A new species of the genus *Microbunodon* (Anthracotheriidae, Artiodactyla) from the Miocene of Pakistan: genus revision, phylogenetic relationships and palaeobiogeography

FABRICE LIHOREAU, CÉCILE BLONDEL, JOHN BARRY & MICHEL BRUNET

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New unpublished remains of small Anthracotheriinae are described. First, materials from the upper Oligocene (MP 30) locality of La Milloque, southwest France, permit a review of the species *Microbunodon minimum*. Thereafter, fossils from the middle and late Miocene of the Potwar Plateau, Pakistan are attributed to the European genus *Microbunodon*. *Microbunodon milaensis* sp. n. from the Nagri Formation (between 10.3 and 9.2 Ma), Pakistan, is described and the species *M. silistrensis* from the Lower Manchar Formation (between 16 and 15 Ma) and from the Chinji Formation (between 12.7 and 11.5 Ma), Pakistan, is reviewed. The new species represents the last occurrence of the subfamily Anthracotheriinae, around 9.3 Ma. Similar materials from the Bugti and Siwalik Hills were previously considered as a small *Anthracotherium*. Comparisons with *M. minimum* from the European late Oligocene lead to a complete revision of the genus and permit definition of a new set of characters, which separate *Microbunodon* from *Anthracotherium*. A cladistic analysis reconsiders phylogenetic relationships among Anthracotheriinae, separating an *Anthracothema–Anthracotherium* clade and an *Anthracokeryx–Microbunodon* clade. *Microbunodon* appears to stem from the Asian late Eocene–lower Oligocene genus *Anthracokeryx*. These results imply a new distribution of the genus *Microbunodon* showing exchanges between Europe and Asia during the late Oligocene and probably the lower Miocene.

Fabrice Lihoreau, Cécile Blondel & Michel Brunet, Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Université de Poitiers, 40 Avenue du Recteur Pineau, 86022 Poitiers cedex, France. E-mail: fabrice.lihoreau@univ-poitiers.fr

John Barry, Department of Anthropology and Peabody Museum, Harvard University, Cambridge, MA 02138, USA. E-mail: jcbarry@fas.harvard.edu

Introduction

The fossil family Anthracotheriidae (Mammalia: Artiodactyla) is known from the late Eocene to the late Pliocene. Because of their abundance, their diversity and their worldwide dispersion (Asia, Europe, North America and Africa), anthracotheres have largely been applied to biochronology and palaeobiogeography. This family is divided into two subfamilies (*sensu* Kron & Manning 1998): the Bothriodontinae and the Anthracotheriinae. Here we focus on the systematic of Anthracotheriinae where the genus *Microbunodon* has been placed (e.g. Pickford 1987).

In 1822, Cuvier created two species for small-sized Anthracotheriinae from the upper Oligocene: *Anthracotherium minus* from Cadibona, Italy and *A. minimum* from Hautesvignes, France. In 1828, Pentland identified similar forms from the Siwaliks of India and attributed them to *A. silistrense*. Later, other species close to those of Cuvier were described: *A. sandbergeri* Von Meyer, 1852 from Gusternhaim, Germany, *A. breviceps* (Troshel, 1859) from Rott, Germany, and *A. laharpei* Renevier, 1879 from Rochette, Switzerland. All of these taxa, except *A. silistrense*, were placed in the genera *Microselenodon* and *Microbunodon* by Depéret (1908). The two genera were synonymized with *Microbunodon* by Stehlin (1910) who also recognized two species: a large one including *M. minus* and *M. laharpei* and a small one regrouping *M. minimum* and *M. breviceps* (the author considered *M. sandbergeri* as an intermediate but did not place it in a defined species). Pilgrim (1910, 1912, 1913) noted the affinities between the Indian specimens, *A. silistrense*, and the two European *Microbunodon* species and proposed to place them in the same genus. This proposition has not been validated (Forster-Cooper 1924; Matthew 1929; Colbert 1935). Brunet (1968)

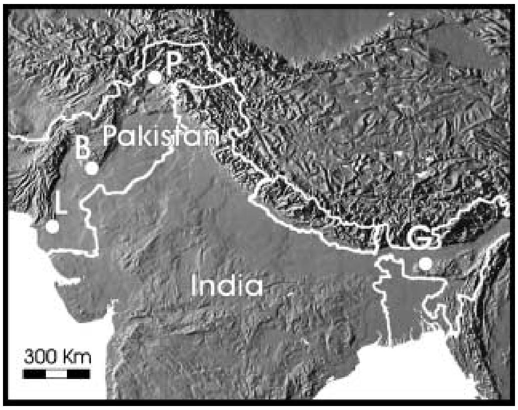

Fig. 1 Location of the studied Asian fossil localities. P, Potwar Plateau; B, Bugti Hills; L, Lower Manchar of Sind; G, Garo Hills.

described a complete cranium of *M. minimum* from La Milloque and showed a great variability in molar size and marked sexually dimorphic upper canines in this species. He proposed to keep only one species in the genus *Microbunodon*, for which he suggested the name *M. minimum.* Pickford (1987) revised the Anthracotheriidae from the Bugti Hills, Pakistan and synonymized three species of small Anthracotheriinae with *A. silistrense*: *A. punjabiense* Lydekker, 1878, *A. mus* Pilgrim, 1908, and *A. exiguum* Forster-Cooper, 1924. Up to now, the genus *Microbunodon* is monospecific and only known from the late Oligocene of Europe. All of the small Anthracotheriinae from the Siwaliks of Pakistan and India are still noted as *A. silistrense*, but this generic attribution following recent authors remains uncertain (Raza *et al*. 1984; Pickford 1987).

New material of Anthracotheriidae, including rare small Anthracotheriinae, have been found by the Geological Survey of Pakistan–Harvard Project since 1973 in the Siwalik formations of the Potwar Plateau, Pakistan (Pilbeam *et al*. 1977, 1979) (Fig. 1). During following campaigns in this area, the project has obtained precise magnetochronological and biochronological ages for these Miocene specimens (Johnson *et al*. 1985; Barry & Flynn 1990). These small Asian Anthracotheriinae represent the latest occurrence of the subfamily.

In order to make systematic attributions to these Asian remains, we describe unpublished material of *M. minimum* from La Milloque found between 1967 and 1970 by Brunet. This allows comparisons to be made with the fossils from the Potwar Plateau. We then review the genus *Microbunodon* and the species *M. minimum* and *M. silistrense*. We also describe a new species, *M. milaensis* sp. n. A phylogenetic analysis based on Anthracotheriinae highlights new hypotheses on the origin of the European and Pakistani forms. Finally, this proposed phylogeny allow us to review some palaeobiogeographical considerations.

Abbreviations

AMNH, American Museum of Natural History in New York; MNHN, Muséum National d'Histoire Naturelle in Paris; NHM, Natural History Museum in London; GSP, Geological Survey of Pakistan. For the synonymy list: V, the authors have seen the referred material; P, only a part of the material is attributed to the species; ?, the attribution is unsure; *, first mention of the name of the valid taxon; in italic, the reference does not provide information on the morphology or the systematic of the taxon.

Systematic palaeontology

Order ARTIODACTYLA Owen, 1848
Family ANTHRACOTHERIIDAE Leidy, 1869
Subfamily Anthracotheriinae Leidy, 1869
Genus *Microbunodon* Depéret, 1908

Type species. Microbunodon minimum (Cuvier, 1822)

Emended diagnosis. Small-sized Anthracotheriinae. Upper and lower incisors mesiodistally enlarged and buccolingually compressed. More selenodont molars than other Anthracotheriinae, with crescentic protocone and protoconid. Upper canine transversally compressed and sexually dimorphic; large tusk in male and short tusk in female. Small lower canine sloped backwards with a mesial wear facet resulting from contact with $I^3/$. Continuous premolar rows with a very small or absent $P/_1$–$P/_2$ diastema. Pre-entocristid joins prehypocristid so that longitudinal valley of second lobe of lower molars is distally open. Talonid on $M/_3$ with a single cusp (hypoconulid). Transverse mandibular narrowing at C–$P/_1$ level. Fused symphysis. Crested ventral edge of symphysis.

Anthracotherium differs from *Microbunodon* by a developed entoconulid, an accessory cusp on upper molar mesial cingulum and on $P^3/$ lingual cingulum, a strong and vertical lower canine in contact with upper canine, a straight mandibular corpus, a flattened ventral border of symphysis, a third hypocristid, on lower molar, that joins pre-entocristid forming a hypolophid, and lower incisors mesiodistally narrowed and high crowned.

Anthracokeryx (*sensu* Colbert 1938) differs from *Microbunodon* by the presence of an accessory cusp on $P^3/$ lingual cingulum, a third protocrista, narrower lower incisors, a proportionally longer $P/_1$–$P/_2$ diastema, a $P/_2$–$P/_3$ diastema, a third hypocristid that joins pre-entocristid forming a hypolophid, a flattened ventral edge of symphysis and unfused symphysis.

Microbunodon minimum *(Cuvier, 1822)*

Synonymy list

v* 1822 *Anthracotherium minimum* Cuvier, p. 404, table 80, fig. 4.
vp 1848 *Anthracotherium minimum* CUVIER, Blainville, pp. 135–136.

1852 *Anthracotherium sandbergeri* sp. n. Von Meyer, p. 305.
1859 *Sus breviceps* sp. n. Troschel, p. 49.
1877 *Anthracotherium breviceps* (TROSCHEL), Boettger, p. 146, fig. 76.
1879 *Anthracotherium laharpei* sp. n. Renevier, p. 146, fig. 76.
1890 *Anthracotherium minimum* CUVIER, Squinabol, pp. 566–567.
1891 *Anthracotherium minimum* CUVIER, Filhol, pp. 162–163, plate 1.
? 1904 *Anthracotherium* cf. *minus* CUVIER, Newton, pp. 285–286, plate 24, fig. 20.
1908 *Microbunodon laharpei* (RENEVIER), Depéret, p. 159.
1908 *Microbunodon sandbergeri* (VON MEYER), Depéret, p. 159.
1908 *Microselenodon minimum* (CUVIER), Depéret, p. 159.
1908 *Microselenodon breviceps* (TROSCHEL), Depéret, p. 160.
p 1910 *Microbunodon minus* (CUVIER), Stehlin, p. 166.
1910 *Microbunodon minimum* (CUVIER), Stehlin, p. 166.
? 1926 *Anthracotherium minus* CUVIER, Forster-Cooper, p. 373.
p 1967 *Microbunodon minus* (CUVIER), Hünermann, p. 679.
1967 *Microbunodon minimum* (CUVIER), Hünermann, p. 678.
vp 1968 *Microbunodon minimum* (CUVIER), Brunet, p. 839.
vp 1970 *Microbunodon minimum* (CUVIER), Brunet, p. 2777.

Holotype. Left lower jaw with M/$_1$–M/$_3$, no. 4219 housed at MNHN (figured by Cuvier 1822: 404, plate 80, fig. 5).

Type locality. France, Lot-et-Garonne, Hautesvignes.

Other localities. France: Bessens; Bourret; Dieupentale; Moissac II; Verdun-sur-Garonne; Réal; Blaymont; Comberatière; Domihac; Fumel; Lacam; La Milloque; Laricardie. Germany: Gusternhaim; Möhren; Rott. Switzerland: Aarau; Ebnat-Kappel; Küttingen; Regensberg; Rochette. Austria: Linz. Turkey: Masatly.

Age. Late Oligocene, known from MP 28 to MP 30 (26–23.8 Ma *sensu* McKenna & Bell 1997).

New material. Left C–M/$_3$ and right C (Ma301–67), right P/$_3$–M/$_3$ (Ma302–67), left P/$_4$–M/$_3$ (Ma320–68), P/$_4$–M/$_3$ and left P/$_1$ (Ma236–69), left P/$_4$–M/$_3$ (Ma240–69), right P/$_3$–M/$_3$ (Ma242–69), symphysis with right P/$_3$–P/$_4$ (Ma312–67), left C–M/$_3$ and right C (Ma4–70), right I/$_1$, C–M/$_3$ and left C–P/$_1$ (Ma57–70), right C–P/$_2$, left P/$_3$–P/$_4$, M/$_2$ (Ma75–70), left P/$_3$–M/$_3$ and right P/$_3$–M/$_3$ (Ma161–70), I/$_1$ (Ma398–70, Ma399–70, Ma400–70, Ma402–70, Ma403–70, Ma404–70, Ma405–70, Ma406–70, Ma407–70, Ma408–70, Ma410–70, Ma412–70), I/$_2$ (Ma329–67, Ma330–67, Ma413–70, Ma414–70, Ma415–70), I/$_3$ (Ma331–67, Ma332–67, Ma333–67, Ma334–67, Ma335–67, Ma336–67, Ma337–67, Ma338–67, Ma339–67, Ma340–67), lower canine (Ma343–68, Ma228–70, Ma231–70), left P/$_1$ (Ma321–67, Ma185–70, Ma186–70, Ma188–70, Ma189–70, Ma190–70, Ma191–70, Ma192–70, Ma193–70, Ma194–70, Ma195–70, Ma196–70), left P/$_2$ (Ma340–68, Ma179–70, Ma180–70), right P/$_2$ (Ma204–69, Ma181–70, Ma182–70, Ma183–70, Ma184–70), left P/$_3$ (Ma158–70, Ma159–70, Ma163–70, Ma164–70, Ma165–70, Ma166–70, Ma167–70, Ma170–70), right P/$_3$ (Ma171–70, Ma172–70, Ma173–70, Ma174–70, Ma175–70, Ma176–70, Ma177–70, Ma178–70), right P/$_4$ (Ma260–69, Ma140–70, Ma141–70, Ma142–70, Ma143–70, Ma144–70, Ma146–70, Ma147–70), left P/$_4$ (Ma332–68, Ma334–68, Ma337–68, Ma338–68, Ma261–69, Ma262–69, Ma263–69, Ma145–70, Ma148–70, Ma149–70, Ma150–70, Ma151–70, Ma152–70, Ma153–70, Ma154–70, Ma155–70, Ma156–70, Ma157–70, Ma158–70, Ma159–70), M/$_1$–M/$_3$ (Ma325–68, Ma3–70, Ma12–70, Ma14–70, Ma32–70, Ma51–70, Ma53–70, Ma315–68, Ma323–68, Ma331–68, Ma336–68, Ma239–69, Ma8–70, Ma6–70, Ma17–70, Ma24–70, Ma26–70, Ma28–70, Ma80–70, Ma84–70, Ma85–70, Ma86–70, Ma160–70), M/$_2$–M/$_3$ (Ma303–67, Ma305–67, Ma306–67, Ma311–68, Ma316–68, Ma319–68, Ma321–68, Ma326–68, Ma247–69, Ma7–70, Ma13–70, Ma15–70, Ma21–70, Ma22–70, Ma23–70, Ma33–70, Ma35–70, Ma39–70, Ma44–70, Ma49–70, Ma50–70, Ma54–70, Ma60–70, Ma66–70, Ma70–70), M/$_1$ (Ma309–67, Ma258–69, Ma115–70, Ma118–70, Ma121–70, Ma123–70, Ma124–70, Ma125–70, Ma126–70, Ma128–70, Ma130–70, Ma138–70), M/$_2$ (Ma335–68, Ma243–69, Ma254–69, Ma257–69, Ma255–69, Ma315–67, Ma31–70, Ma89–70, Ma91–70, Ma93–70, Ma94–70, Ma95–70, Ma97–70, Ma98–70, Ma101–70, Ma102–70, Ma103–70, Ma104–70, Ma105–70, Ma106–70, Ma107–70, Ma82–70, Ma129–70, Ma133–70), M/$_3$ (Ma304–67, Ma307–67, Ma308–67, Ma310–68, Ma324–68, Ma327–68, Ma328–68, Ma235–69, Ma244–69, Ma249–69, Ma250–69, Ma253–69, Ma10–70, Ma16–70, Ma18–70, Ma20–70, Ma25–70, Ma38–70, Ma40–70, Ma42–70, Ma55–70, Ma56–70, Ma43–70, Ma45–70, Ma46–70, Ma47–70, Ma59–70, Ma62–70, Ma63–70, Ma64–70, Ma65–70, Ma67–70, Ma68–70, Ma69–70, Ma71–70, Ma74–70, Ma75–70, Ma87–70, Ma435–70, Ma422–70, Ma52–70), right M^1/–M^2/ (Ma313–67), dP^3/–M^1/ (Ma351–68), right P^4/–M^2/ (Ma278–69), left P^4/–M^1/ (Ma284–69), right I^1/ (Ma350–70, Ma351–70, Ma352–70, Ma353–70, Ma354–70, Ma355–70, Ma356–70, Ma357–70, Ma358–70), left I^1/ (Ma288–69, Ma289–69, Ma359–70, Ma360–70,

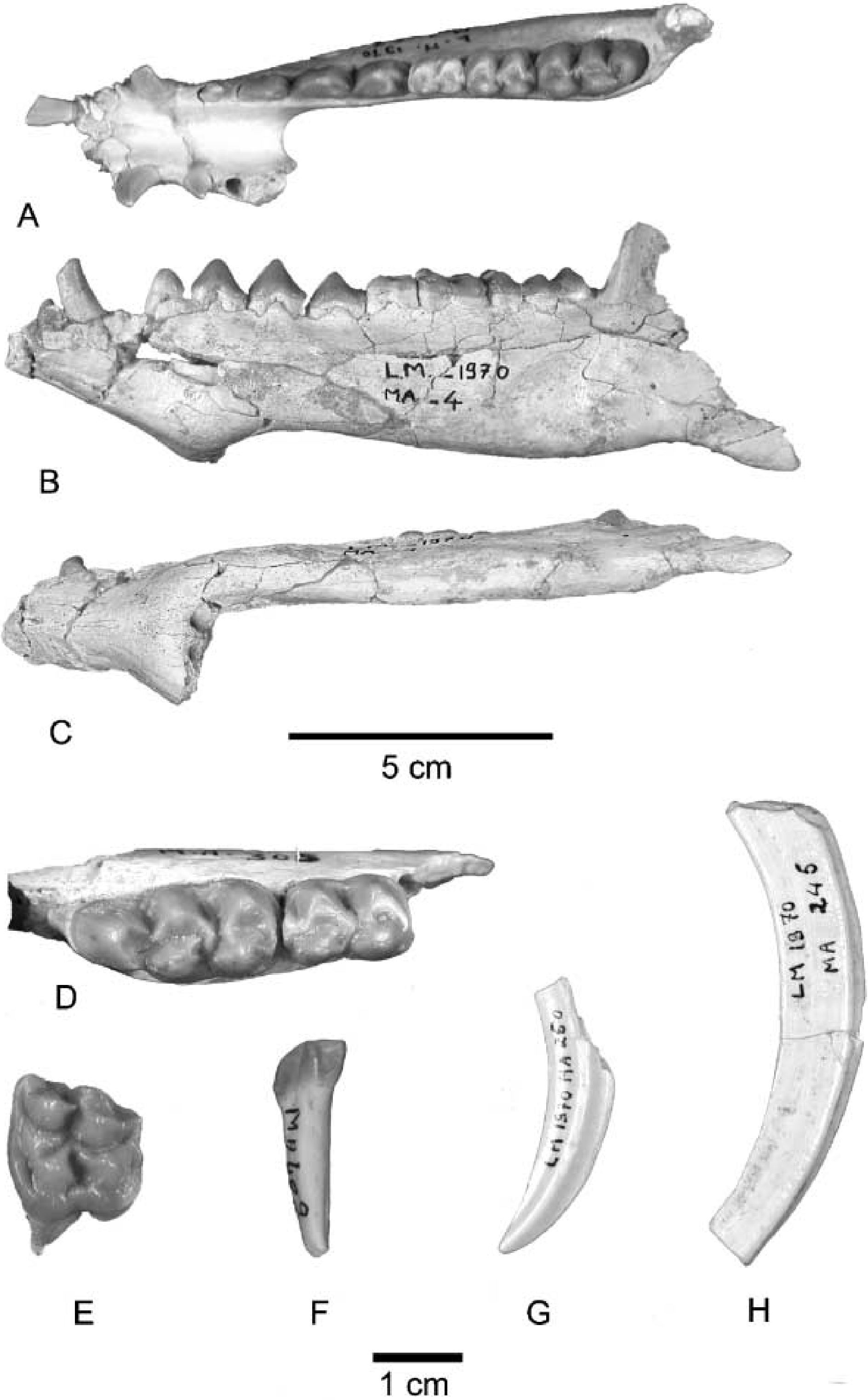

Fig. 2 A–H. —A. *Microbunodon minimum* (MA57–70) fragmentary mandible with right I/$_1$, C–M/$_3$ and left C–P/$_1$ in occlusal view. —B,C. *Microbunodon minimum* (MA4–70) fragmentary mandible with left C–M/$_3$ and right C in labial (B) and ventral (C) views. —D. *Microbunodon minimum* (MA305–67) left M/$_2$–M/$_3$ in occlusal view. —E. *Microbunodon minimum* (MA274–70) left M^3/ in occlusal view. —F. *Microbunodon minimum* (MA409–70) right I/$_2$ in buccal view. —G,H. *Microbunodon minimum* male upper canines in lingual views (G: MA250–70 and H: MA245–70).

Ma361–70, Ma362–70, Ma363–70, Ma364–70, Ma365–70, Ma366–70, Ma367–70), left $I^2/$ (Ma290–69, Ma372–70, Ma373–70, Ma374–70, Ma375–70), right $I^2/$ (Ma291–69, Ma368–70, Ma369–70, Ma370–70, Ma371–70) right $I^3/$ (Ma292–69, Ma376–70, Ma377–70, Ma378–70, Ma379–70, Ma380–70), left $I^3/$ (Ma381–70, Ma382–70, Ma383–70, Ma384–70, Ma385–70, Ma386–70), upper canine (Ma345–68, Ma346–68, Ma347–68, Ma272–69, Ma273–69, Ma274–69, Ma275–69, Ma232–70, Ma233–70, Ma234–70, Ma235–70, Ma236–70, Ma237–70, Ma238–70, Ma239–70, Ma240–70, Ma242–70, Ma243–70, Ma244–70), right $P^1/$ (Ma349–70, Ma387–70, Ma389–70, Ma390–70), left $P^1/$ (Ma388–70, Ma391–70, Ma392–70, Ma393–70, Ma394–70, Ma395–70, Ma396–70, Ma397–70), left $P^2/$ (Ma323–70, Ma329–70, Ma330–70, Ma331–70, Ma332–70, Ma333–70, Ma334–70, Ma335–70), right $P^2/$ (Ma293–69, Ma361–68), right $dP^3/$ (Ma348–70, Ma349–70), left $P^3/$ (Ma321–70, Ma322–70, Ma324–70, Ma325–70, Ma326–70), right $P^3/$ (Ma287–69, Ma360–68, Ma327–70, Ma328–70), right $P^4/$ (Ma260–69 Ma285–69, Ma286–69, Ma306–70, Ma307–70, Ma308–70, Ma320–70), left $P^4/$ (Ma309–70, Ma310–70, Ma311–70, Ma312–70, Ma313–70, Ma314–70, Ma315–70, Ma316–70, Ma317–70, Ma318–70, Ma319–70), right $M^1/$ (Ma279–70, Ma297–70, Ma299–70), left $M^1/$ (Ma300–70, Ma301–70, Ma302–70, Ma304–70), left $M^2/$ (Ma260–70, Ma286–70), right $M^2/$ (Ma358–68, Ma359–68, Ma282–69, Ma281–70, Ma282–70, Ma283–70, Ma284–70, Ma285–70, Ma288–70, Ma293–70, Ma294–70), $M^3/$ (Ma257–70, Ma352–68), right $M^3/$ (Ma279–69, Ma258–70, Ma259–70, Ma262–70, Ma264–70, Ma265–70, Ma266–70), left $M^3/$ (Ma271–70, Ma274–70, Ma276–70). All specimens from La Milloque, France (Fig. 2, Table 1) and housed at the University of Poitiers.

Emended diagnosis. Smallest species of genus. $M/_3$ equal in size with those of *M. silistrense*. Postorbital process closed. Blade-like upper canines very well developed in males, short in females. Geniohyoideus attachment situated on internal side of symphysis or ventrally expanded with two enlarged fossae. Symphysis crested ventrally with a flattened ventral edge at posterior part. Symphysis at posterior border of $P/_2$. Slender limb, hindlimb more robust and longer than forelimb.

Microbunodon silistrensis differs from *M. minimum* by a longer premolar row compared with molar row, less developed parastyles, longer symphysis crested along ventral edge, larger diastema between lower canine and $P/_1$, ventrally expanded genial muscle insertions with reduced genial fossae and developed genial crista.

Description

Mandible. Mandibular narrowing at C–$P/_1$ diastema level (Fig. 2A). Symphysis reaching posterior side of $P/_2$. Fused symphysis. Ventral border of symphysis crested in its anterior part and flattened in posterior (Fig. 2C). Two large fossae separated by a strong crest on internal side of symphysis corresponding to geniohyoideus and digastricus muscle insertions (Fig. 3A). Ventrally expanded insertion in some specimens interpreted as sexual variations but always well-marked fossae and flattened ventral surface below genial spine. Angle 30–33.5° between molar row and anterior edge of symphysis (Fig. 2B).

Table 1 Descriptive statistics of molar measurements of *Microbunodon minimum* from La Milloque.

	n	Mean	Minimum	Maximum	Standard deviation
$M/_1$					
Lmd	38	10.91	9.7	12.3	0.62
L1	38	6.90	6.2	7.7	0.35
L2	38	7.35	6.4	8.3	0.37
$M/_2$					
Lmd	77	13.29	11.7	15.1	0.71
L1	77	9.06	8.1	10.5	0.48
L2	76	9.42	8.2	10.7	0.53
$M/_3$					
Lmd	79	20.49	18.1	23.7	1.16
L1	79	10.22	9.0	12.0	0.55
L2	78	10.48	9.2	12.0	0.60
$M^1/$					
Lmd	11	10.88	10.3	11.4	0.31
L1	11	11.60	11.0	12.2	0.40
L2	11	11.29	10.8	11.7	0.29
$M^2/$					
Lmd	15	13.37	12.0	15.2	0.84
L1	15	14.99	13.0	17.0	1.17
L2	15	13.79	12.2	16.0	0.92
$M^3/$					
Lmd	12	15.03	13.7	17.6	1.07
L1	10	16.71	15.5	17.6	0.55
L2	11	15.05	13.5	17.7	1.05

Lmd, mesiodistal length; L1, buccolingual length between protocone (protoconid) and paracone (metaconid); L2, buccolingual length between metacone (hypoconid) and metaconule (entoconid).

Lower dentition. No diastema between lower incisors and between $I/_3$ and C. Proclivous incisors buccolingually compressed and developed mesiodistally with top edge of crown curved down as it passes distally (Fig. 2F). Reduced lower canine, with curved crown. Mesial wear facet present, corresponding to contact with $I^3/$. Small or absent distal wear facet with upper canine. No sexual dimorphism on this tooth.

Molar row slightly longer than premolar row (Table 2). Short diastema, between C and $P/_1$ (5.4–9.5 mm) and no $P/_1$–$P/_2$ diastema except in a few specimens where it is very short, length ranging from 2 to 5 mm. Triangular outline of lower premolars. Premolars higher crowned than molars. Two crests on premolars: a convex mesial one and a concave

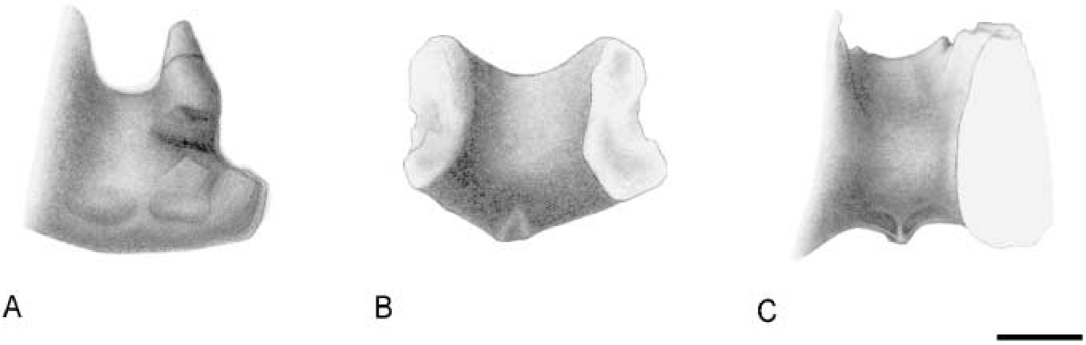

Fig. 3 A–C. Drawing of the distal area of the symphysis in the genial view, showing the different muscular attachment structures. —A. *Microbunodon minimum*, Ma4–LM1970. —B. *Microbunodon silistrense*, Y20446. —C. *Microbunodon milaensis* sp. n., Y10999. Scale bar = 1 cm.

Table 2 Molar and premolar row measurements and mandibular height of *Microbunodon milaensis* sp. n., *M. silistrensis* and *M. minimum* in mm.

Specimens	Species	ML	PL	PL/ML	H
Y10999	*M. milaensis* sp. n.	53	51.6	0.97	34
AM19444	*M. silistrense*	53	58	1.09	25
M11059	*M. silistrense*	44.2	—	—	
Y29194	*M. silistrense*	47	54.2	1.15	26.4
Y21078	*M. silistrense*	43	—	—	
Ma4–70	*M. minimum*	42	39.6	0.94	26.2
Ma236–68	*M. minimum*	41.7	39.8	0.95	21.5
Ma161–70	*M. minimum*	39.8	—	—	25.4
Ma57–70	*M. minimum*	40	36	0.90	20
Ma320–68	*M. minimum*	41.4	37.2	0.90	22.6
Ma242–69	*M. minimum*	43	36.5	0.85	23
Ma302–67	*M. minimum*	41			25.6

ML, molar row length; PL, premolar row length; PL/ML, premolar row and molar row length ratio; H, mandibular height under $M/_2$.

distal one. $P/_1$ shorter than other three premolars. $P/_1$ monoradiculate or, in equivalent frequency, with two fused roots (Tome's root). No diastema between premolars except in some specimens with monoradiculate and small $P/_1$. These show a very short space between $P/_1$ and $P/_2$. $P/_4$ cusp adorned with two distal crests: a strong and straight vestibular one and a less marked and lingually curved one (Fig. 2A). An enlarged distal cingulum on premolars which increases from $P/_2$ to $P/_4$.

Tetracuspidate and rectangular lower molars. Increase in size from $M/_1$ to $M/_3$. Crescentic protoconid and metaconid. Mesial junction between cristid from entoconid and prehypocristid (Fig. 2D). No third cristid from hypoconid. Transverse longitudinal valley between these cusps distally open. Mesial part of prehypocristid invades buccolingual transverse valley, forming a hook. No entoconulid on $M/_3$ but a large loop-like hypoconulid.

Cranium. A complete cranium from La Milloque has been described and figured by Brunet (1968).

Upper dentition. Upper incisors buccolingually compressed. Hypsodont upper canines markedly sexually dimorphic: very well developed in male and short in female. Upper canines transversally compressed, similar to those of extant Moschidae (blade-like) (Fig. 2G–H) but with a triangular cross-section marked by a lingual crest, unlike in contemporaneous pecoran where this crest is vestibular (Jehenne 1985). Pulpal cavity not centred in canine but vestibularly situated so that it is generally opened on vestibular side of tooth. No contact with antagonist lower teeth, but an external wear facet on canine possibly due to ecological habits (Brunet 1968).

Brachyodont and pentacuspidate upper molars, quadrangular in shape. Pronounced selenodonty compared with other members of Anthracotheriinae subfamily. Buccolingual transverse valley interrupted by a fusion between postparacrista, postprotocrista and premetacrista. Parastyle and mesostyle developed and metastyle reduced (Fig. 2E). Two crests from each lingual cusp. Postprotocrista buccolingually orientated. Few specimens with a third crest from metaconule that joins cingulum lingually. Lingual cingulum present. Mesial accessory cusp on cingulum absent or, in rare specimens, weakly developed.

Discussion. The finding of a well-preserved cranium from La Milloque led Brunet (1968) to synonymize all known species of *Microbunodon* (*M. minimum*, *M. minus*, *M. sandbegeri*, *M. breviceps* and *M. laharpei*). With material from La Milloque, he showed that the difference in upper canine development is due to sexual dimorphism and not to interspecific variations (*contra* Hünermann 1967). As a result, he recognized only one species with large size variability, for which he kept the name *M. minimum*. However, the holotype of *M. minus* figured by Cuvier (1822) as an $M/_3$ is actually a $dP/_4$. Indeed, the cast of the piece (1876–7) housed at the MNHN shows a

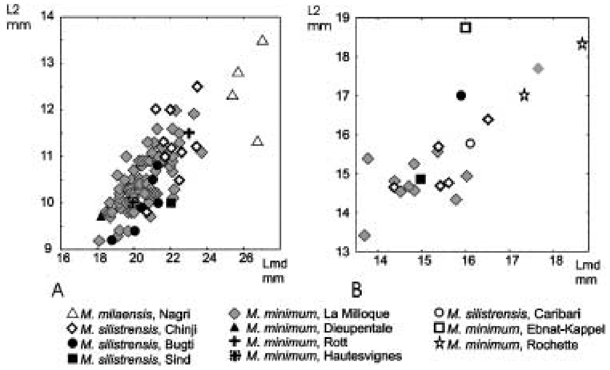

Fig. 4 A, B. Bivariate scatterplots of mesiodistal length (Lmd) on vestibulolingual length (L2). —A. $M/_3$. —B. $M^3/$ of *Microbunodon minimum* (from La Milloque, Dieupentale, Rott, Hautesvignes, Ebnat-Kappel and Rochette), *Microbunodon silistrensis* (from Chinji Formation, Bugti Hills, Lower Manchar near Sind and Garo Hills) and *Microbunodon milaensis* sp. n. (from Nagri Formation).

transversal narrowing of the mesial part of the tooth, a strong distal cingulum and a lingual anteroconid mesially positioned in comparison with the buccal anteroconid. Moreover, the morphology of this deciduous tooth is very close to a mandible of a young specimen of *A. alsaticum* Cuvier, 1822, from Lobsann. They both share the presence of a hypolophid, a postentocristid that joins the posthypocristid and not crescentic buccal cusps. These characters exclude *A. minus* from the genus *Microbunodon*.

The new material from La Milloque allows us to observe the size variability of *M. minimum*. It appears that $M/_3$ (Fig. 4A) of *M. breviceps* (from Rott) are included in the *M. minimum* size variation. Likewise, $M^3/$ (Fig. 4B) of *M. laharpei* (from Rochette) corresponds to large specimens of *M. minimum* from La Milloque. *Microbunodon sandbergeri* is a size intermediate between *M. minimum* and *M. laharpei* and is also included within the *M. minimum* size variation. So, size distribution, which was the main argument that supports these species, is not relevant. Therefore, we agree with Brunet (1968) in synonymizing the European *Microbunodon* species (except *A. minus*) and considering *M. minimum* to be characterized by large size variation in its molars and a sexually dimorphic canine.

Microbunodon silistrensis *(Pentland, 1828)*

Synonymy list

vp*	1828	*Anthracotherium silistrense* Pentland, pp. 393–394.
vp	1848	*Choeromeryx silistrense* (PENTLAND), Pomel, p. 687.
vp	1848	*Anthracotherium silistrense* PENTLAND, Blainville, p. 142.
v	1868	*Anthracotherium silistrense* PENTLAND, Falconer, p. 508, fig. 23.
vp	1877a	*Choeromeryx silistrense* (PENTLAND), Lydekker, p. 77.
	1877a	*Anthracotherium punjabiense* sp. n. Lydekker, pp. 78–79.
	1877b	*Rhagatherium sindiense* sp. n. Lydekker, p. 225.
	1878	*Anthracotherium silistrense* LYDEKKER, Lydekker, p. 77.
	1883	*Anthracotherium silistrense* PENTLAND, Lydekker, pp. 149–150, plate 23, fig. 10 and 12, plate 24, fig. 1.
	1885	*Anthracotherium silistrense* PENTLAND, Lydekker, p. 243.
	1908	*Anthracotherium mus* sp. n. Pilgrim, p. 150.
	1908	*Anthracotherium silistrense* PENTLAND, Pilgrim, p. 161.
	1910	*A.* (*Microselenodon*) *mus* (PILGRIM), Pilgrim, p. 201.
	1910	*A.* (*Microselenodon*) *silistrense* (PENTLAND), Pilgrim, p. 201.
	1912	*Microselenodon silistrensis* (PENTLAND), Pilgrim, plate 14, fig. 2.
	1912	*Microselenodon mus* (PILGRIM), Pilgrim, pp. 46–48, plate 14, fig. 3.
	1913	*Microbunodon mus* (PILGRIM), Pilgrim, p. 317.
	1913	*Microbunodon silistrense* (PENTLAND), Pilgrim.
	1917	*Microbunodon* cf. *silistrense* (PENTLAND), Pilgrim.
v	1924	'*Anthracotherium*' *silistrense* PENTLAND, Cooper, pp. 18–20, figs 15, 16.
v	1924	*Anthracotherium exiguum* sp. n. Cooper, p. 21, fig. 18.
	1929	'*Anthracotherium*' *silistrense* PENTLAND, Matthew, p. 463.
v	1935	*Anthracotherium punjabiense* LYDEKKER, Colbert, pp. 267–272, fig. 120.
v	1976	*Anthracotherium punjabiense* LYDEKKER, Cabard, pp. 119–120.
v	1976	*Anthracotherium mus* PILGRIM, Cabard, p. 120.
v	1984	'*Anthracotherium*' *punjabiense* LYDEKKER, Raza *et al.* pp. 30–32.
	1984	*Anthracotherium punjabiense* LYDEKKER, Raza and Meyer, p. 51.
	1984	*Anthracotherium exiguum* COOPER, Raza and Meyer, p. 51.
	1984	*Anthracotherium silistrense* PENTLAND, Raza and Meyer, p. 51.
v	1987	*Anthracotherium silistrense* PENTLAND, Pickford, pp. 313–316.
v	*1987*	*Anthracotherium silistrense* PENTLAND, Pickford and Rogers, p. 645.

Lectotype. Right $M^3/$, 19041, housed at NHM (figured by Pentland 1828: plate 24, figs 4, 5).

Etymology. The ending of *A. silistrense* must change when placed into *Microbunodon*. Indeed, the former genus is neuter, whereas the latter genus is masculine. Thus, we adopt the combination *M. silistrensis*.

Type locality. India, northeast Bengal, Garo Hills, Caribari.

Other localities. Pakistan, Potwar Plateau, several localities found by the H-GSP in the Chinji Formation (noted loc. y000) and others near Hasnot, Kanatti and Chinji villages. Pakistan, Sind, Bhagothoro area, localities S2, S13 and S14. Pakistan, Bugti Hills, localities of Khumbi and Chur Lando. India, Kashmir, Ramnagar.

Age. Late early Miocene–middle Miocene (last occurrence at 11.5 Ma).

New material. Right $P/_2$ (Y7421, loc. y750), right $M/_3$ (Y13294, loc. y298), frg. Right $M/_2$ (Y18928, loc. y496), right $P^3/$–$P^4/$ (Y19831, loc. y495), symphysis (Y20446, loc. y634), left $P/_4$ (Y20500, loc. y496), left $M/_2$–$M/_3$ (Y21063, loc. y494), left $M/_1$–$M/_3$ (Y21078, loc. y855), left $M^2/$–$M^3/$ (Y24297, loc. y496), left $M/_3$ (Y26382, loc. y496), left $P/_1$ (Y27697, loc. y778), right $P^4/$ (Y27895, loc. y731), subcomplete mandible with left $I/_1$–$I/_2$, C–$M/_3$ and right $I/_2$, C, $P/_2$, $P/_4$, $M/_2$–$M/_3$ (Y28194, loc. y705), frg. left $M/_2$ (Y30507, loc. y750), right $P^3/$–$M^1/$(Y30698, loc. y750), right mandible with $M/_3$ (Y31564, loc. y776), right $P/_1$ (Y31838, loc. y784), frg. left $M/_1$ (Y31990, loc. y695), left $M/_3$ (Y41301, loc. y738), right lower canine (Y41524, loc. y841), right $M/_2$–$M/_3$ (Y42274, loc. y853), left $P/_4$–$M/_1$ (Y45725, loc. y496), symphysis (Y45833, loc. y494) right $P/_4$ (Y47161, loc. y750), all part of the GSP collections (Fig. 5, Table 3). Right $M^3/$ (YPM20098, loc. unknown) from the Yale Peabody Museum collection.

Other material. Fragmentary M (S-3, Sind), left $M/_3$ (S-15, Sind), fragmentary right $M^2/$ (S-17, Sind), fragmentary right $M/_3$ (S-80, Sind), right $M/_2$ (S-84, Sind), left $dP^4/$ (S-99, Sind), fragmentary left $M/_3$ (S-329, Sind), fragmentary right $M/_1$ (S-355, Sind), right $M^3/$ (S-375, Sind), right $M/_1$ (S-377, Sind), right $P/_3$ (S-378, Sind), right $M^1/$ (S-379, Sind) all part of the GSP collections (see Raza *et al.* 1984). Right $M/_1$-$M/_3$ (M11059, Khumbi; see Pilgrim 1913), left $M/_2$–$M/_3$ (M12704, Chur Lando), right $M/_2$–$M/_3$ (M12705, Chur Lando), right $M/_2$–$M/_3$ (M12706, Chur Lando), left $M/_2$–$M/_3$ (M12708, Chur Lando), left $M^3/$ (M12709, Chinji), right $M^1/$–$M^3/$ (M12710, Chur Lando) at NHM. Right $M/_2$–$M/_3$ (B104, Hasnot) at the Geological Survey of India. Mandible with right $P/_1$, $P/_3$–$M/_3$ and left $P/_1$ (AM19444, near Chinji Bungalow), right $M^3/$ (AM94620, Kanatti), right $M/_1$–$M/_2$ (AM94621, Kanatti), right $M^3/$ (AM94625, Ramnagar) at AMNH.

Emended diagnosis. Anthracotheriinae close to *M. minimum.* Premolar row longer than molar row. Geniohyoideus attach keeled and extended anteriorly in ventral view. Small parastyle. Symphysis ventral edge crested along entire length.

Microbunodon minimum differs from *M. silistrensis* in equivalent length of premolar row relative to molar rows, in shorter absolute premolar row length, symphysis ventral edge being less crested with posterior flattening, its shorter and wider symphysis, its two large, well-marked genial fossae, its less transversally compressed mandible at level of C–$P/_1$ diastema, and its strong parastyle.

Description

Mandible. Long and narrow symphysis (Fig. 5A–C). Posterior side of symphysis at anterior $P/_2$ level. Crested and salient ventral edge of symphysis (Fig. 5D) with a prominent ventral development of geniohyoideus and digastricus muscle insertions (Fig. 3B). Anterior position of these muscular attaches forms keel. Two reduced genial fossae without marked separation between them. Angle between molar row and anterior edge of symphysis equal to 33°.

Lower dentition. Mesiodistally enlarged and buccolingually compressed $I/_1$ and $I/_2$. Reduced lower canine, with curved crown. Only a mesial wear facet present corresponding to contact with $I^3/$. No distal wear facet with upper canine.

Triangular outline of lower premolars. Premolars higher crowned than molars. A diastema between C and $P/_1$ (12 mm) and very short diastema between $P/_1$ and $P/_2$ (4 mm). Smaller $P/_1$ than other three premolars with two fused roots (Tome's root) on only known $P/_1$ (Y28194). Buccolingually compressed $P/_2$ and $P/_3$. $P/_4$ cusp adorned with two distal crests: a strong and straight one and a less marked and lingually curved one. Strong enlarged distal cingulum on premolars. Premolar row longer than molar row (Table 2).

Tetracuspidate and rectangular lower molars. Increase in size from $M/_1$ to $M/_3$. Crescentic protoconid and metaconid. Mesial junction between pre-entocristid and prehypocristid. No third cristid from hypoconid. Distally opened transverse longitudinal valley between these cusps. Mesial part of prehypocristid hooked between metaconid and entoconid (Fig. 5F). No entoconulid on $M/_3$ but a large loop-like hypoconulid.

Upper dentition. Bicuspidate $P^4/$. Two mesiodistally orientated crista on buccal cusp. No style on these crista. Concave mesial side of tooth and convex distal one. Unworn crown of $P^3/$ higher than $P^4/$. Transversally compressed $P^3/$with a thin distal edge. No accessory cusp on lingual border of this tooth.

Brachyodont and pentacuspidate upper molars (Fig. 5E). Pronounced selenodonty compared with other members of

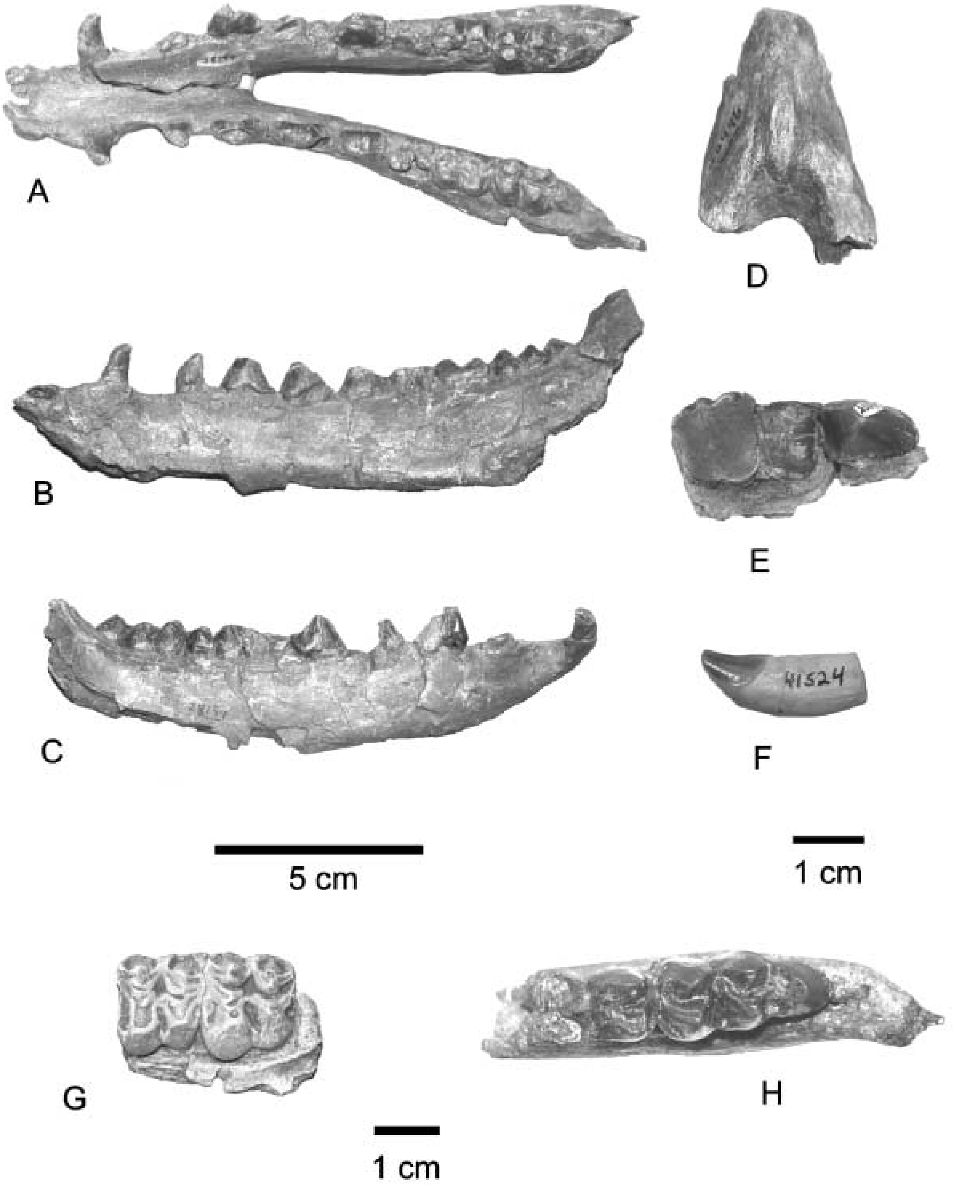

Fig. 5 A–H. *Microbunodon silistrensis* (Y28194) subcomplete mandible with left $I/_{1-2}$, C–$M/_3$ and right $I/_2$, C, $P/_2$, $P/_4$, $M/_2$–$M/_3$. —A. Occlusal view. —B,C. Labial views. —D. *Microbunodon silistrensis* (Y20446) symphysis in ventral view. —E. *Microbunodon silistrensis* (Y30698) right $P^3/$–$M^1/$ in occlusal view. —F. *Microbunodon silistrensis* (Y41524) right lower canine in lingual view. —G. *Microbunodon silistrensis* (Y24297) left $M^2/$–$M^3/$ in occlusal view. —H. *Microbunodon silistrensis* (Y21063) left $M/_3$ in occlusal view.

Anthracotheriinae subfamily. Buccolingual width of molars greater mesially than distally. Buccolingual transverse valley interrupted by fusion between postparacrista, postprotocrista and premetacrista. Small parastyle and no metastyle. Mesostyle poorly developed. Small occlusal surface occupied by buccal cusps and styles, whereas lingual cusps (protocone and metaconule) represent a large surface. Only two crests from each lingual cusp. Postprotocrista buccolingually orientated. No lingual cingulum. The accessory cusp on the molar mesial cingulum does not exist.

Discussion. Pentland (1828) created the species *A. silistrense* from Garo Hills, Bengal, India, on two specimens: a $M^3/$ (19041) and a maxillary fragment with $dP^3/$–$dP^4/$ (19040) housed at NHM. Pentland's (1828) description deals with the adult specimen, but the author does not clearly designate a

Table 3 Molar measurements of *Microbunodon silistrensis* and *M. milaensis* sp. n. in mm.

			Lmd	L1	L2				Lmd	L1	L2
Microbunodon silistrense											
Chur Lando Quarry	M12710	$M^1/$	11.5	13	12.6	Chinji	Y28194	$P/_1$	7.3	4.3	
		$M^2/$	15	15.5	15.7			$P/_2$	14.8	5.3	
		$M^3/$	15.9	18	17			$P/_3$	15	?	
	M12706	$M/_2$	13	7.8	8.9			$P/_4$	13.4	7.7	
		$M/_3$	20.4	9	9.9			$M/_1$	11.6		
	M12708	$M/_2$	12.9	8.1	9			$M/_2$	14.4	?	10.3
		$M/_3$	21	10	10.5			$M/_3$	21.7	11.8	11
	M12705	$M/_2$	13	9.2	8.9		Y30507	$M/_1$	13.5	7.8	8.3
		$M/_3$	20	9.4	9.4		Y13294	$M/_3$	22.5	10.8	10.5
	M12704	$M/_2$	12.3	7.9	8		Y41301	$M/_3$	20.7	10.5	9.8
		$M/_3$	18.8	9.3	9.2		Y21063	$M/_2$	?	?	9.7
Khumbi Quarry	M11059	$M/_1$	9.8	7.2	7.2			$M/_3$	22.6	11.2	11.1
		$M/_2$	12.8	8.2	9.1		Y21078	$M/_2$	12.6	8	8.9
		$M/_3$	21.3	9.8	10.8			$M/_3$	21.3	9.5	10
Bugti Hills	M12709	$M^3/$	16.5	17	16.4		Y24297	$M^2/$	13.8	15.4	13.9
Siwalik Hills	AM19444	$P/_1$	8.8	4.2				$M^3/$	14.4	16.6	14.7
		$P/_3$	15.2	8			Y20098	$M^3/$	15.4	16.7	15.7
		$P/_4$	15.2	9.2			Y31564	$M/_3$	22	10.7	11.2
		$M/_1$	14.9	11.1	8.7		Y30698	$P^3/$	13.4	8.6	
		$M/_2$	16.4	12.0	12.4			$P^4/$	11.3	9	
		$M/_3$	23.4	13.6	12.6			$M^1/$	12.5	13	11.9
	AM94620	$M^3/$	15.4	15.7	14.9		Y7421	$P/_2$	12.5	6.2	
	AM94621	$M/_1$	12.8	8.7	8.9		Y27895	$P^4/$	10.6	11	
		$M/_2$	16	11	10.7		Y27697	$P/_1$	12	4.7	
	AM94625	$M^3/$	15.5	15.7	14.9		Y42274	$M/_2$	14.3	7.5	8
	19041	$M^3/$	16.1	18.8	15.8			$M/_3$	21.6	8.5	?
	B104	$M/_2$	15.2	?	10.6		Y19831	$P^3/$	15	9.5	
		$M/_3$	23.4	?	11.2			$P^4/$	14	11	
Lower Manchar	S-377	$M/_1$	14.1	9.2	9.1		Y26382	$M/_3$	21	11	12
	S-15	$M/_3$	22	9.3	10		Y45725	$P/_4$	13	7.8	
	S-84	$M/_2$	16.4	10.6	11.5			$M/_1$	10	7	7
	S-329	$M/_3$	?	9.4	10.6		Y31838	$P/_1$	7.4	4.4	
	S-80	$M/_3$	?	?	10.1		Y47161	$P/_4$	14	8	
	S-375	$M^3/$	15	16	14.9						
	S-174	$M/_2$	16.6	10.5	12						
Microbunodon milaensis sp. n.											
Nagri	Y16612	$M/_1$	15.2	9.4	9.8	Unknown	M12707	$M/_3$	25.4	13	12.3
	Y10999	$P/_2$	14.4	7			M19442	$M/_3$	27	13	13.5
		$P/_3$	15	8							
		$M/_2$	15.8	10.7	11.6						
		$M/_3$	25.7	12.6	12.8						
	Y11886	$M/_2$	18.0	12.2	12.6						
	Y12448	$M/_2$	18.3	9.8	11.0						
		$M/_3$	26.7	11.0	11.3						
	Y5174	$M/_2$	17.0	10.9	11.8						
	Y11797	$P/_4$	15.7	9							
	Y9799	$P^3/$	17.4	10							
	Y9795	$P/_2$	13	7							

Lmd, mesiodistal length; L1, buccolingual length between protocone (protoconid) and paracone (metaconid); L2, buccolingual length between metacone (hypoconid) and metaconule (entoconid).

holotype. The deciduous teeth, which belong to the syntype made by Pentland, differ dramatically from the $M^3/$ by their high degree of selenodonty and the strong development of the styles, particularly the loop-like structure of the mesostyle fully invaded by the transverse valley. These are Bothriodontinae features (*sensu* Kron & Manning 1998), whereas the $M^3/$ is characteristic of an Anthracotheriinae (the transverse valley does not invaded the mesostyle which is cuspate in shape). Lydekker (1878) separated the two specimens, clearly designating a lectotype for *Choeromeryx silistrensis* (19040) and for *A. silistrense* (19041). Thus, two species were established based on the syntype published by Pentland, but the two had the same species name, which created great confusion in the following publications. We accept the proposition of Lydekker in considering 19041 as the lectotype of *A. silistrense* and excluding 19040. The latter specimen corresponds to a juvenile of a Bothriodontinae that has been synonymized with *Sivameryx paleindicus* by Pickford (1987).

Pentland (1828) did not describe the lower teeth of *A. silistrense*. This led Lydekker (1877) to attribute a mandibular fragment with M/$_2$–M/$_3$ (GSI no. B104) from the Siwaliks to a new species, *A. punjabiense* Lydekker, 1877. In Pakistan and India, all the localities that provided both taxa show an association of *A. silistrense* upper molars and *A. punjabiense* lower molars. These specimens have congruent occlusal patterns. The synonymy between the two species was accepted by Lydekker (1878) and Colbert (1935) who retained the name *A. punjabiense*. Referring to the taxonomical code of nomenclature, the valid species name is the first published. So *A. punjabiense* must be considered as a junior synonym.

The generic attribution of *A. silistrense* has been discussed since Pomel (1848). Pilgrim (1910, 1912, 1913) noted affinities between the specimen from the Garo Hills and the genera *Microbunodon* and *Microselenodon*. The lack of fossil remains and the confusion over the two generic definitions, led authors to reject this proposition (Forster-Cooper 1924; Matthew 1929; Colbert 1935; Cabard 1976; Raza *et al*. 1984; Pickford 1987). The new material from the Potwar Plateau permits attribution with certainty of *A. silistrense* to the genus *Microbunodon*. Indeed, the specimens from Pakistan present very reduced P/$_1$–P/$_2$ diastema, more selenodont molars than in other Anthracotheriinae, a pre-entocristid which joins the prehypocristid so that the longitudinal valley of the second lobe is distally open, a fused symphysis whose ventral edge is crested, a small lower canine with a mesial wear facet, no accessory cusp on the mesial cingulum of the upper molar, only two crista on the protocone (rarely three but not well marked). These characters exclude the species from the genus *Anthracotherium* and place it in *Microbunodon*.

Biometrical comparisons based on M/$_3$, which are the most common remains, cannot discriminate between specimens of *M. minimum* from localities of La Milloque, Dieupentale, Rott and Hautesvignes and specimens of *M. silistrensis* from the Chinji Formation, the Lower Manchar Formation and the Bugti Hills (Fig. 4A). However, they clearly differ by their premolar row length. *Microbunodon silistrensis* is larger with a proportionally smaller M/$_3$ (Table 2). Other differences between these species are seen in the symphysis. The *M. minimum* symphysis reaches the posterior edge of P/$_2$, whereas it only reaches the anterior border of this tooth in *M. silistrense*. The ventral edge of the symphysis in both species is crested, but *M. minimum* shows a flattened area at the posterior part of this surface so that it appears less salient. In *M. minimum* the muscular insertions in the genial area vary in position from an internal one to a ventral one. This variation is due to different muscular developments that could be related to sexual dimorphism. The three symphysis specimens of *M. silistrensis* do not show this variation but always show a very anterior and ventral position. Moreover, the genial fossae are less well developed in *M. silistrensis* and the crest separating these fossae is ventrally expanded in contrast to *M. minimum*. The styles on the upper molar (especially the parastyle and the mesostyle) are less developed in *M. silistrensis* than in *M. minimum*.

Specimens from the Bugti Hills housed at the NHM are included in *M. silistrense*, but are slightly smaller than the material from the Chinji and Lower Manchar Formations (Fig. 4). Their few preserved morphological features do not allow us to differentiate them from *M. silistrensis* or to identify them to this species with certainty. Therefore, we provisionally attribute these specimens to *M. silistrensis* on the basis of the poorly developed parastyle on the upper molar.

Microbunodon milaensis *sp. n.*

Synonymy list

v	1924	*Anthracotherium punjabiense* LYDEKKER, Cooper, p. 20, fig. 17.
?	1978	*Anthracotherium punjabiense* LYDEKKER, Vasishat *et al*., p. 133.
vp	1987	*Anthracotherium silistrense* PENTLAND, Pickford, pp. 313–316.
vp	*1987*	*Anthracotherium silistrense* PENTLAND, Pickford and Rogers, p. 645.

Holotype. Mandible with left P/$_3$–M/$_3$, Y10999, Dhok Mila loc. Y314, in the collections of the GSP (Fig. 6A–C, Tables 2, 3). This specimen was discovered by Martin Pickford.

Paratype. Left M/$_2$–M/$_3$, Y12448, Hasal, loc. y328, in the collections of the GSP (Fig. 6D, Table 3).

Etymology. The species name refers to the Dhok Mila village in Pakistan near the place where the holotype was found.

Type locality. Pakistan, Potwar Plateau, locality y314 in the Nagri Formation near Dhok Mila.

Other localities. All the material attributed to this species is from the Siwalik Hills, and the new material is restricted to several localities (noted loc. y000) in the Potwar Plateau area.

Age. Early late Miocene (10.3–9.2 Ma).

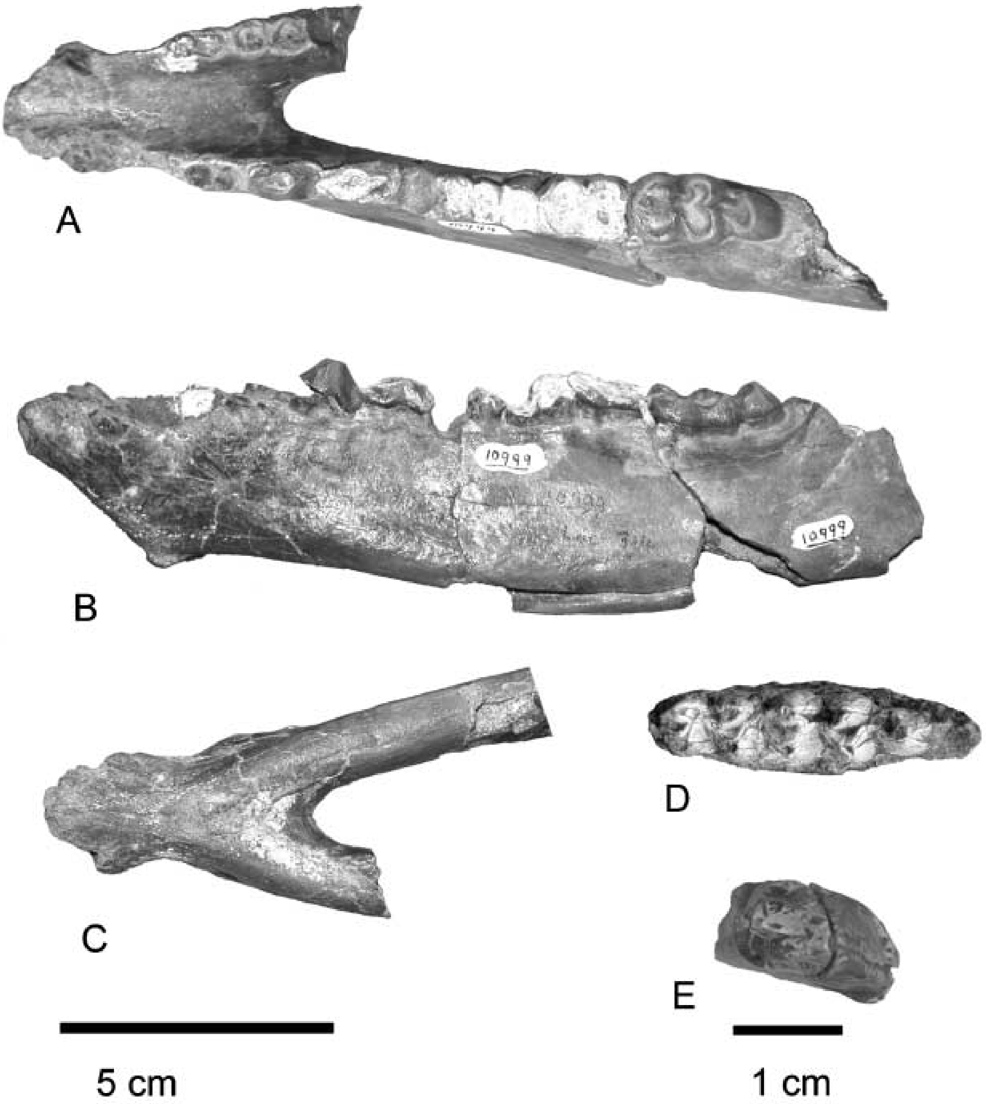

Fig. 6 A–E. *Microbunodon milaensis* sp. n. (Y10999 type) fragmentary mandible with left P/$_3$–M/$_3$. —A. Occlusal view. —B. Labial view. —C. Ventral view. —D. *Microbunodon milaensis* sp. n. (Y12448 paratype) left *M*/$_2$–*M*/$_3$ in occlusal view. —E. *Microbunodon milaensis* sp. n. (Y11797) left P/$_4$ in occlusal view.

New material. Left *M*/$_2$ (Y5174, loc. y211), left *M*/$_3$ (Y9791, loc. y269), left P/$_2$ (Y9795, loc. y269), right P^3/ (Y9799, loc. y269), left *M*/$_2$ (Y11686, Choutriwali loc. y317), left P/$_4$ (Y11797, loc. y317), left *M*/$_2$–*M*/$_3$ (Y12448, loc. y328), left *M*/$_1$ (Y16612, loc. y572), all part of the GSP collections (Table 3).

Other material. Right *M*/$_3$ (M19442), left *M*/$_3$ (M12707) at the NHM (Table 3).

Diagnosis. *M*/$_3$ larger than in *M. silistrensis* and *M. minimum*. Premolar and molar rows equivalent in length. No diastema between P/$_1$ and P/$_2$. Long symphysis. Clearly biradiculate P/$_1$. High angle between anterior edge of symphysis and cheek teeth row (around 46° in Y10999). Deep and robust mandibular corpus. Crested ventral edge of symphysis with a ventrally prominent genial crest and small genial fossae.

Microbunodon minimum and *M. silistrensis* differ from *M. milaensis* sp. n. by lower angle between anterior edge of symphysis and cheek teeth row (around 30–33.5° in *M. minimum* and 33° in *M. silistrense*), monoradiculate P/$_1$ or with a Tome's root, lower dorsoventral height of mandibular corpus and very reduced P/$_1$–P/$_2$ diastema.

In addition, *M. minimum* differs from *M. milaensis* sp. n. by a flattened posterior symphysis ventral edge, two very well-developed and marked genial fossae, absence of prominent ventral expansion of genial crest, and less transversally compressed mandible at level of C–P/$_1$.

Description

Mandible. Long and narrow fused symphysis (Fig. 6A–C) which reaches P/$_2$. Very salient and thin ventral edge of symphysis with strong prominent keel in its posterior part. Very anterior position of genial muscle attachment (Fig. 3C). Two genial fossae not very marked and fused. Angle between anterior edge of symphysis and molar row 46° (measurements made on Y10999). Transversally compressed mandible at level of C–P/$_1$ diastema. Deep mandibular corpus (Table 2).

Lower dentition. No diastema between three incisor alveolus. Small lower canine in contact with I/$_3$. C–P/$_1$ diastema long (15 mm). P/$_1$ with two well-developed roots. No diastema between P/$_1$ and P/$_2$. P/$_2$ and P/$_3$ high crowned: above molar level. Premolars morphologically identical to those of M. silistrensis but larger. Large, rectangular, tetracuspidate molars which increase in size from M/$_1$ to M/$_3$ (Fig. 5B,D). Junction between pre-entocristid and prehypocristid. Distally open longitudinal valley between hypoconid and entoconid. Loop-like hypoconulid on M/$_3$, centred on longitudinal axis of tooth and mesiodistally expanded. No entoconulid.

Upper dentition. P^3/ larger than those of *M. silistrense*. High crowned with sharp cusp. Two distal crests that form a narrow wear facet. Thin distal edge of tooth. Weak contact with P^4/.

Discussion. All the specimens attributed to *M. milaensis* sp. n. are from the Potwar Plateau, except two M/$_3$ housed at the NHM whose origins are unknown. Those two pieces are placed in the new species by reason of their large size. Indeed, *M. milaensis* sp. n. shows larger dimensions and differs markedly from *M. minimum* and *M. silistrense*. M/$_3$ measurements of this species are significantly different from the two others (Fig. 4A). It is the same for the mandibular depth, which is larger in *M. milaensis* sp. n. (Table 2) than in other species. The differences in corpus depth are not interpreted as a sexual dimorphism, because it has not been detected in the large sample of *M. minimum* from La Milloque where males and females are recognized. *Microbunodon milaensis* sp. n. has a prominent and thin ventral symphysis edge that ends in a strong genial spine expanded ventrally. It differs from the bent and wide ventral edge of the symphysis of *M. minimum*, which terminates with a genial flattening. *Microbunodon silistrensis* is intermediate between these two morphologies, but shows closer affinities with *M. milaensis* sp. n. by reason of the genial area. Indeed, the two genial fossae in *M. silistrensis* and *M. milaensis* sp. n. are small, ventrally positioned and without marked separation between them. In comparison, *M. minimum* shows enlarged genial fossae with a clear separating crest (Fig. 3C). In this species, the muscular attachments are on the internal, distal side of the symphysis or, in some specimens from the La Milloque sample, are on the ventral edge. This positional variation can be interpreted as a sexual dimorphism due to variable muscle developments. Nevertheless this species never shows prominent genial structures, but always a flattened area.

Microbunodon milaensis sp. n. also differs from the two other species by a more open angle between the molar row and the anterior edge of the symphysis of between 44 and 46°. It is around 33° in *M. silistrensis* and between 30 and 33.5° in *M. minimum*. In addition, the new species has a clearly biradiculate P/$_1$, whereas *M. silistrensis* and *M. minimum* have P/$_1$ with a single root or a Tome's root.

The phylogenetic relationships within the genus are difficult to establish. Indeed, the two Pakistani species share similar symphysis morphology, particularly the anterior position of the muscular insertions, the ventral expansion of the genial crista and the small genial fossae. This condition, which does not exist in *M. minimum*, could be interpreted as a synapomorphy of the Pakistani species. However, we need to determine the genial structure polarity in the Anthracotheriinae in order to test the primitive condition for this character in *M. minimum*. Moreover, *M. minimum* has blade-like upper canines and closed postorbital processes, which are derived morphological states in the Anthracotheriinae. The state of these two characters is not known in either Pakistani species because of the absence of cranial remains. It does not allow us to speculate on the phylogeny of this genus, which remains unresolved.

Phylogeny of the Anthracotheriinae

In order to test the robustness of the new *Microbunodon* definition and to determine the affinities between the Anthracotheriinae species, a cladistic analysis was conducted. A branch and bound algorithm was used with PAUP version 4.0 (Swofford 1998) on 18 dental and mandibular characters for nine species of Anthracotheriinae (Table 4). We chose *Siamotherium krabiense* Suteethorn *et al*., 1988 from the late Eocene of Thailand (Krabi basin) and Myanmar (Pondaung basin) to be the outgroup because it constitutes the most conservative known Anthracotheriidae (Suteethorn *et al*. 1988; Ducrocq *et al*. 2000). Other selected taxa corresponded to well-known species of Anthracotheriinae with well-preserved specimens. *Microbunodon milaensis* sp. n. was not included in the analysis because of the lack of cranial remains. In terms of this character matrix, *M. milaensis* sp. n. does not seem to be very distinct from the other *Microbunodon* species, as can be seen in Table 4. All characters were unordered and of equal weight.

Table 4 Matrix of characters used for the phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Siamotherium krabiense	0	0	0	0	0	0	?	0	?	0	0	0	0	0	0	0	0	?
Microbunodon minimum	0	0	0	2	0	1	1	0	1	0	1	1	1	1	1	0	1	1
Microbunodon milaensis sp. n.	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*?*	*0*	*1*	*1*	*1*	*1*	*1*	*0*	*1*	*?*
Microbunodon silistrense	0	0	0	1	0	1	?	0	1	0	1	1	1	1	1	0	1	1
Anthracotherium magnum	1	1	1	2	1	1	0	1	0	1	0	0	0	0	0	1	1	0
Anthracotherium monsvialense	1	1	1	2	1	1	0	1	0	1	0	0	0	0	0	1	1	0
Anthracotherium chaimanei	1	1	1	2	1	1	0	?	?	1	0	0	0	0	?	0	0	?
Anthracokeryx ulnifer	0	1	1	2	0	1	1	0	1	0	0	0	0	1	1	0	0	0
Anthracokeryx thailandicus	0	0	1	2	0	1	?	0	1	0	1	1	1	1	1	0	0	1
Anthracothema pangan	1	1	1	0	1	0	0	1	?	1	0	0	?	?	0	0	0	?

1, $P^3/$ without accessory lingual cusp (0), with accessory lingual cusp (1); 2, protocone on upper molars with two crests (0), a marked third crest (1); 3, metaconule on upper molars without a third crest (0), with a marked one (1); 4, parastyle of upper molar absent (0), weak (1), strong (2); 5, accessory cusp on upper molar mesial cingulum absent or very reduced (0), strongly developed (1); 6, centrocrista on upper molars rectilinear (0), V-shaped (1); 7, upper canine with circular cross-section (0), laterally compressed (1); 8, lower canine reduced and sloped backwards (0), strong and vertical (1); 9, wear facet on lower canine due to a C–C contact (0), a $I/_3$–C contact (1); 10, entoconulid on $M/_3$ absent (0), present (1); 11, hypoconid on lower molars with three cristids (0), with two cristids (1); 12, pre-entocristid on lower molars joins the hypoconid (0), joins the prehypocristid (1); 13, symphysal ventral edge of mandible flattened (0), pinched (1); 14, mandible transversally compressed behind lower canine, no (0), yes (1); 15, diastema C–$P/_1$ absent (0), present (1); 16, lateral mandibular apophysis absent (0), present (1); 17, mandibular symphysis not fused (0), fused (1); 18, lower incisors narrow (0), wide and buccolingually compressed (1).
Characters present two or three states quoted 0, 1 and 2. 0 corresponds to the outgroup state. The taxon in italic was not used for the cladistic analysis.

We obtained three equally parsimonious trees of 24 steps, which had low homoplastic rates (consistency index = 0.79, retention index = 0.87). The consensus tree (Fig. 7) discriminated two main Anthracotheriinae clades: one clade includes the genera *Anthracothema* Pilgrim, 1928 and *Anthracotherium*, and the other clade the genera *Anthracokeryx* Pilgrim & Cotter, 1916 and *Microbunodon*.

The *Anthracothema–Anthracotherium* clade is supported by the presence of accessory cusps on the $P^3/$ lingual cingulum (1) and on the upper molar mesial cingulum (5), by the presence of an entoconulid on the $M/_3$ (10), and by the lower canine morphology (8). The latter is strong, vertical, and has a posterior wear surface caused by contact with the upper canine. The younger European *Anthracotherium magnum* Cuvier, 1822 and *A. monsvialense* de Zigno 1888 form a monophyletic group separated from *Anthracothema pangan* Pilgrim, 1916 from the late Eocene of Myanmar and *Anthracotherium chaimanei*, Ducrocq, 1999, from the late Eocene of Thailand, by sharing a fused symphysis (17) and a lateral mandibular apophysis (16). The status of the genus *Anthracotherium* is not resolved on the cladogram because of the position of *Anthracothema pangan*. The latter lacks developed styles (4) and has a rectilinear centrocrista (6) (opposed to the V-shaped of *Anthracotherium*). These character states are primitive features according to Coombs & Coombs (1977) but are treated in the consensus tree as reversions. If we interpret these characters as convergent in the two main clades (*Anthracothema–Anthracotherium* and *Anthracokeryx–Microbunodon*), then *Anthracothema pangan* is the sister group of *Anthracotherium*, which thus becomes monophyletic. However, the characters that separate *Anthracothema* and *Anthracotherium* (4 and 6) show considerable interindividual variability and are progressive from *Anthracothema pangan*, through *A. chaimanei* to European *Anthracotherium*. They cannot be considered as generic distinctions. The presence of *Anthracothema pangan* in the *Anthracotherium* clade is congruent with Ducrocq (1999). This author discussed the validity of *Anthracothema*, emphasizing its great resemblance with *A. chaimanei* and *A. monsvialense*. He then suggested an evolutionary trend for these three taxa, *Anthracothema pangan* being ancestral and *A. monsvialense* the more evolved species. He also proposed attributing *Anthracothema pangan* to *Anthracotherium*. We accept Ducrocq's proposition because of the great variability of the style development and the absence of other derived characters for the genus *Anthracothema*. So *Anthracothema pangan* is reinterpreted as *Anthracotherium pangan*.

The genera *Anthracokeryx* and *Microbunodon* share the following apomorphies: transverse compression of the upper canine (which becomes blade-like in *M. minimum*) (7), mesial lower canine wear facet due to $I^3/$ contact (9), mandibular narrowing behind the lower canine (14), and the presence of a diastema between the canine and the first premolar (15).

The genus *Anthracokeryx* is paraphyletic. *Anthracokeryx thailandicus* Ducrocq, 1999 from the late Eocene of the Krabi basin, Thailand, is separated from *Anthracokeryx ulnifer* by four apomorphies shared with the genus *Microbunodon*. The *A. thailandicus–Microbunodon* clade is supported by the absence of the third transverse cristid of the hypoconid (11), a pre-entocristid that joins the prehypocristid and does not form a hypolophid (*sensu* Coombs & Coombs 1977) (12), the crested ventral edge of the symphysis (13), and the

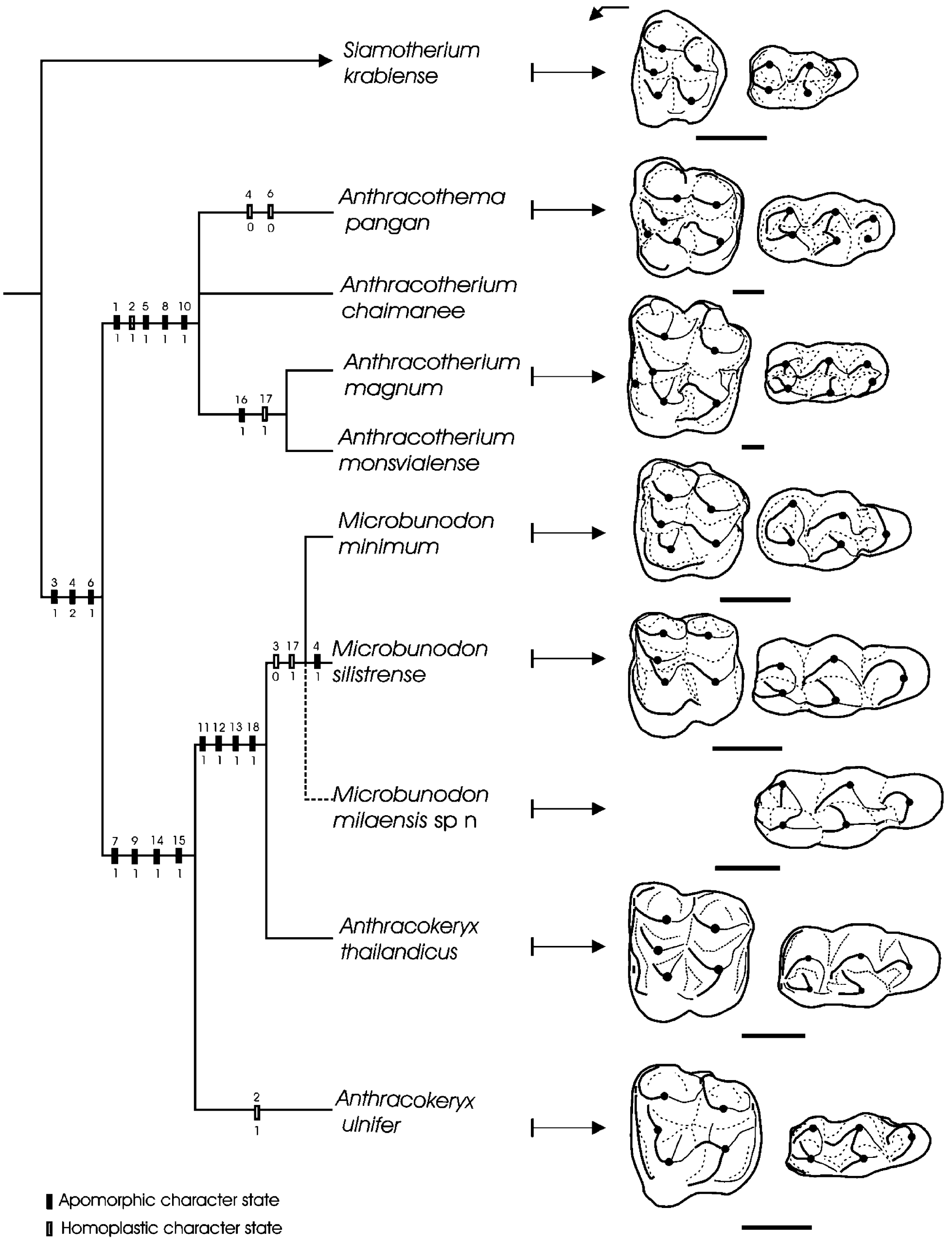

Fig. 7 Cladogram of 10 species of Anthracotheriinae (consistency index = 0.79; retention index = 0.87) obtained by heuristic analysis based on data compiled in Table 3.

buccolingually compressed and mesiodistally enlarged lower incisors (Ducrocq, pers. comm. for *A. thailandicus* lower incisor morphology) (18). *Anthracokeryx thailandicus* also shows the lack of a third protocrista (2). These character states do not fit with the emended diagnosis of *Anthracokeryx* by Colbert (1938). However, *A. thailandicus* has a long P/$_1$–P/$_2$ diastema (15) and an unfused symphysis (17), features that are also not congruent with the new definition of *Microbunodon*. *Anthracokeryx thailandicus* also possesses a very derived, transversely compressed and ventrally expanded symphysis, with a very deep mandibular corpus. Because of these apomorphic characters, *A. thailandicus* does not represent a primitive condition for the *Microbunodon* lineage. However, it is a very close sister taxon, which needs a new generic attribution. A third species, *Anthracokeryx gungkengensis* from the early Oligocene of the Gongkang Formation in Guanxi Province

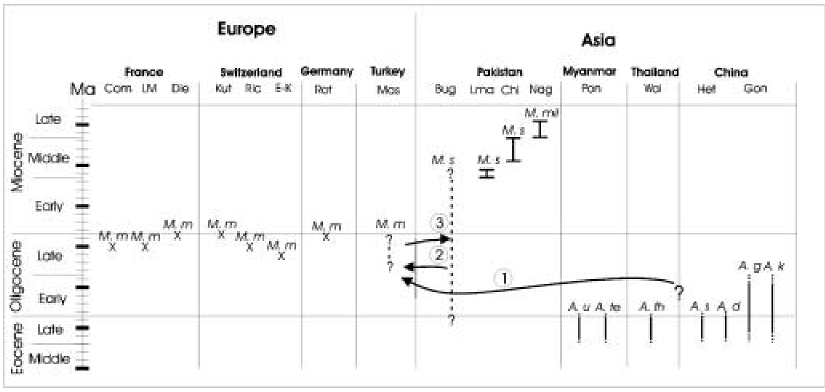

Fig. 8 Spatial and chronological distribution of *Microbunodon* and *Anthracokeryx* following Cabard (1976) and Ducrocq (1999). Com, Comberatière; LM, La Milloque; Die, Dieupentale; Kut, Kuttingen; Ric, Rickenbach; E-K, Ebnat-Kappel; Rot, Rott; Mas, Masatly; Bug, Chur Lando, Khumbi and Dera Bugti quarries; Lma, Lower Manchar Formation; Chi, Chinji Formation; Nag, Nagri Formation; Pon, Pondaung locality; Wai, Wai Lek and Bang Pu Dam (Krabi basin); Het, Heti Formation (Shansi Province); Gon, Gonkgang Formation (Guanxi Province). *M. m*, *Microbunodon minimum*; *M. s*, *Microbunodon silistrense*; *M. mil*, *Microbunodon milaensis* sp. n.; *A. u*, *Anthracokeryx ulnifer*; *A. te*, *Anthracokeryx tenuis*; *A. th*, *Anthracokeryx thailandicus*; *A. s*, *Anthracokeryx sinensis*; *A. d*, *Anthracokeryx dawsoni*; *A. g*, *Anthracokeryx gungkangensis*; *A. k*, *Anthracokeryx kwangsiensis*.

of China (Wang 1992), is poorly known, but it has a lower molar morphology, similar to that of *Microbunodon*. It also lacks a third metacristule on the upper molar. These characters link *A. gungkengensis* to *Microbunodon*, but because the symphysis morphology is not known, we presently cannot attribute it to that genus.

The Pakistani species described in this work are included in the monophyletic genus *Microbunodon*. Characters supporting the clade are the absence of a third metacristule (3) and a fused symphysis (17). The phylogenetic relationships between the three species of *Microbunodon* are not resolved by this analysis. The characters used for their discrimination were not coded because they are quantitative characters and/or are not observed on the other taxa. *Microbunodon milaensis* sp. n and *M. silistrensis* have identical genial structures that suggest close affinities, while the flattened posterior part of the symphysial ventral edge and the small dimensions of *M. minimum* could be interpreted as primitive conditions, but it still needs to be tested.

Palaeobiogeography

The new material from the Potwar Plateau allows us to redefine the geographical distribution of the *Microbunodon* lineage (including the *Anthracokeryx* species) and to propose a migration hypothesis (Fig. 8).

Anthracokeryx is well represented in the late Eocene from Myanmar with the species *A. ulnifer* and *A. tenuis* (Pilgrim 1928; Colbert 1938) and in the late Eocene from Thailand with the species *A. thailandicus* (Ducrocq 1994). *Anthracokeryx sinensis* and *A. dawsoni* are mentioned in the late Eocene from China in the Heti Formation from Shansi Province. The later representatives of the genus, *A. gungkangensis* and *A. kwangsiensis*, occur in the early Oligocene of the Gongkang Formation from Guanxi Province (Wang 1992). Most of these species were not used in the phylogenetic analysis because of the paucity of material. The genus is very specious and is restricted to Southeast Asia.

The earliest known *Microbunodon* is from Switzerland. It occurs in the late Oligocene of Ebnat-Kappel, MP 28 (Brunet & Vianey-Liaud 1987) (around 26 Ma), and is represented by the species *M. minimum*. Similar forms are present at Masatly in the Dardannel, Turkey, in the late Oligocene (Newton 1904), but the age estimate is still uncertain and the fossils are rare. *Microbunodon minimum* is also abundant in France, Germany, Austria, and Switzerland (Cabard 1976) from MP 28 to MP 30 (Fig. 8). Its last occurrence in the Küttingen, Rott and Dieupentale localities is correlated with MP 30 (around 23.5 Ma).

A few specimens housed at the NHM, collected at the end of the 19th and beginning of the 20th centuries in the Chur Lando and Kumbhi quarries from the Bugti Hills, are referred to *M. silistrense*. Those sites are included in the Chitarwata Formation from the Bugti Hills (Raza & Meyer 1984). A recent stratigraphical revision of this formation revealed the existence of early Miocene levels correlated with the Lower Siwalik and Oligocene levels (Welcomme *et al.* 2001). These authors note that each fossiliferous strata is synchronic. Nevertheless, the earlier collection may have mixed fossils of different origins. Therefore, we cannot conclude the age of the Bugti fossils and an Oligocene occurrence of *Microbunodon* in Asia cannot be excluded.

The first well-documented occurrence of *M. silistrensis* was in the S2, S13 and S14 localities from Sind, Pakistan. These sites belong to the basal Lower Manchar Formation near Baghotoro. They are dated between 15 and 16 Ma (Raza *et al*. 1984). *Microbunodon silistrensis* is also present in the Chinji Formation from Potwar Plateau. Specimens are estimated by magnetochronology at between 12.7 and 11.5 Ma (Johnson *et al*. 1985). This species thus has a 4.5 Myr range between 16 and 11.5 Ma. *Microbunodon milaensis* sp. n. is found in the Nagri Formation. Magnetochonological data indicate an age between 10.3 and 9.2 Ma (Johnson *et al*. 1985). Remains of a 'small *Anthracotherium*' from equivalent levels at Haritalyangar, India (Vasishat *et al*. 1978) may correspond to *M. milaensis* sp. n. This species is the last representative of the lineage.

The emergence of *Microbunodon* is not documented, as the earliest known *M. minimum* should be considered as an Asian immigrant into Europe. The genus is monospecific in Europe and has no known European ancestor. *Microbunodon minimum* could stem from an *Anthracokeryx* species morphologically close to *A. thailandicus* or *A. gungkangensis* (hypothesis 1 on Fig. 8). This scenario implies a European diversification of the genus and a migration from Europe to Asia at the late Oligocene (hypothesis 3 on Fig. 8). The second scenario corresponds to an Asian diversification of the genus during the early Oligocene. The Asian *Microbunodon* evolves to *M. silistrensis* and *M. milaensis* sp. n. and *M. minimum* corresponds to a migrant form (hypothesis 2 on Fig. 8), which disappears without descendant. The absence of *Microbunodon* remains in Asia during the late Oligocene suggests a third scenario with an Asian genus diversification, an Asian extinction of the genus, a migration towards Europe (hypothesis 2 on Fig. 8) and a new diversification of the genus from migrant from Europe (hypothesis 3 on Fig. 8). The first and third scenarios can be accepted on the basis that *M. silistrensis* and *M. milaensis* sp. n. possess as derived, upper canine morphology as in *M. minimum*. Up to now, no upper canine remains of these two species have been found, so we cannot support these scenarios. Thus, we cannot conclude whether *M. silistrensis* is an immigrant from Europe or the descendant of an unknown *Microbunodon* lineage in Asia during the late Oligocene. A better datation of the fossils discovered in the Bugti Hills could provide evidence for these palaeoscenarios.

Conclusions

The small Anthracotheriinae from the Miocene of Pakistan previously attributed to *Anthracotherium* are reinterpreted as belonging to *Microbunodon*. The genus is composed of three species: *M. minimum* from the late Oligocene of Europe (26–23.8 Ma), *M. silistrensis* from the middle Miocene of India and Pakistan (16–11.5 Ma) and *M. milaensis* sp. n. from the early late Miocene of Pakistan (10.2–9.3 Ma), the last occurrence of the genus. The description of the new material highlights the evolving trends within this genus, showing an increase in size and the development of a very derived symphysis. This genus is closely related to *Anthracokeryx*. This lineage occurs in the late Eocene of Southeast Asia, where it differentiates from the *Anthracotherium* group. The phylogeny presented in this work establishes that the Anthracotheriinae comprises two evolutionary trends: large bunodont forms (*Anthracotherium*) and small and more selenodont forms (*Anthracokeryx* and *Microbunodon*). This review of the genus *Microbunodon* brings out new data for palaeobiogeography. It implies palaeoscenarios for the place and time of the genus diversification and the subsequent migrations of *Microbunodon*. Questions such as the ambiguous state of the Bugti fossil and the morphology of the upper canine of Pakistani species must be answered in order to confirm one of these scenarios.

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