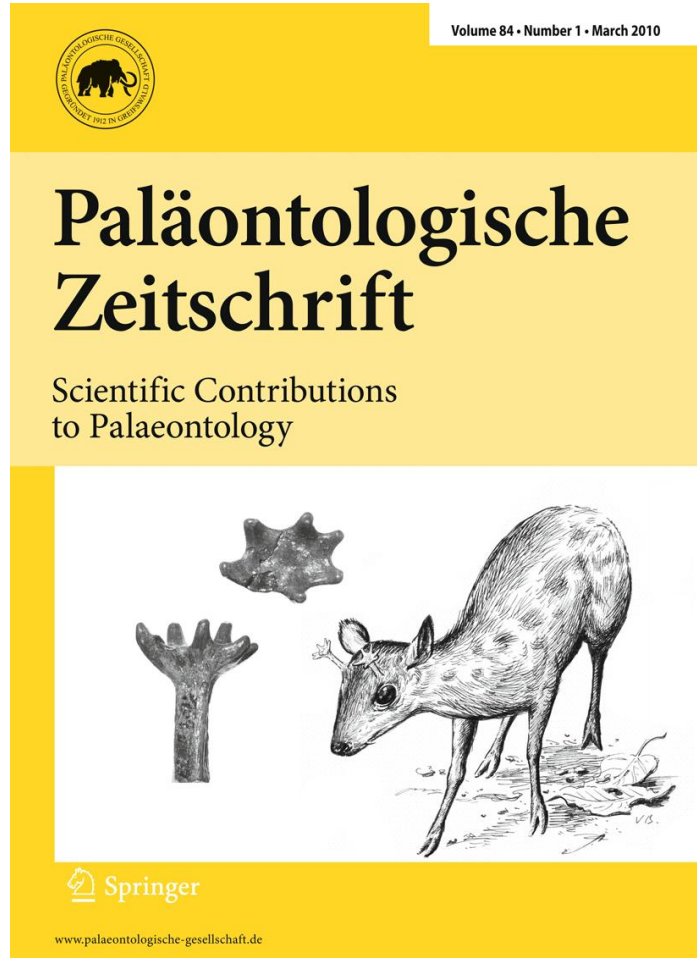


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The Proboscidea (Mammalia) from the Miocene of Sandelzhausen (southern Germany)

Ursula B. Göhlich

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Abstract Presented here is the complete proboscidean assemblage from the vertebrate locality of Sandelzhausen (southern Germany), dated to the Early/Middle Miocene boundary, early middle MN5. The material is preserved as mostly isolated and disarticulated remains and is composed of about 200 dental remains (cheek teeth and tusks), cranial fragments, and postcrania. The main part of this assemblage is identified as belonging to *Gomphotherium subtapiroideum* (Schlesinger, 1917), and a few specimens are attributed to *Zygodon turicensis* (Schinz, 1824). Remarkable is the high percentage of remains of young individuals in this proboscidean assemblage and the lack of *Prodeinotherium* Éhik, 1930. The rich material of *G. subtapiroideum* enables the description of some tooth positions not known before for this taxon. Furthermore, morphological and metrical comparisons with material of more or less contemporaneous taxa from other European localities are provided, especially *G. angustidens* (Cuvier, 1817), *G. sylvaticum* Tassy, 1985, and “*Trilophodon*” *ratisbonensis* Rinnert, 1956.

Keywords Gomphotheres · Mammutids · *Gomphotherium* · *Zygodon* · Upper Freshwater Molasse · Systematics

Kurzfassung Vorliegende Arbeit stellt die vollständige Proboscidea-Fauna der Wirbeltierfundstelle Sandelzhausen (Süddeutschland) aus dem Grenzbereich Unter-/Mittelmiozän, frühe mittlere MN5, vor. Das Material besteht

überwiegend aus isolierten und disartikulierten Resten von über 200 Zähnen (Backen- und Stoßzähne), einigen wenigen Schädelfragmenten und postcranialen Knochen. Der Großteil der Rüsseltierfossilien wird der Art *Gomphotherium subtapiroideum* (Schlesinger, 1917) zugewiesen; nur ein paar wenige Reste als *Zygodon turicensis* (Schinz, 1824) identifiziert. Bemerkenswert an der Probosciderfauna von Sandelzhausen sind der hohe prozentuale Anteil von juvenilen und jungen Individuen sowie das völlige Fehlen von *Prodeinotherium* Éhik, 1930. Das reiche Material von *G. subtapiroideum* ermöglicht erstmals die Beschreibung von bestimmten Zahnpositionen, die von dieser Art bisher noch nicht belegt waren. Darüberhinaus wird das vorgestellte Material morphologisch und metrisch mit anderen etwa zeitgleichen Taxa anderer Europäischer Fundstellen verglichen, wie z.B. mit *G. angustidens* (Cuvier, 1817), *G. sylvaticum* Tassy, 1985 und “*Trilophodon*” *ratisbonensis* Rinnert, 1956.

Schlüsselwörter Gomphotherien · Mammutide · *Gomphotherium* · *Zygodon* · Obere Süßwassermolasse · Systematik

Introduction

The Sandelzhausen locality is a well-known terrestrial vertebrate fossil site. It is located in the Bavarian North Alpine Foreland Basin (southern Germany) near the town of Mainburg, about 70 km north of Munich (Fig. 1). The limnofluvial deposits of Sandelzhausen belong to the Upper Freshwater Molasse. Using mammal biostratigraphy, Heissig (1997) attributed the fauna of Sandelzhausen to Mammal Neogene biozone MN5. Based on recent bio, litho, and magnetostratigraphic investigations of the

U. B. Göhlich (✉)
Naturhistorisches Museum Wien,
Geologisch-Paläontologische Abteilung,
Burgring 7, 1010 Vienna, Austria
e-mail: ursula.goehlich@nhm-wien.ac.at

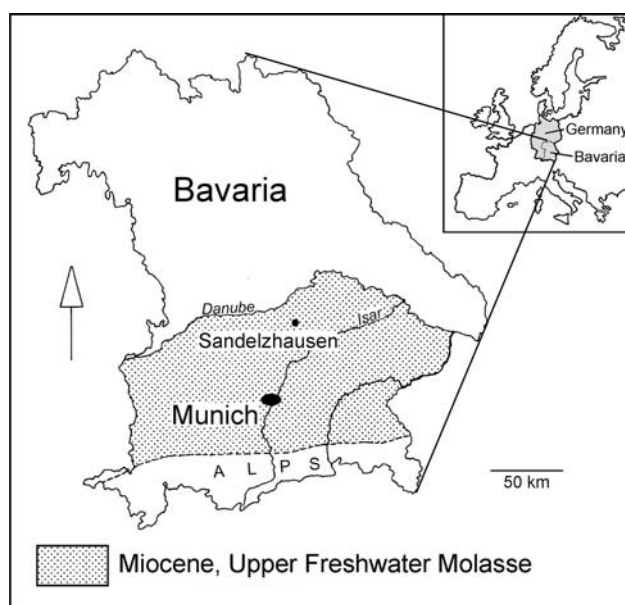


Fig. 1 Geographic position of the Sandelzhausen site (southern Germany) (modified after Göhlich 2002)

stratigraphic position of the locality, Sandelzhausen is situated at or very close to the Early/Middle Miocene (Karpatian/Badenian) boundary (Moser et al. 2009). The deposits arguably cover a time span ranging from some hundreds to thousands of years (Schmid 2002). Several studies on the geology and on different faunal groups of Sandelzhausen have already been published (cited in Falhbusch and Liebreich 1996; Moser et al. 2009).

Proboscideans are known in Europe since the Early Miocene; their invasion from Africa and subsequent expansion in Europe and Asia during the Early Miocene is called the “Proboscidean Datum Event” (Berggren and Van Couvering 1974; Madden and Van Couvering 1976). According to Tassy (1990, 1996b), proboscideans invaded Europe in two waves; the earliest proboscideans in Europe were the elephantoids *Gomphotherium* and *Zygodolophodon* in the Early Miocene (MN3b, Mein 1999); they were followed by *Prodeinotherium* and *Archaeobelodon* in MN4a (Mein 1999). *Prodeinotherium* might possibly have arrived slightly earlier in southeastern Europe, which is suggested by the finding of a *Prodeinotherium* at Lesvos Island (Greece), dated as belonging to the MN3b unit (Koufos et al. 2003). However, proboscideans were subsequently represented throughout the Miocene in Europe by deinotheres, mammutids, gomphotheres, amebelodonts, and choerolophodonts (the last of these are restricted to southeastern Europe).

The oldest evidence of proboscideans in Germany comes from Early Miocene deposits (MN4) of the Upper Brackish and Upper Freshwater Molasse in southern Germany (Göhlich 1998). The following taxa have been identified in the Miocene deposits of the Upper Freshwater

Molasse of south Germany by Schlosser (1917), Stromer (1940), Lehmann (1950), Dehm (1951, 1955), Rinnert (1956), Gaziry (1976), and Göhlich (1998): *Prodeinotherium bavaricum* (Meyer, 1831), *Deinotherium giganteum* Kaup, 1829, *Gomphotherium angustidens*, *G. subtapiroideum*, *G. steinheimense* (Klähn, 1922), “*Trilophodon*” *ratisbonensis* Rinnert 1956, *Tetralophodon longirostris* (Kaup, 1832), *Archaeobelodon filholi*, *Zygodolophodon turicensis*, and *Bunolophodon grandidens* Gaziry, 1976. The last was not accepted as valid taxon by Göhlich (1998), and *T. ratisbonensis* is also a species of uncertain taxonomic status and of doubtful validity (Tassy 1985: 702). Because *Trilophodon* is a junior synonym of *Gomphotherium* (Shoshani and Tassy 1996, Appendix A; Göhlich 1998), the former genus name is given in quotations throughout. Thus far, *A. filholi* has only rarely been mentioned from the Upper Freshwater-Molasse (Tassy 1985; Gregor 2005).

The first study of the proboscideans from Sandelzhausen was made by Schmidt-Kittler (1972). At that time about 20 teeth were available for study. During later excavations, between 1994 and 2002, many dental and postcranial remains were found, which are the topic of this publication. Schmidt-Kittler (1972) attributed all proboscidean specimens, known at that time from Sandelzhausen to *G. angustidens subtapiroides*, with the exception of one molar fragment, which he determined as *Z. turicensis*.

Methods

The material presented here is housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSPG), under the inventory number BSPG 1959 II.... The odontological and osteological terminology used here follow Tassy (1996a), Tobien (1973, 1975), and Nickel et al. (1984). Measurements were taken after Göhlich (1998).

For comparative investigations the following taxa and localities have been considered: *G. subtapiroideum*: Vordersdorf near Eibiswald/Wies (MN5, Styria, Austria, type locality), Viehhausen (MN 5, Germany); *G. sylvaticum*: Artenay (MN4, France, type locality); *G. angustidens*: Simorre (MN7, France, type locality), En Pélouan (MN7, France), Villefranche d’Astarac (MN7, France), Eppelsheim (MN9, Germany), Grund, Guntersdorf (both MN5, Austria); “*T.*” *ratisbonense*: Viehhausen (MN5, Germany, type locality); *G. steinheimense*: Steinheim (MN7, Germany, type locality), Massenhausen (MN8/9, Germany); *G. pyrenaicum*: St Frajou (MN7, France, type locality); *A. filholi*: Sansan (MN6, France, type locality), Bézian (MN4b, France), Pontlevoy (MN5, France), Biorse (Castelnau d’Arbieu) (MN5, France); *Z. turicensis*: Elgg (MN6 or 7, Switzerland, type locality), Simorre, Rajégats, Malartic, Villefranche d’Astarac (all MN7, France), Castelnau-

Picampeau (MN7, France), Baigneaux-en-Beauce (MN4, France), Mistelbach (MN9, Austria), Göriach (MN5, Austria), Devínská Nová Ves (=Neudorf an der March) (MN6, Slovakia).

Most of this comparative material has been studied at the following institutions: BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, Munich; LMJ: Landesmuseum Joanneum, Graz; LPVPH: Laboratoire Paléontologie Vertébrés et Paléontologie Humaine, Paris; NHMW: Naturhistorisches Museum Wien; MNHN: Museum National d'Histoire Naturelle, Paris; PIMUZ: Paläontologisches Institut und Museum der Universität Zürich; SMNS: Staatliches Museum für Naturkunde Stuttgart. Comparisons with the following materials (including the measurements for Figs. 3, 6, 9) are based on publications: *G. sylvaticum* from Artenay (Tassy 1985; Ginsburg and Antunes 1966), partly *G. angustidens* from En Péjouan (Tassy 1985), *A. filholi* from Sansan, Bézian and Pontlevoy (Tassy 1985), and *Z. turicensis* from Baigneaux-en-Beauce, Castelnau-picampeau, Rajégats and Malartic (Tassy 1977, 1985).

Odontological abbreviations: i/I (lower/upper incisor/tusk); d/D (lower/upper deciduous tooth); p/P (lower/upper premolar); m/M (lower/upper molar).

Systematic Palaeontology

Order Proboscidea Illiger, 1811

Superfamily Elephantoidae Gray, 1821

Family Gomphotheriidae Hay, 1922

Genus Gomphotherium Burmeister, 1837

Synonymy: see Shoshani and Tassy (1996: 349f, Appendix A).

Original diagnosis: Burmeister (1837: 795).

Emended diagnosis: Tassy (1985: 670–673).

Type species: *Gomphotherium angustidens* (Cuvier, 1817).

***Gomphotherium subtapiroideum* (Schlesinger, 1917)**

Synonymy: see Göhlich (1998).

Original description: Schlesinger (1917: 30–32).

Lectotype: M2 + M3 dext. (NHMW 3870 ex 1882 (A 4135)) illustrated in Schlesinger (1917: pl. 7 fig. 3). The lectotype was chosen by Osborn (1936: 394).

Paralectotypes: Maxillary portion with dext. M1, D4, P4 and sin. D4, D3, P4 (NHMW C 3874 ex 1882 (A4137)) (Schlesinger 1917: pl. 3 fig. 2, pl. 4 fig. 1); m3 dext. (Schlesinger 1917: pl. 7 figs. 1, 2); M3 sin. (Schlesinger 1917: p. 31 fig. 3). They were mentioned by Osborn (1936: 394) as cotypes.

Type locality and type horizon: Lignites of Vordersdorf near Eibiswald (also sometimes named Vordersdorf

near Wies), Styria, Austria, Middle Miocene (Karpatian), MN5.

Stratigraphic and geographic distribution: Central and probably also Western Europe, Early to early Late Miocene, MN5 (Eibiswald, Sandelzhausen) to MN8/9 (Massenhausen, Göhlich 1998).

Remarks: Schlesinger (1917) described *Mastodon (Bunolophodon) angustidens* forma *subtapiroidea*, from the Lower Miocene Lignites of Vordersdorf near Eibiswald (Styria, Austria), which he separated from *Mastodon (Bunolophodon) angustidens* forma *typica*. According to Schlesinger, the forma *subtapiroidea* represents an intermediate cheek tooth morphology between *M. (B.) angustidens* forma *typica* (= *G. angustidens*) and *M. (Z.) tapiroides* (= *Z. turicensis*). Schlesinger (1917: 146) already pointed to the fact that the cheek teeth morphology of *angustidens* forma *subtapiroidea* can be very similar to those of *Z. turicensis*. Additionally, Schlesinger (1917: 36) took into account that the forma *subtapiroidea* might be a synonym of *M. pyrenaicus* from the Middle Miocene of France.

Later, Osborn (1936) declared Schlesinger's "forma *subtapiroidea*" to be a valid species in his genus *Serridentinus* Osborn, 1923. However, the taxonomic validity and the systematic position of this species were always controversial. Often, it was not accepted as a discrete species, but interpreted as a subtapiroid morphotype of *G. angustidens* (Tassy 1974: 120ff, 1985: 700; Tobien 1976: 177). Also, Lehmann (1950: 159) attributed all trilophodont mastodonts from the Upper Freshwater Molasse of southern Germany to *M. angustidens*, which in his opinion comprises the subspecies *G. angustidens angustidens*, *G. angustidens turicensis* and *G. angustidens tapiroides* (=forma *subtapiroidea*).

Tobien (1972: 172) pointed out that it is extremely difficult and often impossible to attribute certain molars to one or the other taxon. As a consequence, he (Tobien 1972: 171, 1973: 210ff) did not accept "*subtapiroides*" as a valid taxon but included it in the polymorph taxon *G. angustidens*. Tobien (1976: 177) interpreted subtapiroid molars to represent individual variants of *G. angustidens* or a development of local populations.

Schmidt-Kittler (1972) determined the tooth material of Sandelzhausen to be "*G. angustidens subtapiroides*". He concluded that *G. angustidens subtapiroides* and *G. angustidens steinheimense*, known from different stratigraphic deposits, represent taxa of an evolutionary lineage.

Tassy (1985: 700) doubted the validity of a discrete subtapiroid species, but accepted the subspecies *G. angustidens subtapiroideum* to be a member of his "*G. groupe angustidens*" (Tassy 1985: 673), made up by

the species *angustidens* and *inopinatum*. On the other hand, Tassy (1985: 488) subdivided *Z. turicensis* into gracile and robust morphotypes and pointed out that the teeth of the robust type of *Z. turicensis* are morphologically very similar to, and often indistinguishable from, the subtapiroid type of teeth of *G. angustidens*.

Gaziry (1994: 116) described some molars of the Upper Freshwater Molasse as *Bunolophodon subtapiroides*, thereby (Gaziry 1994: 115) fixing *subtapiroides* as the type species for *Bunolophodon*, a genus originally set up by Vacek (1877). This was later generally not accepted as a valid genus, but synonymized with *Gomphotherium* (Coppens et al. 1978: 341; Shoshani and Tassy 1996: 349; Tassy 1985: 670).

In Shoshani and Tassy (1996, Appendix C.1), the taxon *G. a. subtapiroideum* is listed as incertae sedis.

Göhlich (1998) described some molars and tusks from the late Middle Miocene locality of Massenhausen (MN 8) (southern Germany) as *Gomphotherium subtapiroideum*. Dental material

The few specimens that have already been mentioned or described by Schmidt-Kittler (1972) are indicated by the citation. For lack of space in the following only an abridged version (the last number) of the official complete inventory number (BSPG 1959 II ...) is given for the specimens.

d2—d2 dext. (395) (Schmidt-Kittler 1972); d2 dext. (16201); d2 sin. (396) (Schmidt-Kittler 1972); d2 sin. (2250, see juvenile mandible with i2, d2, and d3); d2 sin. (11303).

D2—D2 sin. (391) (determined as p3 dext. in Schmidt-Kittler 1972); D2 dext. (388) (Schmidt-Kittler 1972); D2 dext. (448); D2 sin. (11333); D2 sin. (11334); D2 sin., posterior end lacking (11335); D2 dext. (11363); D2 sin., posteriormost fragment (11373).

d3—d3 sin. (442); d3 dext. (445); d3 sin. (2250, see juvenile mandible with i2, d2); d3 sin. (446, belonging to d4 sin., same number); d3 dext. (11310); d3 dext. (11311); d3 sin. (11312); d3 sin. (11314); d3 sin. (16199), germ; d3 dext., germ, anterior half (11315); d3 dext., posterior lophid (11316); d3 sin. and dext. (sin. 11317c, posterior end; dext. 1137d, anterior end), same individual as d4 sin. and dext., 11317a, b); d3 dext., germ, posterior lophid (11350); d3 dext. (11306); d3 ? (11319).

D3—D3 sin. (451); D3 sin. (441); D3 sin. (11304); D3 sin. (11305); D3 dext. (11323, same individual as D4, same number); D3 dext. (11307); D3 dext., lingual half (11308); D3 sin., lingual half (11309); D3 sin. (11313).

d4—d4 dext. (443); d4 sin. (394) (Schmidt-Kittler 1972, pl. 5 fig. 2); d4 sin. (392) (Schmidt-Kittler 1972); d4 dext. (393) (Schmidt-Kittler 1972); d4 sin. (446, same individual as d3 sin., same number); d4 sin., posterior half (11327); d4

dext., germ (11328, probably same individual as d4 sin., 11331); d4 sin. and dext. (11317a, 11317b, same individual as d3, 11317c, d); d4 sin., anterior end (11331, probably same individual as 11328); d4 sin., posterior end (11332); d4 dext., germ, first and second or third lophid (11319); d4 dext., two posterior lophids, abraded (11371).

D4—D4 dext. (11886); D4 sin. (444); D4 sin. (386) (Schmidt-Kittler 1972); D4 dext. (452, probably same individual as D4 sin., 11324); D4 sin. (11324, probably same individual as D4 dext., 452); D4 dext. (11323, same individual as D3, same number); D4 dext. (11322 probably same individual as D4 sin., 11325); D4 sin., damaged (11325, probably same individual as D4 dext., 11322); D4 dext., totally worn down (11326); D4 dext., germ, anterior half (11321); D4 sin., posterior half (11320); D4 dext. (16198), anterior loph.

p3—p3 sin. (447); p3 dext. (387) (in Schmidt-Kittler 1972, pl. 5 fig. 2, determined as D2); p3 sin. (11647);

P3—P3 dext. (450); P3 sin. (11336); P3 dext. (11337); P3 dext. (11339, possibly belonging to P3 sin. 11341); P3 sin. (11341, possibly belonging to P3 dext. 11339); P3 sin., posterior half (11338); P3 dext., damaged (11340); P3 sin., damaged (11343); P3 sin., damaged (16207); ?P3 (or P2?) dext. (449).

p4—p4 dext. (7939); p4 dext. (11349, probably same individual as P4 sin. 11344 and dext. 11345); p4 sin. (11360, belonging to mandibles sin. and dext. with p4—m3 (all 11360) with both i2 (11410, 11411); p4 dext. (16200) totally worn.

P4—P4 dext., germ (385, Schmidt-Kittler 1972, pl. 5 fig. 3); P4 sin. (11344, probably same individual as P4 dext. 11345 and p4 dext. 11349); P4 dext. (11345, probably same individual as P4 sin. 11344 and p4 dext. 11349); P4 dext. (11346); P4 dext. (11347); P4 dext. (11348);

m1—m1 dext. (439); m1 dext. (42, Schmidt-Kittler 1972, pl. 5 fig. 1); m1 sin. and dext. (11360, belonging to mandibles sin. and dext. with p4—m3 (all 11360) with both i2 (11410, 11411)); m1 sin., totally worn down (453).

M1—M1(?) sin. (440); M1 sin., missing posterior end (11354) and M1 dext., missing posttrite half (11355) of same individual; M1 dext. (11353) and damaged M1 sin. (11352) of same individual (both probably belonging to M2 dext., 11368); M1 dext., damaged (11351); M1 dext., missing posterior end (11356); M1 dext., posterior half (11357); M1 dext., missing anterior end and pretrite portion (11358); M1 sin., posterior fragment (16208); M1 dext., posterior end, worn and abraded (11359).

m2—m2 sin. and dext. (384, in mandible with m3 sin. and i2 sin. and dext., belonging to maxilla with M2 sin. and M3 sin., all same number); m2 sin. and dext. (11360, belonging to mandibles sin. and dext. with p4—m3 (11360) with both i2 (11410, 11411); m2 dext., worn, anterior and posterior end damaged (11376, probably same individual

as m3 dext. 11386 and m3 sin. 11388, possibly as M3 sin. 11389); m2 sin., worn, anterior end and 1st lophid lingually and 3rd lophid labially damaged (11377); m2 sin., worn and damaged (11378, probably same individual as m3 sin. 11381, possibly same individual as m3 dext. 11385); m2 dext., worn and broken (11379); m2 sin., very worn down (11374); m2? dext., totally worn down to the roots (11362); m2 dext., posterior half, totally worn down (11375); m2 sin., posterior half, very worn (11370); m2 sin., posterior half (11361); m2 dext., only roots (11382, same individual as m3, same number).

M2—M2 dext. (11368, probably belonging to M1 sin. and dext. 11352+3); M2 sin. (438); M2 sin. (384) (in maxillary portion with M3 sin. and belonging to mandible sin. and dext. with i2 sin. and dext., m2 sin.+dext., m3 sin., all same number) (illustrated in Schmidt-Kittler 1972, pl. 4 figs. 1–2); M2 sin., very worn (11364); M2 dext., worn and damaged (11369); M2 dext., very worn (11366); M2 sin., totally worn down (11365); M2 sin., totally worn down (11367).

m3—m3 sin. (384, see mandible sin. and dext. with i2 sin. and dext. and m2 sin. and dext., all same number); m3 sin. (11384); m3 sin. (3723, probably same individual as m3 dext. 11383 and prox. ulna fragm., 11383); m3 dext. (11383, probably same individual as m3 sin., 3723); m3 dext. (11386, probably same individual as m2 dext. 11376, m3 sin.-fragment 11388, and possibly M3 sin.-fragment 11389); m3 sin. (11381, probably same individual as m2 sin. 11378 and possibly same individual as m3 dext., 11385); m3 dext., deformed and broken (11385, possibly belonging to m3 sin. 11381 and m2 sin. 11378); m3 dext. (11382, mandible dext. with m3 and roots of m2); m3 sin., posterior 2½ lophids (416);

m3—germs sin. and dext., sin. only anterior 2 lophids (11360, belonging to mandibles sin. and dext. with p4–m3 (all 11360) with both i2 (11410, 11411); m3 sin.-fragm., posterior 1½ lophids (11388, probably same individual as m3 dext. 11386, m2 dext. 11376, and possibly M3 sin.-fragm. 11389); m3 dext.-fragm., posterior 1½ lophids (11390); m3 dext?-fragm., posterior 3 lophids, totally worn down (415); m3-talonid sin. (11391);

M3—M3 sin. (384, belonging to M2 sin and mandible sin. and dext. with i2 sin. and dext. m2 sin.+dext., m3 sin., all same number); M3 sin., damaged anteriorly (3722, possibly same individual as M3 dext. 4783, I2 4782); M3 dext., damaged anteriorly (4783, probably same individual as I2 4782, and possibly same individual as 3722); M3 sin. (4782, possibly same individual as M3 dext. 4783); M3 dext., totally worn to the roots (11380),

M3 sin., fragmentary posterior end (11389, possibly same individual as m3 sin 11388, m3 dext. 11386, and m2 dext. 11376).

di2—di2 dext.? (2221); di2 sin?(2247).

DI2—DI2 sin., complete (11392); DI2 dext., nearly complete (11551); DI2 dext., anterior portion (11393); DI2 sin., midportion lacking tip (16209).

di2 or DI2—fragmentary midportion (11394); fragmentary tip, worn (16210).

i2—i2 sin.? juvenile, lacking posterior end (11395); i2 sin.?, juvenile, anterior portion lacking ultimate tip (11396); i2 sin. juvenile, in situ in juvenile mandible (2250), i2 sin. and dext. (384, in mandible with m2–m3 sin and m2 dext. and belonging to M2–M3 sin., all 384); i2 sin., nearly complete from tip to alveolus (11413); i2 sin., nearly complete (11399, probably belonging to i2 dext. 11412); i2 dext., nearly complete (11412, probably belonging to i2 sin. 11399); i2 dext., nearly complete (397) (illustrated in Schmidt-Kittler 1972, fig. 2); i2 dext. nearly complete (11397); i2 sin. and dext., both nearly complete (11410, 11411, belonging to mandibles sin. and dext. with p4–m3 (all 11360)); i2 sin. and dext., both nearly complete but slivered (11407, 11408); i2 dext., incomplete tusk with tip (11400); i2 dext., incomplete midportion (11404); i2 dext., incomplete midportion (11406); i2 sin. fragmentary midportion (16214); i2 ?, fragmentary midportion (11409); i2 ?, fragmentary midportion (11403); i2 dext?, fragment of a spatula-like tip (11398); i2 sin., juvenile, pointed tip (11405); i2 sin/dext?, very fragmentary midportion (11401); i2 dext., midportion without tip and pulpa (11414).

I2—I2 dext., complete from tip to pulpa (11415); I2 sin., complete from tip to pulpa (11437); I2 dext. and sin., complete from tip to pulpa (11439, 11440); I2 dext., nearly complete from tip to pulpa (11416); I2 dext., nearly complete, no pulpa, relicts of enamel band (11436); I2 sin., nearly complete lacking ultimate tip (11435); I2 sin., nearly complete, lacking tip and pulpa, (398, illustrated in Schmidt-Kittler 1972, Abb. 3); I2 dext, anterior portion missing ultimate tip (16211); I2 dext., fragmentary tip with rest of enamel band (11420); I2 dext.?, midportion of tusk lacking tip and enamel band (11432); I2 sin.?, midportion of tusk lacking tip and enamel band (11433); I2 ?, midportion without enamel band, triangular cross-section (11423); I2 sin./dext.?, small ultimate tips with enamel (47, 11424, 11425, 11427, 11428, 11429, 11430); I2 ?, fragments of midportions with enamel band (11416, 11419, 11421, 11422, 11426, 11434, 16212, 16213, 16215).

I2 or i2—indeterminable tusk fragments (11417, 11418, 11431, 11438).

Description and comparison of dentition

Deciduous teeth

For measurements of the deciduous teeth see Table 1.

d2 (Fig. 2a, f): Four isolated d2 and one d2 in a juvenile mandible are present. The morphology is best preserved in 11303, 2250, and 16201, which are unworn (395 is very worn, 396 is damaged lingually). Tooth “bilophid”; crown oval and labiolingually slender (in occlusal view); main cusp (fused protoconid and metaconid) conical and highest point of crown, occupying about anterior 2/3 of crown; on anterior flank of protoconid very weak crest, in 11303 basal ending in a tiny tubercle (paraconid); weak blunt crest (post-metaconid crest) along posterolingual flank of main cusp; hypoconid of moderate size and height; entoconid small and low; between hypoconid and entoconid low crenulated cingulum; tooth two-rooted. 11303 and 16201 show some morphological variation. In 11303, both entoconid and hypoconid and post-metacone crest stronger than in 16201; in 11303 hypoconid with a serrated labial crest, missing in 16201; in 11303 posterior flank of main cusp marked by median longitudinal furrow (missing in 16201) weakly separating protoconid and metaconid.

The d2 of elephantoids of the European Neogene are extremely rare. Two juvenile mandibular portions of *G. angustidens* containing a d2 are known from its type locality Simorre (MN7, France) (MNHN Si 5 and 6), and an additional one is known from Villefranche d'Astarac (MN7) (MHNT 320, coll. E.+L. Lartet). These d2 of *G. angustidens* are different from those of Sandelzhausen in being roundish in shape (occlusal view) (d2 from Sandelzhausen being longer and labiolingually more slender; Fig. 3) and in being formed by only one main cusp (MNHN Si 5, MHNT 320) but no hypoconid and/or entoconid. However, specimen MNHN Si 6 (which d2 is wrongly implanted inverted in the mandible) also has a posterior loph composed of small tubercles. From Sansan (MN6, France), a portion of a mandible with a d2 and d3 (MNHN Sa 2861) was attributed to *A. filholi* by Tassy (1985, fig. 240A, C (1985: 584). The main cusp of this d2 is described as being composed of two somewhat more separated conids, whereas they are almost fused in the d2 of Sandelzhausen. However, Tassy (1985: 584) pointed out that based on such scanty material it is impossible to distinguish the d2 of *A. filholi* and *G. angustidens*. Mandibular material from En Pélouan (MN 7, France) shows—based on mandibular alveoli for d2—individual variation for *G. angustidens* in the presence or absence of a d2 (Tassy 1985: 377). Tassy (1985: 584) already pointed to the tendency within the gomphotheres for the two anterior cusps (protoconid and metaconid) to fuse in to a single one, as is seen in the d2 of Sandelzhausen.

Table 1 Measurements (in mm) of milk cheek teeth of *G. subtapiroideum* from Sandelzhausen

Inventory number BSPG	L	B	B I	B II	B III	B/L-Index
d2						
1959 II 395	21	12.5				0.60
1959 II 396	17	(10.5)				(0.62)
1959 II 2250	18	12				0.67
1959 II 11303	19.5	12				0.62
1959 II 16201	17.5	12				0.69
D2						
1959 II 391	27	21.5				0.80
1959 II 388	25	20				0.80
1959 II 448	23.5	19.5				0.83
1959 II 11333	26	19.5				0.75
1959 II 11334	24.5	18				0.73
1959 II 11335	—	(21)				—
1959 II 11363	24	17.5				0.73
1959 II 11373	—	—				—
d3						
1959 II 442	35	23	19.5	23		0.66
1959 II 445	36	24.5	(20)	24.5		0.68
1959 II 2250	35.5	24	21	24		0.68
1959 II 446	36	25	20	24.5		0.69
1959 II 11310	35.5	24	21	24		0.68
1959 II 11311	36	24.5	21	24.5		0.68
1959 II 11312	34.5	23.5	21.5	23.5		0.68
1959 II 11306	35	23.5	19.5	23		0.67
1959 II 11314	35.5	25.5	21	25.5		0.72
1959 II 16199	35.5	23.5	21.5	23.5		0.66
1959 II 11315	—	—	21	—		—
1959 II 11316	—	—	—	24		—
1959 II 11317c	—	—	—	24.5		—
1959 II 11317d	—	—	—	—		—
1959 II 11350	—	—	—	22.5		—
1959 II 11319	—	—	—	—		—
D3						
1959 II 451	36	29	25	27.5		0.79
1959 II 441	36	27	24	26.5		0.75
1959 II 11304	36	30.5	—	30.5		0.85
1959 II 11305	36	29	25	28.5		0.81
1959 II 11323	(34)	29.5				(0.87)
1959 II 11307	(37)	—	—	31		—
1959 II 11308	—	—	—	—		—
1959 II 11309	—	—	—	26.5		—
1959 II 11313	(34)	(26)	—	—		(0.76)
d4						
1959 II 443	59	34.5	27.5	32.5	34	0.58
1959 II 394	60	35	28	34	34.5	0.58

Table 1 continued

Inventory number BSPG	L	B	B I	B II	B III	B/L-Index
1959 II 392	57	32.5	25.5	32	31.5	0.57
1959 II 393	51	28	23	27	27.5	0.55
1959 II 446	62	35	26.5	31.5	34	0.56
1959 II 11327	–	–	–	22	22.5	–
1959 II 11328	62.5	35	28	33	34.5	0.56
1959 II 11317a	64.5	35.5	28	33	34.5	0.55
1959 II 11317b	65	36	–	35.5	–	0.55
1959 II 11331	–	–	27	–	–	–
1959 II 11332	–	37	–	32	37	–
1959 II 11371	–	–	–	–	34	–
1959 II 11319	–	–	25	–	–	–
D4						
1959 II 444	56	40	31.5	38	40	0.71
1959 II 386	53	41.5	35	41.5	40	0.78
1959 II 452	61	43	34	42.5	42	0.70
1959 II 11324	60	43.5	35	43	42	0.73
1959 II 11322	57	38	36	38	37.5	0.67
1959 II 11325	(>55)	(38)	–	38	–	(0.69)
1959 II 11323	54.5	36	33.5	–	35.5	0.66
1959 II 11326	54	–	–	–	–	–
1959 II 11320	–	–	–	40	37	–
1959 II 11321	–	–	33.5	–	–	–
1959 II 16198	–	–	30.5	–	–	–
1959 II 11886	58.5	40	32.5	39.5	40	0.68

L, length; B, width; B I, width at 1st loph(id); B II, width at 2nd loph(id); B III, width at 3rd loph(id)

Measurements in parentheses indicate estimated measurements of slightly damaged or very worn specimens

One d2 is known of *G. sylvaticum* from Artenay (Tassy 1985: fig. 280G), which is similar to those of Sandelzhausen in morphology and size (Fig. 3). No d2 is present from Vordersdorf near Eibiswald (MN4, Austria), the type locality of *G. subtapiroideum*.

D2 (Fig. 4a–c): Seven mostly complete, isolated teeth in different stages of wear are present, plus a posterior portion of a D2. Tooth bilophid; crown with mostly pyriform outline (in occlusal view), with slightly concave lingual margin, or ovoid to oval; anterior loph with dominating, large and conical labial main cusp (paracone) and small lingual protocone; protocone variable in size from moderate (e.g. 11363 and 11343) to tiny (e.g. 11333 and 11335); posterior loph composed of middle sized metacone and hypocone separated by deep median sulcus; metacone conical or transversely extended (11335); metacone often accompanied at its posterolabial base by a small low tubercle; paracone mostly with a posterolabial postparacrista; in one specimen (391) metacone with

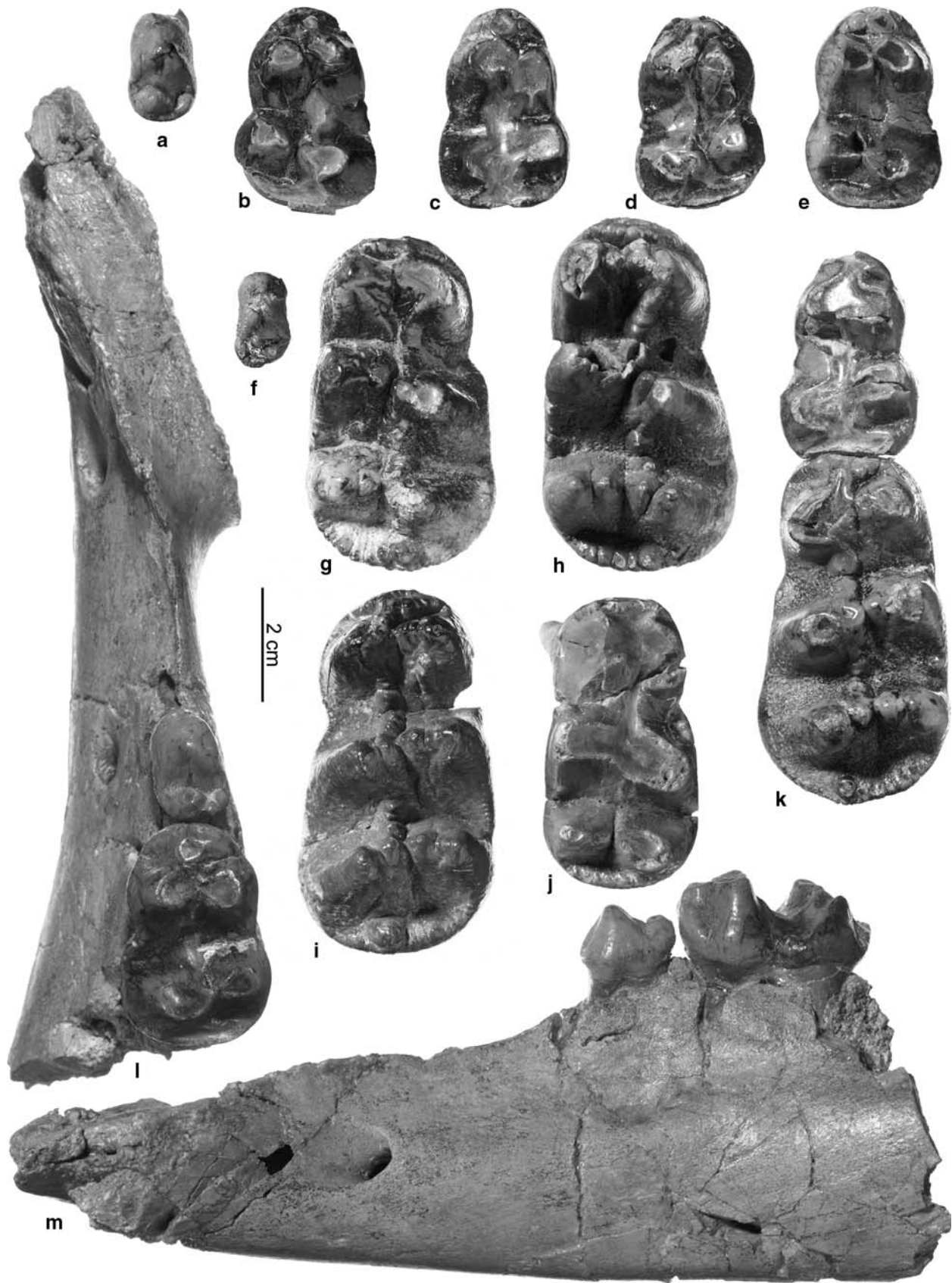
anterolabial premetacrista, in another (11335) with median, serrated crest; hypocone rarely with median serrated crest (391), but mostly merging with posterior low cingulum; anterior end of crown bordered by a low anterior cingulum (no parastyle) often merging with protocone; two-rooted.

The D2 of Sandelzhausen exhibit moderate morphological variability and are all similar in size. No D2 of *G. subtapiroideum* has been described other than those from Sandelzhausen. D2 of other Miocene gomphothere taxa are barely known. *Gomphotherium angustidens* is represented by two D2 from En Pélouan (MN7, France, MNHN SEP 221 and 274) and two from the type locality Simorre (MN7, France; MHN Si 4 and 7). In general, they correspond in morphology and size to those from Sandelzhausen. As far as the attrition allows a statement, all of these D2 of *G. angustidens* have developed a more defined parastyle on the anterior end, whereas the anterior margin of the D2 from Sandelzhausen is formed by a weak, low, and serrated cingulum.

A D2 of *A. filholi* from Sansan (MN6, France; Tassy 1985: 582, fig. 238A, B, D) is distinctly larger than all specimens of Sandelzhausen (Fig. 3) and its crown is more complex with several supplementary tubercles; however, on the basis of this one tooth of *A. filholi*, nothing definitive can be said about intraspecific morphological or metrical variability. The D2 of *G. sylvaticum* from Artenay (MN4) is distinctly narrower (Fig. 3) and not of pyriform shape (Tassy 1985, Fig. 280A, B).

d3 (Fig. 2b–e, k–m): Nine complete d3, all of them mostly worn, and six fragmentary specimens are preserved. Crown bilophid and with pyriform contour (in occlusal view); well-developed paraconid and anterior serrated cingulum; well developed serrated posterior cingulum, anterior lophid almost perpendicular to length of tooth, posterior lophid oriented oblique from lingual anterior to labial posterior; where preserved, all half-lophids consisting of a stronger main cusp and a weaker conelet; valley wide, widening labially; valleys almost unblocked; serrated crescentoid (conule) on posterior flank of anterior pretrite half-loph and on anterior flank of posterior pretrite half-loph (postprotocone crest and prehypocone crest) weak and low; no posttrite conules or crests; in some specimens (e.g. 11312, 445, 11310, 11314) enamel on lingual sides of lophids vertically furrowed; when worn, base of valley and postprotocone and prehypocone crests deep hollowed out.

The d3 of *G. subtapiroideum* from Sandelzhausen are all close in size and are in general smaller than those of *G. angustidens* from Simorre and En Pélouan, and distinctly smaller than those of *A. filholi* from Sansan and Bézian (Fig. 3). In *G. subtapiroideum*, the postprotoconid and prehypoconid crest (posterior and anterior pretrite conule of 1st and 2nd lophid, respectively) of the d3 contact each other in the pretrite half of the valley; this condition is also described for *A. filholi* (Tassy 1985: 584), but differs from



◀ **Fig. 2** Lower deciduous cheek teeth of *Gomphotherium subtypiroides* (Schlesinger, 1917) from Sandelzhhausen (Invent. no. BSPG 1959 II...). **a** d2 sin. (11303); **b** d3 dext. (445); **c** d3 sin. (442); **d** d3 sin. (11312); **e** d3 dext. (11310); **f** d2 sin. (396); **g** d4 dext. (443); **h** d4 dext. (11328); **i** d4 sin. (11317a); **j** d4 dext. (393); **k** d3–d4 sin. (446); **l–m** juvenile mandible with i2, d2–d3 sin. (2250). **a–l** occlusal view, **m** lateral view

that in *G. angustidens* (Tassy 1985: 584), where the postprotocone crest meets with the anterior crescentoid (conule) of the posttrite 2nd half-lophid. However, this feature seems to be variable in *G. angustidens* from Simorre (see MNHN Si 5, 6, 9). No d3 of *G. sylvaticum* or *G. subtypiroides* from their type localities are available for comparison.

D3 (Fig. 4d–f): Five nearly complete and four fragmentary D3 of different stages of wear are preserved. Bilophid; crown contour almost quadrangular, with a step-like lingual broadening anterior to the 2nd loph; 2nd loph oriented oblique from lingual anterior to labial posterior; anterior serrated cingulum, with biggest tubercle in labial corner; posterior serrated cingulum thickened and with strongest tubercle in lingual corner; mostly lingual serrated cingulum with thickened tubercle in interlophid; wear patterns indicating relatively weak conules in the form of an anterior and posterior crescentoid at the 1st loph and an anterior one at the 2nd loph; valley not or only weakly blocked; no posttrite conules; most specimens (e.g. 11304, 11305, 11307, 441) with posttrite “zygodont-crest”-like

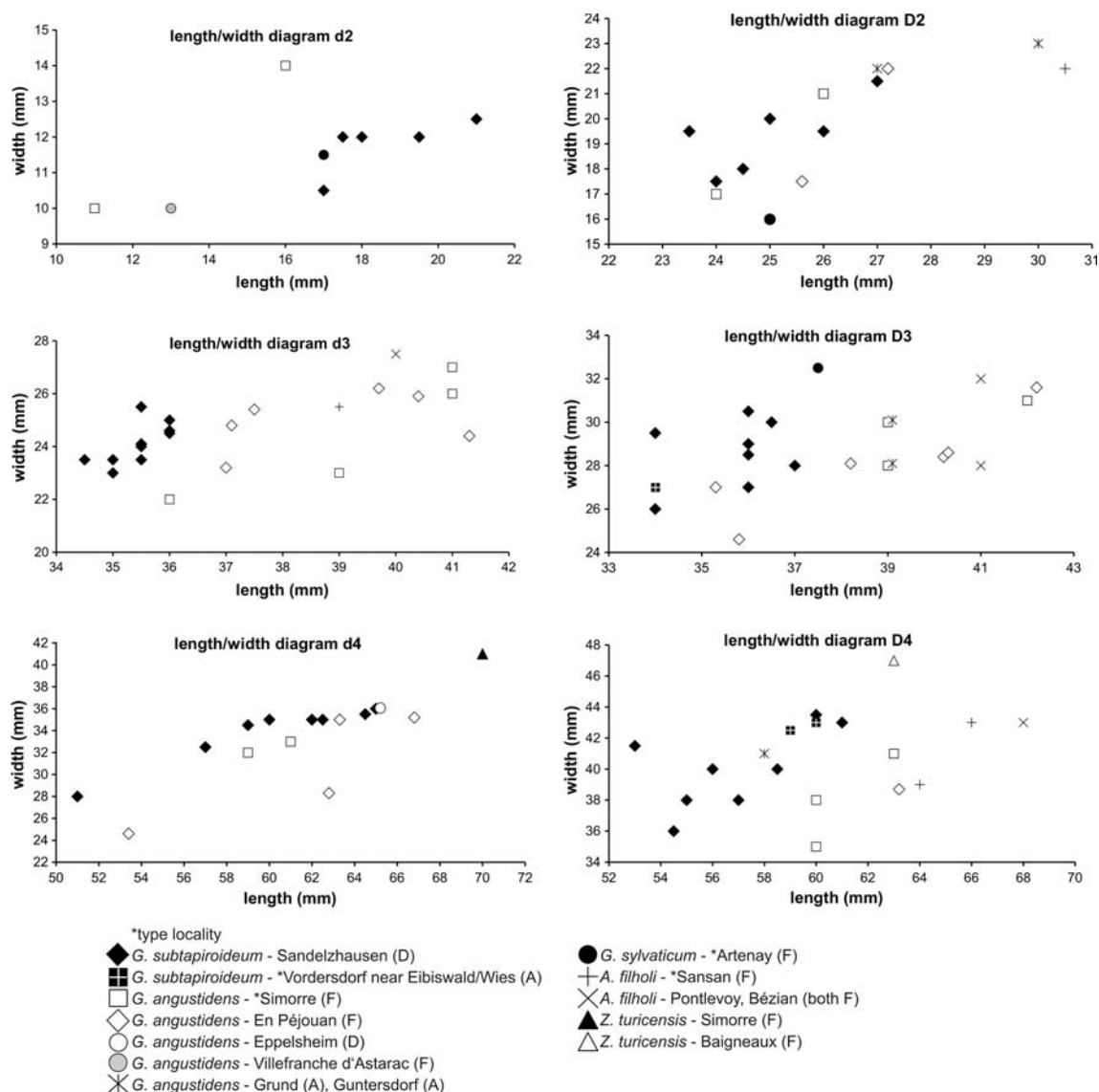


Fig. 3 Scatter diagrams (length and width of teeth) of the lower and upper deciduous cheek teeth of *Gomphotherium subtypiroides* (Schlesinger, 1917) from Sandelzhhausen in comparison with *G.*

subtypiroides, *G. angustidens*, *G. sylvaticum*, *Archaeobelodon filholi*, and *Zygodont turicensis* from different Early to Middle Miocene European localities

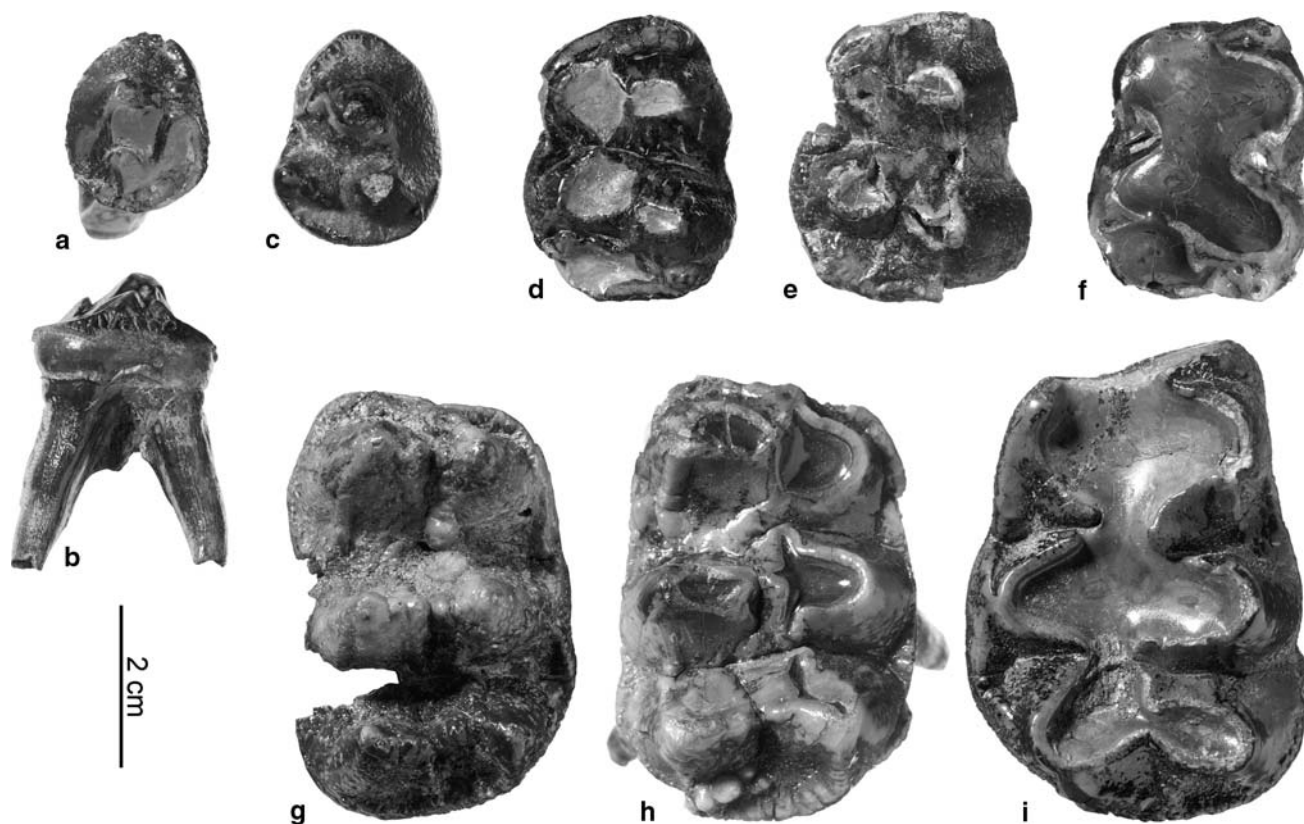


Fig. 4 Upper deciduous cheek teeth of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhausen (Invent. no. BSPG 1959 II ...). **a–b** D2 dext. (448); **c** D2 sin. (391); **d** D3 sin. (441); **e** D3 sin.

(11304); **f** D3 sin. (451); **g** D4 dext. (11323); **h** D4 dext. (11322); **i** D4 sin. (11324). **a, c–i** occlusal view, **b** lingual view

crests on posterior flank of 1st loph and anterior flank of 2nd loph; already in early to middle attrition, base of valley affected by concave wear facets; in some specimens (e.g. 11304, 441, 11305, 11307) enamel on lingual sides of lophids vertically furrowed; when worn, base of valley and postprotocone and prehypocone crests deep hollowed out.

The D3 from Sandelzhausen are smaller than most specimens of *G. angustidens* from Simorre and En Péjouan, except for a very few teeth from En Péjouan, which are mostly narrower (Fig. 3); they are also smaller than those of *A. filholi* from Bézian and Pontlevoy (Fig. 3). The D3 of *G. sylvaticum* from Artenay is slightly longer than those of Sandelzhausen, but conforms with those of *G. subtapiroideum* from Sandelzhausen and Eibiswald in being wider than those of *G. angustidens* or *A. filholi* (Fig. 3). None of the D3 of *G. subtapiroideum* from Sandelzhausen shows a diagonal contact of an additional posterior central conule of the 1st posttrite half-loph with the anterior central conule of the 2nd pretrite half-loph; this pattern can be developed in D3 of *G. angustidens*, but was never observed in *G. sylvaticum* and *A. filholi* (Tassy 1985). No D3 of *Z. turicensis* from Elgg is available for comparison.

d4 (Fig. 2g–k): Eight almost complete and five fragmentary portions of d4 in different stages of wear are

present. Most of the specimens vary in a similar size range (Fig. 3), except for two (393, 11327) which are distinctly smaller (about 20% shorter than the biggest d4). Crown trilophodont with anteroposteriorly slender lophids and relatively weak and low conules; first lophid labiolingually narrower with a labial constriction between 1st and 2nd lophid; lophids oblique and more or less straight, 3rd lophid straight or posteriorly concave; pretrite half-lophids composed of mostly two cusps, posttrite half-lophids with two to four small peaks; pretrite conules relatively weak, comprising serrated spurs; weak posttrite conule (serrated spur) in some specimens (e.g. 11317a+b, 443) on posterior flank of 1st lophid; in specimen 443 weak posttrite serrated spur also on 2nd and 3rd lophid; anterior and posterior cingulum serrated; anterior conule of 1st lophid joining the anterior cingulum; valleys barely blocked and relatively wide; two splayed roots.

The d4 of *G. subtapiroideum* from Sandelzhausen are relatively wider than those of *G. angustidens*, and are smaller than those of *Z. turicensis* (Fig. 3). Two specimens (11328 and 392) from Sandelzhausen show a diagonal contact between the posterior pretrite conule of the 1st lophid and the anterior posttrite conule of the 2nd lophid, as described already above for the d3 of *G. angustidens*

(Tassy 1985). This contact can also be observed in some d4 specimens of *G. angustidens* (e.g. MNHM Si 6) and in *Z. turicensis* (e.g. MNHN Si 11), both from Simorre, France (MN6). A tooththrow of *G. angustidens* (MNHN Si 6) from Simorre shows this contact in both d3 and d4, but it seems to be a variable feature, because other specimens of *G. angustidens* from Simorre (e.g. MNHN Si 5 and 9) lack this contact in d4 and/or d3. However, it has not been observed in d3 or d4 of *A. filholi*, and therefore was supposed to be a distinguishing character of *G. angustidens* (Tassy 1985). In the Sandelzhausen material this feature is developed in two of eight d4, but in none of seven d3. These two specimens show no other distinguishing characters and fall in the middle of the size range of all other d4 from Sandelzhausen. Therefore, this feature is presumed to also be variable in *G. subtapiroideum*. Such a diagonal contact is developed in one D4 specimen (see below), also.

D4 (Fig. 4g–i): Eight almost complete and four fragmentary specimens in different stages of wear are present. Crown trilophodont with anteroposteriorly compressed lophs and relatively weak, low pretrite conules; anterior pretrite conules stronger than posterior ones; crown broadening behind first loph; in unworn teeth pretrite half-lophs made up by three to five conelets; posttrite half-loph (1st and 2nd loph) with strong and high maincusp and one small and low mesoconelet, 3rd loph with more small mesoconelets; most specimens with strong lingual cingulum; valleys wide and barely blocked; three-rooted. Several specimens (11886, 11323, 11322, 11320 and 11325)—especially when unworn—show generally weak posttrite “zygodont-crests” predominantly at the posterior flanks of the 1st and 2nd lophs.

In specimen 11886, the 1st loph lacks a posterior conule, but instead the medial conelet of the posttrite 1st half-loph carries a posterior serrated spur, which contacts the anterior conule of the 2nd pretrite half-loph; such a diagonal contact is also developed in two d4 and is interpreted to be occasional in *G. subtapiroideum* of Sandelzhausen (see above).

In size, the D4 correspond well with those of *G. subtapiroideum* from the type locality Vordersdorf near Eibiswald (Austria) and are smaller than the scanty represented *Z. turicensis* (Fig. 3). The D4 of both *G. subtapiroideum* and *Z. turicensis* are wider than those of *G. angustidens* from Simorre and En Péljouan and of *A. filholi*. The D4 of the latter are also longer. The kind of “zygodont-crest”-like structures in some unworn specimens from Sandelzhausen are also observable, e.g. in a D4 of Simorre (MNHN Si 4).

Premolars

For measurements of the premolars see Table 2.

p3 (Fig. 5b, c): Three specimens are represented, which greatly differ in size—two small-sized (387 and 11647)

Table 2 Measurements (in mm) of lower and upper premolars of *G. subtapiroideum* and *Z. turicensis* from Sandelzhausen

Inventory number BSPG	L	B	B/L-index
<i>Z. turicensis</i>			
p3			
1959 II 11342	30	20.5	0.71
<i>G. angustidens</i>			
p3			
1959 II 387 (p2?)	20	16	0.80
1959 II 11647 (p2?)	20	14.5	0.73
1959 II 447	(30)	22.5	(0.65)
P3			
1959 II 449 (P2?)	30	22	0.73
1959 II 450	40	33	0.83
1959 II 11336	39	28.5	0.73
1959 II 11337	36	27	0.75
1959 II 11339	(34)	30	(0.88)
1959 II 11341	(32)	29	(0.78)
1959 II 11340	32	25	0.88
1959 II 11343	(30)	–	–
1959 II 11338	–	(33)	–
1959 II 16207	–	(26.5)	–
p4			
1959 II 7939	39.5	29.5	0.75
1959 II 11349	42	31	0.75
1959 II 11360	40.5	30	0.74
1959 II 16200	(43)	(31)	(0.72)
P4			
1959 II 385	41.5	35.5	0.86
1959 II 11344	46	42	0.91
1959 II 11345	48	43	0.90
1959 II 11346	(>42)	37	(0.88)
1959 II 11347	(43)	(32)	(0.84)
1959 II 11348	41	35.5	0.87

L, length; B, width

Measurements in parentheses indicate estimated measurements of slightly damaged or very worn specimens

and one specimen about one third larger (447) (Fig. 6). All of them slightly damaged at posterior end; 477 and 387 worn; 11647 is fluviatilly abraded.

Crown shape oval to ovoid; blunt protoconid and metaconid, attached to each other but still separated by median sulcus; protoconid and metaconid higher than more or less strong hypoconid and entoconid; protoconid and hypoconid, and metaconid and entoconid connected by two longitudinal, almost parallel, blunt crenelated crests; longitudinal valley between crests narrow; in small sized p3 (387), hypoconid and entoconid more individualized from

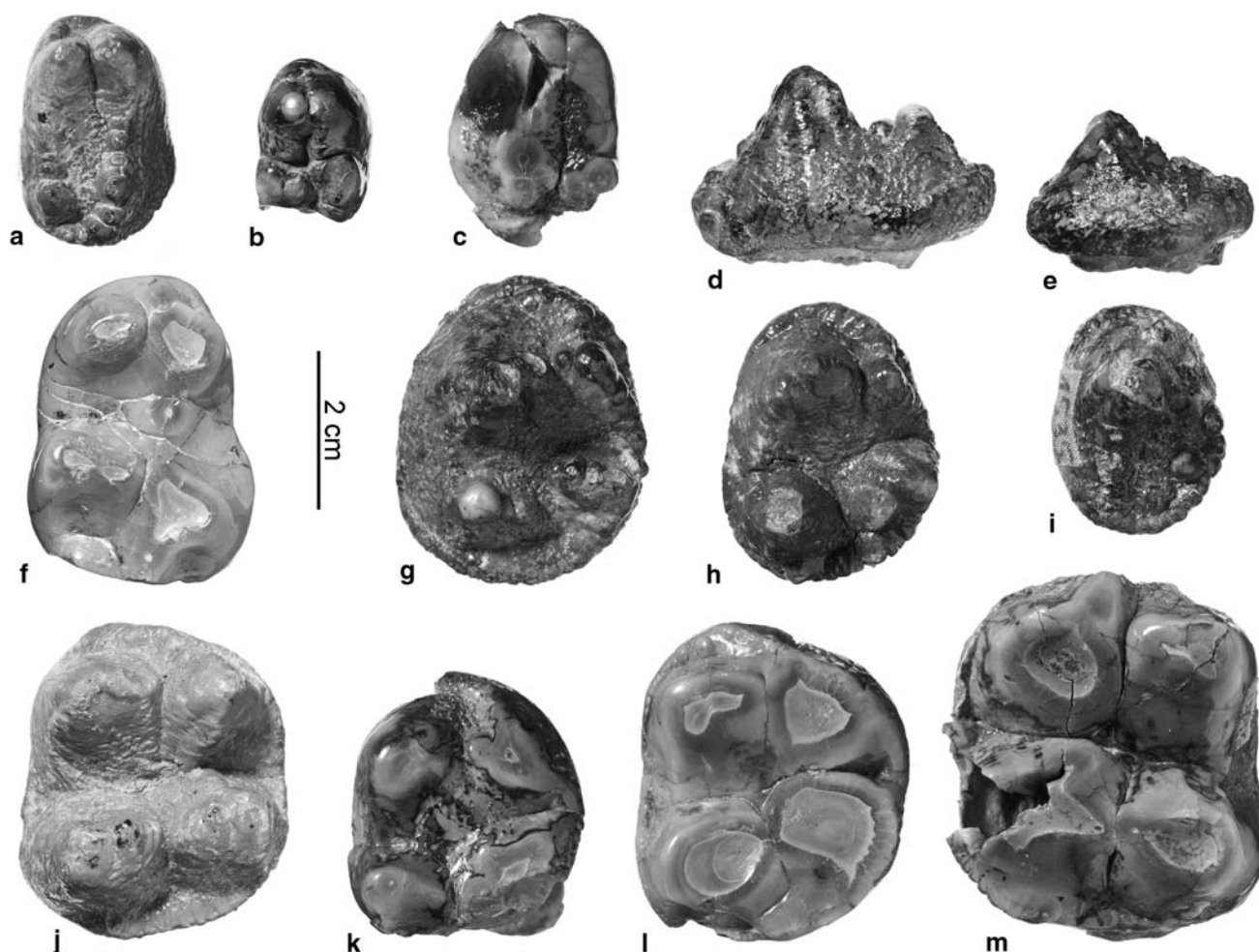


Fig. 5 Lower and upper premolars of *Gomphotherium subtapiroideum* (Schlesinger, 1917) (**b–m**) and *Zygolophodon turicensis* (Schinz, 1824) (**a**) from Sandelzhausen (Invent. no. BSPG 1959 II ...). **a** p3 dext. (11342); **b** p3 (p2?) dext. (387); **c** p3 sin. (447); **d**, **h** P3 dext.

(11337); **e**, **i** P3 (P2?) dext. (449); **f** p4 dext. (7939); **g** P3 dext. (450); **j** P4 dext. (385); **k** P4 dext. (11339); **l** P4 dext. (11348); **m** P4 sin. (11344). **a–c**, **f–m**: occlusal view; **d**, **e**: labial view

crests by sulci; main parts of posterior cingulum broken off; 387 with low, knob-like, anterior cingulum at base of anterior end.

The small sized p3 (387) was identified as D2 by Schmidt-Kittler (1972, pl. 5 fig. 2), but does not correspond with the crown morphology of this tooth position. Remarkable is the enormous size difference of the represented p3. It is not certain whether this is because of size variability (including sexual dimorphism) or if the small p3 might represent another tooth position—namely p2—but which is not known so far to be developed in any *Gomphotherium*, *Zygolophodon*, or *Archaeobelodon*. Support for the first hypothesis is found in the fact that the p3 of *G. angustidens* and *A. filholi* also exhibit a large variation in size (Fig. 6 and Tassy 1985: 588). Based on the similarity in morphology, the small-sized teeth (387 and 11647) are provisionally attributed to p3. However, it cannot be ruled out if a development of a p2 might be possible or typical for *G. subtapiroideum*. Only new findings of such a

small sized tooth in the tooth row will allow a definitive answer to this question.

The bunodont habitus of the crown structure of the p3 differs from the more gracile morphology of the p3 in *Z. turicensis* (see *Z. turicensis* (11342) below), in which the longitudinal crests are lower and more slender—more delicate, and the hypoconid and entoconid are much weaker. The p3 of *G. angustidens* from En Pélouan differs from that of *G. subtapiroideum* from Sandelzhausen by a totally fused metaconid and protoconid; there is no trace of even a median furrow (Tassy 1985: 588). The p3 of *A. filholi* from Bézian, described by Tassy (1985: 588), seems not to differ very much from that of Sandelzhausen. However, the crown of the p3 of *A. filholi* seems to be a little narrower. Because neither taxon has many p3 the variability of both morphology and size cannot be adequately estimated.

P3 (Fig. 5d, g, h): Eight specimens are present; an additional one (449) differs in morphology and is only

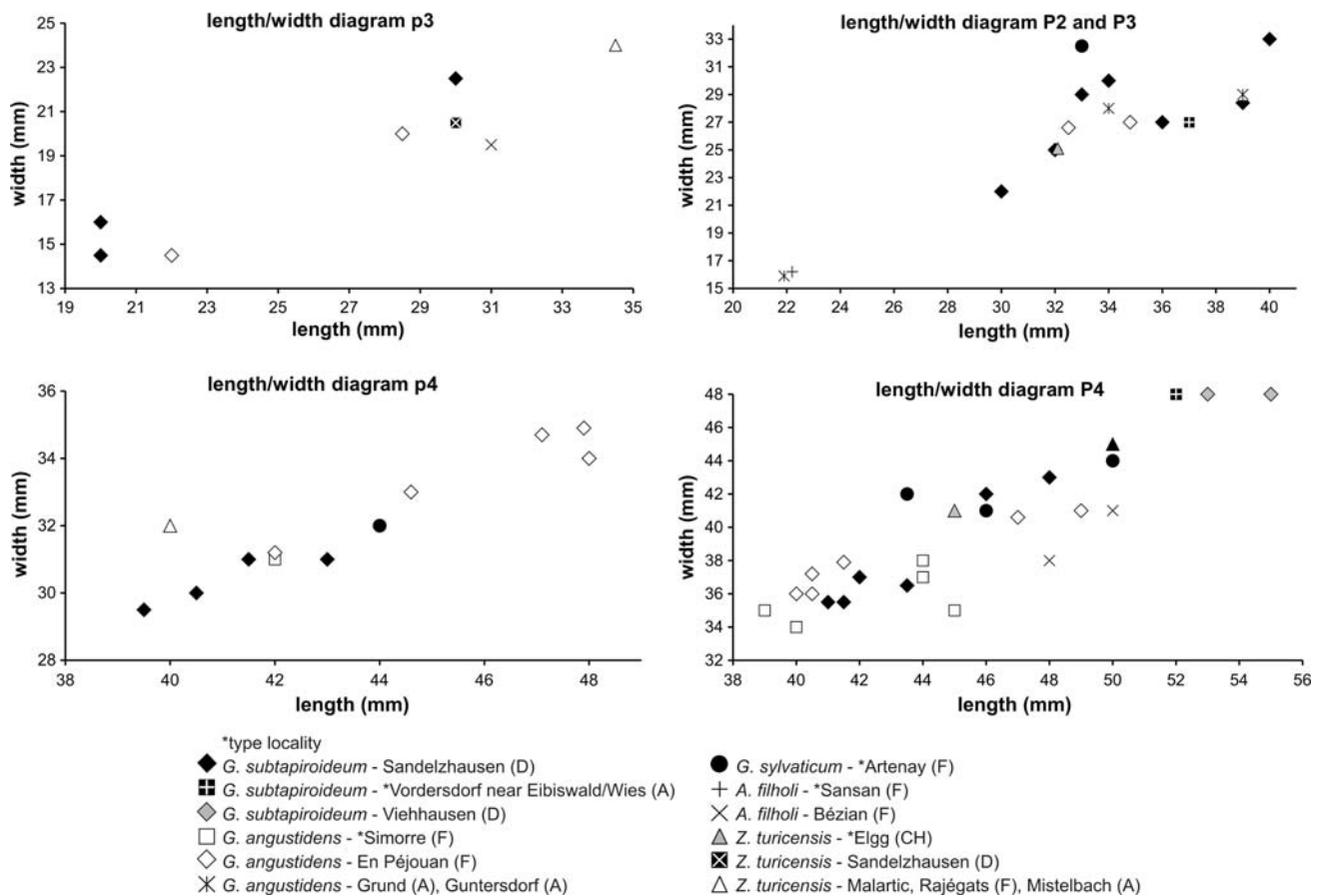


Fig. 6 Scatter diagram (length and width of teeth) of the lower and upper premolars of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhausen in comparison with *G. subtapiroideum*, *G.*

angustidens, *G. sylvaticum*, *Archaeobelodon filholi*, and *Zygolophodon turicensis* from different Early to Middle Miocene European localities

tentatively assigned as P3 (Fig. 5e, i). The crown morphology of P3 is best preserved in 450, 11336, and 11337; the other specimens are worn and/or more or less damaged. Crown of ovoid shape, made up of four main cusps; paracone strongest and highest cone, undivided (450, 11338) or divided into more than one cusp (11336, 11337); metacone second strongest cone, undivided (11337) or divided and with serrated bulges in varying directions (450, 11336, 11338), posterior bulge often merging with posterior cingulum; protocone weakest cone, mostly with anterior and lingual serrated bulges that fuse with anterior and lingual crenulated cingulum; hypocone made up of a variable number and composition of small cusps.

Unworn teeth show a high morphological variability concerning the composition of each main cone. Size comparisons of the Sandelzhausen material with the few known P3 of *Z. turicensis*, *G. subtapiroideum*, and *G. angustidens* (following Tassy 1985, a specimen from Grund (Austria) might be a P3 of *A. filholi*) overlap metrically among these taxa. A single P3 from Artenay identified by Tassy (1985) as belonging to *G. sylvaticum* seems to be

relatively wider. The degree of intraspecific morphological and metrical variability hinders any discussion on morphological differences between the different taxa or diagnostic features.

Specimen 449 (Fig. 5e, i) differs from all other compared P3 specimens by the suppression of the metacone and a very weak hypocone and thus is only tentatively assigned as P3. Instead of a metacone a series of small cusps run from the paracone backwards and fuse with the posterior cingulum. In addition, this tooth is somewhat smaller than all other compared P3 (Fig. 6). On the other hand, all other represented premolar positions also show remarkable variability in size. However, the morphological deviation, especially, gives rise to the question if specimen 449 might represent another tooth position than P3, namely D2, P2, or p2. Specimen 449 falls in the size range of the D2 (Fig. 3), but differs again by the suppressed metacone and hypocone and the shape of the outline (in occlusal view). The development of a p2 is totally unknown so far for any European proboscidean taxon and the P2 are only rarely represented and not known for all European Miocene

taxa. However, the taxa *Z. turicensis*, *A. filholi*, and *G. angustidens* are known to develop at least occasionally a P2. Unfortunately, the size and morphology of the P2 of *Z. turicensis* is unknown, as its existence is only proven by empty alveols in front of a toothrow in a maxilla portion (see Tassy 1985, fig. 190). The P2 of *A. filholi* from Sansan (Tassy 1985, fig. 241) differs morphologically by a central cone (paracone) surrounded by a ring of small protuberances. A P2 of *G. angustidens* from Guntersdorf near Grund (Austria) (Schlesinger 1917, pl. II, fig. 3; Huttunen 2003) (following Tassy 1985, this specimen might belong to *A. filholi*) is made up of a dominating paracone and a number of smaller cones in the posterior half of the tooth. Although there is some resemblance with the morphology with 449, the latter is much larger (Fig. 6). Thus, the determination of specimen 449 to be either a somewhat aberrant P2 or P3 cannot be decided at the moment; in both cases intraspecific variability could be an explanation for the somewhat deviating morphology and size.

p4 (Fig. 5f): Four p4 are preserved, three of them slightly worn, one (16200) totally worn down. Crown bilophid, with pyriform outline; posterior lophid diagonal from lingual anterior to labial posterior; because only worn specimens are known nothing can be said about the number of mesoconelets in each half-lophid; pretrite conule in interlophid worn, but was probably not very strong or high; posterior pretrite conule of 1st and 2nd lophid stronger than anterior one of 2nd lophid; no traces of posttrite conules; two-rooted.

The p4 of *G. subtapiroideum* from Sandelzhausen are relatively small sized (Fig. 6) and tend to be smaller than the comparative material of *G. sylvaticum* and *G. angustidens*, even with a small dimensional overlapping with the latter. They also differ from the p4 of *Z. turicensis* from Mistelbach (Lower Austria, Schlesinger 1917, pl. 21 fig. 3) in being distinctly narrower and in having a stronger pretrite conule, which is very weak in *Z. turicensis*. Morphologically, the p4 from Sandelzhausen seem not to differ clearly from those of *G. angustidens* or *G. sylvaticum*. No comparative material of p4 is known so far for *G. subtapiroideum* from its type locality Eibiswald, or for *A. filholi*.

P4 (Fig. 5j–m): Six P4 are present, of which only one (385) is unworn. Crown bilophid, with an approximate quadrangular outline; well developed cingulum anterior, posterior, lingual, and in some cases labial in the valley; wear pattern indicates anterior pretrite conule on 2nd loph in three specimens (11344, 11345, 11346), which is very weakly developed in germ 385 and absent in 11347 and 11348; in the last two, pretrite interlophid narrow; though worn down, the wear patterns show no evidence of any posttrite conules. P4 in general three-rooted, but splitting of roots variable also intra-individual; in 11344 root splits into

three 2 cm below the crown base, whereas in 11345 posterolingual root undivided as far as root is preserved—3.5 cm below the crown base.

Metrical comparisons (Fig. 6) of the P4 from Sandelzhausen reveal a dimensional overlap with those of *G. angustidens*, *G. sylvaticum*, and *Z. turicensis*. Two P4 from Bézian attributed by Tassy 1985 to *A. filholi* seem to be somewhat more slender than those of the mentioned taxa and of *G. subtapiroideum* from Sandelzhausen. However, the P4 from Sandelzhausen are distinctly smaller than a P4 of *G. subtapiroideum* from Eibiswald (in Bach 1910, pl. 8 fig. 4, 4a determined as *G. angustidens*) and the two large P4 from Viehhausen (Germany, MN6) attributed to *Serridentinus subtapiroidea* by Rinnert 1956. Again, this is indicative of wide metric variability for the taxon *G. subtapiroideum*. The large specimens of P4 from Eibiswald and Viehhausen fall in the size range of tetralophodont gomphotheres (e.g., of the Late Miocene Dinotheriensands in Germany). Unfortunately, the P4 from Viehhausen are deeply worn down and thus lack most morphological information. Tassy (1985: 587) describes the P4 of *A. filholi* as more complex, with posttrite conules, than those of *G. angustidens*. The stage of wear of most P4 from Sandelzhausen hinders detailed morphological information; no posttrite conules are visible, but might have disappeared by progressive attrition. The germ (385) is characterized by multi-pointed, slender lophs and very weak, crenelated conules and thus shows an almost “zygodont” habitus. It is unclear whether its more gracile habitus is due to variability, to the fact that it is a germ, or if this tooth might belong to *Zygodontodon*. However it plots perfectly with the other P4 of Sandelzhausen and is smaller than those of *Zygodontodon* (Fig. 6).

Molars

For measurements of the molars see Table 3.

The intermediate molars (m/M1, m/M2) of the Sandelzhausen fauna also demonstrate a large variability in size, which brings small sized second molars (e.g. 384) into the size range of large first molars (and the converse), thus sometimes hampering identification of isolated intermediate molars.

m1 and m2 (Figs. 7a–c, f, 8a, e): Five m1 (from five individuals) and 14 m2 (from a maximum of 12 individuals) are represented. The following description is mainly based on two unworn specimens of m1 (42, 439) and two slightly worn m2 of individual 11360; all other specimens are too much worn, damaged or too fragmentary to dispose morphological details. Crown trilophodont; lophids anteroposteriorly compressed and slightly oblique transversally; 3rd lophid in weak chevron position; posttrite half-lophids made up by three (to four) conelets, pretrite half-

Table 3 Measurements (in mm) of molars of *G. subtapiroideum* from Sandelzhausen

Inventory number BSPG	L	B	B I	B II	B III	BIV	B/L-index
m1							
1959 II 439	76	44.5	38	42.5	44.5		0.58
1959 II 453	(65)	44	—	—	—		(0.68)
1959 II 42	65	41	32.5	40	39.5		0.63
1959 II 11360							
1959 II 11360	63.5	41	34	39	40.5		0.65
M1							
1959 II 440	85.5	58	52	56	57		0.69
1959 II 11351	(72)	(47)	—	—	—		(0.65)
1959 II 11352	73	55	49	55	(54)		0.75
1959 II 11353	73	(53)	—	—	(50)		(0.73)
1959 II 11354	74	—	—	—	—		—
1959 II 11355	—	50	—	—	—		—
1959 II 11356	—	—	51	51	—		—
1959 II 11357	—	(53.5)	—	52	53.5		—
1959 II 11358	—	(49)	—	—	(49)		—
1959 II 11359	—	—	—	(46)	—		—
1959 II 16208	—	—	—	—	—		—
m2							
1959 II 384	84	54	43	51	54		0.64
1959 II 384	83	53	42	50	53		0.64
1959 II 11360	90	53	43	46.5	53		0.59
1959 II 11360	91	52	42.5	46	52		0.57
1959 II 11374	(>91)	(61)	—	—	61		(0.67)
1959 II 11376	104	62	—	56	62		0.60
1959 II 11377	(107)	(61)	—	56	(61)		(0.57)
1959 II 11378	(112)	(64)	—	59.5	—		(0.57)
1959 II 11362	(80)	(50)	—	—	—		(0.63)
1959 II 11379	—	63	—	58	63		—
1959 II 11370	—	—	—	—	53		—
1959 II 11375	—	—	—	—	(62)		—
1959 II 11361	—	—	—	48	(>52)		—
1959 II 11382	(73)	—	—	—	—		—
M2							
1959 II 438	109	65	63	65	—		0.60
1959 II 384	87	59	55	60	56		0.68
1959 II 11364	95	(65)	—	(65)	(65)		(0.68)
1959 II 11365	98	57	(52)	(57)	(57)		0.58
1959 II 11366	(98)	(65)	—	—	—		(0.66)
1959 II 11367	(91)	59.5	—	(57)	(58)		(0.65)
1959 II 11368	113	68	63	68	66		0.60
1959 II 11369	—	—	63	65	—		—
m3							
1959 II 384	132	60	52	59	59.5	48	0.46
1959 II 3723	(150)	73	66	74	74	64	(0.49)
1959 II 11383	152	74	64	74.5	73	58.5	0.49
1959 II 11381	161	74	69	74	71.5	59	0.46

Table 3 continued

Inventory number BSPG	L	B	B I	B II	B III	BIV	B/L-index
1959 II 11385	155	79	77.5	79	79	67	0.51
1959 II 11382	131	63	55	63	62.5	50	0.48
1959 II 11384	133	62	57	62	61	49	0.47
1959 II 11386	–	–	–	70.5	69.5	55.5	–
1959 II 11388	–	–	–	–	–	57	–
1959 II 11360	–	–	–	–	50	37	–
1959 II 11390	–	–	–	–	48	32	–
1959 II 11391	–	–	–	–	–	–	–
1959 II 415	–	–	–	–	–	–	–
1959 II 416	–	–	–	71	72	64	–
M3							
1959 II 384	128	67	62.5	66	62.5	41	0.52
1959 II 3722	127.5	76	–	76	67	–	0.60
1959 II 4783	137	75.5	73.5	75.5	68	–	0.55
1959 II 11380	(123)	(70)	–	–	–	–	(0.51)
1959 II 11389	–	–	–	–	–	–	–

L, length; B, width; B I–IV, width at 1st, 2nd, 3rd, 4th loph(id)

Measurements in parentheses indicate estimated measurements of slightly damaged or very worn specimens

lophids by predominantly two conelets; pretrite conules of moderate size, anterior conules attached to median-most pretrite mesoconelet, posterior ones to labial main cone; anterior conules more or less single conules, posterior ones composed of crenelated bulges (crescentoids) and small conules at their bases; pretrite conules on 3rd lophid weak (anterior) to absent (posterior); within each lophid, anterior conules slightly stronger (higher) than posterior ones; valleys only blocked at their bases; no posttrite conules developed, but posterior flank of 1st posttrite half-lophid can carry some irregular swellings (42); anterior and posterior cingulum low and crenelated; two-rooted. One m2 (11361) shows an anomaly insofar as the 3rd lophid is much more deeply worn than the 2nd lophid, which might result from a defective position in the jaw.

The anteroposteriorly compressed lophids, composed of several conelets (posttrite), and the moderate to weak conules/crescentoids form the subtapiroid construction of the molars.

Both m1 and m2 of *G. subtapiroideum* from Sandelzhausen show a large variation in size—especially in length (m1: min. 63.5 mm—max. 76 mm; m2: min. 80 mm—max. 112 mm) (Fig. 9), but which is detectable for other taxa (e.g. *G. angustidens*; Fig. 9) also. Sexual dimorphism might be represented by two clusters in the scatter diagrams of the m1 and m2 of *G. subtapiroideum* from Sandelzhausen (Fig. 9).

Concerning size, the intermediate molars of *G. subtapiroideum* from Sandelzhausen coincide with those of *G. angustidens* from Simorre and En Pélouan (both

France); however, most m1 are smaller than those of *G. angustidens*.

Also, morphologically they are difficult to distinguish. *Gomphotherium subtapiroideum* differs by a more subtapiroid crown structure, which is apparent from weaker conules, a higher number of posttrite conelets and slightly wider valleys. But most of these characters disappear with attrition. Also, there are no distinctive morphological differences from *G. sylvaticum*. However, the m1 of *G. subtapiroideum* are narrower than those of *G. sylvaticum*, whereas the large sized m2 of *G. subtapiroideum* from Sandelzhausen partially overlap in length with those of *G. sylvaticum* (Fig. 9). No measurements of the m1 of *A. filholi* are available for comparison, but the m2 in that taxon are slightly longer than in *G. subtapiroideum* from Sandelzhausen. According to Tassy (1985: 592), the lower intermediate molars of *A. filholi* often show posttrite conules anterior to the 2nd and 3rd lophid, but these conules are absent in *G. subtapiroideum* from Sandelzhausen. Both m1 and m2 of *G. subtapiroideum* from Sandelzhausen are smaller and/or narrower than those of *Z. turicensis*. Remarkably, the m2 of *G. subtapiroideum* from Sandelzhausen are smaller (Fig. 9) than those from the type locality Eibiswald (NHMW-M.S.-127 and m2 in Vacek 1877, pl.4 fig. 2 (det. as *G. angustidens*)). The m2 of “*T. ratibonensis*” from Viehhausen falls in the size range of *G. subtapiroideum* from Sandelzhausen, but the tooth is too much worn for any morphological information. An additional, worn m2 from Viehhausen (213d), attributed by Rinnert (1956) to *Serridentinus subtapiroideus*, is larger than those from

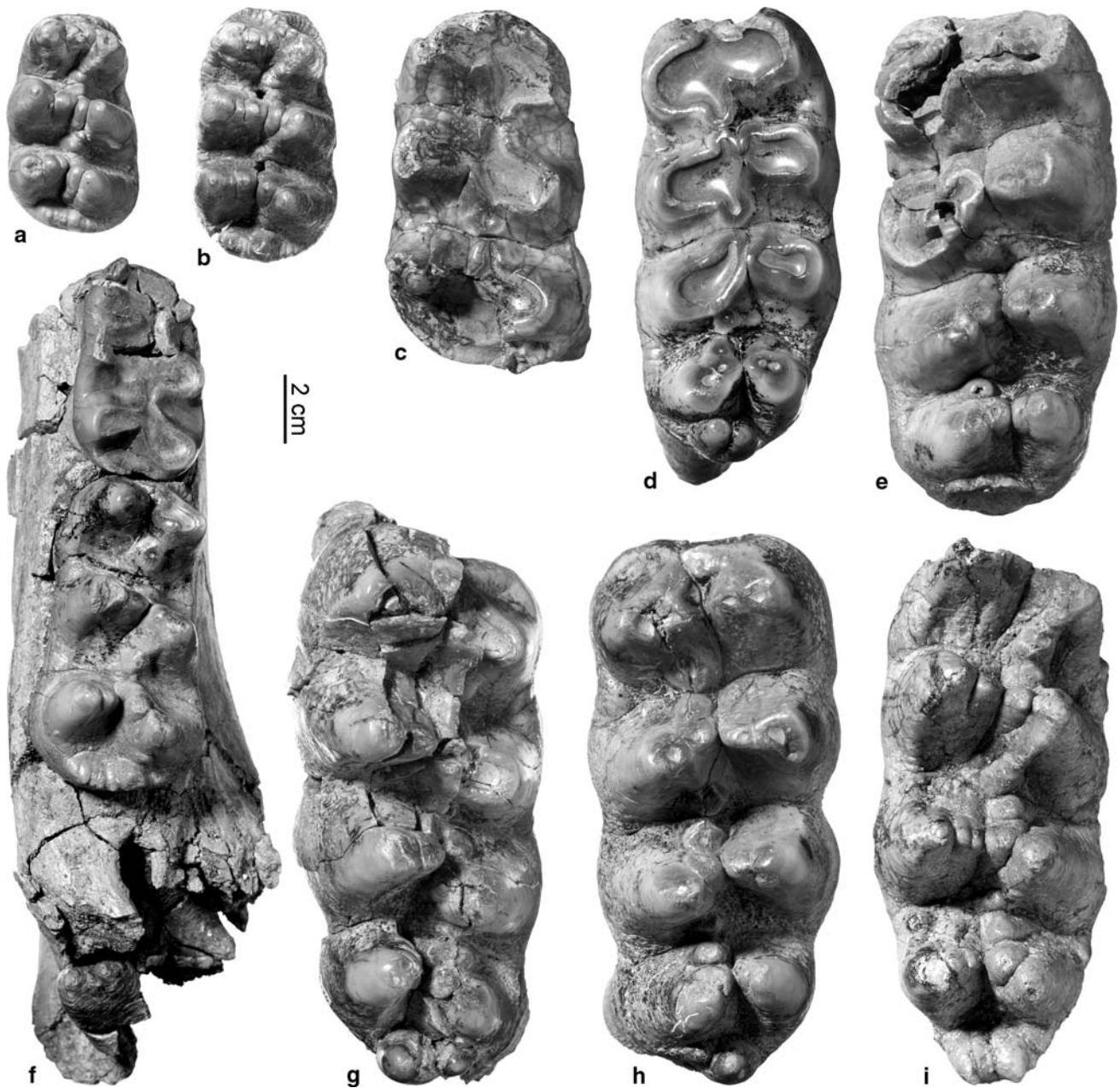


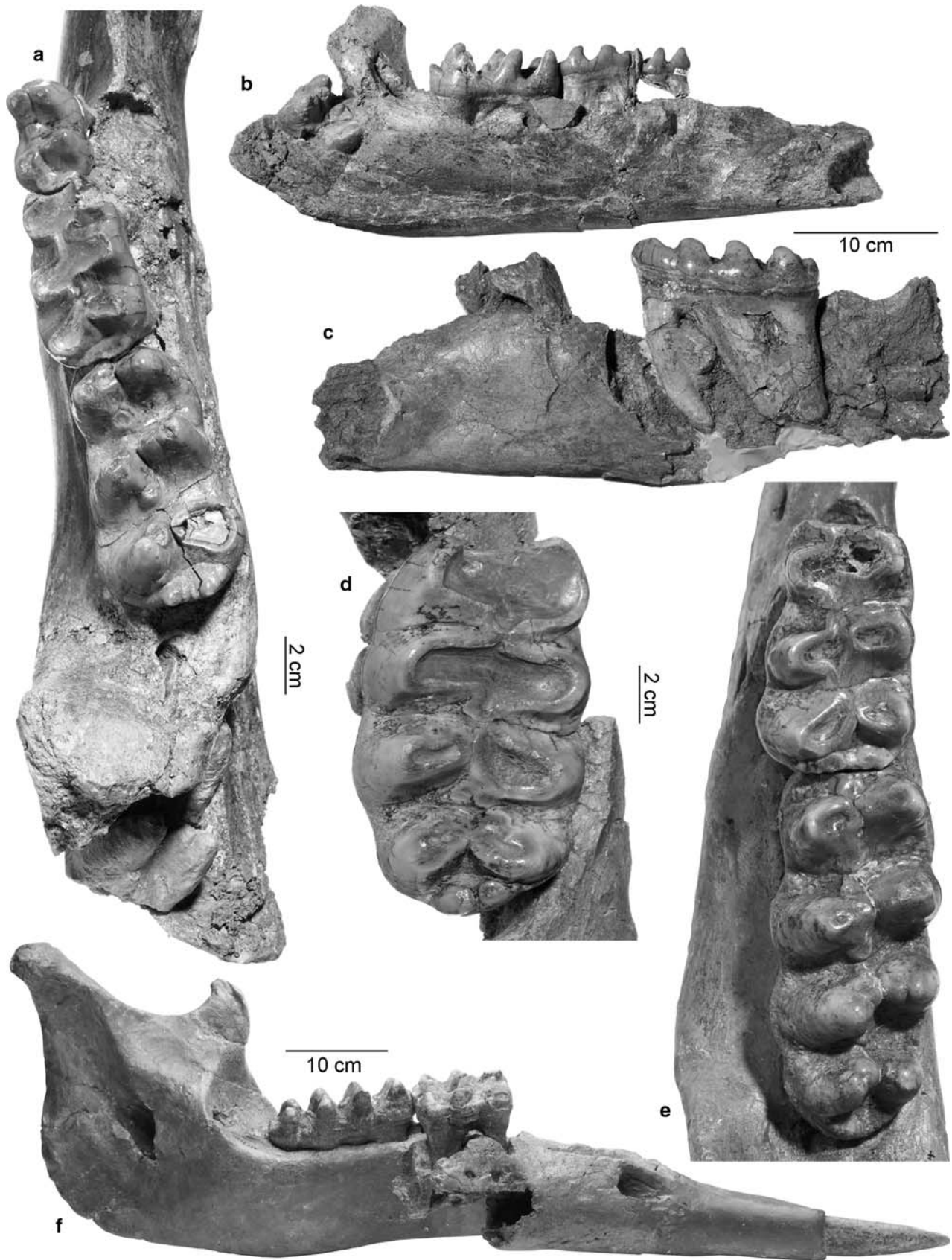
Fig. 7 Lower molars (m1–m3) of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhausen (Invent. no. BSPG 1959 II ...). **a** m1 dext. (42); **b** m1 dext. (439); **c** m2 dext. (11376); **d** m3 sin.

(11384); **e** m3 sin. (3723); **f** ramus of right mandible with m1–m2 dext. (11387); **g** m3 dext. (11385); **h** m3 sin. (11381); **i** m3 dext. (11386). All in occlusal view

Sandelzhausen and Eibiswald, but has weak posttrite anterior conules, which suggests it belongs to *A. filholi* (following Tassy 1985: 592), to which it is also close in dimensions (Fig. 9).

M1 and M2 (Fig. 10a–c, f): 11 M1 (from a maximum of nine individuals) and eight M2 (from eight individuals) are preserved, most of which are very worn and/or fragmentary. The following description of the crown morphology is mainly based on unworn or slightly worn specimens (M1: 11354–5, 11356, 11351; M2: 440, 11368).

Crown trilophodont; pretrite half-lophs made up by a dominating, large main cusp and one or two small to tiny conelets; posttrite half-lophs consisting of three to five conelets; pretrite conules present at all three lochs and always attached to the maincusp; anterior pretrite conules made up by a single cusp, only sometimes divided into two cusps; posterior pretrite conule mostly developed as a crenulated bulge, weak at 1st loph and mostly suppressed at the 3rd loph; anterior pretrite conules stronger and higher



◀ **Fig. 8** Mandibles and mandible fragments with lower dentition of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhhausen (Invent. no. BSPG 1959 II ...). **a, b** ramus of left mandible with p4–m2 and portion of m3 in posterior alveole (11360), **a** close up in occlusal view on p4–m2 sin., **b** medial view on preserved mandible ramus; **c, d** ramus of right mandible with m3 and roots of m2 (11382), **c** close up in occlusal view of m3 dext., **d** medial view of preserved mandible ramus; **e, f** left mandible (partly restored) with m2–m3 and i2 (384), **e** close up in occlusal view of m2–m3 sin., **f** medial view of mandible including largely restored symphysis and lower tusks

than posterior ones of same loph; anterior pretrite conule of 3rd loph in some specimens (M1: 11352+3, 11354+5, 11357, M2: 440, 11368) doubled (bifurcate anterior trefoil); no posttrite conules; posttrite half-lophs often with slender vertical serrated bulges on labial edge of anterior and posterior slopes (M1: 11355, 11356, 11358; M2: 440, 11368, 438, 11369); pretrite and posttrite halves of each loph placed in straight line, only in 3rd loph often shifted or in slight chevron position; valleys mostly quite wide, sometimes moderately wide (M1: 11354+5, 16208); all valleys blocked but usually at a low level; all lophs slightly inclined towards anterior, anterior flanks straight or slightly concave; robust anterior, labial, and posterior serrated cingulum; three-parted root.

Metric comparisons (Fig. 9) for M1 and M2 indicate no clear taxonomic differentiation for most of the considered trilophodont taxa. *G. subtapiroideum* from Sandelzhhausen falls in the size range of *G. angustidens* and overlaps with “*T. ratibonensis*” and largely with *G. sylvaticum*. It also overlaps with some small sized specimens of *Z. turicensis*. M1 and M2 of *G. subtapiroideum* are, in general, smaller than those of *A. filholi*; there is only a marginal dimensional overlap with some large sized (male?) individuals of *G. subtapiroideum*. All specimens of *G. subtapiroideum* from the type locality Eibiswald fall in the size range of the larger sized individuals from Sandelzhhausen. Within the Sandelzhhausen material one M2 (of maxillary tooth row 384) is so small sized that it is close to the size range of the M1. On the other hand, one isolated intermediate molar (440), which is interpreted as a large sized M1, is just slightly smaller than the smallest M2. This large size variation, often in two clusters, which sometimes hampers definite identifications of isolated intermediate molars, is interpreted as a sexual dimorphism, which was also suggested by Tassy (1985, 1996c) for *G. angustidens* from En Pélouan.

Morphologically, the intermediate molars of most trilophodont gomphotheres and even mammutids are hard to distinguish, especially when isolated and attrited. Several M1 and M2 of *G. subtapiroideum* from Sandelzhhausen exhibit at least tendencies of posttrite zygodont crests. However, the pretrite conules are—even if mostly weaker than in *G. angustidens* and *A. filholi*—stronger than in

Zygodontodon. Additionally, the 3rd loph in M1 and M2 from Sandelzhhausen often is in more or less chevron arrangement, whereas it is mostly linear in *Zygodontodon*. In contrast to *A. filholi*, the M1 and M2 from Sandelzhhausen are less bunodont and lack posttrite conules. Even if the morphology of M1 and M2 of *G. angustidens* and *G. subtapiroideum* can be very similar, in general the latter is often more “subtapiroid” by more posttrite mesoconelets per loph, by slightly anteroposteriorly compressed lophs, by weaker pretrite conules and slightly wider valleys. The M1 attributed to “*T. ratibonensis*” is totally worn down and allows no morphological comparisons, the M2 which are at least slightly worn show no apparent difference to those from Sandelzhhausen, neither do so the M2 from Viehhausen attributed by Rinnert (1956) to *S. subtapiroideum*. However, the latter are larger than *G. subtapiroideum* from both Sandelzhhausen and Eibiswald. The M2 of *G. sylvaticum* from Artenay resembles the Sandelzhhausen molars insofar as they are simple and bunodont, with wider valleys and relatively weak pretrite central conules; however, they seem to show no evidence of posttrite zygodont crests.

m3 (Figs. 7d, e, g–i, 8d, e): Eight more or less complete and seven fragmentary m3 from a maximum of 11 individuals are preserved. Most of the m3 are moderately to strongly worn, only 11386 and 384 are unworn or slightly worn, respectively. Crown with four lophids plus a small talonid of two to three lower cusps; lophids slightly oblique and somewhat anteroposteriorly compressed; pretrite half-lophids made up by a main cusp and one smaller mesoconelet; posttrite half-lophids consisting of one main cusp and one to two smaller mesoconelets; anterior and posterior pretrite conules moderately developed and present on anterior three lophids, posterior conule on 3rd lophid very weak; 4th lophid only with anterior conule, posterior one lacking; anterior pretrite conules attached to conelet and stronger than posterior ones (attached to main cusp) of same lophid; no distinct posttrite conules, but sometimes very weak one anterior on 4th posttrite lophid (11386, 416, 11384) and/or posterior one on 1st lophid (11384, 3723); only 11384 with an additional small anterior posttrite conule on 2nd lophid; m3 two rooted.

The m3 of *G. subtapiroideum* from Sandelzhhausen exhibit again a bimodal size distribution that probably indicates sexual dimorphism (Fig. 9). The m3 of *G. subtapiroideum* are slightly broader than those of *G. angustidens* from Simorre and En Pélouan, distinctly broader than *A. filholi* (but which is represented only by one individual), and are shorter and broader than *G. sylvaticum* from Artenay. The large m3 individuals from Sandelzhhausen partially overlap with those of *G. subtapiroideum* from Eibiswald and with “*T. ratibonensis*” from Viehhausen, but also overlap with only the small sized representatives

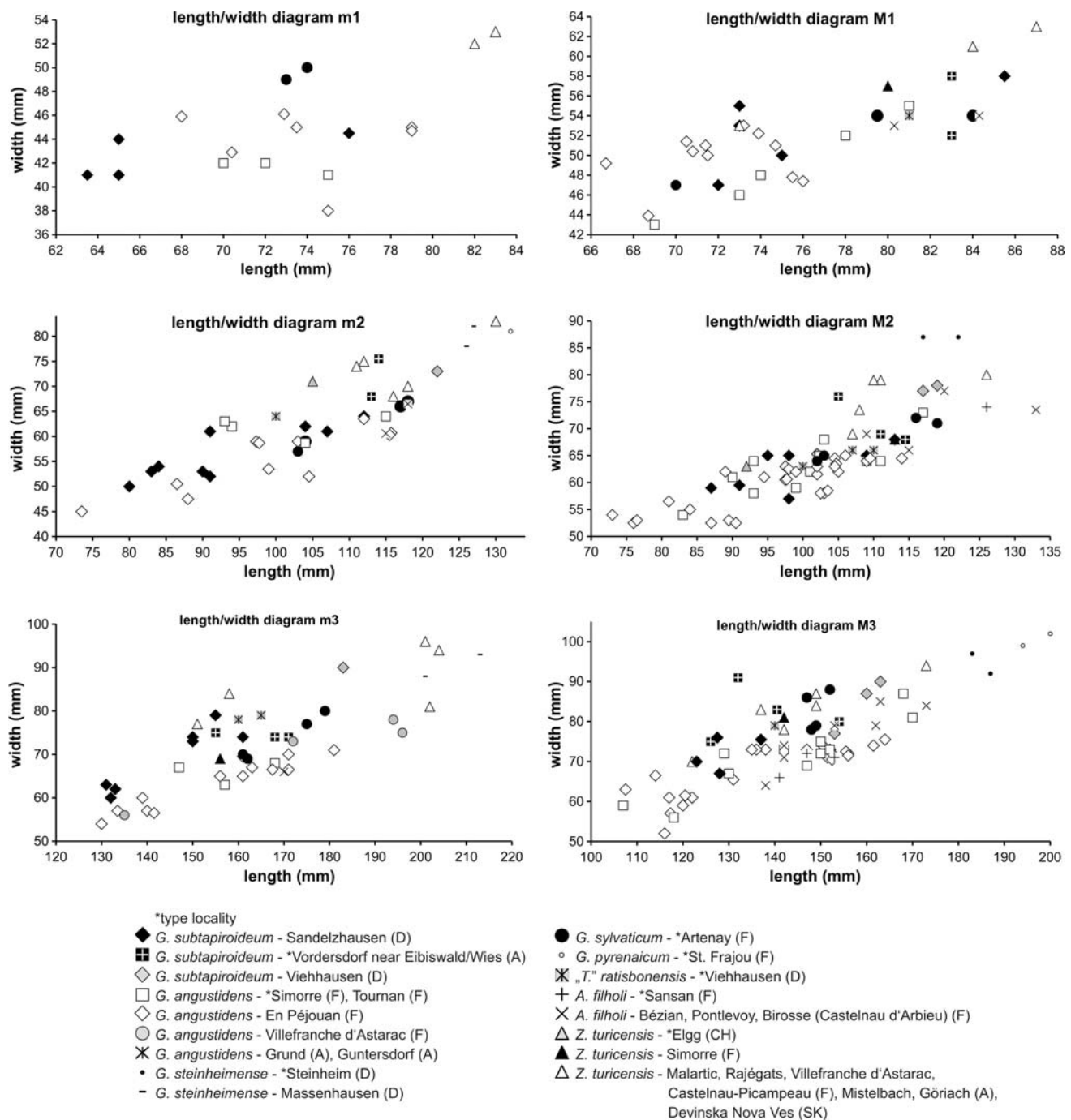


Fig. 9 Scatter diagram (length and width of teeth) of the lower (m1–m3) and upper (M1–M3) molars of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhausen in comparison with *G. subtapiroideum*, *G. angustidens*, *G. sylvaticum*, *Archaeobelodon*

of *Z. turicensis*. The m3 of *G. subtapiroideum* from Sandelzhausen are definitively smaller than *G. steinheimense*, the large sized specimens of *Z. turicensis* and than an m3 from Viehhausen attributed by Rinnert (1956) to *Serridentinus subtapiroideus* (*Serridentinus* is a junior synonym of *Gomphotherium*). Morphologically, *G.*

filholi, *G. pyrenaicum*, *G. steinheimense*, *"T." ratibonensis* and *Zygodolophodon turicensis* from different Early to Middle Miocene European localities

subtapiroideum differs from *G. angustidens* by a more subtapiroid crown structure, with anteroposteriorly more compressed lophids, wider valleys, and weaker central conules. No obvious morphological differences are observable in comparison with *G. sylvaticum* and *"T." ratibonensis*. Specimen 11381 shows clearly how primary



Fig. 10 Upper molars (M1–M3) of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhausen (Invent. no. BSPG 1959 II ...). **a** M1 dext. (11353); **b** M1 sin. (440); **c** M2 dext. (11386); **d** M3 dext. (4783); **e** M3 sin. (3722); **f** M2–M3 sin. (384). All in occlusal view

wear facets can affect the entire anterior and posterior slopes of the posttrite half-lophids and can lead to an additional anteroposterior thinning of the lophids, which can affect the general habitus of teeth.

M3 (Fig. 10d–f): Four M3 of, probably, four individuals are represented, three of them more or less complete and moderately worn, one totally worn down, one very fragmentary. M3 of relatively small size, 384 narrower than 3722 and 4783; crown trilophodont with small talon (3722, 4783) or a weak fourth loph (384); as far as abrasion allows study, pretrite half-lophs made up by main cone and one conelet, posttrite half-lophs by main cone plus two to three conelets (3722); anterior pretrite conule mostly one single cusp, posterior ones weaker and forming a bulge; 3rd loph without posterior conule; no posttrite conules, but often weak vertical bulges (“zygodont-crest”-like) on anterior and posterior slopes of posttrite maincusps; posttrite half-lophids somewhat anteroposteriorly compressed; initial wear facets (384) steep; first valley blocked, second one weakly blocked at its bottom, third one unblocked; valleys

moderately wide; strong anterior and lingual cingulum; three-part root.

The M3 from Sandelzhausen correspond well with the morphology of *G. subtapiroideum* from the type locality Eibiswald in their subtapiroid construction and overlap with the size range of the latter (Fig. 9). The M3 of both assemblages (Sandelzhausen and Eibiswald) fall in the size range of *Z. turicensis*, but they differ from this species by a somewhat less zygodont morphology with relatively strong pretrite central conules and less anteroposteriorly compressed lophs. However, it is known that these taxa are sometimes hard to distinguish. The M3 of *G. subtapiroideum* are broader than those of *A. filholi* from Bézian and Sansan (both France) and also than the most of those from *G. angustidens* from the type locality Simorre and En Pélouan (both France). Moreover, *G. subtapiroideum* differs from *A. filholi* by the lack of posttrite conules, which are frequently developed in the latter. The M3 of *G. subtapiroideum* from Sandelzhausen are much smaller than those of *G. steinheimense* and *G. pyrenaicum* from their

type localities. They are also smaller than those of *G. sylvaticum* from Artenay (type locality, France); however, the latter overlap with the largest specimen from Eibiswald. Morphologically, the M3 from Sandelzhausen correspond well with the M3 type specimens of *G. sylvaticum* from Artenay (Ginsburg and Antunes 1966, pl. IV). Interestingly, the M3 from Viehhausen (Germany) attributed by Rinnert (1956) to *G. subtapiroideum* are mostly larger than those of Eibiswald and Sandelzhausen, whereas the M3 that was attributed to “*T.*” *ratibonensis* falls perfectly in the cluster of *G. subtapiroideum* from the type locality. Several specimens from Sandelzhausen (3722, 4783, 4782) match morphologically well with the M3 type of “*T.*” *ratibonensis*, except that the latter shows some moderate posttrite conules.

Tusks

To simplify matters, the lower and upper permanent tusks and their “milk predecessors” (deciduous tusk, transitory incisors) are referred to as i2, I2, di2 and DI2, respectively, though there has been doubt about the generation and tooth positions, especially of the lower tusks (Tassy 1987). A peculiarity of the Sandelzhausen proboscidean assemblage is the presence of several “milk tusks”, which are rarely found. These transitory tusks are finger sized and carry an enamel cap on their tips. However, it is often difficult to distinguish these from very juvenile permanent lower tusks, which also carry an enamel cap until it is worn away. Juvenile upper permanent tusks initially also carry an enamel cap, which continues in a lateral enamel band, present on all upper permanent tusks of *G. subtapiroideum* from Sandelzhausen. For measurements of lower and upper tusks see Tables 4 and 5, respectively.

di2 (Fig. 11a, b, f–h): The two delicate remains of lower deciduous tusks are almost straight and exhibit a large pulpa proximally; the enamel tips are unworn and apically flattened; the lateral side of the enamel is longer (30 mm for 2247, 27 mm for 2221) than the medial one; the enamel on the medial side is somewhat wrinkled; the cross-section of the tooth is pyriform.

These two lower deciduous tusks differ from the upper deciduous tusks and juvenile permanent tusks by a slightly apically flattened tip (not pointed) and a wrinkled medial enamel surface. The teeth correspond in all details to that described by Stehlin (1926: fig. 3) as a di2 of *G. angustidens* from Baigneaux-en-Beauce. They differ from a lower deciduous tusk of *G. angustidens* from Castelnau-Barbarens (F) in lacking curvature (Tassy 1987, fig. 10).

DI2 (Fig. 11i–q): Four specimens are identified as this tooth position; the best preserved is 11392 with length of 82 mm; 11392 and 16209 do not show a pulpa, but the shorter preserved, 11551 and 11393, do; enamel cap

Table 4 Measurements (in mm) of lower deciduous tusks (di2) and permanent tusks (i2) of *G. subtapiroideum* and cf. *A. filholi* from Sandelzhausen

Inventory number BSPG	L	Lft	Lf	Max H	Max W
<i>G. subtapiroideum</i>					
di2					
1959 II 2221	(64)			10	6.5
1959 II 2245	–	38		11.5	8
i2					
1959 II 11413	(350)			57	40
1959 II 11412	(330)			43	25
1959 II 397	(190)			29	20
1959 II 1397	(210)			36	23
1959 II 11410	(190)			33	21.5
1959 II 11411	(230)			33.5	22
1959 II 11404	(120)			21	12.5
1959 II 384	–	110		35	24
1959 II 384	–	110		38	22.5
1959 II 11399	–	280		41	25
1959 II 11407	–	380		58	38
1959 II 11400	–	(110)		22	13.5
1959 II 11408	–	–	420	(61)	(39)
1959 II 11406	–	–	95	17.5	11
1959 II 11401	–	–	60	18.5	12.5
1959 II 16214	–	–	220	67	53
1959 II 11405	–	42		12	6.5
1959 II 2250	–	–	–	16	10.5
1959 II 11395	–	60	–	16	11
1959 II 11407	–	–	–	–	–
1959 II 11403	–	–	–	–	–
1959 II 11398	–	–	–	–	–
cf. <i>A. filholi</i>					
i2					
1959 II 11414	–	–	270	60.5	34

L, length of nearly complete tusks (including tip and alveole); Lft, length of incomplete tusk fragment including tip (but no alveole); Lf, length of incomplete mid portion fragment of lower tusk; max H, maximum diameter; max W, minimum diameter

Measurements in parentheses indicate estimated measurements of slightly damaged or very worn specimens

pointed and slightly pointing ventrally; enamel cap on lateral side longer (28 mm for 11392, 35 mm for 11551, 34 mm for 11393,) than medial one; no cervix visible at transition from enamel to cement; 11395 with tiny circular wear facet on anteromedial point of tip and long smooth wear facet (36 mm for 11392) along medioventral side of tip; transverse section of tooth inverted pyriform (11392, 16209, 11551, 11393); on posterior half of 11392 concave grooves along medial and lateral side.

Table 5 Measurements (in mm) of the upper deciduous tusks (DI2) and permanent tusks (I2) of *G. subtapiroideum* from Sandelzhausen

Inventory	L	Lft	Lf	At enamel cap		Max. diameter					
Number BSPG				Max H	Max W	Max H	Max W				
DI2											
1959 II 11392	82			13	9	14.5	10				
1959 II 11551	–	(55)		12.5	8	13.5	10				
1959 II 11393	–	(43)		12.5	8.5	13	9.5				
1959 II 16209	–	–	(51)	–	–	14.5	7.5				
I2	L	Lft	Lf	Max. preserved diameter		10 cm behind tip		20 cm behind tip		Max width of Enamel band	Length of wear Facet at tip
				Max H	Max W	Max H	Max W	Max H	Max W		
1959 II 11415	900			113	63	51	43	65	55.5	70	500
1959 II 11437	570			66	50	34	33	51	41	52	260
1959 II 11416	410			62	45	34	32	47	39	45	270
1959 II 11439	270			37	23	31.5	23.5	39	–	33	150
1959 II 11440	210			39	25	–	–	–	–	33	140
1959 II 11436	–	390		53.5	40	36	26	53.5	40.5	–	180
1959 II 11435	–	270		48	36	40	33.5	48	36	37	–
1959 II 16211	–	(200)		41.5	30	(27)	35	–	–	37	–
1959 II 11420	–	125		34	22	34	22	–	–	–	–
1959 II 398	–		400	64	54	–	–	–	–	35	120
1959 II 11432	–	–	140	37	30	–	–	–	–	–	–
1959 II 11433	–	–	160	45	30	–	–	–	–	–	–
1959 II 11423	–	–	100	24	21	–	–	–	–	–	–

L, length of nearly complete tusks (including tip and alveole); *Lft*, length of incomplete tusk fragment including tip (but no alveole); *Lf*, length of mid portion (without tip and alveole); *max H*, maximum diameter; *max W*, minimum diameter

Measurements in parentheses indicate estimated measurements of slightly damaged or very worn specimens

In contrast with di2, the tip of the enamel cap in DI2 is pointed and oriented anteroventrally, and the medial enamel is not very wrinkled. These teeth most resemble in size and morphology the deciduous upper tusk of *G. angustidens* from Baigneaux-en-Beauce described by Stehlin (1926: figs. 1, 2) and Castelnau-Barbarens described by Tassy (1987, fig. 9). However, unlike the latter, in the specimens from Sandelzhausen the lateral extension of the enamel cap is longer.

di2 or DI2: The fragmentary preservation of two fragmentary specimens (11394, 16210) enables no identification as lower or upper tusks, probably deciduous.

Lower permanent tusks (i2) (Figs. 11c–e, 12a–o): Two small sized isolated specimens (11395, 11396) (Fig. 11c–e) carry an enamel cap, but differ slightly morphologically from di2 and DI2 by a longer enamel cap, which extends laterally 45 mm from the tip (11395), and by a more roundish–ovoid cross-section (11396). These two specimens

are interpreted as very juvenile permanent lower tusks (i2), in which the enamel cap is not totally worn. Stehlin (1926: fig. 4) also described such a tooth (whose enamel is laterally about 50 mm long) from Pontlevoy-Thenay, but which he attributed to *Z. turicensis*. However, it corresponds well morphologically with those from Sandelzhausen. In addition, the most juvenile i2 with an enamel cap is preserved in the rostrum of the juvenile mandible from Sandelzhausen (2250) that was dissected earlier by Tassy (1985, fig. 29). The extracted lower tusk of 2250 showed a laterally very long enamel cap and an ovoid cross-section. Tassy (1985) has already identified this lower tusk as the permanent one.

Twenty-one other i2 specimens (but without enamel caps) are preserved; ten of them more or less complete including tip and pulpa (397, 11397, 11399, 11400, 11407, 11408, 11412, 11413). Six specimens (384, 11413, 11407+8, 11414) are large sized (representing three individuals), nine specimens (11397–11399, 11403, 11409–

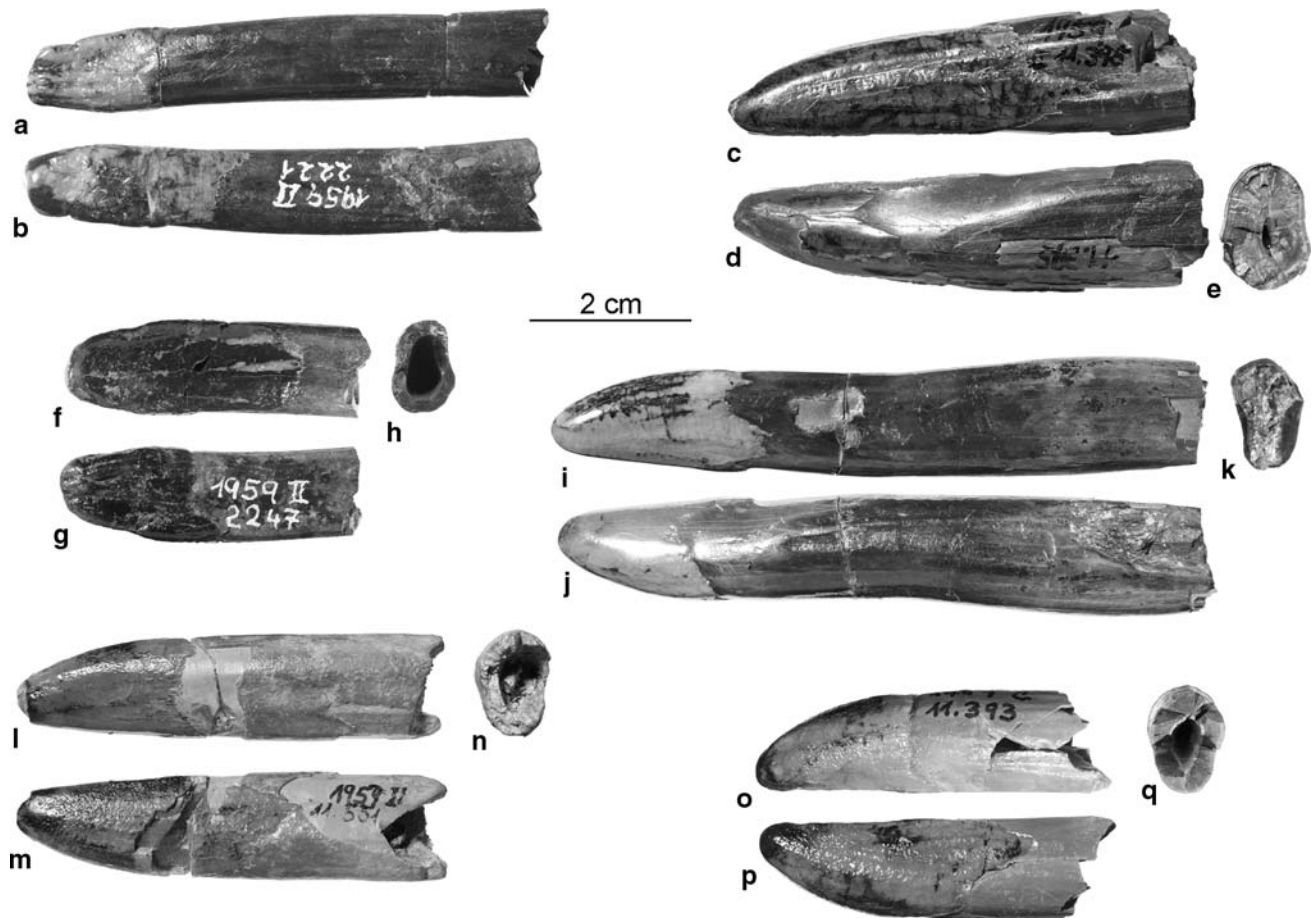


Fig. 11 Lower and upper deciduous (transitory) tusks and juvenile permanent lower tusk of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhausen (Invent. no. BSPG 1959 II ...). **a, b** di2 dext. (2221), **a** medial view, **b** lateral view; **c–e** initially juvenile permanent i2 dext. (?) (11395), **c** lateral view, **d** medial view, **e** cross-section; **f–h** di2

sin. (2247), **f** lateral view, **g** medial view, **h** cross-section; **i–k** DI2 sin. (11392), **i** lateral view, **j** medial view, **k** cross-section; **l–n** DI2 dext. (11551), **l** medial view, **m** lateral view, **n** cross-section; **o–q** DI2 dext. (11393), **o** medial view, **p** lateral view, **q** cross-section

11411, 397) middle sized (representing seven individuals), four specimens (11401, 11404, 11406, 11400) small sized, and two tiny juvenile specimens (2250, 11405); lower tusks mostly straight (in lateral/medial view), but rarely slightly curved upwards (dorsally concave) (e.g. 11399, 11412.); most specimens slightly curved medially (in dorsal/ventral view), except for 11413, which is straight; cross-section slightly pyriform, somewhat mediolaterally flattened, with weak dorsomedial longitudinal furrow (e.g. 397, 11397, 11399, 11400, 11407, 11408, 11410, 11412, 11413); development of lateroventral longitudinal furrow variable: present (11407+8), only weakly denoted (11399, 11410–11413), or absent (397, 11397, 11400, 11404, 11406); tip pointed and worn roundabout with longest facet mostly on dorsal surface; dorsal wear facet polished but not concave; several specimens (e.g. 11399, 11410–11413) with flat medial contact facet on tip; most specimens slightly longitudinally twisted (e.g. slightly in 11407+8, clearly in 397, 11397, 11410+1, 11413, distinctly in 11400); this

longitudinal torsion makes the lower tusks arising from the bony rostrum with the maximum diameter of the cross-section in the vertical position whereas it inclines laterally towards the tip.

The large size variation of the ever-growing permanent lower tusks is probably because of individual age plus sexual dimorphism. The lower tusk in situ in mandible 2250 and the tiny tip (11405) represent very juvenile lower tusks. Whereas the first still carries an enamel cap, the latter shows no traces of enamel and thus seems to represent a slightly older juvenile individual.

By means of the contact facet at the tips of the two tusk pairs 11399 + 11412 and 11410 + 11411 their natural position in vivo can be reconstructed; it indicates that in these individuals the tusks were edgewise (with the maximum diameter in vertical position) implanted in the symphysis. However, in mandible 384 the lower tusks are implanted diagonal in the rostrum; but as the rostrum is completed the implantation might not be the natural one.

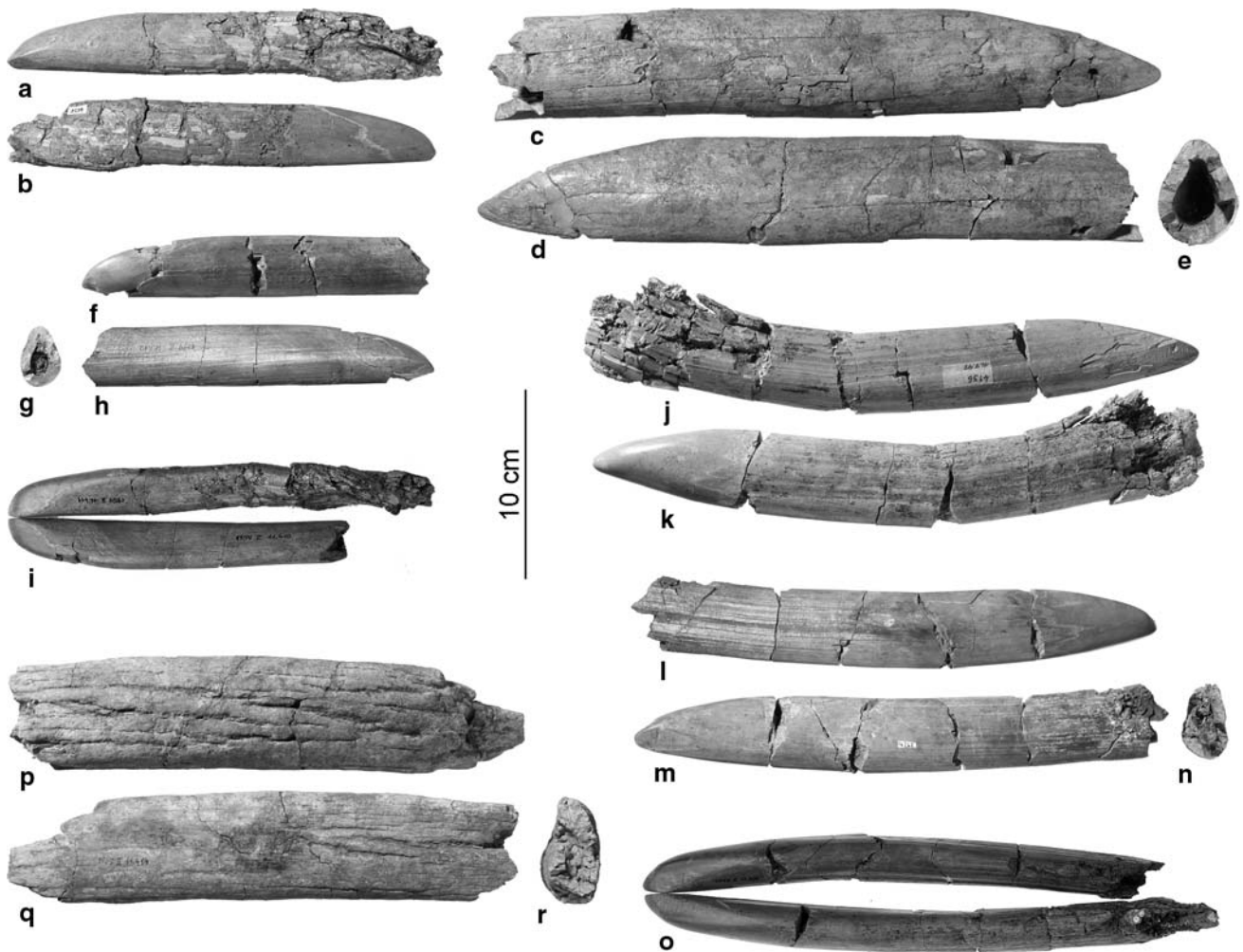


Fig. 12 Lower permanent tusks of *Gomphotherium subtapiroideum* (Schlesinger, 1917) (**a–r**) from Sandelzhausen (Invent. no. BSPG 1959 II ...). **a–b** i2 dext. (11411), **a** medial view, **b** lateral view; **c–e** i2 sin. (11413), **c** medial view, **d** lateral view, **e** cross-section posterior end; **f–h** i2 sin. (11410), **f** lateral view, **g** cross-section posterior end, **h** medial view; **m2** dext. (11376); **i** i2 sin. (11410) and dext. (11411)

of one individual in dorsal view; **j–k** i2 sin. (11412), **j** medial view, **k** lateral view; **l–n** i2 dext. (11399), **l** lateral view, **m** medial view, **n** cross-section posterior end; **o** i2 sin. (11412) and dext. (11399) of one individual in dorsal view; **p–r** i2 dext. (11414), **p** lateral view, **q** medial view, **r** cross-section posterior end

A tip fragment (11398) differs from other lower tusks in forming a sharp, spatula-like edge. But because the tip is so fragmentary preserved it is not possible to identify the direction of the spatula-like edge. It is unclear whether this results from a former break or if this shape has a functional or taxonomic cause.

One large sized specimen (11414), lacking tip and pulpa, differs from all other lower tusks in Sandelzhausen in being dorsoventrally more flattened (Fig. 12p, r). Even if this tooth is superficially cracked, it seems not to be deformed by compression. In cross-section, the dorsomedial side forms a shallow concavity and the dorsal edge almost recurves medially. This condition is close to the lower tusks of *A. filholi*. However, a furrow along the lateroventral side is not traceable, although it should be developed in *A. filholi* (Tassy 1985: 578), even if weaker

than the dorsomedial one. Despite its difference in cross-section from all other preserved lower tusks, and its morphological similarity to *A. filholi*, this specimen is attributed, with reservation, to *G. subtapiroideum*, also because there is no other evidence of *A. filholi* in the Sandelzhausen assemblage. The deviating cross-section is interpreted for the moment to be an extreme within the variability.

The cross-section of all other lower tusks of *G. subtapiroideum* from Sandelzhausen resembles those of *G. angustidens* and *G. sylvaticum*. However, the dorsal wear facet on the tip of *G. angustidens* is mostly concave (Tassy 1985: 349), which is not the case in any of the present lower tusks from Sandelzhausen. Furthermore, most of the lower tusks of *G. angustidens* are slightly upcurved (Tassy 1985: 349f), whereas most specimens from Sandelzhausen are straight (in lateral/medial view), except for one

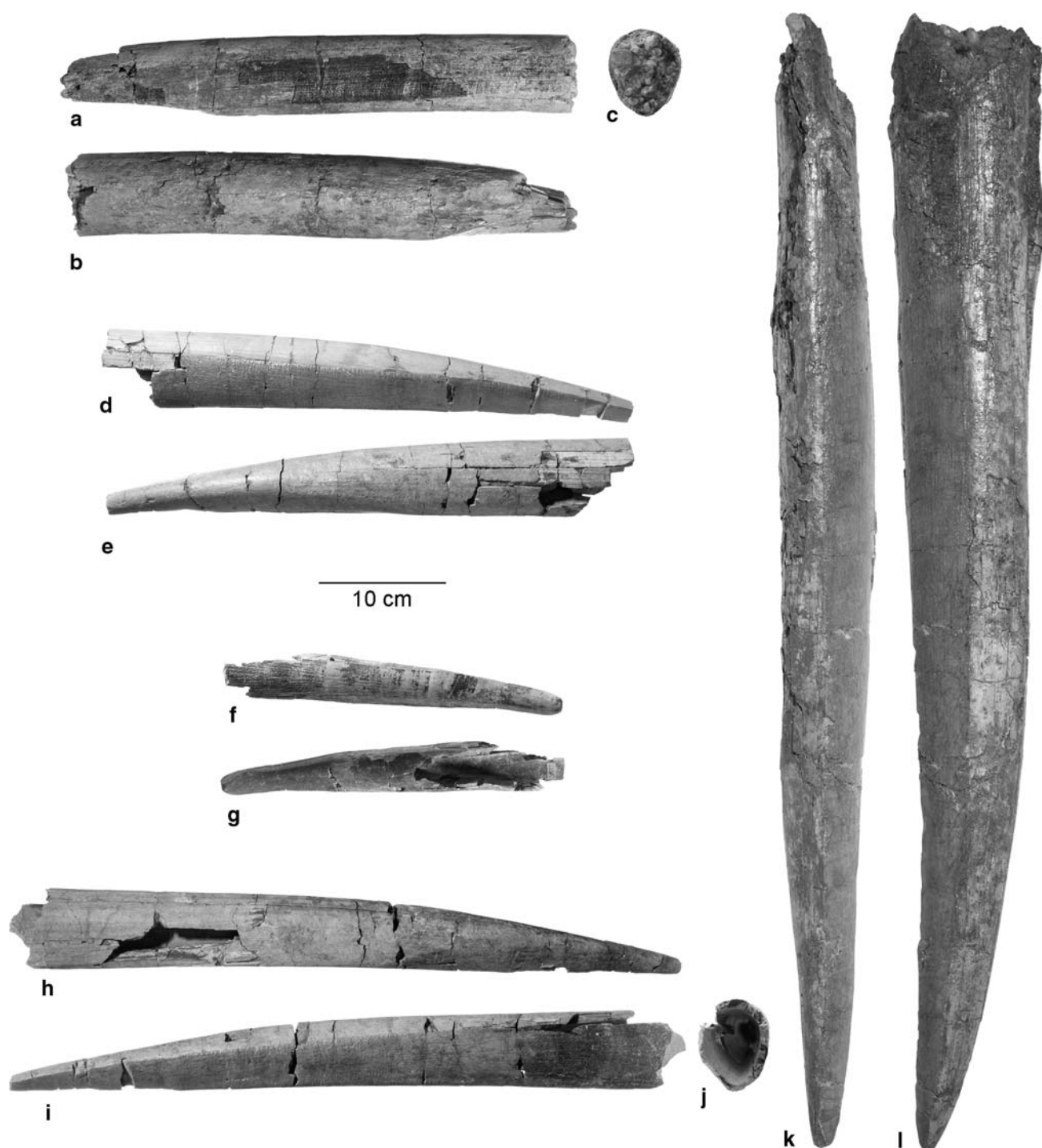


Fig. 13 Upper permanent tusks of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhausen (Invent. no. BSPG 1959 II ...). **a–c** I2 sin. (398), **a** lateral view, **b** medial view, **c** cross-section at posterior end; **d, e** I2 dext. (11416), **d** lateral view, **e** medial view;

f, g I2 dext. (11439), **f** lateral view, **g** medial view; **h–j** I2 sin. (11437), **h** medial view, **i** lateral view, **j** cross-section at posterior end; **k, l** I2 dext. (11415), **k** ventral view, **l** lateral view

individual (11399 + 11412). The lower tusks of *Z. turicensis* differ by an oval cross-section without any longitudinal furrow(s). In *A. filholi* the lower tusks are distinctive in being curved upwards (in lateral/medial view) and being

more flattened (Tassy 1985: 578); they are implanted in the symphysis with the maximum diameter diagonal to sub-horizontal (Tassy 1985, fig. 236). The lower tusks of *G. sylvaticum* correspond to those from Sandelzhausen; they

Table 6 Measurements of mandible (384) of *G. subtapiroideum* from Sandelzhausen (measurements after Göhlich 1998)

Measurements	mm
Dorsal length of ramus mandibulae (from caput mandibulae to processus coracoideus)	215
Max. length of ramus mandibulae (from end of m3 to gonion caudale)	220
Length from caput mandibulae to beginning of symphysis	540
Height of ramus from gonion ventrale to incisura mandibulae	205
Height of ramus from gonion ventrale to proc. coronoideus	280
Height of corpus mandibulae at anterior end of m2	95
Height of symphysis at its caudal end	85
Width of symphysis at its caudal end	150
Max. width of corpus mandibulae	97
Min. width of corpus mandibulae	49

are straight (in lateral/medial view), pyriform with the lateroventral furrow missing. No lower tusks are known of *G. subtapiroideum* from Eibiswald or of “*T.*” *ratibonensis*.

Upper permanent tusks (I2): Twenty-nine upper permanent tusks are represented, of which only nine are sufficiently complete to be informative. Down curved; cross-section inverted egg-shaped and mediolaterally slightly flattened, no longitudinal furrows, except for a very weak medial longitudinal furrow on 398; no torsion; enamel band large and remaining on lateral side to the tip (not helicoidal); medioventral wear facets on tip often quite long (Fig. 13a–l).

The upper tusks of *G. subtapiroideum* from Sandelzhausen differ from those of *G. angustidens*, in which the lateral enamel band is slightly helicoidal so that it terminates at the tip almost ventrally (Tassy 1985: 428). Unlike this derived condition in *G. angustidens*, the enamel band in *G. subtapiroideum* is visible laterally down to the tip. The upper tusks of *G. angustidens* often show a longitudinal furrow along the medial and lateral side, which is not developed in *G. subtapiroideum*. Concerning these features, the tusks of *G. subtapiroideum* resemble those of *G. sylvaticum*, *A. filholi* and “*T.*” *ratibonensis*. However, the tusks of *A. filholi* often carry a medial longitudinal furrow. My own observations of the type material of “*T.*” *ratibonensis* from Viehhausen contradict the description of Rinnert (1956), which says that the lateral enamel band turns ventrally on the tip; the enamel band stays laterally

until the tip. The possible source of misinterpretation might be Rinnert's (1956: 50) assumption that the natural position of tusks is oriented such that their tips point somewhat laterally. No tusks of *G. subtapiroideum* are known from the type locality Eibiswald.

Cranial material

Mandibles—mandible with sin. and fragmentary dext. ramus, with m2 sin. and dext., m3 sin., i2 sin. and dext. (384) (an isolated M2 sin. and M3 sin. also belong to this individual, same number); anterior portion of a juvenile mandible sin. with i2, d2, d3 (2250); fragmentary mandibles sin. and dext. with p4–m3 (11360) and with both i2 (11410, 11411); fragmentary mandible dext. with m3 and roots of m2 (11382); anterior portion of toothless mandibles dext. (11441) and sin. (11442) with tusk alveole and molar alveole. The dentition of these mandibles is listed and described above.

Description

Unfortunately, none of the mandibles (Figs. 2l, m, 8a, b, c, f) is completely preserved. The best specimen is mandible 384; however, in this mandible at least the anterior half of the rostrum, the ventral margin of the corpus mandibulae, and a portion of the incisura mandibulae are artificially completed. Mandible 384 shows that the rostrum projects almost straight from the corpus mandibulae without any angulation. As the rostrum is not completely preserved nothing can be said about its original length. The processus coronoideus is slightly dorsally shorter than the caput mandibulae. The ramus and the corpus are set in, approximately, a right angle. For measurements see Table 6.

Postcranial material

Bones belonging to one individual are listed under the same inventory number, e.g., 16192a–k, representing several bones of a left forearm and hand found in loose articulation. Postcranials probably or possibly belonging to one individual have different inventory numbers but are indicated.

Scapula—scapula dext., lacking margo cranialis and caudalis and cavitas glenoidalis (11447); dist. end of scapula dext., with neck of spina (11443); centre-part of scapula sin., with fragmentary spina (11444); centre-part of scapula sin., with fragmentary spina (11446); cavitas glenoidalis of scapula sin., (11448 + 11576); centre-part of scapula sin.(?), with fragmentary spina (11445) (perhaps belonging to 11449); smashed dist. end of

scapula sin. with neck of spina (11449) (perhaps belonging to 11445).

Humerus—distal half of diaphysis of humerus dext. (juvenile) (11451); diaphysis of humerus dext. (11452) (probably same individual as ulna 11454); medial distal trochlea of humerus dext. (11453); half of humeral distal trochlea sin./dext.? (11329).

Ulna—ulna sin., olecranon broken off, distal diaphysis smashed (16192a); prox. $\frac{3}{4}$ of ulna sin., olecranon missing (11454) (probably same individual as humerus 11452); prox. $\frac{3}{4}$ of ulna sin, olecranon and lat. processus coronoideus missing (11455); proximomedial half of shaft of ulna sin. (11456); prox. $\frac{3}{4}$ of ulna dext., olecranon and processus coronoideus lateralis missing (11457); processus coronoidei, processus anconaeus and portions of shaft of ulna dext. (11460); prox. $\frac{2}{3}$ of ulna shaft sin. (11372); ulna sin., medial part of olecranon, processus coronoideus medialis and distal epiphysis missing (11387).

Radius—prox. $\frac{1}{3}$ of radius sin. (11461); prox. $\frac{1}{3}$ and mid portion of radius sin. (16192b); prox. end and mid portion radius sin. (11462).

Lunate (Os carpi intermedium = Ci)—Ci dext. (11466, same individual as Cu 11465, CII 11469, CIII 11471); Ci sin. (16192c); Ci dext., very worn (11467, eventually same individual as os carpale II, 11470).

Cuneiform (Os carpi ulnare = Cu, triquetrum)—Cu dext. (11463); Cu sin. (16192e); Cu sin., lateral process broken off (11464); Cu dext., lateral process broken off (11465, same individual as Ci 11466, CII 11469, CIII 11471, CIV 11477).

Pisiform (Os accessorium, Ca)—Ca sin. (16192f).

Trapezium (Os carpale I, CI)—CI ? prox. and dist. end (11468).

Trapezoid (Os carpale II, CII)—CII dext. (11469, same individual as Ci 11466, Cu 11465 CIII 11471, CIV 11477); CII sin. fragmentary and worn (11470).

Magnum, (Os carpale III, CIII)—CIII dext. (11471) (same individual as Ci 11466, Cu 11465, CII 11469, CIV 11477); CIII dext., damaged (11472); CIII ?, worn (11473).

Hamate (Os carpale IV, CIV, Unciforme)—CIV dext. (11477, same individual as dext. CIII 11471, Ci 11466, Cu 11465, CII 11469, eventually same individual as sin. CIV 11476); CIV sin. (11476); CIV dext. (11475); CIV sin. (16192d); CIV sin. (11474); CIV dext., very worn (11478).

Metacarpals (Mc)—Mc III? sin. prox. half (11479); Mc III? dext., prox. half (11481); Mc IV? sin., prox. half (11482); Mc IV dext., prox. half (11483); dist. epiphysis (trochlea) of Mc? (11484); Mc II, III?, IV sin. (16192).

Phalanges—Ph prox. III? sin. (16192j); Ph prox. IV? sin. (16192h); Ph prox. V? sin. (16192i); Ph prox. ? (11534); Ph med. III? sin. (16192k); Ph dist. ? sin. (16192g).

Innominate (pelvis)—fragmentary ilium sin. with portion of acetabulum (11485, probably same individual as 11495); fragmentary ilium dext. with portion of acetabulum (11495, probably same individual as 11485); fragmentary ilium dext. with portion of acetabulum (11487); incomplete pubis dext. with portion of ilium, pubis and ischium and smashed acetabulum (11488–11490); portion of acetabulum sin. with cranial part of ischium (11491); portion of pubis sin. with part of acetabulum (11492); portion of acetabulum sin., with cranial part of ischium (11493); portion of acetabulum sin. with lateral part of pubis (11494); portion of acetabulum dext. with lateral part of pubis (11496); portion of acetabulum dext. with cranial part of ischium (11497); portion of acetabulum dext. with fragmentary pubis (11503); fragmentary ilium sin. with portion of acetabulum and part of ischium (11506).

Femur—femur sin., diaphysis (11508, possibly same individual as femur dext. 11510); femur dext., diaphysis (11510, possibly same individual as femur 11508); femur sin./dext.?, broken diaphysis (11509); femur sin./dext.?, broken diaphysis (11511); femur sin./dext.?; half of distal condyle (11512); femur sin./dext, condyle fragments (11513); caput femoris dext. (11318); fragmentary caput femoris sin./dext.? (16193).

Patella—patella sin. (11514); patella sin./dext.? (11515); patella dext. (11330, was found together with individual 16192).

Tibia—tibia sin. with compressed diaphysis (11521) (probably same individual as fibula 11522 and calcaneus 11524); tibia dext., diaphysis (11578).

Fibula—fibula sin., distal $\frac{2}{3}$ (11522, probably same individual as 11521).

Calcaneum—calcaneus sin., distal portion lacking (11523); calcaneus dext., deformed (11524, probably same individual as tibia 11521); portion of prox. articulation facet of calcaneus dext. (11525).

Astragalus (Talus)—astragalus sin., slightly damaged (455); astragalus dext., medial side lacking (454); astragalus sin, medial side lacking (11526); astragalus dext., medial side lacking (11527).

Navicular (Scaphoid, Centrale)—naviculare dext. (11528).

Mesocuneiform (TII)—mesocuneiforme dext., dorsal portion (11529).

Ectocuneiform (TIII)—ectocuneiforme dext. (11530), ectocuneiforme ?, dorsal portion (11519).

Cuboid (TIV)—cuboideum dext., (11531); cuboideum dext., plantar edge lacking (11532).

Metatarsal III—metatarsal III dext, distal end lacking (11481).

Phalanges—phalanx indet. (11533), phalanx indet. prox. portion (11535).

Vertebrae

Atlas—nearly complete atlas, lacking both alae atlantes (11536).

Thoracic vertebrae (T)—vertebra thoracica (T4?, 5?, 6?) (11550); vertebra thoracica, nearly complete (16195); vertebra thoracica, lacking processus spinosus (11538); damaged vertebra thoracica, lacking processus transversus (16196); incomplete vertebra thoracica, end of processus spinosus and portion of corpus broken off (16194); processus spinosus (16197); processus spinosus (11542).

Lumbal vertebrae—vertebra lumbalis, deformed (11539).

Sacrum—sacrum, deformed with caudal end crushed (11540).

vertebrae indet.—fragment of vertebra (11541); fragment of vertebra (11542); epiphysis of vertebra (11543).

ribs—very long and very slender rib with prox. end, caput damaged (11544); long and broad rib, prox. end smashed (11545); prox. half of rib, broad, caput damaged (11546); prox. end of rib (11547); prox. 1/3 of rib with caput, broad and flat (11548); prox. end of rib (11549); portion of rib (11550).

Osteological descriptions

Proboscidean postcrania from Sandelzhausen are attributed to *G. subtapiroideum*, as this is by far the most common proboscidean taxon from that site. The osteological terminology follows Nickel et al. (1984).

Most of the postcrania were found as isolated bones.

Little is known about the postcranial osteology of the taxa represented in Sandelzhausen. So far, no postcranial material has been described of *G. subtapiroideum*, *G. sylvaticum* or *Z. turicensis* and only little is known about the postcranium of *G. angustidens*. Thus, systematic determination of Miocene proboscidean taxa based on osteological features is in its fledgling stages. In most cases, different specimens of each element show few significant morphological differences that could indicate the presence of different proboscidean taxa—except for the remains of two atlases. Like the cheek teeth, the postcranials exhibit a wide size range, which is interpreted as being a result of intraspecific variability, different ontogenetic stages, and sexual dimorphism.

Scapula: Most of the seven scapulae are so fragmentary that they do not reveal any information about dimensions

or osteological features. Specimen 11447 gives a scapula height of about 50 cm; spina inclining cranially with a maximum (lateral) height of about 95 mm; projecting part of tuber spina scapulae and acromion broken off; in distal half margin of spina bends cranially and forms slightly concave shelf; tuberculum supraglenoidale forms strong but blunt protuberance (11443, 11448 + 11576); cavitas glenoidalis craniocaudally strongly concave and oval in shape; lateral margin of cavitas glenoidalis slightly concave (in lateral view) and reaching to lateral surface of angulus ventralis. Dimensions of angulus ventralis (including tuberculum supraglenoidale) (11443): width: 80 mm, depth: 128 mm; cavitas glenoidalis: max. width/depth: 80 mm/105 mm (Fig. 14a).

Humerus: The best preserved humerus (11451) represents a juvenile with proximal half and distal epiphysis missing. Estimated greatest length was around 50 cm or more. Crista humeri originates distally at approximately the same level as proximal end of crista supracondylaris lateralis. Mid-shaft is of triangular shape with concave lateral and caudal surface; its minimum width is 70 mm. Along lateral surface of shaft twists a wide and slightly concave sulcus musculi brachialis. Both, cranial and caudal fossae radiales, are wide and moderate concave. Crista supracondylaris lateralis forms a wide and laterally projecting wing along distal third of the shaft. Two fragmentary portions of distal humeral condyles (11453, 11329) show that the median furrow is deeper caudally than cranially (Fig. 14b).

Ulna: Eight fragmentary ulnas are represented; olecranon is always damaged or broken off; a distal end is only represented in 16192a but is smashed. Processus anconaeus projects dorsally almost as far processus coronoidei (16192a); articular facets of processus coronoidei medialis and lateralis are slightly concave and almost horizontally oriented; the medial one is more than twice as large as the lateral one; a mostly distinct, longitudinal groove is situated dorsally on processus coronoideus medialis; mid-shaft is triangular in cross-section; in some specimens (e.g. 11454, 11455, 11457), mediodorsal edge of shaft swells to a crest in its distal half; in contrast, in 11372, such a crest is very weak and more proximally located in mid-shaft; distal end (16192a) carries rounded triangular articular facet for os carpi ulnare, which is, in general, concave mediolaterally but also slightly convex in its lateral portion. Medially on distal end lies smaller, oval, and concave articular facet (about 35 mm in depth) for radius, forming right angle with distal facet for os carpi ulnare. Broken preservation of palmar margin of distal radius end prevents detection of any small articular facet for os accessorium (pisiforme) (Fig. 15c).

The smallest of the ulnas (11372) is definitely a juvenile as it lacks its distal epiphysis, but it is also stouter (without



Fig. 14 Postcranial bones of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhausen (Invent. no. BSPG 1959 II ...). **a** scapula dext. (11447), lateral view; **b** humerus dext. (juvenile) (11451), cranial view; **c** ulna sin. (16192a), cranial view; **d, e** patella sin. (11514), **d** cranial view, **e** caudal view; **f** pubic portion sin.

(11492), cranial view; **g** thoracic vertebra (6800), caudal view; **h** femur sin. (11508), caudal view; **i** tibia dext. (juvenile) (11578), caudal view; **j** sacrum (11540), dorsal view; **k** thoracic vertebra (T4, 5 or 6) (11550), caudal view; **l** atlas (11536), caudal view; **m** vertebra lumbalis (11539), caudal view

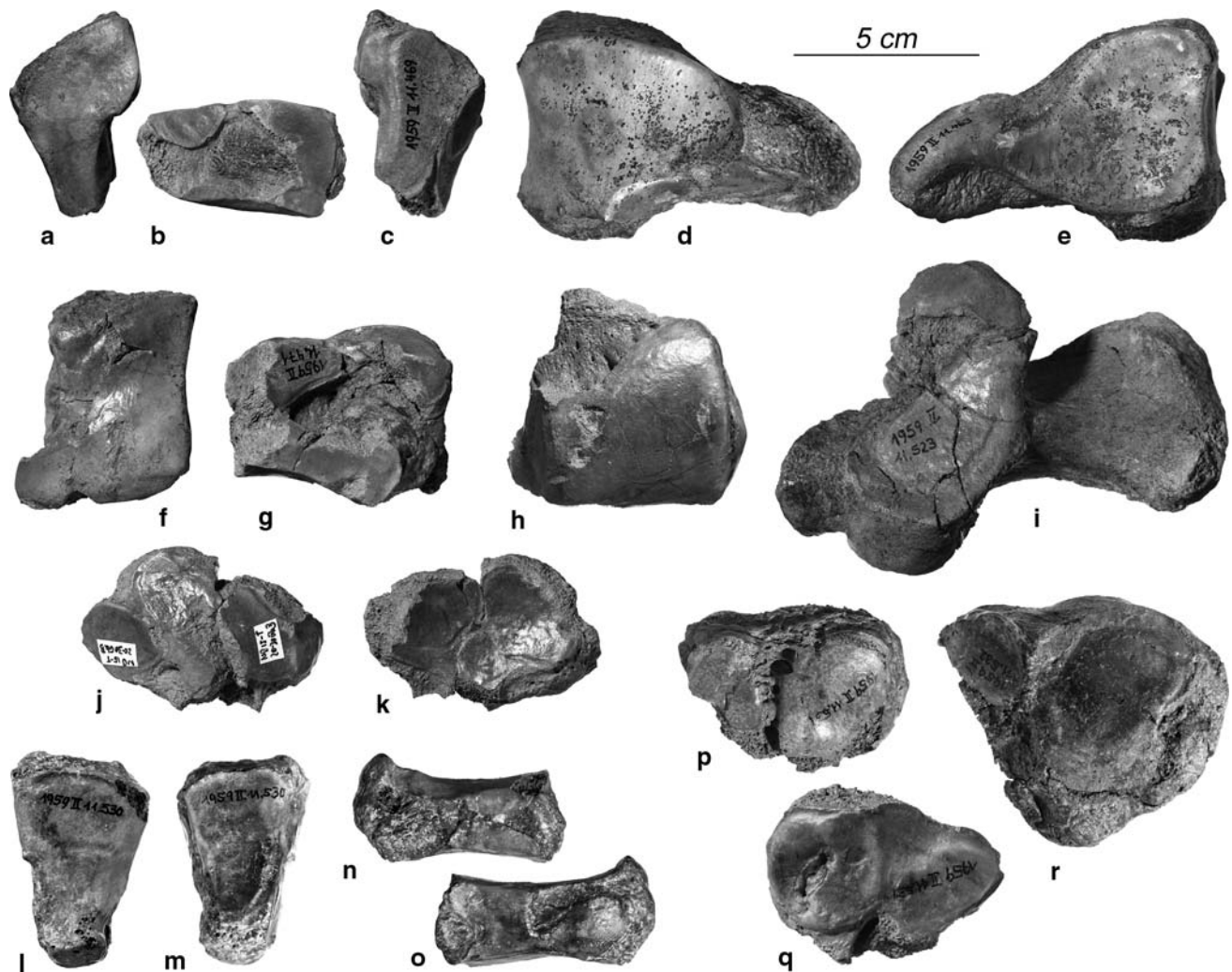


Fig. 15 Carpalia and tarsalia of *Gomphotherium subtapiroideum* (Schlesinger, 1917) from Sandelzhhausen (Invent. no. BSPG 1959 II ...). **a–c** trapezoideum dext. (11469), **a** proximal view, **b** distal view, **c** lateral view; **d, e** cuneiforme dext. (11463), **d** proximal view, **e** distal view; **f, g** magnum dext., **f** proximal view, **g** medial view; **h** astragalus dext. (11527), proximal view; **i** calcaneus sin. (11523),

proximolateral view; **j, k** naviculare dext. (11528), **j** distal view; **k** proximal view; **l–o** ectocuneiforme dext. (11530), **l** proximal view, **m** distal view, **n** lateral view, **o** medial view; **p, q** cuboideum dext. (11532), **p** proximal view, **q** distal view; **r** cuboideum dext. (11431), proximal view

being broader) than the other specimens. Most of the other specimens, even if incomplete, are medium-sized (e.g. 11457, 11454); two individuals (11372, 16192a) are of larger dimensions (Table 7).

Radius: Three proximal portions are present, of which 11462 is distinctly smaller than 11461 and 16192b (Table 7). The fovea capitis radii is saddle-like, medio-laterally convex and dorsopalmar concave. In 16192b the proximal articular surface is broken but seems to be flatter than in 11461 and 11462. 11462 carries a small mediopalmar facet and a bigger longitudinal lateroplantar facet (circumferential articularis radii) for articulation with the incisura radialis of the ulna. A portion of the longitudinal lateroplantar facet is also preserved in 16192b. The lateral margin of the proximal end of 11461 is damaged, but the

medial one does not show a facet of the circumferential articularis radii. The shaft is oblate in all specimens. In 16192b, the proximal shaft carries a longitudinal crest on the lateroplantar aspect.

Manus

Lunate: Three specimens are preserved, one of them very worn (11467). 11467 is distinctly larger than 11466 and 16192c (Table 8). Triangular shape (in proximal/distal view); proximal articulation facet for radius triangular and in plantar half concave; proximal articulation facet for ulna oval, slightly concave and forming an angle of about 150° (in dorsal view) with proximal facet for radius; distal facet triangular in shape in dorsal half strongly convex in plantar

Table 7 Measurements (in mm) of portions of ulnae and radii of *G. subtapiroideum* from Sandelzhausen (measurements after Göhlich 1998)

Measurements			
Ulnae	16192	11454	11455
Width prox. end		88	–
Min. width shaft		47	~60
Min. depth shaft		36.5	–
Min. circumference shaft		145	–
	11457	11372	11387
Width prox. end	–	–	–
Min. width shaft	45.5	40	63
Min. depth shaft	37	31	48
Min. circumference shaft	148	118	190
Radii	16192	11461	11462
Width prox. end	58		
Depth prox. end	40		
Min. width shaft	44		
Min. depth shaft	19		
Min. circumference shaft	–	95	88

half concave; lateral facet for cuneiform elongate oval-shaped along dorsal half of distal edge; medial proximal articular facet for scaphoid thin, medial distal facet somewhat s-shaped.

Cuneiform: One complete (11463), one nearly complete (16192), and two fragmentary (11464, 11465) cuneiforms are preserved. Proximal articular facet for ulna is triangular and mediolaterally convex; proximopalmar articular facet for pisiform long and extending on to lateral process; distal articular facet for hamate slightly concave; distopalmar articular facet on lateral process for metacarpale V elongate and oval-shaped, medial proximal articular facet for lunate low and fluent with proximal facet, medial distal one elongate and oval-shaped. For measurements see Table 8 (Fig. 15d, e).

Pisiform: One pisiform (16192f) is preserved. The hook-like bone measures about 75 mm in length. The distal (free) and proximal ends are damaged. No articular facets for cuneiform or the ulna can be identified.

Trapezium: A proximal and distal portion of one specimen is preserved (11468). Lateral articular facet for magnum and proximal articular facet for scaphoid form angle of about 120°; the latter is concave.

Trapezoid: Two specimens are preserved, of which 11469 is much smaller than 11470 (Table 8). Bone of triangular shape, proximal articulation facet for scaphoid slightly dorsopalmar convex and mediolaterally concave; lateral facet trapezoid but with a marked oval facet for

Table 8 Measurements (in mm) of carpalia of *G. subtapiroideum* from Sandelzhausen (measurements after Göhlich 1998)

Measurements				
Lunatum (Ci)	11466	11467	16192	
Max. width	67	~71	63	
Max. depth	67	~80	66	
Max. height	38	~54	40	
Ulnare (Cu)	11465	11463	16192	11644
Max. width	–	99	~90	–
Max. depth	60	63	–	56
Max. height	33	38	–	28
Width prox. facet	–	63	54	–
Depth prox. facet	47	49	–	47
Trapezoideum (CII)	11469	11470		
Max. depth diagonal	~60	~73		
Max. width	40	55		
Max. height	32	45		
Magnum (CIII)	11471	11472	11473	
Max. width	63	–	~88	
Max. depth	51	54	–	
Max. height	53	55	73	
Hamatum (CIV)	11477	11475	16192	11476
Max. width	~55	–	70	53
Max. depth	50	51	62	–
Max. height	–	47	–	51
	11474	11478		
Max. width	75	–		
Max. depth	75	78		
Max. height	61	71		

trapezium; distal facet for articulation with metacarpal II slightly convex; four separate lateral facets for hamate, of which the two proximal ones are larger than the distal ones (Fig. 15a–c).

Magnum: Specimens 11471 and 11472 are distinctly smaller than 11473 (Table 8). Trapezoid shape in proximal view; proximal articulation facet slightly convex and with a medioplantar extension; medial proximal facet for trapezoid large and tapering towards plantar; lateral proximal facet for hamate recessed in comparison to lateral distal one; distal facet not complete in any of the specimens (Fig. 15f, g).

Hamate: Six fragmentary specimens are preserved, four of them small (11477, 16192, 11475, 11476), and two of them larger sized (11474, 11478) (Table 8). Triangular shape with dorsolateral side curved; bone lowers laterally; proximal facet large and mediolaterally convex; distal facet bifid in two parts of almost equal size forming an angle of

Table 9 Measurements (in mm) of metacarpalia, digital phalanges, and metatarsalia of *G. subtapiroideum* from Sandelzhausen (measurements after Göhlich 1998)

Measurements	II?	III?		
Metacarpale II + III	16192	11480	16192	
Prox width		41	–	
Prox depth		57	–	
Dist. width	45	–	49	
Metacarpale IV	11482	11483	11484	19192
Length	–	–	–	104
Prox width	43	52	–	48
Prox depth	–	~55	–	–
Dist. width	–	–	62	49
Dist. depth	–	–	55	–
Phalanx	III?	IV?	V?	?
Proximales	16192j	16192h	16192i	11534
Length	50	60	50	40
Phalanx	Med. III?	Dist. ?		
Medialis + distalis	16192k	16192g		
Length	30	22		
Max. width	42	26		
Metatarsale III	111481			
Prox width	51			
Prox depth	~56			

about 150°; medial proximal facet for articulation with magnum large and high and becoming slightly lower dorsally; medial distal facet long but low.

Metacarpal: Three proximal portions (11480, 11482, 11483) and one distal trochlea (11484) are present, of which two bones (11480, 11482) represent smaller individuals and two bones (11483, 11484) larger individuals (Table 9). McIII (11480) with a high, proximally extended lateroproximal edge; proximal medial facet triangular, large and strongly inclining medially, proximal lateral facet narrow and inclining laterally; lateral and medial part of proximal facet forming an angle of about 110°; long and low facets on lateral and medial side of proximal end. McIV (11482) with triangular proximal facet dorsopalmally slightly convex and divided in narrow lateral and wide medial parts; medial facet on proximal end sloping and forming an angle of about 110° with proximal facet; lateral facet vertical.

Phalanges: Four proximal phalanges are preserved (16192h–j, 11534); the affiliation to the hand is clear for 16192 (was found in articulation), but unclear for 11534. The more or less symmetric one are identified as IV (16192h) and III (16192j), the slightly asymmetric one (16192) as V; proximal facet oval and slightly concave; Ph

prox. III (16192j) in articulation with Ph med. III (16192k), which is symmetric but shorter. Distal phalanx (16192g) small and short; digit affiliation unclear.

Innominate: Twelve portions of pelves are represented, all of them fragmentary, representing different parts of the pelvis. Corpus ilii short, wide (110 mm in 11495) and craniocaudally flattened; ala widens largely, but no complete ala is present for measurements; medial border of ala thick, medially flattened and thickening towards the level of acetabulum (up to 80 mm in 11495, width of corpus ilii 110 mm); distinct and crest-like tuberculum musculi psoas minoris along ventral edge in middle of medial margin of ala (e.g. 11495, 11485, 11487); medial surface of corpus ilii at level of acetabulum slightly concave; eminentia iliopubica forming a strong blunt protuberance (e.g. 11494), but in two specimens (11494, 11496) with a distinct groove; acetabulum round and moderately concave; dimension of acetabulum in most cases about 90–100 mm in length, but some individuals bigger (e.g. 11506); incisura acetabuli is deep (forming a furrow) and medially bordered by a strong crest (e.g. 11491, 11493, 11497, 11503, 11488–90), which reaches on to the ischium and forms its cranial margin; ramus cranialis ossis pubis carries on its cranial side a characteristic, transversal and longitudinal groove that deepens laterally (11494, 11496, 11492, 11488–90) (Fig. 14f).

Table 10 Measurements (in mm) of portions of femora, patellae, tibiae, and fibulae of *G. subtapiroideum* from Sandelzhausen (measurements after Göhlich 1998)

Measurements			
Femur	11508	11510	11318
Width fem. head			95
Depth fem. head			~82
Min. width shaft	70	72	
Min. depth shaft		42	
Patella	11514	11330	
Max. length	~85	100	
Max. width	62	72	
Max. depth	54	70	
Tibia	11521	11579	
Max. length	460		
Width prox. end	~138		
Min. width shaft	~83	65	
Min. circumference shaft		173	
Width dist. end	~110		
Fibula	11522		
Min. width shaft	<27		
Width dist. End	70		
Depth dist. end	~39		

Femur: Eight portions of femora are represented by isolated and fragmentary diaphyses, condyles, and femoral heads. Diaphyses of 11509 and 11511 broader than those of 11510 and 11508 (Table 10), but this might be a result of their crushing; diaphysis slender and straight, oval in cross-section in the mid-shaft and becoming proximally and distally slightly flatter but wider; distal end of shaft thickened; distinct, longitudinal furrow along laterocranial margin of proximal shaft (11508, 11510); caput femora (11318) hemispherical with a relatively narrow caudal emargination into the fovea capitis; condyle remains (11512, 11513) too badly preserved for any morphological details (Fig. 14h).

Patella: Three patellae are present; two of them nearly complete (Table 10). Oval in shape with small bump-like distal apex; caudal articular facet divided into two almost symmetrical facets, forming an angle of about 100°; each slightly concave; basis slightly damaged in all specimens (Fig. 14d, e).

Tibia: Both tibiae are of similar size (Table 10); 11521 nearly complete, but with shafts crushed dorsoplantarily; juvenile diaphysis (11578) lacks epiphyses; in 11521, only lateral proximal facet preserved, which is oval and slightly concave; the tuberositas tibiae distally forming a bulge and continuing distally in a straight margo cranialis, reaching on to distal half of shaft (11578); mid-shaft oval in cross-section;

distal end of 11521 with malleolus medialis and cochlea tibiae preserved (Fig. 14i).

Fibula: Only one distal half of a fibula is present (11522) (Table 10), probably belonging to tibia 11521. Shaft slender and flattened thickens distally; distal articular facet concave dorsoplantarily, but bending convex on the medial side; medial articulation facet for tibia restricted on plantar half distal shaft, oval in shape, and proximomedially oriented.

Calcaneum: Two nearly complete (11523, 11521) calcanei and a portion of the proximomedial articulation are preserved, 11521 being larger than 11523 (Table 11). Tuber calcanei about half of length of calcaneum and mediolaterally smashed in 11521; lateral articular facet for astragalus large, oval and laterally bent up; medial articular facet for astragalus smaller, elongate, and dorsoplantarily slightly convex; those two facets separated by sulcus widening dorsally; proximal articular facet for fibula rhomboid and dorsoplantarily convex; distal articular facet for cuboid oval; probably no contact facet for the navicular (but slightly damaged in that area) (Fig. 15i).

Astragalus: One larger nearly complete specimen (455) and three smaller incomplete specimens (454, 11526, 11527) are preserved (Table 11). Proximal articular facet

Table 11 Measurements (in mm) of tarsalia of *G. subtapiroideum* from Sandelzhausen (measurements after Göhlich 1998)

Measurements				
Calcaneus	11521	11523	11525	
Max. depth	~145	121	–	
Max width	96	83	–	
Width art. facet for fibula	26	25	–	
Depth art. facet for fibula	45	36	–	
Width over both art. facets for astragalus	75	72	~70	
Width dist. art. facet for cuboid	~50	–	–	
Astragalus	455	454	11527	11526
Max. width	~83		–	–
Max. depth	90		~66	~56
Max. height	55	30	35	39
Naviculare (Tc)	11528	Mesocuneiforme		11529
Max. width	~70	Max. width		27
Max. depth	~45	Max. depth		–
Max. height	~26	Max. height		24
Ectocuneiforme	11530	11577		
Max. width	39	~30		
Max. depth	59	–		
Max. height	30	–		
Cuboideum (TIV)	11532	11531		
Max. width	78	66		
Max. depth	69	–		
Max. height	30	~28		

for tibia dorsoplantarly convex, encroaching in the medial and lateral sides and with its dorsal margin sigmoid; distal lateral articular facet for calcaneum rounded-triangular, medial one in all specimens damaged or missing; dorso-distal articular facet for navicular transverse-oval and slightly mediolaterally convex (Fig. 15h).

Navicular: One nearly complete navicular (11528) is preserved. Small-sized (Table 11) and of oval shape; proximal facet for astragalus transverse oval and concave; distal facet subdivided in four facets for articulation with distal row of the tarsal bones and cuboid; no palmar facet for articulation with the calcaneum preserved. Tassy (1985) pointed out that such a calcaneo-navicular contact is also missing in *G. angustidens*, whereas it is occasional for *A. filholi* (Fig. 15j, k).

Mesocuneiform: Only a dorsal portion of a mesocuneiforme (11529) is preserved. Shape asymmetric triangular; dorsal facet concave, distal facet flat.

Ectocuneiform: One of the two ectocuneiforms (11530) is complete preserved (Table 11). Bone of symmetric triangular shape; proximal and distal facet dorsoplantarly concave, dorsal facet reflected back along lateral margin; lateral side with proximal and distal long and low facets for cuboid; on medial side large dorsal and smaller plantar facet for mesocuneiform, both connected along distal margin (Fig. 15l–o).

Cuboid: The larger of the two cuboids (11532) is complete. Bone low of triangular shape with lateral corner rounded and lateral margin tapering; on proximal side a smaller round medial facet and a larger oval lateral facet, for navicular and calcaneum, respectively; distal facet only weakly separated in medial and lateral half for articulation with metatarsals IV and V, respectively; medial side flat with long and low proximal facet and shorter distal facet for articulation with ectocuneiform (Fig. 15p–r).

Metatarsal III: One worn metatarsal (11481) is identified as Mt III by the medial proximal facet for articulation with Mt II, which is bifid and disconnected by a deep groove; proximal facet with lateral edge proximally extended and separated in two facets; lateral proximal facet worn.

Phalanges: Two phalanges might belong to the pes, but cannot be affiliated with any particular toe.

Vertebrae

Atlas: The description is mostly based on specimen 11536, which is nearly complete and lacks only the ends of both alae atlantes, which rise laterally. Vertebrale foramen is 8-shaped with the dorsal opening wider; dorsal arch dorsally

characterized by a high domed, transverse crest about 10 cm wide, with high and distinct lateral angles, but a very small tuberculum ventrale; foveae articulares craniales kidney-shaped and concave; the caudal ones being flat and round with a little angle medially; fovea dentis in ventral side of foramen vertebrale broad and oval; foramen alare piercing dorsal arch in its cranial half and running straight medially into the foramen vertebrale; tuberculum ventrale on ventral arch forming a blunt protuberance, only very little projecting caudally; foramen transversarium opens caudally at level of mid-height of the fovea articularis caudalis (Fig. 14l, Table 12).

Interestingly, a second atlas (11537), which is bigger, is distinguished from 11536 by the absence of a dorsal transversal crest on the dorsal arch; instead, there is a blunt tubercle laterally next to the tuberculum dorsale. It is difficult from this small sample to decide if this differing morphology is due to age or sexual dimorphism or if it is of systematic importance. However, Olsen (1979: fig. 5) shows these differing atlas morphologies also for the American Mastodon (*Mammot americanum*) and the Woolly Mammoth (*Mammuthus primigenius*), in which the first has a dorsal bump and the latter a dorsal transversal crest. Therefore, 11537 is attributed to the mammutid *Zygodolophodon* (see below).

Thoracic vertebrae: 11550 is from the cranial part of the thoracic vertebral column (T4–T6), because of its long spinous process and because the transverse processes are situated relatively high. Both ends of the vertebral body oval, the cranial one slightly convex, the caudal one slightly concave; foveae costales caudales almost twice the size of cranial ones; processus articulares craniales and caudales minimally projecting with articular facets being quite large, oval, and oriented horizontally; cranial margin of dorsal arch deeply notched caudally between cranial processus articulares; spinous process very long, caudally inclining and its caudal side deep concave (Fig. 14g, k, Table 12).

16195 is of a very similar morphology, but the spinous process, even if not complete, seems to be a little shorter and slightly more inclined caudally. Thus, this specimen probably had a position in the vertebral column slightly caudal to 11550. Transverse process in 16195 squeezed craniocaudally.

16196 is one of the anteriormost thoracic vertebrae, because of the only slightly caudally inclined dorsal arch and long spinous process, the large triangular foramen vertebrale, and the more lateroventral position of the transverse processes. Cranial articular processes projecting moderately cranially, its cranial facets horizontal, caudal ones rising caudally and oriented caudoventrally.

Specimen 16194 is nearly complete but badly crushed; probably, it was positioned in the cranial third of the thoracic vertebral column.

Table 12 Measurements (in mm) of vertebrae of *G. subtapiroideum* from Sandelzhausen (measurements after Göhlich 1998)

Measurements				
Atlas	11536			
Max. height	140			
Width over foveae craniales	140			
Height of foveae craniales	80			
Width over foveae caudales	132			
Height of foveae caudales	54			
Width foramen vertebrale	68			
Height foramen vertebrale	75			
Length arcus dorsalis (mid)	44			
Vertebrae thoracicae	11538	11550	16194	16195
Width over proc. transversi	~168	~200	~200	~225
Width extrem. cranialis	66	~80		~80
Width extrem. caudalis	~75	~75	80	~80
Width over proc. art. cran.	~75	92		–
Width over proc. art. caud.	–	~95	~75	~105
Length over proc. cran. and caud.	–	~77	–	–
Height/length proc. spinosus	–	>320	>260	>270
Width foramen vert. cran.	~140	–	–	–
Width foramen vert. caud.	125	143	–	–
	16196	16197	11542	
Width extrem. caudalis	~130			
Width over proc. art. caud.	~85			
Length over proc. cran. and caud.	72			
Height/length proc. spinosus	>230	>280	>360	
Vertebra lumbalis	11539		Sacrum	11540
Width over proc. transversi	180		Length	~170
Width extrem. cranialis	87			~85
Width extrem. caudalis	94			
Width over proc. art. caud.	52			
Length over proc. cran. and caud.	~90			
Height/length proc. spinosus	~90			

Two long, but fragmentary spinous processes (11542, 16197) represent other thoracic vertebrae also of (probably) the caudal third of the thoracis series.

Specimen 11538, which lacks a spinous process, is probably from the cranial half of the thoracic vertebral column. The cranial end of its vertebral body is almost round, the caudal end oval; cranial foveae costales large, caudal ones only somewhat smaller; foramen vertebrale relatively small; transverse process short and stout and situated high (laterodorsally) on the dorsal arch; facets on cranial articular process flat, oval, and horizontally oriented.

Lumbar vertebrae: One lumbar vertebra is preserved (11539); its body is somewhat deformed. Cranial and caudal end of the vertebral body oval, with their dorsal

margins flattened; transverse process relatively slender and rising laterally; facets of cranial and caudal articular processes strongly inclined medially and laterally, respectively; no processus mamillares developed; dorsal arc craniocaudally elongated and carrying a low median crest becoming caudally the spinous process, but which is broken (Fig. 14m, Table 12).

Sacrum: A fragmentary and badly deformed sacrum (11540) is made of three vertebrae, but it is unclear if this is the complete set. Cranial end of the vertebral body oval and flat; alae sacrales laterally broken; only a fragmentary remnant of the right cranial articular process is preserved; each dorsal arch carrying a laterally flattened spinous process, but which are all incomplete (Fig. 14j, Table 12).

Ribs: Several rib fragments were found in Sandelzhausen; only a few of them have their proximal head and/or the tuberculum costae preserved.

Family Mammutidae Hay, 1922

Genus *Zygodont* Vacek, 1877

Zygodont turicensis (Schinz, 1824)

Synonymy: see Göhlich (1998).

Original diagnosis: Schinz (1824: 248).

Emended diagnosis: Tassy (1985: 480f).

Holotype: m2 (PIMUZ AV 40), illustrated in Schinz (1833, pl. 1 fig. 1); v. Meyer (1867, pl. 2 figs. 5–6); Tobien (1975: fig. 14); Hünermann (1983: fig. 1).

Paratypes: P3 + P4 sin. (PIMUZ A/V 45), illustrated in Schinz (1833, pl. 1 figs. 1, 2, 3).

Type locality: Elgg (Lignites), near the city of Winterthur, canton Zürich, Switzerland, Middle Miocene (MN6 or 7)

Stratigraphic and geographic distribution: *Z. turicensis* is recorded from Eurasia from the Early to the Late Miocene, MN3b up to MN10 (Ginsburg and Bonneau 1994: 326; Mein 1999; Tassy 1985: 480). Tassy (1985, fig. 213) attributed a single molar-fragment from the Early or Middle Miocene of northern Africa (Jebel Cherichera, Tunisia) to *Z. turicensis*, but which was recently determined as *Zygodont* sp. by Pickford (2007).

Remarks: A detailed treatise on the zygodont molar structure and on the Mammutidae in general was published by Tobien (1975, 1996). In general, the taxon *Z. turicensis* is much rarer in the European Miocene than bunodont gomphotheres. Also, the tendency of molar enlargement during the Miocene in gomphotheres is not proved yet for mammutids. But there is a significant variability in crown morphology and proportions (Tassy 1985: 487f), even if not as strong as in bunodont gomphotheres (Tassy 1977c: 1390). Following Tassy (1985: 487, 491), the amplitude of morphological variability stays about the same during the entire Miocene.

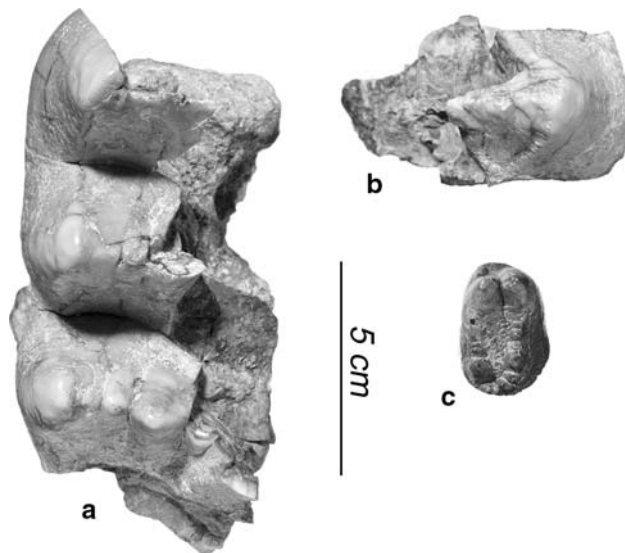


Fig. 16 Molars and premolar of *Zygodontodon turicensis* (Schinz, 1824) from Sandelzhausen (Invent. no. 1995 II ...). **a** m3 sin. (339); **b** M3? sin. fragment (43); **c** p3 dext. (11342)

The presence of *Z. turicensis* in the Upper Freshwater Molasse was first described by Schlosser (1917: 116ff); he described parts of a skeleton and teeth of one individual from the locality of Tutzing (BSP 1912 I 26), (see also Dehm (1955: 9), Lehmann (1950, pl. 14 figs. 28, 29), Osborn (1936: 697f), Schlosser (1917: 116ff) and Stromer (1940: 62)), which, however, was destroyed during World War II. The skull portion with dentition from Freising (BSPG 1879 II 18), illustrated in Lehmann (1950, pl. 14 figs. 26, 27) and Osborn (1936, fig. 657) met the same fate. Göhlich (1998) described some isolated teeth of *Z. turicensis* from different Middle to Late Miocene localities from the Upper Freshwater Molasse of southern Germany.

Material: p3 dext? (11342); fragment of m3 dext., three anterior posttrite half-lophs (399, see also Schmidt-Kittler 1972: 89f); one posttrite half-loph of a probable M3? sin.? (43); right lateral portion of atlas with dorsal arch (11537).

Description and comparison

p3 (Figs. 5a, 16c): Measurement for p3 see Table 2.

Crown unworn, of oval shape, slightly broadened and strongly lowered towards the posterior; protoconid and metaconid strong and high; two longitudinal, crenulated crests running almost parallel from the posterior basal flanks of the protoconid and metaconid to the hypoconid and entoconid, respectively; hypoconid and entoconid weak, barely individualized and only slightly stronger than the denticles within the crenulated crest; hypoconid somewhat higher than entoconid; posterior cingulum originating from hypoconid, weak and short anterior cingulum (almost running vertically) on anterior base of metaconid.

A single p3 found in Rajégats (France, Middle Miocene, MN7) (Tassy 1985: 484, Fig. 192), has previously been attributed to *Z. turicensis*. It corresponds well in occlusal morphology with that of Sandelzhausen; however, the Rajégats tooth is larger (Fig. 6). The crown structure in 11342 is less bunodont than in p3 of *G. subtapiroideum* from Sandelzhausen or in *G. angustidens* from En Pélouan (France), insofar as both longitudinal crests, including the hypoconid and entoconid, are weaker and consist of small tubercles. The p3 of *G. subtapiroideum* from Sandelzhausen, even if worn, also reveals thicker and more bunodont longitudinal crests and a stronger hypoconid and entoconid. In size, the p3 from Sandelzhausen attributed to *Z. turicensis* plots (Fig. 6) between those of *G. subtapiroideum* from Sandelzhausen, *G. angustidens* from En Pélouan, and *A. filholi* from Bézian, but is distinctly smaller than the p3 of *Z. turicensis* from Rajégats.

M3? (Fig. 16b): A probable portion of a M3 is represented only by one posttrite half-loph. However, its sharp-crested shape and the distinct anterior and posterior posttrite zygodont crests permit assignment of this fragment to *Z. turicensis*.

m3 (Fig. 16a): In the m3, the first three posttrite half-lophids are present; in the third lophid a portion of the pretrite half-lophid is preserved. The lophids are quite zygodont, are arranged obliquely, show no chevrons (V-shaped arrangement of half-lophids), and exhibit on the anteriormost preserved lophid a weak pretrite zygodont crest. This combination of characters enables determination as *Z. turicensis*.

Atlas: A right lateral portion of an atlas (11537) is not only bigger than a nearly complete atlas described as *G. subtapiroideum* (11536), but morphologically differs from the latter by forming a blunt hump on the dorsal arch laterally aside the tuberculum dorsale instead of a distinct dorsal transversal crest in 11536. As already mentioned above, these distinctly differing morphologies were also shown by Olsen (1979: fig. 5) for the atlases of the American Mastodon (*Mammot americanum*) (dorsal tubercle) and the Woolly Mammoth (*Mammuthus primigenius*) (transversal crest). Thus, the dorsal tubercle is interpreted to be a feature for mammutids, and therefore 11537 is attributed to *Zygodontodon*.

Discussion and conclusion

Two proboscidean taxa are represented in the fossil vertebrate fauna from Sandelzhausen: *Gomphotherium subtapiroideum* and *Zygodontodon turicensis*.

Remains of 147 cheek teeth and 57 tusks represent a minimum of about 120 individuals. Furthermore, 115 skeletal elements and bone fragments are present. By far

the greatest number of dental remains (144 cheek teeth and all tusks) is identified as belonging to *G. subtapiroideum*, to which nearly all of the postcranial material is attributed (except one portion of an atlas). One lower tusk is more dorsoventrally flattened than the others and resembles in this aspect those of *Archaeobelodon filholi*. However, this differing morphology is interpreted as variability (see discussion in section on lower tusks).

G. subtapiroideum has long been a controversial taxon, as are some other taxa (e.g., “*T.*” *ratibonensis* see below). However, morphological and metrical comparisons of the described dental material result in a combination of features which do not fit with those of *G. angustidens* or *A. filholi*, but corresponds best with *G. subtapiroideum*. Metrical investigations (Figs. 3, 6, 9) show remarkable variability for all of the taxa considered. Several of the diagrams of premolars and molars seem to show, however, two size clusters for the teeth from Sandelzhausen, but the number of teeth is too small for this to be significant. These clusters might indicate simply variability, or perhaps represent male and female specimens. It is conceivable that there might be a better metric differentiation of taxa when considering gender.

It is apparent that it is difficult, and sometimes impossible, to distinguish Early and Middle Miocene gomphotheri taxa in single tooth positions, but nevertheless the combination of features concerning the entire dentition per taxon exhibits some differences.

The cheek tooth crown pattern of *G. subtapiroideum* is usually slightly less bunodont than in *G. angustidens*, a character which is admittedly relatively subjective and is obscured with attrition. In several tooth positions (d3, D3, d4, D4, p3, m3) the teeth of *G. subtapiroideum* are, relatively, slightly wider than those of *G. angustidens* and *A. filholi*. In all cases, except for the m2, the Sandelzhausen material overlaps with that of *G. subtapiroideum* from its type locality Eibiswald (Austria). *Gomphotherium subtapiroideum* from Sandelzhausen also differs from *G. angustidens* by (predominantly) straight lower permanent tusks with the tip smoothly worn (slightly upcurved and with a concave wear facet at the tip in *G. angustidens*) and by non-helicoidal upper permanent tusks with the enamel band laterally on the tip (enamel band helicoidal, thus ventrally on the tip, in *G. angustidens*). Some specimens of d4 and D4 of *G. subtapiroideum* from Sandelzhausen show a diagonal contact of the posterior pretrite crescentoid of the 1st lophid and the anterior posttrite crescentoid of the 2nd lophid; this feature is occasional and also sometimes developed in *G. angustidens*, but has never been observed in *A. filholi* and *G. sylvaticum*. *Archaeobelodon filholi* also differs by the occasional development of posttrite conules (Tassy 1985), which are not typical and if present only very weak in *G. subtapiroideum* from Sandelzhausen. The most

diagnostic feature for *A. filholi* is the flattened lower permanent tusk.

Very few differences have been observed between *G. subtapiroideum* from Sandelzhausen and *G. sylvaticum* in the morphology of the dentary. There are metric differences in some tooth positions, but as the latter taxon is only poorly known, the significance of these should be more rigorously tested in the future when more material is available.

Some unworn deciduous and permanent molars show weak posttrite “zygodont-crest”-like structures, normally, when more distinct, which are more distinct and typical for *Zygolophodon* and *Mammut*; those structures are not essentially interpreted as indicating assignment of those specimens to Mammutidae, as they are also known from other bunodont taxa and localities (e.g. in some M1 of *G. cf. steinheimense* (Göhlich 1998), or a tetralophodont M1 of *T. longirostris* from Eppelsheim, HLMD Din 523).

The molars from Viehhausen (Germany) described by Rinnert (1956) as the new species “*T.*” *ratibonensis* fall in the size range of *G. subtapiroideum* from Sandelzhausen and from the type locality Eibiswald (Fig. 9) and also correspond well to them morphologically. In contrast with Rinnert’s (1956) description of the upper tusks of “*T.*” *ratibonensis* that the lateral enamel band turns ventrally on the tip, my own observations of the type material could not confirm this, but showed a lateral position until the tip, as also observed for *G. subtapiroideum* from Sandelzhausen. Therefore the validity of the taxon “*T.*” *ratibonensis* must be questionable. Additional postcranial comparisons will be necessary to further address this problem. However, the molars from Viehhausen (Germany) attributed by Rinnert (1956) to “*S.*” *subtapiroideum* are mostly larger than those from Sandelzhausen or Eibiswald (Fig. 9).

Postcranial features are poorly known, as there is little material that is identifiable or attributable to a particular taxon. In the Sandelzhausen material, the calcaneum and navicular exhibit no facets for a calcaneo-navicular contact, corresponding to the condition in *G. angustidens*, whereas such a contact is occasional for *A. filholi* (Tassy 1985).

Body mass estimations for *G. subtapiroideum* from Sandelzhausen (Table 13), using minimum limb bone shaft circumferences (and occasionally minimum shaft depth) range between 1,050 and 2,228 kg for subadults to adults. Two juvenile bones give a much lower weight of around 700 kg. Translating the relationship of body masses and shoulder heights of the extant Asian elephant *Elephas maximus* (Christiansen 2004) into the fossil data from Sandelzhausen, results in shoulder heights of about 1.5–2 m for subadults to adults of *G. subtapiroideum*, given that the physique of the two taxa might be similar. Therefore, the body mass estimate for *G. subtapiroideum* is

Table 13 Body mass estimates for *G. subtapiroideum* by means of the available limb bones from Sandelzhausen, according to Christiansen (2004, 2007)

Skeletal element	Inventory no.	Min. circumference or depth* of diaphysis (mm)	$\log(\text{mass}) = a + b(\log X)$	Body mass (kg)
Humerus	1959 II 11451	252	$-1.598 + 2.062(\log 252)$	Mean 2228
	"	82*	$-0.503 + 2.009(\log 82)$	
	1959 II 11452	192	$-1.598 + 2.062(\log 192)$	Mean 1250
	"	61*	$-0.503 + 2.009(\log 61)$	
Ulna	1959 II 11457	148	$-1.349 + 2.022(\log 148)$	1094
	1959 II 11454	145	$-1.349 + 2.022(\log 145)$	1050
(juv.)	1959 II 11372	118	$-1.349 + 2.022(\log 118)$	692 (juv.)
	1959 II 11387	190	$-1.349 + 2.022(\log 190)$	1814
Radius	1959 II 11462	88	$-0.754 + 2.001(\log 88)$	1370
	1959 II 11461	95	$-0.754 + 2.001(\log 95)$	1597
Tibia	1959 II 11578	173	$-2.724 + 2.647(\log 173)$	1585
Femur (juv.)	1959 II 11510	42*	$-0.912 + 2.315(\log 42)$	700 (juv.)

Values with an asterisk are those for the depth of the diaphysis

less than that calculated by Christiansen (2004: Table 6) for *G. angustidens* (2,957–4,104 kg) and *A. filholi* (2,350–3,477 kg).

As shown by Calandra, Göhlich, and Merceron (2008, 2010), dental microwear analyses of *G. subtapiroideum* reflect mixed feeding preference. The microwear signatures of different proboscidean taxa (Calandra, Göhlich, and Merceron 2008) indicate that probably even slight differences in the food spectrum enabled different gomphotheres to be sympatric, and to avoid direct food competition. No diet change is observed in different ontogenetic stages of *G. subtapiroideum* (Calandra, Göhlich, and Merceron 2010).

Zygodolophodon turicensis is poorly represented (~2% of the dental remains, three cheek teeth) in the Sandelzhausen proboscidean sample. This is not exceptional, as in general in the European Miocene mammutids were far less common than gomphotheres and deinotheres and less diversified than the bunodont forms. In most European Miocene localities, where *Zygodolophodon* is found together with gomphothere and deinotheres taxa, the first is much less represented than the last two. The evidence of *Z. turicensis* of Sandelzhausen (MN5) is the oldest record in Central and Eastern Europe.

Worth mentioning is the lack of deinotheres in Sandelzhausen. *Prodeinotherium* is the first representative of European deinotheres which invaded Europe from Africa during the Early Miocene, probably shortly after *Gomphotherium* and *Zygodolophodon* (Tassy 1990, 1996b), and persisted until the early Late Miocene (Huttunen 2001, Table 1). *Prodeinotherium* is known in southern Germany from the Early Miocene localities Baltringen (MN4, personal communication K. Heissig), Langenau 1 (MN4, Heizmann, Ginsburg, and Bulot 1980: 4), and Rauscheröd

(MN4, Ziegler and Fahlbusch 1986: 9). Thus, this species had already colonized the southern German region before the deposition of the Sandelzhausen sediments. However, Dehm (1951, 1955), who based the stratigraphic tripartition of the Bavarian Upper Freshwater Molasse in “Ältere Serie” (MN4–5), “Mittlere Serie” (MN5–6) und “Jüngere Serie” (MN8–9) by means of proboscideans, defined the “Ältere Serie” by the presence of *G. angustidens* but the lack of *P. bavaricum*. The deposits of Sandelzhausen belong to the “Ältere Serie”. On the other hand, Eronen and Rössner (2007, Appendix) list several European MN5 localities in which *P. bavaricum* is present. But it is unclear if the latter are stratigraphically younger MN5 localities than Sandelzhausen or not. If this were to be the case, the definition of Dehm (1951, 1955) of the “Ältere Serie” could still work.

Because *Gomphotherium*, *Zygodolophodon*, *Archaeobelodon* and *Prodeinotherium* are known to be sympatric in several Early and Middle Miocene localities, it can be ruled out that the absence of *Prodeinotherium* in Sandelzhausen is because of the competition with these taxa. The only conceivable reason for the absence of *Prodeinotherium* in Sandelzhausen might be a very specific ecological factor of the early middle MN5 in the Bavarian Upper Freshwater Molasse Basin.

The composition of the proboscidean fauna from Sandelzhausen is remarkable for the disproportionately high ratio of juvenile milk teeth. As Fig. 17 shows, about the half of the specimens found in Sandelzhausen represent juveniles (60 milk teeth versus 59 molars). This might be accounted for in several ways. This ratio probably does not represent the palaeodemographic composition of a gomphothere herd, as extant elephant flocks are dominated by adults (sexually mature) and older adolescents which care

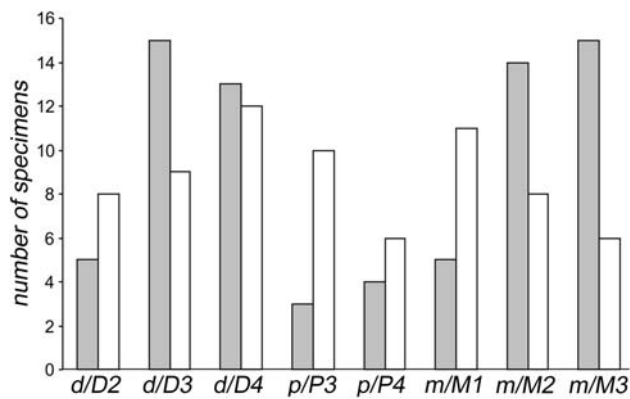


Fig. 17 Frequency of the different cheek teeth of proboscideans from Sandelzhausen

for a few juveniles. One natural reason might be the general higher mortality of juveniles. In extant African elephants mortality within the first year of their life reaches 36%, then until the age of five years it declines to about 10% and further until the age of 40 years to about 3% (Shoshani 1992: 102). Infectious diseases and drought are the usual causes of juvenile-dominated proboscidean mortality in Africa (Shoshani 1992, Sanders personal communication). As in extant elephants, juvenile gomphotheres also had a higher risk of predation than full-grown ones (even if there is no evidence for bite marks in the proboscidean material of Sandelzhausen), or they might have become more easily trapped in the “swampy” sediments of a meadow environment with temporary ponds embedded in a braided river system, the habitat supposed for the Sandelzhausen area and its fossil fauna.

However, the juvenile-dominated composition could also be because of taphonomic factors. Milk teeth are smaller and lighter; thus lower transport energy is necessary to accumulate them in some deposit horizons when the energy might not be high enough to transport heavier and larger items. However, almost none of the specimens show fluvial abrasion that would indicate substantial transport.

For somewhat more than half of the dental specimens, the exact finding position within the geological section of Sandelzhausen is known. By far most of these proboscidean specimens have been found in the deposits below the so called “coal-layer”, predominantly in layer A and B and occasionally C1 (Moser et al. 2009); only a few dental remains have been found in layers C3 and the base of layer D, above the coal layer. Those specimens found above the “coal layer” are all small teeth such as milk teeth, small premolars, and, rarely, small molars (m1). The same tendency holds true for the bone remains. This kind of sorting with most of the proboscidean remains and larger teeth and bones in the lower deposits and smaller proboscidean remains in the higher layers corresponds well with gradual upwards decreasing depositional energy, which is also

reflected by the sedimentological interpretation of the section (Fahlbusch and Gall 1970; Moser et al. in prep.). Thus, the smaller size and weight of the milk teeth give them a higher chance of being not only deposited in the high-energy levels but also in the lower-energy levels.

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