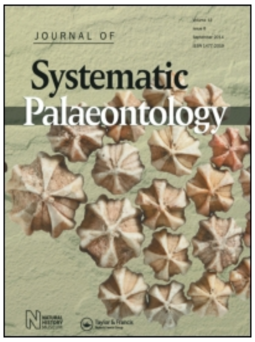

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Reassessing the earliest Oligocene vertebrate assemblage of Monteviale (Vicenza, Italy)

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The faunal assemblage of Monteviale (Vicenza, northern Italy) represents a rare condition among the earliest Oligocene assemblages of south-eastern Europe at the 'Grande-Coupure'. The lignitic fossiliferous strata lie above explosive basaltic breccias produced by a volcanic complex raised within a lagoon where the Calcareniti di Castelgomberto Formation (earliest Oligocene in age) was deposited. Systematic revision of the vertebrate remains from Monteviale reveals the presence of 15 taxa belonging to ?Butidae, Palaeobatrachidae, Trionychidae, Geoemydidae, Diplocynodontinae, Dugongidae, ?Pantolesta, Chiroptera, Rhinocerotidae, Anthracotheriidae and Palaeochoeridae. The fossiliferous deposit of Monteviale probably originated in a coastal lagoon characterized by salinity fluctuations, from brackish to fresh water, the latter evidenced by the presence of palaeobatrachid larvae. The terrestrial vertebrate assemblage indicates a humid forest environment with an age close to the Eocene–Oligocene boundary, lowermost Rupelian, MP21. Some of the mammal taxa (e.g. *Epiaceratherium*, *Anthracotherium* and ?*Propalaeocherus*) of Monteviale show a clear affinity with older (late Eocene) southern Asian species, suggesting a dispersal pattern across the several plates of south-eastern Europe and western Asia. By contrast, the herpetofauna (e.g. *Trionyx*, *Bergouniouxchelys* and *Diplocynodon*) suggests a closer relationship to European taxa.

Keywords: systematics; palaeobiogeography; biochronology; palaeoenvironment; earliest Oligocene; Italy

Introduction

The lignite-bearing deposits of Monteviale (Vicenza Province, Veneto Region, northern Italy) (Fig. 1) have been extensively exploited for more than a century, resulting in the collection of numerous fossil vertebrate remains. The Monteviale outcrops became famous when these remains were traded and often incorrectly attributed to the more famous Bolca Lagerstätte (Verona Province, Veneto Region, northern Italy) whose exposures are not far from those of Monteviale. The first documented report of fossil vertebrate remains from Monteviale dates back to 1832, when the outstanding Swiss palaeontologist Louis Agassiz reported the presence of some articulated fish skeletons and assigned them to the species *Cottus papyraceus*. A few years later these fossil remains were described in detail in the Agassiz magnum opus *Recherches sur les poissons fossiles* (Agassiz 1833–45). The first mammal remains collected at Monteviale, referable to an anthracothere, were described by Beggiato (1865), and subsequently by Zigno (1888) who ascribed them to the new species *Anthracotherium monsvialense*. Meschinelli (1903) described the remains of a large bat, while Dal Piaz (1926, 1929, 1930a, b, c, d, 1931, 1932, 1937a, b, c) illustrated the mammals collected at the site, in a series of monographs. In recent decades, only a few mammalian taxa have been re-examined to refine their systematics (see Kotsakis 1986 and references therein; Schutt & Simmons 1998). Finally, reptile and amphibian remains were described by Portis (1885), Negri (1892, 1893), Sacco (1895) and Fabiani (1915), and subsequently reviewed by Bergounioux (1954), Broin (1977), Kotsakis (1977, 1985), Franco *et al.* (1992), Franco & Piccoli (1993), Del Favero (1999) and Kotsakis *et al.* (2004).

According to Fabiani (1915), the vertebrate-bearing deposits of Monteviale are of Rupelian age. Subsequently, Fabiani (1952) referred the deposits to the early Oligocene in general. Dal Piaz (1929) referred the mammal

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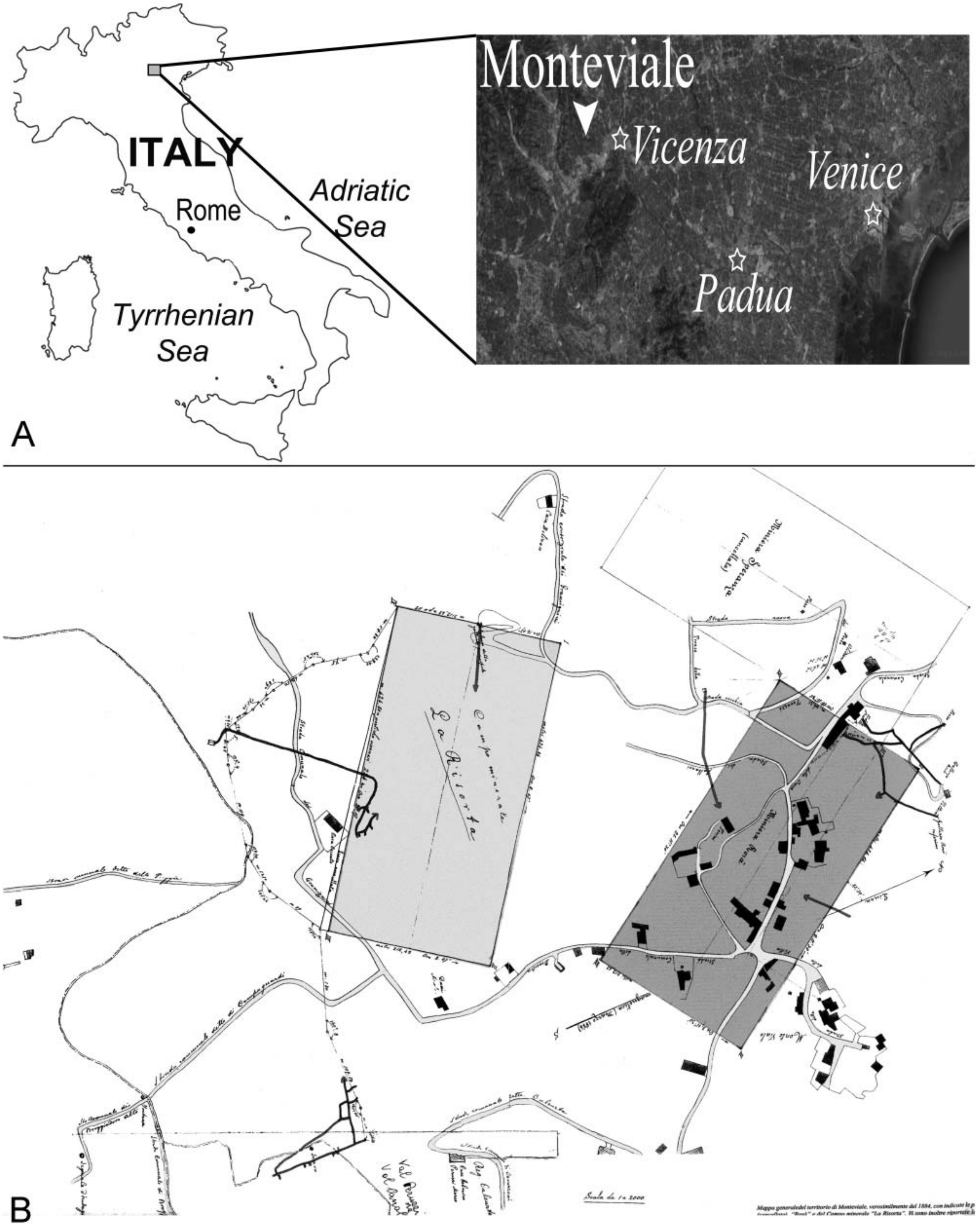


Figure 1. Oligocene vertebrate locality of Monteviale, Veneto, northern Italy. **A,** locality map; **B,** lignite mines and mineral concession map of 1884 (from Mietto 2006).

assemblage from Monteviale to the early Oligocene (Sannoisian), while Thenius (1959) considered this assemblage coeval with that of Ronzon (early Oligocene, France). According to Brunet (1977), the faunal assemblage might be correlated with that from Villebramar (late early Oligocene, France), whereas Altichieri (1980), Savage & Russell (1983) and Kotsakis (1986) suggested that it should be referred to the earliest Oligocene, and particularly to the Mammal Paleogene (MP) 21 level (Kotsakis *et al.* 1997). Franco & Piccoli (1993) attempted to date the deposit using calcareous nannoplankton, obtaining an Eocene–early Oligocene (Rupelian) age.

The aim of the present contribution is to review and update the systematics of the vertebrates collected at Monteviale and to discuss their palaeobiogeographical, palaeoenvironmental and biochronological implications.

Geological and stratigraphical framework

The lignite-bearing horizon of Monteviale basically consists of bituminous schists with reduced lignite content that were deposited above basaltic breccias resulting from explosive volcanic activity. Fabiani (1915) produced the first contribution to the stratigraphical interpretation of the Monteviale outcrop, placing the lignite horizon above the tuff and alternating with the Calcareniti di Castelgomberto (Fig. 2A). According to Mietto (2006), however, the lignite strata overlie basalt breccias (Fig. 2B, C) and were deposited within a lagoon that originated as a volcanic structure which became flooded by the sea. In this lagoon, the Calcareniti di Castelgomberto also accumulated (Frost 1981). In such a context, brackish thalassogenic waters, episodically influenced by the sea, were present in depressions caused by explosive events. The two interpretations are not completely dissimilar because the reconstruction by Fabiani (1915) might be considered valid for the peripheral zones of the system. Similar environmental conditions have been proposed for other localities, such as Ignago, north of Monteviale, and Monte San Lorenzo di Gambugliano, west of Monteviale, or Gazzo di Zovencedo in the Berici Hills (Mietto 2006 and references therein). Third-order eustatic oscillations possibly allowed temporary communications of the insular systems with the mainland, thus favouring dispersal events of land vertebrates (Gianolla *et al.* 1992).

Fabiani (1915) referred the lignite deposits of Monteviale (numbered 2–10 in Fig. 2A) to the Rupelian stage and the basal limestone (numbered 1 in Fig. 2A) to the Lattorfian on the basis of the molluscan assemblage which was compared to that from the Castelgomberto Formation (Fabiani, 1915, 1930; Ungaro 1978). The ‘Lattorfian’ stage is not currently used in the geological time scale but is correlated with the late Eocene (Gradstein & Ogg 2012).

The Eocene–Oligocene boundary in the Priabonian unit stratotype locality of Priabona (Vicenza) occurs at the level of the contact between the Priabona Formation and the Calcareniti di Castelgomberto (Cita & Piccoli 1964; Hardenbol 1969; Setiawan 1983; Barbin 1986), based on the last occurrence of *Nummulites fabianii*. However, based on dinoflagellates, Brinkhuis & Biffi (1993) and Brinkhuis (1994) have recently placed the Eocene–Oligocene boundary within the Priabona Formation, below the so-called ‘bryozoan strata’, traditionally considered typical of the Priabonian stage. This was accomplished by correlation with the Rupelian Global Stratotype Section and Point (GSSP) at Massignano. The Monteviale calcarenites in the Castelgomberto locality are interrupted by an erosional surface at the top of which a siliceous layer, characterized by exotic sands, can be observed (Bassi *et al.* 2007, 2008; Bassi & Nebelsick 2010). Overall, stratigraphical evidence suggests an early Oligocene age for the Monteviale locality. However, Böhme *et al.* (2014) have highlighted faunal affinities between the North Vietnamese Na Duong mammalian fauna and that of Monteviale, thereby suggesting a late Eocene age. Samples from lignite levels at Valle dei Peruzzi in the Monteviale area (Mietto 2006) contain nannoplankton of Priabonian age, but the environmental context suggests sedimentary reworking.

History of the collections from Monteviale

The Monteviale mines have been known since the beginning of the eighteenth century as a source of lignite and were exploited until 1952 (Mietto 2006). Fossils were commonly found during the excavations, most of which are currently housed in the Museo di Geologia e Paleontologia of the Università di Padova (MGP-PD). The collection consists of about 360 specimens, comprising fishes (91 specimens), amphibians (two specimens), reptiles (47 specimens) and mammals (222 specimens), acquired by the museum at different times, as revealed by the manuscript catalogue, and the labels associated with the fossils (1875, 1886, 1890, 1892, 1911, 1912, 1914, 1920, 1921, 1922, 1924, 1925, 1942, 1944 and 1946).

Giovanni Meneguzzo (1831–1912), a ‘geological guide’ with a deep knowledge of the Veneto Prealps, was very active in the fossil trade and sold the first specimens to the MGP-PD in 1875 (Fig. 3A). In 1886, Attilio Cerato (1826–1904), the owner of the celebrated Pesciara di Bolca, sold some fossils from Monteviale to the director of the MGP-PD, Prof. Giovanni Omboni (1829–1910). In 1890, Cerato traded additional fossils from Monteviale, claiming that they were collected from Bolca (Fig. 3B). Prof. Giorgio Dal Piaz (1872–1962) subsequently identified the correct

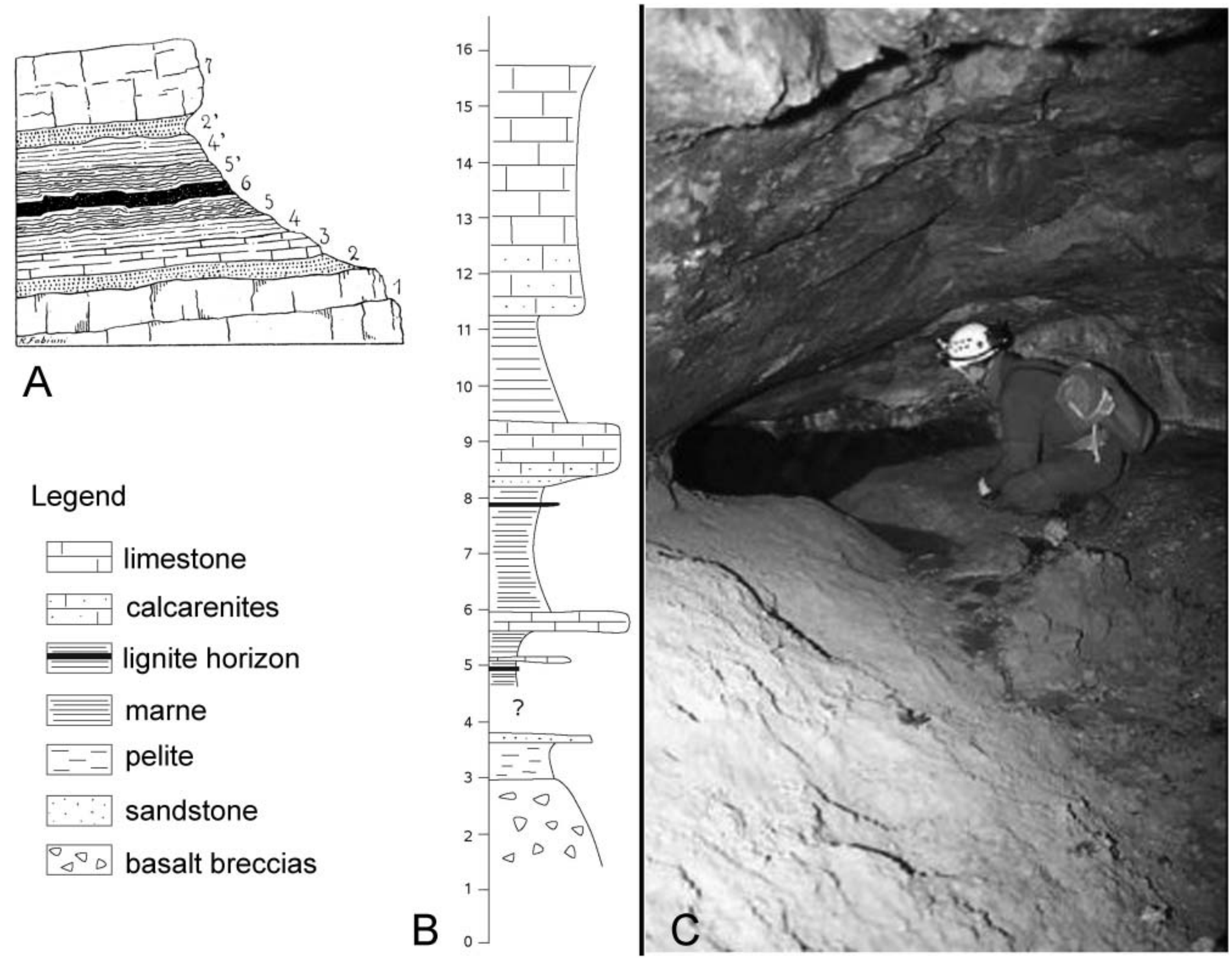


Figure 2. Stratigraphical sections. **A,** lignite mines at Monteviale (after Fabiani 1915); **B,** Valle dei Peruzzi, (from Mietto 2006); **C,** mine tunnel Canale 1 at Valle dei Peruzzi (from Mietto 2006).

locality, as indicated in a label associated with the fossils. During the twentieth century, specimens were probably sold to geologists and palaeontologists of the Università di Padova directly by miners of the lignite seams, who were aware of their commercial value (Mietto 2006).

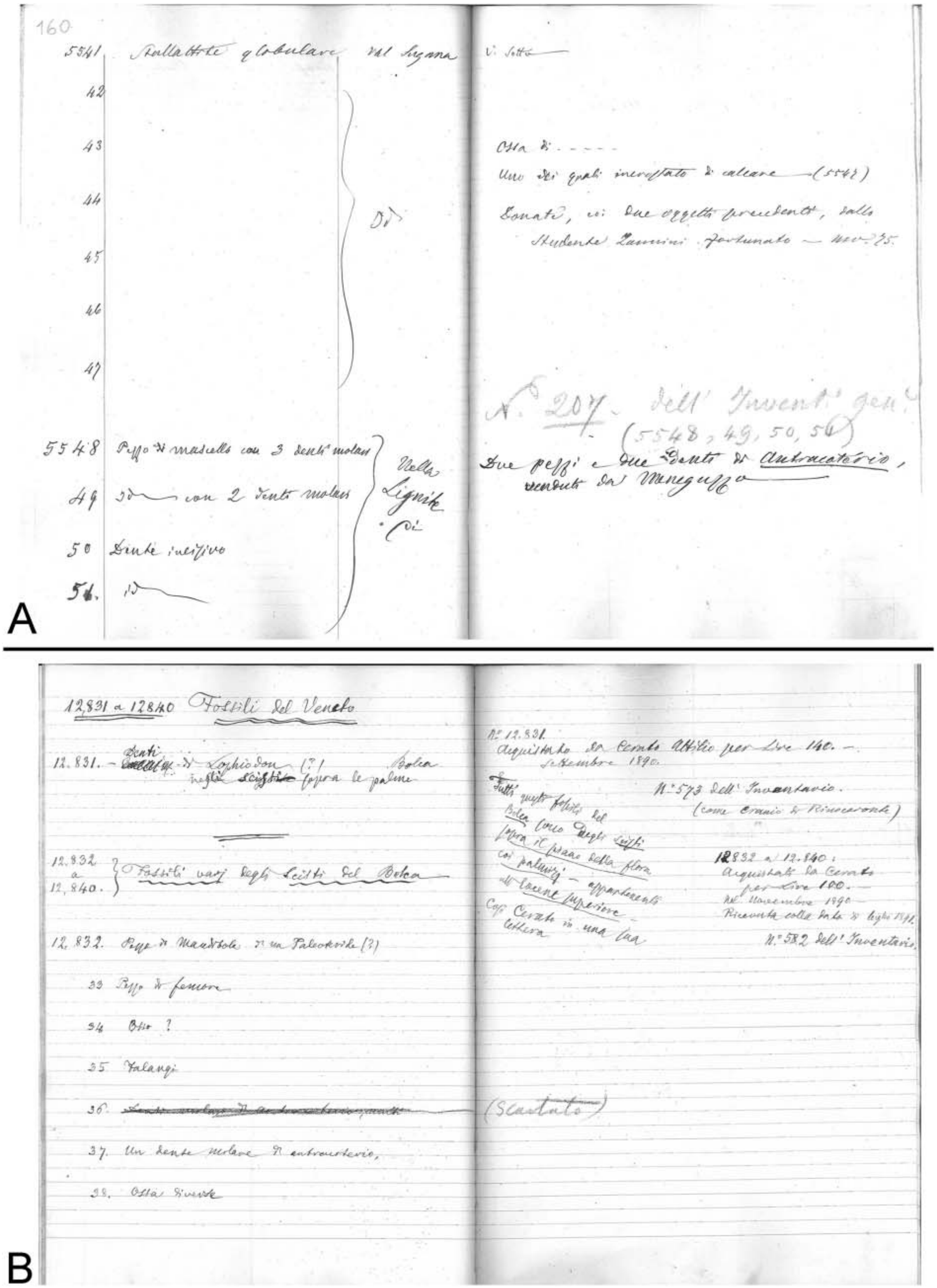
A few mammal remains collected at Monteviale are currently housed at the Naturhistorisches Museum in Basel (Switzerland) and consist of several fragmentary specimens of rhinocerotids, a crushed rhinocerotid skull, a few fragmentary remains of anthracotheres and a well-preserved specimen of *Anthracochoerus*. Fragmentary remains of *Trionyx* (s. l.) *italicus* and four tadpoles of a palaeobatrachid are housed at the Museo di Montecchio Maggiore in Vicenza (Veneto). Finally, two carapaces of trionychids are stored in the collections of the Museo Regionale di Scienze Naturali, Torino, and two additional specimens in the Museo di Paleontologia of the Università 'Federico II' di Napoli.

Institutional abbreviations

MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MGP-PD**: Museo di Geologia e Paleontologia, Università di Padova, Padova, Italy; **MP-CMSNF**: Museo di Paleontologia, Centro Musei delle Scienze Naturali e Fisiche, Università 'Federico II' di Napoli, Napoli, Italy; **NMB**: Naturhistorisches Museum, Basel, Switzerland; **PU**: Museo Regionale di Storia Naturale, Torino, Italy.

Systematic palaeontology

Superclass **Osteichthyes** *sensu* Rosen, Forey,
Gardiner & Patterson 1981
Subclass **Actinopterygii** *sensu* Rosen, Forey,
Gardiner & Patterson 1981
Subdivision **Teleostei** *sensu* Patterson & Rosen
1977



160
5541 Stallattite globulare val Lagana V. sotto —
42
43
44 Id
45
46
47

5548 Pezzo di mascella con 3 denti molari
49 Id — con 2 denti molari
50 Dente incisivo
51. Id —
Nella Lignite · Ci

Ossa di - - - -
Uno dei quali incrostato di calcare —(5547)
Donati, cioè due oggetti precedenti, dallo
Studente Zannini fortunato — nov. 75.

N.° 207 dell' Invent.° gen.le
(5548, 49, 50, 51)
Due pezzi e due denti di Antracoterio,
venduti da Meneguzzo —

12,831 a 12840 Fossili del Veneto

12.831. – ~~[illegible]~~ denti di Lophiodon (?) Bolca
negli ~~scisti~~ sopra le palme

12.832 a 12,840. } Fossili varj degli Scisti del Bolca

12.832. Pezzo di Mandibola di un Paleoterio (?)
33 Pezzo di femore
34 Osso ?
35 Falangi
36. ~~[illegible]~~ — (Scartato)
37. Un dente molare di antracoterio,
38. Ossa diverse

N.° 12.831.
acquistato da Cerato Attilio per Lire 140. —
settembre 1890.

N.° 573 dell' Inventario.
(come cranio di Rinoceronte)

Tutti questi fossili del
Bolca cioè degli scisti
sopra il piano della flora
coi palmizj – appartenenti
all'Eocene superiore –
Così Cerato in una sua
lettera

12832 a 12.840:
acquistati da Cerato
per Lire 100. —
nel Novembre 1890 —
Ricevuta colla data di luglio 1891.
N.° 582 dell' Inventario.

Figure 3. Historical catalogues housed in the Museo di Geologia e Paleontologia of the Università di Padova (MGP-PD). **A,** description of specimens bought from Giovanni Meneguzzo; on the bottom of the right page are reported: 5548 – fragment of maxilla with three molars, 5549 – idem with two molars, 5550 – incisor tooth, 5551 – idem, all collected from the lignite; on the bottom of the left page are reported two specimens and two teeth of an anthracothere bought from Meneguzzo. **B,** description of specimens bought from Attilio Cerato; the indicated locality is Bolca.

Order **Gobiiformes** Günther, 1880
Suborder **Gobioidei** Jordan & Evermann, 1896
Family **?Butidae** Bleeker, 1874
'Lepidocottus' papyraceus (Agassiz, 1832)
(Figs 4, 5)

1832 *Cottus papyraceus* Agassiz: 137.
1839 *Cottus papyraceus* Agassiz; Agassiz: 187, pl. 32, fig. 1.
1875 *Lepidocottus papyraceus* (Agassiz); Sauvage: 637.
1901 *Lepidocottus papyraceus* (Agassiz); Woodward: 583.
1922 *Lepidocottus papyraceus* (Agassiz); D'Erasmo: 136.
1961 *Lepidocottus papyraceus* (Agassiz); Obrhelová: 111.
1978 *Gobius papyraceus* (Agassiz); Gaudant: 3, figs 1–3, pls 1, 2.
2006 *Gobius papyraceus* (Agassiz); Mietto: 30, fig. 18/3-4.
2013 *Lepidocottus papyraceus* (Agassiz); Gierl, Reichenbacher, Gaudant, Erpenbeck & Pharisat: 15.
2014 '*Gobius*' *papyraceus* (Agassiz); Přikryl: 194.

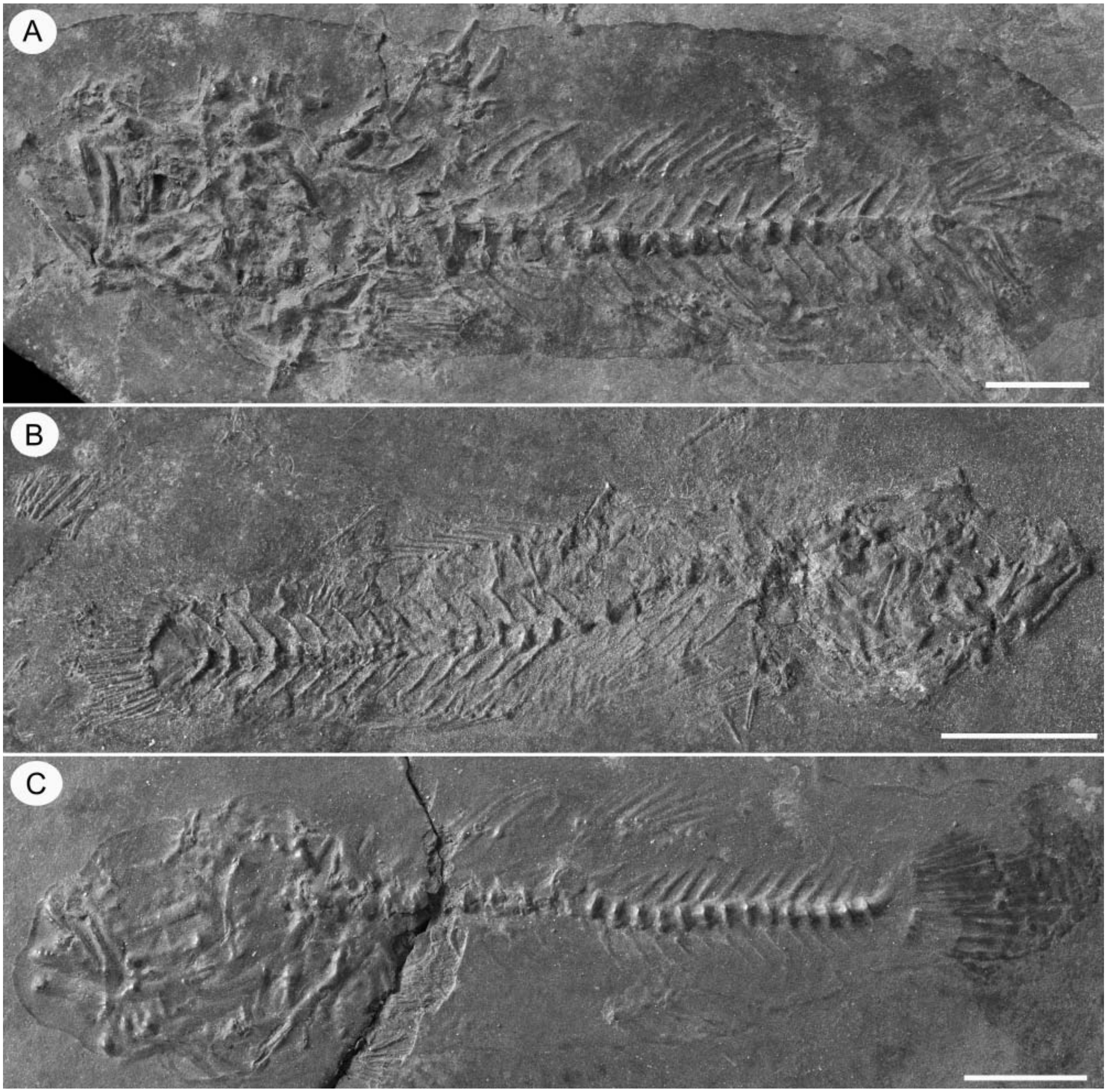


Figure 4. '*Lepidocottus*' *papyraceus* (Agassiz, 1832) from Monteviale. **A,** MGP-PD 7506Z; **B,** MGP-PD 9247; **C,** MGP-PD 9250. Scale bars = 10 mm.

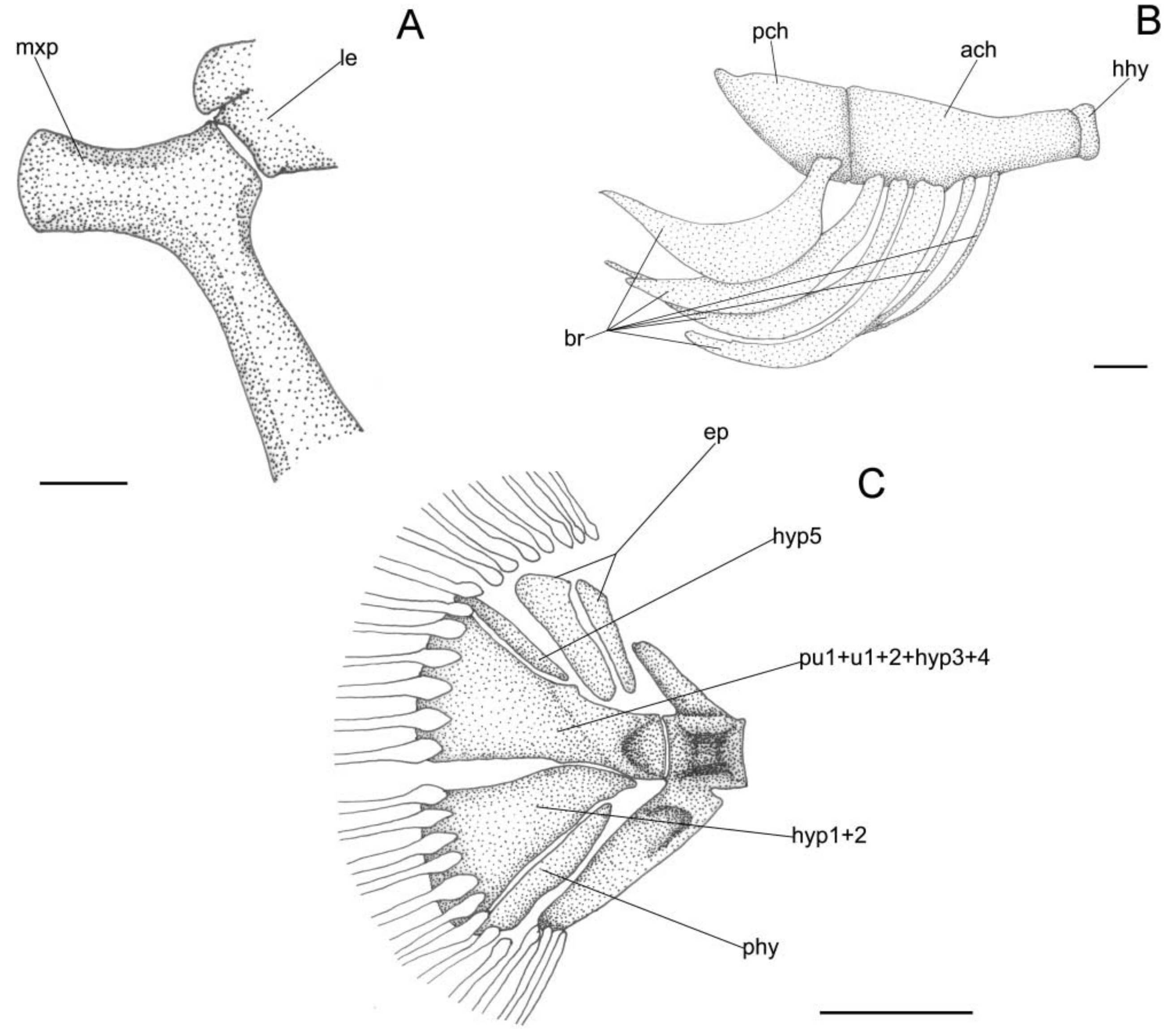


Figure 5. '*Lepidocottus*' *papyraceus* (Agassiz, 1832) from Monteviale. **A,** MGP-PD 9267, left palatine, lateral view, scale bar = 1 mm; **B,** MGP-PD 9265, right hyoid bar and branchiostegal rays, lateral view, scale bar = 1 mm; **C,** MGP-PD 9247, caudal skeleton, right lateral view, scale bar = 2 mm. Abbreviations: ach, anterior ceratohyal; br, branchiostegal rays; ep, epural; hhy, hypohyal; hyp, hypural; le, lateral ethmoid; mxp, maxillary process of the palatine; pch, posterior ceratohyal; phy, parhypural; pu, preural centrum; u, ural centrum.

Holotype. MCZ 5262, a moderately well preserved articulated skeleton, 36 mm standard length (SL).

Other material. 91 specimens housed in the MGP-PD; the available specimens mainly consist of poorly preserved and incomplete articulated skeletons with bones usually not exposed, covered by a thin layer of organic-rich sediment. Specimens examined: 6942Z, 7392C (two specimens), 7399C, 7401C, 7403C, 7406C, 7407C, 7416C, 7503Z, 7504Z, 7505Z, 7506Z (Fig. 4A), 9247 (Fig. 4B), 9248, 9248, 9250 (Fig. 4C; figured in Gaudant 1978, pl. 1, fig. 1), 9251, 9252, 9253, 9254, 9255, 9256, 9257, 9258, 9259, 9260, 9261, 9262, 9263, 9264, 9265, 9266, 9267 (figured in Gaudant 1978, pl. 2, fig. 3), 9268, 9393, 9653, 9808C (two specimens), 18428, 27009, 27010, 27011, 27012, 27013, 27014, 27015, 27016 (four specimens), 27017 (14 specimens), 27018, 27019 (16 specimens), 27020 (two specimens), 27021, 27022, 27023, 27024, 27025, 27026, 27039.

Measurements. Based on holotype MCZ 5262: total length 44.5 mm; SL 36 mm. Other measurements as percentage of SL: head length: 33.3; maximum body depth: 25; caudal peduncle length: 23.6; caudal peduncle depth: 15.2; predorsal (first fin) distance: 40.2; predorsal (second fin) distance: 58.3; preanal distance: 63.8; prepelvic distance: 33.3; first dorsal fin base length: 11.1; second dorsal fin base length: 16.6; anal fin base length: 11.2.

Description. The morphology of the available specimens is difficult to describe due to a thin layer of black, organic-rich sediment that covers the skeletons, preventing detailed observation of anatomical structures (Fig. 4). Overall, the body is moderately elongate, its maximum depth four to five times the standard length. The head is relatively large, its length slightly more than three times the standard length. The caudal peduncle is well developed, longer than the second dorsal-fin base, its length four to five times the standard length. The orbit is relatively large. The mouth is terminal, with a slightly oblique gape; its posterior end extends beyond the vertical under the anterior margin of the orbit.

The head skeleton is only partially recognizable. The frontals are the largest bones of the skull roof. There is no evidence of the parietals and basisphenoid. The thickened parasphenoid is clearly exposed in the lower third of the orbit. The premaxilla bears well-developed separate ascending and articular processes; numerous small conical teeth of variable size are irregularly arranged along the ventral margin of the alveolar process. The maxilla is robust and characterized by an expanded posterior end. The lower jaw teeth are similar to those of the upper jaw. The overall structure of the suspensorium is consistent with that of other gobioid fishes (e.g. Harrison 1989; Winterbottom 1993). The palatine is L-shaped, characterized by a large maxillary process and a short and stout articulatory process for the lateral ethmoid (Fig. 5A). What appears to be an endopterygoid can be recognized in specimen MGP-PD 7506Z. There is a relatively large gap between the posterior margin of the symplectic and the anterior margin of the preopercle (suspensorial interspace of Harrison 1989). The hyoid bar is massive. There are six branchiostegal rays, one of which is greatly expanded and articulates with the posterior ceratohyal (Fig. 5B).

The vertebral column comprises 25(26) [10+15(16)] vertebrae. The abdominal vertebrae bear thick and relatively large parapophyses. The general architecture of the caudal skeleton (Fig. 5C) is consistent with that of many other gobioid fishes, with a large triangular epaxial hypural plate (hyp 3+4) fused with the urostyle, autogenous triangular hypural plate (hyp 1+2), rod-like autogenous fifth hypural, autogenous parhypural, and penultimate vertebra bearing a short neural spine and an expanded haemal arch and spine fused to the centrum (e.g. Miller 1973; Hoese 1984; Winterbottom 1993); two epurals appear to be present. The caudal fin is rounded and consists of 15 principal rays (13 bifurcated distally), plus seven upper and six lower procurrent rays. The supraneurals are absent. There are two separated dorsal fins. The first dorsal fin contains six slender and flexible spines while the second dorsal fin contains a single spine followed by nine or 10 soft rays. The dorsal pterygiophore formula (Birdsong *et al.* 1988) is difficult to determine, primarily due to difficulties in interpretating the insertion of the first dorsal-fin pterygiophore; however, the anterior portion of the first dorsal fin and the underlying vertebrae are partially recognizable in specimen MGP-PD 27011 in which the dorsal pterygiophore formula appears to be 3-2211. The interneural gap appears to be absent. The anal-fin origin is located well beyond the insertion of the second dorsal fin. The anal fin consists of a single spine plus seven or eight soft rays; two anal fin pterygiophores insert anterior to the first anal fin pterygiophore. The pectoral girdle is always badly damaged and difficult to interpret. The pectoral fin comprises (14) 15−17 rays. The pelvic fins are separated from each other; each fin contains a single spine plus five rays.

Most of the body is densely covered with ctenoid scales; cycloid scales seem to be recognizable in the predorsal and abdominal regions. Lateral-line scales are absent.

Remarks. Fossil fish remains from the lignite-bearing deposits of Monteviale were described for the first time by Agassiz (1832, 1839) and assigned to the species *Cottus papyraceus*. Subsequently, Sauvage (1875) referred the species established by Agassiz (1832) to the genus *Lepidocottus*. One century later, Gaudant (1975) considered the genus *Lepidocottus* to be a junior synonym of *Gobius* s. l. and included all of the species previously referred to *Lepidocottus*, including *L. papyraceus* from Monteviale (Gaudant 1978), within the genus *Gobius*. More recently, in a detailed study of *Lepidocottus* material from the Oligocene of Aix-en-Provence, southern France, Gierl *et al.* (2013) regarded the species from Monteviale as belonging to this genus.

The fossil fishes from the laminated lignites of Monteviale exhibit a suite of characters that unquestionably support their placement within the Gobioidei, including the overall physiognomy of the body, lack of parietals, basisphenoid and supraneurals, general architecture of the caudal-fin skeleton, absence of lateral-line scales, and presence of suspensorial interspace (e.g. Miller 1973; Springer 1983; Hoese 1984; Harrison 1989; Winterbottom 1993).

The assignment of these fossils to the genus *Lepidocottus*, as proposed by Sauvage (1875) and reiterated by Gierl *et al.* (2013), is problematical because of the lack of an unambiguous diagnosis of this genus. The external morphology of the body (Fig. 4), osteology, meristics and squamation pattern that characterize the gobioid fishes from Monteviale are consistent with those of the type species of *Lepidocottus*, *L. aries* (Agassiz) from the Oligocene of southern France. The gobioid from Monteviale, however, clearly differs from *L. aries* in having a more anterior insertion of the first dorsal-fin pterygiophore and no interneural gap (dorsal pterygiophore formula 3-2211 vs 4-22110; see Gierl *et al.* 2013). However, these differences might be indicative of a separation at the species rather than the genus level, and for this reason the gobioid fishes from Monteviale are tentatively referred herein to the extinct genus *Lepidocottus*.

The position of *Lepidocottus* within Gobioidei is even more difficult to determine. Molecular studies (Thacker 2009) suggested that Gobioidei includes at least six families (Butidae, Eleotridae, Gobiidae, Gobionellidae, Odontobutidae, Rhyacichthyidae), and the familial status of two additional gobioid clades, Milyeringidae and Thalasseleotrididae has been subsequently demonstrated (Chakrabarty 2010; Gill & Mooi 2012). Agassiz (1832, 1839) and Sauvage (1875) regarded the fishes from Monteviale as members of the family Cottidae. Obrhelová (1961) considered the fishes from Monteviale to be closely related to the extinct gobioid family Pirskeniidae (= Eleotridae; see Přikryl 2014), and Gaudant (1978) placed them within Gobiidae (see also Přikryl 2014). Gierl *et al.* (2013) referred the genus *Lepidocottus*, including the species *L. papyraceus* from Monteviale, to the gobioid family Butidae. The fish from Monteviale show a number of features that support their assignment to the gobioid families Butidae or Eleotridae (e.g. Akihito 1969; Springer 1983; Hoese 1984; Birdsong *et al.* 1988; Harrison 1989; Hoese & Gill 1993), including: palatine L-shaped with short process articulating medially with the lateral ethmoid; endopterygoid present; six branchiostegal rays; two epurals; pelvic fins widely separated from each other; caudal peduncle well-developed, longer than second dorsal fin base; dorsal pterygiophore formula 3-2211; interneural gap absent; and caudal fin with 15 principal rays of which 13 are bifurcated distally. These two families have been traditionally regarded as closely related to each other but recent molecular studies (Thacker 2009) have demonstrated their phylogenetic separation and that a group that includes Butidae and Eleotridae would be paraphyletic. Gierl *et al.* (2013) assigned *Lepidocottus* to the Butidae based on a handful of morphological features. In this scenario, *Lepidocottus* has been interpreted as the sister taxon of the extant genus *Kribia*. The hypothesis proposed by Gierl *et al.* (2013) is tentatively followed herein. However, before such a familial placement can be unambiguously demonstrated further comparative information is required.

Class **Amphibia** Linnaeus, 1758
Order **Anura** Fischer von Waldheim, 1813
Suborder **Palaeobatrachina** Bolkay, 1919
Family **Palaeobatrachidae** Cope, 1865
Genus ***Palaeobatrachus*** Tschudi, 1838
Palaeobatrachus (*s. l.*) sp.
(Fig. 6)

1885 *Palaeobatrachus* sp.; Portis: 1189, figs 3, 4.
1887 *Palaeobatrachus* sp.; Wolterstorff: 101.
1915 *Palaeobatrachus* sp.; Fabiani: 303.
1972 Palaeobatrachidae; Vergnaud-Grazzini & Hoffstetter: 170.
1972 *Palaeobatrachus* sp.; Špinar: 40.
1980 *Palaeobatrachus* sp.; Altichieri: 173.
2003 *Palaeobatrachus* sp.; Roček: 2003: 595, 605.
2006 *Palaeobatrachus* sp.; Mietto: 32, fig. 18/1.
2012 Palaeobatrachidae; Wuttke, Přikryl, Ratnikov, Dvořák & Roček: 388 (in fig. 7).

Material. Two tadpoles: MGP-PD 9396 and 9397, part and counterpart (counterpart as impression only), Length (L) = 28.7 mm (Fig. 6); and MGP-PD 9392, a poorly preserved partially complete skeleton, L = 23.9 mm.

Description. Amphibians are represented at Monteviale by two tadpoles. Despite the inadequate preservation of the first specimen, it is possible to make a few

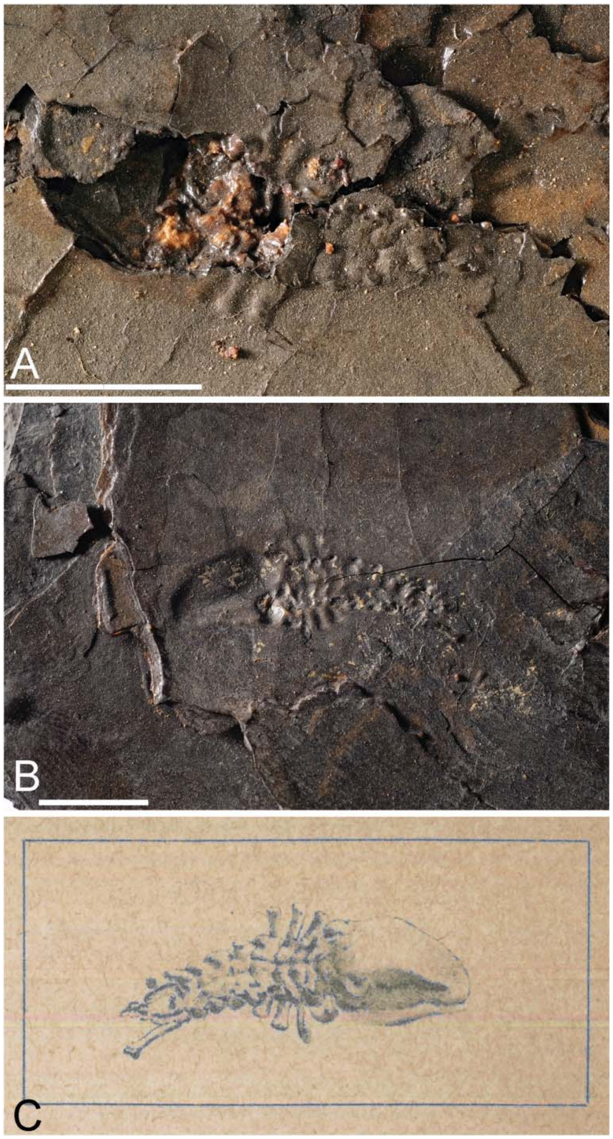


Figure 6. *Palaeobatrachus* (s. l.) sp. from Monteviale. **A,** MGP-PD 9396, part; **B,** MGP-PD 9397, counterpart; **C,** historical drawing of MGP-PD 9396 by Portis (1885). Scale bars = 10 mm.

observations. The head is large whereas the tail is long and thin (Fig. 6A). In the counterpart five pairs of free ribs are evident, while on the part the frontoparietal is undivided and smooth (Fig. 6B). Concerning the post-cranial region, it is possible to observe the beginning of ossification of the cleithrum. The right femur (L = 3.9 mm) is ossified. The second specimen is badly preserved, preventing any accurate morphological observation.

Remarks. Portis (1885) first described the Monteviale tadpoles and assigned them to *Palaeobatrachus* sp. The presence of five pairs of autogenous ribs and the morphology of the frontoparietal confirm the attribution of the remains to the family Palaeobatrachidae, excluding any attribution to Pelobatidae (Špinar 1972; see also Roček 2003 and Maus & Wuttke 2004). The developmental stage of the first specimen corresponds (at least for the number of ribs) to stage NF 59b of Roček (2003), even though the ossifications of other elements reported by this author were not observed. Portis (1885) referred to the genus *Palaeobatrachus* a partially complete tadpole, from upper Oligocene deposits of Laverda (Vicenza, Veneto), for which Petters (1877) previously established the taxon *Protobatrachus vicetinus* (now *Palaeobatrachus vicentinus*; see Martin *et al.* 2012). Woltersdorff (1887) excluded any possible attribution of the palaeobatrachids of Monteviale and Laverda to the same taxon. However, the advanced development stage of *P. vicentinus* does not allow an easy comparison with the tadpoles of Monteviale.

At least three Palaeogene European genera were assigned to the family Palaeobatrachidae, including *Palaeobatrachus*, *Messelobatrachus* and *Albionbatrachus* (Rage & Roček 2003). According to Wuttke *et al.* (2012, and references therein), both *Messelobatrachus* and *Albionbatrachus* should be considered synonyms of *Palaeobatrachus*. However, Venzel *et al.* (2013) assigned remains of an anuran from the Rupelian (MP23–24) of Suceag (Romania) to the genus *Albionbatrachus*, for which they established the species *A. oligocenicus*. Since there are conflicting opinions about the systematics of the family Palaeobatrachidae, and finding a solution is well beyond the scope of this work, we prefer to assign our fossils to *Palaeobatrachus* (s. l.) sp.

Class **Reptilia** Laurenti, 1768

Remarks. The reptiles from Monteviale belong to two orders: Testudines and Crocodylia. Although the fossil turtles of Monteviale have been recently reviewed (Kotsakis 1977, 1985; Hervet 2004), a brief summary of *Trionyx* and *Palaeochelys* is presented here.

Order **Testudines** Batsch, 1788
Suborder **Cryptodira** Cope, 1868
Infraorder **Eucryptodira** Gaffney, 1975
Superfamily **Trionychoidea** Gray, 1825
Family **Trionychidae** Gray, 1825
Subfamily **Trionychinae** Gray, 1825
Genus ***Trionyx*** Geoffroy Saint-Hilaire, 1809
Trionyx (s. l.) ***italicus*** von Schauroth, 1865
(Fig. 7)

(Selected synonym)
1865 *Trionyx italicus* Schauroth: 265, pl. 29.
1892 *Trionyx capellinii* var. *montevialensis* Negri: 39, pl. 4.
1893 *Trionyx schaurothianus* Negri: 5, pls 1, 2.
1895 *Trionyx capellinii* var. *gracilina* Sacco: 544, fig. 2.
1895 *Trionyx capellinii* var. *perexpansa* Sacco: 546, fig. 1.
1934 *Trionyx (Amyda) italicus* Schauroth; Bergounioux: 279.
1934 *Trionyx (Amyda) capellini* var. *perexpansa* Sacco; Bergounioux: 279.

Figure 7. *Trionyx* (s. l.) *italicus* (Schauroth, 1865) from Monteviale. **A,** MGP-PD 9273, carapace in dorsal view, holotype of *Trionyx capellinii montevialensis*; **B,** MGP-PD 10818Z, carapace in dorsal view with fragments of skull and limbs, holotype of *T. schaurothianus*; **C,** MGP-PD 26560, carapace in dorsal view, holotype of *T. insolitus*. Scale bars = 5 cm.

1934 *Trionyx (Amyda) capellinii* var. *gracilina* Sacco; Bergounioux: 279.
1934 *Trionyx (Amyda) capellinii* var. *schaurothiames* [sic] Negri; Bergounioux: 279.
1954 *Trionyx (Amyda) capellinii* var. *monsvialensis* Negri; Bergounioux: 5, figs 19–23, pls 7–11.
1954 *Trionyx (Amyda) capellinii* var. *schaurothianus* Zigno; Bergounioux: 63, fig. 24, pl. 12.
1954 *Trionyx (Amyda) capellinii* var. *gracilina* Sacco; Bergounioux: 66, fig. 25.
1954 *Trionyx (Amyda) capellinii* var. *perexpansa* Sacco Bergounioux: 66, fig. 26.
1954 *Trionyx insolitus* Bergounioux: 67, fig. 27, pl. 13.
1955 *Trionyx (Amyda) capellinii* var. *monsvialensis* Negri; Bergounioux: 535, fig. 36.
1955 *Trionyx (Amyda) capellinii* var. *schaurothianus* Zigno; Bergounioux: 535, fig. 37.
1977 *Trionyx capellinii montevialensis* Negri; Kotsakis: 214.
1977 *Trionyx italicus* Schauroth; Broin: 189.
1980 *Trionyx (Amyda) capellinii monsvialensis* Negri; Altichieri: 173, fig. on page 174.
1980 *Trionyx capellinii montevialensis* Negri; Barbera & Leuci: 3, figs 1, 2, pls 1–3.
1980 *Trionyx capellinii schaurothianus* Zigno; Barbera & Leuci: 11, figs 1, 2, pls 4, 5.
1985 *Trionyx italicus* von Schauroth; Kotsakis: 163.
2005 *Trionyx italicus* von Schauroth; Kotsakis, Argenti, Barisone, Delfino, Palombo, Pavia & Piras: 132, fig. 11.
2006 *Trionyx italicus* Schauroth; Mietto: 31, figs 19, 20.

Material. Carapace in dorsal view, holotype of *Trionyx capellinii montevialensis* (MGP-PD 9273) (Fig. 7A); carapace in dorsal view and posterior limbs (MGP-PD 27634); partial endoskeleton in ventral view (MGP-PD 27636); carapace and plastron in ventral view with part of an anterior and a posterior limb (MGP-PD 27637); carapace in dorsal view with fragments of skull and limbs, holotype of *T. schaurothianus* (MGP-PD 10818Z) (Fig. 7B); carapace in dorsal view, holotype of *T. insolitus* (MGP-PD 26560) (Fig. 7C); two carapaces in dorsal view, holotypes of *T. c. gracilina* (PU 17285) and *T. c. perexpansa* (destroyed but illustrated in Sacco 1895); two carapaces in dorsal view (MP-CMSNF 7562 and MP-CMSNF 7563), the first one with a partial and distorted skull.

Description. The trionychids from Monteviale were described by Kotsakis (1977) and reviewed by the same author (Kotsakis 1985).

Remarks. The first description of a carapace fragment of a trionychid from Monteviale dates back to 1865 (Schauroth 1865) with the institution of the species *Trionyx italicus*. A few years later, Negri (1892, 1893) and Sacco (1895) examined the abundant material of the Monteviale collection and created several species and subspecies. Most of the trionychids of Monteviale were attributed to several subspecies of a species previously reported from the middle Eocene locality Purga di Bolca (Verona Province, Veneto Region, Italy). Negri (1892) described two species of *Trionyx*, *T. capellinii* and *T. gemmelaroi*, from Purga di Bolca. The second taxon was considered a synonym of *T. capellinii* by Kotsakis (1977). The forms described from Monteviale are as follows: *T. capellini montevialensis* Negri, 1892, *T. schaurothianus* Negri, 1893 (attributed by this author to Zigno *in schaedis*), *T. c. gracilina* Sacco, 1895, and *T. c. perexpansa* Sacco, 1895. Bergounioux (1954) described a carapace and added a further species, *T. insolitus*, to the long list of trionychids from Monteviale. Broin (1977) suggested that all these forms should be attributed to a single species, *T. italicus* Schauroth, 1865. This suggestion was corroborated by Kotsakis (1985). The carapace of *T. italicus* shows strong similarities to that of *T. capellinii* from the Lutetian of Purga di Bolca and therefore the Monteviale turtle has been considered as a chrono-subspecies of *T. capellinii* (Kotsakis 1977, 1985). It is very likely that the two above-mentioned species belong to the same group.

Meylan (1985, 1987) proposed a new classification for the living members of the family Trionychidae based on cranial morphology and post-cranial elements. The fossils of Monteviale exhibit the following carapace and plastron characters: width/length ratio greater than 3; peripherals absent; prenuchal absent; disc shape as wide as long; large eighth pleurals; unfused hyoplastra and hypoplastra; neural reversal always at same neural; only the eighth pleurals meeting at mid-line. Two specimens consist of badly deformed skulls, the type of *T. schaurothianus* (MGP-PD 10818Z) and specimen MP-CMSNF 7562. The preservational quality of the second individual allows some observations. On the right side, the jugal does not contact the squamosal as well as the parietal on the skull surface (characters 32 and 34 in Meylan 1987). These characters indicate morphological affinities (among the living members of the family) with *Trionyx triunguis* (Forskäl, 1775), the only species of the family assigned to the nominal genus by Meylan (1987).

Karl (1998) proposed the attribution of all remains of the European Cenozoic trionychids to three species: *Rafetoides henrici* (Owen, 1849), *R. austriacus* (Peters, 1858) and the extant *Trionyx triunguis* (Forsskål, 1775). Furthermore, Karl (1999) mentioned the material of Monteviale in his list of European localities bearing trionychid fossil remains but without any systematic comments, and later (Karl 2007) reported the presence of *T. triunguis* in the early Oligocene of Italy without any further indications. Finally, Karl & Müller (2008) reported the presence of *R. austriacus* from the early Eocene to Rupelian of Italy without any further indications. It is not clear which Italian Oligocene species and specimens are considered in this latter work. For this reason, we prefer to follow the classification proposed by de Lapparent de Broin (2001), and assign the species of Monteviale to *Trionyx sensu lato*.

Superfamily **Testudinoidea** Batsch, 1788
Family **Geoemydidae** Theobald, 1868
Genus ***Bergouniouxchelys*** Hervet, 2004
Bergouniouxchelys vallisnerii (Bergounioux, 1954)
(Fig. 8)

1915 *Emys vallisnerii* Fabiani: 303 (*nomen nudum*).
1953a *Anthracochelys vallisnerii* Bergounioux: 223 (*nomen nudum*).
1953a *Cyclochelys perexpansa* Bergounioux: 223 (*nomen nudum*).
1953a *Cyclochelys complanata* Bergounioux: 223 (*nomen nudum*).
1953b *Anthraxochelys vallisnerii* Bergounioux: 388 (*nomen nudum*).
1953b *Cyclochelys perexpansa* Bergounioux: 388 (*nomen nudum*).
1953b *Cyclochelys complanata* Bergounioux: 388 (*nomen nudum*).
1954 *Paralichelys vallisnerii* [sp. nov.] Bergounioux: 72, figs 29, 30, pl. 15.
1954 *Paralichelys complanata* [sp. nov.] Bergounioux: 77, figs 31–33, pls 16, 17, fig. 1.
1977 *Palaeochelys vallisnerii* (Bergounioux); Broin: 237, fig. 79.
1990 *Palaeochelys vallisnerii* (Bergounioux); Jiménez-Fuéntes, Ramos Guerrero, Martín de Jesús, Pérez Ramos & Mulas Alonso: 153.
2004 *Bergouniouxchelys vallisnerii* (Bergounioux); Hervet: 39, pl. 6, figs D–F.
2012 *Bergouniouxchelys vallisneri* (Bergounioux); Schäfer: 19.

Material. Plastron and partial carapace, holotype of *Paralichelys vallisnerii* (MGP-PD 26562) (Fig. 8A); carapace (MGP-PD 27630) (Fig. 8B); fragment of carapace and plastron, holotype of *Paralichelys complanata* (MGP-PD 26563); fragment of carapace (MGP-PD 27631).

Description. See Hervet (2004).

Remarks. Fabiani (1915) was the first author to mention an '*Emys*' collected in Monteviale for which he proposed the name *Emys vallisnerii*. Bergounioux (e.g. 1953a, b) described three specimens and created two new genera and three new species: *Anthracochelys vallisnerii*, *Cyclochelys perexpansa* and *Cyclochelys complanata*. All of these taxa are currently *nomina nuda*. In 1954, Bergounioux created two new species, *Paralichelys vallisnerii* and *Paralichelys complanata*, and assigned them to the suborder Pleurodira, family Polysternidae (see Hervet 2004 on the generic attribution). Broin (1977) assigned *P.*

Figure 8. *Bergouniouxchelys vallisnerii* (Bergounioux, 1954) from Monteviale. **A,** MGP-PD 27630, carapace; **B,** MGP-PD 26562, plastron and partial carapace, holotype of *B. vallisnerii*. Scale bars = 5 cm.

vallisnerii to the genus *Palaeochelys* (Cryptodira, Emydidae) and synonymized *Paralichelys complanata* with *Palaeochelys vallisnerii*. Hervet (2004) also considered *P. complanata* to be a synonym of *P. vallisnerii*, and proposed the creation of a new genus for this species, *Bergouniouxchelys*, belonging to the cryptodiran family Geoemydidae. Claude & Tong (2004) synonymized *Bergouniouxchelys* (along with other geoemydid genera) with *Palaeochelys* without any justification. However, in a subsequent contribution, Claude *et al.* (2012) accepted the validity of the genus created by Hervet (2004).

Nevertheless, there are two questions about the systematic status of *P. vallisnerii*. The first is its authorship. In the recent literature Bergounioux is considered to be the author of the species (Bergounioux 1954; Broin 1977; Hervet 2004). Fabiani (1915, p. 303) proposed the name *Emys vallisnerii* for the remains of a turtle discovered at Monteviale and considered this form different from the early Eocene *Emys capellinii* Zigno, 1890 (now *Neochelys capellinii*; see Bergounioux 1954; Broin 1977; Kotsakis 1978) from Monte Bolca. The Eocene species was considered by Fabiani (1915) as a possible ancestor of the Monteviale turtle. We consider the short mention of *E. vallisnerii* by Fabiani (1915) as inadequate to validate authorship as it does not fulfill the requirements of Article 12.2 of the International Code of Zoological Nomenclature (ICZN 2000).

The second problem concerns the generic attribution of the Monteviale geomyidid. Two different opinions have already been mentioned above. The first hypothesis regards the Monteviale species as belonging to *Palaeochelys*, a genus with a wide geographical distribution in the European Palaeogene (Broin 1977; Claude & Tong 2004). The second hypothesis (Hervet 2004) assigns the Monteviale species to a monospecific genus, endemic for the area, *Bergouniouxchelys*. However, after Claude *et al.* (2012), some of the fossils collected in Provence (France) referred to the genus *Provencemys* by Hervet (2004) should be placed in *Bergouniouxchelys*. The diagnosis of the genus *Bergouniouxchelys* seems to be adequate to recognize this taxon as separate from *Palaeochelys*, and we here follow Hervet (2004) and Claude *et al.* (2012) in assigning the fossils from Monteviale to *Bergouniouxchelys*.

Superorder **Crocodyliformes** Hay, 1930 (*sensu* Benton & Clark 1988)
Order **Crocodylia** Gmelin, 1789 (*sensu* Brochu 2003)
Superfamily **Alligatoroidea** Gray, 1844 (*sensu* Brochu 2003)
Subfamily **Diplocynodontinae** Brochu, 1999
Genus **Diplocynodon** Pomel, 1847
Diplocynodon cf. ***ratelii*** Pomel, 1847
(Figs 9, 10)

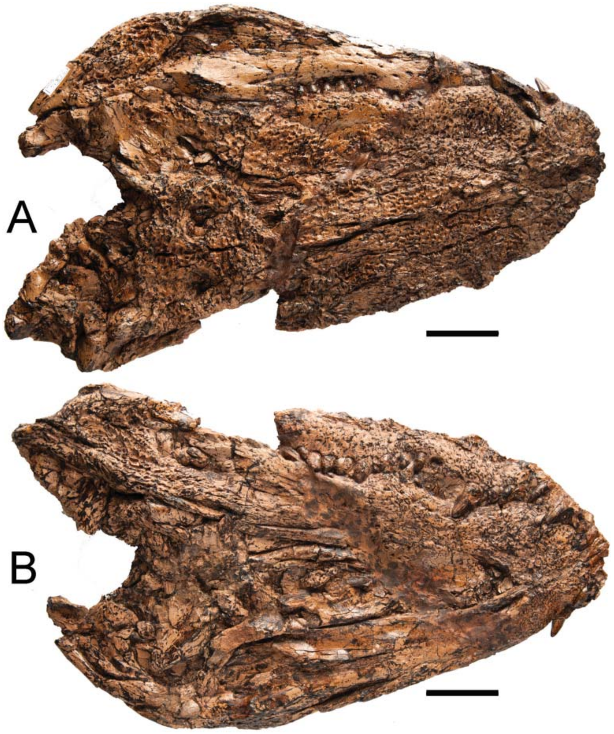


Figure 9. MGP-PD 26814, *Diplocynodon* cf. *ratelii* Pomel, 1847 from Monteviale, lectotype of *Diplocynodon dalpiazi*. **A,** dorsolateral view; **B,** ventrolateral view. Scale bars = 5 cm.

1914 *Crocodilus monsvialensis* Fabiani: 233 (footnote 2).
1915 *Crocodilus dalpiazi* Fabiani: 306 (*nomen nudum*).
1915 *Crocodilus monsvialensis* Fabiani; Fabiani: 306.
1966 ?*Diplocynodon monsvialensis* (Fabiani); Berg: 40.

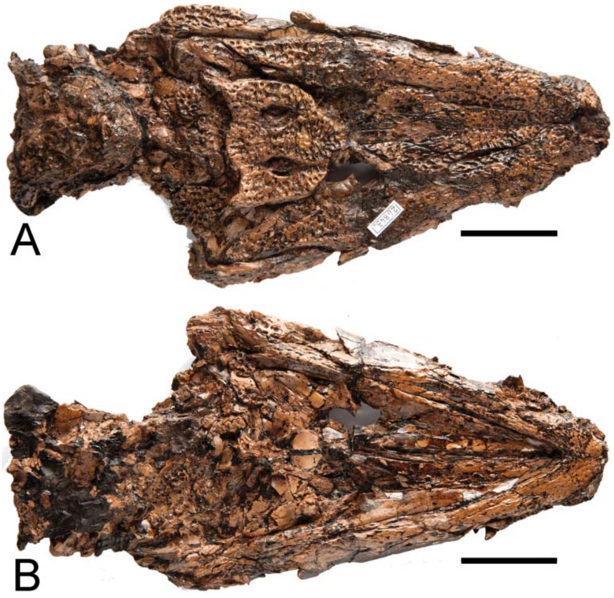


Figure 10. MGP-PD 26843, *Diplocynodon* cf. *ratelii* Pomel, 1847 from Monteviale, lectotype of *Asiatosuchus monsvialensis*. **A,** dorsal view; **B,** ventral view. Scale bars = 5 cm.

1980 ?*Diplocynodon monsvialensis* (Fabiani); Altichieri: 173.

1980 '*Crocodilus dalpiazi*' Fabiani; Altichieri: 173.

1992 *Diplocynodon dalpiazi* (Fabiani); Franco, Piccoli & Tchaprassian: 130, figs 1–17, pls 1–3.

1993 *Asiatosuchus monsvialensis* (Fabiani); Franco & Piccoli: 101, figs 1–12, pls 1–3.

1995 *Diplocynodon dalpiazi* (Fabiani); Franco: 271, fig. 1 (1).

1995 *Asiatosuchus monsvialensis* (Fabiani); Franco: 271, fig. 1(2).

1995 *Diplocynodon dalpiazi* (Fabiani); Rauhe & Rossmann: 84.

1995 *Diplocynodon monsvialensis* (Fabiani); Rauhe & Rossmann: 85.

1998 *Diplocynodon ratelii* Pomel; Brinkmann & Rauhe: 307.

1999 *Diplocynodon* cf. *D. ratelii* Pomel; Del Favero: 109, figs 1–3.

2004 *Diplocynodon* cf. *D. ratelii* Pomel; Kotsakis, Delfino & Piras: 70.

2005 *Diplocynodon* cf. *D. ratelii* Pomel; Kotsakis Kotsakis, Delfino & Piras: 133.

2006 *Diplocynodon* cf. *D. ratelii* Pomel; Mietto: 32, fig. 21.

Material. Thirty-seven published specimens, almost all figured by Franco *et al.* (1992) and Franco & Piccoli (1993) who chose the lectotypes of *Diplocynodon dalpiazi* (MGP-PD 26814, incomplete skull with lower jaw, lacking a small piece of the snout, dorsal cranial length: 324 mm, Fig. 9), and of *Asiatosuchus monsvialensis* (MGP-PD 26843, skull with lower jaw, dorsal cranial length 195 mm, Fig. 10). Besides the lectotypes, the material also includes 17 skulls, most of which are fragmentary (MGP-PD 11407, MGP-PD 26815, MGP-PD 26816, MGP-PD 26817, MGP-PD 26819, MGP-PD 26820, MGP-PD 26835, MGP-PD 26837, MGP-PD 26838, MGP-PD 26842, MGP-PD 26844, MGP-PD 26845, MGP-PD 26846, MGP-PD 26856, MGP-PD 26857, MGP-PD 26858, MGP-PD 26861), many isolated teeth (not numbered), and 28 postcranial remains consisting of partial dorsal and ventral armours, parts of vertebral columns, girdles and limbs, and many isolated osteoderms (MGP-PD 26821, MGP-PD 26822, MGP-PD 26823, MGP-PD-26824, MGP-PD 26825, MGP-PD 26827, MGP-PD 26828, MGP-PD 26829, MGP-PD 26831, MGP-PD 26832, MGP-PD 26840, MGP-PD 26841, MGP-PD 26847, MGP-PD 26848, MGP-PD 26849, MGP-PD 26852, MGP-PD 26853, MGP-PD 26854, MGP-PD 26855, MGP-PD26856, MGP-PD 26859, MGP-PD 26860, MGP-PD 26861, MGP-PD 26862, MGP-PD 26863, MGP-PD 26864, MGP-PD 26865, MGP-PD 26866).

Description. See Franco *et al.* (1992) and Franco & Piccoli (1993).

Remarks. Crocodiles from Monteviale are numerous but generally poorly preserved. Complete specimens have not been found. Most of the remains were collected during the nineteenth and the beginning of the twentieth century, the bulk housed at the MGP-PD. It mainly consists of remains referable to at least a dozen individuals, and many isolated teeth and osteoderms. The fossils were originally studied by Fabiani, who created the new species *Crocodylus monsvialensis* Fabiani, 1914 and *C. dalpiazi* Fabiani, 1915. Unfortunately, Fabiani only provided a short description of the material and did not figure any specimens. Berg (1966) tentatively included *'C'. monsvialensis* within the genus *Diplocynodon* but scarcely justified this attribution. No mention of *C. dalpiazi* was made by Berg. In the 1990s, Franco *et al.* (1992) and Franco & Piccoli (1993) described and figured most of the specimens originally studied by Fabiani, and assigned them to *Diplocynodon dalpiazi* (Fabiani, 1915) and *Asiatosuchus monsvialensis* (Fabiani, 1914). They also selected lectotypes for both species, regarded as valid by these authors. They considered the size of the skull (larger in *D. dalpiazi*) and the presence of fine striae on the surface of the teeth as diagnostic for *D. dalpiazi*. Rauhe & Rossmann (1995) referred both species to *Diplocynodon*, while Brinkmann & Rauhe (1998) considered them to be junior synonyms of *Diplocynodon ratelii* Pomel, 1847, an opinion shared by Kotsakis *et al*. (2004).

We carried out a review of the most characteristic material, confirming that *C. monsvialensis* and *C. dalpiazi* are referable to the genus *Diplocynodon.* This generic attribution is justified by a combination of several characters, including: the presence of two enlarged and subequal alveoli in the maxilla (4th+5th); two enlarged subequal alveoli in the mandible (3rd+4th); a short dentary symphysis extending between the third and fourth alveoli; dorsal margin of lower temporal fenestra formed by the quadratojugal, preventing the quadrate from reaching the fenestra; and rounded dorsal margin of the iliac blade with a smooth border and the presence of a ventral armour consisting of bipartite osteoderms [e.g. Franco *et al.* 1992, pl. 3, fig. 4, fig. 6 (p. 134); Franco & Piccoli 1993, pl. 1, fig. 2, pl. 2, fig. 2, fig. 5 (p. 105), fig. 7 (p. 107)]. We also agree with the opinion of Brinkmann & Rauhe (1998) that all of the remains from Monteviale represent a single species. On the other hand, a combination of characters suggests that the Italian species might be slightly different from *D. ratelii.* The snout in dorsal view exhibits a strong lateral festoon and is shorter and stouter than that seen in *D. ratelii*. Nevertheless, this feature can be partly related to ontogeny or to post-mortem distortion. The nasal bones are short and weakly pointed mesially; they end at the level of the maxillary-premaxillary notch (first maxillary alveolus, in some cases at the second), never reaching the narial rim. The frontal-parietal suture is straight and located at the level of the posterior third of the supratemporal fenestrae; in some specimens the postorbital-squamosal suture exhibits a similar condition. The postorbital is wider than long and there is no contact between it and the parietal; the supraoccipital is well exposed in dorsal view in the skull table.

A detailed systematic revision of the Monteviale material is needed in order to assess better the taxonomic position of these remains.

Class **Mammalia** Linnaeus, 1758
Cohort **Placentalia** Owen, 1837

Remarks. Ten species of placental mammals occur in the fossil assemblage of Monteviale: two pantolestans, a single bat, one primitive rhinocerotid, four anthracotherioids, a single suoid and a single sirenian. The best-known species is the large bat *Archaeopteropus transiens*. Because several recent publications have described the morphological characteristics of this taxon (Habersetzer & Storch 1987; Simmons & Geisler 1998; Schutt & Simmons 1998), and as the original fossil was destroyed during the Second World War, only a brief summary of this taxon is reported here.

Superorder **Afrotheria** Stanhope, Waddell, Madsen, De Jong, Hedges, Cleven, Kao, & Springer, 1998
Order **Sirenia** Illiger, 1811
Family **Dugongidae** Gray, 1821
Dugongidae gen. et sp. indet.

1937c *Halitherium* sp. Dal Piaz: 1.

Material. Two fragments of ribs (MGP-PD 26584; MGP-PD 31399).

Remarks. Dal Piaz (1937c) referred a rib fragment (MGP-PD 26584) to the genus *Halitherium*. The two fragments are clearly pachyostotic and typical of a sirenian. Nevertheless, the material is too fragmentary for a definitive generic attribution.

Superorder **Boreoeutheria** Springer & De Jong, 2001
Grandorder ***incertae sedis***
Order ?**Pantolesta** McKenna, 1975
Family ***incertae sedis***
Genus ***Epapheliscus*** Van Valen, 1966
Epapheliscus italicus Van Valen, 1966
(Fig. 11)

1930b cf. *Dyspterna woodi* Hopwood; Dal Piaz: 3, pl. 1, figs 1–3.
1943 cf. *Dyspterna woodi* Hopwood; Kretzoi: pl. 1, fig. 13.
1958 *Dyspterna* cf. *woodi* Hopwood; Thenius: 56.
1966 *Epapheliscus italicus* Van Valen: 88.
1967 *Epapheliscus italicus* Van Valen; Van Valen: 249.
1973 *Epapheliscus italicus* Van Valen; Cray: 57.
1980 cf. *Dyspterna woodi* Hopwood; Altichieri: 174.
1986 *Epapheliscus italicus* Van Valen; Kotsakis: 142.
1997 *Epapheliscus* Van Valen; McKenna & Bell: 362.
2005 *Epapheliscus italicus* Van Valen; Zack, Penkrot, Krause & Maas: 811.
2006 *Epapheliscus italicus* Van Valen; Mietto: 36, fig. 23/1, 2.

Material. The holotype consists of a right maxillary fragment bearing P4-M3 (MGP-PD 27284) (Fig. 11).

Description. (Dental terminology follows Hooker & Russell 2012). The dental series P4-M3 is 19.8 mm in length.

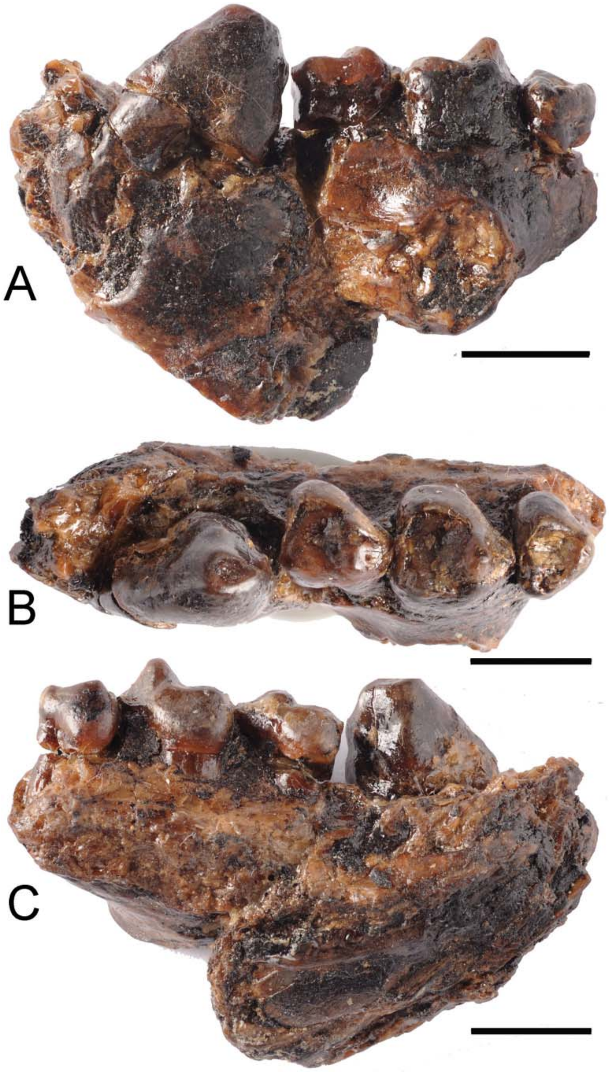


Figure 11. MGP-PD 27284, holotype of *Epapheliscus italicus* Van Valen, 1966 from Monteviale, right maxillary fragment bearing P4-M1. **A,** labial view; **B,** occlusal view; **C,** lingual view. Scale bars = 5 mm.

P4 is the most robust tooth (L = 6.2 mm; Width (W) = 4.5 mm) and possesses a very large and robust paracone; the metacone is absent, while the protocone is reduced and displaced to the postero-lingual edge of the tooth. A cingulum occurs on the mesial, distal and lingual sides of the premolar. Among the molars, M2 is larger than M1, whereas M3 represents the smallest element. M1 (L = 4.6 mm; W = 4.2 mm) is characterized by a deep trigon basin. The metacone is more robust than the paracone. The metastyle is present, even if not well developed. The protocone expands mesio-distally with the development of the preprotocrista and postprotocrista. The hypocone is absent. M2 (L = 5.1 mm; W = 4.8 mm) has a deep trigon basin as well, and a metacone better developed than the paracone. The protocone and adjoining cristae are similar to those of M1. The metastyle is visible, while the hypocone is absent. M3 (L = 3.1 mm; W = 4.1 mm) is triangular and displays a paracone much more robust than the metacone. A protocone and well-developed pre- and postprotocristae are present. Hypocone is absent. In the antero-labial portion, the paracingulum is divided into two cristae and seems to form an additional cusp with the parastyle.

Remarks. Dal Piaz (1930b) described and illustrated this fossil, devoid of collection number, and provisionally assigned it to cf. *Dyspterna woodi* Hopwood, 1927. This species, established by Hopwood (1927), is based on a mandibular fragment with m2−m3, collected in the Hamstead Member of the Bouldnor Formation, Isle of Wight (UK), and of earliest Oligocene age (Hooker *et al.* 2005; Hooker 2010a). No maxillary remains of this species are known. Cray (1973) described and assigned a second species to the genus as *Dyspterna hopwoodi* Cray, 1973, found at Headon Hill (Isle of Wight) and late Eocene in age. *D. hopwoodi* is also known only from a mandible and two additional lower teeth. It was transferred by Russell & Godinot (1988) to a new genus, *Euhookeria*. Hooker *et al.* (2005) reported this species as *Dyspterna hopwoodi* and listed it only from the Hatherwood Limestone Member of the Headon Hill Formation at Headon Hill. The genus is not found outside England. Therefore, it is not possible to compare the fossil remains of Monteviale with those ascribed to *Dyspterna*.

Van Valen (1966) established a new taxon, *Epapheliscus italicus*, for the fossil of Monteviale. He assigned it to the subfamily Apheliscinae, recorded from the Paleocene and Eocene of North America. As pointed out by Zack *et al.* (2005), Van Valen indicated MGP-PD 6834 as the type of the species, finding out that it is actually the holotype of ?*Dyspterna helbingi* Dal Piaz, 1930 (see following species). Nevertheless, the material described by Van Valen (1967) is clearly specimen MGP-PD 27274. Indeed, only this specimen displays the morphological characters described by Van Valen; these characters are not present in MGP-PD 6834. So, we suggest maintaining the name *E. italicus* as a valid taxon despite the mistake in the transcription of the inventory number. In a second publication, Van Valen (1967) excluded *E. italicus* as being derived from *Apheliscus insidiosus* (Cope, 1874) because of the morphology of the P4, characterized by a well-developed protocone in the latter species. Van Valen (1967) hypothesized that it could not have been derived from any other member of the subfamily Apheliscinae. McKenna & Bell (1997) assigned the monotypic genus *Epapheliscus* to the subfamily Apheliscinae, family Hyopsodontidae, order Condylarthra. Zack *et al.* (2005) elevated the subfamily Apheliscinae to the rank of family and indicated the presence of a well-developed hypocone on M1 and M2, as the main feature that justifies the rank change, a feature totally absent in the fossil from Monteviale. Zack *et al.* (2005) did not exclude *E. italicus* from Apheliscidae but suggested that this species could belong to another group such as a primitive artiodactyl, amphilemurid, erinaceomorph or primate. The systematic position of the Apheliscidae has undergone numerous changes in the last decade. Apheliscidae, Louisinidae, Adapisoricidae and Amphilemuridae are considered by some researchers to belong to Macroscelidea (Penkrot *et al.* 2008; Hooker & Russell 2012) (in this case the elephant-shrews should not be included in Afrotheria), while for others Apheliscidae should still be considered part of the order Condylarthra (Rose *et al.* 2012).

A comparison with several species of Apheliscidae − *A. insidiosus* (Cope, 1874), *A. nitidus* Simpson, 1937, *A. wapitiensis* (Van Valen, 1967), *A. chydaeus* Gingerich, 1974, *Phenacodaptes sabulosus* (Jepsen, 1930), *Gingerichia geoteretes* Zack, Penkrot, Krause & Maas, 2005, *G. hystrix* Zack, Penkrot, Krause & Maas, 2005, *Haplomylus speirianus* Cope, 1880, *H. simpsoni* Rose, 1981, *Litomylus grandaletes* Scott, Fox, & Youzwyshyn, 2002, *Dorraletes diminutivus* Gingerich, 1983 and *Aletodon quadravus* Gingerich, 1983 − all North American taxa ranging from middle Paleocene to early Eocene, shows that *E. italicus* is considerably different from all of the members of the family in the morphology of P4, M1 and M2 (Simpson 1935, 1937; Gazin 1959; Van Valen 1967; Delson 1971; Rose 1981; Gingerich 1983, 1994; Robinson & Williams 1997; Scott *et al.* 2002; Gingerich & Smith 2006; Zack *et al.* 2005; Hooker & Russell 2012; Rose *et al.* 2012). Therefore, we concur with the suggestion of Zack *et al.* (2005) and exclude the Monteviale species from the family Apheliscidae.

A comparison between *Epapheliscus italicus* and several species of the European family Louisinidae (middle Paleocene−early Eocene) shows substantial morphological differences. Members of Louisinidae possess a fourth upper premolar with a well-developed metacone, whereas this is absent in the last premolar of the Monteviale specimen. Another peculiar feature is the presence of a hypocone in M1 and M2 in the louisinids, which is missing in the Monteviale specimen (Tabuce *et al.* 2006; Hooker & Russell 2012). Amphilemuridae, a European (and dubiously North American) Eocene family traditionally assigned to Erinaceomorpha (McKenna & Bell 1997) but recently transferred to Macroscelidea (Hooker & Russell 2012), is characterized by different morphologies of P4 and upper molars with a hypocone still present in the molars (Hooker 1986; Hooker & Weidmann 2000; Maitre *et al.* 2006).

A comparison with the members of the order Pantolesta demonstrates the impossibility of assigning the Monteviale fossil to the European family Paroxyclaenidae (early–late Eocene) as suggested by McKenna & Bell (1997), primarily because M1 is larger than M2, and the morphology of P4 and molars is completely different (labio-lingually elongated) among all genera for which upper teeth are reported (*Paroxyclaenus, Spaniella, Kopidodon, Pugiodens, Vulpavoides* (= *Russelites*), *Paravulpavoides*) (Van Valen 1965; Crusafont Pairo & Russell 1967; Hooker 1986; Koenigswald 1992; Rose 2006; Harrison 2009). Additionally, it is difficult to assign *Epapheliscus* to Pantolestidae because the dental morphologies of the genera belonging to this family (*Palaeosinopa* and *Buxolestes* among others) are completely different in having molars labio-lingually elongated (in Pantolestinae) and a semimolariform P4 (in Pentacodontinae) (Koenigswald 1980; Gunnell *et al.* 2007; Hooker 2010b; Rankin 2014). The Asian members of Pantolesta, *Kiinkerishella zaisanica* Gabuniya & Biryukov, 1978 (paroxyclaenid) and *Oboia argillaceous* Gabuniya, 1989 (pantolestid or paroxyclaenid), both from the late Eocene of the Zaysan basin (Kazakhstan), and *Gobiopithecus khan* Dashzeveg & Russell, 1992 (dyspternine) from the early Oligocene of Mongolia, are known only from mandibular remains (Dashzeveg & Russell 1992; Lucas & Emry 2004). *Bogdia orientalis* Dashzeveg & Russell, 1985 (pantolestid) from the middle Eocene of the Valley of Lakes (Mongolia) possesses a developed protocone on P4 and M1 with a hypoconular shelf (Dashzeveg & Russell 1985), thereby showing a morphology completely different with respect to that of the fossil from Monteviale. Members of the early Oligocene African family Ptolemaiidae appear to be morphologically distant. These have been traditionally assigned to Pantolesta (McKenna & Bell 1997), currently elevated to the rank of order (Simons & Bown 1995; Gunnell *et al.* 2010).

Finally, the subfamily Dyspterninae, erected as a family by Kretzoi (1943) and assigned to the family Paroxyclaenidae by Russell & Godinot (1988) and to the family Pantolestidae by McKenna & Bell (1997), includes (in addition to the nominal genus *Dyspterna* which is probably a junior synonym of *Cryptopithecus*, as suggested by Hooker 2010a): *Cryptopithecus* [including *Androconus* and *Opsiclaenodon*, the latter considered a synonym of *Cryptopithecus* by Van Valen (1967) and Heißig (1977), but regarded as valid by Cray (1973) and Hooker *et al.* (2005)] from the late Eocene–early Oligocene of Europe; *Kochictis* from the late Oligocene of Hungary; and *Gobiopithecus* from the early Oligocene of Mongolia (Kretzoi 1943; Heißig 1977). The genus *Fordonia*, assigned to Pantolesta by Marandat (1989) and regarded by McKenna & Bell (1997) as a member of the subfamily Dyspterninae, was transferred by Hooker (2013) to the family Pseudorhyncocyonidae. The P4 of *Kochictis centenii* Kretzoi, 1943 bears a well-developed protocone, being totally different from the P4 of *E. italicus*. The (partially preserved) lingual half of M1 displays the presence of a small hypocone (Kretzoi 1943; Russel & Godinot 1988). The upper molars of *Cryptopithecus major* (Lydekker, 1887) (= *Opsiclaenodon major*) and *C. sideroolithicus* Schlosser, 1890 are known only from isolated specimens, and thus it is impossible to assess whether M2 was larger than M1. The upper molars are very different (presence of a small hypocone, L/W proportions) from those of the Monteviale fossil (Cray 1973; Heißig 1977). Nevertheless, the P4 of *C. sideroolithicus*, illustrated by Heißig (1977, figs 6, 7), displays similarities to the P4 of *E. italicus*.

In conclusion, *Epapheliscus italicus* does not belong to the family Apheliscidae. The similarity of its P4 morphology with that of *C. sideroolithicus* seems to suggest an attribution to the order Pantolesta. However, a new cladistic analysis, similar to that performed by Hooker & Russell (2012) for the Apheliscidae and Louisinidae, could possibly clarify the relationships of the Monteviale taxon with the members of Pantolesta. We doubtfully ascribe *E. italicus* to ?Pantolesta, family *incertae sedis*.

?Pantolesta *incertae sedis*

(Fig. 12)

1930b ?*Dyspterna helbingi* Dal Piaz: 6, pl., fig. 4.
1943 ?*Dyspterna helbingi* Dal Piaz; Kretzoi: pl. 1, fig. 12.
1958 *Dyspterna helbingi* Dal Piaz; Thenius: 56.
1966 ?*Dyspterna helbingi* Dal Piaz; Van Valen: 88.
1973 ?*Dyspterna helbingi* Dal Piaz; Cray: 57.
1980 cf. *Dyspterna helbingi* Dal Piaz; Altichieri: 174.
1986 ?*Dyspterna helbingi* Dal Piaz; Kotsakis: 142.
2006 ?*Dyspterna helbingi* Dal Piaz; Mietto: 36, fig. 18/3.

Figure 12. MGP-PD 6834, ?Pantolesta *incertae sedis*, from Monteviale, left side of the cranium having a maxilla bearing P3 and P4–M3 roots. Scale bar = 5 mm.

Material. Cranial fragment embedded in the matrix including the left side of the cranium with maxilla bearing P3 and P4–M3 roots (MGP-PD 6834).

Description. The type of this species (approximate length = 60.0+ mm) bears a P3 and the roots of P4–M3 (length of P3–M3 = 20.5 mm). P3 (L = 4.96 mm, W = 4.58 mm) has a single and partially worn large cusp (paracone). A small accessory crest corresponding to the protocone occurs in the distal portion of the lingual side of the tooth. The sizes of the molars are similar to those of *E. italicus* with M2 > M1 > M3. However, M1 has a different outline (at the root level) than that drawn by Dal Piaz (1930b, fig. 4). The lingual border appears to be definitely squared as if the tooth possessed a hypocone. The outline of the P4, triangular with the apex on the lingual side, notably differs from that of *Epapheliscus italicus*.

In the catalogue of the MGP-PD, a cranial fragment (MGP-PD 6835Z), figured by Dal Piaz (1930b), and a mandibular fragment, very poorly preserved (MGP-PD 6836Z), are recorded under the name ?*D. helbingi*. The skull is elongated with a strong sagittal crest. Dal Piaz (1930b) did not assign these remains to a particular taxon but mentioned them as belonging to creodonts. Unfortunately, there are no adequately preserved morphological characters to assign these remains to a particular taxon.

Remarks. Dal Piaz (1930b) doubtfully assigned this fossil (MGP-PD 6834) to the genus *Dyspterna* and erected a new species, ?*Dyspterna helbingi*. The fossil does not have enough characters for a specific diagnosis (Van Valen 1966), and the conservation procedures used in the 1930s obscured part of the original root morphology. P3 resembles the morphology of the corresponding premolar of *Cryptopithecus sideroolithicus* Schlosser, from the early Oligocene of Möhren 13, Franconia (Germany), illustrated by Heißig (1977). However, it displays a wider expansion in the distal region of the tooth. The Monteviale fossil is slightly larger than *C. sideroolithicus*. However, the outlines of the molars, and particularly the M2 and M3, look completely different. Currently, ?*Dyspterna helbingi* should be considered as *nomen vanum*, as proposed by Simpson (1945, 1948) and further clarified by Mones (1989).

Grandorder **Laurasiatheria** Waddell, Okada, & Hasegawa, 1999
Order **Chiroptera** Blumenbach, 1799
Suborder ***incertae sedis***
Family ***incertae sedis***
Subfamily **Archaeopteropodinae** Simpson, 1945
Genus ***Archaeopteropus*** Meschinelli, 1903
Archaeopteropus transiens Meschinelli, 1903
(Fig. 13)

(Selected synonymy)
1903 *Archaeopteropus transiens* Meschinelli: 1329, pl. 1.
1912 *Archaeopteropus transiens* Meschinelli; Andersen: 37.
1937 *Archaeopteropus transiens* Meschinelli; Dal Piaz: 1, figs 1–3, pl. 1.
1970 *Archaeopteropus transiens* Meschinelli; Russell & Sigé: 168.
1987 *Archaeopteropus transiens* Meschinelli; Habersetzer & Storch: 119, fig. 8.
1998 *Archaeopteropus transiens* Meschinelli; Simmons & Geisler: 10.
1998 *Archaeopteropus transiens* Meschinelli; Schutt & Simmons: 19, figs 4, 9.

Material. Cast of a slab (part and counterpart, Fig. 13) with a partial skeleton (MGP-PD 27401 and 27402). The holotype, originally stored at the Museo Civico of Vicenza (Veneto, Italy), was destroyed during World War II.

Description. This fossil has been described and interpreted by several authors. For a recent discussion, see Schutt & Simmons (1998).

Remarks. *Archaeopteropus transiens* is the most studied fossil taxon among those collected at Monteviale. Additional observations on the cast, beyond those given by previous authors (e.g. Meschinelli 1903; Andersen 1912; Dal Piaz 1937a; Habersetzer & Storch 1987; Simmons & Geisler 1998; Schutt & Simmons 1998), are prevented by its moderate preservation which precludes observation of diagnostic anatomical features of the bat for a correct systematic revision. *Archaeopteropus* was considered as the oldest megachiropteran by Meschinelli (1903) and by several researchers who later studied its systematic position (Andersen 1912; Dal Piaz 1937a; Habersetzer & Storch 1987). Habersetzer & Storch (1987, fig. 31; see also Schutt & Simmons 1998, fig. 9A) reconstructed the wing and associated membranes of *Archeopteropus* with a typical megachiropteran uropatagium. According to other authors, this taxon should be assigned to Microchiroptera (Russell & Sigé 1970; Schutt & Simmons 1998). Schutt and Simmons (1998) attributed it to the clade Microchiroptera on the basis of the presence of a well-developed calcar. Recent molecular analyses proposed a different phylogenetic scenario in which megachiropterans represent the sister group of several families of microchiropterans within the Yinpterochiroptera, a clade of the order Chiroptera (Teeling *et al.* 2005). The validity of this clade has been accepted by several authors (Simmons 2005; Simmons *et al.* 2008, fig. 4). The presence of a calcar in *A. transiens* would represent a plesiomorphic character that was subsequently lost in pteropodids. *Archaeopteropus* could therefore be considered as a basal member of the clade Pteropodidae. However, a molecular study by Angarsson *et al* (2011) has led to a different conclusion,

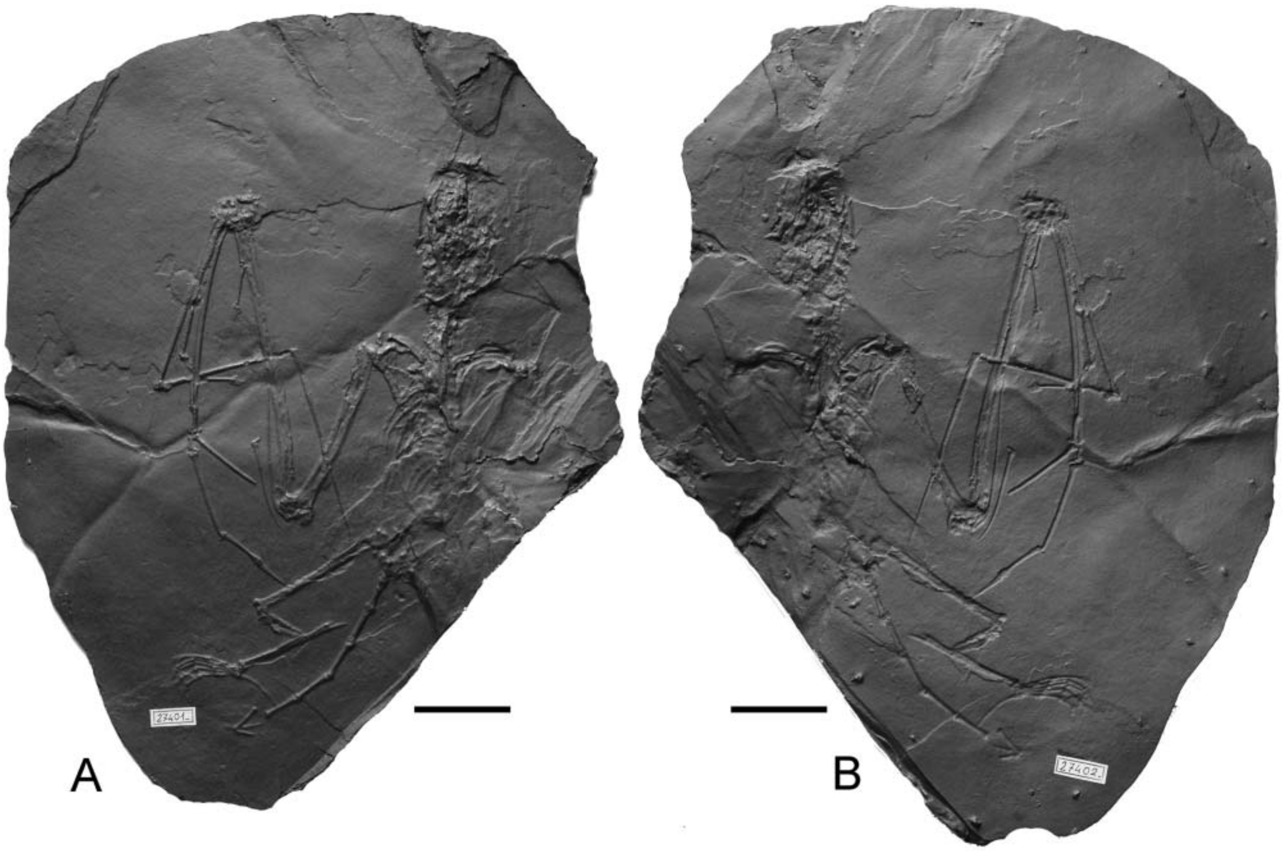


Figure 13. *Archaeopteropus transiens* (Meschinelli, 1903) from Monteviale. **A,** MGP-PD 27401, cast of a slab positive print; **B,** MGP-PD 27401, cast of a slab negative print. Scale bars = 4 cm.

separating once again pteropodids from other bats. Therefore, it would be more prudent to refer *A. transiens* to Chiroptera *incertae sedis*.

Order **Perissodactyla** Owen, 1848
Suborder **Ceratomorpha** Wood, 1937
Superfamily **Rhinocerotoidea** Gray, 1821
Family **Rhinocerotidae** Gray, 1821
Genus ***Epiaceratherium*** Abel, 1910
Epiaceratherium bolcense Abel, 1910
(Figs 14, 15)

(Selected synonymy)
1910 *Epiaceratherium bolcense* Abel: 20, pl. 2, fig. 5.
1915 *Hyracodon ombonii* Stehlin (*in litteris*); Fabiani: 297.
1915 *Epiaceratherium bolcense* Abel; Borissiak: 784.
1930d *Trigonias ombonii* Dal Piaz: 1, pls 1–10.
1932 *Epiaceratherium bolcense* Abel; Wood: 169.
1958 *Epiaceratherium bolcense* Abel; Viret: 438.
1980 *Trigonias ombonii* Dal Piaz; Altichieri: 174, fig. on page 173.
1986 *Epiaceratherium bolcense* Abel; Kotsakis: 142.
1996 *Epiaceratherium bolcense* Abel; Uhlig: 135, fig. 2.
2003 *Epiaceratherium bolcense* Abel; Antoine *et al.*: 366.
2005 *Epiaceratherium bolcense* Abel; Kotsakis *et al.*: 134, figs 15, 16.
2006 *Epiaceratherium bolcense* Abel; Mietto: 36, fig. 24.
2015 *Epiaceratherium bolcense* Abel; Pandolfi: 69, fig. 2M–P.

Holotype. MGP-PD 12831 (26553), a basal skull with right and left maxillae bearing P1–M2 and a fragment of the right M3 (Fig. 14A).

Other material. 99 specimens of which 77 were published or partly cited by Dal Piaz (1930d) but with different collection numbers (65 housed at MGP-PD, 12 housed at NMB), and 22 unpublished specimens (20 housed at MGP-PD, two housed at NMB). The material includes: seven skulls and fragmentary skulls [MGP-PD 12831 (26553), 27286, 27288, 27289, 27290, 27295; NMB Bc1 (Fig. 14B)], six maxillae [MGP-PD 27292 (Fig. 15A), 27293 (Fig. 15B), 28009, 28012; NMB IO23, IO22a-d], 12 mandibles and fragmentary mandibles (MGP-PD 27231, 27287, 27291, 27294, 27296, 27297, 27298, 27299, 27301, 28011, 31386; NMB IO23a-b), eight isolated teeth (MGP-PD 27230, 27300, 27302, 27303, 27304, 27305, 27306; NMB Bc8), 39 specimens referable

Figure 14. *Epiaceratherium bolcense* Abel, 1910 from Monteviale. **A,** MGP-PD 12831 (26553), holotype of *E. bolcense*, basal skull; **B,** NMB Bc1, basal skull. Scale bars = 5 cm.

to the forelimbs (33 housed at MGP-PD, 27307, 27308, 27310, 27312–27317, 27319–27322, 27325, 27331, 27333, 27334, 27336–27340, 27342, 27814, 28010, 31381–31384, 31390, 31394, 31397, 31401; six housed at NMB, Bc2, IO24, IO25a-b–IO27) and 27 specimens referable to the hindlimbs (24 housed at MGP-PD, 11553, 27309, 27311, 27318, 27323, 27324, 27326–27330, 27332, 27335, 27341, 27815, 31385, 31387–31389, 31391–31393, 31395, 31396; three housed at NMB, IO28–IO30). The rhinocerotid material of Monteviale

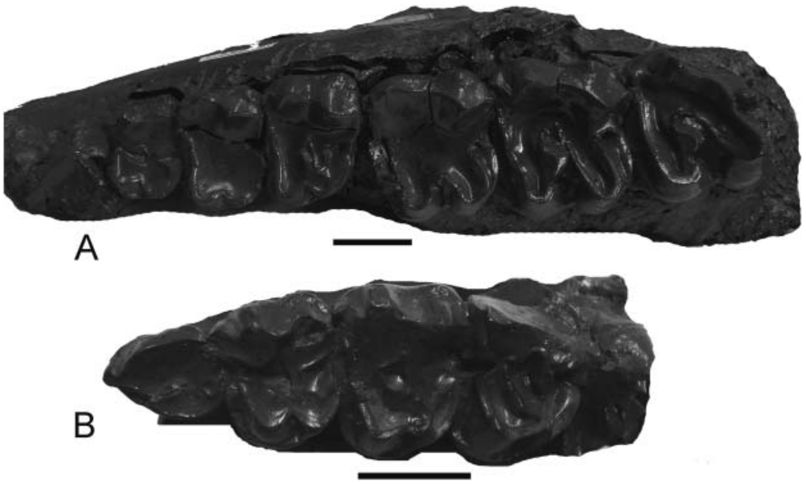


Figure 15. *Epiaceratherium bolcense* Abel, 1910 from Monteviale. **A,** MGP-PD 27293, maxilla with P1-M3, occlusal view; **B,** MGP-PD 27292, P1-P4, occlusal view. Scale bars = 2 cm.

can be referred to at least 10 individuals, nine adults (MGP-PD 27286, 12831 (26553), 27295, 27289, 27292, 27293, 28012; NMB Bc1, IO22a-d) and one juvenile individual (MGP-PD 28011).

Description. Several specimens collected at Monteviale were originally described by Dal Piaz (1930d). Nevertheless, the descriptions were not exhaustive and several morphological characters were not included or considered in Dal Piaz's work (1930d). Here, we provide a complete description of the holotype along with new cranial, mandibular and dental characters.

The holotype [MGP-PD 12831 (26553)] is represented by a basal skull with both maxillae. P1 possesses a straight lingual and distal border and a convex mesio-labial border. An oblique labial cingulum occurs on the distal side of the tooth. A lingual cingulum is also evident. The paracone fold is slightly pronounced, the parastyle fold is sharp, whereas the parastyle is less developed than that of other premolars.

The paracone fold is marked on P2; the parastyle fold is sharp, whereas the parastyle is well developed. Protocone and hypocone are joined by a lingual bridge, and the protocone is slightly more developed than the hypocone. A mesio-lingual cingulum and a slight distal cingulum occur on P2.

The morphology of P3 is similar to that of P4, but the metaloph appears slightly longer, whereas the labial-lingual length is slightly shorter than that of P4. The protocone is lingually elongated. The hypocone is separated from the protocone.

P4 has a pronounced paracone fold, a sharp parastyle fold and a short parastyle; the metastyle is slightly marked. In occlusal view, the protoloph of P4 is long whereas the metaloph appears very short. The mediofossette opens distally. A continuous and evident mesio-lingual cingulum and a slight distal cingulum characterize the P4 morphology. The protocone has a convex lingual border and it appears separated from the hypocone.

M1 is heavily worn, the antecrochet is wide, the paracone and the metacone folds are marked and the mesial cingulum is present. Protoloph and metaloph are similar in length. The latter is S-shaped in occlusal view, whereas the former is straight. The labial cingula are missing on the molars of the holotype.

The right M2 lacks the distal half of the labial side, whereas the left M2 lacks the mesial half of the ectoloph. M2 displays a pronounced mesial cingulum and a wide antecrochet, whereas crista and crochet are absent. The metaloph is slightly longer than the protoloph. Both metaloph and protoloph are straight.

The holotype lacks the left M3, and the right molar is represented only by the mesio-lingual portion of the protoloph where the presence of a mesial cingulum is evident.

Complete skulls are unknown and the descriptions are based on observations of several specimens. The nasal bones are narrow and totally separated, the anterior end of the nasal bones lies above the premaxilla (MGP-PD 27287, 27295), the median nasal horn is absent, the posterior border of the nasal notch is above the P3 or above the P3/P4 boundary (MGP-PD 27287, 27289, 27295), the frontal-parietal crests are close (MGP-PD 27287), the anterior border of the orbit lies above the M1 (MGP-PD 27289, 27290) or M2 (MGP-PD 27295), the nuchal crest is slightly forked in dorsal view (MGP-PD 27290), the external auditory pseudomeatus is partially closed ventrally (MGP-PD 27288, 27290), the processus postglenoidalis is massive and short, the processus paraoccipitalis is long and narrow and its ventral end is straight and lying below the processus postglenoidalis, the processus posttympanicus is little developed and fused with the processus paraoccipitalis (MGP-PD 27290).

The ventral border of the mandibular horizontal ramus is straight (MGP-PD 27296), the posterior border of the

Table 1. Estimated body mass ($\ln X = \ln Y * 1.564 + 3.267$; X corresponds to weight and Y to m1 area: Legendre 1989), Gracility Index (GI = 100 * Transverse Diameter of the diaphysis/Length: Guérin 1980) and Hypsodonty Index (HI = 100 * Height/Length: Guérin 1980) of *Epiaceratherium bolcense* and several Rhinocerotoidea from European Oligocene and early Miocene localities (data from Becker 2003, 2009). Abbreviations: M, upper molar; p, lower premolar; m, lower molar, d, lower deciduous. For *Ronzotherium romani* the GI was estimated only for the third metatarsal (Becker 2003).

Species	Weight (kg)	GI	HI
Eggysodon osborni	273–357	18.9	37.2 (m)
Eggysodon gaudry	484–544		46.9 (p); 58.3 (m)
Protaceratherium minutum	427–723	22.5	62.5 (m)
Ronzotherium romani	1820–2260	23.7 (MT III)	82.1 (m)
Ronzotherium fiholi	1812–2091	20.2	64 (m)
'Epiaceratherium' magnum	476–736	22.7	71 (M)
Epiaceratherium bolcense	372–519	22.4–23.43	64.8 (m); 73.8 (d)
Lartetotherium sansaniense		27.4	89.4 (M); 86 (m)
Diaceratherium aginense	1696–2278	30.8	86 (m)
Pleuroceros pleuroceros		28.5	53.4 (m)

symphysis is ahead of p1 (MGP-PD 27296), the ascending ramus of the mandible is vertical, the processus coronoideus is well developed (MGP-PD 27294), the foramen mentale lies below the p2 (MGP-PD 27298). The second incisors are straight and slightly divergent (MGP-PD 27296).

The estimated body mass (following Legendre 1989) ranges from 372 to 519 kg (based on 5 m1; MGP-PD 27294, 27297, 27296, 27301 and NMB IO27); the Gracility Index measured on the MCIII ranges from 22.4 to 23.43 (Table 1). These results suggest that *E. bolcense* was a cursorial species.

Remarks. Fossil remains of Perissodactyla from Monteviale were originally described by Omboni (1901) and assigned to the genus *Lophiodon* Cuvier, 1822. Nevertheless, the fossil remains had been bought by Omboni as specimens collected from Monte Bolca. Stehlin (1901) referred the remains figured by Omboni (1901) to the genus *Hyracodon* Leidy, 1856, whereas Abel (1910) erected a new genus and a new species of rhinocerotid, *Epiaceratherium bolcense*. Fabiani (1915) recognized these remains as collected from Monteviale and proposed assigning them to *Hyracodon ombonii* Stehlin (*in schaedis*).

The material originally described by Omboni (1901), along with new material collected during mining activities, was studied by Dal Piaz (1930d) who assigned it to the American genus *Trigonias* and the species *T. ombonii*. Dal Piaz (1930d) explicitly rejected the name *Epiaceratherium bolcense* proposed by Abel (1910). However, *E. bolcense* has been considered a valid taxon by several authors (Wood 1932; Simpson 1945; Viret 1958; Radinsky 1966; Heißig 1969).

A new species of the genus *Epiaceratherium*, *E. magnum*, was named by Uhlig (1999) for material collected at Möhren 13 in Germany (MP22). According to Becker *et al.* (2013), *E. magnum* should be assigned to a new genus *incertae sedis*, and the genus *Epiaceratherium*, represented by the species *E. bolcense*, would appear as paraphyletic in their cladogram. Indeed, *E. magnum* is larger (estimated body mass between 476–736 kg) and displays more derived morphological features than *E. bolcense* (e.g. strong reduction of the metacone in M1 and M2, presence of enamel folds in the median valley, reduced metacone on M3 and others; see Uhlig 1999). Therefore, attribution to a different genus cannot be excluded.

The new species *Epiaceratherium naduongense* was recently described by Böhme *et al.* (2014) for material collected at Na Duong in Vietnam. This Asiatic rhinocerotid is considered the sister taxon of *E. bolcense* (Böhme *et al.* 2014). As indicated by Böhme *et al.* (2014), *E. naduongense* differs from *E. bolcense* in being slightly larger (~10%) and in having a partially closed auditory pseudomeatus, a lingual wall on P3-P4, the usual absence of labial and lingual cingula on the upper molars, a generally constricted protocone on M1-M2, a long metaloph with respect to the protoloph on M1, a trigonid forming an acute dihedron on lower cheek teeth, and a usually closed posterior valley on p2. Nevertheless, new morphometric data on *E. bolcense*, also based on unpublished material, highlights the wide variability of this species (with an estimated body size ranging between 372 and 519 kg; Table 1). Moreover, two fragmentary skulls of *E. bolcense* (MGP-PD 27288; MGP-PD 27290) have a partially ventrally closed pseudomeatus. Some specimens display a lingual wall on P3-P4 (MGP-PD 27289), whereas others (MGP-PD 27290) show a faint labial cingulum on M1 as in *E. naduongense*. The constriction on M1-M2 also occurs in *E. bolcense* as noted by Böhme *et al.* (2014), whereas the metaloph of M1 is slightly longer than the protoloph in a few cases (NMB Bc1; MGP-PD 27290). The characters of the lower teeth of *E. naduongense* are also evident in *E. bolcense* (Böhme *et al.* 2014; closed posterior valley on p2 is present in the specimen MGP-PD 27298, whereas a trigonid forming an acute dihedron on lower cheek teeth occurs in several specimens). Taking into account the morphological similarities, *E. naduongense* and *E. bolcense* are closely related.

The estimated body mass of *Epiaceratherium bolcense* is considerably less than that of *Ronzotherium romani* Kretzoi, 1940 (1820−2260 kg) and *Ronzotherium filholi* (Osborn, 1900) (1812−2091 kg) (Becker 2003), and slightly less than *'E.' magnum* (476−736 kg) and *Protaceratherium minutum* (Cuvier, 1822) (427−723 kg) (Table 1). In comparing the estimated body masses of European hyracodontids, *E. bolcense* is larger than *Eggysodon osborni* (Schlosser, 1902) (273−357 kg) and is comparable in size to *Eggysodon gaudry* (Rames, 1886) (484−544 kg). The Gracility Index (GI) values of *Epiaceratherium bolcense* are close to those of *P. minutum* (22.5), *R. romani* (23.7) and *'E.' magnum* (22.7), whereas they are lower than those of mediportal and graviportal taxa such as *Lartetotherium sansaniense* (Lartet in Laurillard, 1848) (27.4), *Diaceratherium aginense* (Répelin, 1917) (30.8) and *Pleuroceros pleuroceros* (Duvernoy, 1853) (28.5) (Table 1).

Order **Artiodactyla** Owen, 1848 (*sensu* Asher & Helgen 2010)
Suborder **Whippomorpha** Waddell, Okada & Hasegawa, 1999
Superfamily **Anthracotherioidea** Leidy, 1869
Family **Anthracotheriidae** Leidy, 1869
Subfamily **Anthracotheriinae** Leidy, 1869
Genus ***Anthracotherium*** Cuvier, 1822
Anthracotherium monsvialense Zigno, 1888
(Figs 16−18)

?1865 *Anthracotherium* sp. Beggiato: 7, pl. 1, figs 6, 7.
?1876a ?*Anthracotherium minus* Cuvier; Hoernes: 107.
?1876a ?*Anthracotherium hippoideum* Rütimeyer; Hoernes: 107.
?1876b ?*Anthracotherium minus* Cuvier; Hoernes: 230.
?1876b ?*Anthracotherium hippoideum* Rütimeyer; Hoernes: 230.
1888 *Anthracotherium monsvialense* Zigno: 37, pl. 1.
1897 *Anthracotherium magnum* (Cuvier); Flores: 93.
1910a *Anthracotherium monsvialense* Zigno; Stehlin: 176, figs 1, 2.
1915 *Anthracotherium monsvialense* Zigno; Fabiani: 308.

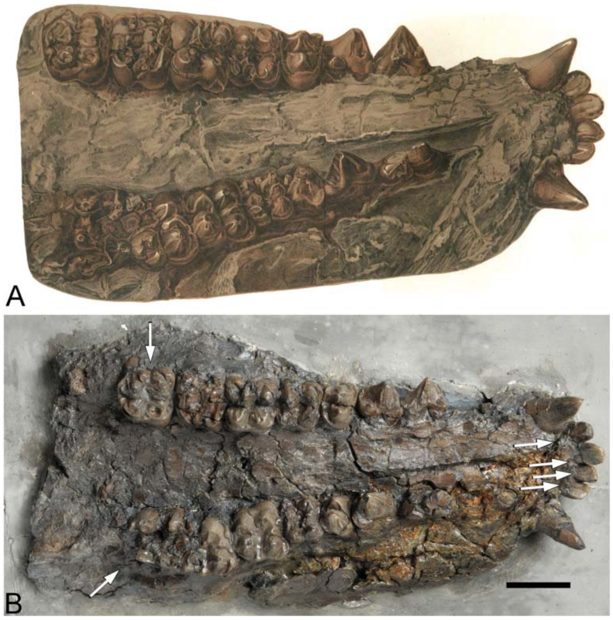


Figure 16. *Anthracotherium monsvialense* Zigno, 1888 from Monteviale, MGP-PD 26556, holotype, palate with right and left tooth rows. **A,** the first representation published by Zigno (1888); **B,** the same specimen today. The fossil was embellished by adding two upper molars and four lower incisors (indicated by arrows). Scale bar = 4 cm.

1926 *Anthracotherium monsvialense* Zigno; Dal Piaz: 55.
1929 *Anthracotherium monsvialense* Zigno; Dal Piaz: 911.
1932 *Anthracotherium monsvialense* Zigno; Dal Piaz: 1, pls 1−16.
1980 *Anthracotherium monsvialense* Zigno; Altichieri: 174, fig.
1986 *Anthracotherium monsvialense* Zigno; Kotsakis: 143.
1999 *Anthracotherium monsvialense* Zigno; Benammi, Chaimanee, Jaeger, Suteethorn & Ducrocq: 547.
2004 *Anthracotherium monsvialense* Zigno; Lihoreau, Blondel, Barry & Brunet: 110, fig. 7.
2005 *Anthracotherium monsvialense* Zigno; Kotsakis *et al.*: 135, fig. 18.
2006 *Anthracotherium monsvialense* Zigno; Mietto: 37, fig. 25.

Holotype. Palate with right and left tooth series (MGP-PD 26556) (Fig. 16).

Other material. Several finds from Monteviale were ascribed to *Anthracotherium monsvialense* and cited by Dal Piaz (1932) without inventory numbers. The fossils described are housed at the MGP-PD. Most of the collection includes fragmentary cranial and dental remains (splancnocranium: MGP-PD 5740, 26556, 27359, 27360, 27382, 31503; isolated upper canines: MGP-PD 27367, 27369, 31490; isolated upper incisors: MGP-PD 27371, 27372, 27373, 27385, 31477a, 31477c, 31478a, 31489,

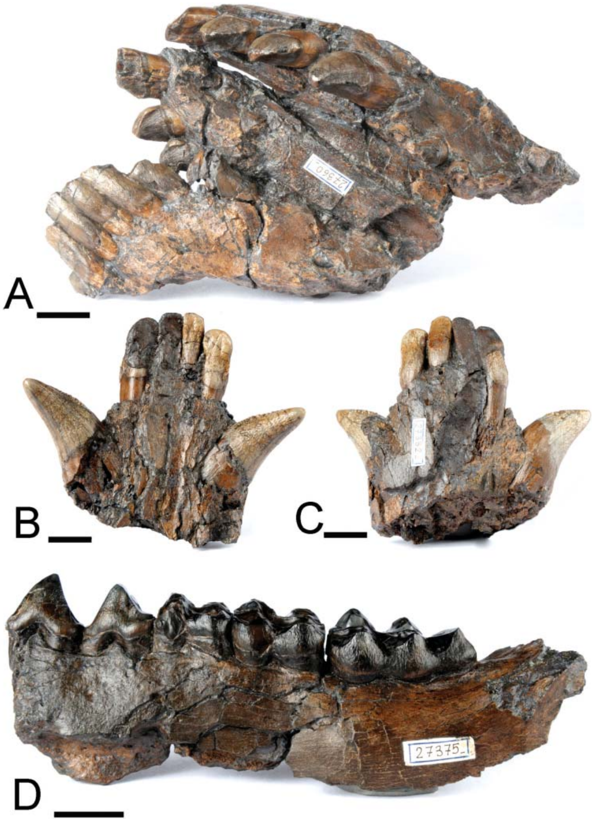


Figure 17. *Anthracotherium monsvialense* Zigno, 1888 from Monteviale. **A,** MGP-PD 27360, upper and lower incisors on ventral view; **B,** MGP-PD 27382, rostrum with first and second right lower incisors and canines (left incisors are reconstructed) in dorsal view; **C,** MGP-PD 27382 in ventral view; **D,** MGP-PD 27375, left mandible with p3, p4, m1, m2, and m3 in lateral view. Scale bars = 2 cm.

27370 (cf. *A. monsvialense*); isolated upper premolars and molars: MGP-PD 31410, 31411, 31492, 31496, 31499, 31500, 31506a, 31506b, 31512; upper tooth series: MGP-PD 5548, 27363, 27364, 27366, 27388, 31413, 31486, 31488, 31491, 31495, 31501, 31502); fragments of teeth bearing mandibles (MGP-PD 27377, 27378, 27379, 27384, 27386, 27387, 31412, 31432, 31479, 31480, 31493, 31507b); isolated lower teeth (canines: MGP-PD 27368; incisors: MGP-PD 5551, 31415, 31497, 31498; premolars and molars MGP-PD 5549, 12837, 27376, 27380, 27381, 31414, 31478b, 31482a, 31484, 31494, 31504, 31505, 31513a-c; fragmented teeth: MGP-PD 31477b, 31478c, 31482b, 31483); a few juvenile decidual teeth (MGP-PD 27361, 27362, 27383, 31481). Postcranial remains are represented by a complete but fragmented hindlimb (MGP-PD 12900); isolated postcranial remains such as scapula (MGP-PD 31517, illustrated by Dal Piaz 1932, fig. 3), tibia (MGP-PD 31507a), patella (MGP-PD 27390, 31487), metapods (MGP-PD 27393, 27394, 27395, 27396), carpals and tarsals (MGP-PD 27391, 27392, 31485), and phalanxes (MGP-PD 27397, 27398, 27399).

Figure 18. MGP-PD27364, palate of *Anthracotherium monsvialense* Zigno, 1888 from Monteviale with the distal fragment of left M1, right and left M2 and M3. Detailed pictures show symmetrical stage of wear on both series. Scale bars = 2 cm.

Within the NMB collection, *A. monsvialense* is represented by an M1–M3 series (NMB I.O. 31), a fragment of a right mandible bearing m2–m3 (NMB I.O. 32a), a fragment of a left mandible bearing m2–m3 (NMB I.O. 32b), a fragment of a right mandible bearing p4–m1 (NMB I.O. 32c), a fragment of a proximal femur, a fragmentary MT III and IV and fragmentary phalanges (NMB I.O. 33), a left navicular (NMB I.O. 34a), a first phalanx from posterior digit IV (NMB I.O. 34b) and a left upper canine (NMB I.O. 75).

Description. In dorsal view, the nasal notch opens at the level of the canines. In ventral view, the palate is narrow, the rostrum is prognathous and, as a consequence, the upper incisors form a convex arch. The existence of a mandibular bulge (apophysis), present in *Anthracotherium magnum* Cuvier, 1822 (specimens from Cadibona), is somewhat evident below the third premolar on MGP-PD 27359, and developed on the ventral outline of the mandible, just posterior of the end of the mandibular symphysis.

The first upper incisor has an enlarged and horizontally directed spatulate outline (wider than that of lower incisors) with a lateral and distal cingulum (Fig. 17). The second and third incisors are canine-like, equally spaced from each other and from the canines. The premolars have a single main cusp, with a lobed and enlarged distal border. The size of these teeth increases from the first to the last. The third premolar has a triangular shape due to the development of a distal lingual cusp. The fourth premolar transversely emerges on the dental series with a wide concave medial edge and a convex distal one. The masticatory surface is characterized by well-developed paracone and protocone. The cingulum forms a wall on the mesial and distal outline with evident parastyle and distostyle. The succeeding low-crowned, brachydont molars are pentacuspid with a noticeable paraconule and a small mesio-lingual accessory cusp. The neck is evident in correspondence to the main cusps, in particular on paracone and metacone. The premetacristule reach the trigonid only when the enamel is worn, and the premetacrista joins the postparacrista at a labial mesostyle. The upper molars have similar morphology (Fig. 18). The M2 can be distinguished from M3 by having the metaconule bearing a reduced border compared to that of the protocone. These lobes show the same trend on M3 and the protocone is more convex. The second molar has similar morphology and different size if compared to the former, and both are smaller than the following tooth. The mesial outline of M2 has a mesially increasing surface on the parastyle and is partially compressed for the accommodation of the previous molar. In the first molar the mesial end is straight or concave; the smaller parastyle is not always present.

The lower incisors are mesio-distally compressed and spatulate (Fig. 17). They emerge horizontally from the mandibular mesial end, sub-parallel to the dorsal axes. *Anthracotherium monsvialense* possesses three lower incisors. The existence of i3 can be presumed from the presence of a third alveolus on MGP-PD 27382 (Fig. 17B, C), while it is well preserved on MGP-PD 27360 (Fig. 17A). The incisor crowns protrude fully from the muzzle, are dorso-ventrally compressed and elongated, and very close to each other, forming a curved spatula. There are no diastemata between incisors and canines, and the same follows for premolars. Therefore, the lower dentition is more crowded than the upper one. The premolars have one cusp, which is similar in morphology and size to the cusps of the upper teeth, but more slender. The first and second premolars are smaller than the others. The last premolar has a wide middle cusp with an enlarged distal talonid (Fig. 17D). The molars differ in size and the main cuspids show a basal bulged neck. On the medial edge, the first and second enlargements are equally developed while the distal one is characterized by a longer surface due to an enlarged talonid. The latter has two cuspids, the labial hypoconulid and a smaller lingual entoconulid. The preprotocristid mesially joins the premetacristid at the mesiostylid, and the prehypocristid is medially directed and does not reach the entoconid. The postcranial remains are fragmentary and not easily recognizable. However, the autopodials of the hindlimbs show a reduced size for the lateral digits.

Remarks. The first occurrence of Anthracotheriidae from the Venetian region at Zovencedo (Vicenza) was reported in a letter sent from Prof. Massalongo to De Visiani in 1858. After this first record, many authors discussed the presence, the taxonomic attribution and the origin of several fossils of *Anthracotherium* in northern Italy (Dal Piaz 1926). The debate ended when Zigno (1888) established the new species *A. monsvialense* based on the material collected in Monteviale and stored in the MGP-PD. He stated that, while other remains from several localities should be ascribed to *A. magnum*, the small bones from Monteviale belonged to *A. monsvialense*, characterized by an overall smaller size, a distinctive upper dentition and unique features of the I1. Fabiani (1915) and Dal Piaz (1926, 1930a, 1932) highlighted the fact that the Venetian *Anthracotherium* came from a few localities only, excluding previous and incorrect records from Bolca, Praticini Bolca, Schio and Torricelle (Schauroth 1865; Stehlin 1910a; and recent references cited in Scherler 2011). Remains of *Anthracotherium* have been reported from two other localities of Veneto, Zovencedo and Chiuppano (Beggiato 1865; Hoernes 1876a, b; Leonardi 1950; Accordi 1951), but the specific attribution is still debated and the material needs systematic revision.

Anthracotheridae probably evolved during the early Eocene in South East Asia (Pilgrim 1928; Suteethorn *et al.* 1988; Ducrocq 1994; Ducroq *et al.* 2000; Tsubamoto *et al.* 2002; Lihoreau & Ducroq 2007) and then spread into Europe for the first time during the late Eocene together with the genus *Elomeryx* (Hellmund 1991). In addition to *Elomeryx*, the anthracotheriid *Diplopus* and *Prominatherium dalmaticum* occurred in Europe early in the late Eocene (Meinolf & Kurt 1994; Hooker 2010b). The genus *Anthracotherium* was first recorded in the Pondaung Formation (Myanmar), dated as latest middle Eocene (Tsubamoto *et al.* 2002), and then spread into Europe, Africa and North America during the late Eocene (Ducrocq 1995; Tsubamoto *et al.* 2002). It is recorded for the first time in Europe in the ?late Eocene locality of Dětaň in the Czech Republic (Fejfar 1987; Ducrocq 1995). It was well represented after the ‘Grande Coupure’ (Stehlin 1910a, b) but the genus had disappeared in Europe before the end of the Oligocene (Lihoreau & Ducrocq 2007). In this scenario, Monteviale with the small *A. monsvialense* represents one of the earliest European occurrences of these browsing animals along with records of the species from a few localities in the Czech Republic, France, Germany, Switzerland and Spain (Becker *et al.* 2004; Fejfar & Kaiser 2005; Scherler 2011 and references therein). It is questionably recorded also at Çavuşlu and Karakaya (early Oligocene, Turkish Thrace) by Lebküchner (1974). Therefore, the geographical range of *A. monsvialense* was not limited to Monteviale, where the most abundant remains were collected.

Following the observations on dental robustness by Ducrocq (1999) and Tsubamoto *et al.* (2002), the size and specific characteristics of *A. monsvialense* fit better within a gradual trend of increasing body mass from the older Asian to the younger European species, rather than isolated evolution in an insular environment. In fact, size comparison with the most primitive species from Pondaung and Europe reveals that the size of upper and lower molars are representative for the increasing body size of this taxon, from Asian species to the last European species *A. magnum* (Fig. 19A). Only *Anthracotherium pangan* Pilgrim & Cotter, 1916 from the middle Eocene of Asia fits within the size range of *A. monsvialense*.

Anthracotherium monsvialese is similar in size to the early Oligocene *A. alsaticum* Cuvier, 1822. Sudre (1995) discussed the similarity between these two species, but dental differences, mainly in upper incisors and deciduous teeth (Stehlin 1910a; Scherler 2011), seem to rule out a possible synonymy. The species is larger than the late Eocene *Prominatherium dalmatinum* (von Meyer, 1854) which displays a bulged protocone and developed ectostyle and parastyle compared to *A. monsvialense* (Meinolf & Kurt 1994). In the M3 of anthracotheres from Pondaung and in *P. dalmatinum,* both paracone and protocone are larger than the talonid (Meinolf & Kurt 1994; Tsubamoto *et al.* 2002); in *A. monsvialense* the masticatory surface of M3 has instead a squared shape.

Fossil remains of *A. monsvialense* are abundant at Monteviale, with both juveniles and adults represented. Moreover, a complete upper and lower dental series has been recovered. The presence of a supernumerary upper molar has been discussed by several authors (Zigno 1888, 1890a, 1890b; Schlosser 1889; Teller 1889; Gaudry 1890) but Stehlin (1910a) demonstrated that this was due to a fake reconstruction probably made by a fossil dealer. The teeth are brachyodont, with low crowns, and bunodont. The upper molars typically had five major cusps whereas the lower ones had four, with the exception of the elongated m3. Different sizes and morphologies of the canines are reported as indicative of sexual dimorphism. Both sexes are represented in the Monteviale collection; males show lower massive and bulging canines (Fig. 17B, C), while females possess shorter and slender ones. Furthermore, different features of the canines are also notable in artiodactyls, suggesting the plesiomorphic state of these characters. In contrast, the size of the third lower molar does not show any variation between sexes. Measurements of the molars of specimens from the MGP-PD show a normal distribution, incompatible with the bimodality typically expected in sexually dimorphic taxa, suggesting that at least the lower m3 cannot be used for sex determination (Fig. 19B).

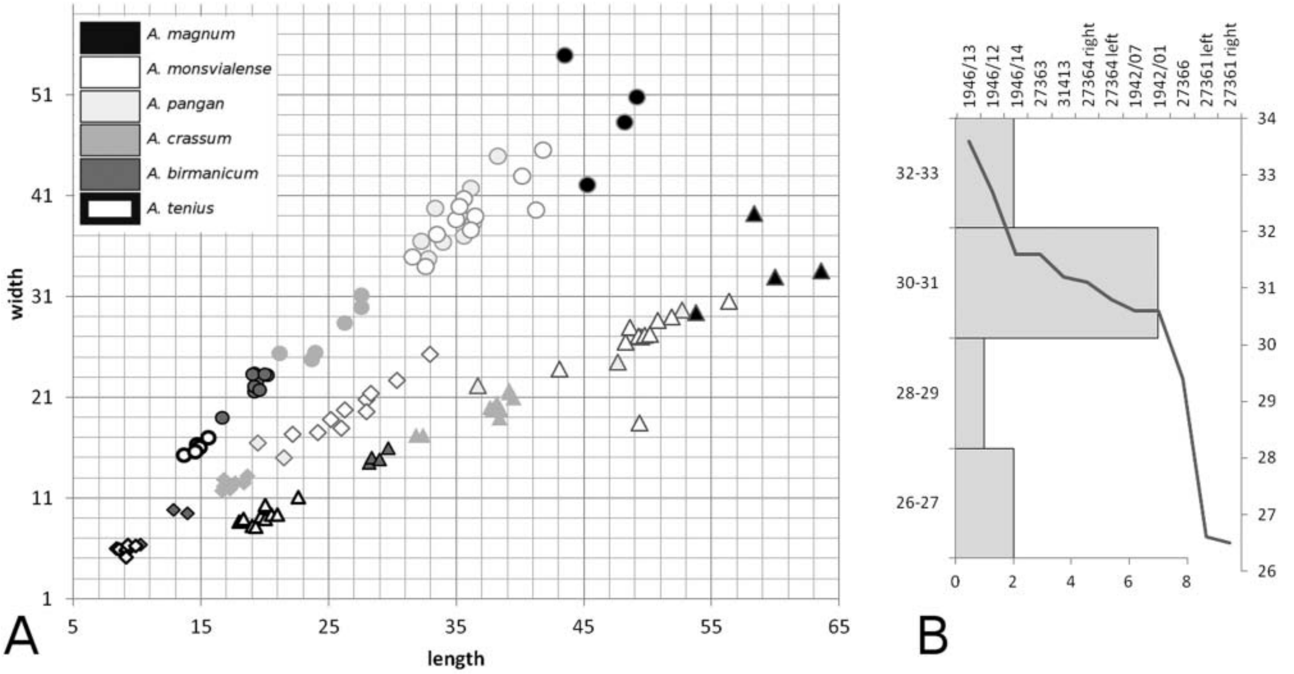


Figure 19. Morphometrics of *Anthracotherium*. **A,** scatter chart with different species of *Anthracotherium*; comparison among M3 (circles), m1 (diamonds) and m3 (triangles); *Anthracotherium pangan* (data from Tsubamoto *et al.* 2002) and *A. monsvialense* have the same range of variability, while smaller species are clearly clustered (data on *A. magnum* from Cadibona have been collected on specimens stored at Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze, Florence). **B,** bar chart and respective linear representation of length sets of m3 in *A. monsvialense*; the trend from smaller to larger specimens (right x axis) has a slope that flattens before returning to a normal inclination, giving no evidence of sexual dimorphism.

Figure 20. *Anthracochoerus* Dal Piaz, 1930 from Monteviale. **A,** MGP-PD 27352, fragment of mandible with m2 and m3 of *A. stehlini* Dal Piaz, 1930 in labial view; **B,** MGP-PD 27352 in occlusal view; **C,** MGP-PD 26555 fragment of mandible of *A. fabianii* Dal Piaz, 1930 with molars and last premolar in labial view; **D,** MGP-PD 26555 in occlusal view. Scale bar = 1 cm.

The tooth morphology strongly suggests a browsing feeding mode; the structure and configuration of the postcranial bones point to a close association with freshwater environments (Tsubamoto *et al.* 2002).

The postcranial long bones are quite fragmented and poorly preserved, but reduced lateral digits are visible distally on the limbs. Kowalevsky (1873) stated that this characteristic is indicative of the split of *Anthracotherium* into two groups: anisodactyls with reduced lateral digits and subisodactyls with similar-sized lateral digits. According to this division, *A. monsvialense* should be included in the former group.

Subfamily (?) **Bothriodontinae** Scott, 1940
Genus ***Anthracochoerus*** Dal Piaz, 1930
(Figs 20–22)

Description. Like other Bothriodontinae, *Anthracochoerus* has high-crowned lower molars compared to members of the Anthracotheriinae with slender and elongated teeth. The labial and lingual sides are straight and vertical, giving a selenodont appearance to the molars. The lower molar cuspids are comparable in size to each other, and cristids are less frequent compared to anthracotheriids such as *Microbunodon*. Labial cuspids are not sickle-shaped as in *Microbunodon*, but are rounded.

Both species described by Dal Piaz (1931) have a convex ventral edge of the mandibular horizontal ramus. The trigonid of the lower molars is clearly separated from the talonid, and labial cuspids tend to join their antimeres, forming a perpendicular wall to the parasagittal plane. The prehypocristid joins the preentocristid in the middle of the tooth, producing a mesial deep transverse valley. There is a similar distal trasverse groove, which is straight in *A. stehlini* but distally curved in *A. fabianii* due to the more lobate features of the hypoconid and entoconid. The entoconulid is completely absent in both species and there is no constriction between hypoconulid and ento- and hypoconids, typically visible in some Oligocene ruminants such as *Lophiomeryx* and *Iberomeryx* (Janis 1987; Antoine *et al.* 2011; Mennecart 2012) as much as in other Bothriodontinae, such as in the genus *Elomeryx* (Ducrocq & Lihoreau 2006).

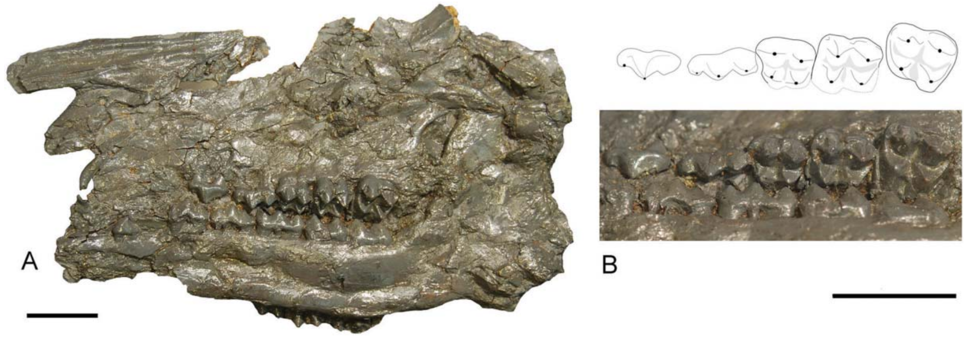


Figure 21. *Anthracochoerus stehlini* Dal Piaz, 1930 from Monteviale, MGP-PD 26554, holotype of the species. **A,** fragmented skull and mandible of a relatively young individual, lateral view; **B,** upper tooth row (dP3, dP4, M1, M2 and M3) in occlusal view with M1–M3 showing four unworn cusps. Scale bars = 2 cm.

Figure 22. *Anthracochoerus stehlini* Dal Piaz, 1930 from Monteviale; NMB Bc. 3a–n, paratype; crushed skull with an anterior limb. Scale bar = 5 cm.

Remarks. Dal Piaz (1931) included *Anthracochoerus* within the family Anthracotheriidae, before Scott (1940) had erected a subfamily rank classification. Since then, the taxonomic position of *Anthracochoerus* has not been investigated. Specific characters described below are considered indicative of the Bothriodontinae, and therefore we have included the taxon within this subfamily.

After brief note (Dal Piaz 1930a), the genus *Anthracochoerus* was validly established by Dal Piaz (1931) when describing the species *A. stehlini* and *A. fabianii* (Fig. 20). In the original publication, *Anthracochoerus* was described as a typical anthracotheriid characterized by several postcranial features and buno-selenodont teeth, upper molars with four main cusps and no paraconule ('protoconulus' in Dal Piaz 1931), and m3 with a single distal cuspid (hypoconulid).

The lack of a paraconule (Dal Piaz 1931) was recognized in the large bothriodontine *Hemimeryx* from Pakistan (Lydekker 1883), dated to the late early to early middle Miocene. No further anthracotheres with four cusps on the upper molars have been reported for the early Oligocene in Europe, raising doubts about the close relationship of *Anthracochoerus* to Anthracotheriidae. However, the post-cranial features (Dal Piaz 1931), buno-selenodont lower teeth, and all specific dental characters justify the placement of this genus within Bothriodontinae. The dental morphology (in particular of the lower teeth), lack of entoconulid on m3, as well as the overall size, distinguish *Anthracochoerus* from *Brachyodus*, suggesting a closer affinity of *Anthracochoerus* with the genus *Elomeryx*. In fact, some features of *Anthracochoerus* (i.e. the separated ectoentocristid and postectometacristid) are almost identical to those displayed by *Elomeryx borbonicus* (Gervais, 1852). However, the fossils from Monteviale differ from *E. borbonicus* in the lack of an evident talon constriction, presence of a diastema between the first and second lower premolars, and smaller size. For instance, m3 length of *A. stehlini* is about 13–15 mm, 10.2 mm in *A. fabianii*, and around 30 mm in *E. borbonicus*. In addition, *A. stehlini* and *A. fabianii* differ from *Elomeryx crispus* (Gervais, 1849) (late Eocene; Hooker 2010a) and *Elomeryx cluai* (Depéret, 1906) (recorded only in Spain from early Oligocene deposits) in their smaller size, features of the cuspids of the lower molars, and presence of a deep transverse valley between trigonid and talonid. Finally, we cannot exclude the possibility that *A. stehlini* and *A. fabianii* might belong to the same species with an exceptionally extreme sexual dimorphism, as suggested by Tsubamoto *et al.* (2002) for two species from Pondaung. Nevertheless, the sample is too small for a statistical analysis.

Anthracochoerus stehlini Dal Piaz, 1930
(Figs 20A, B, 21, 22)

1930a *Anthracochoerus stehlini* Dal Piaz: 63.

1931 *Anthracochoerus stehlini* Dal Piaz; Dal Piaz: 6, pls 1–3, pl. 4, figs 1–5, 7–10, pl. 5.

1941 *Anthracochoerus stehlini* Dal Piaz; Stehlin & Hürzeler: 272, figs 1–3.

1980 *Anthracochoerus stehlini* Dal Piaz; Altichieri: 174.

1986 *Anthracochoerus stehlini* Dal Piaz; Kotsakis: 143.

2005 *Anthracochoerus stehlini* Dal Piaz; Kotsakis *et al.*: 135: fig. 17.

2006 *Anthracochoerus stehlini* Dal Piaz; Mietto: 41, fig. 26/1, 4.

Holotype. MGP-PD 26554, fragmented skull and mandible of a relatively young individual (Fig. 21).

Other material. Fossils determined as *Anthracochoerus stehlini* are represented by cranial material (MGP-PD 27378, 27346, 27345, 27351, 27344, 27343) and mandibles (MGP-PD 31514, 12832, 27378, 27349, 31515a–b, 31516, 7509, 27353, 27350, 27354, 27355, 27352, 27353) bearing teeth. A few other postcranial remains have been attributed to *A. stehlini*, both forelimbs (partially preserved arm: MGP-PD 31509; humerus: MGP-PD 31508; radius and ulnae: MGP-PD 27356) and hindlimbs (MGP-PD 12839, 27357). Three isolated upper teeth (MGP-PD 27347) and a MC IV (MGP-PD 31400) are also dubitatively recorded as cf. *A. stehlini*. A single individual, constituted by a crushed skull with an anterior limb, represents the paratype of this species currently housed at the NMB (Bc. 3a–n; Fig. 22). The NMB collection also includes fragmentary and isolated teeth (NMB Bc. 4c), a fragmentary skull with the lower tooth rows (NMB Bc. 4e: N. 23 in Dal Piaz 1932), a right mandible with m1–m3 and a fragmentary maxillary tooth row (NMB I. O. 35). Several fragmented postcranial remains (NMB Bc. 4a–b, 4d and Bc. 5: N. 23, 24 and 25 in Dal Piaz 1932) are also housed in the collection of the NMB.

Description. The mandible has short diastemata between the canine and first premolar, and the first and second lower premolars. The upper canine is conical and small, partially laterally compressed, posteriorly curved and unworn. We did not find clear evidence of the lower incisors because the rostra are strongly fragmented.

Anthracochoerus fabianii Dal Piaz, 1930
(Fig. 20C, D)

1929 *Lignitohyus fabianii* Dal Piaz: 912 (*nomen nudum*).
1930a *Anthracochoerus fabianii* Dal Piaz: 63.
1931 *Anthracochoerus fabianii* Dal Piaz; Dal Piaz: 25, pl. 4, figs 6, 11–14.
1980 *Anthracochoerus fabianii* Dal Piaz; Altichieri: 174.
1986 *Anthracochoerus fabianii* Dal Piaz; Kotsakis: 143.
2005 ?*Anthracochoerus fabianii* Dal Piaz; Kotsakis *et al.*: 135.
2006 *Anthracochoerus fabianii* Dal Piaz; Mietto: 41, fig. 26/2–3.

Holotype. MGP-PD 26555, left mandible with molars and p4.

Other material. In addition to the holotype, a single left mandible (MGP-PD 27358) was assigned to *A. fabianii* by Dal Piaz (1930a).

Remarks. *Anthracochoerus fabianii* was collected from Monteviale in 1924. It is smaller than *A. stehlini* and the fourth premolar is higher. Unfortunately, there are no cranial or postcranial remains, thereby preventing a full comparative analysis between the two species.

Anthracotheriidae indet.

1937b cf. *Ancodon* sp. Dal Piaz: 1, fig. 1.
1980 cf. *Ancodon* sp. Altichieri: 174.
1986 cf. *Bothriodon* sp. Kotsakis: 145.
2006 cf. *Bothriodon* sp. Mietto: 41.

Material. Single fragment of a right radius (MGP-PD 27400).

Remarks. A single radius was referred to cf. *Ancodon* by Dal Piaz (1937b). Kotsakis (1986) transferred it to *Bothriodon* because *Ancodon* is considered a junior synonym of *Bothriodon*. This hypothesis was confirmed by Lihoreau & Ducrocq (2007) for European species assigned to *Ancodon*. However, the presence of *Bothriodon* at Monteviale is based on a fragmentary radius which does not allow a precise taxonomic attribution. We prefer to classify this specimen, larger than *A. monsvialense* and *Anthracochoerus*, as Anthracotheriidae indet.

Suborder **Suiformes** Jaeckel, 1911
Superfamily **Suoidea** Gray, 1821
Family **Palaeochoeridae** Matthew, 1924
Genus **?*Propalaeochoerus*** Stehlin, 1899

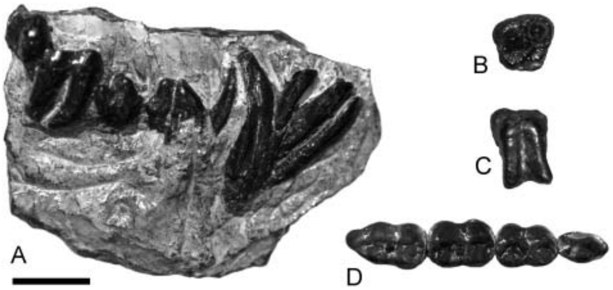


Figure 23. ?*Propalaeochoerus paronae* Dal Piaz, 1930 from Monteviale. **A,** MGP-PD 26557, holotype, a lower tooth row with i1–m2 in labial view; **B,** MGP-PD 27280/4, third upper left molar in occlusal view; **C,** MGP-PD 27280/5, upper molar in lingual view; **D,** MGP-PD 27283, lower left tooth row with p4–m3 in occlusal view. Scale bar = 1 cm.

?*Propalaeochoerus paronae* Dal Piaz, 1930
(Fig. 23)

1930c *Propalaeochoerus paronae* Dal Piaz: 1, pl. 1, figs 1–3, 6–14.
1974 *Palaeochoerus paronae* (Dal Piaz); Ginsburg: 69.
1978 *Propalaeochoerus* aff. *paronae* Dal Piaz; Heißig: 243.
1980 *Propalaeochoerus paronae* Dal Piaz; Altichieri: 174.
1986 *Propalaeochoerus paronae* Dal Piaz; Kotsakis: 143.
1987 *Propalaeochoerus* cf. *paronae* Dal Piaz; Fejfar: 259, fig. 9/1–6.
1992 *Propalaeochoerus paronae* Dal Piaz; Hellmund: 11.
1994 *Palaeochoerus paronae* (Dal Piaz); van der Made: 8.
2006 *Propalaeochoerus paronae* Dal Piaz; Mietto: 39, fig. 23/4, 5.
2010 *Palaeochoerus paronae* (Dal Piaz): van der Made: 115.
2011 *Propalaeochoerus paronae* Dal Piaz; Pickford: 573.
2012 *Palaeochoerus paronae* (Dal Piaz); Mennecart, Scherler, Hiard, Becker & Berger.: 171.

Holotype. MGP-PD 26557, a lower tooth row with i1–m2 (Fig. 23A).

Material. The collection of *Propalaeochoerus paronae* housed at MGP-PD includes 10 specimens originally described by Dal Piaz (1930c): a left p1 (MGP-PD 27278), a left M2 (MGP-PD 27280/1), a left M1 (MGP-PD 27280/2), a left M3 (MGP-PD 27280/3), an upper molar (MGP-PD 27280/5; Fig. 23B), a left M3 (MGP-PD 27280/4; Fig. 23C), a lower molar (MGP-PD 27280/6), a partial left maxilla bearing DP1–M1 (MGP-PD 27281), a partial right maxilla with DP1–M2 (M2 in eruption) and P (MGP-PD 27282), and a lower left tooth row with p4–m3 (MGP-PD 27283; Fig. 23D). Four isolated teeth belonging to this taxon are housed at the NMB, two upper molars (I.O.37 and I.O.38a) and two lower molars (I.O.36 and I.O.38b).

Description. (Based on Dal Piaz 1930c). The canine is rather robust with a concave and sharp distal edge, and a convex mesial side. The incisors possess long roots with a large, robust and spatulate crown. The upper molars are typically bunodont with a crown bearing four main cusps. The M1 and M2 are squared with a rounded paracone. A ridge runs from the protocone towards the main valley of the crown. The paraconule has three ridges; the first one runs mesially terminating near the paracone, and the third one connects the paraconule with the protocone. A ridge connects the protocone and metaconule lingually. The metaconule joins the basal cingulum that runs distally through the crown and terminates near the mesostyle. The M3 shows plesiomorphic features. It is rounded and does not possess any talonid. The metacone and metaconule are small and the cingulum exhibits cementum. The latter is connected to the metaconule by a small ridge. The crown appears more pronounced than that of M1 and M2. The lingual roots of the upper molars are fused and divergent.

Only lower premolars are present in the Monteviale collection. The p1 is pointed with a single root, while p2 is similar to p3 but higher and shorter. The p3 has a pyramidal shape with a single major cusp. It is laterally compressed and bears a mesial ridge more oblique than the distal one. The talonid is slightly prominent.

The p4 has two major cusps. A narrow ridge runs mesially from the labial cusp to the small basal tubercle. This latter extends outwards, onto the labial edge of the crown, giving rise to a small oblique crest. Two main crests run from the two cusps of the premolar to the distal edge, where the talonid is located.

The lower m1 and m2 possess similar morphology with the exclusion of the talonid. They have an evident basal cingulum on the distal edge. The m3 possesses a talonid constituted by the hypoconulid from which a median ridge runs towards the hypoconid. The metaconid joins the protoconid and paraconid mesially, originating a pronounced ridge in correspondence to the transversal valley. The protoconid is half-moon shaped, and exhibits three small cusps mesially. The paraconid is pyramidal in shape and represents the largest cusp of the tooth. The entoconid appears less robust than the protoconid. The protoconid and paraconid are higher than the other cusps. A basal cingulum is observable on the mesial edge of the molar. The roots of the lower molars are connected through a bony lamina on both sides.

Remarks. Dal Piaz (1930c) described the material from Monteviale and created a new species assigned to the genus *Propalaeochoerus* Stehlin, 1899, *P. paronae*, belonging to the family Palaeochoeridae Matthews, 1924 (van der Made 2010; Pickford 2011; Mennecart *et al.* 2012), though a recent paper has highlighted how the familial attribution cannot be properly determined (Hellmund & Heizmann 2011). The validity of *Propalaeochoerus* has been debated in several works (Ginsburg 1974; Hellmund 1992; van der Made 1994). Recently, two different major views about the generic attribution of *P. paronae* have emerged; several authors have considered it a member of *Propalaeochoerus* (Hellmund 1992; Pickford 2011), whereas others have assigned it to *Palaeochoerus* Pomel, 1847 (van der Made 1994; Boisserie *et al.* 2010; van der Made 2010; Mennecart *et al.* 2012).

Stehlin (1899) originally described *Propalaeochoerus* based on material from Quercy in France. This genus possesses upper molars with fused and divergent lingual roots. By contrast, *Palaeochoerus* (*P. typus*), erected by Pomel (1847) on material from Saint-Gérand-Le-Puy in France, shows upper molars with separate roots (Ginsburg 1974; Hellmund 1992). However, Stehlin (1899) did not assign any type species to the genus and did not indicate the material that he studied. Stehlin (1929) subsequently assigned *P. elaverensis* to *Propalaeochoerus* which thus became the type species (Hellmund 1992; van der Made 1994).

Ginsburg (1974) reviewed *Palaeochoerus* and *Propalaeochoerus* and argued that dental characters, along with other anatomical features of the tooth crown and skull, previously used for a generic distinction, are inadequate to justify their separation. Therefore, he moved *Propalaeochoerus paronae* into the genus *Palaeochoerus*.

Hellmund (1992) followed the indications of Stehlin (1899) and after a revision of the material, concluded that *P. paronae* is a valid species pertaining to the genus *Propalaeochoerus.* Its generic identity was considered valid until 1994. Van der Made (1994) described *Propalaeochoerus* sp. A and B based on material from Montaigu and Cetina (Mammal Neogene unit (MN)2, Spain), and Tomerdingen (MN1, Germany; described as *Propalaeochoerus pusillus* by Hellmund 1992), respectively. Van der Made (1994) identified and proposed new morphological characters to distinguish the two genera: (1) M3 elongated in *Propalaeochoerus* and wide in *Palaeochoerus*; (2) m1 and m2 having a hypoconulid nearby or fused with the hypoconid after wear in *Propalaeochoerus*, whereas it is separated from the hypoconid and placed along the major axis of the tooth in *Palaeochoerus*; and (3) lingual roots of upper molars fused and convergent in *Propalaeochoerus*, whereas they are separated (or joined by a thin lamina) and divergent in *Palaeochoerus*. Van der Made (1994) assigned *Propalaeochoerus paronae* to the genus *Palaeochoerus*, on the basis of his emended diagnosis, even though he also pointed out that such a generic attribution is not properly supported.

Revision of the material from Monteviale led to the recognition of the fused lingual roots of the upper molars of *Propalaeochoerus paronae* (the terminal tips appear slightly divergent; Fig. 23B), rounded M3 (Fig. 23C), and hypoconulid almost fused with hypoconid into a single cusp (Fig. 23D). Therefore, if the emended diagnosis

Table 2. Morphological character comparison among species of *Propalaeochoerus* and *Palaeochoerus*. NA = not available; ? = unclear.

	M3	Lingual roots of upper molars	Hypoconulid (m1 and m2)
?*Propalaeochoerus paronae*	Rounded	Fused and divergent	Close to hypoconid
Propalaeochoerus elaverensis	Elongated	Fused	Close to hypoconid
Propalaeochoerus leptodon	NA	NA	Isolated
Propalaeochoerus sp. A	Elongated	NA	NA
Propalaeochoerus sp. B	Elongated	Fused and convergent	Isolated
Palaeochoerus pusillus	Wide	Divergent and fused (?)	NA
Palaeochoerus typus	Wide	Divergent and unfused (?)	Isolated
Palaeochoerus gergovianus	NA	NA	Isolated
Palaeochoerus aquensis	Rather wide	NA	Isolated

of van der Made (1994) is considered valid, the Monteviale palaeochoerid has to be attributed to the genus *Palaeochoerus* and not to *Propalaeochoerus*. However, the anatomical features proposed as discriminatory by van der Made (1994) show inter- and intraspecific variability that does not permit a clear systematic attribution of this taxon. In addition, *P. paronae* possesses an intermediate M3 shape, a root character of upper molars similar to *Palaeochoerus*, and hypoconulid morphology (fused with the hypoconid) similar to *Propalaeochoerus*. Therefore, in agreement with Stehlin (1899) and Hellmund (1992), we tentatively maintain the original generic attribution of Dal Piaz (1930c) as ?*Propalaeochoerus* (see Table 2 for character comparisons among species of *Propalaeochoerus* and *Palaeochoerus*). Heißig (1978) and Fejfar (1987) described the material from Germany (MP21–22, Möhren 13 and 19) and Bohemia (MP21, Dětaň) as *Propalaeochoerus* aff. *paronae* and *P.* cf. *paronae*, respectively, highlighting that this taxon was probably not endemic to the Monteviale area. However, Hellmund (1992) reviewed the Möhren and Dětaň material and attributed it to *Propalaeochoerus gergovianus* because of its larger size. We agree with Hellmund (1992) since we have noted a difference in the overall morphology of p4 and, in particular, the shape of the entoconid.

Discussion

The biochronological, palaeoecological and palaeobiogeographical implications of the Monteviale faunal assemblage are discussed below. Great care has to be taken in the evaluation of these implications because no systematic fossil collecting and screenwashing of bulk samples from this site have ever been carried out by researchers. Almost all of the specimens were collected by miners in the second half of the nineteenth century and the first decades of the twentieth, and sold to the Università di Padova. The discussion is limited to taxa that provide useful information.

Biochronology

The genus *Diplocynodon* has nine valid species in Europe, ranging from late Paleocene to middle Miocene (e.g. Buscalioni *et al.* 1992; Vasse 1993; Ginsburg & Bulot 1997; Kotsakis *et al.* 2004; Piras & Buscalioni 2006; Martin & Gross 2011; Delfino & Smith 2012; Martin *et al.* 2014). *Diplocynodon ratelii*, to which the material from Monteviale has been tentatively assigned (e.g. Brinkmann & Rauhe 1998; Kotsakis *et al.* 2004), spans from the early Oligocene to the early Miocene (Brinkmann & Rahue 1998). In addition to the specimens from Monteviale, an individual of *Diplocynodon* reportedly from Purga di Bolca (Verona, Veneto) is present in the MGP-PD, but the provenance of this fossil, currently ascribed to *Diplocynodon* cf. *ratelii*, has been debated (Del Favero 1999; Kotsakis *et al.* 2004). According to Del Favero (1999) it is possible that this crocodile was found in one of the other Eocene–Oligocene sites of the Vicenza area (e.g. Cornedo Vicentino, Chiuppano or Monteviale). Kotsakis *et al.* (2004) tentatively referred this specimen to Monteviale, but there is no conclusive evidence to support this hypothesis. The matrix in which this crocodile is embedded contains nannofossils indicating an age spanning middle Eocene to early Oligocene (NP16–NP21, Del Favero, 1999). A similar age interval has been reported by Franco & Piccoli (1993) for some nannoplankton samples from Monteviale.

The genus *Epiaceratherium*, including tentatively assigned species, ranges from late Eocene to the end of the early Oligocene. The species ‘*E.*’ *magnum* occurred in Europe from MP21 to MP23 (Uhlig 1999; Becker *et al.* 2013), while the record of *E.* cf. *magnum* at Paali-C2 (Pakistan) has been referred to MP22 (Antoine *et al.* 2003). The record of *Epiaceratherium* at Habach 5 (Germany, MP25) has been recently reassigned to *Molassitherium* (see Becker *et al.* 2013). *‘E.’ magnum* is larger and displays more advanced morphological features than *E. bolcense* (cf. Uhlig 1999; Becker *et al.* 2013). In addition, the records of this taxon in the MP21 level are questionable because they are based on an isolated third lower deciduous collected at Soumailles (France) and previously referred to *Eggysodon* sp. by Brunet (1979), an isolated third lower deciduous from Möhren-16, and a juvenile hemimandible with a third lower deciduous from Grafenmühle 11, Germany. The latter locality as well as Möhren-19 and Weißenburg 16 (Uhlig 1999) yielded remains of *Eggysodon osborni*, whereas Möhren-16 and Ronzon (France) yielded remains of the large-sized rhinocerotid *Ronzotherium* Aymard, 1854 (Heißig 1987; Uhlig 1999). The specimen from Dětaň attibuted to *Epiaceratherium* was reassigned to *Ronzotherium* by Fejfar & Kaiser (2005). The Na Duong Formation, from which *E. naduongense* has been collected, was considered to be late Bartonian−Priabonian in age (39−35 Ma) by Böhme *et al.* (2014), and early or middle Priabonian by Ducrocq *et al.* (2015). *Eggysodon naduongense* is morphologically similar to *E. bolcense* and probably closely related to it.

The first occurrence of the family Anthracotheriidae is reported in South East Asia from the Pondaung Formation (Myanmar), dated to the middle Eocene, and the late Eocene site of Krabi (Thailand) with the genus *Siamotherium*. The oldest evidence of the genus *Anthracotherium* was reported from this geographical area in the same localities (Ducrocq *et al.* 2000; Tsubamoto *et al.* 2002; Soe 2008). The broad diversity of these first fossils testifies to a rapid diversification and divergence of Anthracotheriidae, and the family's rapid dispersal through all of South Asia. The first doubtful European record of *A. monsvialense* was reported from Dětaň, a site ascribable to MP21 (earliest Oligocene), based on the rich mammalian fauna (Fejfar 1987; Fejfar & Kaiser 2005). However, Fejfar (1987) assigned a radiometric [potassium/argon (K/Ar)] age of 37.7 ± 1.5 Ma to this site, which corresponds to the early Priabonian (late Eocene) (Cohen *et al.* 2013). Ducrocq (1995) showed the contradiction between radiometric age and biochronological assignment, suggesting an Eocene age for the Dětaň fauna. The discrepancy between the two ages could be explained by a remarkable delay in the chronological distribution of the various taxa between the faunas of Western Europe and those of Central and Eastern Europe. The radiometric age of the locality should be reanalysed using modern techniques; K/Ar dating was one of the earliest isotopic dating techniques and its use is now limited as it occasionally produces anomalously old ages attributed to an argon excess (Kelley 2002). *Anthracotherium monsvialense* is well represented at Monteviale and has been identified in a few other European localities, based on size instead of morphological comparison of the material. The species probably ranged from MP21 to MP23.

Palaeoenvironment and palaeoecology

Extant members of the gobioid family Butidae primarily occur in tropical fresh and brackish waters and only occasionally thrive in normal marine contexts (Thacker 2011; Gierl *et al.* 2013). Therefore, the ecological requirements of butid fishes are consistent with the brackish lagoon hypothesized by Mietto (2006) as the palaeobiotope in which the lignite-bearing deposits of Monteviale originated.

A brackish lagoon might also explain the presence of rib fragments of a dugongid. By contrast, the presence of larvae of palaeobatrachids, an exclusively freshwater clade (Špinar 1972; Roček & Wuttke 2010), suggests that this lagoon was occasionally isolated from the sea with salinities that became very low. Alternatively, the presence of small streams flowing into the lagoon might explain the presence of tadpoles. Post-mortem transport of tadpoles is unlikely due to their extremely fragile skeletons.

The trionychids were probably autochthonous, as suggested by the rather abundant remains. The extant members of the genus *Trionyx* (s. l.) are usually found in fresh water, both lakes and rivers, but there are also populations living in brackish or coastal marine waters (Taskavak & Akcinar 2009). The geoemydid of Monteviale belongs to the extinct genus *Bergouniouxchelys*. The majority of extant members of the family Geoemydidae live in freshwater environments (from mountain streams to estuaries or along coastal waters), but the family also includes terrestrial forms (Vitt & Caldwell 2014 and references therein). Therefore, this taxon appears not to be useful palaeoenvironmentally.

Diplocynodon was a short-snouted, caiman-like crocodile widespread in freshwater habitats. Its ecological success was likely due to its unspecialized dentition that made it a generalist and adaptive predator. The remains from Monteviale are poorly preserved and no complete individual has ever been reported from this locality. Nevertheless, some almost-complete skulls, ranging from about 20 to 30 cm in dorsal cranial length, suggest that individuals were rather small.

The estimated body mass of *Epiaceratherium bolcense* indicates that this species was the smallest among the early representatives of Rhinocerotidae in Europe. The GI values suggest that *E. bolcense* was a cursorial rhinocerotid, whereas the values of the Hypsodonty Index (HI) suggest that it was a 'browser feeding above the ground level' (*sensu* Becker *et al.* 2009). Unfortunately, the skulls of *E. bolcense* are crushed and the posture of the head cannot be verified. Nevertheless, ecological data suggest that this small rhinocerotid was most probably related to humid or partially humid open forests.

Dental features of *Anthracotherium monsvialense* are putatively related to a browsing diet by the presence of low-crowned molars, well-differentiated upper and lower premolars (if compared to the successive teeth), and the position and morphology of the lower incisors. It probably fed on soft vegetation or roots (Kowalevky 1873; see Damuth & Janis 2011 for a general discussion). Blondel

(2001) included anthracotheriids in her Category 2 of the dental patterns of Palaeogene European ungulates – that is artiodactyls with a lophed structure on their brachyodont molars that prefigure the selenodonty adapted to a mixed frugivorous/folivorous diet (Janis 1995).

The generally poor preservation and lack of postcranial remains of ?*Propalaeochoerus paronae* do not allow a detailed investigation of the palaeoenvironment inhabited by this suoid. As argued by Kotsakis *et al.* (2005), the stratigraphy of the site and the association of ?*P. paronae* with anthacotheres suggest an open forest and marshy environment (Mietto 2006). The brachyodont and bunodont dental morphology of this palaeochoerid indicate a frugivorous-omnivorous diet (Janis 1995; Blondel 2001).

Palaeobiogeography

Today, the 39 living species of the gobioid family Butidae are found in the Old World tropics (Africa, Asia, Australia and Oceania), where they comprise a moderately abundant component of the coastal fauna and, in some cases, of the inland freshwater fauna, primarily in Australia, New Zealand and New Guinea where ostariophysan fishes are absent (Thacker 2011). Species of the extinct butid genus *Lepidocottus* were present in Europe (Mediterranean basin, Paratethys, Upper Rhine Graben) during the Oligocene and early Miocene (see Gierl *et al*. 2013). The species '*Lepidocottus*' *papyraceus* appears to be restricted to Monteviale.

The morphological similarity of *Trionyx italicus* with *T. capellinii* of Monte Bolca suggests the presence of a group of related species, from the beginning of the middle Eocene up to the Eocene–Oligocene transition, in several small and/or large islands of the Tethys.

If part of the material assigned to *Provencemys* by Hervet (2004) should instead be assigned to the genus *Bergouniouxchelys*, as suggested by Claude *et al.* (2012), the presence of this genus in the Alpine High and in the West European Island would indicate the possibility of migration of these aquatic turtles through narrow seaways. In fact, some extant species of Geoemydidae (*Batagur baska* (Gray, 1830) and *B. borneoensis* (Schlegel & Müller, 1845)) are regularly found in coastal marine waters during nesting (Iverson 1991).

Diplocynodon is a geographically widespread genus, occurring in many European localities. It has been recorded in several Spanish (early Eocene–early Oligocene) (Buscalioni *et al*. 1992; Piras & Buscalioni 2006), French (late Paleocene–early late Oligocene, MP6–MP24) (Vignaud *et al*. 1996; Brinkmann & Rahue 1998; Martin 2010; Antoine *et al*. 2011; Martin *et al.* 2014), British (late Eocene–early Oligocene) (Wood 1846; Wolff *et al*. 2007) and German (middle Eocene–?early Oligocene) (Kuhn 1938; Gramann 1958; Berg 1966; Rauhe & Rossmann 1995; Hellmund 1997; Martin 2010; Delfino & Smith 2012) localities. Paunović (1992) referred a fragmentary right mandibular ramus and an isolated tooth found in the Oligocene coal pit of Novi Golubovech in Croatia to *Diplocynodon* cf. *styriacus*. These remains are too scarce and poorly preserved to allow a specific attribution and we believe they should be referred only tentatively to *Diplocynodon*. The type locality of the type species *D. ratelii* is Saint Gérand Le Puy (Allier, France; early Miocene) (Pomel 1847). The genus also occurs in several other Miocene European fossiliferous sites (Huene & Nikoloff 1963; Buffetaut & Cornée 1982; Schleich 1994; Ginsburg & Bulot 1997; Martin & Gross 2011).

The dispersal pattern of *Diplocynodon* in Europe appears unclear. According to Martin *et al*. (2014), the genus might have reached Europe from North America before the Paleocene–Eocene Thermal Maximum (PETM), or it could have been endemic to Europe before the late Paleocene. Based on its taxonomic affinities, Kotsakis *et al*. (2004) suggested a Central or Western European origin for the *Diplocynodon* of Monteviale. The immigration of this taxon into the supposed insular system of Monteviale is puzzling because the genus has been found almost exclusively in freshwater deposits and probably is thus poorly competent in salt waters. Moreover, if one considers the distribution of extant Alligatoroidea (e.g. *Alligator*, *Melanosochus*), *Diplocynodon* would be strongly related to continental fresh waters. However, it cannot be excluded that species of *Diplocynodon* could have survived in brackish environments (Buffetaut & Cornée 1982), as do the extant caimans *Caiman latirostris* (Daudin, 1801) and *C. crocodilus* (Linnaeus, 1758) in estuaries and mangrove swamps (Grigg *et al*. 1998). Furthermore, alligatoroids seem to be able to cross narrow seaways, as is evident from the occurrence of *C. crocodilus* in Trinidad and the palaeogeographical distribution of fossil Alligatoroidea (Brochu 2001 and references therein).

Epiaceratherium bolcense is currently known only from Monteviale. '*Epiaceratherium' magnum*, tentatively retained within the genus *Epiaceratherium* (cf. Becker *et al.* 2013), occurs in several German (Möhren 13 and 16, Grafenmühle 7, 11 and 12, Ronheim 1), French (Soumailles, Villebramar), Swiss (Kleinblauen) and Czech (Dětaň, Markvartice) localities, chronologically related to MP21–23 (Uhlig 1999). However, the MP21 records of this taxon are questionable and based mainly on three third lower deciduous teeth. Uhlig (1999) reported *E.* aff. *magnum* in a few German (Offenheim and Grafenmühle 11, MP21–23) and French (Monclar-de-Quercy, MP21–23) localities, and cf. *Epiaceratherium* sp. at Habach 5 (MP25) and Weißenburg 16 (MP21) (Germany). Becker *et al.* (2013) recently referred the specimens from Kleinblauen, Offenheim, Habach 5 and Monclar-de-Quercy to *Molassitherium delemontense*, suggesting that this species was partly coeval with *'E.' magnum*. However, all of the early Oligocene localities, where *'E.' magnum* has been found, were not located on the Alpine High (Popov *et al.* 2004; Kocsis *et al.* 2014). This latter area was separated from the Western and Central European territories by a marine basin (Popov *et al.* 2004). A few dental remains from Pakistan (Paali C2), morphologically similar to those of *'E.' magnum*, have been attributed by Antoine *et al.* (2003) to *E.* cf. *magnum*. If the *Epiaceratherium* from Na Duong is reliably dated as early or middle Priabonian (Ducrocq *et al.* 2015), a dispersal pattern can be hypothesized for this taxon from South East Asia to Western Europe. Most probably the genus reached the Alpine High and later Central Europe via an island chain consisting of micro-continents and volcanic back-arcs (Böhme *et al.* 2014).

The range of *Anthracotherium monsvialense* was probably not restricted to Monteviale. This species has been recorded from MP21 to MP23 in several localities, such as Dětaň (Czech Republic; *A.* cf. *monsvialense*), Villebramar, Caylux, Bach, Nassiet, Quercy (France), Weinheim (Germany), Vaulruz (Switzerland), and Montalbán (Spain) (Kotsakis 1986; Sudre 1995; Becker *et al.* 2004; Fejfar & Kaiser 2005; Scherler 2011 and references therein). The presence of *A. monsvialense* in other Venetian localities (Zovencedo and Chiuppano) is uncertain. As a consequence, Monteviale can be considered the first well-documented evidence of this species. *Anthracotherium monsvialense* was previously reported as a 'small-sized animal' (related to the larger and younger *A. magnum*) but comparisons with late Eocene Asian species revealed that its size is better related to an increasing size trend from the older Asian species to the younger European ones. According to Benammi *et al.* (1999), the morphology and size of *A. monsvialense* closely resembles *A. chaimanei* from Krabi (Thailand, late Eocene). In addition, the cladistic analysis performed by Lihoreau *et al.* (2004) suggests a close relationship between the South Asian anthracotheres [*A. pangan* (= *Anthracothema pagan* in Lihoreau *et al.* 2004) and *A. chaimane*] and the European clade (*A. monsvialense* and *A. magnum*). These results support the hypothesis of a dispersal of the ancestors of *A. monsvialense* from South Asia, which also appears to be supported by the presence of a few dental fragments from the early Oligocene of Karakaya and Çuvaşlu (Turkish Thrace: Ünay-Bayraktar 1989) belonging to a taxon close to *A. monsvialense* (Lebküchner 1974; Russell *et al.* 1982). The affinity of *A. monsvialense* with *A. alsaticum* has been hypothesized by some authors (Sudre 1995). These two species share the same chronological interval and their ranges overlap, but the limited material of *A. alsaticum* does not allow a conclusive statement about their relationship.

Investigating the palaeobiogeography of the genus *Propalaeochoerus* is challenging. Recent contributions have mentioned the problematical taxonomic position of this genus and its relatives, and it is uncertain whether *Propalaeochoerus*, together with several other basal suoids, belongs to Suidae, Tayassuidae or Palaeochoeridae (Liu *et al.* 2002; van der Made 2010; Orliac *et al.* 2010; Hellmund & Heizmann 2011; Pickford 2011; Mennecart *et al.* 2012; Scherler *et al.* 2013), with implications for the understanding of the early palaeobiogeographical histories of these groups. Further, the taxonomic ambiguity already mentioned makes its palaeobiogeographical context even more intricate.

The species ?*Propalaeochoerus paronae* shares some primitive features with several suoideans from the late Eocene of eastern Asia. These Asian taxa (Ducrocq *et al.* 1998; Liu 2001) appear to exhibit close affinities with the European genera. *Egatochoerus*, *Palaeochoerus*, *Propalaeochoerus*, *Odoichoerus* and *Siamochoerus* show similar upper molars (Liu 2001), evidencing a clear eastern Asian origin of the group (Ducrocq 1994; Ducrocq *et al.* 1998; Orliac *et al.* 2011). In addition, a recent palaeogeographical study (Böhme *et al.* 2014) is consistent with the possible palaeobiogeographical scenario and dispersal route of these taxa towards Europe.

Conclusions

The reassessment of the vertebrate assemblage of Monteviale, which includes 15 taxa, represents a remarkable opportunity to understand the structure and composition of the Southern European earliest Oligocene faunas. Unfortunately, no systematic fossil collecting or screen-washing of bulk samples from the site have ever been carried out by researchers, almost all of the specimens having been collected by miners in the second half of the nineteenth century and the first decades of the twentieth and sold to the Università di Padova.

The Monteviale fauna currently includes several endemic species. In fact, potentially only *Anthracotherium monsvialense* and ?*Propalaeochoerus paronae* are recorded from other European localities.

The assemblage was traditionally included within the mammal faunas of the earliest Oligocene, MP21 (Kotsakis 1986; Kotsakis *et al.* 1997), but Böhme *et al.* (2014) recently suggested a latest Eocene age (?MP20) for this locality. The inclusion of the Monteviale assemblage within MP21 was primarily based on the presence of the genus *Anthracotherium*, which characterized the European Oligocene mammal faunas after the 'Grande Coupure' (Stehlin 1910b; Costa *et al.* 2011). However, Monteviale was part of a geographical area (Alpine-Dinaric) located at the south-eastern margin of the European area and geographically isolated from Western Europe (Fig. 24; Popov *et al.* 2004; Kocsis *et al.* 2014). The occurrences of taxa of Asian origin in south-eastern

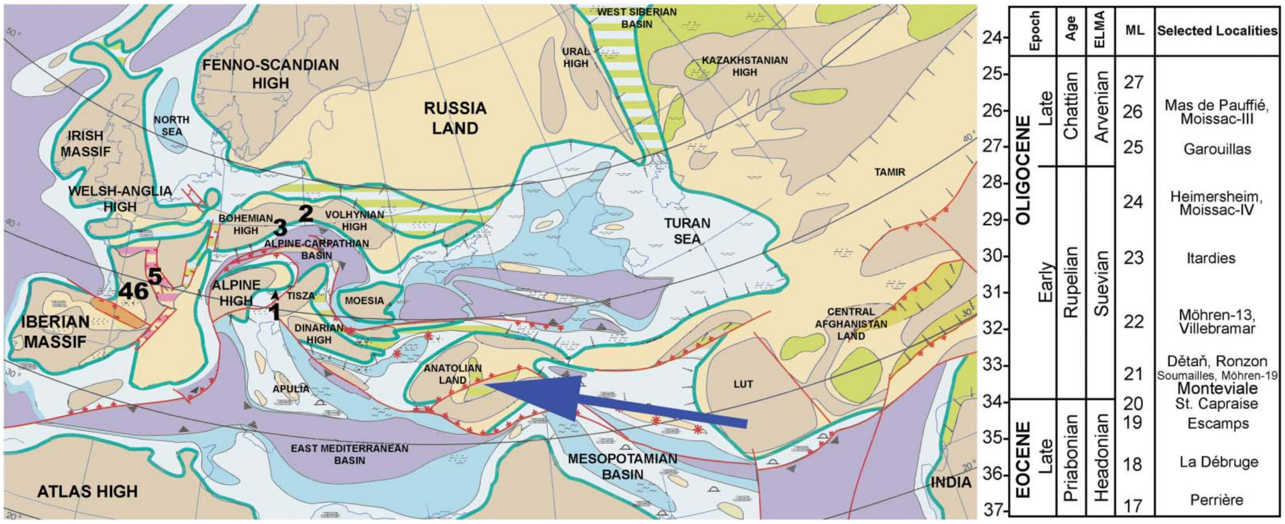


Figure 24. Palaeogeographical and chronological position of Monteviale and other selected European MP21−22 localities during the earliest Oligocene (after Popov *et al.* 2004; Böhme *et al.* 2014; Kocsis *et al.* 2014). 1 = Monteviale; 2 = Dětaň; 3 = Möhren-13 and Möhren-19; 4 = Ronzon; 5 = Villebramar; 6 = Soumailles. Arrow indicates the hypothetical dispersal route of south-eastern Asian taxa around the Eocene-Oligocene boundary. The ages of selected localities are deduced from Aguillar *et al.* (1997); Uhlig (1999); Becker *et al.* (2004); Antoine *et al.* (2011); Maridet *et al.* (2013); Kocsis *et al.* (2014).

Europe probably occurred earlier than in Western Europe, as suggested by Ducrocq (1995); thereafter, a few genera (*Anthracotherium*, *Propalaeochoerus* and maybe *Epiaceratherium*), along with several other species, reached Central and Western Europe ('Grande Coupure'). The stratigraphical position of the lignite deposits above the Calcareniti di Castelgomberto Formation allows to exclude an age older than late Priabonian. The evolutionary stage of the Monteviale rhinocerotid, morphologically similar to the Na-Duong species (late Eocene) and less advanced than *'E.' magnum* of Central Europe (MP22−23), suggests an age close to the Eocene−Oligocene boundary or earliest Oligocene (MP21). This age is also supported by the evolutionary stage of *?P. paronae*. Some nannoplankton samples from Monteviale suggest attribution to zones NP16−NP21, from *c.* 43.5 Ma to *c.* 32.8 Ma (Franco & Piccoli 1993; Del Favero 1999).

Based on this evidence, and considering the recent calibration of MP21 by Costa *et al.* (2011), the Monteviale assemblage is here assigned to the earliest Oligocene, lowermost Rupelian, MP21 (which is only 0.5 myr younger than the Eocene−Oligocene boundary; Costa *et al.* 2011).

Geological and palaeontological data suggest that the area in which the Monteviale deposits accumulated was characterized by the presence of humid forests. It was probably located close to a coastal brackish lagoon that was characterized by salinity fluctuations suggested by the concurrent presence of marine taxa (e.g. Dugongidae) and strictly freshwater taxa (e.g. Palaeobatrachidae).

Regional geological evidence suggests that the Monteviale lagoon was situated along the coast of a small island 1 km long. However, this island was probably close to a larger continental area (or a larger island?), as indicated by the relatively high ungulate biodiversity (five or six species). The taxa that constitute the Monteviale fauna are much more diverse (for large mammals in particular) than those of extant insular assemblages, as well as of those of the Mediterranean islands in the Pleistocene (Geer *et al.* 2010). The close proximity to a large area of dry land probably allowed the passage of mammals and freshwater taxa (e.g. palaeobatrachids) via a small emergent land bridge.

With regard to the palaeobiogeography of Monteviale, the palaeobatrachids are exclusive to the European area, *Bergouniouxchelys vallisneri* is endemic to Monteviale but clearly related to the Western European species of Geoemydidae, whereas *Diplocynodon* is also present in Central and Western Europe. By contrast, the ungulates (*Epiaceratherium*, *Anthracotherium*, ?*Propalaeocherus* and probably *Anthracochoerus*) appear to be related to southern Asian taxa, supporting a dispersal pattern of these mammals across the south-eastern Europe and western Asia plates during the late Eocene and early Oligocene (Heißig 1979; Kotsakis 1986; Ducrocq 1995; Kotsakis *et al.* 2004).

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