the best-represented population besides the type material from Sansan (MN6, France) (Filhol 1891). Moreover, one new genus and two new species are documented with a considerable quantity of specimens: the palaeomerycid *Germanomeryx* n. g. *fahlbuschi* n. sp. and the cervid *Heteroprox eggeri* n. sp.

Besides the material described here, Sandelzhausen yielded many identifiable ruminant postcranials, which will complete the knowledge of the described species and are planned to be published in the near future.

For details on the fossil site see Moser, Rössner et al. (2009).

This study is an extract of an unpublished Habilitationsschrift (Rössner 2002).

Materials and methods

The described material comprises more than 1,000 teeth (partially in situ in a mandible or maxilla fragment), nearly 70 antler fragments, and one skull. It was collected at the Sandelzhausen fossil site from 1959 to 2001 by the Department für Geo- und Umweltwissenschaften, Sektion Paläontologie, Ludwig-Maximilians-Universität München in association with the Bayerische Staatssammlung für Paläontologie und Geologie München (BSPG) (Fahlbusch 2003; Moser, Rössner et al. 2009). The material is curated at the BSPG under the inventory numbers: BSPG 1959 II... (mainly and omitted in the following text), 1975 IX ..., 1985 II

Careful and extensive morphometric comparison led to the taxonomical identification of five ruminant species. The terminology of tooth crown elements and manner of

measurements of teeth and antlers follows Rössner (1995) or Gentry et al. (1999: Fig. 23.1).

The investigated ruminant material is extensive enough to provide reliable data on some palaeoecological aspects. In detail I chose the taxonomical composition and body mass, because of their far-reaching importance in all ecological levels (autecologic, demecologic, synecologic). Thus a substantial number of possible predictions enable relatively detailed palaeoecological characterisation.

Yet modern faunas show that qualitative taxonomical composition is not convincing with regard to the ecological roles of the species (May 1975; Wing et al. 1992: 8). In order to reconstruct the community structure, quantitative analysis was undertaken. Therefore, all ruminant teeth from Sandelzhausen were counted and the relative abundances of the species were calculated (Table 1). This “total specimen number” approach was chosen to make the dataset adaptable to a comparison with datasets of the ruminant communities from the fossil sites of Walda 2 (middle MN5), and Thannhausen (early MN6), both NAFB, Middle Miocene (for details on these localities see Rössner 2002, 2004). Checking the “minimum number of individuals” approach (maximum number in tooth positions of either the left or the right body side) for the Sandelzhausen community the relative abundance remains more or less the same.

Because body size is a major factor in an animal’s adaptation to its environment (Peters 1983) body-mass estimation has been chosen for the purpose of bringing ecology and physiology of mammals into an evolutionary context. It has been successfully used to characterise ancient physiological condition, population dynamics, and habitats (Legendre 1986; Fortelius et al. 1996; Eronen and Rössner 2007). Here, body mass has been estimated by use of regression lines already set up to correlate variables of physiological significance with body mass in extant ruminants via allometric equations ($\log \text{ body mass} = a + b \log x$; where a is the intercept, b is the slope, and x is the variable) from Janis (1990) and Scott (1990). The variables which had been used are defined linear measurements on bones and teeth with high correlation values (r^2) to body mass (humerus distal width, radius proximal width, metatarsal length, lower molar row length, second lower molar

length, second upper molar length). For this, postcranial material not described here has been used to provide measured values of, if possible, several specimens for each variable, to ascertain body mass estimates for each of the selected high correlation values (Table 2). Specific differentiation of postcranial elements is doubtlessly possible because of size differences and morphological differences, in the case of the identical sized *Heteroprox eggeri* n. sp. and *Dorcatherium crassum*, and because of the richness of the material. The single variables of each ruminant species from Sandelzhausen display large differences in correlated body masses, reflected by a standard deviation up to more than one half of their arithmetic mean (Table 2). These differences are because of specific, yet unknown adaptations in size and morphology deviating from the general trend in extant species (Janis 1990; Scott 1990). However, the ascertained means of body mass estimation give a principal idea on the body masses of each represented species, indicate some aspects in autecology and population ecology, and show the general body mass pattern in the ruminant community.

The body mass estimates well complete the ecological characterization of the Sandelzhausen ruminant species classified in diet categories based on reconstructions of the palaeodiet from Kaiser and Rössner (2007).

Abbreviations for institutions: BMNH = The Natural History Museum London; BSPG = Bayerische Staatssammlung für Paläontologie und Geologie, Munich; HLMD = Hessisches Landesmuseum Darmstadt; MNHN = Musée Nationale d’Histoire Naturelle, Paris; NMA = Naturmuseum Augsburg.

Abbreviations for tooth positions: Cf = upper canine female; Cm = upper canine male; D = upper deciduous tooth; d = lower deciduous tooth; i = lower incisor; M = upper molar; m = lower molar; P = upper premolar; p = lower premolar.

Taxonomic description

The identified ruminant species are listed in systematic order with information on holotype, type locality, chronological occurrence, and description. Newly established

Table 1 Characteristic statistical values of the taxonomic composition of the ruminant assemblage from Sandelzhausen

Species	Number of specimens	Relative abundance of specimens (%)	Minimum number of individuals	Relative abundance individuals (%)
<i>Dorcatherium crassum</i>	94	9	9	12
<i>Germanomeryx fahlbuschi</i>	104	10	6	8
<i>Lagomeryx parvulus</i>	98	10	8	11
<i>Lagomeryx pumilio</i>	274	26	19	25
<i>Heteroprox eggeri</i>	470	45	33	44

Table 2 Body mass estimates for the ruminant species from Sandelzhausen by means of six different highly correlative variables after Janis (1990) and Scott (1990)

Species	Humerus distal width (according to Scott (1990), H5 Ruminantia; $a = 0.2574$, $b = 2.6372$, $r^2 = 0.9599$) (kg)	Radius proximal width (according to Janis (1990), R4 Ruminantia; $a = 0.3872$, $b = 2.4226$, $r^2 = 0.9587$) (kg)	Metatarsal length (according to Janis (1990), Mt1 Ruminantia; $a = -1.8978$, $b = 2.9135$, $r^2 = 0.6219$) (kg)	m1 to m3 length (according to Janis (1990), all selenodonts; $a = -0.80$, $b = 3.27$, $r^2 = 0.92$) (kg)	m2 length (according to Janis (1990) to Janis (1990) all selenodonts; $a = 0.92$, $b = 3.21$, $r^2 = 0.90$) (kg)	M2 length (according to Janis (1990) to Janis (1990) all selenodonts; $a = 0.94$, $b = 3.15$, $r^2 = 0.89$) (kg)	x (kg)	±s
<i>Dorcatherium crassum</i>	2.5 cm/ 20.3	2.1 cm/ 14.7	9.6 cm/ 9.2	4.0 cm/ 14.7	1.2 cm/ 14.9	1.2 cm/ 15.5	14.9	±1.0
<i>Germanomeryx</i> n. g. <i>fahlbuschi</i> n. sp.	7.3 cm/ 342.1	5.2 cm/ 132.4	Not available	8.7 cm/ 187.1	2.6 cm/ 178.7	2.8 cm/ 223.1	212.7	±35.8
<i>Heteroprox eggeri</i> n. sp.	2.8 cm/ 27.3	2.2 cm/ 16.5	18.4 cm/ 61.3	3.8 cm/ 12.5	1.2 cm/ 14.9	1.1 cm/ 11.7	24.0	±8.6
<i>Lagomeryx pumilio</i>	1.1 cm/ 2.3	0.9 cm/ 1.9	Not available	2.0 cm/ 1.5	0.6 cm/ 1.6	0.6 cm/ 1.7	1.8	±0.2
<i>Lagomeryx parvulus</i>	1.5 cm/ 5.3	1.3 cm/ 4.6	11.4 cm/ 15.2	2.4 cm/ 2.8	0.7 cm/ 2.6	0.8 cm/ 4.3	5.8	±3.6

Given are measured value and ascertained value of appendant body mass (in bold), calculated via the regression line, and, for every species, arithmetic mean and standard deviation. Missing measurements and estimated values are because of skeleton elements not documented here. (Abbreviations see “Material and methods”; ±s standard deviation)

Fig. 1 Dental remains of *Dorcatherium crassum* (Lartet 1839) from Sandelzhausen (Inventory-No. BSPG 1959 II ...). **A:** 6635 right jaw fragment with d2 and alveoli of d1; **A1:** lingual view; **A2:** occlusal view, 1.5 times larger than indicated by the scale at the bottom; **A3:** labial view. **B:** 4144 right maxilla fragment M1 to M3; **B1:** labial view; **B2:** occlusal view, 1.5 times larger than indicated by the scale at the bottom. **C:** 6644 left D4, 1.5 times larger than indicated by the scale at the bottom. **D:** 1974 I 10 right jaw with p3 to m3, occlusal view. **E:** 2212 right jaw fragment with m1 to m3; **E1:** lingual view; **E2:** occlusal view, 1.5 times larger than indicated by the scale at the bottom; **E3:** labial view. **F:** 5206 right P2; **F1:** lingual view; **F2:** occlusal view, 1.5 times larger than indicated by the scale at the bottom; **F3:** labial view. **G:** 11660 left P3, **G1:** lingual view; **G2:** occlusal view, 1.5 times larger than indicated by the scale at the bottom; **G3:** labial view. **H:** 4158 left jaw fragment with p4 to m3, occlusal view, 1.5 times larger than indicated by the scale at the bottom. **I:** 3927 left D3, occlusal view, 1.5 times larger than indicated by the scale at the bottom. **J:** 4150 left jaw fragment with p1 to p3; **J1:** occlusal view, 1.5 times larger than indicated by the scale at the bottom; **J2:** labial view. **K:** 1975 I 39 left m3; **K1:** labial view; **K2:** occlusal view, 1.5 times larger than indicated by the scale at the bottom. **L:** 6662 right P4, occlusal view, 1.5 times larger than indicated by the scale at the bottom. **M:** 4146 left jaw fragment with p4 to m3; **M1:** lingual view; **M2:** occlusal view, 1.5 times larger than indicated by the scale at the bottom; **M3:** labial view. **N:** 4157 right jaw with p3 to m1 and alveoli of p1 and p2; **N1:** lingual view; **N2:** occlusal view, 1.5 times larger than indicated by the scale at the bottom; **N3:** labial view. **O:** 4342 left d3, occlusal view, 1.5 times larger than indicated by the scale at the bottom. **P:** 4140 left m3, occlusal view, 1.5 times larger than indicated by the scale at the bottom

species are completed by a synonymy list, diagnosis and differential diagnosis.

Superorder Cetartiodactyla Montgelard et al., 1997

Order Artiodactyla Owen, 1848

Suborder Ruminantia Scopoli, 1777

Infraorder Tragulina Flower, 1883

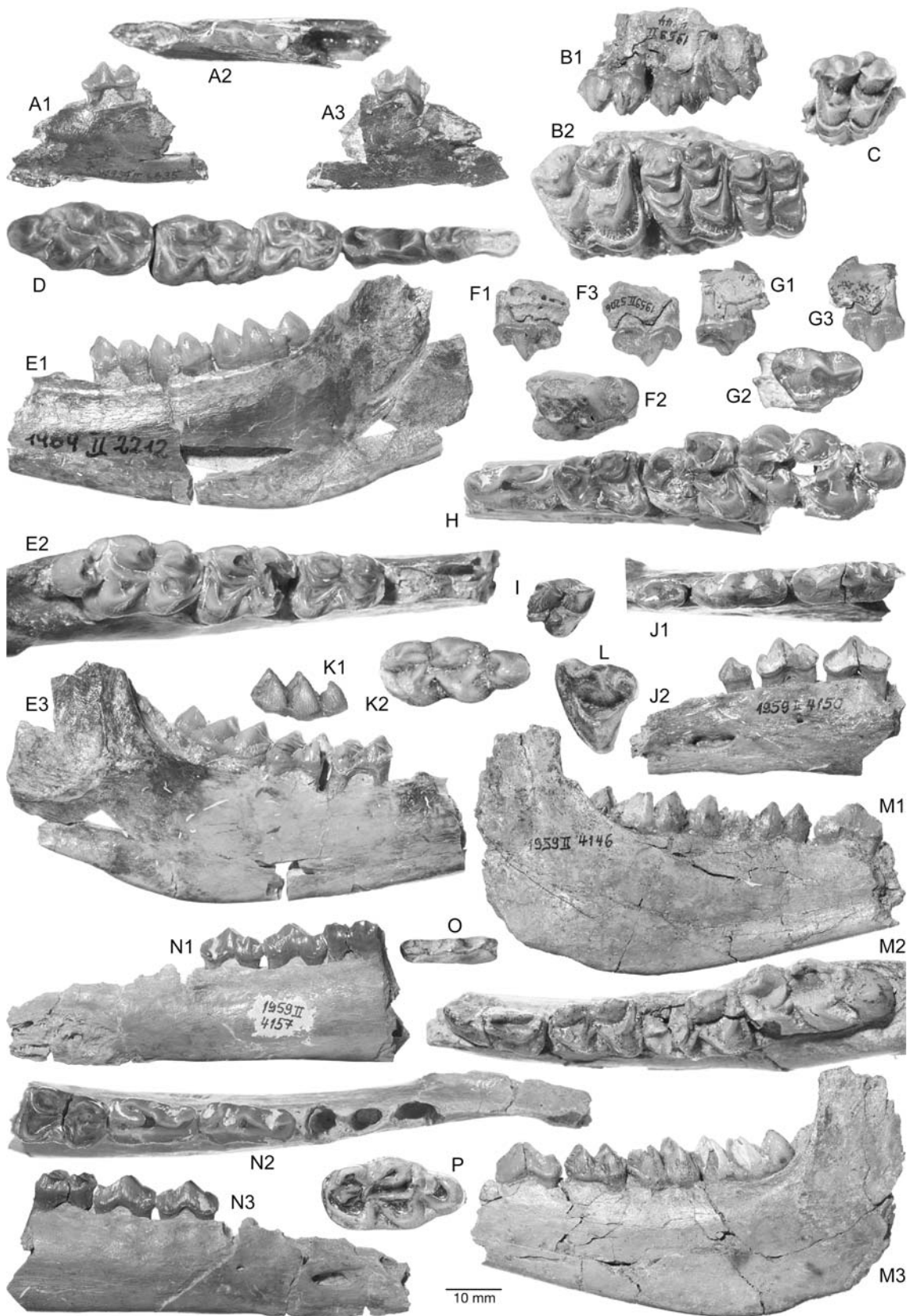
Family Tragulidae Milne-Edwards, 1864

Genus *Dorcatherium* Kaup and Scholl, 1834

Type species: *Dorcatherium nauii* Kaup and Scholl, 1834

Chronological and geographical occurrence of the genus: MN4 (late Early Miocene, early Karpatian, middle Orlanian) (Sach and Heizmann 2001) to MN13 (latest Late Miocene, late Pontian or early Dacian, late Turolian) (Arambourg and Piveteau 1929), eventually Pliocene (Bakalov and Nikolov 1962), in Europe, Middle Miocene (Qiu and Gu 1991) to Early Pliocene (Lydekker 1876) in Asia, late Early Miocene (Set II) (Pickford 2001) to Early Pliocene (Pickford et al. 2004) in Africa.

General information: The genus *Dorcatherium* was established by Kaup and Scholl (1834). The type specimen is a right jaw with m3 to p3 with alveoli of p2 and p1 (Kaup 1839a, b: pl. 23 Fig. 1, 1a, 1b), now lost, but from which casts were made and are stored at the BMNH (M. 3714) (Lydekker 1887). Much information about the genus comes from a skull with both jaws and complete dentition (Kaup 1839a, b: pl. without number between pl. 22 and pl. 23, pl. 23A Figs. 1, 2; pl. 23B Figs. 1–4), two jaw fragments (Kaup 1839a, b: pl. 23 Figs. 1, 1a, 1b, 4, 4a) and



several postcranials (Kaup 1839a, b: pl. 23C Figs. 2, 2a, 2b, 3, 4, 6a, 6b) of *D. nauti* from Eppelsheim (Germany, MN9), which are stored at the HLMD (Kurz and Gruber 2004: 42) and BMNH. The skull comprises brain and a nose capsules of nearly the same length. The nasalia contact the full length of the praemaxillae. Strong elongated sabre-like upper canines can be interpreted as life-long growing, because of a constant tooth diameter and growing stripes over the whole length of the tooth. Two-thirds of the canine is housed in a long maxillary alveolus, which curves back above the cheek tooth row, close to the nasomaxillar contact, to the level of P3. In 1864, Milne Edwards noticed the strong osteological and odontological similarity between the fossil deer *Dicrocerus ? crassus* Lartet 1839 from Sansan (France, reference locality MN6) and the living *Hyemoschus aquaticus*; this prompted him to change the assignment of the species and he included it in *Hyemoschus* and in his newly established family Tragulidae. Currently the genus comprises most of the Mio-Pliocene Eurasian and African tragulids (Rössner 2007). Their teeth are bunoselenodont to selenodont with more or less strong cingula and cingulidae and mostly strong styli and stylidae at the molars. The upper molars increase in size from M1 to M3 (Fig. 1B). The lower molars show a special crest complex called the ‘Dorcatherium-fold’. It is formed by the bifurcation of the posterior slopes of the protoconid and the metaconid resulting in a ‘Σ’ shape (Fig. 1D, E2, H, K2, M2, P). The premolars are comparatively long and consist mainly of the labial conid/conidae and crests. Lingual crown elements are underrepresented. At the p4 the entoconid fuses with the postprotocristid (Fig. 1D, H, M2, N2). The p3 has only a short lingual entocristid originating at the hypoconid (Fig. 1D, J1, N2). An exception is the P4, which is shorter and does not have an anteroposterior longish shape (Fig. 1L). p1 (Fig. 1F) and d1 are optional and variable in length, as is P2 (Fig. 1F), and cuspid number (one or two, not recorded from Sandelzhausen, but from other localities in the German NAFB; Rössner 2002).

***Dorcatherium crassum* (Lartet 1839) Appendix**

Lectotype: Hitherto not established. Type material illustrated in Filhol (1891: pl. XXII Figs. 9–11; pl. XXIII Figs. 1–12; pl. XXX Figs. 1–2), stored at the MNHN. The material was under revision by J. Morales and I.M. Sanchez (both Madrid) and the resulting paper with the title “Les Tragulidae (Ruminantia, Mammalia) de Sansan.” is submitted for publication in the special volume “La faune miocène de Sansan, vol. 2” in “Mémoires du Museum National d’Histoire Naturelle”.

Type locality: Sansan, Molasse marine de Salles, Gers, France, Neogene European Land Mammal Unit MN6 (reference locality).

Chronological and geographical occurrence: MN4 (late Early Miocene, early Karpatian, middle Orleanian) (Sach and Heizmann 2001) to MN6 (Middle Miocene, Badenian, early Astaracian) (Morales and Sanchez submitted, see above) in Europe.

Description and comparison: *D. crassum* forms with the contemporaneous *D. vindebonense* (MN5 to MN6) and the younger *D. nauti* (MN9 to MN11) the group of medium sized Central European *Dorcatheriums* with bunoselenodont teeth. Within this group *D. vindebonense* is the largest. *D. crassum* and *D. nauti* are similar in size (see measurements in Table 3). *D. crassum* is more brachyodont than *D. nauti* and therefore excludes synonymy with *D. nauti*, as has often been argued (Rütimeyer 1883; Hofmann 1893; Roger 1898:32, 1900: 67f, 1902:4f; Hünermann 1983; Gentry et al. 1999: 254). In contrast, *D. crassum* is less brachyodont than *D. vindebonense*. Besides *D. crassum* and *D. vindebonense* two more contemporaneous species exist: the larger *D. peneckeii* (MN5 to MN6) with slightly lower molars and the smaller *D. guntianum* (MN4 to MN7), with selenodont and slightly higher molars.

The medium sized *Dorcatherium* from Sandelzhausen corresponds in tooth size with the type material of *D. crassum* from Sansan (see measurements in Table 3). Its tooth crown height is lower than in *D. nauti*. The back fossette of m3 has a middle position (Fig. 1D, E2, H, K2, M2, P) like *D. crassum* from Sansan (personal observation) and *D. vindebonense* from Wackersdorf (Fahlbusch 1985), in contrast with the more lingual position in *D. nauti* (Kaup 1839b: Table 23 B Fig. 3). p3 and p2 have three labial conids (Fig. 1D, J, N) and d3 and d2 (Fig. 1A, O) in contrast with double-pointed teeth in *D. nauti* (already mentioned in Rinnert 1956), which are shorter and lower crowned than their successor. The very short p1 is mainly built up by the protoconid accompanied by a tiny hypoconid and an anterior and posterior crest (Fig. 1J). The two roots are fused in the upper part. Specimen 6635 shows the posterior part of an alveolar for a d1 with 4 mm distance to the alveolar of d2 (Fig. 1A). The upper molars are characterised by a very strong cingulum surrounding the protoconus and, often weakly, the hypoconus. Parastyle, mesostyle, and paraconus column are very strong (Fig. 1B). The neocrista is weak. The upper premolars show labially a strong paraconus with a prominent column but a poor parastyle. P4 has a strong hypoconus and a weak cingulum surrounding the hypoconus. The posthypocrista enters the metaconus leaving the metastyle outside the fossette and making the shape asymmetrical (Fig. 1L). Labial styles and columns are strong. Lingually the P3 is only equipped with a weak hypoconus, in contrast with a lingually two-cusped P3 in *D. nauti* (Kaup 1839b: Table 23 B Fig. 2), and a weak posterior cingulum (Fig. 1G). The P2 is longer than the P3 with only a tiny hypoconus attached to the base of the paraconus (Fig. 1F). The D4 is extremely low crowned with a strong cingulum surrounding the lingual part of the tooth (Fig. 1C). An also very low crowned D3 is only partly preserved with a clear postprotocrista and a very weak protoconus (Fig. 1I). The D2 is not recorded. Only one fragment represents the C (Fig. 2). It is flat with a slender-drop-shaped cross-section and a very sharp posterior crest. A thin layer of enamel covers just the labial side of the tooth. Labial

Table 3 Tooth measurements for *Dorcatherium crassum* from Sandelzhausen, and for type materials of *D. crassum*, *D. nauti*, and *D. vindebonense* measured by the author

		d1	D2	d2	D3	d3	D4	d4	M1	m1	M2	m2	M3	m3	p1	P2	p2	P3	p3	P4	p4
<i>Dorcatherium crassum</i> , Sandelzhausen, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany)																					
l	N	–	–	1	–	1	3	–	2	11	6	13	7	10	1	1	3	1	3	2	11
	Min	–	–	11.0	–	11.9	9.0	–	10.0	10.5	11.0	11.0	12.0	17.5	6.1	13.0	10.6	11.0	11.3	10.0	10.8
	Max	–	–	11.0	–	11.9	10.5	–	10.3	11.9	12.3	14.0	12.7	20.9	6.1	13.0	11.5	11.0	12.5	10.0	13.0
antw/w	N	–	–	2	1	2	3	–	2	11	4	14	4	11	1	1	3	1	3	2	11
	Min	–	–	3.4	7.4	3.4	9.7	–	11.0	6.3	12.8	7.4	14.1	7.9	3.5	6.6	4.2	7.5	4.0	10.0	5.2
	Max	–	–	3.5	7.4	3.5	10.9	–	11.1	8.5	14.0	10.0	14.5	10.2	3.5	6.6	5.5	7.5	5.2	11.9	6.0
<i>Dorcatherium crassum</i> , Sansan, Musée National d'Histoire Naturelle Paris (France) (described in Filhol 1891)																					
l	N	–	–	1	–	1	1	1	4	5	4	5	3	3	–	–	1	–	3	–	4
	Min	–	–	11.5	–	11.9	11.3	13.3	9.7	10.2	11.8	11.1	12.3	18.2	–	–	12.0	–	12.1	–	11.9
	Max	–	–	11.5	–	11.9	11.3	13.3	11.6	11.8	12.3	13.3	12.9	19.4	–	–	12.0	–	12.5	–	14.5
antw/w	N	–	–	1	1	1	1	1	4	5	4	5	3	3	–	–	1	–	3	–	4
	Min	–	–	3.7	8.2	4.3	10.9	6.6	11.0	6.3	12.5	7.9	13.3	8.8	–	–	4.1	–	4.4	–	5.0
	Max	–	–	3.7	8.2	4.3	10.9	6.6	12.6	7.0	13.7	8.4	14.1	8.9	–	–	4.1	–	5.1	–	6.5
<i>Dorcatherium nauti</i> , Eppelsheim, Hessisches Landesmuseum Darmstadt (Germany) (described in Kaup 1839a)																					
l	N	–	–	–	–	–	–	–	–	3	–	3	–	3	–	–	1	–	2	–	3
	Min	–	–	–	–	–	–	–	–	11.3	–	11.9	–	18.5	–	–	10.5	–	13.6	–	11.8
	Max	–	–	–	–	–	–	–	–	12.1	–	12.8	–	20.6	–	–	10.5	–	13.7	–	12.6
antw/w	N	–	–	–	–	–	–	–	–	3	–	3	–	3	–	–	3	–	2	–	3
	Min	–	–	–	–	–	–	–	–	5.1	–	7.7	–	8.2	–	–	3.5	–	4.1	–	4.7
	Max	–	–	–	–	–	–	–	–	6.7	–	8.0	–	8.7	–	–	3.5	–	4.7	–	5.1
<i>Dorcatherium vindebonense</i> , Neudorf, Naturhistorisches Museum Wien (Austria) (described in Thenius 1952)																					
l	N	–	–	–	–	–	2	1	2	–	4	3	3	2	–	1	1	2	2	1	–
	Min	–	–	–	–	–	12.5	16.3	12.6	–	14.0	14.2	15.9	20.7	–	17.4	14.9	14.8	14.7	12.1	–
	Max	–	–	–	–	–	13.0	16.3	13.3	–	15.4	14.6	17.3	22.4	–	17.4	14.9	15.7	15.3	12.1	–
antw/w	N	–	–	–	–	–	2	1	2	–	4	3	3	2	–	1	1	2	2	2	–
	Min	–	–	–	–	–	11.0	7.5	13.4	–	15.2	9.5	16.9	10.4	–	7.1	15.5	8.5	5.8	12.2	–
	Max	–	–	–	–	–	11.9	7.5	13.4	–	16.6	10.0	18.0	10.6	–	7.1	15.5	9.8	6.1	12.2	–

l largest length; antw/w largest anterior width for Ms, ms, and D4 s or largest width for Ps, ps, D3s, D2s, and ds; N number of measurements; Min minimum value measured; Max maximum value measured. Measurements in mm

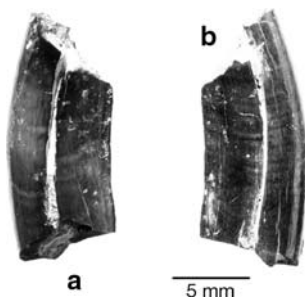


Fig. 2 Fragment of upper canine of *Dorcatherium crassum* (BSPG 1959 II 15648) from Sandelzhausen showing “growth rings”. a: lingual view, b: labial view

and lingual sides show growth stripes produced by longitudinal undulated irregularities of the tooth surface. Filhol (1891) associated upper canines of *Dicrocerus elegans* and

Heteroprox larteti (pl. XXII Figs. 1–4), which show an increasing anteroposterior diameter from the tip to the root and a comparably low crown, with the dentition of *Dorcatherium crassum*.

Comments: Tooth specimens of the above mentioned medium sized representatives of *Dorcatherium* are difficult to separate, because of similar morphology and size. Besides Mottl (1961) only Fahlbusch (1985) discusses differences and different authors’ opinions in detail, but finally found no better solution than the systematics as they were. Fortunately, *Dorcatherium* from Sandelzhausen is represented by a reasonable number of specimens, which give an insight in stable features and variability. In principle these correspond to those of the type material of *D. crassum* from Sansan (see measurements in Table 3 for comparison). Although in some tooth positions there is a

clear overlap in size with the type material of *D. vindebonense*, teeth belonging to one tooth row can never all be assigned to *D. vindebonense*, because of a too small size. However, the spectrum of intraspecific size variability in *D. crassum* is large and enables sexual dimorphism in body size to be hypothesized. However, in extant tragulids females are a little larger than males (Dubost 1965; Terai et al. 1998), as is generally true for small ruminants (Loison et al. 1999). Therefore, it can be assumed for *D. crassum*, also. Sexual dimorphism in the size and length of the sabre-like upper canines, as in extant tragulids (Milne-Edwards 1864; Smit-van Dort 1989; Terai et al. 1998) is not yet recorded for *D. crassum*.

Infraorder Pecora Linnaeus, 1758

Superfamily Cervoidea Goldfuss, 1820

Family Palaeomerycidae Lydekker, 1883

General information: From the Early to the early Late Miocene the now extinct exclusively Northern hemisphere palaeomerycids were a customary faunal element in ruminant communities. In Europe they usually represented the largest body size within these communities. Plesiomorphic characters in common with all Cervoidea are a closed dorsodistal metatarsal gully, a posterior tuberosity of the metatarsus, metatarsal II remnant proximally fused, side toes partially lost, raised cubonavicular facet on proximal metatarsus, two lacrimal orifices on the dorsal rim of the orbit, a lacrimal fossa, brachyo- to mesoselenodont dentition with *Palaeomeryx*-fold in lower molars and neocrista in upper molars, a more prominent entostyle in upper molars, posteriorly situated and directed protocone on P3, weak cingula, an optional p1, and a sabre-like upper canine (Duranthon et al. 1995; Janis and Scott 1987). Their position within the superfamily Cervoidea (Janis and Scott 1987; Gentry et al. 1999) and the extent of the family (including North-American Dromomerycinae, e.g. Janis and Scott 1987; Janis and Manning 1998; Janis 2000; e.g. excluding North-American Dromomerycinae, Duranthon et al. 1995; Gentry et al. 1999; including the Oligomiocene European genus *Bedenomeryx*, e.g. Ginsburg 1999; excluding *Bedenomeryx*, Gentry et al. 1999; Prothero and Liter 2007; including the Early Miocene European genus *Oriomeryx*, e.g. Ginsburg 1985; Ginsburg 1999; Prothero and Liter 2007; excluding *Oriomeryx*, e.g. Gentry et al. 1999; inclusion of the Early Miocene European genus *Amphitragulus*, e.g. Janis and Scott 1987; exclusion of *Amphitragulus*, e.g. Gentry et al. 1999; inclusion of the Middle Miocene European genus *Triceromeryx*, e.g. Gentry et al. 1999; Prothero and Liter 2007; excluding *Triceromeryx*, e.g. Janis and Scott 1987; inclusion of the North African genus *Prolibytherium*, Janis and Scott 1987, exclusion of *Prolibytherium*, e.g. Gentry et al. 1999) are still under discussion. In Janis and Scott (1987) and Janis and Manning (1998) the family is defined by a suite of dental features: reduced metastyles in the upper molars,

attenuated metacone on P4, bifurcated posterior wing of the metaconule (here spur of the posthypocrista), and double posterior lobe (here third lingual conid) on m3 that is closed posteriorly. However, all of these characters are not only present in the Palaeomerycidae, but also in early cervids or moschids, and display variability, and are therefore difficult to verify as indicative. Real unique features are the combination of unbranched occipital appendages and supraorbital ossicones (Duranthon et al. 1995). These were most likely of dermal origin and fuse with the frontal in old individuals because of similarities to the giraffid ossicones. European palaeomerycids are known to possess a long legged habitus (Köhler 1993).

The name giving genus *Palaeomeryx* with the type species *Palaeomeryx kaupi* and its type material, a right jaw with p3 to m3 stored at the BSPG (1893 I 501) and a left m2 (BSPG 1893 I 502), were published and illustrated by von Meyer (1834: pl. X Figs. 77 and 78). The type material was recovered from the fossil site of Georgensgmünd (Germany), dated as MN6 in the literature (de Bruijn et al. 1992), but currently discussed as representing MN5 (G. Berger, M. Rummel and K. Heissig, personal communication), which would better support the hypothesis about a constant size increase within the family during time (Duranthon et al. 1995; Ginsburg and Heintz 1966; Ginsburg 1985, 1999). For more than a century, teeth with the same brachyo-selenodont morphology, but of different size were placed in the genus *Palaeomeryx*, which was considered a representative of the Cervoidea (distally closed central groove at the dorsal surface of the metatarsal) with an appendage-less skull. Roger (1885: 93ff, pl. 1 Figs. 1–3) was the first to illustrate a supraorbital appendage of a palaeomerycid. It came from Mering (Augsburg, Germany, Middle Miocene, NAFB) and he assigned it to *Chalicotherium*. Ginsburg and Heintz (1966) attributed two supraorbital appendages discovered at Artenay (MN4, France) to *Palaeomeryx*. Duranthon et al. (1995) discuss the problem of the insufficient type material (some teeth and postcranial elements) compared with current record conditions: more recently found skulls of palaeomerycids from different localities of different ages (Villalta et al. 1946; Qiu et al. 1985; Astibia and Morales 1987; Astibia et al. 1998) always show the same homogeneous and plesiomorphic teeth, but also supraorbital and parietooccipital appendages. The latter are characterised by a wide range of morphologic variability and do not enable positioning within one genus. Because the type material from Georgensgmünd does not include any skull remains no statement concerning the morphology of potential appendages of the genus *Palaeomeryx* is possible. Therefore, Duranthon et al. (1995) suggest that *Palaeomeryx kaupi* from Georgensgmünd be regarded as a species inquirenda. Moreover, they suggest abandoning widespread usage of the genus name *Palaeomeryx* for the time being,

but keeping the family “Palaeomerycidae”. In this paper I comply with the latter suggestion in contradiction with the recommendation of Ginsburg (1999) to keep the genus *Palaeomeryx*. The arguments are given above or below.

Comparison of metrical data for teeth gives evidence for the same size of “*P. kaupi*” and *Ampelomeryx ginsburgi* from Els Casots (Spain, MN4) and Montréal-du-Gers (France, MN4) (Duranthon et al. 1995) (Table 4). Therefore synonymy of both species is most likely, but has to be covered by skull remains of “*P. kaupi*”, not yet available.

Genus *Germanomeryx* n. g.

Type species: *Germanomeryx fahlbuschi* n. sp.

Chronological and geographical occurrence: see type species.

Derivatio nominis: the name refers to Germany (=Germania [Latin]) as the hitherto sole country with a record of this palaeomerycid genus.

Description and differential diagnosis: see type species.

***Germanomeryx fahlbuschi* n. sp.** Figs. 3, 4, 5, Appendix.

.1956 *Palaeomeryx eminens* v. Meyer, 1847; Rinnert, p. 12

.1970 *Palaeomeryx*; Fahlbusch and Gall, p. 394

.1974 *Palaeomeryx eminens* H. v. Meyer; Fahlbusch et al. p. 126

.1993 *Palaeomeryx eminens*; Köhler, p. 52.

.1997 *Palaeomeryx eminens* Meyer 1852; Rössner, p. 611

.2003 Palaeomerycidae n. g. n. sp.; Fahlbusch, p. 119

Holotype: caudal part of a skull with left P2 to P3 and M2 to M3 and right P4 to M3, 7801 (Figs. 3, 4B, C, D).

Paratypes: right mandible with p2 to m3 (Fig. 5G) and left mandible with p3 to m3, 2499, belonging to one individual (Fig. 5H).

Type locality: Sandelzhausen, Upper Freshwater Molasse, Bavaria, Germany, early middle MN5.

Chronological and geographical occurrence: early Middle MN5 (boundary Early/Middle Miocene, topmost Burdigalian or basalmost Langhian) in Germany.

Derivatio nominis: in honour of Volker Fahlbusch†, for his 40 years of outstanding commitment to the fossil site of Sandelzhausen.

Diagnosis: *G. fahlbuschi* is a very large representative of the Miocene European Palaeomerycidae with short, flattened, and posteriorly rounded parieto-occipital appendages, strongly brachyodont teeth without p1 and enlarged and elongated upper canines.

Description and comparison: Besides a single m1 from Undorf (Germany) (BSPG 1896 XI 258, Rinnert 1956: 12) *G. fahlbuschi* is hitherto exclusively known from Sandelzhausen. The material includes a skull with teeth, jaws, with nearly complete tooth rows, and several

incomplete jaws, isolated teeth, and bones. The skull (Fig. 3) is preserved from the frontalia caudalwards with a length of 300 mm. It is badly flattened with a displacement of the skull roof over the right skull half. The suture between the frontals and parietals can be assumed from a fracture just behind the orbits. Each of the parietals show a clear crest running from rostral to caudal resulting in the edge of a posterior elongation (90 mm), which is dorsoventrally flattened and has blunt endings. Those protuberances are most likely homologous with the parietooccipital appendages characterizing all skulls of male palaeomerycids. Because of the bad preservation the suture with the occipitals are lost. The lateral portion of the frontals, potential attachment areas for supraorbital appendages, and supraorbital appendages themselves, which are characteristic in palaeomerycids also, are not preserved either. The occipital condyles are both recorded and have a caudal area with a height of 43 mm. The teeth are extremely large and P2, P3, P4, and M1 are strongly worn, which indicates an especially large and senile individual.

The teeth are extremely brachyodont. The upper molars show strong columns of the paraconus, parastyles, and mesostyles and an isolated neocrista often oriented in anteroposterior direction posteriolingually of the paraconus (Fig. 4B, C, M, N). There is a clear cingulum surrounding the lingual half of the teeth. The spur of the posthypocrista is weak. The entostyle is elongated and clings to the hypoconus. The P4 is horseshoe-shaped with weak labial elements, cingulum, medial crista, and spur (Fig. 4B). P3 and P2 show a lingually well rounded shape, a strong paraconus column and parastyle, and a partially weak lingual cingulum (Fig. 4D, K). The D4 has strong labial elements and a weak lingual cingulum, neocrista, and spur (Fig. 4J). D3 is relatively short and compact with weak labial elements, neocrista, and spur (Fig. 4L). The D2 is also relatively short and compact with weak labial elements and a comparably strong protoconus (Fig. 4I). Two upper sabre-like canines are recorded. They differ strongly in size, but both show from anterior a slight bending to lateral. The smaller one (Fig. 5B) is assigned to a female, which shows posteriorly and anteriorly sharp edges made from rows of pearled enamel and, laterally, a blunt and low central crest. The enamel is thin and developed only on the lateral side. The size corresponds to the size of the cervid *Procervulus dichotomus* (Rössner 1995), but, in contrast, in *P. dichotomus* only posteriorly is a sharp edge developed, but laterally a rounded crest. The larger (Fig. 5A) is a fragment of the tooth crown and is more than the double the size of the smaller one; it has therefore been assigned to a male individual. The specimen is badly preserved, but still shows thin enamel on its lateral side only.

Table 4 Tooth measurements for *Germanomeryx n. g. fahlbuschi n. sp.* from Sandelzhausen and from type materials of *Ampelomeryx*, “*Palaeomeryx kaupii*”, and Palaeomerycidae of the size “*magnus*” and “*eminens*” measured by the author. Measurements of the palaeomerycid of the size “*eminens*” from Öhningen from von Meyer (1852: Table XIII Fig. 5)

		D2	d2	D3	d3	D4	d4	M1	m1	M2	m2	M3	m3	P2	p2	P3	p3	P4	p4	Cf	Cm
<i>Germanomeryx n. g. fahlbuschi n. sp.</i> , Sandelzhausen, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany)																					
l	<i>N</i>	2	2	1	4	3	4	7	8	2	10	1	7	1	3	3	5	1	6	1	–
	Min	20.0	18.0	24.0	19.0	19.0	25.0	22.0	22.0	26.5	22.2	28.6	33.0	24.1	18.5	22.3	18.9	19.0	14.0	13.0	–
	Max	22.0	19.0	24.0	22.2	21.0	26.0	24.0	25.8	29.9	26.7	28.6	39.0	24.1	20.0	22.6	24.1	19.0	25.0	13.0	–
antw/w	<i>N</i>	1	2	1	5	1	4	6	8	1	9	1	8	0	5	3	5	1	6	1	–
	Min	11.2	7.6	17.1	9.6	20.5	12.0	24.7	16.4	32.5	15.0	32.7	17.2	–	9.4	19.2	11.4	22.9	13.4	6.0	–
	Max	11.2	8.5	17.1	11.8	20.5	15.6	27.0	18.1	32.5	18.7	32.7	21.9	–	10.7	20.6	13.5	22.9	24.8	6.0	–
<i>“Palaeomeryx kaupii”</i> , Georgensgmünd, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany) (described in von Meyer 1834)																					
L	<i>N</i>	–	–	–	–	–	1	1	–	–	4	3	4	2	–	2	–	3	1		
	Min	–	–	–	–	–	23.5	19.4	–	–	13.5	19.7	16.3	18.4	–	17.7	–	13.6	16.9		
	Max	–	–	–	–	–	23.5	19.4	–	–	24.5	21.1	30.6	20.6	–	18.4	–	19.5	16.9		
antw/w	<i>N</i>	–	–	–	–	–	1	1	–	–	4	3	4	2	–	2	–	3	1		
	Min	–	–	–	–	–	11.6	21.6	–	–	15.2	23.0	13.9	15.5	–	15.5	–	11.2	9.9		
	Max	–	–	–	–	–	11.6	21.6	–	–	24.9	23.9	16.1	15.7	–	18.5	–	18.4	9.9		
<i>Ampelomeryx ginsburgi</i> , Els Casots, Institut Paleontològic Dr. M. Crusafont Sabadell (Spain) (described in Duranthon et al. 1995)																					
l	<i>N</i>	–	–	1	–	3	–	5	4	5	4	4	5	1	3	6	5	9	6		
	Min	–	–	16.3	–	15.5	–	18.6	16.1	19.8	17.2	18.5	24.7	16.0	14.1	16.5	16.2	12.8	16.7		
	Max	–	–	16.3	–	15.9	–	22.4	19.5	20.9	19.3	21.6	29.1	16.0	15.9	18.7	17.2	15.0	18.1		
antw/w	<i>N</i>	–	–	1	–	3	–	6	3	5	4	4	7	1	3	6	5	9	6		
	Min	–	–	11.7	–	13.7	–	16.7	11.4	19.7	13.0	17.9	12.2	12.9	6.5	13.5	9.1	16.1	9.9		
	Max	–	–	11.7	–	14.6	–	21.3	11.9	23.2	13.9	22.7	13.8	12.9	7.3	17.3	11.9	18.3	11.5		
<i>Ampelomeryx ginsburgi</i> , Montréal du Gers, Museum d’Histoire Naturelle Toulouse (France) (described in Duranthon et al. 1995)																					
l	<i>N</i>	–	–	–	–	–	–	1	1	1	1	1	1	2	2	2	1	2	1		
	Min	–	–	–	–	–	–	19.3	21.6	21.3	20.7	30.2	16.5	13.8	11.9	18.0	13.9	19.9			
	Max	–	–	–	–	–	–	19.3	21.6	21.3	20.7	30.2	17.7	14.2	17.6	18.0	14.4	19.9			
antw/w	<i>N</i>	–	–	–	–	–	–	1	1	1	1	2	1	2	2	2	1	2	1		
	Min	–	–	–	–	–	–	19.7	13.3	24.7	14.2	22.2	14.8	14.3	6.6	16.3	9.8	12.2	11.4		
	Max	–	–	–	–	–	–	19.7	13.3	24.7	14.2	23.3	14.8	14.5	8.3	16.9	9.8	17.3	11.4		
Palaeomerycidae of the size “ <i>magnus</i> “, Sansan, Musée National d’Histoire Naturelle Paris (France) und Naturhistorisches Museum Basel (Switzerland) (described in Filhol 1891)																					
l	<i>N</i>	–	–	–	–	2	2	3	5	3	6	3	4	2	3	3	5	2	5		
	Min	–	–	–	–	20.6	24.0	22.5	21.6	26.0	19.5	24.0	32.3	15.9	13.5	19.5	19.3	16.4	19.5		
	Max	–	–	–	–	21.0	25.2	23.9	23.0	26.4	26.3	26.5	35.6	19.8	17.4	21.1	21.6	16.4	22.4		
antw/w	<i>N</i>	–	–	–	–	2	2	2	4	3	5	3	4	1	3	3	4	2	4		
	Min	–	–	–	–	19.3	12.7	24.9	15.5	25.7	17.6	25.8	18.2	17.2	8.3	17.5	11.7	21.0	15.4		
	Max	–	–	–	–	19.8	13.9	24.9	16.9	26.8	19.3	28.1	19.3	17.2	10.7	28.8	13.7	21.3	20.0		
Palaeomerycidae of the size “ <i>eminens</i> “, Öhningen, type lost (described in von Meyer 1852)																					
l	<i>N</i>	–	–	–	–	–	–	–	–	–	1	–	1	–	1	–	1	–	1		
	Min	–	–	–	–	–	–	–	–	–	24.5	–	37.0	–	16.0	–	19.5	–	20.0		
	Max	–	–	–	–	–	–	–	–	–	24.5	–	37.0	–	16.0	–	19.5	–	20.0		
antw/w	<i>N</i>	–	–	–	–	–	–	–	–	–	1	–	1	–	1	–	1	–	1		
	Min	–	–	–	–	–	–	–	–	–	17.0	–	15.5	–	9.0	–	11.0	–	13.0		
	Max	–	–	–	–	–	–	–	–	–	17.0	–	15.5	–	9.0	–	11.0	–	13.0		

Table 4 continued

		D2	d2	D3	d3	D4	d4	M1	m1	M2	m2	M3	m3	P2	p2	P3	p3	P4	p4
Palaeomerycidae of the size “ <i>eminens</i> “, Steinheim, Naturhistorisches Museum Basel (Switzerland) (described in Fraas 1870 and Rüttimeyer 1881)																			
1	<i>N</i>	–	–	–	–	1	–	2	–	2	–	2	–	2	–	2	–	1	–
	Min	–	–	–	–	21.8	–	23.1	–	27.8	–	16.9	–	20.0	–	20.0	–	18.3	–
	Max	–	–	–	–	21.8	–	23.8	–	28.6	–	28.1	–	21.2	–	20.3	–	18.3	–
antw/w	<i>N</i>	–	–	–	–	1	–	2	–	2	–	2	–	2	–	2	–	1	–
	Min	–	–	–	–	22.3	–	25.0	–	30.4	–	30.5	–	16.2	–	19.0	–	23.3	–
	Max	–	–	–	–	22.3	–	27.9	–	30.6	–	31.2	–	16.7	–	19.2	–	23.3	–

l largest length; *antw/w* largest anterior width for Ms, ms, and D4s or largest width for Ps, ps, D3s, D2s, and ds; *N* number of measurements; *Min* minimum value measured; *Max* maximum value measured. Measurements in mm

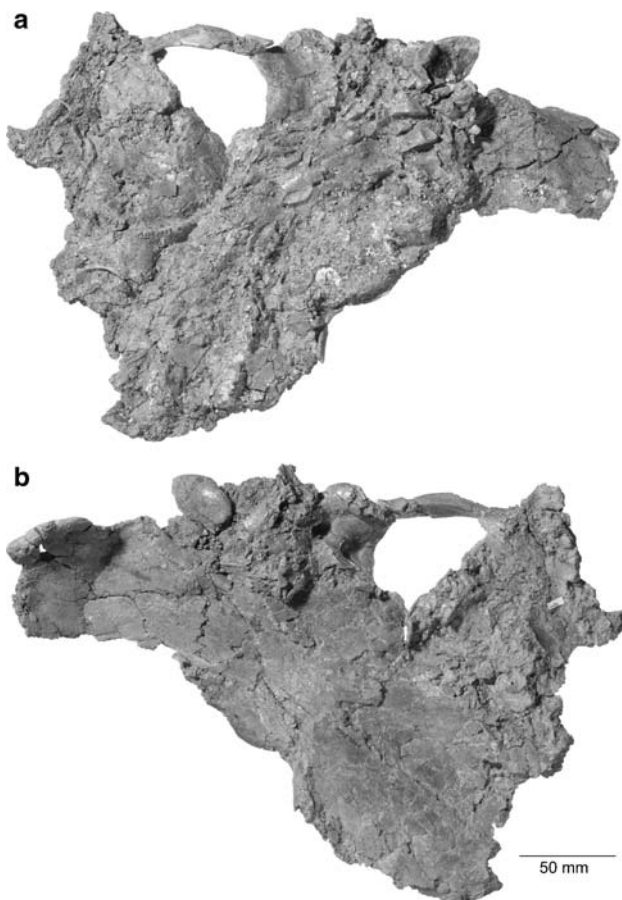


Fig. 3 Skull of *Germanomeryx* n. g. *fahlbuschi* n. sp. from Sandelzhausen (BSPG 1959 II 7801). **a:** ventral view, **b:** dorsal view

The lower molars show a weak metastylid and *Palaeomeryx*-fold (Figs. 5G, H, I, 4A, E, H). Their strong cingulid is only anteriorly and posteriorly developed. The entoconulid of the m3 is closely attached to the labial wall of the postentocristid (Figs. 5H, I, 4H). The labial portion of the column of the entoconid is strongly oriented to

posterior and forms in advanced wear an outstanding fold (Fig. 5I). At its base an additional small cristid running to the posterior end of the posthypocristid is occasionally developed (Fig. 4H). The exostylid is strong, also, but low. The lower premolars have a compact shape. p4 to p2 show a postprotoconulidcristid (Figs. 5G, H, I, 4F). If a preprotoconulidcristid was developed, it cannot be seen from the wear stages preserved. At the p4 a metaconid is present. p1 is lacking. The d4 shows weak labial stylids, a *Palaeomeryx*-fold, a spur, and a cingulid (Figs. 5F, 4E, G). Anterior and posterior cingulids are strong. The d3 has a weak metaconid and lingually dichotomous pre- and postprotoconulidcristids (Fig. 4E1, 5F1). In specimen 11651 (Fig. 5F) an additional transversal crest is developed between protoconid and hypoconid. The d2s have no metaconid and the preprotoconulidcristid is occasionally dichotomous (Fig. 4E1). The incisors are shovel-like (Fig. 5C, D, E) with a lingually stump ridge at the posterior portion. From i1 to i3 the posteriorwards bending of the crown increases.

Differential diagnosis:

G. fahlbuschi differs from *Oriomeryx* (Ginsburg 1985) by a larger size and by the existence of occipital appendages; it differs from *Palaeomeryx kaupi* (von Meyer 1834) by a larger size; it differs from *Ampelomeryx ginsburgi* (Duranthon et al. 1995) by a larger size and shorter occipital appendages; it differs from *Tauromeryx turiasonensis* (Astibia and Morales 1987; Astibia et al. 1998) and from *Triceromeryx pachecoi* (Villalta et al. 1946) by a larger size, shorter occipital appendages, and dorsoventrally flattened occipital appendages; it differs from Palaeomerycidae of the size “*magnus*” (Lartet 1851; Ginsburg 1985, 1999) by a larger size; and it differs from Palaeomerycidae of the size “*eminens*” (von Meyer 1852; Fraas 1870; Rüttimeyer 1883) by less molarised premolars and milk molars.

Comments: The palaeomerycid material from Sandelzhausen differs from all other known representatives of this

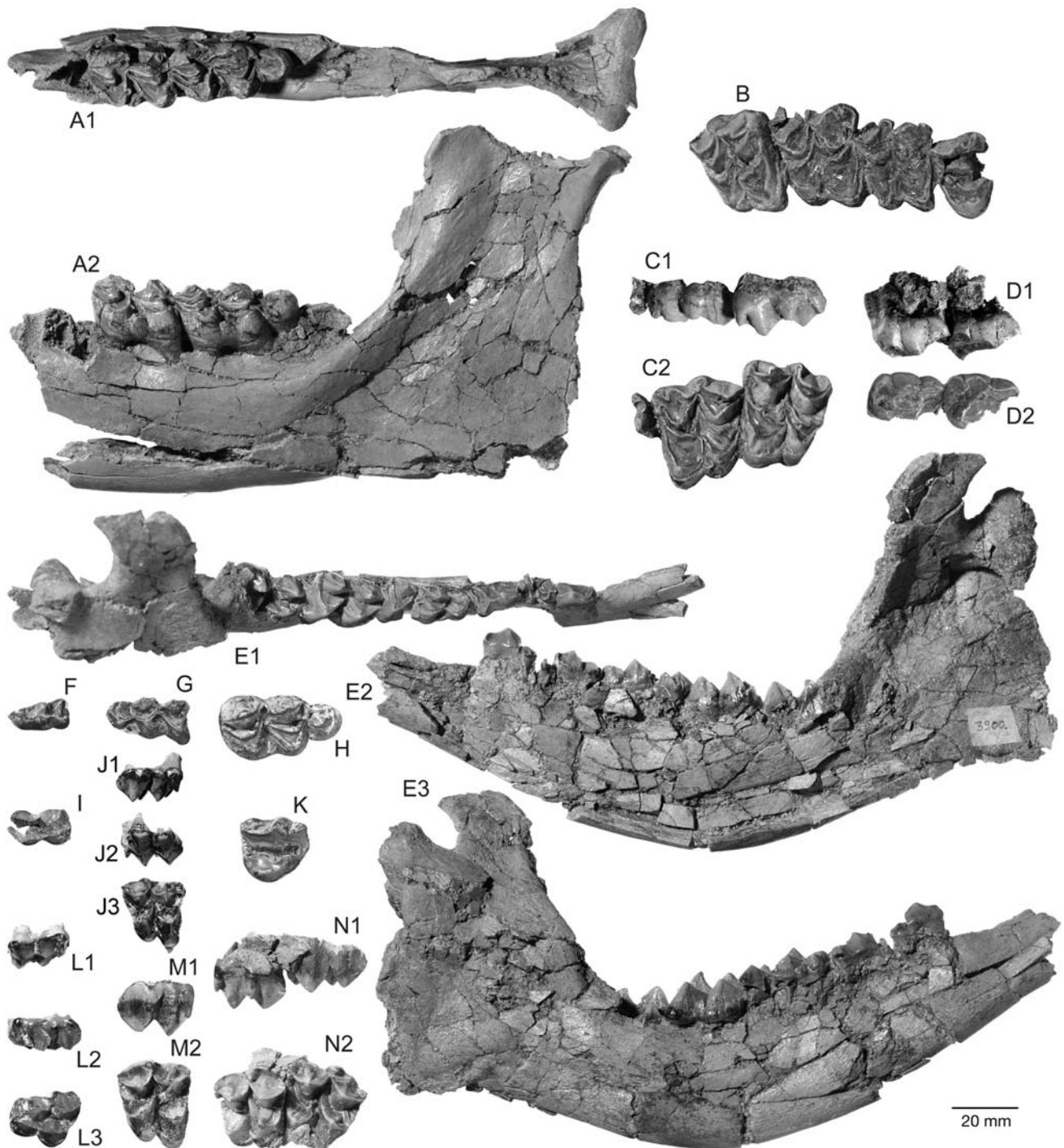


Fig. 4 Dental remains of *Germanomeryx* n. g. *fahlbuschi* n. sp. from Sandelzhausen (Inventory-No. BSPG 1959 II ...). **A**: 4662 left jaw fragment with m2 and m3; **A1**: occlusal view; **A2**: labial view. **B–D**: 7801 upper dentition belonging to the skull specimen 7801 in Fig. 3; **B**: right P4 to M3, occlusal view; **C**: left M2 to M3, **C1**: labial view, **C2**: occlusal view; **D**: left P2 to P3, **D1**: labial view, **D2**: occlusal view. **E**: 11651 right jaw with d2 to d4 and m1 to m2; **E1**: occlusal

view; **E2**: lingual view; **E3**: labial view. **F**: 5207 left d3, occlusal view. **G**: 5191 left d4, occlusal view. **H**: 5219 left m3, occlusal view. **I**: 5211 dex D2, occlusal view. **J**: 5197 right D4; **J1**: labial view; **J2**: lingual view; **J3**: occlusal view. **K**: 5200 right P3, occlusal view. **L**: 5210 right D3; **L1**: lingual view; **L2**: labial view; **L3**: occlusal view. **M**: 5184 right M1; **M1**: labial view; **M2**: occlusal view. **N**: 7802 left maxilla fragment with M1 to M2; **N1**: labial view; **N2**: occlusal view

family by the morphology of its occipital appendages. Hence, with reference to the known wide range of morphologies in occipital appendages of palaeomerycids, and

excluded from belonging to one of the previously existing genera (see above), the new genus *Germanomeryx* with the new species *fahlbuschi* is established.

Germanomeryx fahlbuschi is definitively a species of the Palaeomerycidae, which disproves the hypothesis of a constant size increase in the family with time (Ginsburg and Heintz 1966; Ginsburg 1985, 1999). Its size corresponds to that one of the hitherto known largest representatives of the family the Palaeomerycidae of the size “*eminens*” from MN7 + 8 (Ginsburg and Heintz 1966: 979; Ginsburg 1985:1077 and Table 4). The MN5-locality Undorf yielded a fragmentary m1 (BSPG 1896 XI 258, Rinnert 1956: 12) of a palaeomerycid which corresponds in size with *G. n.g. fahlbuschi* n.sp. from Sandelzhausen. This clearly supplies evidence for a more differentiated and complex body size development within the family than previously thought (Ginsburg and Heintz 1966; Ginsburg 1999). Moreover, the large sample size of the fossil site clearly demonstrates considerable size differences within the teeth of this palaeomerycid (differences of 6 mm in length in m3s). For ecological reasons a second sympatric palaeomerycid at this locality seems hardly probable, so sexual dimorphism with smaller females and larger males, known from extant large ruminants (Loison et al. 1999), would be the most likely explanation. This argumentation is supported by the usual size variation observed in every palaeomerycid assemblage (Ginsburg 1985, 1999).

Family Cervidae Goldfuss, 1820

Gattung *Heteroprox* Stehlin, 1928

Type species: *Heteroprox larteti* (Filhol, 1891).

Further European species: *Heteroprox moralesi* Azanza, 2000; *Heteroprox anatoliensis* Geraads, 2003; *Heteroprox eggeri* n. sp.

Chronological and geographical occurrence range in Europe: from early middle MN5 (around boundary Early/Middle Miocene, topmost Burdigalian or basalmost Langhian) (Sandelzhausen) to MN7 (late Middle Miocene, Sarmatian) (Steinheim am Aalbuch, Germany, Fraas 1870).

General information: The genus *Heteroprox* comprises medium-sized cervids of the Middle Miocene of Europe. Its species are characterized by cranial appendages with deciduous dichotomously forked to multibranching antlers without a burr, but longitudinal sculpturing in the vicinity of the antler fork. Their position on the skull is supraorbital and extracranial. The dentition of *Heteroprox* is early-cervid typical brachyoselenodont with elongated and molarised lower premolars (p4 with posterior and sometimes anterior cristid of the metaconid, p3 with almost always present metaconid, longer transversal crests). The lower molars show a weak *Palaeomeryx*-fold and a third lingual conid on the m3s. The upper canines of males are sabre-like elongated and enlarged. At the frontal the foramen supraorbitale is close to the appendage base and in a characteristic lancet-shaped depression of the outer bone layer (present at lectotype, personal observation, but nowhere illustrated).

The genus *Heteroprox* was established by Stehlin (1928) for cranial appendages from Steinheim am Aalbuch, (Germany, MN7) which he synonymised with *Cervus larteti* described by Filhol (1891) from Sansan (France, reference locality MN6). Ginsburg and Crouzel (1976, Fig. 9) established the lectotype of *H. larteti*, MNHN Sa 3317 right frontal appendage, illustrated in Filhol (1891).

Cranial appendages and dentitions of *Heteroprox* are similar in morphology and size to those of the Early to Middle Miocene *Procervulus*, the oldest cervid known, and in the spectrum of variability single specimens are hard to assign to one of these genera (see antler specimens from Reisenburg (MN4) described and illustrated by Rüttimeyer (1881, pl. 1 Fig. 8) and Dehm (1944 Figs. 6–9) and assigned to *Heteroprox* by Dehm (1944)). Therefore, a close evolutionary relationship between both genera has often been hypothesized (Ginsburg and Crouzel 1976; Azanza 1993:6; Gentry 1994: Fig. 6; Azanza 2000: 277ff). Because of their more or less successive stratigraphical occurrence a direct *Procervulus*-*Heteroprox*-lineage has been assumed (Ginsburg 1968:12; Ginsburg and Crouzel 1976).

Heteroprox eggeri n. sp. Fig. 6, Appendix

p1956 *Procervulus dichotomus*; Rinnert, Taf. 1 Fig. 9.

.1970 *Euprox*; Fahlbusch and Gall, p. 394.

.1970 *Heteroprox*; Fahlbusch and Gall, p. 394.

.1974 *Euprox furcatus* (Hensel); Fahlbusch, Gall and Schmidt-Kittler, p. 122.

.1974 *Heteroprox larteti* (Filhol); Fahlbusch, Gall and Schmidt-Kittler, p. 123.

.1997 *Heteroprox* n. sp.; Rössner, p. 611ff.

.2003 *Heteroprox* n. sp.; Fahlbusch, p. 119.

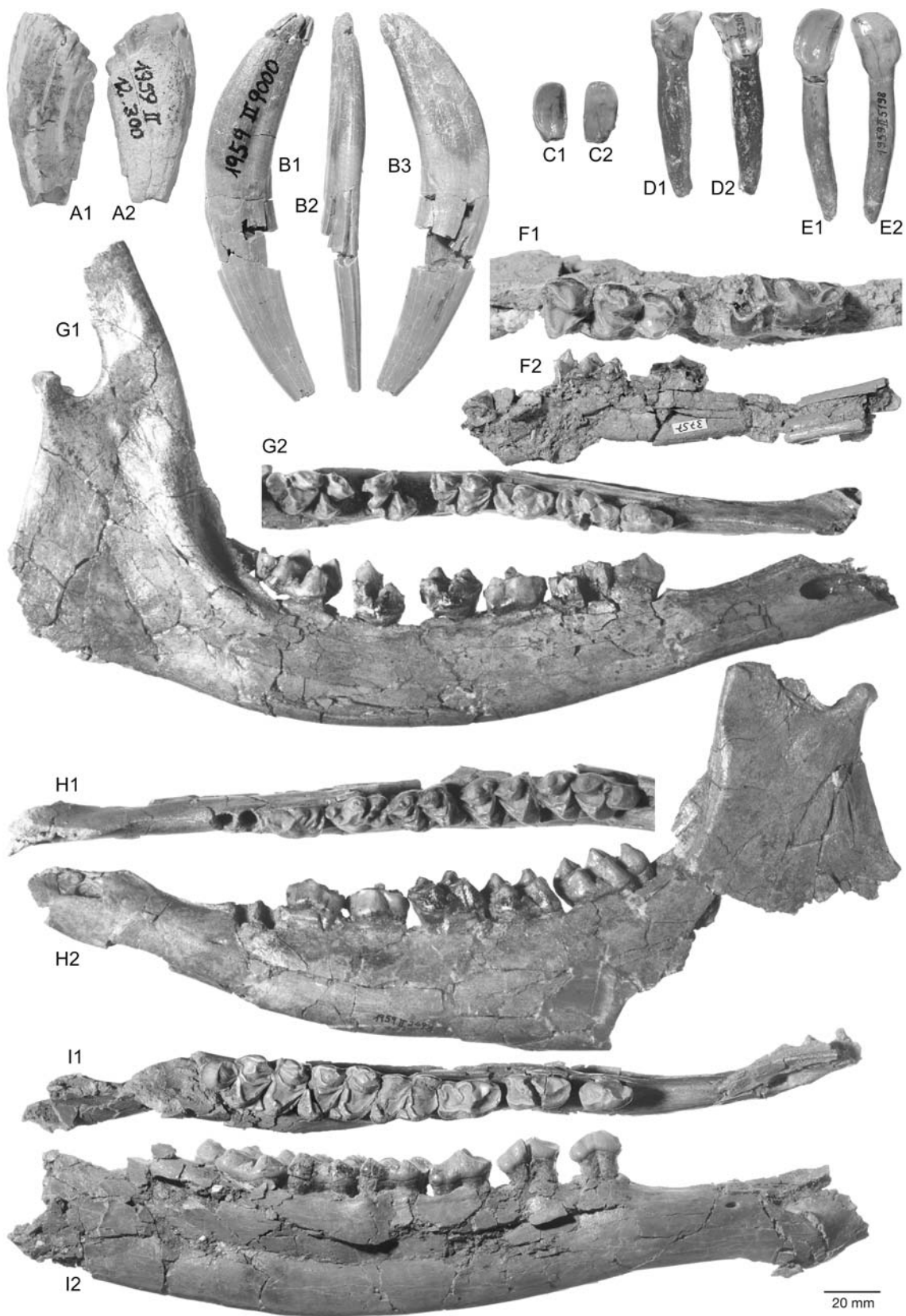
Holotype: Right adult frontal appendage, 5249 (Fig. 6A).

Paratypes: Right juvenile frontal appendage, 2502 (Fig. 6B); right adult frontal appendage, 5247 (Fig. 6F); right adult appendage, 5248 (Fig. 6D); antler cast, 5268 (Fig. 6C); antler cast, 5258 (Fig. 6E); right maxilla with M1 to M3, 3749 (Fig. 6Q); right mandible with p2 to m3, 1975 IX 27 (Fig. 6K); right maxilla with P2 to P4, 5299 (Fig. 6P); right mandible with p2 to p4, 2504 (Fig. 6U); left male C, 5301 (Fig. 6O); left female C, 8992 (Fig. 6N); left mandible with p2 to m3, 4315 (Fig. 6R); left mandible with p3 to m3, 6619 (Fig. 6T); left D3, D4, M1, 3911 (Fig. 6L); left jaw with d2 to d4, 3870 (Fig. 6S).

Type locality: Sandelzhausen, Upper Freshwater Molasse, Bavaria, Germany, early middle MN5.

Chronological and geographical occurrence: early middle MN5 (boundary Early/Middle Miocene, topmost Burdigalian or basalmost Langhian) in Germany.

Derivatio nominis: In honour of Josef Egger (Mainburg), former mayor of the town of Mainburg, who



◀ **Fig. 5** Dental remains of *Germanomeryx* n. g. *fahlbuschi* n. sp. from Sandelzhausen (Inventory-No. BSPG 1959 II ...). **A**: 12300 right male C, 1.5 times larger than indicated by the scale at the bottom, original size; **A1**: labial view; **A2**: lingual view. **B**: 9000 left female C, 1.5 times larger than indicated by the scale at the bottom, original size; **B1**: labial view; **B2**: anterior view; **B3**: lingual view. **C**: 5204 right i1, 1.5 times larger than indicated by the scale at the bottom, original size; **C1**: lingual view; **C2**: labial view. **D**: 5201 left i3, 1.5 times larger than indicated by the scale at the bottom, original size; **D1**: labial view; **D2**: lingual view. **E**: 5198 right i2, 1.5 times larger than indicated by the scale at the bottom, original size; **E1**: lingual view, **E2**: labial view. **F**: 3757 right fragmentary jaw with d3 and d4; **F1**: occlusal view, 1.5 times larger than indicated by the scale at the bottom, original size. **F2**: labial view. **G, H**: 2499 right and left jaw with dentition belonging to one individual; **G**: right jaw with p2 to m3; **G1**: labial view; **G2**: occlusal view; **H**: left jaw alveol of p2 and p3 to m3; **H1**: occlusal view, **H2**: labial view. **I**: 3733 right jaw with p2 to m3; **I1**: occlusal view; **I2**: labial view

essentially supported the excavations in Sandelzhausen from 1994 to 2001.

Diagnosis: *Heteroprox eggeri* is the smallest and stratigraphically oldest species of the genus. Its antlers are dichotomously branched, its pedicles are extracranial, supraorbital inserted in a more or less upright position. There is no trace of a burr, but only weak longitudinal sculpturing. The lower tooth row lacks a p1. The upper canine in males is sabre-like elongated and enlarged with a prominent crest on the labial side. The dentition is brachyoselenodont with elongated and molarised lower premolars.

Description: The frontal appendages of *H. eggeri* are seated on the orbitae roofs some two or three millimetres from the orbitae rims. The pedicles are straight and stood in parallel on the skulls in a more or less upright position, as seen from two appendages originally belonging to the same individual (Fig. 6D). Anteromedially of the appendage base a lancet-shaped depression in the skull roof contains the supraorbital aperture (Fig. 6D, F2). The transitional area pedicle/antler and the antler fork are slightly sculptured with longitudinal grooves and ridges. Different ontogenetic stages of the cranial appendages are recorded: non-forked to weakly forked juvenile stages with a posteriorly bent tip (Fig. 6B, D); forked adult stages (Fig. 6C, E, F); advanced adult stages with shortened pedicle, strengthened sculpture, and occasionally accessory prongs (Fig. 6A). Dropped antlers with cast areas showing bone with rounded absorbing structures are also recorded (Fig. 6C, E).

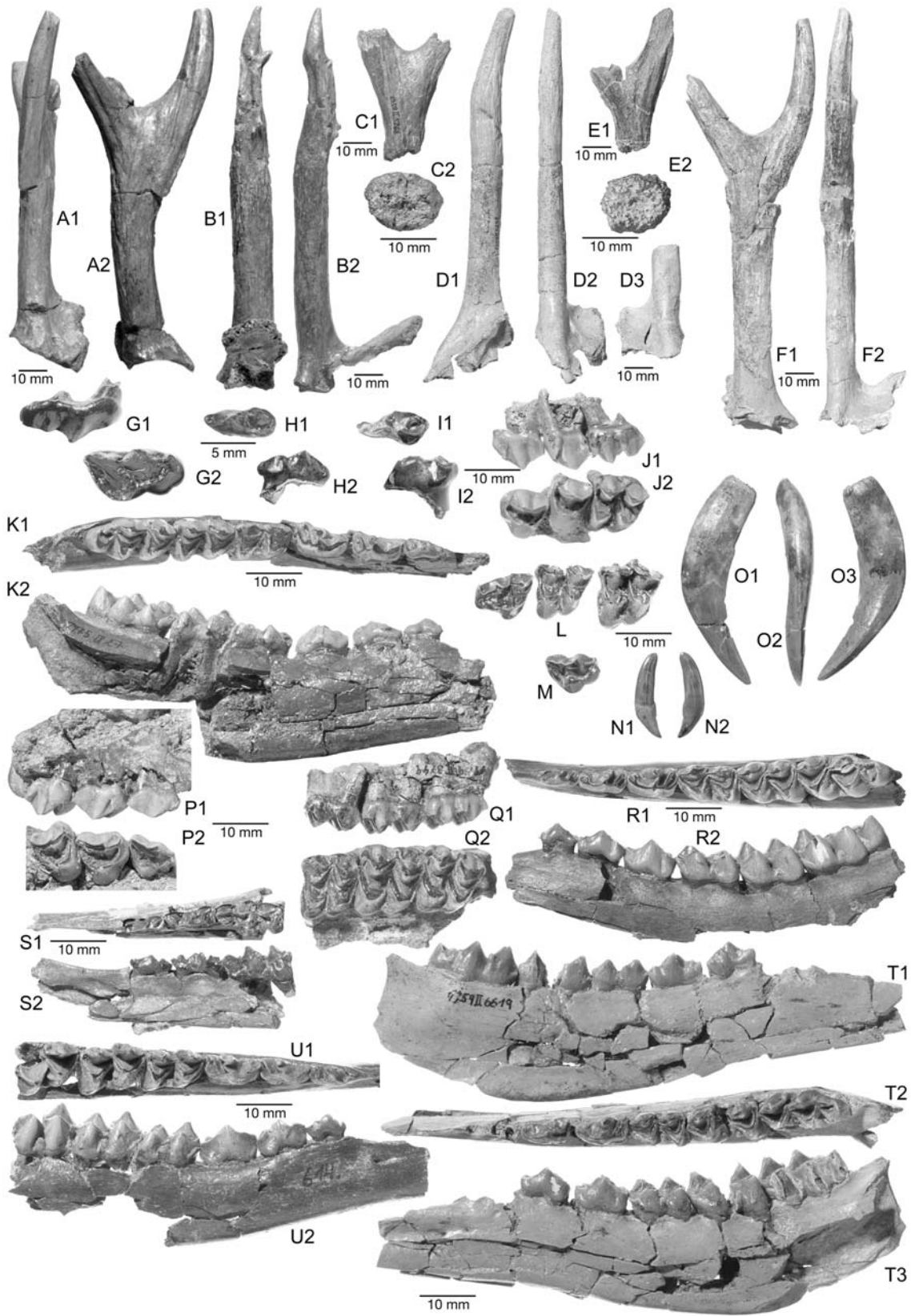
The teeth are similar in height and size to those of *P. dichotomus* from La Romieu (Roman and Viret 1934) and Bézian (Ginsburg and Bulot 1987) (see measurements in Table 5). They are smaller than in *P. dichotomus* from Rauscheröd (Rössner 1995) (see measurements in Table 5). The upper molars show a strong neocrista and a clear spur (Fig. 6J, L, Q). The cingulum is distinct in M1 and M2 on the anterior, lingual and posterior surfaces. In M3 it completely surrounds the lingual part of the tooth and is

sometimes posteriolabially present. The upper premolars have a medial crista and sometimes a weak cingulum (Fig. 6J, P). The P4 is more or less symmetrical horseshoe-shaped. P3 and P2 are triangular-shaped, but differ in a clearly larger width of the P3. The P2 is slender. Both have a very prominent paraconus column. D4 and D3 carry a spur (Fig. 6L). D4 has a strong anterior and lingual cingulum and a neocrista. D3 has a prominent parastyl and mesostyl and a weak anterior and lingual cingulum. The D2 is slender with a prominent paraconus column (Fig. 6G). The upper male canines are enlarged and elongated but clearly shorter than in *Procervulus* (Obergfell 1957, pl. 12 Fig. 43; pl. 13 Figs. 444–449) (Fig. 6O). In anterior view they are bent slightly outwards. Posteriorly they are indicated by a sharp edge, labially and anteriorly by a blunt edge. The labial edge is prominent, which gives the tooth a triangular diameter. One upper female canine is recorded, showing the same morphologic features, but is not enlarged and elongated (Fig. 6N).

All lower molars have strong ectostylids (Fig. 6K, R, T, U). The *Palaeomeryx*-fold is small but clear. Anterior and posterior cingulidae are medium in size. The m3 is characterized by a strong entoconulid, which is still smaller than the metaconid and the entoconid and often isolated or fused with the postentocristid, posthypoconulidcristid, praehypoconulidcristid, and/or posthypocristid. In the lower premolar row the p1 is absent and the individual teeth are relatively long and slender (Fig. 6K, R, T, U). p4 and p3 always have metaconid and postprotoconulidcristid. In p4 the postmetacristid is always developed, the praemetacristid occasionally. In p3 a postmetacristid is occasional. The p2 includes a long postprotocristid, entocristid, and hypocristid. The d4 has a strong anterior and posterior ectostylid, little anterior and posterior cingulid, a prominent mesostylid, and a clear *Palaeomeryx*-fold (Fig. 6S). d3 and d2 are slender and long (Fig. 6S). The d3 is equipped with a metaconid and long pre- and postprotoconulidcristids. The d2s vary substantially in length with differences up to 30% and have a clear entoconid. The preentocristid sometimes fuses with the postprotocristid forming a posterior fossette. Pre- and postprotoconulidcristid are very short. d1 is lacking.

Differential diagnosis:

Among other early cervids with dichotomous forked antlers *H. eggeri* differs from *Acteocemas* Ginsburg, 1984 (Azanza 2000) by a larger size, an absent proto-burr in the frontal appendages, a gradual transition from pedicle to fork in the frontal appendages, and a lancet-shaped depression of the outer bone layer of the frontal containing the foramen supraorbitale; it differs from *Procervulus praelucidus* (Obergfell 1957; see also Rössner 1995) by weak sculpture in the frontal appendages, proportionally longer pedicles in the frontal appendages, parallel oriented



◀ **Fig. 6** Cranial appendages and dental remains of *Heteroprox eggeri* n. sp. from Sandelzhausen (Inventory-No. BSPG 1959 II ...). **A:** 5249 right antler of an adult individual; **A1:** anterior view; **A2:** lateral view. **B:** 2502 right antler of a juvenile individual; **B1:** median view; **B2:** anterior view. **C:** 5268 cast antler fragment of an adult individual; **C1:** lateral/medial view; **C2:** proximal view of cast area. **D:** 5248 pair of antlers of a juvenile individual; **D1:** medial view of right antler; **D2:** anterior view of right antler; **D3:** anterior view of left antler. **E:** 5258 cast antler fragment of an adult individual; **E1:** lateral/medial view; **E2:** proximal view of cast area. **F:** 5247 right antler of an adult individual; **F1:** lateral view; **F2:** anterior view. **G:** 9032 right D2; **G1:** labial view; **G2:** occlusal view. **H:** 3920 left d2; **H1:** occlusal view; **H2:** labial view. **I:** 3922 left d2; **I1:** occlusal view; **I2:** labial view. **J:** 6629 left P3 to M1; **J1:** labial view; **J2:** occlusal view. **K:** 1975 IX 27 right mandible with p2 to m3; **K1:** occlusal view; **K2:** labial view. **L:** 3911 left D3, D4, M1; occlusal view. **M:** 5316 right P2, occlusal view. **N:** 8992 left female C; **N1:** labial view; **N2:** lingual view. **O:** 5301 right male C; **O1:** lingual view; **O2:** anterior view; **O3:** labial view. **P:** 5299 fragment of right maxilla with P2 to P4; **P1:** labial view; **P2:** occlusal view. **Q:** 3749 fragment of left maxilla with M1 to M3; **Q1:** labial view; **Q2:** occlusal view. **R:** 4315 fragment of left mandible with p2 to m3; **R1:** occlusal view; **R2:** labial view. **S:** 3870 fragment of left mandible with d2 to d4; **S1:** occlusal view; **S2:** labial view. **T:** 6619 left mandible with p3 to m3 and alveoli of p2; **T1:** lingual view; **T2:** occlusal view; **T3:** labial view. **U:** 2504 fragment of right mandible with p2 to m3; **U1:** occlusal view; **U2:** labial view

frontal appendages, a slightly more medial position of the frontal appendages, a lancet-shaped opening of the outer bone layer of the frontal containing the foramen supraorbital, higher crowned teeth, shorter and straighter upper canines, a prominent labial edge at upper canines, an only weak metaconus column and a stronger neocrista in the upper molars, a more prominent hypoconid column in the lower molars, more slender lower premolars, and molarised p3s (general existence of a metaconid and longer transversal crests); it differs from *Procervulus dichotomus* (Gervais 1849; see Rössner 1995) by a straight orientation of the frontal appendages pedicles in anterior and posterior view, shorter prongs in the frontal appendages, weak sculpture in the frontal appendages, a slightly more medial position of the frontal appendages, a lancet-shaped leave-out of the outer bone layer of the frontal containing the foramen supraorbital, shorter and straighter upper canines, a more prominent and more centrally positioned lateral edge at upper canines, an only weak metaconus column, stronger neocrista, shorter spur in upper molars, and molarised p3s (general existence of a metaconid and longer transversal crests); it differs from *Procervulus ginsburgi* (Azanza 1993; see also Azanza 2000) by only two prongs at the frontal appendages (besides accessorial prongs), stronger sculpturing of the frontal appendages, a lancet-shaped opening of the outer bone layer of the frontal containing the foramen supraorbital, and a lack of d1; it differs from *H. larteti* (Filhol 1891; see Ginsburg and Crouzel 1976) by a smaller size (Tables 5, 6), weaker sculpture of the frontal appendages, proportionally shorter prongs in the frontal appendages, and a stronger

Palaeomeryx-fold in the lower molars; it differs from *H. moralesi* (Azanza 2000) by a smaller size (Tables 5, 6), weaker sculpture of the frontal appendages, only two prongs in the frontal appendages (besides accessorial prongs), and proportionally shorter and wider upper canines; it differs from *H. anatoliensis* Geraads 2003 by weaker sculpture of the frontal appendages, longer prongs in the frontal appendages, and straight orientation of the pedicles in the anterior and posterior views; it differs from *Dicroceros elegans* (Lartet 1837; see Filhol 1891; Stehlin 1939; Ginsburg and Azanza 1991) by a smaller size, weaker sculpture of the frontal appendages, straight orientation of the frontal appendage pedicles in anterior and posterior views, the absence of a proto-burr on the frontal appendages, a gradual transition from pedicle to fork in the frontal appendages, shorter prongs in the frontal appendages, a lancet-shaped leave-out of the outer bone layer of the frontal containing the foramen supraorbital, more sel-enodont teeth and more slender premolars, and longer male upper canines; it differs from *Euprox* (Stehlin 1928) by weaker sculpture of the frontal appendages, straight orientation of the pedicles in the anterior and posterior views, an absent proto-burr, shorter prongs in the frontal appendages, a lancet-shaped leave-out of the outer bone layer of the frontal containing the foramen supraorbital, and lower crowned teeth; and it differs from *Amphiprox* (Haupt 1935; see Azanza and Menendez 1990; Kaup 1839b: Table 24 Figs. 2–4) by a smaller size, weaker sculpture of the frontal appendages, an absent proto-burr in the frontal appendages, shorter fork basis in the frontal appendages, and shorter prongs in the frontal appendages.

Comments: In comparison with all European cervids from the Miocene with dichotomous antlers general correspondence exists between *H. eggeri* n. sp. and *H. larteti* in morphological features of dentition and frontal appendages, even in the single equivalent stages of the antler cycle (compare with Filhol 1891: pl. 35 Fig. 4; Stehlin 1939: Fig. 1; Ginsburg and Crouzel 1976: Figs. 6, 7). They differ in the clearly smaller metrical values of *H. eggeri*. Hence the establishment of a new *Heteroprox* species is appropriate.

As described above, similarities in the morphology of dentition and antlers of Early to Middle Miocene *Procervulus* and Middle Miocene *Heteroprox* have hitherto been interpreted as evidence for an evolutionary lineage. Since the distinction of both genera often seems to be difficult because of overlapping morpho-metric character variability, different opinions concerning the stratigraphical occurrence of the transition within MN5 (Rössner 1995: 108) or at the border between MN5/MN6 (Ginsburg 1999: 113) exist and the synonymisation of *Procervulus* and *Heteroprox* has been discussed. With the extensive material of *H. eggeri* n. sp. striking new distinctive features have been revealed and documented, namely the shorter

Table 5 Tooth measurements for *Heteroprox eggeri* n. sp. from Sandelzhausen, for *Procervulus dichotomus* from Rauscheröd, La Romieu, Bézian, and for type materials of *H. larteti* measured by the author. Tooth measurements for *Heteroprox eggeri* n. sp. from Viehhausen and Undorf taken from Rinnert (1956). Tooth measurements for type materials of *H. moralesi* taken from Azanza (2000)

		D2	d2	D3	d3	D4	d4	M1	m1	M2	m2	M3	m3	P2	p2	P3	p3	P4	p4	Cm	Cf
<i>Heteroprox eggeri</i> n. sp., Sandelzhausen, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany)																					
l	N	1	3	1	2	4	2	33	36	33	46	29	41	11	13	15	31	32	38	12	1
	Min	9.4	6.0	11.8	9.4	9.7	12.3	9.4	9.5	10.7	11.0	9.8	11.5	8.9	6.8	9.0	8.8	7.0	9.4	8.5	4.1
	Max	9.4	8.0	11.8	9.8	10.9	13.3	12.3	12.3	12.4	13.3	12.4	18.3	10.0	8.2	11.0	10.9	9.3	11.9	11.0	4.1
antw/w	N	1	5	2	3	4	2	30	39	22	51	24	48	9	13	15	37	30	41	11	1
	Min	4.7	2.6	7.0	3.4	9.6	5.8	10.3	6.3	11.8	7.2	11.9	7.0	5.6	3.1	8.2	4.2	9.9	4.7	4.6	2.4
	Max	4.7	3.9	7.9	4.0	10.4	5.9	13.0	8.0	14.3	9.0	14.6	8.6	7.8	4.0	11.2	5.6	11.2	6.3	5.8	2.4
<i>Heteroprox eggeri</i> n. sp., Viehhausen und Undorf, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany) (described in Rinnert 1956)																					
L	N	–	–	–	–	–	–	1	–	1	3	1	–	1	–	1	1	1	2	–	–
	Min	–	–	–	–	–	–	11.0	–	12.0	12.0	12.5	–	10.0	–	9.7	10.0	8.0	11.2	–	–
	Max	–	–	–	–	–	–	11.0	–	12.0	12.4	12.5	–	10.0	–	9.7	10.0	8.0	12.0	–	–
antw/w	N	–	–	–	–	–	–	1	–	1	3	1	–	1	–	1	1	1	2	–	–
	Min	–	–	–	–	–	–	13.0	–	14.7	7.4	14.0	–	7.3	–	9.3	5.0	11.3	6.0	–	–
	Max	–	–	–	–	–	–	13.0	–	14.7	8.5	14.0	–	7.3	–	9.3	5.0	11.3	6.5	–	–
<i>Procervulus dichotomus</i> , Rauscheröd, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany) (described in Rössner 1995)																					
l	N	–	–	–	–	–	–	1	2	2	2	2	2	2	2	2	2	1	2	2	–
	Min	–	–	–	–	–	–	11.7	11.3	13.0	11.6	13.7	19.0	10.1	7.9	10.7	10.8	9.0	11.0	11.0	–
	Max	–	–	–	–	–	–	11.7	11.7	13.2	12.6	13.9	19.1	11.2	8.1	11.0	10.9	9.0	11.7	11.0	–
antw/w	N	–	–	–	–	–	1	2	2	2	2	2	2	2	2	2	1	2	–	–	–
	Min	–	–	–	–	–	–	13.9	7.9	16.6	9.2	16.3	9.7	7.5	3.6	11.3	5.1	11.3	6.7	–	–
	Max	–	–	–	–	–	–	13.9	8.1	17.9	9.3	16.7	10.1	8.3	3.7	11.5	5.8	11.3	7.1	–	–
<i>Procervulus dichotomus</i> , La Romieu, Centre de Paléontologie stratigraphique et Paléoécologie, Université Claude Bernard Lyon (Villeurbanne, France) (described in Roman and Viret 1934)																					
l	N	–	–	–	–	–	–	1	3	2	4	1	6	1	–	1	2	1	2	–	–
	Min	–	–	–	–	–	–	10.8	11.2	11.5	12.6	10.9	17.1	11.6	–	7.7	9.4	7.5	10.2	–	–
	Max	–	–	–	–	–	–	10.8	12.9	12.0	14.8	10.9	19.0	11.6	–	7.7	9.9	7.5	10.3	–	–
antw/w	N	–	–	–	–	–	–	1	3	2	4	1	6	1	–	1	2	1	2	–	–
	Min	–	–	–	–	–	–	11.5	7.7	12.5	9.5	11.5	8.0	7.9	–	10.6	5.2	11.0	6.0	–	–
	Max	–	–	–	–	–	–	11.5	8.5	12.8	9.7	11.5	9.9	7.9	–	10.6	5.2	11.0	6.3	–	–
<i>Procervulus dichotomus</i> , Bézian, Musée National d'Histoire Naturelle Paris (France) (described in Ginsburg and Bulot 1987)																					
l	N	1	–	2	–	3	2	4	8	3	5	4	10	2	1	2	3	2	3	–	–
	Min	9.7	–	12.0	–	9.6	13.1	11.6	11.9	13.3	12.0	12.3	15.8	9.4	7.3	11.3	8.9	9.2	9.4	–	–
	Max	9.7	–	13.4	–	11.9	13.9	12.6	13.2	14.0	13.9	13.3	19.7	10.7	7.3	11.4	10.5	9.6	10.3	–	–
antw/w	N	1	–	2	–	3	2	4	7	3	5	4	10	2	1	2	2	2	5	–	–
	Min	4.8	–	7.4	–	9.1	6.0	12.7	7.5	13.5	9.1	13.6	8.4	7.0	3.6	8.4	5.3	10.7	5.1	–	–
	Max	4.8	–	9.1	–	11.0	6.6	14.2	8.7	14.9	10.0	14.2	10.4	7.3	3.6	9.1	5.3	10.7	6.5	–	–
<i>Procervulus ginsburgi</i> , Artesilla, Museo Paleontológico de la Universidad de Zaragoza (Spain) (described in Azanza 1993)																					
l	N	–	–	–	–	–	–	3	13	5	12	5	6	1	6	4	11	7	11	–	–
	Min	–	–	–	–	–	–	11.3	10.0	11.5	10.1	12.1	16.0	10.2	6.8	9.7	9.1	7.7	9.2	–	–
	Max	–	–	–	–	–	–	11.8	11.4	12.3	12.2	12.5	17.5	10.2	7.9	10.7	10.0	8.9	10.5	–	–
antw/w	N	–	–	–	–	–	–	2	12	5	11	3	5	–	6	5	12	6	12	–	–
	Min	–	–	–	–	–	–	12.2	6.6	12.7	7.0	12.6	7.4	–	3.2	8.2	4.4	9.4	5.2	–	–
	Max	–	–	–	–	–	–	12.5	7.7	13.7	8.6	13.3	8.8	–	3.6	8.9	5.4	10.5	6.3	–	–

Table 5 continued

		D2	d2	D3	d3	D4	d4	M1	m1	M2	m2	M3	m3	P2	p2	P3	p3	P4	p4	Cm	Cf
<i>Heteroprox larteti</i> , Sansan, Musée National d'Histoire Naturelle Paris (France) (described in Filhol 1891 and Ginsburg and Crouzel 1976)																					
l	<i>N</i>	–	–	–	–	–	–	2	4	3	4	3	3	–	2	1	4	3	4	–	–
	Min	–	–	–	–	–	–	13.0	12.0	12.5	13.9	12.0	18.4	–	8.5	11.7	10.4	8.9	11.0	–	–
	Max	–	–	–	–	–	–	13.1	13.9	14.7	14.7	13.5	23.3	–	10.0	11.7	11.4	9.9	12.3	–	–
antw/w	<i>N</i>	–	–	–	–	–	–	2	4	3	4	3	3	–	2	1	4	3	4	–	–
	Min	–	–	–	–	–	–	13.8	8.2	14.3	9.4	13.5	8.8	–	4.0	11.3	5.6	11.4	6.6	–	–
	Max	–	–	–	–	–	–	14.0	9.4	15.7	11.0	14.9	10.7	–	5.0	11.3	6.3	12.2	7.5	–	–
<i>Heteroprox moralesi</i> , Puente Vallecas, Museo Nacional de Ciencias Naturales Madrid (Spain) (described in Azanza 2000)																					
l	<i>N</i>	–	–	–	–	–	–	2	6	2	4	2	4	1	1	2	3	3	5	1	–
	Min	–	–	–	–	–	–	14.0	13.0	15.4	15.7	16.8	21.3	11.8	9.9	11.0	10.9	10.1	11.8	11.0	–
	Max	–	–	–	–	–	–	14.1	14.3	15.6	16.3	17.0	22.8	11.8	9.9	12.4	12.7	11.5	14.4	11.0	–
antw/w	<i>N</i>	–	–	–	–	–	–	2	6	1	4	2	6	–	1	2	3	3	5	–	–
	Min	–	–	–	–	–	–	15.2	8.8	17.3	11.5	18.1	11.2	–	5.0	12.6	6.6	13.9	7.2	–	–
	Max	–	–	–	–	–	–	15.4	10.0	17.3	12.4	19.2	12.4	–	5.0	13.4	7.4	14.8	8.5	–	–

l largest length; *antw/w* largest anterior width for Ms, ms, and D4s or largest width for Ps, ps, D3s, D2s, and ds; *N* number of measurements; *Min* minimum value measured; *Max* maximum value measured. Measurements in mm

and straighter shape and different morphology of the upper canines of males (indicative of the whole genus; Filhol 1891: pl. XXII Fig. 3; Fraas 1870: pl. VIII Fig. 10) and the lancet-shaped leave-out of the outer bone layer of the frontal close to the appendage basis containing the foramen supraorbital. Without a doubt they justify the maintaining of two different genera and corroborate the evidence of *Procervulus dichotomus* and *H. larteti*, which show different morphology in the caudal cranium (Rössner 1995:108).

The here described new and hitherto earliest representative of *Heteroprox* makes it impossible to reconstruct an evolutionary lineage transforming *Procervulus* to *Heteroprox*. First, the appearance of *H. eggeri* n. sp. in the early middle MN5 conflicts with records of *P. dichotomus* from other contemporaneous localities (e.g. Tavers and La Romieu (type locality of *Procervulus dichotomus*; type species *Antilope dichotoma*). Moreover the biochronologically older *P. dichotomus* from Rauscheröd (MN4, Germany) (Rössner 1995) is larger than *H. eggeri* n. sp. But *H. eggeri*'s correspondence in morphology with *H. larteti* (MN5–MN7) and *H. anatoliensis* (MN6) and its chronological earlier occurrence makes it a probable ancestor of both species. The origin of the genus *Heteroprox* might be an offshoot from the *Procervulus* line. Such an event has been already assumed in the middle of MN5 or at the beginning of MN6 (Rössner 1995; Ginsburg 1999 respectively) for *H. larteti*, but with *H. eggeri* this event has to be set back to early middle MN5. An urgently necessary revision of both genera would shed more light on this phylogeny.

The antlers of *Procervulus dichotomus* from Viehhausen (Rinnert 1956: Table 1 Figs. 9, 10) correspond in size and morphology to those of *H. eggeri* n. sp., which was therefore synonymised with the latter species.

Genus *Lagomeryx* Roger, 1904

Type species: *L. ruetimeyeri* Thenius, 1948 (proposed by Gentry and Heizmann (1993) to the ICZN and accepted by the ICZN in 1994 (ICZN Opinion 1790, *Bulletin of Zoological Nomenclature* 51: 290, 1994).

Type specimen: left frontal appendage, BSPG 1881 IX 55 m, from Reisenburg (MN4, Germany) (Rüttimeyer 1883, pl. I Figs. 2–5; Stehlin 1937: Fig. 9; Gentry et al. 1999: Fig. 23.11).

Further European species: *L. parvulus* (Roger, 1898), *L. pumilio* (Roger, 1896).

Chronological occurrence in Europe: MN3? (late Early Miocene, Eggenburgian, early Orleanian) (Ginsburg et al. 2000), MN4 (late Early Miocene, late Otnangian) (Rössner 1998; Eronen and Rössner 2007) to early MN6 (middle Middle Miocene, late Badenian) (Rössner 2006).

General information: *Lagomeryx*'s European representatives are restricted to small Cervidae from the Lower to Middle Miocene of Europe. Their frontal appendages differ from those of the most early cervids by a multipointed antler with 5 to 7 hierarchical equal prongs, radially branching from a basal plate and sitting on a long pedicle without proto-burr (Rüttimeyer 1881: pl. I Figs. 2–3; Schlosser 1916: pl. 1 Fig. 21; Stehlin 1937: Fig. 9; Rinnert 1956: pl. 1 Fig. 13; Fahlbusch 1977: Fig. 2; pl. 16 Figs. 1–7; Gentry et al. 1999: Fig. 23.11). The prongs are short and mostly upwards curved. The surface of the cranial appendages is smooth. They were supraorbital, extracranial, and diverging positioned on the skull with a slight inwards curving. The brachyoselenodont dentition of the European *Lagomeryx* belongs to the lowest crowned within the Miocene cervids in common with *Procervulus*, *Heteroprox*,

Table 6 Antler measurements for *Heteroprox eggeri* n. sp. from Sandelzhausen and closer relatives. Measurements for *Procervulus praelucidus* from Wintershof-West and for *Procervulus dichotomus* from Rauscheröd were taken by the author. Measurements for *Procervulus dichotomus* from Bézian are from Ginsburg and Bulot

(1987), for *H. larteti* done by the author and taken from Ginsburg and Crouzel (1976), and for *H. moralesi* were taken from Azanza (2000). Comparable measured distances are not preserved for the antlers from Viehhausen and Undorf (Rinnert 1956)

Inventory-No.	l	papd	pml
<i>Heteroprox eggeri</i> n. sp., Sandelzhausen, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany)			
1959 II 5247 adult	105	14.0	11.1
1959 II 5249 senil	86	19.0	13.8
1959 II 7894 senil	99	16.0	15.4
1959 II 12314 juvenil	–	12.5	10.9
1959 II 5246 juvenil	–	12.5	12.1
1959 II 5248 right juvenile	–	13.2	10.6
1959 II 5248 left juvenile	–	14.0	11.5
<i>Heteroprox larteti</i> , Sansan, Musée National d'Histoire Naturelle Paris (France) (described in Ginsburg and Crouzel 1976)			
Sa 3317 adult, holotype	116.0	18.3	15.2
Sa 3399 right senile	104.0	24.0	18.0
Sa 3399 left senile	96.0	18.0	
Sa 3316 right juvenile	114.0	18.0	–
Sa 3315 right adult	105.0	21.0	–
<i>Heteroprox moralesi</i> , Puente de Vallecas, holotype, Museo Nacional de Ciencias Naturales Madrid (Spain) (described in Azanza 2000)			
MNCNM/CR-3054	141.0	21.2	20.3
<i>Procervulus praelucidus</i> , Wintershof-West, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany) (described in Rössner 1995)			
BSPG 1937 II 16841	115.0	N 45	47
BSPG 1937 II 16803	96.2	Min 9.5	7.3
BSPG 1937 II 16794	94.6	Max 19.2	17.0
BSPG 1937 II 16852	72.9		
<i>Procervulus dichotomus</i> , Rauscheröd, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany) (described in Rössner 1995)			
1979 XV 555 right adult	136.6	17.0	14.0
1979 XV 555 left adult	122.6	17.0	14.0
<i>Procervulus dichotomus</i> , Bézian, National d'Histoire Naturelle Paris (France) (described in Ginsburg and Bulot 1987)			
Be 7518 left adult	130.0	–	–
Be At 7150 right adult	110.0	–	–

l length from orbita edge to bifurcation; papd proximal anteroposterior diameter; pml proximal mediolateral diameter; N number of measurements; Min minimum value measured; Max maximum value measured. Measurements in mm

and *Dicrocerus*. The upper canines are enlarged and elongated in males. They are laterally flattened, curved to the posterior and to labial, and equipped with a sharp posterior edge. They are proportionally similar to the canines of *Procervulus* and therefore clearly longer than in all other remaining genera.

The establishment of a family Lagomerycidae based on characters of the cranial appendages has been discussed repeatedly, most recently in Ginsburg and Chevrier (2003). However, because of always insufficient evidence this paper does not make that distinction.

Lagomeryx parvulus (Roger, 1898), Appendix Figs. 7, 8

Holotype: left mandible with p3 to m3 and alveoli of p2, 86-500 stored in the NMA, original of Roger (1898: pl. 2 Fig. 7) and Roger (1900: pl. 3 Fig. 9).

Type locality: Reischenau, Upper Freshwater Molasse, Bavaria, Germany, most likely MN5.

Chronological and geographical occurrence: see genus.

Description and comparison: *L. parvulus* is the medium sized species within European *Lagomeryx* (Fig. 7). *L. pumilio* is a little smaller and *L. ruetimeyeri* a little larger

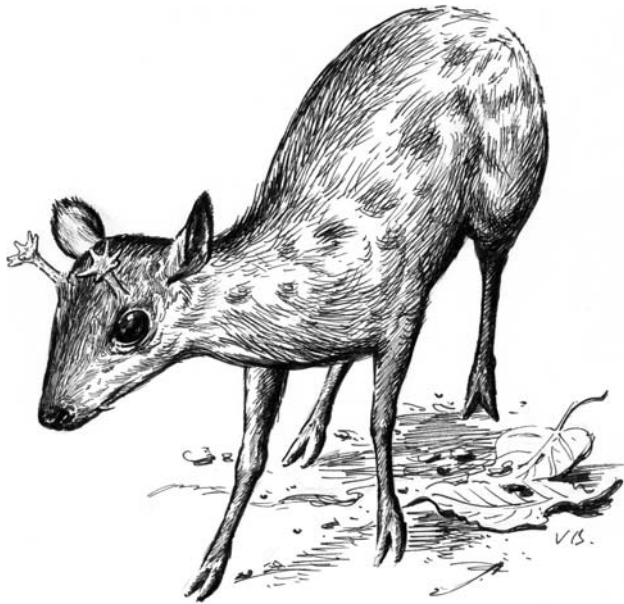


Fig. 7 Reconstruction of *Lagomeryx parvulus* in lifetime appearance (drawing W. Balat, Munich)

(Table 7). From Sandelzhausen a nearly completely preserved antler (678, Fig. 8Y) is recorded with very similar morphology to the genus type antler of *L. ruetimeyeri* (see above), but smaller size. It has seven prongs (one is broken) of similar size positioned with more or less the same distance in between them around the oval basal plate, described in detail in Fahlbusch (1977: pl. 16 Figs. 1–7). Two further fragmentary antler specimens (4594 and 7803, Fig. 8AF, AG) show a less regular prong arrangement and a possible proximal cast area (Fig. 8AF1). Moreover, two right pedicles still attached to the dorsal part of the orbita are recorded (Fig. 8AD, AE). They are similar in size and morphology with slight inwards bending. They are different in the lateral bounding just above the orbit, where specimen 8979 shows smooth morphology without any protuberance (Fig. 8AE2) whereas specimen 4646 possesses a lateral foramen (Fig. 8AD2).

In the upper molars (Fig. 8G, Q) parastyle, metastyle, and the paraconus column are quite prominent and slender. A neocrista is clearly developed, but no spur. The cingulum is weak with the exception of M3, where it is stronger. The M2 is the largest tooth within the upper molar row. The P4 is horseshoe-shaped with prominent parastyle, paraconus column, and metastyle, and a medial crista (Fig. 8AB, AC). P3 and P2 are triangular, but P3 (Fig. 8V, W) is much wider than P2 (Fig. 8M, N), which is relatively slender. Parastyle and paraconus column are very prominent. The medial crista is weak. The cingula are weak on P4 and lacking on P3 and P2. The D4 has a comparably strong cingulum and a spur at the posthypocrista (Fig. 8P). D3s are only partially preserved showing no specific feature besides size. The D2s are much slender than P2s with a prominent paraconus column

(Fig. 8O, X). An upper male canine is partly preserved. It is very slender, medially enamel-free, with a sharp posterior edge and a drop-shaped diameter (Fig. 8F). In the lower molars (Fig. 8Z, AA) the *Palaeomeryx*-fold is weak. The back fossette of the m3 usually completely closes with the postentocristid and/or posthypocristid. The cingulid is strong anterior and posterior. The lower premolars are various in shape from compact to slender. The p4 has a strong metaconid and a crestfallen postprotocristid (Fig. 8I, K). The p3 often has a metaconid (Fig. 8J, S). The p2 lacks metaconid and postprotoconulidcristid (Fig. 8H, R) and has two roots. The p1 shows the protoconid and short and weak protocristid, *Palaeomeryx*-fold, postprotocristid, entocristid, and hypocristid (Fig. 8A, B, C, D). The deciduous lower cheek teeth are elongated trapezoidal shaped. The d4 has strong anterior and posterior ectostylids (Fig. 8T, U). d2 and d3 lack a metaconid (Fig. 8E, L). The d3 possesses a very short postprotoconulidcristid. The d1 is not documented.

The morphology and size of the dentition of the Sandelzhausen *L. parvulus* is close to Early and Middle Miocene Moschidae. The size is slightly below that of *Pomelomeryx boulangeri* and slightly larger than that of *Micromeryx flourensianus* (Table 7). The dentition of the moschid *P. gracilis* has the same size and similar morphology, but *L. parvulus* differs in more crescent-shaped cusps on lower molars with lingually uncurved metaconid and entoconid, in a metastylid less closely attached to postmetacristid, in a postmetacristid on p4, in more isolated styles on upper molars, in a stronger spur and further extended posthypocrista, in an always present medial crista, in a more prominent labial profile, in an anterior more incised P3 with stronger medial crista, and in a weaker entostyle (Rössner and Rummel 2001: 51). Compared with *P. boulangeri* the tooth cusps are more selenodont, the posterior fossettes of the lower molars are proportionally more slender, and the crown height is slightly larger. It differs from *M. flourensianus* by a lower crown height, a lacking third lingual cuspid in m3 and a lacking closing of the anterior valley in p4 (Rössner 2006). The lower tooth row includes a p1 (Fig. 8A, B, C, D) in contrast with *L. pumilio*, *P. boulangeri*, and *M. flourensianus*. The upper molars are rectangular in shape (Fig. 8G, Q) in contrast with the square shape in *L. pumilio* Table 8.

Discussion: Considering previously found small-sized Miocene ruminants from Europe (see above) the lectotype jaw of *Lagomeryx parvulus*, NMA 86-500, found in Reischenau, an area in the Bavarian Molasse Basin, corresponds very well to the larger small-sized cervid from Sandelzhausen. Although the lectotype is medium to strongly worn and several details are missing, the available evidence suggests the lower dentition of *L. parvulus* from Sandelzhausen is identical in size and morphology. Further upper and deciduous dentitions of the same size group recorded from Sandelzhausen are also assigned to *L. parvulus*.

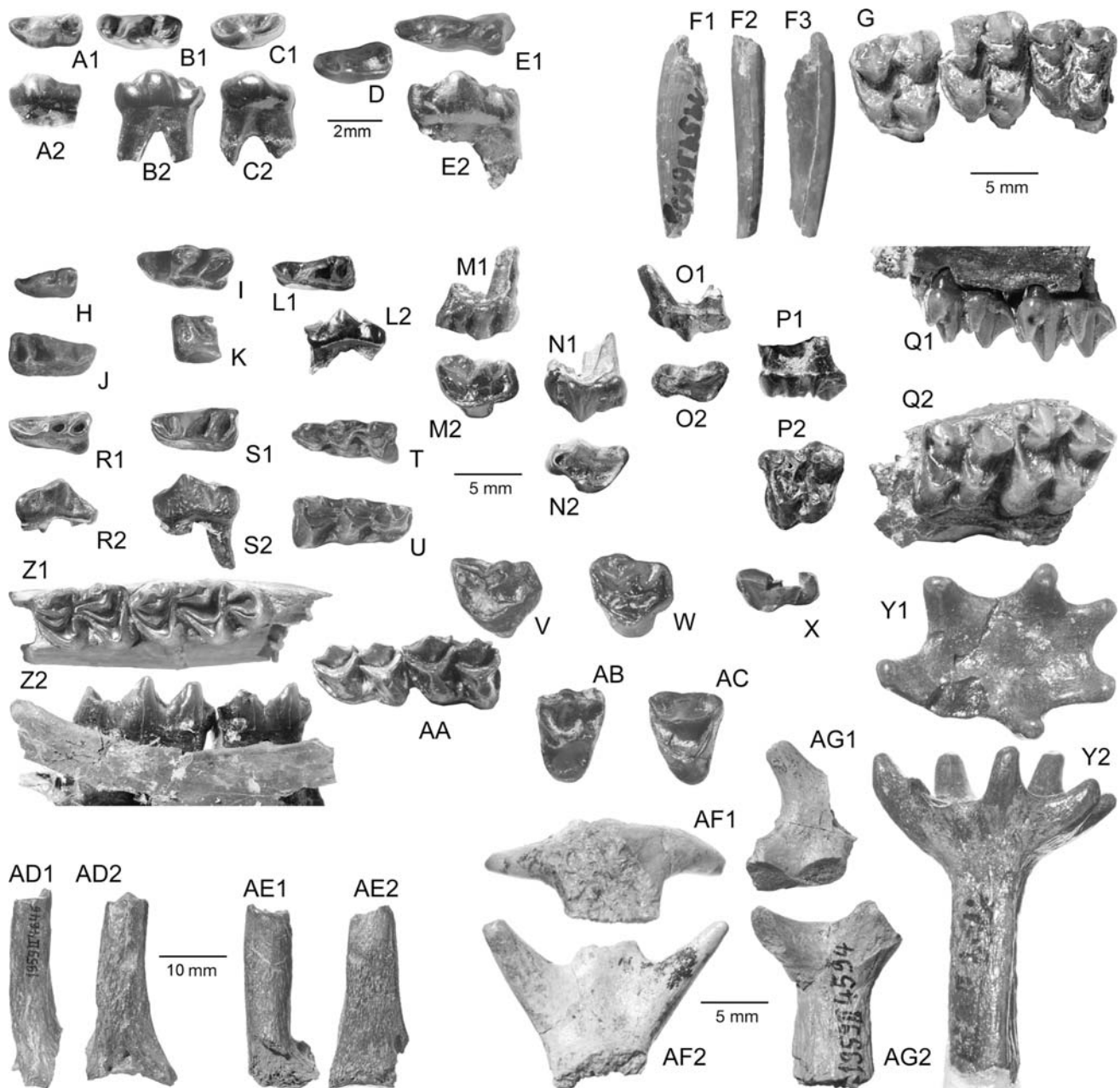


Fig. 8 Dental remains and cranial appendages of *Lagomeryx parvulus* (Roger, 1898) from Sandelzhausen (Inventory-No. BSPG 1959 II ...). **A:** 4321 left p1; **A1:** occlusal view; **A2:** labial view. **B:** 9066 left p1; **B1:** occlusal view; **B2:** labial view. **C:** 9067 left p1; **C1:** occlusal view; **C2:** labial view. **D:** 6604 left p1, occlusal view. **E:** 9073 left d2; **E1:** occlusal view; **E2:** labial view. **F:** 6603 right male C; **F1:** labial view; **F2:** anterior view; **F3:** lateral view. **G:** 4313 right M1 to M3, occlusal view. **H:** 7814 left p2, occlusal view. **I:** 4611 left p4, occlusal view. **J:** 7825 right p3, occlusal view. **K:** 4115 fragmentary right p4, occlusal view. **L:** 4015 left d3; **L1:** occlusal view; **L2:** labial view. **M:** 3954 right P2; **M1:** labial view; **M2:** occlusal view. **N:** 3964 left P2; **N1:** labial view; **N2:** occlusal view. **O:** 3961 left D2; **O1:** labial view; **O2:** occlusal view. **P:** 3967 left D4; **P1:** labial view; **P2:** occlusal view. **Q:** 4609 left M1 to M2; **Q1:** labial view; **Q2:** occlusal view.

R: 3952 left p2; **R1:** occlusal view; **R2:** labial view. **S:** 4062 left p3; **S1:** occlusal view; **S2:** labial view. **T:** 4045 left d4, occlusal view. **U:** 7824 right d4, occlusal view. **V:** 3973 right P3, occlusal view. **W:** 4012 right P3, occlusal view. **X:** 4097 fragmentary right D2, occlusal view. **Y:** 678 antler of an adult individual (original to Fahlbusch 1977); **Y1:** distal view; **Y2:** side view. **Z:** 4312 fragment of left mandible with m2 to m3; **Z1:** lingual view. **AA:** 6614 left m1 to m2, occlusal view. **AB:** 3953 left P4, occlusal view. **AC:** 5370 right P4, occlusal view. **AD:** 4646 right antler pedicle; **AD1:** anterior view; **AD2:** lateral view. **AE:** 8979 right antler pedicle; **AE1:** anterior view; **AE2:** lateral view. **AF:** 7803 fragmentary cast antler; **AF1:** view of cast area; **AF2:** distal view. **AG:** 4594 fragmentary antler; **AG1:** distal view; **AG2:** side view

Table 7 Tooth measurements for *Lagomeryx parvulus* and *Lagomeryx pumilio* from Sandelzhausen and for the type material from Reischenau, *Lagomeryx ruetimeyeri* from Landstrost and Oberdorf, *Pomelomeryx boulangeri* type material from St-Gérard-le-Puy, *Pomelomeryx gracilis* type material from Montaigu-le-Blin, and *Micromeryx flourensianus* type material from Sansan. All measured by the author

		d1	D2	d2	D3	d3	D4	d4	M1	m1	M2	m2	M3	m3	p1	P2	p2	P3	p3	P4	p4	Cm	Cf
<i>Lagomeryx parvulus</i> , Sandelzhausen, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany)																							
l	N	–	4	–	–	2	1	2	7	4	10	7	6	5	13	5	2	3	3	3	1	–	–
	Min	–	5.1	–	–	5.8	6.4	7.9	6.4	5.9	6.5	7.0	6.5	9.4	2.0	5.0	4.7	5.0	6.3	5.0	6.9	–	–
	Max	–	6.1	–	–	6.1	6.4	8.8	7.1	8.1	8.0	7.8	7.4	10.7	3.5	6.3	6.1	7.0	6.4	6.8	6.9	–	–
antw/w	N	–	5	2	1	2	1	3	6	6	8	8	6	6	13	5	3	2	5	3	2	–	–
	Min	–	2.5	2.1	5.4	2.4	5.8	3.0	7.1	4.1	7.5	4.5	7.1	3.7	1.0	3.5	2.2	5.7	2.6	6.1	3.1	–	–
	Max	–	3.1	2.2	5.4	2.7	5.8	3.9	8.4	5.2	8.8	5.1	8.5	5.4	1.5	5.7	3.1	6.0	3.4	6.9	3.3	–	–
<i>Lagomeryx pumilio</i> , Sandelzhausen, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany)																							
l	N		11	2	3	–	4	4	19	29	8	18	16	16		8	8	6	10	11	15	–	–
	Min		3.5	4.0	4.9	–	4.6	6.0	5.0	4.5	5.6	5.4	4.8	5.9		4.0	3.0	4.6	3.8	3.9	4.2	–	–
	Max		4.8	4.4	5.0	–	5.3	6.7	5.9	6.3	6.2	6.4	5.8	8.8		5.4	3.9	5.1	4.9	4.7	5.7	–	–
antw/w	N		12	3	6	–	4	6	18	31	6	20	17	20		9	10	4	13	9	18	–	–
	Min		1.6	1.3	3.0	–	4.2	2.3	5.1	2.1	5.9	3.2	5.3	3.1		3.0	1.5	3.4	1.8	4.7	2.2	–	–
	Max		2.9	1.5	4.4	–	5.3	3.0	6.6	3.8	6.6	4.2	6.8	4.9		4.4	2.8	5.3	3.4	5.3	3.1	–	–
<i>Lagomeryx parvulus</i> , Reischenau, Naturmuseum Augsburg (Germany) (described in Roger 1898, 1900)																							
l	N	–	–	–	–	–	–	–	–	1	–	1	–	1	–	–	–	–	1	–	1	–	–
	Min	–	–	–	–	–	–	–	–	5.8	–	7.2	–	10.0	–	–	–	–	5.9	–	5.7	–	–
	Max	–	–	–	–	–	–	–	–	5.8	–	7.2	–	10.0	–	–	–	–	5.9	–	5.7	–	–
antw/w	N	–	–	–	–	–	–	–	–	1	–	1	–	1	–	–	–	–	1	–	1	–	–
	Min	–	–	–	–	–	–	–	–	4.0	–	4.9	–	5.0	–	–	–	–	2.7	–	3.2	–	–
	Max	–	–	–	–	–	–	–	–	4.0	–	4.9	–	5.0	–	–	–	–	2.7	–	3.2	–	–
<i>Lagomeryx pumilio</i> , Reischenau, Häder, Naturmuseum Augsburg (Germany) (described in Roger 1898, 1900)																							
l	N	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	1	–	1	–	–
	Min	–	–	–	–	–	–	–	–	4.4	–	–	–	8.0	–	–	–	–	4.5	–	5.0	–	–
	Max	–	–	–	–	–	–	–	–	4.4	–	–	–	8.0	–	–	–	–	4.5	–	5.0	–	–
antw/w	N	–	–	–	–	–	–	–	–	1	–	1	–	1	–	–	–	–	1	–	1	–	–
	Min	–	–	–	–	–	–	–	–	2.8	–	3.2	–	3.5	–	–	–	–	2.0	–	2.5	–	–
	Max	–	–	–	–	–	–	–	–	2.8	–	3.2	–	3.5	–	–	–	–	2.0	–	2.5	–	–
<i>Lagomeryx ruetimeyeri</i> , Landstrost, Bayerische Staatsammlung für Paläontologie und Geologie in München (Germany)																							
l	N	–	–	–	–	–	–	–	–	4	–	2	–	2	–	–	1	–	4	–	3	–	–
	Min	–	–	–	–	–	–	–	–	8.0	–	9.5	–	13.3	–	–	6.1	–	6.7	–	7.4	–	–
	Max	–	–	–	–	–	–	–	–	9.3	–	9.6	–	13.4	–	–	6.1	–	8.2	–	8.8	–	–
antw/w	N	–	–	–	–	–	–	–	–	4	–	2	–	2	–	–	1	–	4	–	3	–	–
	Min	–	–	–	–	–	–	–	–	4.9	–	6.5	–	6.8	–	–	2.7	–	2.7	–	3.8	–	–
	Max	–	–	–	–	–	–	–	–	5.8	–	6.8	–	6.8	–	–	2.7	–	2.7	–	4.6	–	–
<i>Lagomeryx ruetimeyeri</i> , Oberdorf, Naturhistorisches Museum Wien (Austria) (described in Rössner 1998)																							
l	N	–	1	1	–	–	–	–	–	–	1	–	2	3	1	4	4	1	1	3	4	–	–
	Min	–	8.4	6.0	–	–	–	–	–	–	9.7	–	9.8	14.7	3.5	7.6	6.3	8.5	8.3	6.8	6.7	–	–
	Max	–	8.4	6.0	–	–	–	–	–	–	9.7	–	10.8	14.8	3.5	8.9	6.5	8.5	8.3	9.4	8.8	–	–
antw/w	N	–	1	1	–	–	–	–	–	–	1	–	2	3	1	4	4	1	2	2	4	–	–
	Min	–	4.1	2.5	–	–	–	–	–	–	12.3	–	11.2	7.2	1.7	6.2	3.1	7.8	4.2	9.1	4.3	–	–
	Max	–	4.1	2.5	–	–	–	–	–	–	12.3	–	12.8	8.0	1.7	7.0	3.6	7.8	4.4	10.0	5.0	–	–

Table 7 continued

		d1	D2	d2	D3	d3	D4	d4	M1	m1	M2	m2	M3	m3	p1	P2	p2	P3	p3	P4	p4	Cm	Cf
<i>Pomolomeryx boulangeri</i> , St-Gérard-le-Puy, Musée Guimet d'Histoire Naturelle de Lyon (France) (described in Filhol 1891, Viret 1929)																							
l	<i>N</i>	–	–	–	–	–	–	–	–	1	–	1	–	1	–	–	–	1	–	1	–	–	
	Min	–	–	–	–	–	–	–	7.8	–	8.4	–	13.3	–	–	–	6.8	–	7.1	–	–		
	Max	–	–	–	–	–	–	–	7.8	–	8.4	–	13.3	–	–	–	6.8	–	7.1	–	–		
antw/w	<i>N</i>	–	–	–	–	–	–	–	–	1	–	1	–	1	–	–	–	1	–	1	–	–	
	Min	–	–	–	–	–	–	–	5.3	–	6.3	–	6.5	–	–	–	3.3	–	3.9	–	–		
	Max	–	–	–	–	–	–	–	5.3	–	6.3	–	6.5	–	–	–	3.3	–	3.9	–	–		
<i>Pomolomeryx gracilis</i> , Montaignu-le-Blin, Musée Guimet d'Histoire Naturelle de Lyon (France) and Centre de Paléontologie stratigraphique et Paléocéologie, Université Claude Bernard Lyon (Villeurbanne, France) (described in Filhol 1881, Viret 1929)																							
l	<i>N</i>	–	1	–	1	–	1	3	4	3	4	3	2	–	1	1	2	2	2	3	–	–	
	Min	–	4.3	–	6.0	–	8.5	6.6	6.4	7.5	7.1	7.1	10.4	–	6.3	4.9	6.4	5.7	5.3	5.6	–	–	
	Max	–	4.3	–	6.0	–	8.5	6.8	7.3	7.6	7.5	7.3	10.5	–	6.3	4.9	6.6	5.9	5.3	6.8	–	–	
antw/w	<i>N</i>	–	1	–	1	–	1	3	4	3	4	3	2	–	–	1	1	2	2	3	–	–	
	Min	–	2.5	–	2.5	–	3.4	7.5	4.1	8.4	5.0	7.8	5.0	–	–	1.9	5.1	1.9	5.5	3.0	–	–	
	Max	–	2.5	–	2.5	–	3.4	7.6	4.3	8.5	5.4	7.9	5.0	–	–	1.9	5.1	2.4	6.2	3.3	–	–	
<i>Micromeryx flourensianus</i> , Sansan, Musée National d'Histoire Naturelle Paris (France) and Naturhistorisches Museum Basel (Switzerland) (described in Filhol 1891)																							
l	<i>N</i>	6	1	5	1	4	1	5	7	3	7	2	6	–	5	3	5	4	3	5	–	–	
	Min	5.1	3.6	5.7	5.1	5.3	7.0	6.0	5.8	6.7	6.2	6.8	8.7	–	5.7	3.8	5.5	5.5	4.5	5.1	–	–	
	Max	5.7	3.6	6.6	5.1	6.2	7.0	6.7	6.6	7.0	6.9	7.0	10.4	–	6.1	4.5	6.2	5.8	5.8	6.5	–	–	
antw/w	<i>N</i>	6	1	5	1	4	1	5	5	3	6	2	5	–	5	3	4	3	3	4	–	–	
	Min	3.0	1.8	4.0	2.5	5.2	3.2	6.0	3.8	7.4	4.0	6.7	4.2	–	3.8	1.9	4.9	2.9	4.7	3.4	–	–	
	Max	3.8	1.8	4.8	2.5	5.6	3.2	6.8	4.4	6.9	4.8	7.0	4.5	–	5.9	2.1	5.4	3.3	5.7	3.5	–	–	

l largest length; *antw/w* largest anterior width for Ms, ms, and D4s or largest width for Ps, ps, D3s, D2s, ds, and Cs; *N* number of measurements; *Min* minimum value measured; *Max* maximum value measured. Measurements in mm

Moreover, the documented fragments of *Lagomeryx*-like frontal appendages of a small sized deer complete the picture of this species nicely. However, so far frontal appendages of the small sized European *Lagomeryx*-species have only been found isolated, which makes determination difficult. But the assemblage with teeth of a restricted number of ruminant size groups gives options for assignment. So, Roger (1885: pl. I Fig. 13; 1898: pl. II Fig. 4) described a base of a frontal appendage, a simple pedicle of 10 mm diameter, and finally assigned it to *L. parvulus*; according to the size of the teeth this seems probable. Fahlbusch (1977) associated the nearly completely preserved *Lagomeryx*-antler from Sandelzhausen (Fig. 8Y) to *L. pumilio*, which is also recorded in Sandelzhausen. However the extremely small size of the latter species makes this improbable.

In contrast with the assertion in Fahlbusch (1977: 228), that *Lagomeryx* is known to have possessed a non-drop-pable antler, nowadays antler specimens are known which document an antler cycle indicating periodic casting and redeveloping with continuous increase in prong number (Rössner in preparation).

The exact fossil site from which the lectotype originates is unknown. The lectotype was collected by

a member of the Naturwissenschaftlicher Verein für Schwaben und Neuburg in Augsburg (Roger 1885: 99) and is stored in the collection of the NMA. Roger (1885: 104; 1896: 550) first identified it as “*Micromeryx Flourensianus*”. Later he clarified the error and illustrated the specimen (1898: 38, pl. II Fig. 4, 7). For the whole collection from this area Roger (1885: 99) gave as localities Breitenbronn and Kutzenhausen in the “Reischenau”, which is the name of a landscape in the valley of the little river Zusam West of the city of Augsburg. Therefore the age of the lectotype can only be determined by comparison with neighbouring sites, e.g. Häder, which is positioned in the European mammal unit MN5.

In Ginsburg et al. (2000: 623) the type material is stated as missing and a specimen from the Bavarian locality Häder, with no further identifying information, is proposed as the neotype. Because the type material has since been located, the established neotype is invalid.

The type of *Calomeryx nitidus* from the Bavarian locality Häder (Roger 1900: pl. III Fig. 7), fragment of a right mandible with m1, d4 and d3, NMA 79.5012) corresponds in size and morphology to the lectotype of *L. parvulus*, which implies synonymy and makes *C. nitidus* an invalid name.

Similarity in morphology and size of the teeth of *L. parvulus* and *Pomelomeryx gracilis* is the reason for discrepancies in assessing the first appearance datum of *L. parvulus*. Some French localities from MN3 yielded specimens which were identified as *L. parvulus*. Only a few of these are poorly described with reference to the type material (Ginsburg et al. 2000: 623), but the characteristic cranial appendages have never been found. Additionally, the similarity between *L. parvulus* and *P. gracilis* never is mentioned. Until today the reference locality for MN3 Wintershof-West in southern Germany yielded the most extensive material of the latter species, described as *L. aff. parvulus* by Obergfell (1957). In Rössner (1997) this material was synonymised with *P. gracilis*. No further *L. parvulus* materials older than MN4 are described elsewhere besides the French material. Consequently the first appearance datum of *L. parvulus* in MN3 has to be taken as uncertain until detailed revision of the French records.

***Lagomeryx pumilio* (Roger, 1896), Fig. 9, Appendix**

Holotype: right m3, 80-45 stored in the NMA, original of Roger (1898: 39, pl. 2 Fig. 5).

Type locality: Reischenau, Upper Freshwater Molasse, Bavaria, Germany, most likely MN5.

Chronological and geographical occurrence: early middle MN5 (boundary Early/Middle Miocene, topmost Burdigalian or basalmost Langhian) (this study) to early MN6 (middle Middle Miocene, early Serravalian) (Rössner 2002) in Europe.

Description and comparison: smallest representative of Miocene European Ruminantia. The lower molars have a comparably large ectostylid (Fig. 9F, Q, T, U, V, W, Y, AB, AC). The p4 has a strong metaconid protruding lingually, mostly with a postmetacristid, and often long pre- and postprotoconulidcristids, which are oriented to lingual (Fig. 9F, P, U, V, Y, AB, AC). The p3s have a weak metaconid (Fig. 9F, S, V, AB, AC). Pre- and postprotoconulidcristid are long, the latter is lingually oriented. The p2 has a very weak postprotocristid and entocristid, but no postprotoconulidcristid (Fig. 9F, V, X, AC). The d4 has a strong posterior ectostylid in correspondence with the lower molars and a weak cingulum (Fig. 9N, R). d3 is not recorded. The d2 is long and slender with protocristid and entocristid oriented posteriorly (Fig. 9O). There is no preprotoconulidcristid. The upper molars have a prominent paraconus column and a nearly lacking metaconus column (Fig. 9Z, AA). The neocrista is strong. At the posthypocrista a spur is sporadically developed. The entostyle and anterior, posterior and lingual cingulum are clear. The P4 is more or less triangular (Fig. 9L, M, AA). A medial crista is sometimes present. P3 and P2 have a strong paraconus and a strong, isolated hypoconus (Fig. 9G, H, I, J, K, AA). The P3 is triangular and the P2 is more slender and longer. When there is a medial crista, it is only a weak one. A metaconus is never developed. The D4 has a larger length/

width ratio than in *L. parvulus*, which means it is more rectangular than the square upper molars (Fig. 9D, E). A neocrista and a spur at the posthypocrista are developed, and an anterior and lingual cingulum with a clear entostyle. In D3 and D2 the protoconus is very poor (Fig. 9A, B, C).

The teeth of *L. pumilio* are even smaller as in the dainty moschid *Pomelomeryx gracilis* from MN2 and MN3 localities (Rössner and Rummel 2001), but the tooth crown height is larger. *L. pumilio* from Sandelzhausen differs from *L. parvulus* and *L. ruetimeyeri* by a lacking p1 (Fig. 9F, V, X, AC), more triangular upper premolars (Fig. 9G–M), nearly square upper molars (Fig. 9Z, AA), and an m3 with an enlarged entoconulid forming a third lobe with the hypoconulid (Fig. 9Q, T, V, W, Y, AB, AC).

Comments: The holotype of *L. pumilio*, a right m3 with an enlarged entoconulid forming a third lingual cusp (Roger 1898: 39, pl. 2 Fig. 5), corresponds in size and morphology to all the m3s from Sandelzhausen. Based on that, all the other teeth belonging to this smallest ruminant dentition from Sandelzhausen can be assigned to *L. pumilio*.

The general differences in the dentition of *L. pumilio* compared with *L. parvulus* and *L. ruetimeyeri*, documented with the material from Sandelzhausen (see above), and missing evidence for typical cranial *Lagomeryx*-appendages doubtlessly belonging to *L. pumilio* make the belonging of the species *L. pumilio* to another genus most likely and needs urgently to be revised.

Because as type locality for *L. pumilio* the area Reischenau is mentioned in Roger (1896: 550), as he does for *L. parvulus*, the same problematic nature appears here concerning an unknown exact locality and only an estimated age of MN5 (see above).

Palaeoecological interpretation

Generally the large number of ruminant remains at Sandelzhausen is a rich source for ecological information. In the past only the teeth and cranial elements have been studied, and these continue to be the main basis for palaeoecological deductions in this paper. Postcranial elements are used only for some of the estimates of body mass (Table 2), because body mass is an important tool (Peters 1983) in reconstructing palaeoecological relationships (Damuth and Mc Fadden 1990). The following portraits of comparative ecology of the Sandelzhausen species are compiled with the additional aid of deductions about their autecology at other localities.

Dorcatherium crassum

The tragulid *D. crassum* is quite similar in its skeleton and body mass (14.9 ± 1.0 kg; Table 2) to the extant aquaphil tragulid *Hyemoschus aquaticus* (Milne-Edwards 1864; Carlsson 1926; Dubost 1965; Barrette 1982). Therefore a strong attachment to wet, forested habitats with

dense understory can be assumed, where the animals could hide in vegetation or water from predators. The general absence of *Dorcatherium* from dry karstic palaeoenvironments (Rössner 2004) strongly supports this supposition. Given the dental similarity between *D. crassum* and *H. aquaticus*, it is noteworthy that abrasion/attrition facets on the tooth crowns (mesowear method of Fortelius and Solounias 2000) indicate contrasting feeding strategies (unpublished data Rössner and Kaiser). *Hyemoschus aquaticus* is mainly a frugivore feeder on a diverse spectrum of fruit and seeds, but also on flowers, leaves, petioles, stems, fungi, and animal matter (Dubost 1984). But *D. crassum* groups in a mesowear analysis with typical representatives of the browsing guild (*Okapia johnstoni*, the okapi; *Odocoileus virginianus*, the white-tailed deer). Such animals feed on a broad array of leaves, shoots, and buds with high protein content, and also on limited amounts of vegetation with abrasive particles (Kaiser 2009) and find their food in lowland forests and ecotones to open areas (Stuart and Stuart 1997: 100; Geist 1998: 258). Therefore, for *D. crassum* a browse diet with a wide spectrum including water plants and occasional fruit and grass intake can be assumed.

The difference between feeding strategies of *H. aquaticus* and *D. crassum* does not lead to any change in deduction of wet forested habitats for *D. crassum*, because the habitats of the extant browsing guild overlap the skeletal-related habitat interpretation for *D. crassum*. Closed high canopy forest with minimal ground cover would have been just as unsuitable for *D. crassum* as it is for its extant feeding analogue *Okapia* and for *Hyemoschus*, but the habitats of all three do overlap in wet lowland forests (Stuart and Stuart 1997).

Modern tragulids live solitary, non-territorial, but sedentary on a limited home range (Dubost 1978; Barrette 1982). There is no reason to assume that *D. crassum* had different behaviour. Further protection from predators could have been offered by exclusive or partial nocturnal activity. This is known in living tragulids (Dubost 1978; Matsubayashi et al. 2003) and indicated by the rather large orbits of the Eppelsheim (MN9, Germany) fossil skull of *D. kaupi* (Kaup 1839a).

Lagomeryx pumilio and *Lagomeryx parvulus*

The cervids *L. pumilio* and *L. parvulus* (Fig. 7) had body masses of 1.8 ± 0.2 and 5.8 ± 3.6 kg, respectively (Table 2) and are thus the smallest ruminant representatives in Sandelzhausen close to the lower limit within extant ruminants (e.g. *Tragulus kanchil* (Tragulidae), 1.5–2.5 kg in Rössner 2007). According to Barrette (1982), Köhler (1993) and Scott (1987) small extant ruminants without exception prefer more or less closed habitats (loose bush veld to dense understory in forests), show exclusive or partial nocturnal or crepuscular activity, and have either solitary behaviour or at most live in small families. Therefore, such behaviour can be assigned to both *Lagomeryx* species from Sandelzhausen. According to

Fig. 9 Dental remains of *Lagomeryx pumilio* (Roger, 1896) from Sandelzhausen (Inventory-No. BSPG 1959 II ...). **A:** 4288 right D2, occlusal view. **B:** 6606 left D3, occlusal view. **C:** 4065 right D3, occlusal view. **D:** 4602 right D4, occlusal view. **E:** 4599 right D4, occlusal view. **F:** 3718 left mandible with p2 to m2; **F1:** lingual view; **F2:** occlusal view; **F3:** labial view. **G:** 4607 right P2, occlusal view. **H:** 5153 right P3, occlusal view. **I:** 4308 left P3, occlusal view. **J:** 3979 left P3, occlusal view. **K:** 4010 right P3, occlusal view. **L:** 4086 left P4, occlusal view. **M:** 4079 fragmentary right P4, occlusal view. **N:** 4287 right d4, occlusal view. **O:** 3986 left d2, occlusal view. **P:** 4021 right p4, occlusal view. **Q:** 4291 left m3, occlusal view. **R:** 4119 right d4, occlusal view. **S:** 4033 right p3 to p4, occlusal view. **T:** 4292 left m3; **T1:** occlusal view; **T2:** lingual view. **U:** 4293 left p4 to m1, occlusal view. **V:** 679 left mandible with p2 to m3; **V1:** occlusal view; **V2:** labial view; **V3:** lingual view. **W:** 6616 fragment of right mandible with m2 to m3, occlusal view. **X:** 3950 fragment of left mandible with p2 and alveoli of p3 and p4; **X1:** occlusal view; **X2:** labial view. **Y:** 5161 left p4 to m3, occlusal view. **Z:** 5311 fragment of left maxilla with M2 to M3; **Z1:** labial view; **Z2:** occlusal view. **AA:** 4071 right P3 to M3, linguoocclusal view. **AB:** 5325 fragment of left mandible with p3 to m3, occlusal view. **AC:** 3719 left mandible with p2 to m3; **AC1:** occlusal view; **AC2:** lingual view; **AC3:** labial view

Kaiser (2009) both species show a mesowear on their dentition, which is close to those of the extant giraffe (*Giraffa camelopardalis*) and mule deer (*Odocoileus hemionus*), which have a higher graze/browse ratio in their feeding strategy than the okapi and the white-tailed deer. Therefore, a general browsing feeding adaptation for both *Lagomeryx* species can be postulated, but probably it was less opportunistic than in *D. crassum*. Because this is in congruence with the habitats of the extant body mass analogues, a similar habitat is thus confirmed for *L. pumilio* and *L. parvulus*. The sympatric occurrence of both very small cervid species is known from several more localities also (Rinnert 1956; Rössner 1997; Kaiser and Rössner 2007) and indicates the likelihood that adaptations were required to two different niches.

Heteroprox eggeri

With a body weight of 24.0 ± 8.6 kg (Table 2) *H. eggeri* n. sp. is either comparable with modern small solitary forest deer (up to 25 kg, Barrette 1982) or with the larger representatives of modern deer (under 100 kg) which are mainly adapted to dense thickets and bush (Scott 1987) and live in families or small herds (Köhler 1993). But, *H. eggeri* n. sp. is also comparable with the highly territorial Chinese Water Deer (*Hydropotes inermis*) (mean body mass 12 kg, Geist 1998) which inhabits open environments with high grasses and reeds in swampy areas solitary or in pairs. Therefore, irrespective of social behaviour, at least dense vegetation can be deduced for the palaeohabitat of *H. eggeri* from its extant analogues. The existence of periodically cast antlers in *H. eggeri* could indicate ritualized combats between two solitary individuals or within a group, although Barrette (1982) claims that there is no evidence for territoriality from observations in the wild for small solitary forest deer.

According to Kaiser (2009) the mesowear on the dentition of *H. eggeri* classifies with those of typical extant

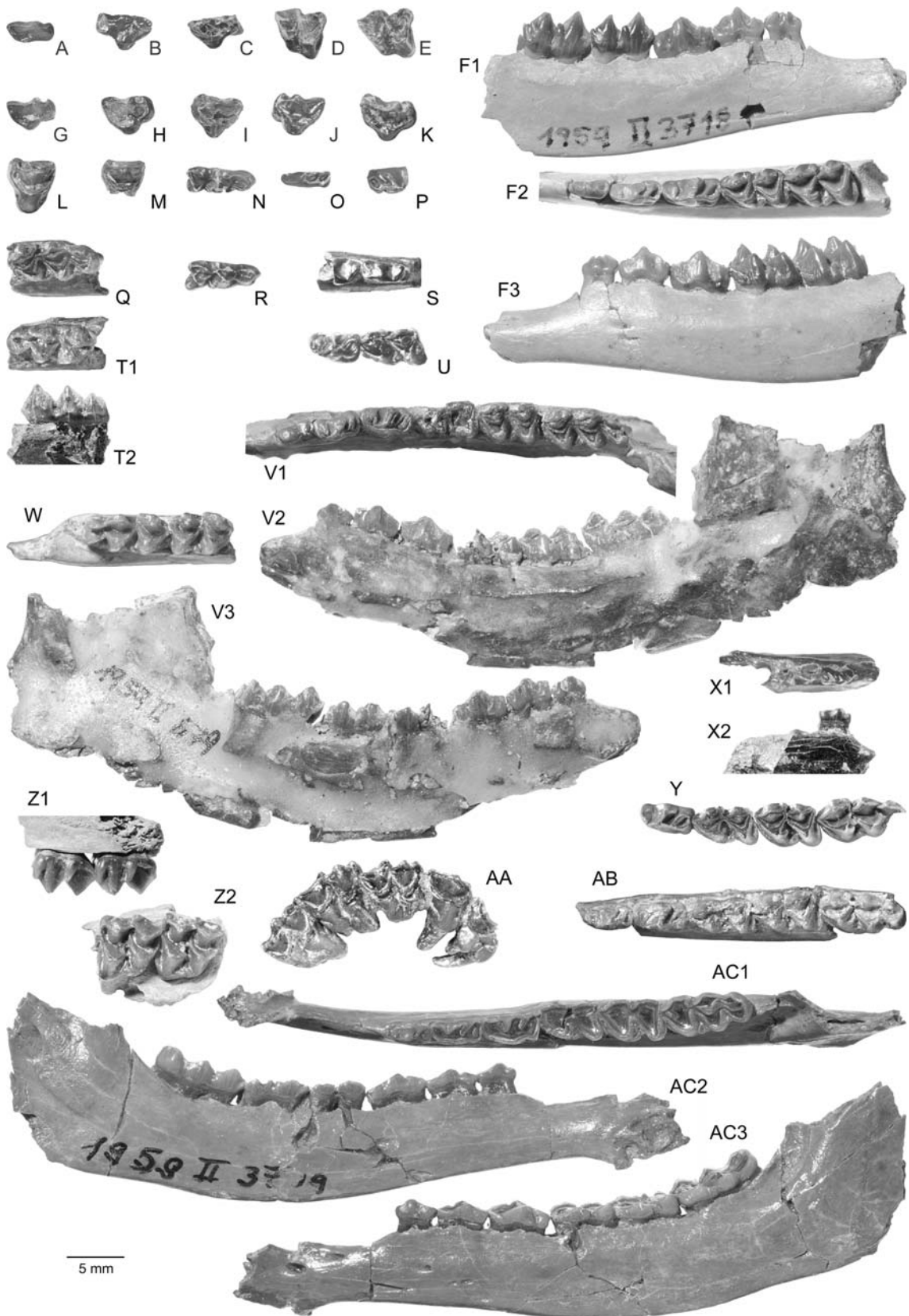


Table 8 $\delta^{13}\text{C}$ values of the tooth enamel of the ruminant species from Sandelzhausen

Specimen	Species	Tooth	$\delta^{13}\text{C}$ (‰)	Mass (mg)
1959 II 5322	<i>Heteroprox eggeri</i> n. sp.	M3	-11.9	50.3
1959 II 4096	<i>Lagomeryx parvulus</i>	M2	-11.8	8.0
1959 II 4297	<i>Lagomeryx pumilio</i>	M3	-12.2	1.7
Without number	<i>Germanomeryx</i> n. g. <i>fahlbuschi</i> n. sp.	?	-12.7	90.5
1959 II 3899	<i>Dorcatherium crassum</i>	p4	-10.8	25.0

browsers (*Okapia johnstoni*, the okapi; *Odocoileus virginianus*, the white-tailed deer). Because the mesowear of more frugivorous nibbling modern small solitary forest deer (Barrette 1982), which feed on small rich parts on the forest floor or saplings, was not included in the analysis, we cannot exclude this style of feeding for *H. eggeri*. Tütken and Vennemann (2009) deduce a water-dependent understory browser in a partially closed forest environment for *H. eggeri* from $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of its enamel carbon and oxygen isotope composition. However, either feeding strategy would fit the interpretation of a more or less closed wooded habitat with dense thickets which provide shelter from predators.

Interestingly, mesowear documents a different niche occupation for *H. eggeri* than for its descendant or sister species *H. larteti*, which is grouped with extant mixed feeders (Kaiser and Rössner 2007). This suggests a change in ecology between *eggeri* and *larteti* (if the latter is a descendant), and a range of ecology within *Heteroprox*.

Germanomeryx fahlbuschi

The palaeomerycid *Germanomeryx* n. g. *fahlbuschi* n. sp. represents, with its body mass estimate of 212.7 ± 35.8 kg (Table 2), an unusually large size class within the Ruminantia of early Middle MN5 of Central Europe, comparable with an extant western European *Cervus elaphus* (Geist 1998). This body mass is not restricted in modern ruminants to any specific habitat or feeding type. Traditionally, the palaeomerycids are compared with the extant Okapi, which is a shy and solitary living inhabitant of the dense African rainforest with habitats close to streams, because of the similarities in body size, in the long legged habitus, in the ontogeny of cranial appendages, and in the tooth morphology. But, studies of Köhler (1993: 52f) show, that the body proportions of large palaeomerycids correspond to those of large Bovinae (length of fore and hind limbs nearly the same). Their phalanges articulate in a straight line and are positioned more or less flat on the ground with splaying ability (documented for *G. fahlbuschi* in Köhler 1993:52f). This would enable the individual to progress slowly in swampy or waterlogged ground and probably to remain longer in water, as the moose (*Alces*). This supports an interpretation of *G. fahlbuschi* as an inhabitant of boggy forests, which lived solitary or in pairs, perhaps even in small groups.

In the analysis of Kaiser (2009), however, the teeth of *G. fahlbuschi* resemble in their mesowear mostly those of *Dicerorhinus sumatrensis*, the Sumatran rhino, which is a pure browser feeding on high-quality protein-rich plant parts, for example saplings, leaves, and fruits. This is in congruence with the very low crowned dentition of *G. fahlbuschi*, supposed to be best adapted to a soft and juicy diet. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of its tooth enamel support such a diet in general, but also allow differentiation of canopy feeding in *G. fahlbuschi* in contrast with understory feeding of *H. eggeri* (Tütken and Vennemann 2009). Because browsers are highly selective feeders, *G. fahlbuschi* individuals must have had occupied large territories in order to select a sufficient amount of food for their body size. They might, therefore, possibly have preferred dense forests as habitat, to restrict the size of their territory. A diet with a high proportion of aquatic plants as in *Alces*, as suggested by Köhler (1993: 52), can be rejected on the basis of the $^{12}\text{C}/^{13}\text{C}$ ratio of the tooth enamel of *G. fahlbuschi*. The $\delta^{13}\text{C}$ value of -12.7‰ (Table 8) is too low for a substantial amount of aquatic plants in a diet (O'Leary 1981).

The autecological characterisation of the Sandelzhausen ruminants will essentially be completed in the near future with analysis of the postcranial elements (as shown in Scott 1985, 1987; Kappelman 1988; Köhler 1993). Meanwhile several calculations of species-distributions and ecomorph-distributions should offer support to infer synecological conditions (Damuth 1992). Considering all listed specimens in a stratum-independent analysis we find that *H. eggeri* is the dominant species of the assemblage and is represented by nearly half of the specimens (Table 9). This is in concordance with its inferred potential social organisation in families or small herds (see above) and the assumed more or less solitary-sedentary behaviour of all other species. The next most abundant species is *L. pumilio* covering one-fourth of the complete assemblage and indicating a comparable high population density within the community. For *D. crassum*, *G. fahlbuschi*, and *L. parvulus* with relative abundances of only around 10% a clearly lower population density is most likely.

Considering the estimated body masses (Table 2) the ruminant community from Sandelzhausen is made up of 45% of very small-sized forms (2–20 kg), 45% of small-sized forms (more than 20–100 kg), and 10% of medium to

Table 9 Stratum-dependent species distribution within the ruminant community from Sandelzhausen

Species	A total	A relative (%)	B total	B relative (%)	C total	C relative (%)	D total	D relative (%)	E total	E relative (%)
<i>Heteroprox eggeri</i> n. sp.	1	1	89	50	72	42	11	6	0	0
<i>Lagomeryx parvulus</i>	0	0	8	29	13	46	6	21	1	4
<i>Lagomeryx pumilio</i>	0	0	16	33	21	45	10	21	1	1
<i>Germanomeryx</i> n. g. <i>fahlbuschi</i> n. sp.	0	0	39	90	4	9	0	0	1	1
<i>Dorcatherium crassum</i>	0	0	18	26	11	15	42	59	0	0

For details on the section's strata see Moser, Rössner et al. (2009)

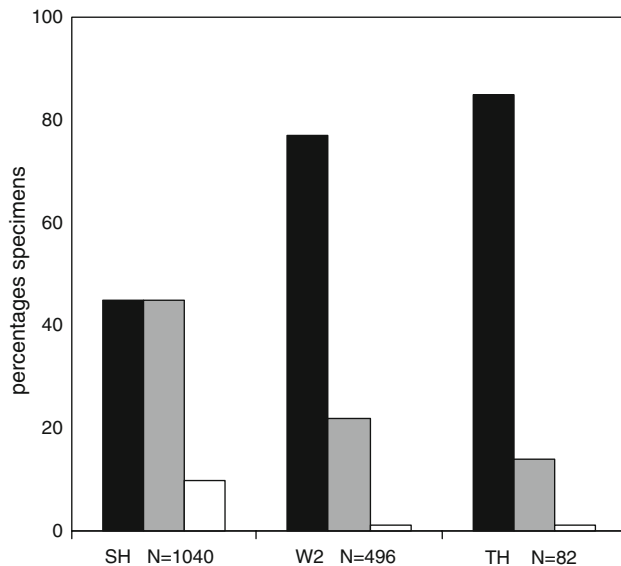


Fig. 10 Relative abundances of body mass categories in the ruminant communities of Sandelzhausen (SH) (early middle MN5), Walda 2 (W2) (middle MN5), and Thannhausen (TH) (early MN6) (all NAFB, Germany) calculated on specimen numbers. *Black* = very small-sized, 2 to 20 kg; *grey* = small-sized, more than 20 to 100 kg, *white* = medium to large-sized, more than 100 kg

large-sized forms (more than 100 kg) (Fig. 10). Looking at the distribution of diet categories according to Kaiser (2009) we see a purely browsing community which occasionally fed on small portions of abrasive plants (Fig. 11). This is well in accordance with the $\delta^{13}\text{C}$ values of the tooth enamel (Table 8; Tütken and Vennemann 2009). These are slightly higher than those known for a pure C_3 (browsing) diet with -13.1 to -19.1‰ and clearly distinct from a pure C_4 (grazing) diet (-2.3‰ to 0.1‰ , O'Leary 1988). All ruminant species from Sandelzhausen can therefore be classed as browsers with only minor, if any, amounts of C_4 -grasses; this is well in accordance with the mesowear data.

The distribution of the Sandelzhausen species within the section provides another insight. However, only a portion of the specimens come from known horizons (A at the base, B, C, D or E at the top; Moser, Rössner et al. 2009) (Table 9), so this calculation has to be performed with care.

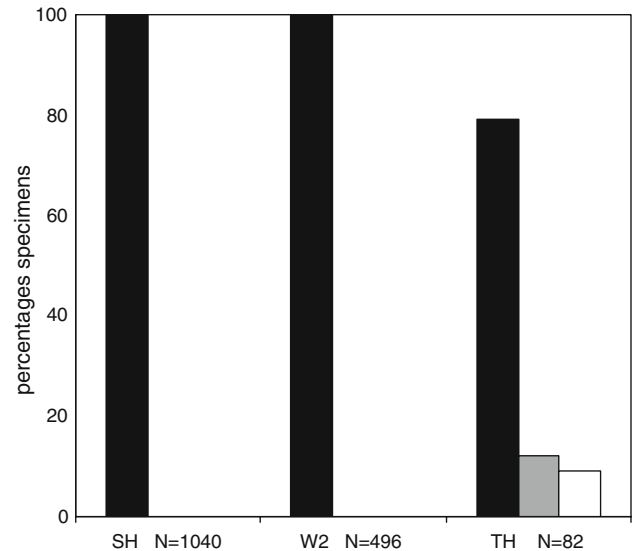


Fig. 11 Relative abundances of diet categories in the ruminant communities of Sandelzhausen (SH) (early middle MN5), Walda 2 (W2) (middle MN5), and Thannhausen (TH) (early MN6) (all NAFB, Germany) calculated on specimen numbers. *Black* = browser, *grey* = browse dominated mixed feeder, *white* = unknown

The data are taken from the Sandelzhausen database (data may be requested from the Bayerische Staatssammlung für Paläontologie und Geologie in Munich) and include the described teeth plus the described and undescribed skeletal elements. Figure 12 reveals that stratum B yielded most of the specimens followed by stratum C, stratum D, stratum E, and finally stratum A with only one specimen of *Heteroprox*. On the one hand, this distribution probably reflects taphonomic effects of the fluvial environment caused by grain size sorting and energy intensity. Thus the large-sized *Germanomeryx* was mainly found in stratum B which contains many pebbles (Moser, Rössner et al. 2009) and much more rarely in stratum C (the coal layer), whereas both very small-sized *Lagomeryx* species come mainly from stratum C. On the other hand, the dominant occurrence of *Dorcatherium*, with very few *Heteroprox* and no *Germanomeryx* in stratum D cannot be explained by taphonomic processes and might have ecological reasons.

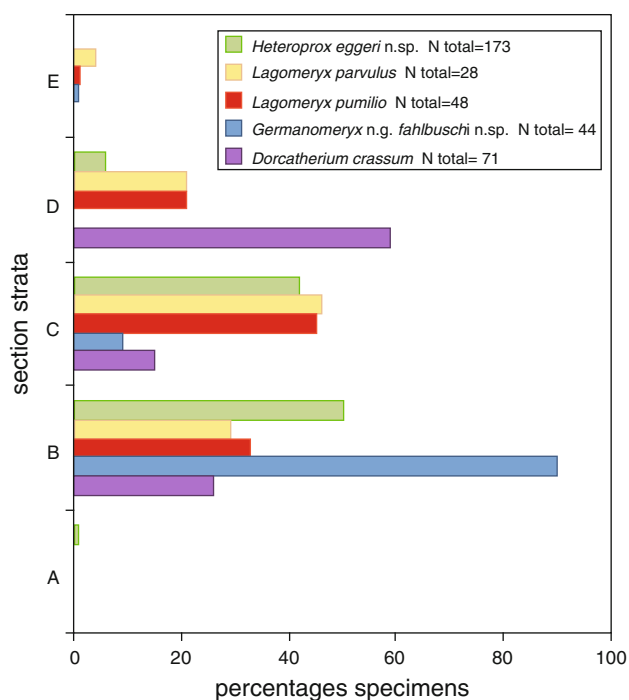


Fig. 12 Distribution of ruminant specimens in the Sandelzhausen section. For details on the section's strata see Moser, Rössner et al. (2009)

According to the gastropod and the ectothermic vertebrate communities a persistent lake in a fluvial network and a humid canopy forest evolved in stratum D, in contrast with temporary ponds with a semi-open bushy hinterland which gave rise to layer C to lower D (Böhme 2010 this volume; Moser, Rössner et al. 2009). Because *D. crassum* is assumed to have had the same behaviour as its extant African descendant *Hyemoschus aquaticus* (see above), it can be suspected that it was especially frequent around persistent water bodies with a closed hinterland and lowland forests in between, in contrast with all other ruminants. Moreover, according to palaeoprecipitation estimates, based on the ecophysiological categories of reptiles (Böhme et al. 2006), strata B, C and lower D reflect a mean annual precipitation of 571 ± 252 mm and strata upper D and E reflect a mean annual precipitation of 847 ± 254 mm (Böhme 2010 this volume). This would mean less pronounced seasonality in upper D and E supporting less variation of the regional ground water table and leading to the establishment of a pond with permanent water conditions. A more pronounced seasonality in B and C would mean alternating wet and dry seasons, which are in fact suggested by the sedimentology in lower D (Schmid 2002).

Overall, the species composition of the palaeocommunity seems to have been stable during sedimentation of the complete section. The slight differences from stratum to stratum might well have been because of taphonomic sorting effects reflecting, e.g., changes in the sedimentary conditions but could also arise from changes in the

local environment related to moving of the nearby river channel.

In summary, the dominance of cervids and of browsing in the ruminant community from Sandelzhausen reflects an environment of mainly closed forest. A significant representation of tragulids and palaeomerycids with adaptations to ecotonal wet and swampy habitats indicates humid conditions with temporary and perennial lentic and lotic waters. Some additional consumption of C_4 -grasses, or at least abrasive plants, which could well include riparian vegetation, also, signifies the presence of accompanying open areas.

In comparison with other rich ruminant materials from younger localities of the Middle Miocene of the German NAFB (Rössner 2004) the community from Sandelzhausen differs generally by a lower species number, by a much higher abundance of Cervidae and much lower abundance of Tragulidae, and much higher relative abundance of the

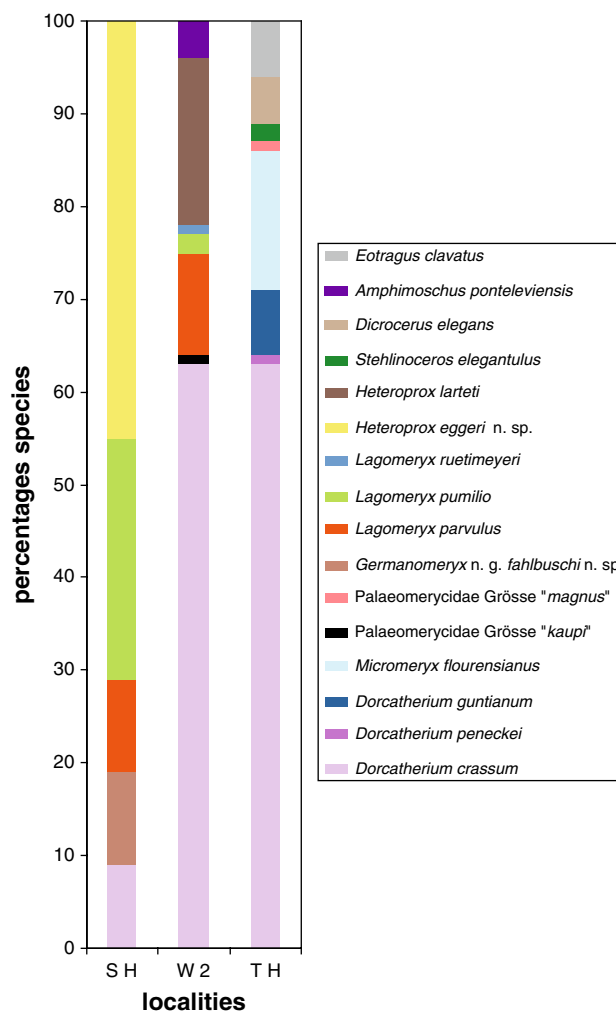


Fig. 13 Relative abundances of ruminant species in the community of Sandelzhausen (SH) (early middle MN5), Walda 2 (W2) (middle MN5), and Thannhausen (TH) (early MN6) (all NAFB) calculated on specimen numbers

Palaeomerycidae (Fig. 13). A further peculiarity is the comparably extraordinary high abundance of the small cervid *Lagomeryx pumilio* and the complete absence of *Amphimoschus*. Thus, the community from Sandelzhausen was clearly less taxonomically differentiated than all the others. The higher species numbers in the other localities were produced by higher numbers of very small-sized and small-sized ruminants.

The body mass distribution in Sandelzhausen differs from the others in the proportion of very small-sized species (45% specimens) being the same as the proportion of the small-sized ruminants. The other communities do not exceed 25% relative specimen abundance of small-sized ruminants (Fig. 10), whereas the number of very small-sized species increase or decrease with the species number of small-sized ruminants (Rössner 2004). Instead, individuals of the very small-sized Ruminantia were much less abundant in Sandelzhausen and the large-sized palaeomerycids are much more common than in the other communities, although principally a small proportion (10%).

The distribution in diet preferences (Fig. 11) shows exclusively browsing adapted Ruminantia in Sandelzhausen, Walda 2, and Thannhausen (all Germany). Besides several browsers, two mixed feeding species with a browse-dominated diet are included with not more than 10% relative species abundance.

The specific composition of dietary traits in the Sandelzhausen ruminant fauna is thus different from what Kaiser and Rössner (2007) found in general for the early Middle Miocene Molasse Basin ruminant community, for which they report a more abrasion-dominated dietary trait in the tragulids *Dorcatherium guntianum* and *Dorcatherium crassum* and the cervid *Dicrocercus elegans*.

Discussion

The combination of a large number of specimens and a comparatively small number of ruminant species at Sandelzhausen means that the structure of the paleocommunity is most probably not a product of taphonomical effects, but can be taken as real. That opens the way to a discussion on ecological similarities and differences, and stability or changes in space and time with consequences for phylogeny and biostratigraphy.

The ruminant assemblage from Sandelzhausen reflects a qualitative taxonomic structure well known from other communities in the emerging terrestrial areas of Central and Western Europe in the late Early and early Middle Miocene (Schlosser 1902; Roman and Viret 1934; Rinnert 1956; Ginsburg and Bulot 1987; Gentry 1994; Rössner 1997, 1998, 2005; Gentry et al. 1999; Sach 1999; Sach and Heizmann 2001; Eronen and Rössner 2007). Those areas

were created by the successive phases of drying of the Paratethys in the Miocene and were characterised by widely distributed forests in a limnofluvial depositional area (Fortelius et al. 1996; Steininger et al. 2004; Bernor et al. 2004). Cervids, tragulids, and palaeomerycids are characteristic ruminant elements of those communities. The lack of giraffids is also a feature of these regions, although giraffids were found in other European regions at the time (de Bonis et al. 1997).

However, the ruminant composition from Sandelzhausen is peculiar in many aspects. A lack of both bovids and moschids and the comparatively low species number (five) are remarkable. Within the identified taxa two new species and one new genus (*Germanomeryx* n.g. *fahlbuschi* n. sp., *Heteroprox eggeri* n. sp.) are included. The commonness of *L. pumilio* and the palaeomerycid differs from other localities (see above). Finally, the typical dominance of tragulids in the early Middle Miocene of the NAFB (Fig. 13; Rössner 2004) is not evident at Sandelzhausen.

The body-size distribution pattern (based on qualitative and quantitative taxonomy) of the Sandelzhausen ruminants corresponds in general to other NAFB localities in which mainly the very small and small-sized categories are represented (Fig. 10). In comparison with body size distribution patterns (based on species numbers) in extant ruminant communities, a clear correspondence of Sandelzhausen and all the younger NAFB localities exists with more or less closed biomes based on the dominance of very small to small-sized species in contrast with a higher portion of small to large-sized species from more open biomes (Barrette 1982; Köhler 1993). This correlates very well with the reconstruction of a closed forest as environment from the autecologic characterisations of the Sandelzhausen ruminants (see above).

The diet category distribution pattern (based on qualitative and quantitative taxonomy) of all NAFB localities compared show an increase of mixed feeders toward the end of the early Middle Miocene (MN5) (Fig. 11) (see also Eronen and Rössner 2007). This record indicates not only an increase in differentiation of diet strategies, but also an increase in diversity of available plants and with this an increase in the differentiation of the environment.

According to biostratigraphical dating of the fossil site as latest Burdigalian (Early Miocene) or earliest Langhian (Middle Miocene) (Moser, Rössner et al. 2009), the Sandelzhausen fauna is exceptional in being a stratigraphical unit not yet recorded anywhere else. The specific taxonomic composition in Ruminantia with *Dorcatherium*, *Germanomeryx* n. g. *fahlbuschi* n. sp., *Lagomeryx* and an early *Heteroprox* simply might reflect a transitional stage between Burdigalian and Langhian MN5 assemblages (Eronen and Rössner 2007). Most probably they are a foreshadowing of typical MN5 ruminants from this region (e.g. the moschid *Micromeryx* or the cervid *Stehlinoceros*).

Because the extraordinary large sized palaeomerycid *Germanomeryx* n. g. *fahlbuschi* n. sp. is not known from any other community except for an incomplete lower molar from the MN5-locality Undorf (BSPG 1896 XI 258, Rinnert 1956: 12) it seems even to have been a taxon unique for this time span.

What is left unsolved by biostratigraphic explanations is the absence of the bovid *Eotragus* and the genus *Amphimoschus* (a ruminant with still unknown taxonomic affiliation) because both genera are known from older (MN4; Schlosser 1902; Sach and Heizmann 2001) and from younger (MN5, MN6; Rössner 1997, 2004, 2006; Eronen and Rössner 2007) localities in the Molasse Basin and beyond (Hofmann 1893; Moyà-Solà 1983; Ginsburg and Heintz 1968; Ginsburg 1989; Gentry 1994; van der Made 2010). *Eotragus* is completely unknown from MN5 localities of the German NAFB but reappears in early MN6 (Rössner 2006; Eronen and Rössner 2007). *Amphimoschus* is a typical, although less abundant, genus from late MN4 until the end of MN5 or beginning of MN6 (Schlosser 1902; Rinnert 1956; Rössner 1997, 2004; Eronen and Rössner 2007). Therefore, the absence of *Eotragus* in Sandelzhausen can be assumed to be because of general ecological conditions in MN5 in the Molasse Basin. The lack of *Amphimoschus* seems to be an ecological peculiarity in Sandelzhausen.

This hypothesis is supported by the ruminant communities from the localities Undorf and Viehhausen from the northwestern edge of the Molasse Basin described by Rinnert (1956), which are taxonomically most similar and therefore probably nearly contemporaneous with that of Sandelzhausen. They include even the newly established taxa *H. eggeri* n. sp. and *Germanomeryx* n.g. *fahlbuschi* n. sp. (see synonymy lists in the taxonomical description above), but also *Amphimoschus*. Admittedly, the sediments from Undorf and Viehhausen are of lignitic origin and might therefore document a more swampy environment compared with Sandelzhausen, but younger and more centrally situated MN5 localities in the NAFB do not, which makes that aspect unimportant to further discussions.

Comparing the species abundance data from Sandelzhausen with those of the other NAFB communities, the much smaller representation of tragulids in Sandelzhausen can be interpreted as a less successful adaptation in competition with the cervids (Fig. 13). In contrast the dominance of the small-sized cervid *H. eggeri* n. sp. and the relatively high abundance of the large-sized *Germanomeryx* n. g. *fahlbuschi* n. sp. caused a comparably large mean body mass. This might have been supported by the smaller species diversity with less competition. *L. pumilio* seems to have found much better conditions in Sandelzhausen than in other localities, where it is clearly less commonly documented. Because those communities have

in common that the tragulids have highest abundances, these might have replaced *L. pumilio* in a widespread region.

The described inhomogeneities in the ruminant compositions from the late Early Miocene (MN4 to beginning of MN5) to the early Middle Miocene (MN5, beginning of MN6) South German NAFB can be most likely linked to changes in the ecological conditions. The occurrence of tragulids, no matter if dominant or non-dominant, in contrast with their complete absence from the northwards neighbouring karst biome strongly indicates wetland conditions, because of their postcranial adaptations similar to today's West-Central African aquaphil tragulid *Hyemoschus* (Rössner 2004; Eronen and Rössner 2007; Kaiser and Rössner 2007). Further arguments for the existence of wetland conditions are given by the geological history of the NAFB, which emerged from a marine basin to become a lowland surrounded by highlands (Lemcke 1988), and the varied sediment types (Fahlbusch et al. 1972; Fiest 1989; Schmid 2002; Seehuber 2002) which document a mosaic limno-fluvial environment. According to Böhme (2003) and Reichenbacher et al. (2004) during the Karpatian (late Early Miocene, late MN4) and early Badenian (early Middle Miocene, MN5) a warm seasonal climate with pronounced dry periods can be reconstructed on the basis of a variety of evidence. Pronounced dry periods premise interjacent times of heavy precipitation. Heavy precipitation in the region of the then South German Molasse Basin would have caused marked flood seasons because of the geomorphological situation of a Basin surrounded by mountain chains and highlands. If we assume that a seasonal character gradually developed in the aforementioned time span, then gradually developing flood seasons were concomitant. The alternation of dry and flood seasons would have caused a highly differentiated mosaic ecotone environment, which would have offered an outstanding number of habitats and niches and consequently an exceptionally large number of species (Eronen and Rössner 2007). Because of alternation of ground conditions seasonal migration events might have occurred.

With such a scenario the appearance/disappearance of species can be explained. So, at the first emergence of the NAFB the seasons might have been more uniform, offering habitats for many adaptations (e.g. *Amphimoschus* and *Eotragus*). With increased seasonality a pattern of long rainy seasons interrupted by short dry seasons might have appeared. The resulting more or less wet environment could have been inconvenient for *Eotragus* and would imply its adaptation to more or less dry habitats, such as were found in the neighbouring karst environment. With the later establishment of longer dry seasons (MN6) *Eotragus* came back to the NAFB, at least seasonally. The occurrence of *Amphimoschus* is recorded for the late MN4 and the complete MN5. Therefore, its absence from

Sandelzhausen is an exception, but can hardly be attributed to taphonomic conditions (see above). This local gap might indicate that the Sandelzhausen fauna is definitively autochthon to parautochthon fauna of the closer ambit, which for unknown ecological reasons was avoided by *Amphimoschus*.

The increase in ruminant diversity in younger NAFB localities might have been assisted by the incremental establishment of a mosaic environment and by migrations from and to the surrounding highlands, as is known, for example, from the modern South American Pantanal wetland (Eronen and Rössner 2007). In such an environment deciduous trees would have lost their leaves during the dry season, thereby limiting the amount of available leaves and fruits and favouring the emergence of a mixed feeder flexible feeding strategy.

Mesowear analyses exclude the chalicotheres and equids as immediate competitors for food of the ruminants in Sandelzhausen and reflect a resource partitioning of brachyodont herbivorous mammals on a broad spectrum, even implying pronounced niche segregation in the Sandelzhausen environment. The dietary niche of the equid *Anchitherium aurelianense* is reconstructed as one of a browse-dominated mixed feeder, probably an opportunistic “dirty browser” or at least flexible (selective to non-selective) feeder in this community (Kaiser 2009). For the chalicothere *Metaschizotherium bavaricum* Schulz and Fahlke (2009) reconstructed a dietary niche of a mixed feeder or an abrasion dominated browser, which shows an even more abrasion dominated mesowear signature.

Besides the here described five species of ruminants, the chalicothere and the equid species, the ungulate fauna from Sandelzhausen comprises three rhino species (Heissig 1972; Peter 2002), at least two proboscidean species (Schmidt-Kittler 1972; Göhlich 2010 this volume), and two suoid species (Schmidt-Kittler 1971; van der Made accepted, this volume). All of these are more or less brachyodont species. In total there are at least 14 brachyodonts. This number is unusual in modern world biomes, where the highest number of brachyodonts is represented in tropical rain forests with nine species (Janis et al. 2000). But, it corresponds to the composition of Middle Miocene ungulate faunas from Northern America (Janis et al. 2000, 2002, 2004), which is associated with higher terrestrial primary productivity in the Middle Miocene. This is well in accordance with recently documented elevated atmospheric CO₂ in the earlier Middle Miocene (Kürschner et al. 2008).

Conclusions

The Ruminantia from Sandelzhausen are documented by outstandingly rich material. On the one hand it increases

knowledge of the odontological morphometric characters of the tragulid *Dorcatherium crassum* and the cervids *Lagomeryx parvulus* and *Lagomeryx pumilio*. Despite the commonness of those species in the European Miocene, descriptions were hitherto only based on fragmentary material. On the other hand, it completes the picture of the faunal composition of Miocene European Ruminantia with the newly discovered cervid *Heteroprox eggeri* n. sp. and palaeomerycid *Germanomeryx* n.g. *fahlbuschi* n.sp. The autecological characterisations of all five species support the reconstruction of an environment mainly shaped by humid canopy forests interspersed with temporary and perennial waters and are thus consistent with current environmental interpretations for the Central European Miocene.

The qualitative and quantitative community composition displays several peculiarities in contrast with other NAFB communities, but is mainly in agreement with those from the Middle Miocene lignite localities Undorf and Viehausen from the northwestern edge of the NAFB. This strengthens the similar age of both faunas.

Finally, the hypothesized dynamics in community structure of the NAFB ruminants suggest the existence of a vast wetland environment with alternating dry and flood seasons which forced a mosaic of ecotonal habitats with an endless number of niches and corresponding adaptations.

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Appendix

Studied material

Dorcatherium crassum (Inventory-No. BSPG 1959 II...)
2212 right m1–m3, 3852 left D4, 3927 right D3, 4120 right p4, 4121 left p, 4122 right p, 4123 right p2, 4126 left

D4, 4127 right m1, 4128 right m3, 4129 left m2, 4130 left p4, 4131 right M2, 4132 right M2, 4133 left M3, 4134 left m2, 4135 left M2, 4136 left M3, 4137 right P4, 4138 left M2, 4139 left p4, 4140 left m3, 4142 left m1, 4144 right M1–M3, 4146 left p4–m3, 4148 right m1–m2, 4150 left p1–p3, 4152 right M1, 4153 right m1–m2, 4154 right M2, 4155 left M3, 4157 right p3–m1, 4158 left p4–m3, 4160 right m2, 4161 right m1, 4162 left m2, 4163 right M3, 4164 left m1–m3, 4165 left p3–m3, 4166 right m2, 4167 right m3, 4168 right m2–m3, 4168 right m2, 4316 right d3, 4338 right M2, 4339 right M3, 4340 left m2, 4342 left d3, 4343 right D, 4344 left p, 4345 right p4, 4590 left M3, 5206 right P2, 5292 left p4–m3, 5300 right p4–m1, 5371 left p2, 6621 right m2–m3, 6635 right d2, 6639 right p4, 6644 left D4, 6659 left M3, 6661 left m3, 6662 right P4, 6663 right M3, 11658 left p4, 11659 right d2, 11660 left P3, 15648 C.

Germanomeryx n. g. *fahlbuschi* n. sp. (Inventory-No. BSPG 1959 II...)

41 right M1, 300 left P4, 2499 right mandible with p2 to m3 and left mandible with p3 to m3, 3733 right mandible with p2 to m3, 3747 left m2, 5183 left D4, 5184 right M1, 5185 right D4, 5186 right m, 5187 left M1, 5188 right m2, 5191 left d4, 5192 right p3, 5193 left d4, 5194 left d3, 5195 left m1, 5196 right m1/m2/m3, 5197 right D4, 5198 right i1/i2/i3, 5200 right P3, 5201 left i1/i2/i3, 5202 right m1/m2/m3, 5203 right d4, 5204 right i1/i2/i3, 5205 right d4, 5207 left d3, 5208 left p3, 5209 left p4, 5210 left D3, 5211 right D2, 5212 left d4, 5213 right m1/m2/m3, 5214 right M1/M2/M3, 5216 left M1/M2/M3, 5217 right M1, 5218 right P3, 5219 left m3, 5220 right p2 to p4 and m2 to m3, 5221 left p4 and m2 to m3, 5298 right P3, 5302 left M1/M2/M3, 5303 right M1, 6628 right m3, 6652 left D4, 7801 left P2 to P3 and M2 to M3, 7802 left D2–M2, 9000 left Cm, 11648 left mandible with m2 to m3, 11649 left mandible with m1 to m2, 11650 right mandible with m2, 11651 right mandible with d3 to d4, 11652 right mandible with d2 to d4 and m1 to m2, 11653 left m1, 11654 left M1, 11655 right m2, 11656 left p2, 12300 sin Cm, 12320 left p2, 12321 left p2, 12323 left D2, 12324 left I, 12332 right M, 12337 left d4, 15652 right p4.

Heteroprox eggeri n. sp. (Inventory-No. BSPG 1959 II ...)

301 left m3, 302 right M3, 2502 right juvenile cranial appendage, 2504 right mandible with p2 to m3, 2505 right Cm, 2515 right Cm, 3734 left M1, 3735 right M3, 3736 left M2, 3737 right M2, 3738 left m3, 3739 right M3, 3740 left M3, 3741 left M2, 3742 left M3, 3743 left M2, 3744 left M1/2/3, 3745 right M2, 3746 left M2, 3748 left M1–M2, 3749 right maxilla with M1 to M3, 3750 left M2, 3751 right M1/2, 3752 left M2, 3753 right M1/2, 3754 right M2, 3755 right M3, 3756 left M1/2/3, 3757 left M1, 3758 left M3, 3759 left M1/2, 3760 right M3, 3761 left M3, 3762 right M2, 3763 right M2, 3764 left M3, 3765 right M1,

3766 left M1, 3767 right M2, 3768 left M2, 3769 left M3, 3770 right M3, 3771 left M1, 3772 left M3, 3773 right M2, 3774 right M2, 3775 left M3, 3776 right M3, 3777 right M1, 3778 left M2, 3779 right M2, 3780 right M1, 3781 right M2, 3782 left M2, 3783 right M1, 3784 right M2–M3, 3785 left M1, 3786 left M2, 3787 left M1, 3788 left M3, 3789 right m3, 3790 right m3, 3791 right m3, 3792 right m2, 3793 right m3, 3794 left m3, 3795 right m3, 3796 left p2–p4, 3797 right p2–m1, 3798 right m3, 3799 right m2–m3, 3800 right m2–m3, 3801 left m2, 3802 right m3, 3803 right m3, 3804 left m2, 3805 right m1, 3806 left m3, 3807 right m1, 3808 left m2, 3809 right m1, 3810 right m2, 3811 left m2, 3812 left m2–m3, 3813 right m3, 3814 left m2, 3815 right m3, 3816 left m2, 3817 right m3, 3818 left m1, 3819 left m1/2/3, 3820 right m2, 3821 right m2, 3822 right m3, 3823 left m1, 3824 right m3, 3825 left m1, 3826 right m3, 3827 left m, 3828 right m2, 3829 right m2, 3830 left m2, 3831 right m1, 3832 left m2, 3833 right m3, 3834 right m3, 3835 left m2, 3836 right m3, 3837 right m3, 3838 left p4, 3839 right p3, 3840 right p4, 3841 right p4, 3842 left p3, 3843 left p3, 3844 right m1, 3845 right p3, 3846 left p3, 3847 left p4, 3848 left p3, 3849 right p4, 3850 left p3–p4, 3853 left d4, 3854 right D4, 3855 right M1, 3856 right M2, 3857 right M, 3858 left p4, 3859 left m1–m3, 3860 left m2, 3861 left m1, 3862 left m3, 3863 right M1, 3864 left m1–m2, 3865 right p4–m3, 3866 right p3–p4, 3867 left p4, 3868 right p3–m2, 3869 right p4–m1, 3870 left d2–d4, 3871 left p3–p4, 3872 right P4, 3873 left P4, 3874 right P3, 3875 left P4, 3876 right P4, 3877 left P3–P4, 3878 right P4, 3879 right M1, 3881 left P4, 3882 left p4, 3883 left p2, 3884 right P4, 3885 left P3, 3886 right m1, 3887 right P4, 3888 right P2, 3889 left P4, 3890 left m3, 3891 right m3, 3892 right M1, 3893 left p4, 3894 left M1, 3895 left P4, 3896 left M1, 3897 right P2/3, 3898 right P2, 3899 left p4, 3900 left P2, 3901 left P4, 3902 right P3, 3903 right P2, 3904 right P2, 3905 right P3, 3906 left P4, 3907 right P3, 3908 left P3, 3909 left P4, 3910 right P2, 3911 left D3–M1, 3915 left d2–m2, 3916 left P4, 3917 right m2, 3918 left M2, 3919 right M3, 3920 left d2, 3921 right P3, 3922 left d2, 3923 left m2, 3924 right m1, 3925 right d2, 3926 left m2, 3928 left p3, 3929 right M1/2, 3930 left m1, 3931 left m1, 3932 right m2, 3933 right p3, 3934 right P4, 3935 right P4, 3936 left P4, 3937 right p3–p4, 3938 left p3–m2, 3939 left p2–p4, 3940 left m2–m3, 3941 right p3–m3, 3942 right p2–m1, 3943 right m2–m3, 3944 right P3–M1, 3945 left P2–M1, 3951 left D3, 4031 right m, 4051 left d3, 4053 left p4, 4067 right p2, 4124 left m3, 4125 left M1, 4141 left M, 4143 right Cm, 4145 left Cm, 4147 left Cm, 4149 left Cm, 4151 left Cm, 4156 right m2–m3, 4159 left Cm, 4219 right M3, 4283 left M1, 4304 left p2–p3, 4314 left m1–m3, 4315 left mandible with p2 to m3, 4327 left P4, 4335 right Cm, 4593 left P4, 4605 left p3, 4608 left M, 4610 right p3, 4612 left m3, 4714 left m3, 4985 left M3, 5150 right D3, 5249

right adult cranial appendage, 5290 left p3–m3, 5291 right p4–m3, 5299 Right maxilla with P2 to P4, 5301 right Cm, 5304 right p3, 5305 right p3–m2, 5306 left p3–p4, 5313 right m1, 5316 right P2, 5317 right P4, 5318 right P4–M3, 5319 left M2, 5320 right m3, 5321 left m2, 5322 right M3, 5323 right P3, 5324 right P4, 5368 right m1, 6090 fragment of pedicle, 6619 left mandible with p2 to m3, 6620 left p3–m3, 6622 left p4–m3, 6623 left p4–m3, 6624 right p3–m3, 6625 right p2–m3, 6626 left p4–m1, 6627 right m1–m2, 6629 left P3–M1, 6630 right P4–M2, 6631 right m1–m2, 6632 right p2–p4, 6633 right p3–m1, 6634 right m3, 6636 right m2, 6637 left p2–m3, 6638 right M3, 6640 right M2, 6641 right M1, 6642 left P4, 6643 right m3, 6645 right M2, 6646 left P4, 6647 right m3, 6648 left M3, 6649 left m3, 6650 right m2, 6651 right p4, 6653 left m3, 6654 left M3, 6655 right m2, 6656 right M1, 6657 left P4, 6658 right D4, 6660 right M3, 6665 left m1–m3, 7842 right p3, 7843 right D4, 7844 right P3, 7845 right Cm, 7861 left m3, 8031 left male C, 8987 left M3, 8988 left m3, 8989 right m1/2/3, 8990 left m1/2/3, 8992 Left female C, 9016 right m1, 9029 right Cm, 9030 right Cm, 9032 right D2, 10781 right m3, 11657 basis of left cranial appendage, 11661 left M1, 11662 left M2, 11663 right M2, 11664 right P3, 11665 left M1, 11666 right P3, 11667 right p4, 11668 right p4, 11669 right p3, 12183 basis of right cranial appendage, 12309 left Cm, 12316 base of right frontal appendage, 12310 left M2, 12311 left M3, 12312 left male C, 12313 right M2, 12314 left juvenile frontal appendage, 12315 base of left frontal appendage, 12317 base of left frontal appendage, 12318 right mandible with m1 to m3, 12325 right P2, 12327 right p3, 12328 right p2, 12329 left P2, 12330 left M1, 12331 right m3, 12334 left M1, 12335 right P2, 12339 right d3, 15646 left male C, 15647 left P4, 15649 right M3, 15650 left M1, 1975 IX 27 right mandible with p2 to m3, 1985 II 142 left P4.

Lagomeryx parvulus (Inventory-No. BSPG 1959 II ...)

678 antler (original to Fahlbusch 1977), 3851 left M2, 3948 right M3, 3952 left p2, 3953 right P4, 3954 right P2, 3955 right M1, 3958 right P2, 3960 left m1, 3961 left D2, 3963 left m1, 3964 left P2, 3967 left D4, 3973 right P3, 3974 right M1, 3977 left p3, 3987 left p3, 3992 left p2, 4002 right m2, 4004 left M1, 4006 left p3, 4008 right m2, 4012 right P3, 4015 left d3, 4018 left D2, 4020 right p1, 4024 right m3, 4028 left D2, 4036 right d4, 4045 left d4, 4054 left p2, 4057 left d2, 4064 right D2, 4066 right P3, 4069 left m1/2/3, 4070 right M2, 4072 left M3, 4073 right P4, 4080 right m1, 4081 left d3, 4083 left M3, 4089 left M3, 4095 left M2, 4096 right M2, 4097 right D2, 4099 left p1, 4106 left d4, 4115 right p4, 4227 right p1, 4302 left m3, 4305 left p3, 4310 right m2, 4311 left m2–m3, 4312 left m2–m3, 4313 right M1–M3, 4321 left p1, 4322 left d2, 4323 right p1, 4332 right m3, 4594 antler fragment, 4598 left m2, 4604 left P2, 4609 left M1–M2, 4611 left p4, 4646

basis of right frontal appendage, 5152 right p1, 5156 right M2, 5159 right D2, 5307 left M1, 5309 left m1/2/3, 5310 left D3, 5370 right P4, 6601 right P2, 6603 right Cm, 6604 left p1, 6610 right m3, 6614 left m1–m2, 6615 left M2–M3, 7803 antler fragment, 7814 left p2, 7817 left p1, 7818 left p1, 7824 right d4, 7825 right p3, 7826 left m2, 7827 left M1, 8979 basis of right frontal appendage, 8991 left M1, 9064 left p1, 9065 left p1, 9066 left p1, 9067 right p1, 10782 right m1, 10783 right M3, II 12308 left M2.

Lagomeryx pumilio (Inventory-No. BSPG 1959 II ...)

3718 left p2–m2, 3719 left p2–m3, 3946 right m2, 3947 right m2, 3949 right m1/2, 3950 right p2, 3956 left M3, 3957 right m2, 3959 left P3, 3962 right p3, 3965 right m3, 3966 left m1, 3968 right m3, 3969 left m1/2/3, 3970 right M, 3971 right D2, 3972 left m1, 3975 right M, 3976 right M1, 3978 left m2, 3979 right P3, 3980 left m2, 3981 right M2, 3982 left m3, 3983 left m1/2/3, 3984 right m1, 3985 right P3, 3986 left d2, 3988 left m1, 3989 left M, 3990 left P4, 3991 left P2, 3993 left P4, 3994 right m3, 3995 right m1/2/3, 3996 left P2, 3997 left m2, 3998 right m2, 3999 right m2, 4000 right m1, 4001 right M, 4003 left m3, 4005 left P4, 4007 right M2, 4009 left P4, 4010 right P2, 4011 right M1, 4013 left m3, 4014 left p4, 4016 right D2, 4017 left p4, 4021 right p4, 4022 left P2, 4023 right D3, 4025 right d4, 4026 right m1/2/3, 4027 right m1, 4029 right M3, 4030 left m1, 4032 left M1/2/3, 4033 right p3–p4, 4034 left m3, 4035 right m1, 4037 left M1, 4038 right D4, 4039 right P2, 4040 right p4, 4041 left m1/2/3, 4042 left m3, 4043 right m1, 4044 right m1/2/3, 4046 left m1, 4047 left m2, 4048 left M1, 4049 right m1, 4050 right m2, 4052 left m, 4055 left P2, 4056 left m3, 4058 left M1, 4059 right m3, 4060 left D2, 4061 right M, 4062 left M1, 4063 right p4, 4065 right D3, 4068 left M1, 4071 right P2 + P4–M3, 4074 right M3, 4075 left M1, 4076 right M1, 4077 right M2, 4078 right M3, 4079 right P4, 4082 left M3, 4084 right P2, 4085 right M1, 4086 left P4, 4087 left d4, 4088 right D2, 4090 left m1, 4091 left M3, 4092 left M3, 4093 right P3, 4094 left M3, 4098 right d4, 4100 right p3, 4101 left p2, 4102 right D4, 4103 right p3, 4104 left P3, 4107 right D2, 4108 left D2, 4110 right m1, 4111 right m1, 4112 right M2, 4113 left P4, 4114 right M1, 4116 left M1, 4117 right p2, 4119 right d4, 4226 right M1/2, 4228 right P4, 4229 left M, 4287 right d4, 4288 right D2, 4291 left m3, 4292 right m3, 4293 left p4–m1, 4294 right p4–m1, 4295 right M1, 4296 right M3, 4297 right M3, 4298 right M1, 4299 right m1, 4300 right d4, 4301 right m2–m3, 4303 right M3, 4306 left m3, 4307 left M1, 4308 left P3, 4309 left P4, 4317 left M1/2/3, 4318 right m1–m2, 4319 left p4, 4320 left D3, 4324 left p2, 4325 right M1/2/3, 4328 left D2, 4329 right p4, 4330 right M2, 4331 right M3, 4333 right m1–m2, 4599 right D4, 4600 right M3, 4601 right P4, 4602 right D4, 4603 left P2, 4606 left D3, 4607 right D2, 4613 left M1–M3, 4614 right m1, 4650 right m1, 5151 left m1, 5153 right

P2, 5154 left d4, 5155 left M3, 5157 right M2, 5158 right d4, 5160 left m3, 5161 left p4–m3, 5308 right M1, 5311 left M2–M3, 5312 right M2–M3, 5325 left p3–m3, 6600 right p4, 6602 left D4, 6605 right m1, 6606 left D3, 6607 left M1, 6608 right m1, 6609 left p3, 6611 left M3, 6612 left m3, 6613 right p3–m1, 6616 right m2–m3, 6618 right M3, 6664 right m2, 679 left p2–m3, 7804 left M3, 7805 left m3, 7806 left p4, 7807 left m1, 7808 left m3, 7809 left D3, 7810 left D4, 7811 right m3, 7812 right p3, 7813 right D2, 7815 left P2, 7816 right p2, 8092 left m2 to m3, 8093 right P3, 9017 left p4, 9018 right p4, 9019 right m1, 9020 left m1, 9021 right m2/3, 9022 right m3, 9023 right P4, 9024 right M1, 9025 right M1/2/3, 9026 right M1/2/3, 9068 left p2, 9069 right m2 to m3, 9070 right p3, 9071 right D2, 9072 right m3, 9073 left d2, 9074 right d2, 12304 right M1, 12305 left M, 12306 left m1, 12307 right p4, 12319 left p2, 12326 left M3, 12333 left m1, 12338 right m1, 15651 left p4.

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