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Research article

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A taxonomic and morphological re-evaluation of “*Halitherium*” *cristolii* Fitzinger, 1842 (Mammalia, Sirenia) from the late Oligocene of Austria, with the description of a new genus

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Abstract. The fossil sirenian material from the upper Oligocene Linz Sands of Upper Austria is reviewed and re-described in detail following a recent approach on the invalidity of the genus *Halitherium* Kaup, 1838. This morphological study provides the first evidence for the synonymy of “*Halitherium*” *cristolii* Fitzinger 1842, “*H.*” *abeli* Spillmann, 1959 and “*H.*” *pergense* (Toula, 1899), supporting the hypothesis that only a single species inhabited the late Oligocene shores of present-day Upper Austria. In the course of the taxonomic revision of the “*Halitherium*” species-complex, this taxon is now assigned to the new genus *Lentiarenium* Voss gen. nov. It represents a more derived sirenian compared to Eocene and early Oligocene taxa distributed across Central Europe and North Africa, which is in accordance with the stratigraphical data. An updated inventory list of all identifiable and referable skeletal material is provided, including a detailed synonymy list for the new taxonomic combination.

Keywords. Sea cows, Oligocene, Austria, morphology, taxonomy.

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Introduction

The upper Oligocene sands from the Linz Basin in northern Austria are well-known for producing fossils belonging to the marine mammal group Sirenia, or sea cows. Linz is likewise the type locality of a late Oligocene sirenian species, *Halitherium cristolii* Fitzinger, 1842, the intra- and interspecific diversity of which has long been a subject of controversial debate.

In this study, the sirenian species from Linz is taxonomically revised. The genus *Halitherium* Kaup, 1838 has served as a wastebasket name for a variety of Eocene to Pliocene sirenian fossils found worldwide (Domning *et al.* 2010), and *H. cristolii* was traditionally being considered as one of three valid European *Halitherium* species (Domning *et al.* 2010; Voss 2012), although none of them are sister taxa (e.g., Velez-Juarbe & Domning 2015). At the same time, this species was also hypothesised as a potential member of the *Metaxytherium*-species complex (Laurillard 1846; Domning *et al.* 2010). The need for a revision of the genus *Halitherium* was recently also demonstrated by Voss (2014, and references therein) by pointing out that its early Oligocene type species, *Halitherium schinzii* Kaup, 1838, is a *nomen dubium*. As a result, this taxon name is not applicable to any other species previously assigned to congeneric taxa and thus the genus name *Halitherium* becomes unavailable and is, apart from the synonymy list, subsequently given between quotation marks.

“*Halitherium*” *cristolii*, named after the French palaeontologist Jules de Christol, was established by Fitzinger in 1842 and considered to represent the only sirenian species in Linz and the surrounding area. Subsequently, this hypothesis was challenged by Toula (1899), who additionally described the new species *Metaxytherium pergense* (Toula, 1899) on the basis of a fragmentary skull roof and natural endocranial cast from coeval sediments from the town of Perg, situated some 25 km from Linz. Conversely, Abel (1904) assigned all finds from northern Austria to a single species, “*H.*” *christoli* [sic], and attributed skeletal differences to intraspecific variability or ontogeny. Spillmann (1959) revived the debate on the splitting and lumping of sirenian taxa from the Linz Basin in that he distinguished three sirenian morphospecies. In addition to “*H.*” *christoli* [sic], this author confirmed the validity of *M. pergense*, in the combination “*Halitherium*” *pergense*, and simultaneously proposed a new species, “*Halitherium*” *abeli* (Spillmann, 1959), mainly based on a lower jaw from Linz. Today, only a single species is regarded as valid since Domning (1994, 1996) and Domning *et al.* (1994) subjectively synonymised both taxa under “*H.*” *christoli* [sic]. However, this synonymy has not been validated.

The present paper aims at testing Domning’s (1996) hypothesis by providing a morphological re-evaluation of all available material referred to, and synonymised under, “*H.*” *cristolii*, and hence to gain a largely objective basis for the lumping of taxa. Consequently, a new genus is established for the Linz species by providing an up to date synonymy. A cladistic analysis reflecting the results presented herein in a phylogenetic framework as performed in Voss (2013) is in progress to be published, but is not within the scope of this paper.

Geological setting

The area around Linz (Fig. 1) is geologically situated in the Molasse Zone of Upper Austria, between the crystalline basement of the Bohemian Massif in the north, and the main overthrust of the Alpine orogenic front in the south (e.g., Peschel 1982; Steininger *et al.* 1996; De Ruig & Hubbard 2006). It forms part of the North Alpine Foreland Basin (NAFB) and is a classical asymmetric foredeep that was formed as a result of the collision between the Apulian continental microplate and the North European craton (De Ruig & Hubbard 2006; Steininger *et al.* 1996). The northern part of the Molasse Basin in Upper Austria contains marine and terrestrial deposits of Oligocene to Pliocene age. In the Kiscellian to Egerian (i.e., Chattian to Aquitanian), well-sorted, shallow-marine and deltaic sands were deposited along the northern margin of the eastern NAFB (Peschel 1982; Rupp 2011). These sands, which yielded the sirenian skeletal remains of “*H.*” *cristolii* that form the focus of the present paper, are commonly referred to as “Linzer Sande” (Linz Sands) (Fig. 1), and are part of the Linz-Melk Formation (Rupp 2008: 56).

Spanning the upper Kiscellian and entire Egerian (i.e., Chattian to Aquitanian), the Linz-Melk Formation is insufficiently defined at present (Rupp 2011). Although numerous outcrops of coastal sandstones and unconsolidated sands exist along the northern margin of the NAFB, these are usually small and difficult

to correlate with more completely preserved formations of the deeper Molasse Basin. Moreover, recent studies show that these distal deposits are younger than previously recognised (e.g., Grunert *et al.* 2015). Based on the fossil content of the Linz Sands, however, which includes, e.g., age-diagnostic foraminifera (Rögl & Steininger 1969), mollusc faunas (Grill 1935) as well as allochthonous terrestrial mammals (Sickenberg 1934; Spillmann 1969), the coastal sediments that crop out within the city limits of Linz are still being regarded as lower Egerian (= upper Chattian). The well-cemented sandstones occurring further east along the northern margin of the NAFB, such as those of Wallsee and near the town of Perg, the type locality of “*H.*” *pergense*, are today considered as stratigraphic and lateral facies equivalents of the Linz Sands (Krenmayr & Roetzel 2000; Rupp 2011).

Material and methods

The fossil sirenian specimens stored in the Geoscience Collections of the Oberösterreichisches Landesmuseum Linz in Austria (OLL) were collected during the 19th and early 20th centuries from the lower Egerian (late Chattian) Linz Sands of the Linz-Melk Formation in the Linz and Perg regions in the Federal State of Upper Austria. All specimens were personally examined following a thorough morphological and morphometric approach. The focus was placed on the investigation of holotypes and on well-preserved associated material. Isolated elements such as teeth and individual bones were also considered if appropriate.

The macroscopic descriptions consider the cranial and postcranial osteology making up the basis for the morphological re-evaluation of the Linz species. Measurements were carried out with either a digital

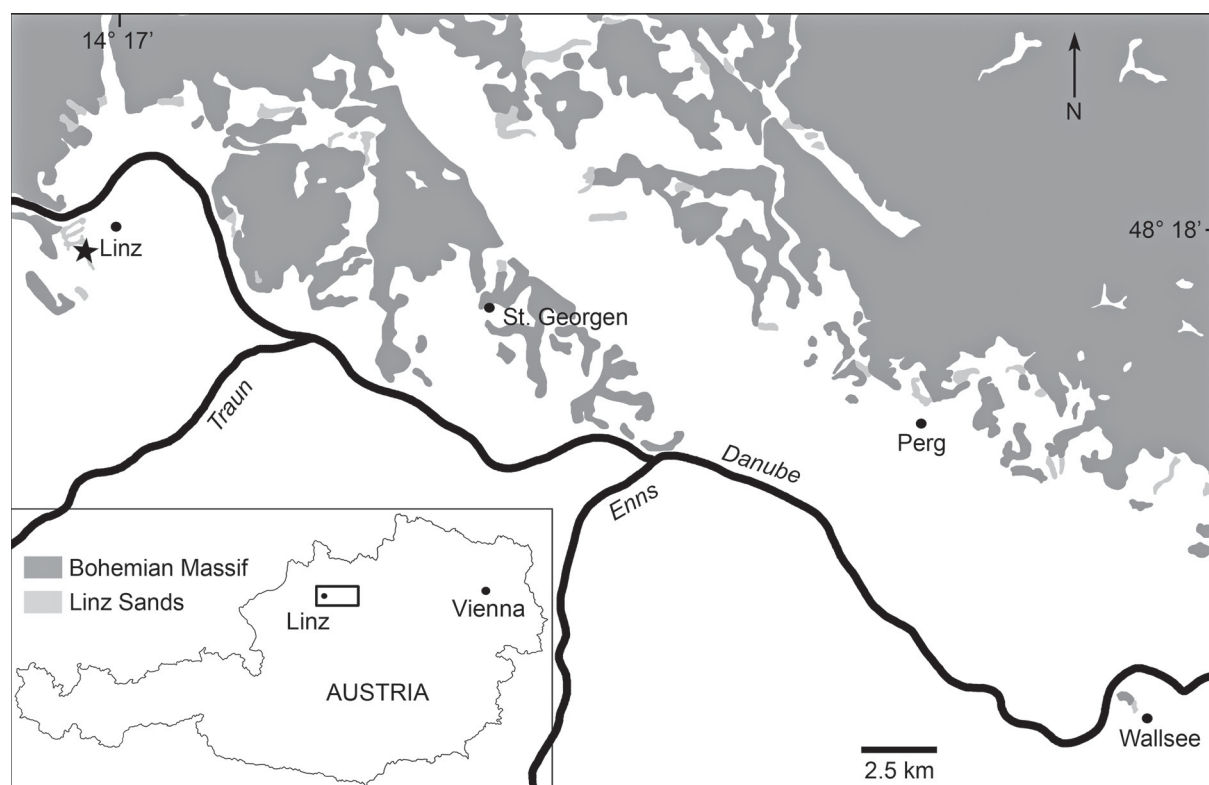


Fig. 1. Geographic and geologic overview of the Linz region, including the localities of St. Georgen/Gusen, Perg and Wallsee. Asterisk indicates approximate type locality of *Lentiarenium cristolii* (Fitzinger, 1842).

calliper of standard size (max. 150 mm) or a large scale caliper (up to 200 cm). All measurements are quoted in millimetres, unless otherwise stated, and are listed in Tables 2–5.

Images were taken with a digital camera in all relevant views, mostly using the macro-function under normal light, or on a special photo-desk with camera-stand and lights. Line drawings of important skeletal elements, especially cranial remains in different views complement the documentation of the fossil Sirenia.

Additionally, in the course of the investigations the severely damaged, historical *in situ* arrangement of the postcranial skeleton OLL 1854/327, which was first reported and figured by Ehrlich (1855: pl. 1), was restored and reconstructed (Reiter & Mittermayr 2013).

Anatomical abbreviations

| | | |
|-------------|---|--|
| a | = | acromion |
| ac | = | anterior cingulum |
| amef | = | accessory mental foramen |
| amr | = | ascending mandibular ramus |
| as | = | alisphenoid |
| bf | = | bony falx cerebri |
| bigr | = | bicipital groove |
| bl | = | break line |
| bs | = | basisphenoid |
| C1–7 | = | cervical vertebra 1–7 |
| cap | = | caput |
| cnf | = | coronoid foramen |
| cnp | = | coronoid process |
| colsc | = | collum scapulae |
| corp | = | coracoid process |
| decr | = | deltoid crest |
| dh | = | diaphysis of humerus |
| DP1–5/dp1–5 | = | upper/lower deciduous premolar or alveolus 1–5 |
| e | = | ethmoid |
| eam | = | external auditory meatus |
| exocr | = | external occipital crest |
| exopr | = | external occipital protuberance |
| f | = | frontal |
| fproc | = | frontal process |
| fpsut | = | frontoparietal suture |
| fs | = | fracture surface |
| gcav | = | glenoid cavity |
| gt | = | greater tubercle |
| hmr | = | horizontal mandibular ramus |
| hy | = | hypocone |
| ifsut | = | interfrontal suture |
| ispf | = | infraspinous fossa |
| j | = | jugal |
| lt | = | lower tubercle |
| M1–3/m1–3 | = | upper/lower molar or alveolus 1–3 |
| ma | = | mandibular angle |
| mas | = | masticating surface |

| | | |
|-----------|---|--|
| mc | = | mandibular condyle |
| mcan | = | mandibular canal |
| mcaud | = | margo caudalis |
| mcl | = | metaconule |
| mcran | = | margo cranialis |
| mdf | = | mandibular foramen |
| me | = | metacone |
| mef | = | mental foramen |
| mfos | = | mandibular fossa |
| ml | = | metaloph |
| msym | = | mandibular symphysis |
| mx | = | maxilla |
| ncr | = | nuchal crest |
| os | = | orbitosphenoid |
| p | = | parietal |
| P1–5/p1–5 | = | upper/lower premolar 1–5 |
| pa | = | paracone |
| pal | = | palatine |
| pb | = | posterior basin |
| pc | = | posterior cingulum |
| per | = | periotic |
| pet | = | petrosal |
| pgp | = | postglenoid process |
| pl | = | protoloph |
| pr | = | protocone |
| prl | = | protoconule (= paraconule according to Thenius (1989)) |
| prv | = | processus retroversus |
| ps | = | presphenoid |
| pt | = | pterygoid |
| ptp | = | pterygoid process |
| ptymp | = | posttympanic process |
| rart | = | articulation for rib |
| scsp | = | scapular spine |
| so | = | supraoccipital |
| sop | = | supraorbital process |
| sq | = | squamosal |
| sqzp | = | zygomatic process of squamosal |
| sr | = | sigmoid ridge |
| sspf | = | supraspinous fossa |
| tcr | = | temporal crest |
| to | = | tentorium osseum |
| tproc | = | tentoric process |
| trsul | = | transverse sulcus |
| tub | = | tuberculum |
| tv | = | transverse valley |
| v | = | vomer |
| zobr | = | zygomatic-orbital bridge |

Institutional abbreviations

OLL = Oberösterreichisches Landesmuseum Linz, Austria

UF = Florida Museum of Natural History, University of Florida, Gainesville, USA
MNHN = Muséum national d'Histoire naturelle, Paris, France
NHMW = Naturhistorisches Museum Wien, Vienna, Austria

Results

Systematic Palaeontology

Following Voss (2014), the subfamily Halitheriinae Carus, 1868, in which “*H.*” *cristolii* was originally grouped, is not considered in the systematic scheme provided below. This taxon proved to be invalid for two reasons: 1) the type genus *Halitherium* is declared a *nomen dubium*, and 2) this subfamily is considered paraphyletic in all known studies (e.g., Domning 1994; Velez-Juarbe *et al.* 2012; Springer *et al.* 2015), and this study aims at using a classification comprising only monophyletic taxa. The family Dugongidae Gray, 1821 has also been considered to be paraphyletic as, for instance, in the phylogenetic analyses by Domning (1994) and Voss (2013), who included an extensive set of taxa representing the order Sirenia. In contrast, although a number of dugongid taxa were neglected, such as the multispecific genera *Eosiren* and *Prototherium*, Springer *et al.* (2015) included representatives of all major groups and recovered the Dugongidae as monophyletic. Other recent works using smaller datasets (e.g., Velez-Juarbe & Domning 2014a, 2015) support this hypothesis and consider the taxon studied herein as a member of the family Dugongidae.

Class Mammalia Linnaeus, 1758
Superorder Afrotheria Stanhope *et al.*, 1998
Mirorder Tethytheria McKenna, 1975
Order Sirenia Illiger, 1811
Family Dugongidae (Gray, 1821)

Genus *Lentiarenium* Voss gen. nov.

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Type species

Halitherium cristolii Fitzinger, 1842

Diagnosis

Dugongid based on the following combination of synapomorphies: absence of alisphenoid canal, open *foramen ovale*, loss of permanent fifth premolar, and squamosal reaching temporal crest. Differs from the Dugonginae (*Crenatosiren* Domning, 1991, *Nanosiren* Domning & Aguilera, 2008, *Dugong* Lacépède, 1799, *Rytiodus* Lartet, 1866, *Corystosiren* Domning, 1990, *Callistosiren* Vélez-Juarbe & Domning, 2015, *Bharatisiren* Bajpai & Domning, 1997, *Domningia* Thewissen & Bajpai, 2009, *Kutchisiren* Bajpai, Domning, Das, Vélez-Juarbe & Mishra, 2010, *Dioplotherium* Cope, 1883 and *Xenosiren* Domning, 1989), the Hydrodamalinae Simpson, 1932 (*Dusisiren* Domning, 1978 and *Hydrodamalis* Retzius, 1794), and other dugongid genera (*Eotheroides* Palmer, 1899, *Prototherium* De Zigno, 1887, *Eosiren* Andrews, 1902, *Caribosiren* Reinhart, 1959, *Priscosiren* Vélez-Juarbe & Domning, 2014b, *Metaxytherium* De Christol, 1840, and other species formerly lumped under “*Halitherium*”) by displaying the following unique combination of plesiomorphies: frontal roof flat; supraorbital process of the frontal dorsoventrally flattened with well-developed, prominent posterolateral corner; supraoccipital wider dorsally than ventrally; exoccipitals meet in a suture dorsal to the *foramen magnum*; posttympanic process with a prominent anteroventral process for attachment of *m. sternomastoideus*; paroccipital process of exoccipital long, reaching as far ventrally as occipital condyles; accessory mental foramina present; horizontal ramus of mandible slender dorsoventrally; permanent premolars (P2/p2 – P4/p4) present. Synapomorphies: nasals reduced and not meeting in midline (shared with *Eosiren imenti* Domning

et al., 1994, *Caribosiren*, *Priscosiren*, and all later dugongid taxa), nasal incisure at posterior end of the mesorostral fossa deep, extending posterior to the supraorbital processes of the frontals (shared with some *Metaxytherium* spp., dugongines, and *Hydrodamalis*); strongly concave ventral border of the horizontal mandibular ramus (shared with *Priscosiren*, *Metaxytherium* spp., and dugongines), masticating surface of mandible broad (shared with *Metaxytherium* spp., dugongines, and hydrodamalines). In contrast to the similar species *Priscosiren atlantica* it has a supraorbital process with the posterolateral corner projecting posteriorly; prominent temporal crests on frontal and parietal; supraoccipital distinct in height, only slightly wider than high.

Etymology

A combination of the Latin terms for the Linz Sands (*Lentia* and *arenium*), the informal name for the upper Oligocene sediments in which the species was found.

Lentiarenium cristolii (Fitzinger, 1842) comb. nov.

Figs 2–10, Tables 1–5

Halitherium cristolii Fitzinger, 1842: 71, pl. 1.

Metaxytherium(?) pergense Toulou, 1899: 459, pl. 12.

Halitherium abeli Spillmann, 1959: 36, pls. 1–4, figs 19–20, 22, 24–27, 29b, 31–32, 33b, 34.

Manatus christolii – De Blainville 1844: 122.

Metaxytherium christolii – Laurillard 1846: 172.

Halianassa collinii – Meyer 1847: 189, 578 (partim). — Ehrlich 1850: 14–15, figs a–c. — Ehrlich 1855: 3, pls. 1–2, corresponding figs on pages 14–17.

Halitherium schinzii – Peters 1867: 310.

Halitherium schinzi – Lepsius 1882: 164 (partim).

Halitherium christoli – Abel 1904: 25, pl. 1, figs 12–13, pl. 2, figs 4, 11, 17, pl. 5, fig. 8, fig. 1. — Spillmann 1959: 17, figs 8–18, 21, 23, 28, 29a, 30, 33a; 1969: 62, pl. 8, fig. 2; 1973: 198, pl. 40, fig. 4.

Halitherium pergense – Spillmann 1959: 11, figs 6–7; 1969: 61, fig. 1; 1973: 197, pl. 39, figs 1–2.

Halitherium abeli – Spillmann 1969: 62, pl. 9, fig. 3; 1973: 205.

Diagnosis

As for the genus.

Type Material

Lectotype (present designation)

A mandible (OLL 2012/1) of an adult individual (based on the presence of a large retromolar space and erupted m3 in wear) with left dp5–m2 and right m1–3, “Sicherbauer” sandpit, Linz.

Paralectotypes

Fragment of right maxilla with worn M1 crown and remnants of DP5 roots (OLL 2012/2), and an isolated crown of M3 (OLL 2012/3) from the right side, both from the “Sicherbauer” sandpit, Linz.

Holotype (by monotypy) of *Metaxytherium pergense*

Cast of a parietal-supraoccipital skullcap (OLL 1899/11), sandstone quarry near the town of Perg.

Holotype (by original designation) of *Halitherium abeli*

Mandible of an adult individual (based on the presence of a large retromolar space and erupted m3 in wear), fragments of basicranium, cervical and other vertebrae (OLL 1939/257), “Limoni” sandpit, Linz.

Table 1. List of the preserved skeletal parts of *Lentiarenium cristolii* (Fitzinger, 1842) in the OLL.

| OLL collection numbers | numbers used by Spillmann (1959) | Locality | Material | Original identification | Remarks |
|------------------------|----------------------------------|-------------------|--|-------------------------|---|
| 1854/327 | Sir. 9 | Linz | Partial skeleton (left scapula, vertebrae, ribs) | <i>H. cristolii</i> | |
| 1863/184 | Sir. 55 | Wallsee | Rib fragments | <i>H. cristolii</i> | |
| 1899/11 | Sir. 10 | Perg | Parietal-supraoccipital skullcap | <i>H. pergense</i> | Holotype of <i>H. pergense</i> Toula, 1899 |
| 1917/7 | Sir. 50 | Perg | Rib fragments | <i>H. pergense</i> | |
| 1921/71 | Sir. 19 & 20 | St. Georgen/Gusen | Vertebrae, fragments of vertebrae and ribs | <i>H. abeli</i> | |
| 1926/394 | Sir. 11 | Linz | Partial skull | <i>H. cristolii</i> | |
| 1926/395 | Sir. 33 | Linz | Rib fragment | <i>H. cristolii</i> | |
| 1927/200 | Sir. 35 | Linz | Rib fragment | <i>H. cristolii</i> | |
| 1928/82 | Sir. 37 | Linz | Fragments of skull and rib | <i>H. cristolii</i> | |
| 1931/21 | Sir. 38 | Linz | Rib fragment | <i>H. cristolii</i> | |
| 1931/263 | Sir. 34 | Linz | Vertebral fragment | <i>H. cristolii</i> | |
| 1939/257 | Sir. 59 | Linz | Mandible, fragments of basicranium, cervical and other vertebrae | <i>H. abeli</i> | Holotype of <i>H. abeli</i> Spillmann, 1959 |
| 1948/33 | (?)to Sir. 60 | St. Georgen/Gusen | Sternal fragment | <i>H. abeli</i> | |
| 2012/1 | Sir. 1 | Linz | Mandible with left dp5–m2, right m1–3 | <i>H. cristolii</i> | Lectotype of <i>L. cristolii</i> |
| 2012/2 | Sir. 2 | Linz, | Maxillary fragment with M1 and DP5 root | <i>H. cristolii</i> | Paralectotype of <i>L. cristolii</i> |
| 2012/3 | Sir. 3 | Linz | Isolated M3 crown | <i>H. cristolii</i> | Paralectotype of <i>L. cristolii</i> |
| 2012/4 | Sir. 4 | Linz, | Proximal humerus fragment | <i>H. cristolii</i> | |
| 2012/5 | Sir. 5 | Linz | Sternal fragment | <i>H. cristolii</i> | |
| 2012/6 | Sir. 6 | Linz | Left m3 | <i>H. cristolii</i> | |
| 2012/7 | Sir. 8 | Linz | Skull fragment | <i>H. cristolii</i> | |
| 2013/1 | Sir. 60 | St. Georgen/Gusen | Partial skeleton with left scapula and distal humerus fragment | <i>H. abeli</i> | Spillmann (1959: fig. 2); vertebrae and ribs of partial skeleton now lost |

Referred material

OLL 1854/327, 1863/184, 1917/7, 1921/71, 1926/394, 1926/395, 1927/200, 1928/82, 1931/21, 1931/263, 1948/33, 2012/4, 2012/5, 2012/6, 2012/7, 2013/1. For a detailed listing of the preserved skeletal parts see Table 1.

Type horizon and locality

“Sicherbauer-Sandgrube”, a former sandpit within the city limits of Linz (Upper Austria). Linz-Melk Formation, Linzer Sande (= Linz Sands), upper Oligocene, lower Egerian (Chattian).

Range and distribution

Known only from the upper Oligocene of Linz and the surrounding area.

Description

The following description is based on the available sirenian material housed in OLL, regardless of the different species that were proposed in the past. It will be outlined in detail in the Discussion why the respective skeletal material represents a single species.

Lentiarenium cristolii is known from cranial and postcranial elements. However, the premaxilla and lacrimal are unknown as are the pelvis, zeugopod and autopod. The following description is mainly based on a partial skull (OLL 1926/394) and two mandibles (OLL 1939/257 and OLL 2012/1).

PREMAXILLA. The premaxilla is not preserved in any specimen but some morphological characters can be indirectly determined. The external nares are retracted and enlarged (Fig. 2), as in all sirenians, and reach beyond the anterior margin of the orbit. Judging from the recesses in the anterior margin of the frontal, the nasal processes are not broadened and bulbous at their posterior ends but taper, having lengthy overlap with the frontals. The angle of the rostrum most likely exceeds 50° considering the deflection of the mandibular symphysis of about 60° (Fig. 7).

NASAL. The exact status of the nasals cannot be determined without doubt due to the poor preservation of the nasal area in specimen OLL 1926/394 (Fig. 2). Judging from the right anteromedial margin of the frontals, which is not damaged, but smooth without an attachment area for the nasals, these elements are at least considered to have been small without meeting in the midline. A nasal incisure is present at

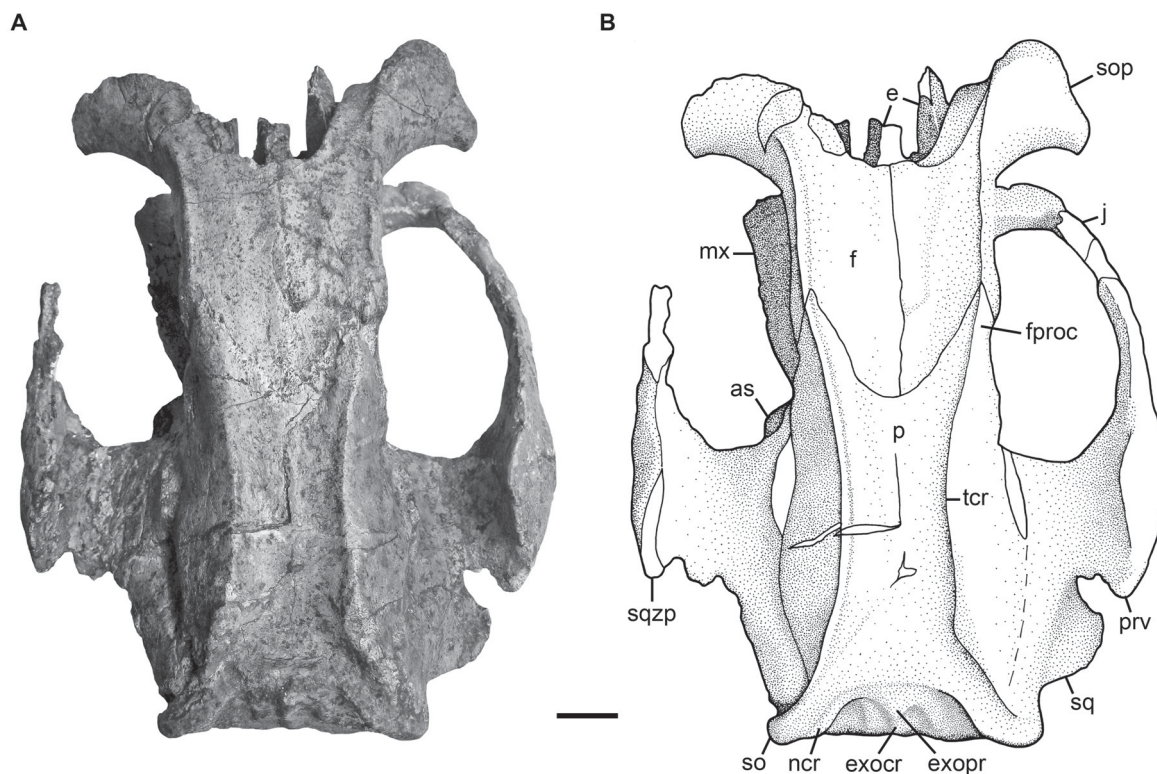


Fig. 2. Cranium of *Lentiarenium cristolii* (Fitzinger, 1842) (OLL 1926/394) in dorsal view. **A.** Photograph. **B.** Drawing. White areas indicate either missing or reconstructed parts. Scale bar = 2 cm.

Table 2. Measurements (in mm if not otherwise stated) of crania of *Lentiarenium cristolii* (Fitzinger, 1842). Letters in parentheses denote the standard dimensions established by Domning (1978: fig. 7, table 2). Measurements in parentheses indicate preserved lengths.

| | OLL 1926/394 | OLL 1939/257 |
|---|-----------------|-----------------|
| Zygomatic width (CC') | 179 | – |
| Width across occipital condyles (ff') | – | 127 |
| Length of zygomatic process of squamosal (OP) | 129 | (94) |
| Dorsoventral height of zygomatic process of squamosal (WX) | 37 | 31 |
| Anteroposterior length of root of zygomatic process of squamosal (QR) | (36) | 49 |
| Length of frontals in midline (LFr) | 76 | – |
| Length of frontals, level of tips of supraorbital processes to frontoparietal suture (F) | 130 | – |
| Width across supraorbital processes (FF') | (136) | – |
| Width of cranium at frontoparietal suture (GG') | 62 | – |
| Minimum width of parietals | 57 | – |
| Width of <i>foramen magnum</i> (gg') | – | 50 |
| Length of parietals, frontoparietal suture to rear of external occipital protuberance (P) | 89 | – |
| Maximum width of parietals | 80 | – |
| Anteroposterior length of zygomatic-orbital bridge of maxilla (no) | – | (47) |
| Dorsoventral thickness of zygomatic-orbital bridge (T) | – | (17.5) |
| Maximum width between labial edges of left and right alveoli (rr') | (87) | – |
| Maximum width between pterygoid processes (yy') | (68) | – |
| Height of supraoccipital (HSo) | 61 | – |
| Width of supraoccipital (WSo) | 83 | – |
| Angle between supraoccipital and parietal (degrees) | 120 | – |

the posterior end of the mesorostral fossa, but unlike in *Metaxytherium albifontanum* (Velez-Juarbe & Domning, 2014a) and *Priscosiren atlantica* (Velez-Juarbe & Domning, 2014b) it is deep, extending posterior to the supraorbital processes of the frontals, though not to the extent seen in dugongines like *Crenatosiren olseni* (Domning 1997). It is uncertain whether the nasals were fused or coalesced with the frontals.

ETHMOIDAL REGION. The ethmoid is incompletely preserved and not easily observable in all aspects. A prominent perpendicular plate of the mesethmoid is visible in dorsal and anterior views of the skull OLL 1926/394 (Fig. 2). This vertical wall measures 10 mm to 15 mm in width, is narrower dorsally and ventrally, and apparently also becomes thinner posteriorly. Ventrally, the perpendicular plate is fused with the likewise distinctly developed vomer. On the right side of the skull, and medial to the frontal (Fig. 2), the almost complete large ethmoturbinal (*concha maxima ethmoidalis* (Kaiser 1974)) extends nearly parallel to the mesethmoid. Its left counterpart is only fragmentarily preserved. The *crista galli* and *lamina papyracea* are either not preserved or not visible.

VOMER. The vomer is exposed on the ventral side of the skull OLL 1926/394 but broken anteriorly (Fig. 3). It is fused with the presphenoid posteriorly and forms the cranial extension of its median crest. The vomer is triangular in cross section, firmly fused with the ethmoid via its flat dorsal surface, and contacts the maxilla laterally. In lateral view (Fig. 4B), the vomer is also visible through the orbit due to the incomplete preservation of the skull.

FRONTAL. In dorsal view (Fig. 2), the frontal roof is flat between the temporal crests, and bears no knoblike bosses as present in some dugongines (e.g., *Crenatosiren olseni* (Domning 1997)). The straight to slightly concave anterior margin of the frontal has no internasal process. The temporal crests form distinct keels (morphotype B; Domning 1988) and are as prominent on the frontal as on the parietal. In lateral view (Fig. 4B), the supraorbital process is dorsoventrally flattened with its dorsal surface inclined gently ventrolaterad. Its lateral margin is not divided, and it has a prominent posterolateral corner that projects posteriorly. An orbitotemporal crest is distinct relative to what is observed in *Metaxytherium albifontanum* (Velez-Juarbe & Domning 2014a), and forms a craniocaudally-extending ridge. The *lamina orbitalis* is significantly less than 10 mm thick.

PARIETAL. The parietal roof (Fig. 2) is flat between the temporal crests and characterised by a strong intertemporal constriction that reaches its maximum behind the centre of the skull roof with the parietal bulging laterally. An external sagittal crest is not developed. The frontal processes of the parietal are short and do not exceed half the length of the frontal in the midline, a condition similar to that in *Priscosiren atlantica* (Velez-Juarbe & Domning 2014b). The parietal is longer than the frontal, and the overall proportions of the cranial roof indicate a slight brachycephaly when the value of the frontal length is divided by the width of the supraoccipital, i.e., the ratio l_{FP}/w_{SO} , which is below 2. In endocranial view (Fig. 3), the bony *falx cerebri* extends from a prominent tentoric process and flattens out anteriorly before reaching the frontoparietal suture. The *tentorium osseum* is well developed and

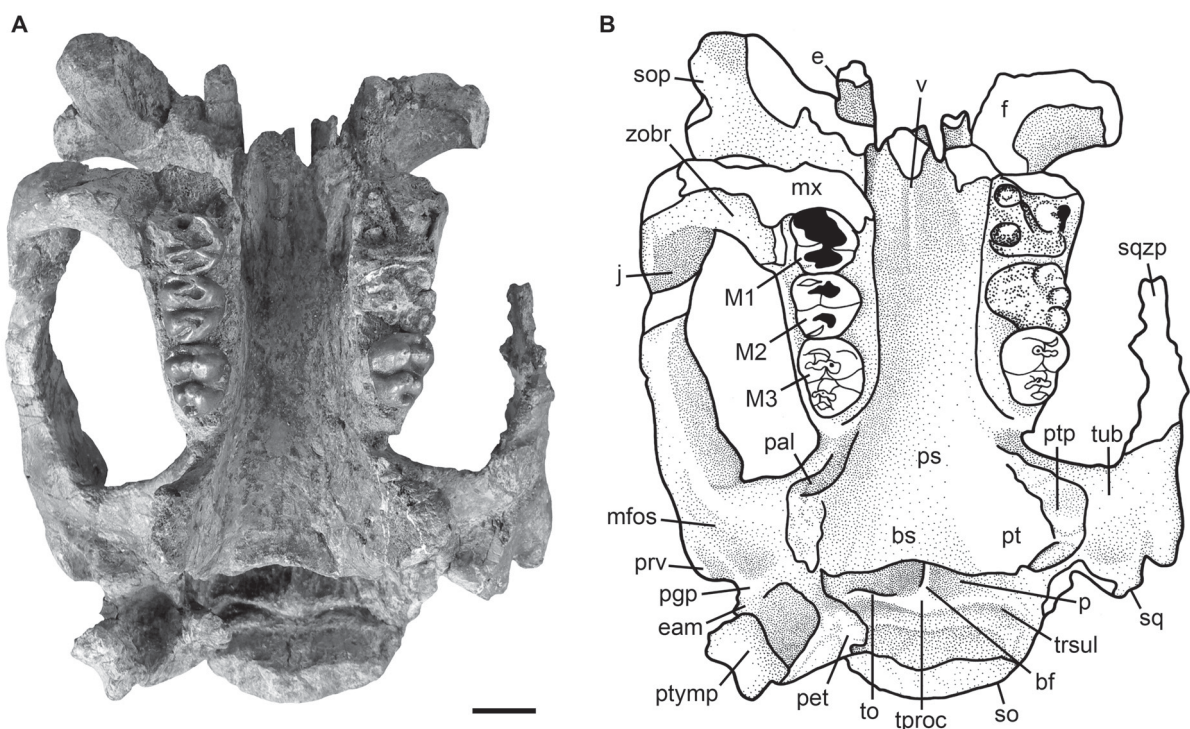


Fig. 3. Cranium of *Lentiarenium cristolii* (Fitzinger, 1842) (OLL 1926/394) in ventral view. **A.** Photograph. **B.** Drawing. White areas indicate either missing or reconstructed parts. Scale bar = 2 cm.

an internal parietal spine (or tentorial process as illustrated in Voss (2008: Fig. 4B)) is missing. On both sides of the bony *falx*, the flat internal parietal surface shows the depressions for the superior parts of the brain hemispheres.

SUPRAOCCIPITAL. This element is widest dorsally rather than ventrally (Fig. 4A), relative to what is observed in *Metaxytherium* spp. (e.g., *M. albifontanum* (Velez-Juarbe & Domning 2014a)). The supraoccipital is only slightly wider than high (width to height ratio < 1.5), which is similar to the contemporaneous species *Crenatosiren olseni* (Domning 1997). Dorsally, the nuchal crest is constantly narrow along its transversal length and relatively sharp-edged. It makes up the dorsolateral margin of the supraoccipital. The external occipital protuberance rises above the parietal roof and is also prominent posteriorly. Ventrally, the protuberance continues as the external occipital crest that forms a distinct ridge, which slightly flattens out after one third of the supraoccipital's height, almost reaching its ventral margin. Dorsolateral to this median ridge the deep and large insertions for the *semispinalis capitis* muscle occupy about the upper third of the external lamina. The area of the muscle insertion is triangular and defined by distinct ridges medioventrally and the nuchal crest dorsolaterally. The ventral margin of the supraoccipital forms an angle of approximately 135° in specimen OLL 1926/394. Specimen OLL 1899/11 (Fig. 5), formerly designated as the holotype of "*Halitherium*" *pergense* but now referred to *Lentiarenium cristolii*, also shows a distinct nuchal crest. However, the protuberance, median ridge and definitions of the muscle insertions are less prominently developed than in OLL 1926/394, indicating its juvenile status. In interior view (Fig. 3), the supraoccipital is flat with the exception of longitudinal bulges dorsolaterally that are merged in the median plane and separated by a deep transverse sulcus from the *tentorium osseum*. Posterolaterally, the parietals extend between the supraoccipital and squamosal, forming a short flange.

EXOCCIPITAL. The dorsal parts of these paired elements are not preserved in any specimen. However, the total length of the ventral margin of the supraoccipital in OLL 1926/394 (Figs 3, 4A) reveals the articulation surface for the exoccipitals, indicating that these bones evidently meet in a suture dorsal to the *foramen magnum*. Additionally, specimen OLL 1939/257 preserves the ventralmost parts of the exoccipitals, which Spillmann (1959: fig. 19) illustrated in ventral view. During the personal examinations, the paroccipital processes were detected to be long, projecting as far ventrally as the occipital condyles, which is similar to what can be observed in some dugongines (e.g., *Nanosiren garciae* Domning & Aguilera, 2008 and *N. sanchezi* Domning & Aguilera, 2008 (Domning & Aguilera 2008: fig. 3, 11)). Medioventral to the paroccipital processes, the hypoglossal foramen is not opened to form a

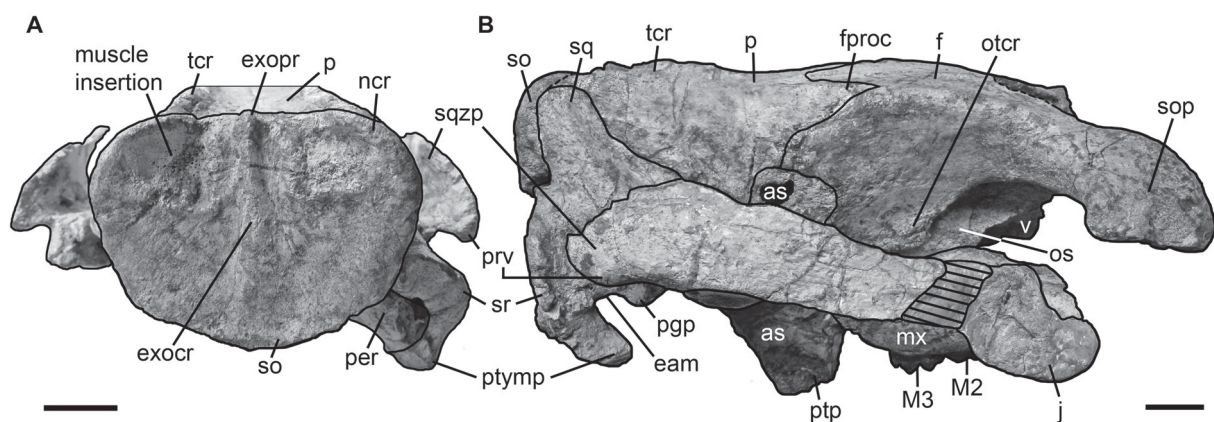


Fig. 4. Cranium of *Lentiarenium cristolii* (Fitzinger, 1842) (OLL 1926/394). **A.** In caudal view. **B.** In right lateral view. Shaded area indicates either missing or reconstructed part. Scale bars = 2 cm.

notch or incisure but is well surrounded by bone. The supracondylar fossae are distinct and define the occipital condyles across their entire width.

BASIOCCIPITAL. An isolated basioccipital fused with the lower parts of the exoccipitals is preserved in specimen OLL 1939/257 (Spillmann 1959: fig. 19). It contributes to the occipital condyles ventrolaterally and extends cranial as a short, columnar bone. On its ventral side, the sphenoccipital eminences for the *longus capitis* muscles are concave and separated by a short but distinct ridge. Specimens OLL 1939/257 and 1926/394 (Fig. 3), in which either the basioccipital or basisphenoid is preserved, show smoothed attachment areas for the adjacent bone, indicating that the basioccipital and basisphenoid were not fused. On that basis, both specimens can be determined as subadults.

BASISPHENOID, PRESPHENOID, ORBITOSPHENOID. In specimen OLL 1926/394, the sphenoidal region is clearly observable (Fig. 3). The basisphenoid has a flat ventral surface that is defined laterally by antero posteriorly-broad pterygoid processes. Cranially, the basisphenoid continues with a slight anterodorsal slope into the presphenoid. Both bones are firmly fused with each other and with the orbitosphenoid anterolaterally, the alisphenoid dorsolaterally, and the pterygoid posterolaterally. The median crest of the presphenoid is not prominently developed, which might be related to the state of preservation of the skull in this area, and only becomes distinct at the level of the adjacent vomer. On the lateral side of the skull (Fig. 4B), the orbitosphenoid is exposed and contributes to the anteromedial wall of the temporal fossa. The orbitosphenoid is defined by the frontal dorsally, the alisphenoid posterodorsally, and apparently by the maxilla ventrally. Its sutures with the palatine are not detectable.

ALISPHENOID. The alisphenoid is visible in the lateral view of the skull (Fig. 4B). Its sutural contacts with the frontal, parietal and squamosal can be clearly determined. Furthermore, the alisphenoid forms the slightly uneven posterolateral side of the pterygoid process. An alisphenoid canal is absent, and the *foramen ovale* is opened to form a notch or incisure.

PTERYGOID. As in other sirenians, the pterygoid is present on the posteromedial side of the pterygoid process but fully fused with the surrounding bones (Fig. 3). Though not well preserved in OLL 1926/394, the wing-shaped pterygoid processes each bear a dorsoventrally elongated pterygoid fossa posteriorly that extends above the level of the roof of the internal nares, relative to the condition observed in some dugongines like *Dioplotherium manigaulti* (Domning 1989). The distal ends of both pterygoid

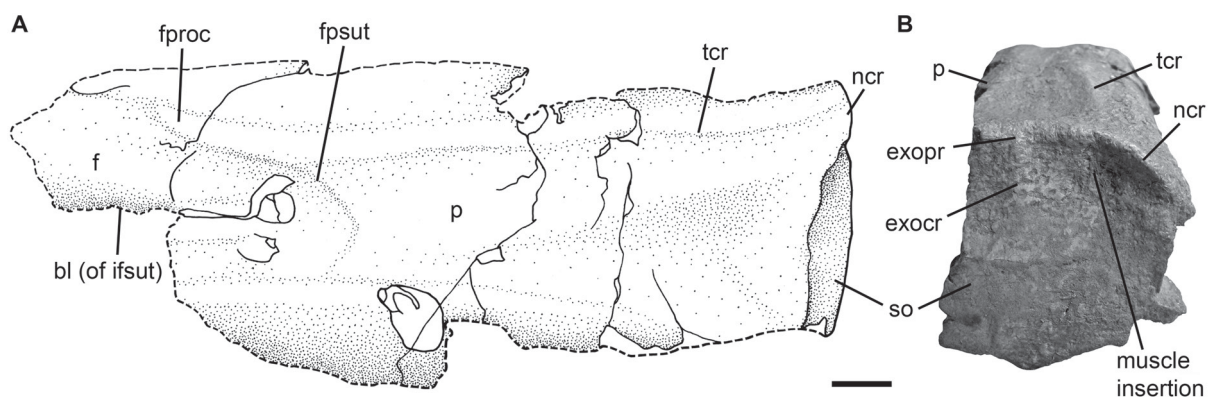


Fig. 5. Parietal-supraoccipital skullcap of *Lentiarenium cristolii* (Fitzinger, 1842) (OLL 1899/11, holotype of “*Halitherium*” *pergense* (Toula, 1899)). **A.** Drawing in dorsal view. **B.** Photograph in caudal view. White areas indicate either missing or reconstructed parts. Dashed lines pertain to broken parts. Scale bar = 1 cm.

processes are somewhat damaged, although the distomedial angle of the right pterygoid process is still distinct and indicates a hamula process.

PALATINE. Only the posteriormost parts of the palatines are preserved in OLL 1926/394, and are best observable on the right side (Fig. 3). There the palatine forms the anteromedial margin of the pterygoid process. Its sutures with the surrounding bones are only barely visible on the distal and medial sides of the pterygoid process and on the posterior side of the maxillary alveolar margin.

MAXILLA. The zygomatic-orbital bridge (Fig. 3) is not completely preserved in any of the specimens. However, in the maxillary fragment of OLL 1939/257 its dimensions are 47 mm in minimum length and 17.5 mm in nearly original height (Spillmann 1959: fig. 20). On the basis of these data, the zygomatic-orbital bridge can be clearly determined to be long anteroposteriorly, relative to what is observed in the genus *Hydrodamalis* (Domning 1978; Velez-Juarbe & Domning 2014a). Additionally, and in contrast to some hydrodamalines, e.g., *Dusisiren jordani* Kellogg, 1925 and *Hydrodamalis cuetae* Domning, 1978 (Domning 1978; Velez-Juarbe & Domning 2014a), it is only slightly elevated above the alveolar margin, and its posterior edge is thickened. Remnants of the infraorbital canal reveal no obstruction.

SQUAMOSAL. The cranial part of the squamosal (Figs 2, 4B) extends up to the temporal crests but does not interrupt the course of the temporal crests, so that these reach the occipital nuchal crest. The posttympanic process is not club like distally (Fig. 4B), but concave anteroventrally for the attachment of the sternomastoid muscle. In the posterior view of the skull (Fig. 4A), a prominent sigmoid ridge is visible forming the laterocaudal margin of the squamosal. Posterolaterally, the mastoid foramen is present, filled by the periotic, and enclosed by the squamosal anteriorly, the exoccipital posteriorly, and the supraoccipital dorsally. Lateral to the braincase (Figs 2, 4B), each of the zygomatic processes projects from a zygomatic root that, though partially broken, is characterised by a distinct notch posteriorly. The zygomatic process is triangular in shape, tapering anteriorly. Its lateral and medial sides are flat to concave with the dorsal margin distinctly inclined inwards to form a sigmoid ridge. The posterodorsal end of the zygomatic process is straight to concave. The external auditory meatus is short mediolaterally and about as wide as high anteroposteriorly. Ventrally (Fig. 3), the elements of the mandibular articulation surface are elongated transversely. The mandibular fossa forms a distinct depression relative to the slightly convex *tuberculum* anteriorly. Posterior to the mandibular fossa, the postglenoid process forms a rounded and longitudinal knob, which rises above the level of the *tuberculum*. The posterior end of the zygomatic process, the *processus retroversus*, shows a moderate inward-directed inflection in contrast to what is observed in the living dugong (e.g., Domning & Aguilera 2008; Velez-Juarbe & Domning 2014a).

JUGAL. Only a fragmentarily preserved middle part of the right jugal is known from specimen OLL 1926/394 (Fig. 4B), indicating that a postorbital process is probably present. Considering the position and shape of the supraorbital processes of the frontal, the development of a postorbital bar can be excluded. The zygomatic process of the jugal is not preserved but according to its imprint on the ventral side of the zygomatic process of the squamosal it reaches the *tuberculum*, exceeding the diameter of the orbit.

EAR REGION. In specimen OLL 1926/394, the right periotic is poorly preserved (Figs 3, 4A). It is not fused with the adjacent skull bones, and is set in a closely-fitting socket in the squamosal. The *tegmen tympani* is only indicated by its imprints on the dorsolateral side of the squamosal. It was most likely about as big as the mastoid or slightly smaller. The petrosal is fragmentarily preserved medioventrally, with the perilymphatic foramen apparently not separated into a *fenestra rotunda* and *cochlea canaliculus*. The *processus fonticulus* fills the mastoid foramen posteriorly (Fig. 4A).

MANDIBLE (Table 3). The mandibular symphysis is broad, as is the masticating surface that is lacking a median furrow and houses four large and shallow alveoli for vestigial incisors and canines. This is best visible in OLL 1939/257 (Fig. 6A), which exhibits a completely preserved masticating surface, whereas in OLL 2012/1 (Figs 6B, 7A) the ventralmost end is broken. In lateral view (Fig. 7), the symphysis is higher than long and bears the mental foramen laterally, which is joined dorsoposteriorly by two accessory mental foramina on each side in specimen OLL 1939/257 (Fig. 7B). The accessory mental foramina are large relative to what is observed in more plesiomorph dugongid taxa, e.g., “*Halitherium*” *taulannense* (Sagne 2001a), but they are still smaller than the principal foramen. This observation is interpreted here in analogy with *Trichechus* (Domning 1982, 1994, and personal observations), as “true” accessory mental foramina, which are present in addition to and usually posterior to the large principal foramen. In the lectotype (OLL 2012/1; Fig. 7A), the mental foramen is broken off dorsoposteriorly, and therefore the accessory mental foramina are not identifiable, but their open canals are merged with the main foramen. The overall build of the horizontal mandibular ramus appears to be broad dorsoventrally, but it is evaluated to be slender on the basis of its minimum dorsoventral height, which is smaller than $0.25 \times$ the length of the mandible. The ventral border of the mandible is strongly concave and not tangent to the angle posteriorly. The ascending mandibular ramus is incomplete, lacking most of the coronoid process, but still reveals a slight slope of it in the anterior direction. Posteriorly, the mandible is missing a distinct *processus angularis superior* and rather has a broadly convex outline. The mandibular condyle is well preserved in both specimens, with an articulation surface of even elliptical outline on a mediolateral axis. In OLL 1939/257 (Fig. 6A), the condyle is partially covered by plaster today but it is originally preserved as also stated by Spillmann (1959: 44, fig. 25). Behind m3 at the base of the ascending ramus (Fig. 6A), the coronoid foramen (canal) is enlarged and varies between 7.5 mm and 9.5 mm in maximum diameter. The retromolar space, i.e., the distance between m3 and the rear of the coronoid canal, is large in both specimens, measuring approximately 17 mm in OLL 2012/1 and 22 mm in OLL 1939/257. According to Domning (1978, 1988), it increases with age, indicating the adulthood of both specimens

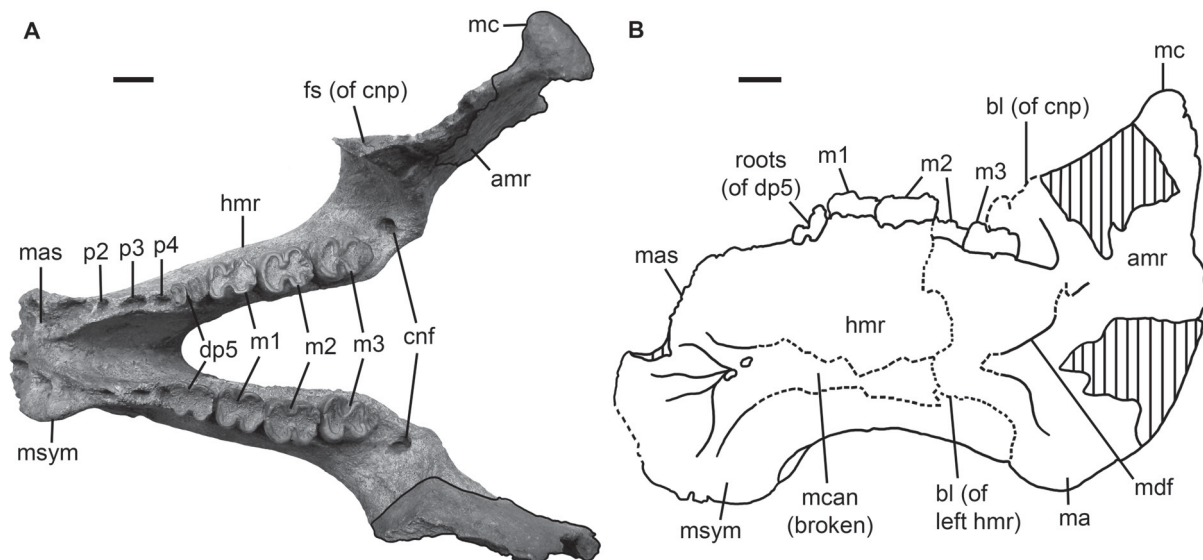


Fig. 6. Mandibles of *Lentiarenium cristolii* (Fitzinger, 1842). **A.** Photograph of OLL 1939/257 (holotype of “*Halitherium*” *abeli* (Spillmann, 1959)) in occlusal view. **B.** Outline drawing of OLL 2012/1 (lectotype) in left lateral view revealing information on the medial side of the right mandible. Dashed lines indicate broken parts. Both outlined (A) and shaded (B) areas indicate either missing or reconstructed parts. Scale bars = 2 cm.

Table 3. Measurements (in mm, if not otherwise stated) of mandibles of *Lentiarenium cristolii* (Fitzinger, 1842). Letters in parentheses denote the standard dimensions established by Domning (1978: table 7). Measurements in parentheses indicate preserved lengths, “e” estimated dimensions, “l” and “r” measurements from the left and/or right side.

| | OLL 2012/1 | OLL 1939/257 |
|--|---------------|-----------------|
| Total length (AB) | (307) | 305 |
| Anterior tip to front of ascending ramus (AG) | (170) | 176 |
| Anterior tip to rear of mental foramen (AP) | – | 60 |
| Anterior tip to front of mandibular foramen (AQ) | (174) | 164 |
| Length of symphysis (AS) | (82) | 90 |
| Posterior extremity to front of ascending ramus (BG) | (150) | (136) |
| Posterior extremity to front of mandibular foramen (BQ) | (160) | 154 |
| Distance between anterior and posterior ventral extremities (DF) | 176 | 176 |
| Height at mandibular notch (DK) | – | 206 |
| Height at condyle (DL) | (256) | 220 |
| Height at deflection point of horizontal ramus (EF) | (110.5) | 120 |
| Deflection point to rear of alveolar row (EU) | 122 | 132 |
| Minimum anteroposterior length of ascending ramus (GH) | 126 | 116 |
| Front of ascending ramus to rear of mental foramen (GP) | (100) | 110 |
| Top of ventral curvature of horizontal ramus to line connecting ventral extremities (MN) | 48 | 46 |
| Minimum dorsoventral height of horizontal ramus (MO) | 73 | 74.5l; 74r |
| Maximum width of masticating surface (RR') | (58.5) | 59.5 |
| Rear of symphysis to front of mandibular foramen (SQ) | 127 | 133 |
| Length of the alveolar row (m1–3) (TU) | 76 | 80 |
| Maximum width between labial edges of left and right alveoli (VV') | 81 | 82 |
| Minimum width between angles (WW') | – | 190 |
| Minimum width between condyles (XX') | – | 220.5e |
| Retromolar space | 17 | 22 |
| Maximum diameter of coronoid foramen | 7.5 | 9.5l; 7.7r |
| Deflection of symphyseal surface from occlusal plane (degrees) (MD) | ~60 | 60 |

(see also Sagne 2001b). In medial view (Fig. 6B), a single and undivided mandibular foramen reveals the dental capsule of m3 to be exposed posteroventrally.

DENTITION (Table 4). The premaxilla and anterior part of the maxilla are missing and therefore no conclusion on the absence or presence of incisor tusks can be drawn. However, the complete lower tooth arcade is preserved in two mandibles, one of which is the lectotype (OLL 2012/1). Accordingly, the dental formula in the lower jaw is interpreted to be i0, c0, p2–4, dp5, m1–3. Considering the logical

occlusion pattern and the conditions in similarly derived sirenians, the second and third upper incisors are considered to be absent as are the upper canines while the permanent premolars P2–4 and the persistent DP5 are present. Consequently, the lifetime dental formula in the upper jaw is estimated to have been most likely ?I1, C0, P2–4, DP5, M1–3.

Upper dentition. Besides the paralectotypes OLL 2012/2 and 2012/3, only two specimens have upper teeth or parts of these preserved. For example, OLL 1939/257 preserves a right maxillary fragment exhibiting the broken crowns and roots from M1–3 and DP5 (Spillmann 1959: fig. 20). The anterior part of the maxilla, especially the area where M1 and DP5 are positioned, is damaged and was restored. The medial and posterolateral roots of M1 are clearly preserved, whereas the anterolateral root is missing. The DP5 is three-rooted, as is characteristic for a molariform premolar that remains unreplaced. Its medial root is preserved but it is uncertain whether the anteriormost root in this maxillary fragment indeed belongs to DP5, representing one of the lateral roots, or may even be that of a single-rooted P4. In the first case, the fragment including the anteriormost root was presumably fixed in the wrong position. The skull of specimen OLL 1926/394 preserves M1–3 from the right tooth arcade, the left M3, and the roots of the left M1–2, and therefore is the principal reference for the following description (Figs 3, 8).

The molars are three-rooted, not reduced in size relative to the skull and have well-developed enamel of about 2 mm thickness on average. Mesiobuccally, the right M1 is broken where the anterior *cingulum* might have been present, but it can be clearly identified as the smallest molar. M1 is strongly worn in OLL 1926/394 as it is in the paralectotype OLL 2012/2, preventing any description of its cusp pattern except for the presence of two transverse lochs, an apparently deep central valley, and the *postcingulum*. The crown of M1 is heart-shaped in outline as is that of the slightly larger M2.

The right M2 (Fig. 8) is moderately worn and has distinct *pre-* and *postcingula* that attach to the two main transverse lochs mesio- and distolingually, and open labially by decreasing in height. The anterior and posterior basin each represent a deep furrow of similar size. Centrally, a deep transverse valley separates the protoloph from the metaloph but without being obstructed by the metaconule. The protoloph bears a continuous wear surface connecting the paracone labially, the protoconule centrally,

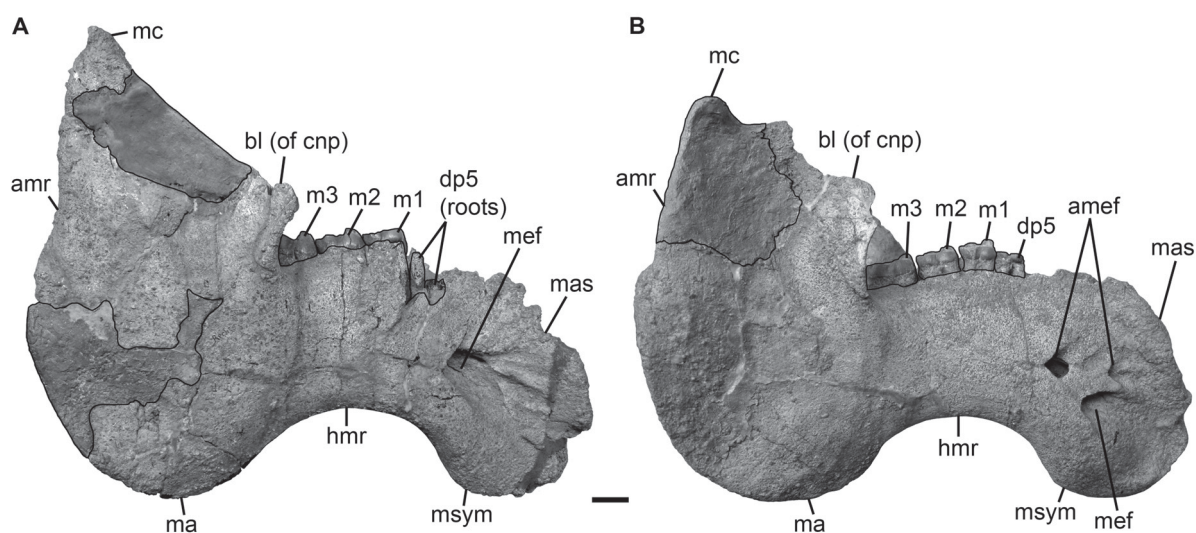


Fig. 7. Mandibles of *Lentiarenium cristolii* (Fitzinger, 1842) in right lateral views. **A.** OLL 2012/1 (lectotype). **B.** OLL 1939/257 (holotype of “*Halitherium*” *abeli*). Outlined areas of the ascending mandibular rami (amr) indicate either missing or reconstructed parts. Scale bar = 2 cm.

and the protocone lingually, which are each still discernible as single cusps. The metaloph is slightly less worn and reveals the nearly transverse row consisting of metacone and hypocone from labial (or buccal) to lingual, with the metaconule in between only very slightly shifted anteriorad. Despite tooth wear, these posterior cusps can still be clearly distinguished from each other.

The right upper M3 is well preserved in specimen OLL 1926/394 and only slightly worn (Fig. 8). This stands in contrast to the state of preservation of the paralectotype OLL 2012/3, an isolated right M3 that shows a strongly worn protoloph and is broken distolingually. However, both teeth resemble each other in shape and are also similar in their preserved morphology. The M3 is larger than M2 with its crown in the shape of an elongated heart due to the distal metaloph being transversally shorter than the mesial protoloph. Proto- and metaloph are each characteristically composed of three cusps. Accessory cusps or cuspules are not present. The main cusps of the protoloph form a transverse row, and are clearly separated and distinct from each other. Lingually, the protocone represents the largest and highest cusp followed in the buccal direction by the smaller protoconule and paracone, both of about the same size. A cuspid *precingulum* is attached mesiolingually to the protocone and opens labially by decreasing in height. The anterior basin forms a deep furrow. Proto- and metaloph are separated by a distinct transverse valley that is somewhat obstructed but not closed by the slightly anterad-shifted metaconule. The hypocone is slightly larger than the subequally-sized metaconule and metacone, and closely adjacent to the metaconule but still separated from it by a distinct furrow. The posterior basin is large and deep, and enclosed by two cingular cusps that form the *postcingulum*, which is connected to the hypocone lingually and opens labially.

Lower dentition. Two individuals of approximately the same age or state of tooth wear preserve the lower dentition. Mandible OLL 1939/257 preserves both tooth arcs (Fig. 6A), and the lectotype specimen OLL 2012/1 has only the right arcade complete while the left one is broken behind m2 (Figs 6B, 7A). The masticating surface of the mandibular symphysis (Fig. 6A) bears four large and irregularly-rounded alveoli that are not very deep, and may have housed three pairs of vestigial incisors and one

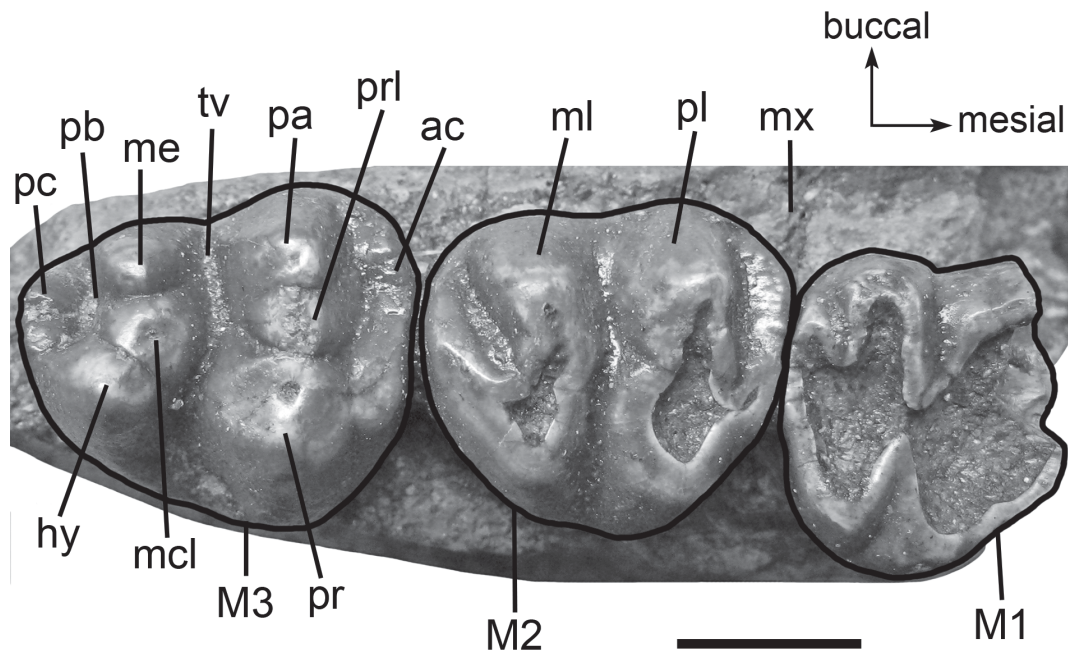


Fig. 8. The right upper molars M1–M3 of *Lentiarenium cristolii* (Fitzinger, 1842) (OLL 1926/394) in occlusal view. Scale bar = 1 cm.

Table 4. Linear dimensions (in mm) of cheek teeth of *Lentiarenium cristolii* (Fitzinger, 1842). Letters in parentheses denote the preserved lengths, “e” estimated dimensions, “l” and “r” measurements from the left and/or right side.

| Tooth | Specimen (all OLL collection) | Length | Anterior width (AW) | Posterior width (PW) |
|-------|----------------------------------|----------------|------------------------|-------------------------|
| M1 | 1926/394 | (15)r | (16) | 17.8 |
| M2 | 1926/394 | 20r | 20.4 | 17.6 |
| M3 | 1926/394 | 23.5l; 24r | 19.8 | 14.5 |
| dp5 | 1939/257 | (17.4)l | 15l | 15.6l |
| m1 | 2012/1 | (21)l; 21.5r e | 18.4l; 18r e | (17)l; 17r e |
| | 1939/257 | 21l; 21.5r | 16l; 16.5r | 15.5 |
| m2 | 2012/1 | 24l; 23.8r | 19l e; 18.7r | 17.5l; 17r |
| | 1939/257 | 25l; 24.5r | 19l; 19.5r | 19 |
| m3 | 2012/1 | 24.5r | 18 | 17 |
| | 1939/257 | 26l; 25.5r | 20l; 20.5r | 19l; 19.5r |

pair of vestigial canines. These alveoli gradually diminish in size top down, with the topmost alveolus measuring approximately 20 mm × 15 mm in diameter and the lowermost alveolus measuring 15 mm × 10 mm in diameter. The teeth themselves are not known, nor are the permanent premolars p2–4.

A further alveolus is present at the junction between the masticating surfaces of the horizontal mandibular ramus and the mandibular symphysis. It resembles in size and outline the alveoli of the vestigial lower incisors and canines, and is interpreted here to have possibly housed a vestigial dp1, which is not replaced at this locus. The paired roots of dp5 are preserved in both mandibles, but in specimen OLL 1939/257 (Fig. 6A), though heavily worn, the left crown is present, indicating a molariform tooth. Its protolophid and hypolophid have about the same transversal length.

Molars m1–3 are preserved in both specimens and characterised by having two roots and mesiodistally-elongated crowns that slightly increase in size from anterior to posterior within the tooth arcade (Fig. 6A). All crowns are moderately to heavily worn, preventing most details of their cusp pattern from being observed except for the two main transverse lophs, which are separated by a deep transverse valley. The protolophid and hypolophid are nearly perpendicular to the longitudinal axis of the tooth arcade. In the lectotype specimen, m2 and m3 are slightly less worn than in specimen OLL 1939/257 and reveal the transverse valley to be obstructed by an accessory cuspule that is connected to the hypoconid mesiointernally. This might have also been the case on m1, which, however, is too heavily worn to draw unambiguous conclusions. While the protolophid is about as large transversally as the hypolophid on m1, the hypolophid decreases in size from m2 onwards and becomes distinctly shorter on m3. Additionally, the bicuspid morphology of the protolophid and hypolophid is still discernible on m3. This becomes more obvious in a nearly unworn isolated m3 (OLL 2012/6) from the left side (Abel 1904: pl. 1: fig. 13). There the metaconid forms a prominent lingual cusp that is slightly larger than the protoconid on the labial side. On the hypolophid, the entoconid is about as large as the hypoconid. Also the isolated m3 (OLL 2012/6) displays a mesiointernal accessory cuspule of the hypoconid. A *precingulum* is not detectable on any molar. The hypoconulid lophule is distally composed of two cusps in OLL 2012/1 that are vaguely observable also in OLL 1939/257 (Fig. 6A). Specimen OLL 2012/6 shows two additional cuspules between the two cusps that might no longer be observable in the former two specimens due to wear.

HYOID APPARATUS. Not preserved in any specimen.

VERTEBRAL COLUMN. The vertebral column is only incompletely known by a few cervicals, several thoracics, some lumbar, and caudals. Most of the vertebral remains are associated with two partial skeletons, OLL 1854/327 and 2013/1. The ribs and vertebrae of specimen OLL 2013/1 are lost today and only documented in Spillmann (1959: fig. 2). Otherwise, the vertebrae are only known by fragments as also indicated by Spillmann (1959), but these also seem to no longer be available in the collections of the OLL. Relative correlation to a position within the column is partly possible.

Cervicals. The atlas is almost completely preserved in specimen OLL 1939/257. Both cranial articular facets are well defined and form concave and kidney-shaped areas for articulation with the occipital condyles. The caudal articular facets are slightly flatter and have a rounded outline without the large dorsoventral extension as in their cranial counterparts. The lateral margins of the articular facets flare out so that the articular surfaces are somewhat directed medially, toward the vertebral canal. The vertebral foramen is large, occupying the centre of the atlas, and partially obstructed at about half its height by a small bony knob on the right side for the transverse ligament. This knob certainly was present also on the left side but it is no longer preserved, and this area is replaced by plaster now. The neural arch is a low ridge with a small triangular surface anterodorsally that possesses a narrow and low median keel about 10 mm long. The anterior surface rises slightly in the dorsocaudal direction, whereas dorsocaudally the neural arch is not inclined but forms a smooth and rounded ridge.

Laterally, the atlas shows caudad-projecting aliform transverse processes, the left one broken to its base. Ventral and medial to the transverse processes the *foramen transversarium* is located, measuring about 2 mm in diameter. The vertebral foramen is defined ventrally by a bony bridge about 10 mm long anteroposteriorly and missing the caudad-projecting articulation surface for the second cervical, the area of which is replaced by plaster now.

Specimens OLL 1939/257 and OLL 1854/327 preserve a further vertebra from the cervical series, the latter only observable in caudal view, due to its arrangement on the *in situ* reconstruction, and missing the transverse and caudal articular processes. Both vertebrae represent elements of the series C3–7, but their exact position within the cervical column cannot be determined. The centra are short anteroventrally and form the flat floor of the vertebral foramen that is overall rounded although slightly peaked dorsally. Dorsal to the centra the neural arch is preserved, with a short neural spine rising straight up and having a slight keel cranially and a somewhat concave surface caudally.

Thoracics. Both partial skeletons, OLL 1854/327 and 2013/1, as well as specimen OLL 1939/257 preserve thoracic vertebrae. Their morphology does not importantly differ from that of other Oligocene sirenians like *P. atlantica* (Velez-Juarbe & Domning 2014a) and those formerly lumped under “*Halitherium schinzi*” and now in the process of being published (Voss & Hampe accepted). The description is therefore generalised in the following.

Specimen OLL 1939/257 preserves the first thoracic, T1, which is similar to the T1 remains illustrated for *M. albifontanum* (Velez-Juarbe & Domning 2014a: fig. 10C). The cranial and caudal epiphyses are more or less equal in size, but flat to concave cranially and slightly convex caudally. Lateral to the centrum, wing-shaped transverse processes are present, the right one broken to its base. The left transverse process extends laterad with a slight slope in caudal and ventral directions. The rear side of the process is flat to slightly concave. In cranial view, the prezygapophyses are flat dorsally and directed anterolaterad. In caudal view, the right postzygapophysis is present dorsal to the transverse process at a somewhat higher level than the prezygapophyses. Although the posterior tip is broken, it can be clearly determined that the articular facet for the adjacent cervical is directed ventrad and posteromedial. The

neural spine rises straight up from the neural arch and is broken at about half of its height, but clearly shows a slight keel cranially and a somewhat concave surface caudally.

The centra of the remaining thoracics are compact elements with a roughly heart-shaped outline that is caused by a more or less pronounced ventral crest and a shallow longitudinal depression dorsally. Dorsolaterally, the centra show deeply concave cranial and caudal articular facets for the *capitula* of the corresponding ribs while the remaining lateral surface is flat to slightly concave. The cranial and caudal extremities are flat and always wider than high. Lateral to the base of the neural arch, the transverse processes originate as very short and wedge-shaped elements with a slight dorsad slope. In ventral view, the transverse process bears the rounded articular facet for the *tuberculum* of the corresponding ribs. The mammillary processes form prominent knobs on the cranial sides of the transverse processes. Dorsal to the rounded and keyhole-shaped vertebral foramen, the cranial and caudal zygapophyses are present with the former flattened dorsally and the latter flattened ventrally. In anteroposterior direction, the neural spines are about as long as the centra and rise straight up with their cranial surface keeled and the caudal surface cleaved. Some thoracics are preserved in a somewhat oblique position in OLL 1854/327 and reveal a tuberosity on the distal end of the neural spine that seems to extend longitudinally in the anteroposterior direction. Vascular canals can be variably present on the vertebrae, especially on the ventrolateral and dorsal surfaces of the centra.

*Lumbar*s. Specimen OLL 1854/327 preserves a single lumbar composed of the centrum and the transverse processes. This vertebra is only observable in cranial view due to its arrangement on the *in situ* reconstruction. The vertebral body is massive with an oval outline that is wider than high. Its lateral and ventral surfaces are flat and the cranial epiphysis is slightly concave. The neural arch is not preserved. Though partially broken on the left side, the transverse processes are long mediolaterally, and attach with craniocaudally-broad bases lateral to the mid-section of the centrum. In cranial view, they extend more or less horizontally and show only a slight ventrocaudad inclination. The dorsal and ventral surfaces of the transverse processes are smooth and terminate in narrow and blunt distal ends. Therefore, this vertebra is not considered to represent a sacral vertebra as it evidently did not serve for the attachment of the pelvic ligaments, but has to be assigned to the lumbar series. Its exact position within the lumbar segment remains uncertain.

Caudals. Some caudal vertebrae were present in the partial skeleton OLL 2013/1, which is the only reliable information up to now. As mentioned above, however, this specimen is no longer available or at least not recognisable in the OLL collections. Additionally, the caudals are simply recorded in Spillmann (1959) but neither described in detail nor illustrated except for the schematic documentation of the original find context, which, however, barely deals with these elements.

CHEVRONS. Not known in any specimen assignable to *Lentiaenium cristolii*.

RIBS. Abundant rib fragments are known while the two partial skeletons OLL 1854/327 and 2013/1 (now lost) provide several complete ribs. Most elements are known from specimen OLL 1854/327, which preserves 34 ribs and rib fragments. However, no example of the first rib exists. No measurements could be taken from the preserved ribs in specimen OLL 1854/327, because the bones are mounted in their original position. Nonetheless, the ribs are identified as long, slightly arching elements, having an overall morphology that does not differ from other Oligocene sirenians like those formerly lumped under “*Halitherium schinzi*” (Voss & Hampe accepted). The ribs are pachyosteosclerotic, mediolaterally flattened, and hence have an elliptical cross section similar to what is observed in *P. atlantica* and *M. albifontanum* (Velez-Juarbe & Domning 2014a, b).

STERNUM. Two sternal fragments are preserved, OLL 2012/5 (Fig. 9C; Abel 1904: fig. 1; Spillmann 1959: fig. 33a) and 1948/33. Specimen OLL 1948/33 (Spillmann 1959: fig. 33b) was found in 1944, as was the partial skeleton OLL 2013/1. However, it is not certain if both belong to a single individual, and this uncertainty is also indicated by a separate collection number for the sternal part. Therefore, OLL 2013/1 and 1948/33 are treated here as two different specimens.

Specimen OLL 2012/5 measures 84 mm in maximum length and 65 mm in maximum width, and is the smaller of the two sternal fragments as well as the better-preserved one (Fig. 9C). Abel (1904: 36) identifies that element as the “*processus ensiformis*” of the xiphisternum. Spillmann (1959) considered it to be part of the corpus. In this study, Abel’s (1904) interpretation is confirmed, and this element is considered to represent the anterior part of the xiphisternum. The bone has smooth dorsal and ventral surfaces, the former slightly convex and the latter slightly concave. In the caudal direction the bone slightly widens, while a blunt process is present anteriorly. The lateral margins are thickened anteriorly, each characterised by two articulation facets for the attachment of ribs. The lateral margins become thinner caudally forming sharp edges. OLL 1948/33 most likely represents a fragment of the manubrium, which preserves a single rib articulation facet on each side. The bone has smooth surfaces and lacks a ventral keel.

SCAPULA (Table 5). Three scapular remains were described by Spillmann (1959), one of which represents the distal two-thirds of the left element (OLL 1854/327; Fig. 10). Additionally, the partial skeleton OLL 2013/1 preserves parts of the left scapular blade. The right element of this specimen was originally also present (Spillmann 1959) but is now lost.

The scapular blade is sickle-shaped, defined by the *margo cranialis* anteriorly, the *margo dorsalis* proximally, and the *margo caudalis* posteriorly. The anterior margin steeply rises craniodorsad with an

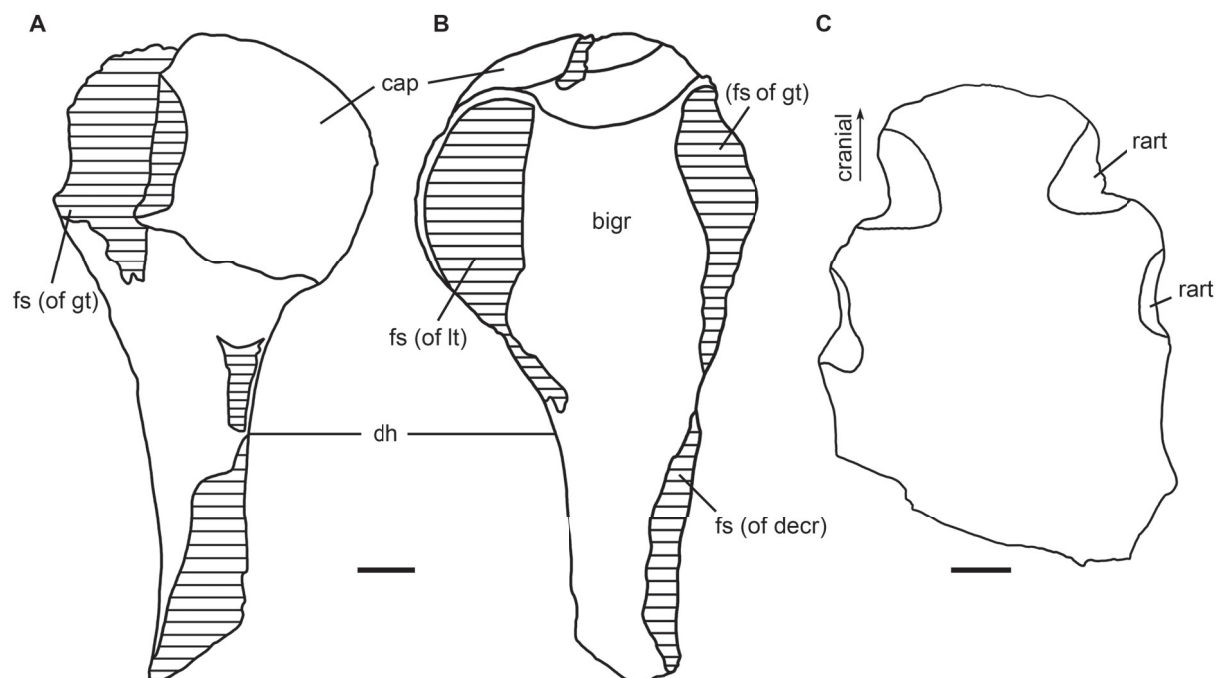


Fig. 9. Outline drawings of the left humerus LI 2012/4 and the xiphisternum OLL 2012/5 of *Lentiarenium cristolii* (Fitzinger, 1842). **A.** Humerus in posterior view. **B.** Humerus in anterior view. **C.** Xiphisternum in ventral view. Shaded areas indicate missing parts. Scale bars = 1 cm.

Table 5. Dimensions (in mm) of the scapula of *Lentiarenium cristolii* (Fitzinger, 1842). Letters in parentheses denote the standard dimensions established by Domning (1978: fig. 7, table 16). Measurements in parentheses indicate preserved lengths.

| | OLL 1854/327 (l) | OLL 2013/1 (l) |
|---|---------------------|-------------------|
| Maximum scapular length, vertebral border to border of glenoid fossa (AB) | (200) | (290) |
| Length of scapular spine | 95 | 145 |
| Maximum width of blade dorsally (CD) | (96) | 124 |
| Transversal width of infraspinous fossa at about mid-length of scapular spine | 21 | 23 |
| Mediolateral width of glenoid fossa (BI) | 25 | – |
| Anteroposterior length of glenoid fossa (MN) | 48 | – |
| Lateral border of glenoid fossa to inside of concave distal end of spine (BJ) | 50 | (46) |
| Minimum anteroposterior width of neck (EF) | 35 | 45 |

angle of about 50° from the *collum scapulae*, i.e., the scapular neck, and turns at nearly a right angle to run more or less straight dorsad for about 100 mm. Specimen OLL 1854/327 is broken at this level (Fig. 10; Spillmann 1959: fig. 30), but the left scapula of OLL 2013/1 (Spillmann 1959: fig. 31) preserves the proximal end that shows a dorsocaudal slope of about 45° into the *margo dorsalis*. The latter extends approximately 100 mm almost parallel to the vertebral column and, finally, forms an angle of about 90° with the *margo caudalis*. It is only this short *margo dorsalis* that is broadened and roughened for attachment of a scapular cartilage, in contrast to the thin and sharp anterior edge immediately distal to it. The posterior margin is largely convex cranially, and converges distad together with the *margo cranialis* to form the long and slender *collum* of about 50 mm in dorsoventral length, which is best visible in OLL 1854/327 (Fig. 10).

The external surface (Fig. 10A) is divided by the scapular spine into a large and shallow supraspinous fossa, and a narrow and more concave infraspinous fossa. The scapular spine forms a rounded flange without a proximal rugosity and does not exceed half the length of the scapular blade. It starts with a broad base at about the middle portion of the blade and rises slightly but steadily towards its distal end.

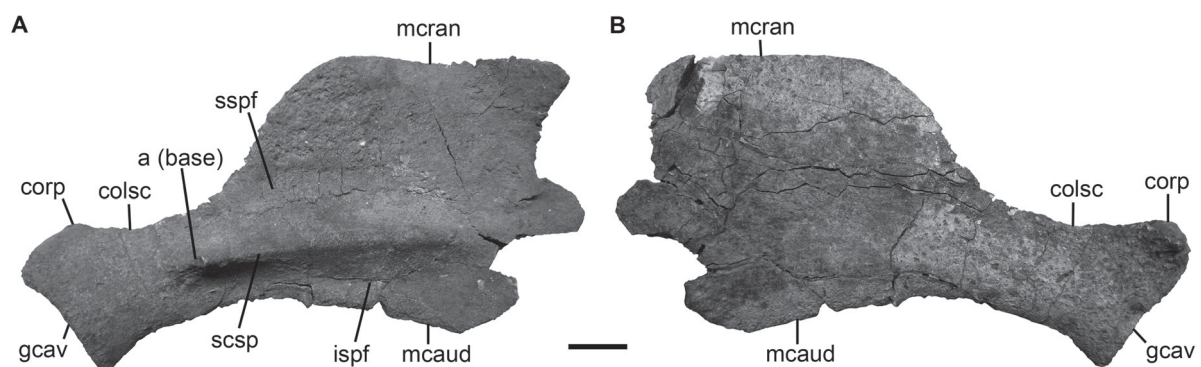


Fig. 10. Left scapula of *Lentiarenium cristolii* (Fitzinger, 1842) (OLL 1854/327). **A.** In lateral view. **B.** In medial view. Scale bar = 2 cm.

The spine becomes narrower in the distal direction by sloping slightly caudad and, finally, terminates in the acromion. Although the acromion is broken in all specimens, it can be clearly stated that it did not pass the level of the glenoid cavity. Similar to what is observed in *M. albifontanum* (Velez-Juarbe & Domning 2014a), the coracoid process is moderately developed, inclined medially, and is not disjunct from the anterior apex of the articular glenoid (Fig. 10B). The glenoid cavity is shallow and oval, narrower mediolaterally and wider anteroposteriorly, about 25 mm × 48 mm in OLL 1854/327. Medially (Fig. 10B), the costal surface is overall flat and smooth, only slightly convex in its central part according to the curvature of the ribs.

HUMERUS. Two single fragments of the left humerus from different individuals are known. Specimen OLL 2012/4 represents a left proximal half of 115 mm length in its maximum dimensions (Fig. 9A–B), and specimen OLL 2013/1 preserves a distal fragment that was excavated together with the partial skeleton in 1944. Although incompletely preserved, the humerus is seen to be compact and having distinctly developed epiphyses. The diaphysis forms a strong shaft but it is broken in both specimens and preserves only remnants of the deltoid crest anteriorly in OLL 2012/4 (Fig. 9B). The humeral head is rounded and separated by a deep furrow from the lesser tubercle. Both the lesser and greater tubercles are broken. The bicipital groove is deep and wide, serving for the passage of the biceps muscle. On the distal fragment (Spillmann 1959: fig. 32), the lateral and medial epicondyles are barely preserved. However, the trochlea can be identified as an hourglass-shaped and smooth articulation surface for the radius and ulna. Its inclination relative to the shaft appears to be perpendicular but cannot be certainly determined due to the incomplete state of preservation.

Remarks

Lentiaerenium cristolii was originally based on a type series according to Fitzinger (1842). This type series was composed of a mandible with left dp5–m2 and right m1–3 (OLL 2012/1), two isolated molars (OLL 2012/2 + 3), an isolated m3, ribs and vertebrae. In the above order, all syntypes were found in the “Sicherbauer” sand quarry in 1839 (Spillmann 1959: 4), but in succession and not at the same time as indicated by Fitzinger (1842: 62). Hence, it is not certain whether the original type series represents a single specimen. In the interest of nomenclatural stability, the mandible is designated here as lectotype. Accordingly, the remaining syntypes in the type series of Fitzinger (1842) represent paralectotypes. The ribs and vertebrae mentioned by Fitzinger (1842) are no longer traceable in the OLL. According to Fitzinger (1842), an isolated m3 was sent to the Naturhistorisches Museum Wien, Austria (NHMW) but it is neither listed in the catalogue of Pia & Sickenberg (1934) nor present in the NHMW vertebrate collection itself (pers. comm. U. Göhlich). These elements are now considered to be lost.

Furthermore, it is proposed in this study to maintain the original spelling of the species name *cristolii* as established by Fitzinger (1842), and to regard the use of “*christoli*” and “*christolii*” as incorrect subsequent spellings. Although Fitzinger (1842) established this species in honour of Jules de Christol, he spelled the name “de Cristo” (p. 67) and consistently applied the spelling “*cristolii*” throughout his entire work, which shows that it is not a lapsus calami or printer’s error. Therefore, “*cristolii*” (Fitzinger 1842: 71) is the “correct original spelling” according to Articles 32.1., 32.2. and 33.4. of the Code (ICZN 1999), and is not to be considered as a spelling that must be corrected following Article 32.5.1.

As already stated by Marx *et al.* (2010) and Berning (2013), the OLL collection numbers are another source of confusion. Some of the fossil finds of the 19th and early 20th century were apparently not given a collection number when they came to the museum. At some stage between 1914 and 1937 the fossil vertebrates were transferred from the palaeontological collection to the biological collections, which were then curated by the vertebrate specialist Theodor Kerschner. It was he who gave consecutive numbers to the fossil vertebrate remains using his own system, ignoring that some of the specimens already had official collection numbers. Kerschner’s unofficial numbers, however, which start with an

abbreviation of the respective taxon (e.g., “Sir.1”=Sirenia #1), were often used in publications during the 20th century (e.g., Spillmann 1959). For the sake of conformity with the numbers of the larger part of the palaeontological collection, we return here to using the official collection numbers (see Table 1 for comparison between Kerschner’s and the official numbers). Specimens without such an official collection number, i.e., those we could not trace in the collection register, were given new numbers.

Discussion

Based on a comparative morphological analysis of the type material of “*Halitherium*” *cristolii* and the respective holotypes of the species “*H.*” *abeli* and “*H.*” *pergense*, we hypothesise that only a single species is present in the late Oligocene of Upper Austria, and that, therefore, the two latter species are junior synonyms of the former. Corroborating Domning’s (1996) earlier claim, the sirenian specimens did not yield distinct morphological differences to justify the presence of different morphospecies in that region and time. Based on the following morphological and taxonomical comparisons, and on the critical approach concerning the validity of the genus *Halitherium* by Voss (2014), the new genus *Lentiarenium* is established for “*H.*” *cristolii*.

“*Halitherium*” *abeli* was established on a nearly complete mandible (OLL 1939/257; Figs 6A, 7B), while some cranial elements were also found subsequently (Spillmann 1959). This provides an ideal basis for direct comparisons with the lectotype and mandible, respectively, of *L. cristolii*. Both mandibles are morphologically identical and correspond in the following observable features: a broad and high symphysis, a slender horizontal ramus, a strongly concave ventral border that is not tangent to the angle posteriorly, and a *processus angularis* being absent. Additionally, measurements given in Table 2 display significant similarities also in the maximal dimensions of both elements. This indicates that the respective specimens are of the same life-age, but likewise excludes potential differences at the species level referring to size.

The overall mandibular morphology is diagnostic for *L. cristolii*, which can be clearly distinguished from other more or less coeval dugongid taxa other than dugongines. These include an early Oligocene species from Europe formerly known as “*Halitherium schinzii*” Kaup, 1838, the revision of which is currently in process of publication (Voss 2012; Voss & Hampe accepted), *Eosiren imenti* Domning *et al.*, 1994 from the early Oligocene of Egypt, *Caribosiren turneri* Reinhart, 1959 and *Priscosiren atlantica* Velez-Juarbe & Domning, 2014b from the early Oligocene of Puerto Rico, ?“*Halitherium*” *antillense* Matthew, 1916 from the late Oligocene of Puerto Rico, and *Metaxytherium albifontanum* Velez-Juarbe & Domning, 2014a from the late Oligocene of Florida and South Carolina. A major contrast between the species formerly lumped under “*H. schinzii*” and *L. cristolii* is that the former shows a horizontal mandibular ramus that is only moderately concave ventrally, and sharply downturned at the level of the symphysis (Voss & Hampe accepted). Furthermore, the mandibles of *abeli* and *L. cristolii* share a dental formula, each composed of three permanent premolars and three molars. This reflects a significant difference with regard to *Eosiren imenti* (only known by maxillary teeth), which retains canines (Domning *et al.* 1994), as well as to *C. turneri* (likewise only the upper dentition is known) (Reinhart 1959), *P. atlantica* (Velez-Juarbe & Domning 2014b: 963), and *M. albifontanum* (Velez-Juarbe & Domning 2014a: 445), all of which having a postcanine dental formula that lacks permanent premolars. The interpretation of p2–4 as permanent premolars is substantiated here by the presence of their respective alveoli, which are separated, deep, and have a clear outline in both specimens (OLL 1939/257 and OLL 2012/1). Additionally, both mandibles known from *L. cristolii* represent at least young adult individuals based on fully erupted m3s clearly in wear, and a large retromolar space. As such, one would expect that no more alveoli are present anterior to dp5 when no tooth replacement occurs at the respective loci, similar to what can be observed in the living dugong (*Dugong dugon*). Following Mitchell (1973) and Marsh (1980) on the relative age determination of the dugong, the cheek teeth erupt sequentially during the animal’s growth, and the most anterior teeth are shed (or resorbed)

before the latter become functional. This mode of cheek-tooth succession is also reported for samples of *M. krahulecki* (Domning & Pervesler 2001), *M. floridanum* (Domning 1988) and *M. serresii* (Carone *et al.* 2013), all of which are more derived than *L. cristolii* and show the cheek dentition to be reduced to M1-3 in adults. In young individuals, e.g., *M. floridanum* (Domning 1988: 411), a dp4 is still represented by a pair of alveoli, characteristically separated by a thin septum of bone as it is described for *P. atlantica* (Velez-Juarbe & Domning 2014b: 958). However, this condition is not observable in *L. cristolii*. Instead, the series of alveoli anterior to dp5 in *L. cristolii* is most similar to the condition in the contemporaneous species “*Halitherium*” *antillense* from Puerto Rico (Matthew 1916: fig. 1; personal observations). Although poorly known by a single specimen, its holotype, this species preserves the posterior part of the left mandible with worn m1–m3 and four alveoli anterior to m1, which are interpreted here as those of a two-rooted dp5 and single-rooted p4 and p3. In contrast, “*H.*” *antillense* differs from *L. cristolii* by having a horizontal mandibular ramus that appears to be more slender and has a ventral border that is only moderately concave (Matthew 1916; pers. obs.). The evaluation of the horizontal ramus as being rather slender dorsoventrally in *L. cristolii* stands in contrast to how this character is generally scored for this species (e.g., Domning 1994; Domning & Aguilera 2008; Velez-Juarbe & Domning 2015), and hence is considered here as a further morphological difference to *Priscosiren* (Velez-Juarbe & Domning 2014b), *Metaxytherium* spp. (e.g., *M. albifontanum* (Velez-Juarbe & Domning 2014a)), and dugongines (e.g., *Crenatosiren olsenii* (Domning 1997)).

Although a systematic study to support the taxonomical and morphological review performed here is still in progress, it is worth commenting on the phylogenetic position of *L. cristolii*. According to the cladistic analyses conducted by Domning (1994) and Domning & Aguilera (2008), *L. cristolii* is uniformly shown as a more derived sirenian compared to Eocene and early Oligocene taxa distributed across Central Europe and North Africa, and occupies a position basal to a clade including the Dugonginae, the Hydrodamalinae, *Caribosiren*, and the *Metaxytherium* assemblage. However, more recent phylogenies (Velez-Juarbe & Domning 2014a, 2015) place *L. cristolii* as a stem dugongid basal to two early Oligocene taxa, *C. turneri* and *P. atlantica* from the West Atlantic-Caribbean region, which is less in accordance with the fossil record. In any case, all studies, including Voss (2013), reveal that *L. cristolii* is not sister to any of the taxa included in the cladistic analyses, and that it is neither related to representatives of the former “*Halitherium*”-species complex, nor close to the paraphyletic *Metaxytherium* assemblage. Hence, Laurillard’s (1846) consideration of the species studied herein as a member of the genus *Metaxytherium* is not corroborated. Instead, *L. cristolii* is introduced here as a distinct and so far monospecific genus.

In fact, the morphological comparison of the mandibles and the resulting synonymy of the species *abeli* with *L. cristolii* imply a revision of the scoring for character 123 used in the phylogeny performed by Velez-Juarbe & Domning (2015), which is the most recent analysis including *L. cristolii*. This character defines the presence of accessory mental foramina in addition to, and usually posterior to, the large principal foramen on the lateral sides of the symphyseal region as the plesiomorph condition, and the absence of such as the derived state. Velez-Juarbe & Domning (2015) scored accessory mental foramina to be absent in the lectotype mandible (OLL 2012/1) of *L. cristolii*. This would imply a potential morphological difference compared to the findings of the present study. However, close inspection of specimen OLL 2012/1 suggests that accessory mental foramina are not necessarily lacking but are simply not preserved. While the left lateral wall of the mandibular canal is broken along the entire length of the horizontal ramus (Fig. 6B), the right symphyseal region (Fig. 7A) is damaged to such a degree that no reliable conclusion on the absence or presence of the respective foramina can be drawn, at least for the lectotype. On the other hand, accessory mental foramina are well preserved and clearly visible on both sides of the mandibular symphysis in the holotype of *abeli* (OLL 1939/257; Fig. 7B). As already outlined, the condition seen in OLL 1939/257 is interpreted here in analogy with *Trichechus* (Domning 1982, 1994, and pers. obs.), as “true” accessory mental foramina, which are present in addition to and

usually posterior to the large principal foramen (Velez-Juarbe & Domning 2015: character 123(0)). The number of accessory mental foramina in the three extant *Trichechus* species is highly variable, and ranges from specimens with five or more foramina that are distinctly smaller than the principal foramen (e.g., UF 15187, 24954, 24969), to specimens showing two relatively large accessory foramina, such as in *L. cristolii* (e.g., UF 25062; MNHN 1878-490, 1900-247), or even specimens with only a single large foramen posterior to the principal one (e.g., Domning 1982: fig. 6B; Domning 1994: fig. 2C; UF 15175; MNHN 1930-261, 1940-397). Other works (Domning 1988; Carone & Domning 2007; Carone *et al.* 2013) provide a different interpretation for a similar observation in some specimens of *Metaxytherium floridanum* and *M. serresii*. These authors consider accessory mental foramina to be absent in the respective individuals by defining the posteriormost foramen as the “principal” mental foramen, because of its position behind the deflection point of the alveolar margin, and score all specimens as derived for character 123. This scoring is based on the assumption that the respective interpretation of the mental foramina seems to be most phylogenetically congruent (Carone *et al.* 2013: 193). Beside the fact that this reflects a subjective *a priori* decision neglecting intraspecific variation in this character, it is emphasised here that relatively large samples of *M. serresii* (Carone & Domning 2007; Carone *et al.* 2013) and *M. floridanum* (Domning 1988) are known. While a number of *Metaxytherium* specimens reflect the derived state (accessory mental foramina clearly absent), a few individuals show the condition as in *L. cristolii*. However, such large samples are not known from *L. cristolii*, of which only two mandibles are preserved while only one of these has an undamaged symphyseal region. Hence, the polymorphism documented in representatives of the genus *Metaxytherium* is not corroborated for *L. cristolii* in the present study and, if present at all, can only be clarified when additional material is found. Moreover, the position of the principal foramen also varies in extant *Trichechus* (personal observations). A position well in front of the deflection point of the alveolar border always appears to be present in specimens with many small accessory mental foramina, whereas specimens with only one or two accessory foramina have the principal foramen either at about the level of the deflection point (or slightly in front of it), as in *L. cristolii*, or somewhat behind it. Therefore, the interpretation of the mental foramen in *L. cristolii* as a large one lying just posterior to the deflection point, and with the mental gutter divided anteriorly by bony bridges (Carone *et al.* 2013), is not followed here. Instead, the condition in *L. cristolii* is considered as representing a plesiomorphic trait, which can recur in more derived taxa like *M. floridanum* (Domning 1988: 408). Considering *abeli* as being synonymous with *L. cristolii* and, in consequence, that mandible OLL 1939/257 completes the morphological information available for *L. cristolii*, the original scoring of character 123 inferred from the data matrix of Velez-Juarbe & Domning (2015) should be updated. Instead, character 123 should be scored as “accessory mental foramina present, in addition to and usually posterior to the large principal foramen”.

As indicated above, the species *pergense* also proves to be a junior synonym of *L. cristolii*, as previously suggested by Domning (1996). Toula (1899) established *pergense* on the basis of the partial skull roof OLL 1899/11 (Fig. 5), which is the only known material referable to that name besides a few rib fragments. Direct comparisons between *pergense* and the skull OLL 1926/394 known from *L. cristolii* (Figs 2–4) reveal no relevant differences. Despite the limited availability of cranial features in *pergense* due to its incomplete preservation, both skull elements correspond in showing prominent temporal crests that, on the one hand, reach a likewise distinct nuchal crest and, on the other hand, show a maximum constriction behind the centre of the skull roof. This combination of morphological features is in contrast to the taxa for comparison listed above. While a constriction of the temporal crests in *M. albifontanum* and *P. atlantica* is not developed at all (Velez-Juarbe & Domning 2014a, b), *E. imenti* (Domning *et al.* 1994), *C. turneri* (Reinhart 1959), and “*Halitherium schinzii*” (Voss & Hampe accepted) show a constriction at about the centre of the skull roof, though weak in the former two species and strong in the latter.

The only deviation of *pergense* from the skull morphology observable in OLL 1926/394 is the distinctly smaller size of its skull roof, as well as less pronounced cranial structures such as the external occipital

protuberance. However, as outlined above, these differences are considered to indicate immaturity and reveal that the type of *pergense* is a juvenile specimen. This can be corroborated by personal observations in juvenile skulls of the dugong, for example, that, in addition to differences in size, are likewise characterised by smoothly developed crests, processes and protuberances compared to adult individuals.

Furthermore, *L. cristolii* is also considered to be the only species present in the late Oligocene of the Austrian northern Molasse Basin based on geological and biostratigraphical data. Notwithstanding the uniformly reported Chattian age of the Linz Sands, including the well-cemented sandstone from Perg and Wallsee, Spillmann (1959) justified the establishment of three different sirenian species in the Linz Basin on the basis of different type localities and beach terraces. However, assessing Spillmann's (1959) thorough review on the history of the discovery of the respective sirenian finds may lead to a different conclusion. According to Spillmann (1959), all specimens originally assigned to "*H.*" *cristolii* come from three very closely spaced sandpits in or near the city of Linz. This information also corresponds to the records of Fitzinger (1842) on the sandpits present around 1840 (Reiter & Mittermayr 2013). "*Halitherium*" *abeli* was found in another sandpit, the "Limonikeller" (Spillmann 1959: 5), which, however, is only 400 m away from the type locality of "*H.*" *cristolii*. The only other sirenian described from outside the city limits of Linz is "*H.*" *pergense* (Toula, 1899) from Perg, some 25 km to the east. Yet, as already outlined, the sandstone from Perg (Fuchs & Thiele 1987) is regarded as coeval with the Linz Sands, i.e., of Chattian age (Rupp 2011 and references therein).

In summary, the distribution of all sirenian specimens now assigned to *L. cristolii* not only reflects a restricted range, the larger region of the Linz Basin (while the species certainly had a wider distribution in the Molasse Basin and other Paratethyan regions), but is also limited to lower Egerian (Chattian) sediments. In addition to the stratigraphical and palaeobiogeographic point of view, evidence for the presence of sympatric morphospecies in the Linz area is clearly lacking, and therefore it is concluded that "*H.*" *abeli* and "*H.*" *pergense* are synonymous with the species now designated as *Lentiaenium cristolii*. The synonymy of the species in question is demonstrated here on an objective morphological basis for the first time, and corroborates the hypothesis already postulated by Domning (1996).

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