

NEW DRYOLESTOID MAMMALS FROM THE BASAL CRETACEOUS PURBECK LIMESTONE GROUP OF SOUTHERN ENGLAND

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ABSTRACT. The dryolestoid mammal *Dorsetodon haysomi* gen. et sp. nov. is described from the Purbeck Limestone Group (Lower Cretaceous) of southern England, on the basis of lower molars. *Dorsetodon* is assigned to the Paurodontidae, a family of Theria previously known only from North America. The distinction between Paurodontidae and Henkelotheriidae (from the Upper Jurassic of Portugal), although maintained for lack of solid contrary data, is argued to have been based on variable or subjective characters. A further small mammal, *Chunnelodon alopekodes* gen. et sp. nov., representing an undetermined cladotherian family, is also described from lower molar teeth. The non-procumbent paraconid on the lower molar places *Chunnelodon* as a sister-taxon to the Laurasian Dryolestoidea.

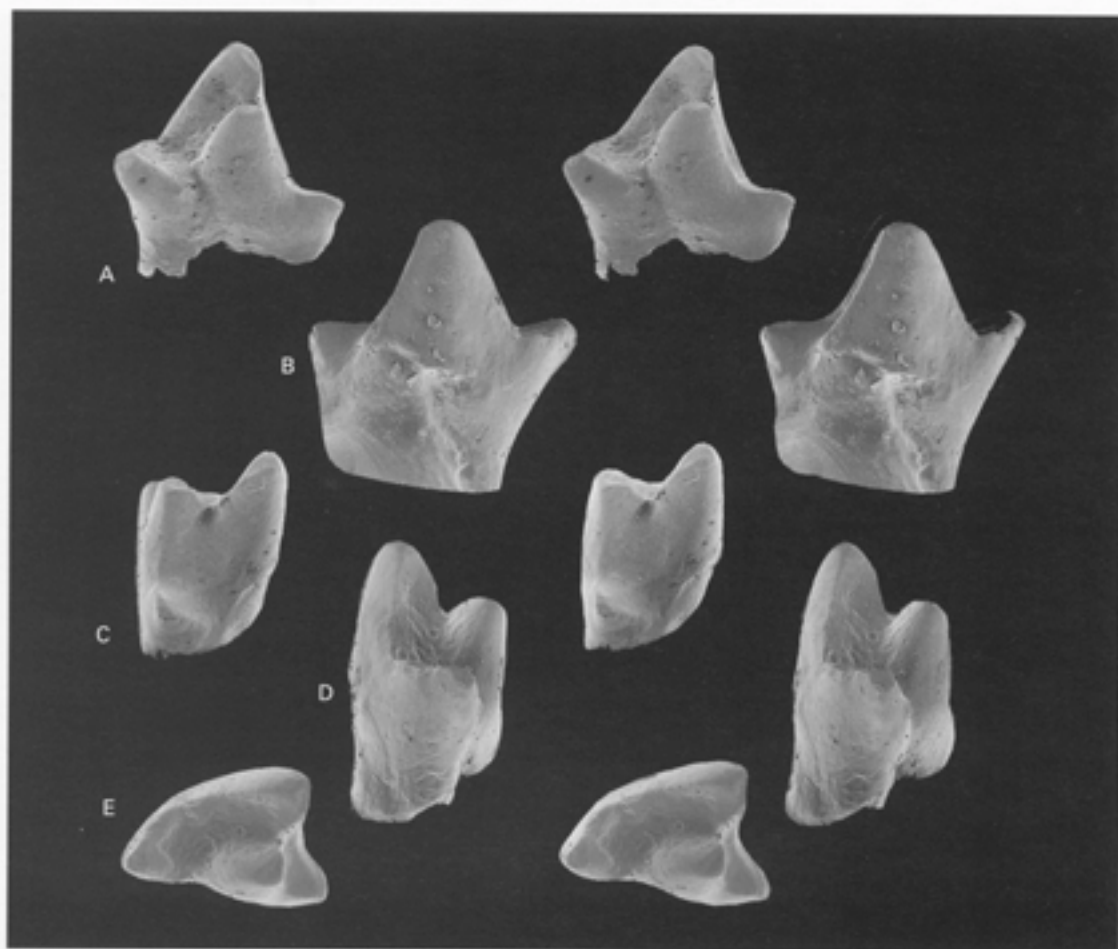
THE Purbeck Limestone Group has been known as a rich source of fossil vertebrates for approximately 150 years. An important new microvertebrate and dinosaur footprint site on the Isle of Purbeck at Sunnydown Farm near Langton Matravers continues to provide valuable new information on the coeval faunas within the Purbeck Limestone Group. New discoveries and increasing knowledge of the fauna, which includes fishes (Woodward 1916–19), amphibians (Ensom *et al.* 1994), reptiles (Benton and Spencer 1995) and mammals (Owen 1871; Simpson 1928; Kielan-Jaworowska and Ensom 1992, 1994; Sigogneau-Russell and Ensom 1994), in addition to vertebrate trace fossils (Ensom 1995*a*, 1995*b*) have led to the following statement by Howse and Milner (1995): 'the Purbeck fauna is becoming one of the richest mid-Mesozoic continental assemblages known'. The two new mammalian taxa described below further confirm this assessment.

LOCALITY AND STRATIGRAPHY

The new locality was first reported by Ensom (1987) and subsequently described in more detail by Kielan-Jaworowska and Ensom (1992). Two horizons were exploited. Both horizons lie within the Cherty Freshwater Member of the Purbeck Limestone Group (Clements 1993), which, along with much of the Purbeck Limestone Group, is increasingly considered to be of early Berriasian, Early Cretaceous, age (Allen and Wimbledon 1991) (this point has been discussed by Kielan-Jaworowska and Ensom 1994, and Sigogneau-Russell and Ensom 1994).

The mammal teeth described below have been picked from residues derived from samples of clay collected from the higher of the two horizons at the Sunnydown Farm Quarry sauropod footprint site (NGR SY 9822 7880), 5 km west of Swanage, and from its equivalent in Durlston Bay NGR (SZ 035 780) just south of Swanage, both in Dorset, southern England.

The upper horizon lies at the junction of a clay, locally termed the 'Sly', which immediately underlies the 'Cap' bed, 2.6 m below the base of the Cinder Member. This clay-limestone interface can be equated confidently with beds DB 102/103 in Durlston Bay (Clements 1993). The sedimentology and environmental setting of the upper horizon has been described by West (1988). Both horizons are thought to represent clays bordering shallow freshwater lakes.



TEXT-FIG. 1. *Dorsetodon haysoni* gen. et sp. nov.; holotype, DORCM GS 433, resin cast; lower right molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. SEM stereophotographs; $\times 45$.

Kielan-Jaworowska and Ensom (1992, 1994) described a significant number of the multituberculate mammals so far recovered from this horizon, and Sigogneau-Russell and Ensom (1994) recorded the only known example of a tribosphenic molar from the Purbeck Limestone Group, possibly the earliest so far recovered (this was from the lower horizon at Sunnydown Farm). Apart from the Multituberculata and Tribosphenida, all the main groups of mid Mesozoic mammals are represented amongst the teeth collected so far. These include Triconodonta, Docodonta, Symmetrodonta and Cladotheria. A general faunal list was prepared by Ensom *et al.* (1994).

MATERIALS AND METHODS

Sampling methods have been described in more detail in Kielan-Jaworowska and Ensom (1992). Approximately 3 tonnes of clay were collected from the site, in addition to smaller samples from

other locations. The clay samples have been sieved down to a mesh size of 0.3 mm. Residues are being picked down to and including the ratio retained by the 0.5 mm mesh.

The teeth described in this paper come from the following samples: DORCM GS 376, 377 and 378 from sample 40; DORCM GS 433 from sample 34, DORCM GS 438 from sample 68, DORCM GS 747 from sample 83, DORCM GS 501 and 502 from sample 85 and DORCM GS 625 from sample 98. These samples were all from the excavation at Sunnydown Farm Quarry, Langton Matravers, within an area of 60 m². The equivalent of the upper horizon at Durlston Bay yielded DORCM GS 313 and 315 (sample 01).

Abbreviations. DORCM, Dorset County Museum; L, length; W, width.

SYSTEMATIC PALAEOLOGY

Order DRYOLESTOIDEA Butler, 1939

Family PAURODONTIDAE Marsh, 1887

Genus DORSETODON gen. nov.

Derivation of name. Allusion to the geographical origin of the genus.

Type species. *D. haysomi* sp. nov.

Differential diagnosis (based only on type). Protoconid moderately high, less so than in *Paurodon* or *Archaeotrigon*; lingual face concave and anteriorly oriented. Paraconid forming a distinct, but not tubular, cusp, inclined lingually as well as anteriorly, narrower than the metaconid, which distinguishes it from that of other paurodons except *Archaeotrigon* and *Tathiodon*. Metaconid of moderate height. Posterior face of trigonid more strongly concave than in other paurodons. Talonid relatively long, especially more so than in *Paurodon* and *Araeodon*; sub-triangular as in *Araeodon*, low and medio-lingually situated without a well-defined cusp. Lower molars closest to *Araeodon* in labial 'convexity' (flatter in other genera, including *Henkelotherium*). Closest to *Tathiodon* for general proportions, but paraconid more inclined lingually and anteriorly; metaconid less stout; trigonid flatter; talonid less sharply triangular.

Differs from *Henkelotherium* by posterior trigonid face more concave, less compressed trigonid, para- and metaconid relatively more gracile, talonid less wide; but to be noted is the variation of the talonid along the dental series in this genus (as well as in *Foxraptor*): short, wide and triangular in most molars, it becomes semicircular at the rear of the jaw.

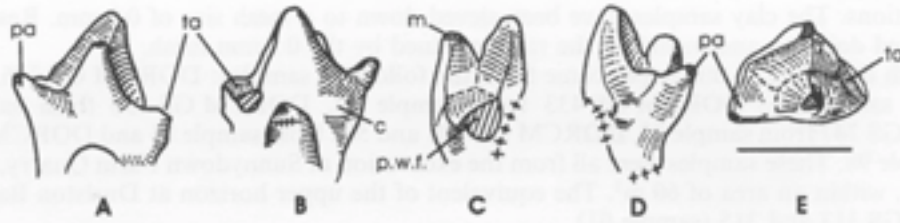
Dorsetodon haysomi sp. nov.

Text-figures 1-6

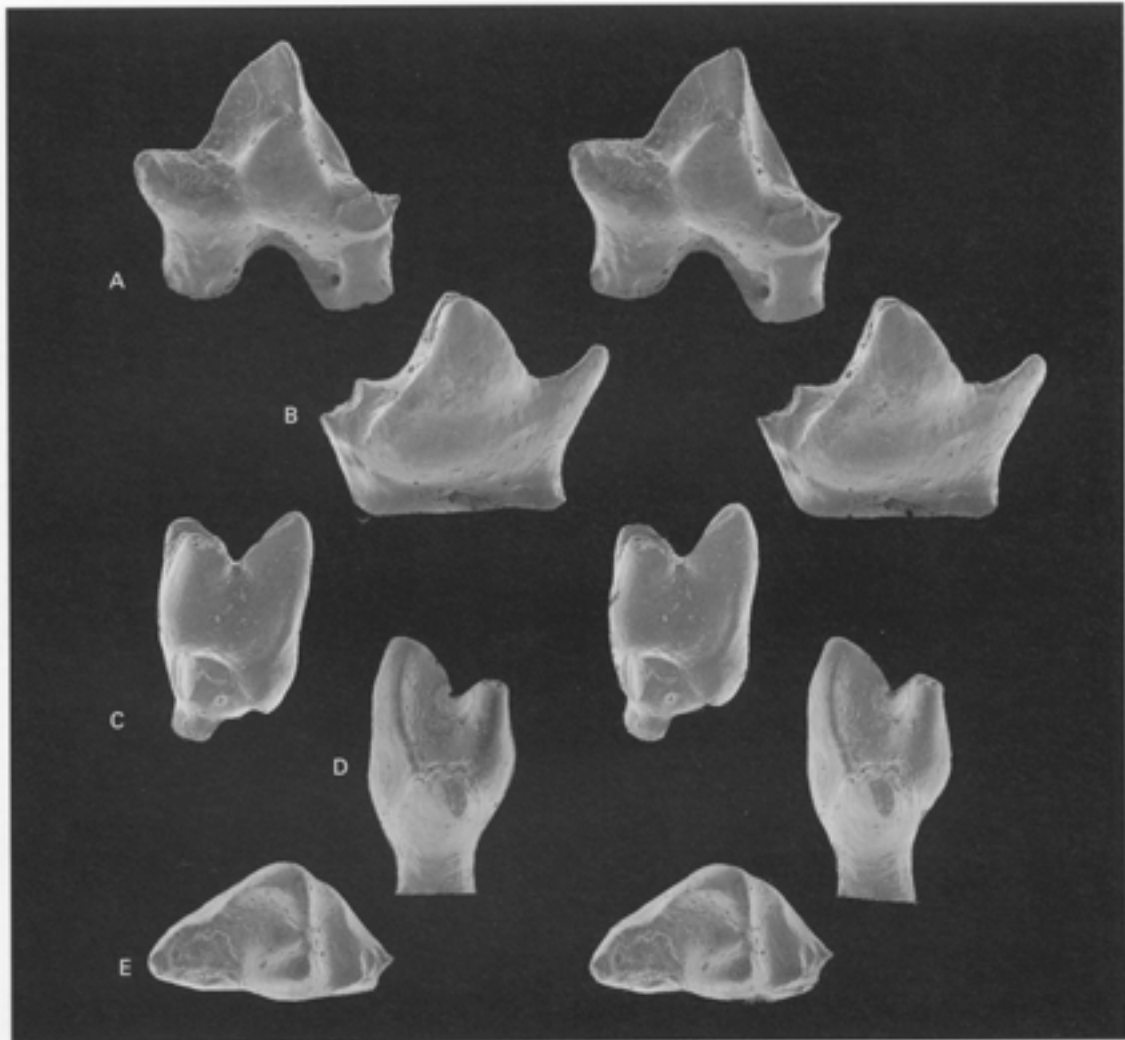
Derivation of name. In honour of W. T. Haysom, a quarry owner on the Isle of Purbeck, who drew the attention of the senior author to the Sunnydown site.

Holotype. DORCM GS 433, a right lower molar (Text-figs 1-2). L = 0.65 mm; W = 0.42 mm.

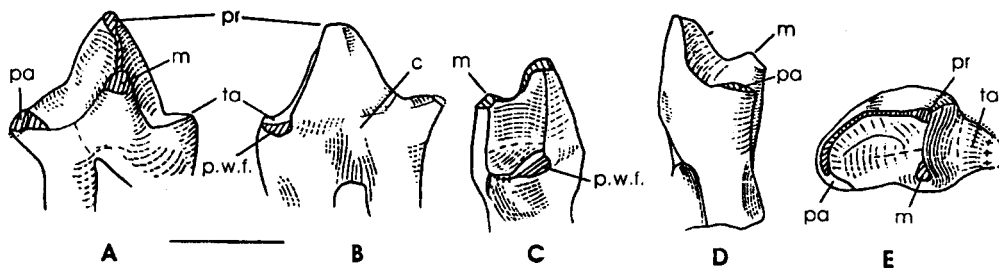
Attributed material. DORCM GS 376, a right lower molar (L = 0.72 mm; W = 0.41 mm) (Text-figs 3-4); DORCM GS 502, a right lower molar (L = 0.70 mm; W = 0.38) (Text-fig. 5); DORCM GS 438, a left lower molar (L as preserved = 0.76 mm; W = 0.43 mm) (Text-fig. 6); DORCM GS 501, a left lower molar (L = 0.70 mm; W = 0.42 mm); DORCM GS 625, a left lower molar (L = 0.72 mm; W = 0.50 mm); DORCM GS 747, a right lower molar (L = 0.82 mm; W = 0.41 mm).



TEXT-FIG. 2. *Dorsetodon haysomi* gen. et sp. nov.; holotype DORCM GS 433; lower right molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. Key: m, metaconid; pa, paraconid; pr, protoconid; p.w.f., posterior wear facet; ta, talonid. Hatching, wear; cross-hatching or crosses, broken areas or edges. Scale bar represents 0.5 mm.



TEXT-FIG. 3. *Dorsetodon haysomi* gen. et sp. nov.; DORCM GS 376, resin cast; lower right molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. SEM stereophotographs; $\times 45$.



TEXT-FIG. 4. *Dorsetodon haysomi* gen. et sp. nov.; DORCM GS 376.; lower right molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. Key as for Text-figure 2. Scale bar represents 0.5 mm.

Horizon and locality. Sunnydown Farm, Dorset, England; Cherty Freshwater Member, Lulworth Formation, Purbeck Limestone Group, basal Cretaceous (?Berriasian).

Diagnosis. As for genus, this being the only species.

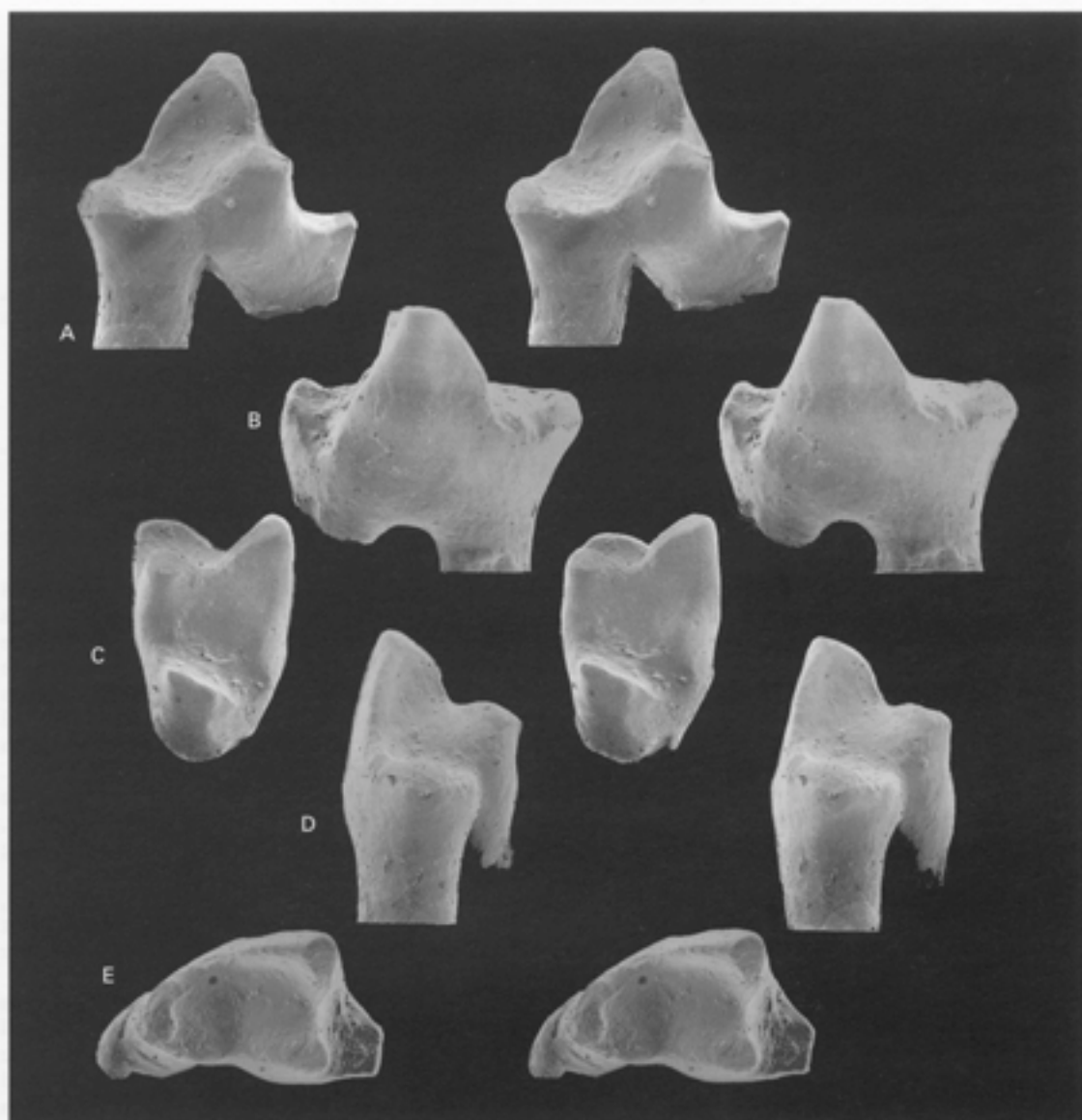
Description of type. In addition to the diagnosis, some points should be stressed. In lingual view, para- and metaconid form a widely open V, the paraconid being strongly inclined towards the front. The metaconid is relatively high but distinctly shorter than the protoconid, the lingual face of which is deeply concave. The anterior crest of the protoconid is very finely denticulated. A faint bump is visible at the anterior labial base of the protoconid (also visible in the last preserved molar of *Paurodon*). In posterior view, the median crests of the meta- and protoconid delimit a wide and concave U, and each ends respectively on the labial and lingual border of the talonid. The latter is at present relatively small in occlusal surface, asymmetrically triangular with the apex being postero-lingual, aligned with the tip of the metaconid; the hypoconulid itself remains very low.

The roots are not preserved: their bases are visible lingually, but labially a break occurred at the base of the protoconid. However, given the flattening of this face and of the cusps, as well as the position of the talonid, it can be safely concluded from what is left that the two roots were subequal, the posterior one following anterior and not being situated entirely lingual to it as in dryolestids.

The tooth is in almost unworn condition, only the tips of the main cusps having been abraded. In contrast, the labial face of the talonid is strongly worn, even excavated, which may be partly responsible for its present triangular shape. This excavates an indentation at the base of the posterior trigonid crest, which is very characteristic. Another wear facet may be detectable at the anterior base of the protoconid.

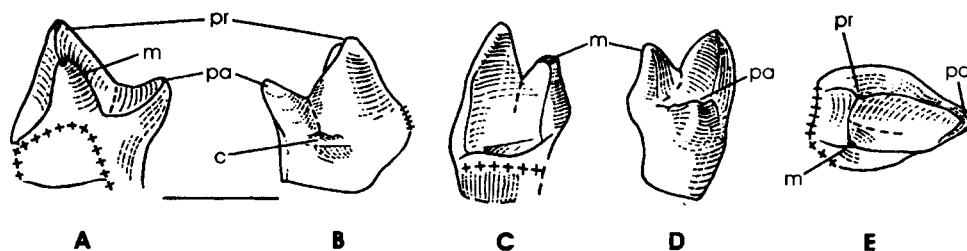
DORCM GS 376, 438, 501, 502, 625 and 747 are also interpreted as lower paurodontid teeth: their two roots were undoubtedly subequal and the open trigonid is as flat as or even flatter labially than that of the type. All teeth are slightly longer than the latter. As in DORCM GS 433, the posterior face of the trigonid of all these molars is hollowed between the same crests, and the lingual face of the protoconid is clearly concave and anteriorly oriented. A very slight elevation is again visible at the labial base of the protoconid, except in DORCM GS 625, where it may have been worn. However there are differences. On DORCM GS 376, the paraconid is even more shelf-like than that of the type but less inclined lingually (as in *Archaeotrigon*) and lower (even if we admit that the tip is missing); the lingual V between para- and protoconid is even more open, while the metaconid appears to have been relatively lower. Finally, the talonid appears to be significantly different from that of the type tooth, being relatively longer, situated at mid-width of the tooth, and having a quadrangular shape, the lingual angle being slightly displaced medially and another angle being present postero-labially. However, scrutiny of this distal border suggests that it may have been slightly abraded, which may be partly responsible for the difference in shape between the latter and that of the type. A wear facet is again visible on the labial face of the talonid, cutting into the posterior crest of the protoconid. Also, there may be an incipient triangular wear facet on the anterior base of the labial face of the protoconid.

On DORCM GS 502, the paraconid is more inclined anteriorly than on the type; the talonid lacks a chip of enamel posteriorly, but it is strongly worn labially, a wear that indents the posterior crest of the protoconid as on the preceding teeth; wear has also touched the antero-labial face of the protoconid and the posterior edge of the paraconid. DORCM GS 501 has a lower paraconid, separated from the metaconid by a wide U-basin;



TEXT-FIG. 5. *Dorsetodon haysomi* gen. et sp. nov.; DORCM GS 502, resin cast; lower right molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. SEM stereophotographs; $\times 45$.

the talonid, which is clearly complete and unworn, is definitely triangular as on the type. On DORCM GS 625, again the paraconid is lower and more shelf-like, the talonid is triangular but shorter; wear is clearly visible on the anterior face of the protoconid, and on the occluso-labial face of the talonid, but the posterior crest remains untouched. Finally, on DORCM GS 747 and 438, the paraconid is quite extended anteriorly; on the former, the talonid is short and wide, worn labio-occlusally but again the posterior crest of the protoconid is not indented. The latter tooth is unworn but, unfortunately, the talonid is missing. These differences are likely to be attributable to a different position in the dental series.



TEXT-FIG. 6. *Dorsetodon haysomi* gen. et sp. nov.; DORCM GS 438; lower left molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. Key as for Text-figure 2. Scale bar represents 0.5 mm.

Legion CLADOTHERIA McKenna, 1975

Order INCERTAE SEDIS

Family INCERTAE SEDIS

Genus CHUNNELODON gen. nov.

Derivation of name. To emphasize the French-British collaboration as demonstrated by this paper, and the Channel Tunnel inaugurated in the year of the discovery of the taxon.

Type species. *C. alopekodes* sp. nov.

Diagnosis. Lower molars with trigonid very flattened transversely. Cusps sharp. Protoconid moderately high; small paraconid not inclined anteriorly but recurved, and not shelf-like; metaconid high, slightly visible in labial view; strong backwards inclination of the posterior wall of the trigonid. Talonid reduced to a sharp, lingual and relatively high cusp. Roots slightly unequal, with a pre-eminence of the anterior one; but labially, the two roots are nearly aligned antero-posteriorly.

Chunnelodon alopekodes sp. nov.

Text-figures 7-9

Derivation of name. From the Greek, ἀλοπηκώδης, sly as a fox: an allusion to the horizon in the Cherty Freshwater Member from which the material comes, which is called the 'Sly' by the quarrymen of the Isle of Purbeck.

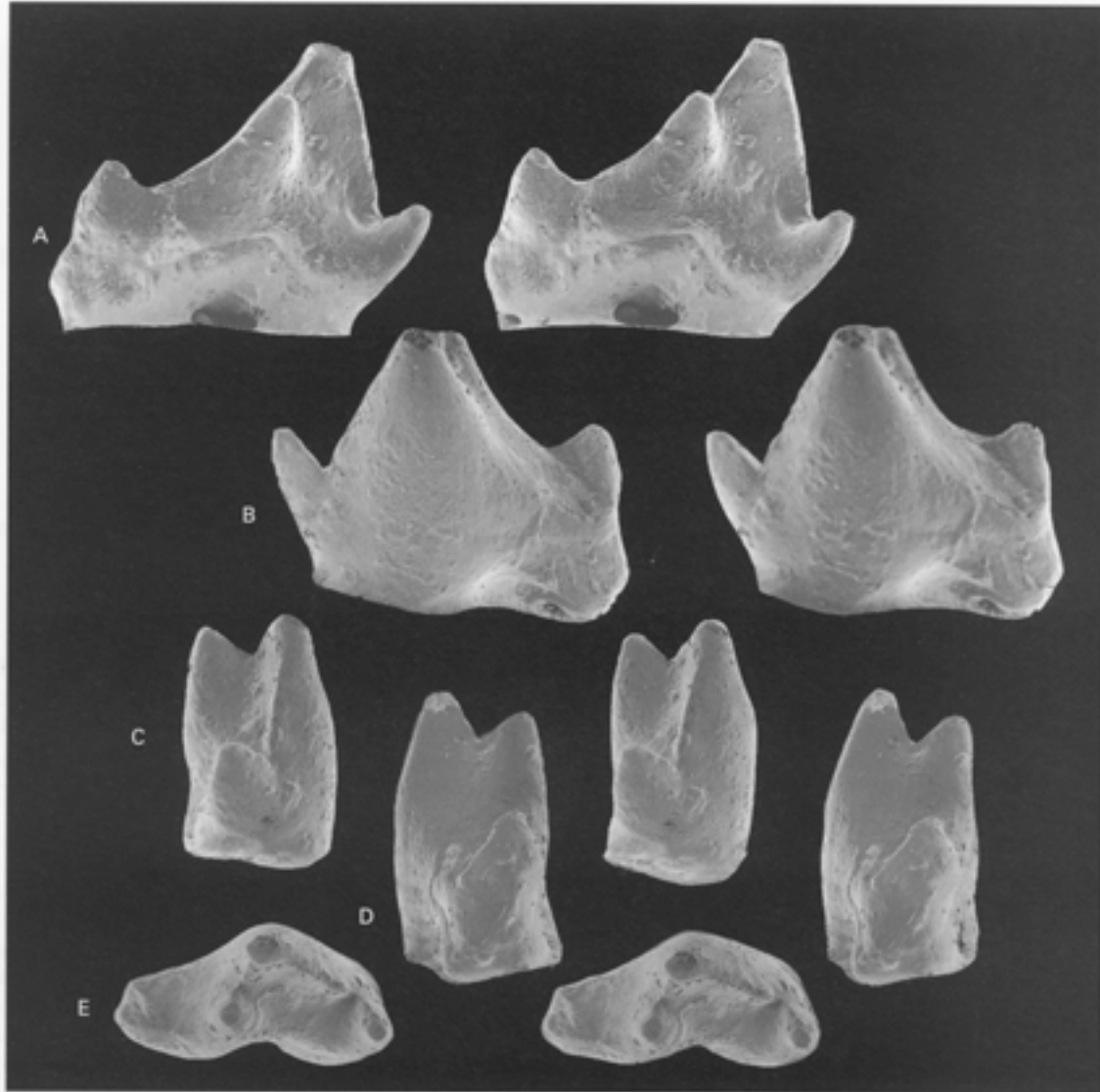
Holotype. DORCM GS 378, a left lower molar (Text-figs 7-8). L = 0.72 mm; W = 0.36 mm.

Attributed material. DORCM GS 377 (Text-fig. 9), a right lower molar (probably from the same individual as the type, but the two molars did not occupy the same position in the dental series). L = 0.72 mm; W = 0.41 mm.

Horizon and locality. Sunnydown Farm, Dorset; Cherty Freshwater Member, Lulworth Formation, Purbeck Limestone Group, basal Cretaceous (?Berriasian).

Diagnosis. As for the genus, this being the only species.

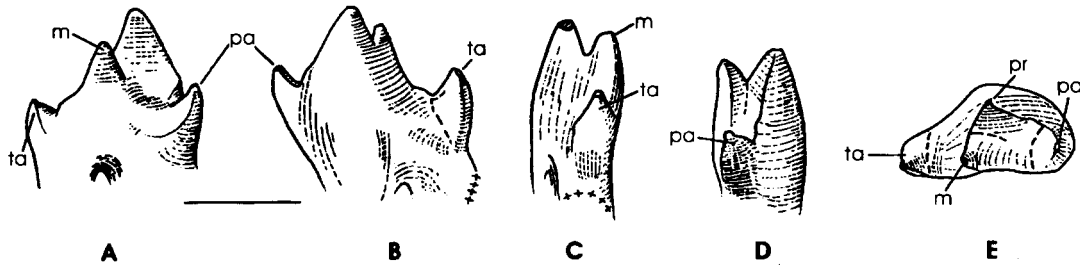
Description. DORCM GS 377 is the more complete of the two teeth in having the two roots partially preserved, but a small chip of enamel has come off between trigonid and talonid. These two teeth are very peculiar, with paraconid, metaconid and hypoconulid sharp and lingually aligned; the metaconid is notably longer and higher than the paraconid, itself slightly recurved. The protoconid is barely concave lingually. Another very distinctive feature is the backward and labial inclination of the posterior wall of the trigonid, a



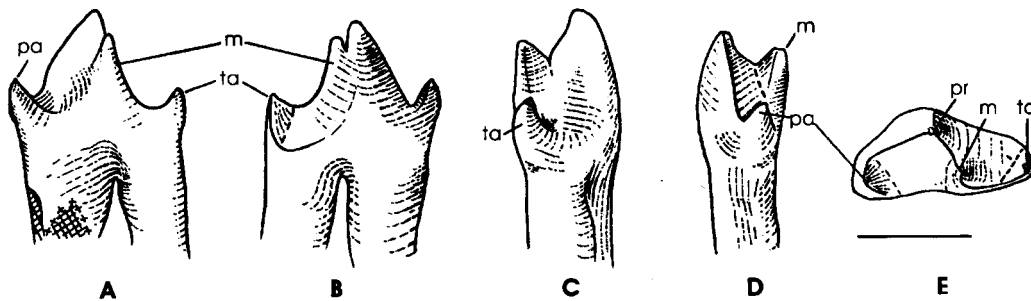
TEXT-FIG. 7. *Chunnelodon alopekodes* gen. et sp. nov.; holotype, DORCM GS 378, resin cast; lower left molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. SEM stereophotographs; $\times 45$.

wall practically flat with no trace of any crest; in occlusal view, this inclination gives the impression of an expanded talonid, whereas the latter is in fact reduced to the hypoconulid, a high triangular cusp entirely lingual: such characteristics are found in no other Theria.

The two specimens differ only slightly. The differences concern the paraconid, slightly more forwardly inclined on the holotype DORCM GS 378, and the metaconid, a little less visible. On DORCM GS 377, the presence of a minute bump at the labial base of the paraconid can be observed (rather like in *Dorsetodon*). These two teeth are unworn and show no clear wear facets, and, in particular, no paraconal sulcus.



TEXT-FIG. 8. *Chunnelodon alopekodes* gen. et sp. nov.; holotype, DORCM GS 378; lower left molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. Key as for Text-figure 2. Scale bar represents 0.5 mm.



TEXT-FIG. 9. *Chunnelodon alopekodes* gen. et sp. nov.; DORCM GS 377; lower right molar. A, lingual view; B, labial view; C, posterior view; D, anterior view; E, occlusal view. Key as for Text-figure 2. Scale bar represents 0.5 mm.

DISCUSSION

History of paurodontid classification (Table 1)

Butler (1939) created the suborder Dryolestoidea to separate, within the Pantotheria *sensu* Simpson, 1928, three families (Paurodontidae Marsh, 1887 (including *Peramus*), Amphitheriidae Owen, 1846 and Dryolestidae Marsh, 1879) from the suborder Docodontoidea. This term Dryolestoidea has the same contents (as a sublegion) in Prothero (1981), with the exclusion of *Peramus*, since in this work, the term is used in opposition to the sublegion Zatheria McKenna, 1975 (*Peramuridae* plus *Tribosphenida*) within the legion Cladotheria McKenna, 1975. Sigogneau-Russell (1991) included her new family Donodontidae (from Morocco) in the Dryolestoidea (misspelled) on the basis of the upper molars; but the characteristics of the protoconid and of the roots of the attributed lower molars are not those of dryolestoids. Finally Krebs (1991) attributed his new family Henkelotheriidae to the order Eupantotheria Kermack and Mussett, 1958 (which is not equivalent to Pantotheria *sensu* Simpson, 1928, but which includes the same families as Dryolestoidea in Butler 1939 and Prothero 1981). One of us (DS-R) considers that Amphitheriidae is closer to *Peramuridae* and hence should be excluded from Dryolestoidea. Dryolestoidea would then include three families: Dryolestidae, Paurodontidae and Henkelotheriidae.

However, Bonaparte (1992, 1994) has included four more monospecific South American families in the infraclass Dryolestida Prothero, 1981 (Dryolestoidea minus Amphitheriidae). We will not discuss these forms here, limiting our considerations to the Laurasian forms, but we would like to temper the proposals made by Bonaparte (1994) concerning the affinities between the North African and the Argentinian cladotheres. A relationship had indeed also been suggested by Sigogneau-Russell (1991) between *Donodon* Sigogneau-Russell, 1991 and *Mesungulatum* Bonaparte, 1986, on the basis of the upper molars; but the lower molars attributed to these taxa (Bonaparte 1986),

TABLE 1. History of the classification of the families mentioned in the text.

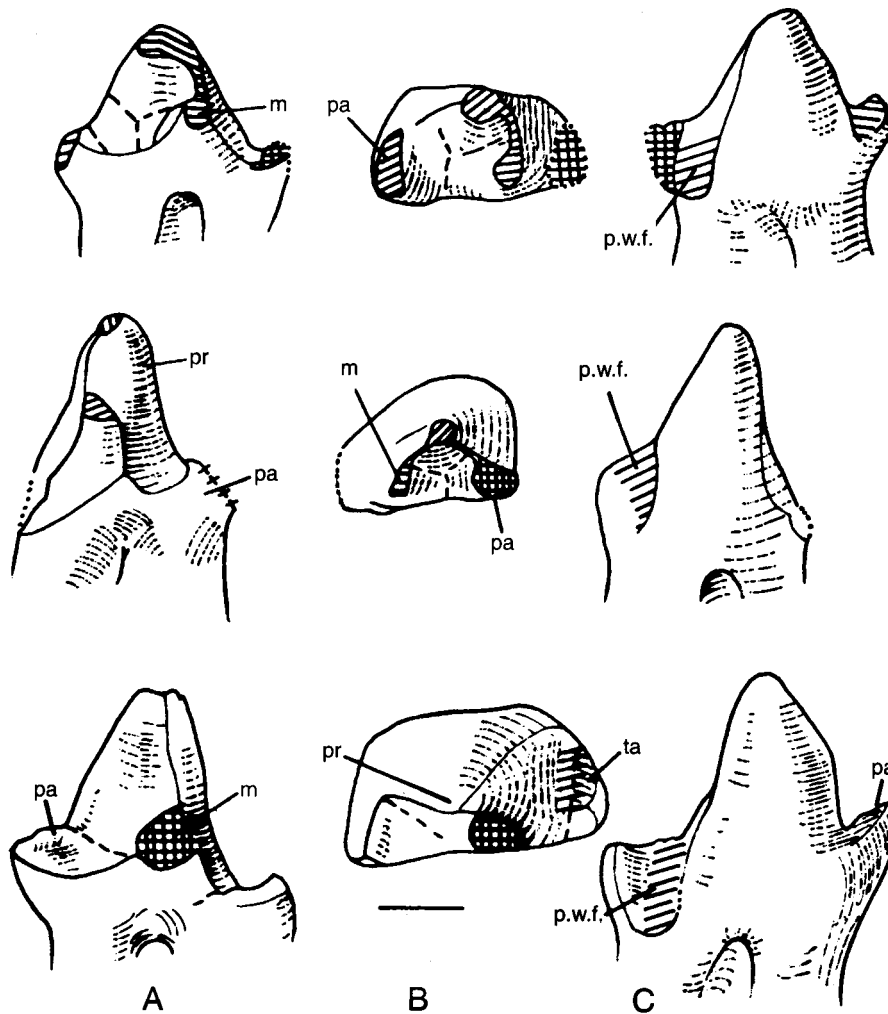
Butler 1939: Order Pantotheria Simpson, 1928	
Suborder Dryolestoidea	Amphitheriidae Paurodontidae Dryolestidae
Suborder Docodontoidea	
Prothero 1981: Legion Cladotheria	
Sublegion Dryolestoidea	Amphitheriidae Paurodontidae Dryolestidae
Sublegion Zatheria	Peramuridae Tribosphenida
Krebs 1991: Order Eupantotheria	Amphitheriidae Paurodontidae Dryolestidae Henkelotheriidae
Sigogneau-Russell 1991:	
Suborder Dryolestoidea	Amphitheriidae Paurodontidae Dryolestidae Donodontidae
This paper: Legion Cladotheria	
Sublegion Dryolestoidea*	Dryolestidae Paurodontidae Henkelotheriidae Donodontidae <i>Chunnelodon</i>
Sublegion nov.	Amphitheriidae Peramuridae Tribosphenida
Sublegion Zatheria	

* South American families not considered here.

devoid of talonid, do not support this relationship, and the rest of the mammalian fauna renders it even more tenuous. The Los Alamos Campanian mammalian assemblage does seem to testify to a long isolation of that part of Argentina from the rest of the subcontinent and hence from the rest of Gondwana.

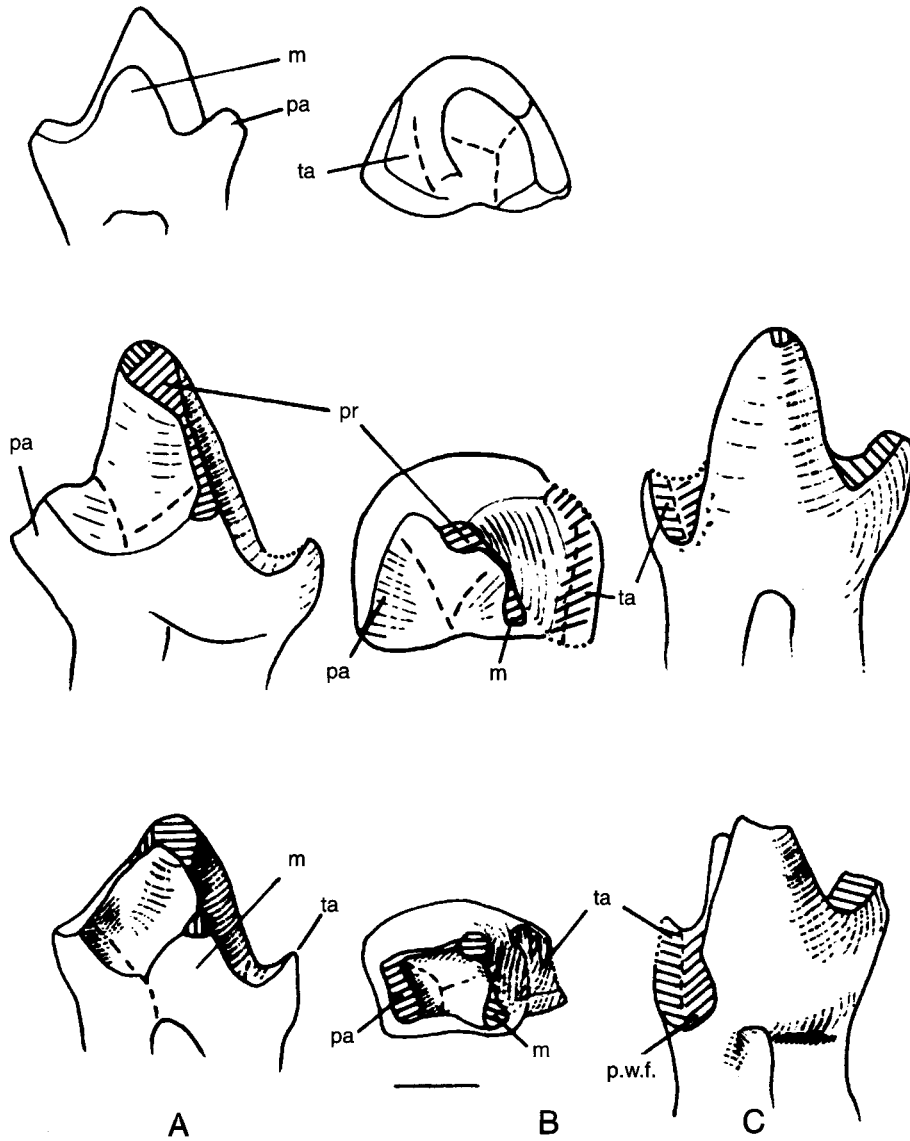
Of the three Laurasian families in the suborder Dryolestoidea (Paurodontidae, Henkelotheriidae and Dryolestidae), only the last was known from the Purbeck Limestone Group (Simpson 1928; Lillegraven *et al.* 1979). However, the new discoveries of mammals made by one of us (PE) in the Lulworth Formation of the Purbeck Limestone Group (basal Cretaceous) in Dorset include, among lower teeth which are undoubtedly of a dryolestoid type (shelf-like and procumbent paraconid, asymmetrical trigonid, transverse paracrista-metacristid shear), a few elements that show a morphology incompatible with the definition of the Dryolestidae. The asymmetrical trigonid excludes the Gondwanan Donodontidae (insofar as the attribution of the lower teeth to the type upper molar of the only donodontid genus is correct); so their inclusion in Paurodontidae or Henkelotheriidae had to be envisaged (the four South American families, except Mesungulatidae, are known only from upper teeth).

The family Paurodontidae itself was created for the genus *Paurodon* Marsh, 1887. It was united with Amphitheriidae by Gregory (1922), but Simpson (1927a) validated Marsh's distinction of



TEXT-FIG. 10. Lower molars of, from top to bottom: *Araeodon*, *Paurodon*, *Archaeotrigon brevimaxillus*. A, lingual view; B, occlusal view; C, labial view. Scale bar represents 0.5 mm.

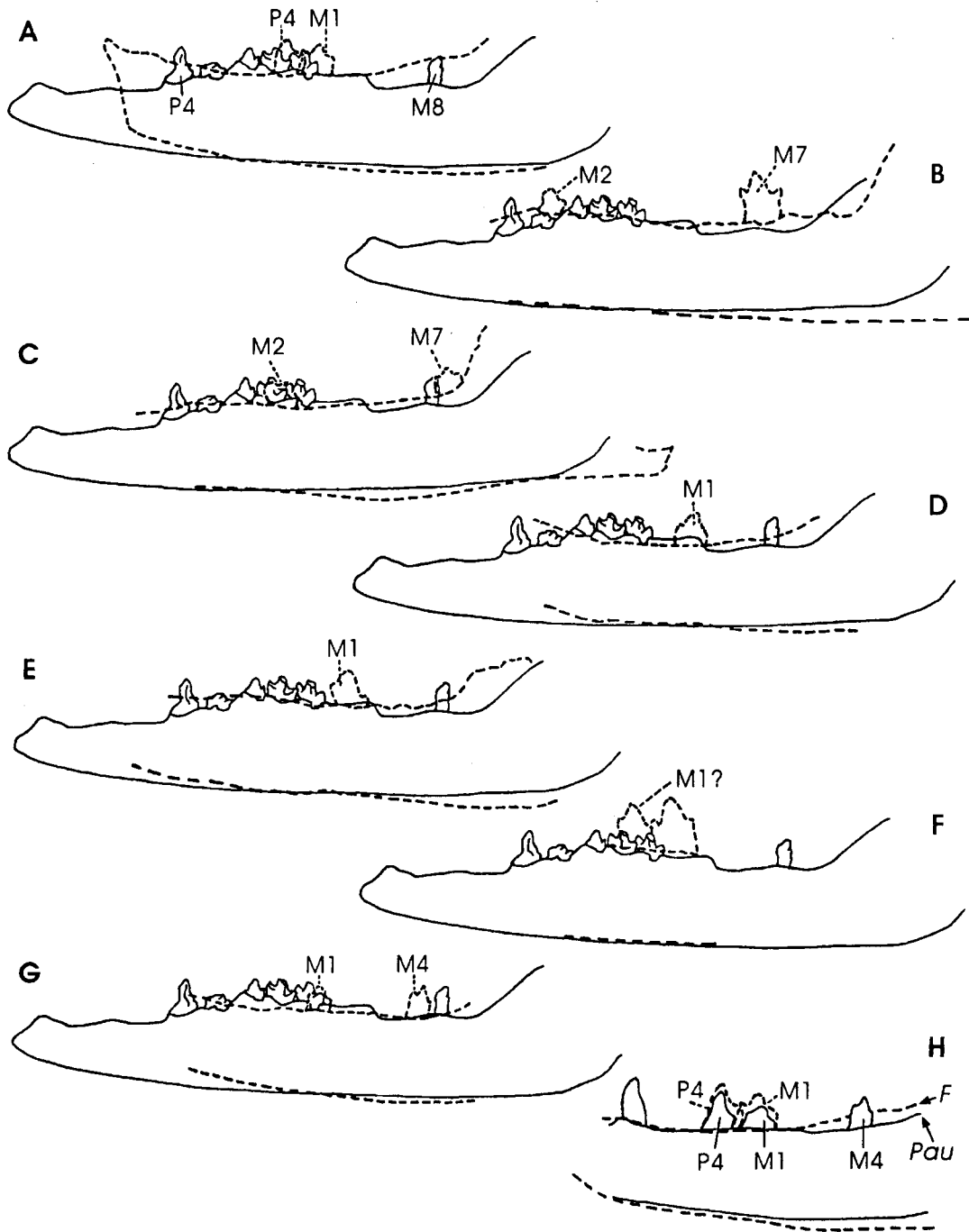
Paurodon from *Amphitherium*. As indicated by the name, Marsh (1887) and later Simpson (1929) differentiated Paurodontidae from Dryolestidae by the reduced dental formula, as well as by the shape of the lower molars, not compressed transversely and supported by two subequal roots. Simpson's diagnosis includes, moreover, the non-reduction of the unicuspid talonid (in fact, the paurodontid talonid is longer but not wider than that of the dryolestid, but as the tooth is flatter, hence longer, the talonid occupies a greater part of the total width), the smallness of the metaconid relative to the protoconid, and the shortness and stoutness of the lower jaw. Later, Prothero (1981) defined the family by what he considered to be a unique set of derived characters: 'broad shelf-like paraconid and talonid with reduced cusps, molars broaden antero-posteriorly, loss of anterior cusp on last lower premolar'. Krebs (1991) distinguished Paurodontidae from his Henkelotheriidae by its smaller dental formula, the greater reduction of the para- and metaconid (paraconid forming a ledge and metaconid very blunt), the situation of the semicircular talonid in the middle of the tooth



TEXT-FIG. 11. Lower molars of, from top to bottom: *Tathiodon*, *Foxraptor*, *Henkelotherium*. A, lingual view; B, occlusal view; C, labial view. Scale bar represents 0.5 mm.

width and the shorter and stouter lower jaw; finally, Bakker and Carpenter (1990) emphasized the proportions of the jaw (more especially the symphysis) in defining Paurodontidae.

Simpson (1927a) enlarged Paurodontidae with four new genera: *Archaeotrigon*, *Tanaeodon* (to become *Tathiodon* Simpson 1927b), *Peramus* and *Brancatherulum*. He acknowledged, however, that this group was rather heterogenous; indeed *Peramus*, isolated in the family Peramuridae by Kretzoi (1946), and later united with Amphitheriidae by Mills (1964), was reinstated in a distinct family by Clemens and Mills (1971), a distinction accepted by Lillegraven *et al.* (1979) and Prothero (1981).



TEXT-FIG. 12. Profile of the lower jaw of various Dryolestoidea (dashed line), compared with that of *Kepolestes* (uninterrupted line, from Prothero 1981), with mandibular height below M/1 as a constant. A, *Foxraptor* (from Bakker and Carpenter 1990); B, *Laolestes* (from Prothero 1981); C, *Henkelotherium* (from Krebs 1991); D, *Archaeotrigen* (from Simpson 1929); E, *Araeodon* (from Simpson 1937); F, *Tathiodon* (from Simpson 1929); G, *Paurodon* (from Simpson 1929). H, *Foxraptor* (dashed line) compared with *Paurodon* (uninterrupted line). Tooth contour schematic.

TABLE 2. Distribution of characters in the lower molars of the genera considered in this paper. Formula for incisors and canines not known.

	Dental formula pm + m	Protoconid	Paraconid
<i>Paurodon</i>	2 + 4	High Median ridge lingually Convex labially	Low
<i>Archaeotrigon brevimaxillus</i>	2 + 3 to 4	High Median ridge lingually Slightly convex labially	Very low and narrow Anteriorly directed
<i>Tathiodon</i>	2 to 3 + 3 to 4	High Convex labially	Low Anteriorly directed
<i>Araeodon</i>	3 + 4	High? Median ridge lingually Convex labially	Low Anteriorly directed?
<i>Foxraptor</i>	3 + 5	High Median ridge lingually Flat labially	Moderate Tubular Anteriorly directed
<i>Henkelotherium</i>	4 + 6 to 7	Moderate? Median ridge lingually Slightly convex labially	Low Slightly anteriorly directed
<i>Dorsetodon</i> GS 433	—	Moderate height Concave lingually Slightly convex labially	Short Moderately high Anteriorly directed
<i>Dorsetodon</i> GS 376	—	Moderate Slightly concave lingually Slightly convex labially	Short Low Anteriorly directed
<i>Dorsetodon</i> GS 438	—	Moderate Slightly concave lingually Slightly convex labially	Long Low Very anteriorly directed

As for *Brancatherulum*, the edentulous lower jaw that constitutes the type and only specimen of the genus was reviewed by Heinrich (1991), who concluded that it was not possible to decide between a paurodont and a peramurid on the basis of the dental formula alone.

To the three remaining genera of Paurodontidae, *Araeodon* was added by Simpson (1937). Finally, Bakker and Carpenter (1990) described a new therian genus, *Foxraptor*, which they attributed to the same family. These five genera are known only from lower teeth. However, Simpson (1929) had suspected that the dryolestid genus *Pelicopsis* Simpson 1927a, known from upper teeth, might in fact be a paurodont. This opinion was adopted by Prothero (1981). Later, Krebs (1991), citing what he considered to be similarities between the upper molars of *Henkelotherium* from the Kimmeridgian of Guimarota, Portugal and the Morrison genus *Pelicopsis*, as well as those between the lower molars of *Henkelotherium* and of another Morrison genus *Tathiodon*, included these two North American genera in his family Henkelotheriidae, thus leaving only four genera in Paurodontidae.

All the paurodontid genera come from the Morrison Formation (late Jurassic, and, for *Foxraptor*, possibly basal Cretaceous). No contemporaneous or older locality has so far yielded paurodont remains (except for possibly *Brancatherulum* and *Henkelotherium*).

TABLE 2 (CONT).

Metaconid	Talonid	Trigonid posterior face	Wear
Moderate	Sloping Semicircular Shelf-like Wide and short 'No true cusp'	Narrow and flat	More posterior than labial
Moderate	Semicircular Wide and long Cusp postero-lingual	Flat	Posterior and labial?
Relatively high	Triangular Wide and long Cusp postero-lingual	Flat?	?
Moderate	Sub-triangular? Very small No cusp?	Flat	Posterior and labial?
Low to moderate	Semicircular Wide Cusp postero-lingual	Slightly concave	Posterior and labial?
'Not reduced'	Triangular Wide and short Postero-lingual cusp	Slightly concave	Posterior and labial base
Moderate	Triangular? Relatively long No cusp	Strongly concave	Postero-labial base
Moderate	Triangular? Longer and wider No cusp	Strongly concave	Postero-labial base
Relatively high	—	Strongly concave	—

Position of Dorsetodon

By the subequality of the roots, the lack of compression of the crown, the relative extension of the talonid, these teeth are closer to those of paurodontids/henkelotheriids than to those of dryolestids. However, one possibility mentioned by Krebs (pers. comm. 1994) should be considered: could the teeth attributed to the new genus (especially DORCM GS 438) represent lower milk-molars of Dryolestidae? As far as we know, no such teeth have been described or mentioned. The slighter compression of the first molar in one or two dryolestid lower jaws would seem to give support to this interpretation. However, in no dryolestid specimen have we observed such a flattening, nor symmetry of the roots; the situation of the milk molars may of course have been different. But we consider that the type of wear is critical in determining the affinities: never, in dryolestids, is there an indentation at the base of the posterior crest of the protoconid; in these forms, wear is perfectly transverse. On the contrary, talonid wear, with an indentation of the base of the posterior crest of the protoconid such as noted on DORCM GS 433 and others, can be observed in *Henkelotherium*, *Araeodon*, *Foxraptor* and possibly *Archaeotrigon* (cast damaged in this area) (Text-figs 10–11). Again the situation is different in typical dryolestids, where the labial cingulum may be affected by wear, but such a facet is completely independent from the talonid (unfortunately, wear cannot be

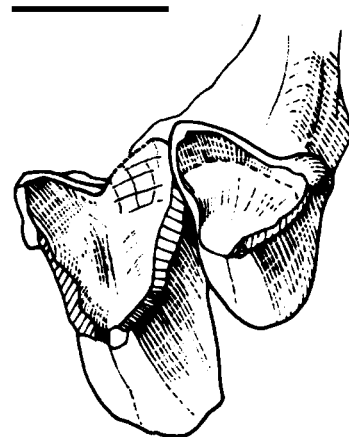
observed on our incomplete cast of the Purbeck dryolestid *Peraspalax*, which also has a slightly concave posterior trigonid surface). Wear is not recorded in *Tathiodon* and we remain uncertain of the shape of the posterior trigonid face, which, combined with the slight differences mentioned above, prevents us from attributing the Dorset specimens to a small species of this genus.

The presence of at least one paurodontid-henkelotheriid in the Purbeck Limestone Group is thus well established. There remains the matter of the distinction between these two families and the establishment of to which one *Dorsetodon* should be attributed. One of the differentiating characters of henkelotheriids cited by Krebs (1991) concerns the relative slenderness of the lower jaw. Given the fragmentary state of most paurodont remains, it is difficult to express this objectively. We measured (from the published figures): (1) the height of the jaw under M/1 with respect to the height of this M/1: the results varied considerably according to the source used for the measurement, and from the value estimated for M/1 on imprecise drawings of partly worn teeth; (2) the height of the jaw under M/1 with respect to the length of the alveolar border comprised between the anterior limit of the ultimate premolar and the posterior limit of M/3; the latter measurement excludes *Tathiodon* for which we have a figure of only the molar part of the preserved jaw (but said by Simpson (1929) to be more slender than in *Paurodon* and *Archaeotrigon*). As shown in Text-figure 12, there does not seem to be a clear distinction between Paurodontidae and Dryolestidae as concerns the relative height of the jaw at that level, much less between Henkelotheriidae and the former. In fact, the difference lies mainly in the respective elongation of the molar series and of the anterior part. Unfortunately the shape and length of the symphysis, short in all paurodonts except *Tathiodon*, are unknown in the type specimen of *Henkelotherium*, the only specimen of this taxon described by Krebs.

It also appears that the two other characters cited by Krebs as differentiating Paurodontidae and Henkelotheriidae are not familiarly diagnostic: the relative extension of the para- and metaconid and that of the talonid vary along the dental series in *Henkelotherium* itself, and also in paurodonts (for example, M/1-M/2 of *Archaeotrigon brevimaxillus*, or *Foxraptor*). Even the shape of the talonid varies, since it is essentially triangular in most molars of *Henkelotherium*, but becomes semicircular in the last molar. In fact, the lingual view of the molars of *Foxraptor* (a genus not included in Krebs' comparison) and *Henkelotherium* superpose nearly perfectly and the trigonids are very similar in details. The difference between *Henkelotherium* and *Foxraptor* lies mainly in the talonid, which is longer and more developed in *Foxraptor*, even though in this genus also there is some variation along the series. The dental formula of *Foxraptor* (3 or 4 Pm/ +5 M/) is intermediate between that of other paurodonts and *Henkelotherium* (4 Pm/ +6 or 7 M/). But, as already noted by Clemens (1970), and accepted by Lillegraven *et al.* (1979), the reduction of the dental formula may have occurred progressively within the family Paurodontidae. Finally, the type of wear in *Henkelotherium* is the same as that described in paurodonts and even more accentuated: the indentation at the base of the posterior protoconid crest is very characteristic. Therefore, with the data available, it is tempting to consider either *Foxraptor* as a member of Henkelotheriidae, or Henkelotheriidae as a junior synonym of Paurodontidae.

The situation is not made any clearer by the inclusion of *Tathiodon* in Henkelotheriidae. The similarities invoked by Krebs (1991, pp. 95-96) are as follows: (1) non-shortened lower molars; (2) two subequal roots; (3) paraconid inclined anteriorly: these three characters are valid for all Paurodontidae (and the shortening of the molar is in fact greater in *Tathiodon* than in *Henkelotherium* and most paurodonts); (4) three trigonid cusps well developed: it is very difficult to evaluate this point; besides being vague, it is rare to find paurodont teeth with their cusps intact; they are in any case well developed in *Foxraptor* also; (5) triangular talonid with cusp lingually situated: however, this seems also to occur in *Araeodon* and is in any case more clearly indicated in *Tathiodon* than in *Henkelotherium* (see Simpson, 1929, fig. 22, p. 46; in Bakker and Carpenter (1990), the figures listed as *Archaeotrigon* and *Tathiodon* (fig. 7), clearly taken from Simpson 1929, have been inverted). Besides, in Krebs' table 2 (p. 51), there remain only two characters shared by *Henkelotherium* and *Tathiodon* and separating the latter from the other paurodonts: (1) talonid cusp not reduced: but the hypoconulid is even better developed in *Archaeotrigon* and *Foxraptor*; (2)

TEXT-FIG. 13. DORCM GS 313 and 315; last two upper molars of a possible paurodontid. Scale bar represents 0.5 mm.



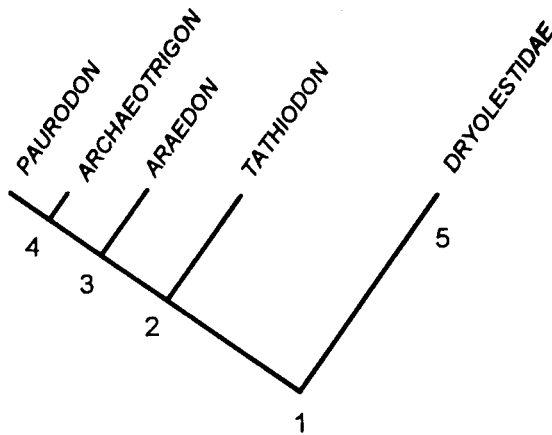
paraconid and metaconid not much lower than the protoconid: the height of the metaconid relative to the protoconid may indeed be a good differential character. The trigonid angle may also be a good indicator. However, more significant is the type of wear at the level of the talonid: as mentioned above, that of *Henkelotherium*, with an excavation at the base of the posterior crest of the protoconid delimiting a slight concavity, is similar to the condition in *Dorsetodon* and *Paurodon*, only more accentuated. Again the mode of wear is unknown in *Tathiodon*. To sum up, the distinction of Henkelotheriidae and Paurodontidae founded on the lower molars needs to be confirmed by further comparative material and studies. Hence the conservative approach of this paper, in which we place *Dorsetodon* in Paurodontidae.

The characteristics of *Dorsetodon* and the other paurodontid genera are listed in the table below (Table 2). We wish to stress once more that these evaluations are subject to variations (1) along the dental series; (2) according to state of preservation; and (3) which are subjective: an attempt at quantification is itself devalued by (1) and (2).

Obviously we have envisaged the possible presence, in the new Purbeck collection, of upper molars corresponding to the lower molars of *Dorsetodon*. In the available sample, 36 upper molars could be attributed to Dryolestidae. Without doubt 26 of them represent typical Dryolestidae, even if some do not perfectly correspond to any of the three taxa so far known in this fauna: *Amblotherium nanum*, *A. pusillum* and *Kurtodon* (some of the lower molars also indicate the presence of new dryolestid taxa). The teeth which cannot be identified as dryolestids make potential candidates as upper molars of Paurodontidae.

As no paurodont genus is known from both upper and lower dentition, the peculiarities of the paurodont upper molars remain uncertain. *Pelicopsis*, as already mentioned, has been tentatively attributed to this family by Simpson (1929), mainly from the number of molars and the shape of the intermolar embrasures. Krebs (1991) went further by placing the genus in Henkelotheriidae. The common characters cited for the two genera (Krebs 1991, p. 50) are the non-compression of the trigon and the reduced stylocone. However, the latter is much more reduced in some Dryolestidae, e.g. *Kurtodon*. The only remaining character possibly linking the teeth of *Henkelotherium* and *Pelicopsis* is the proportions of the trigon; but these should be expressed objectively, and measured along the dental series. In the absence of such data, we can only suggest that some teeth, such as DORCM GS 313 and 315 (Text-fig. 13), might represent upper molars of our new paurodontid.

The establishment of this new taxon demands the search for the phylogenetic relationships of the various forms mentioned above. Prothero (1981) proposed a cladogram for the then known genera (Text-fig. 14). The knowledge acquired since 1981 exposes a few incongruities: *Foxraptor*, recognized as the most primitive paurodont by its authors, must indeed diverge before *Tathiodon*



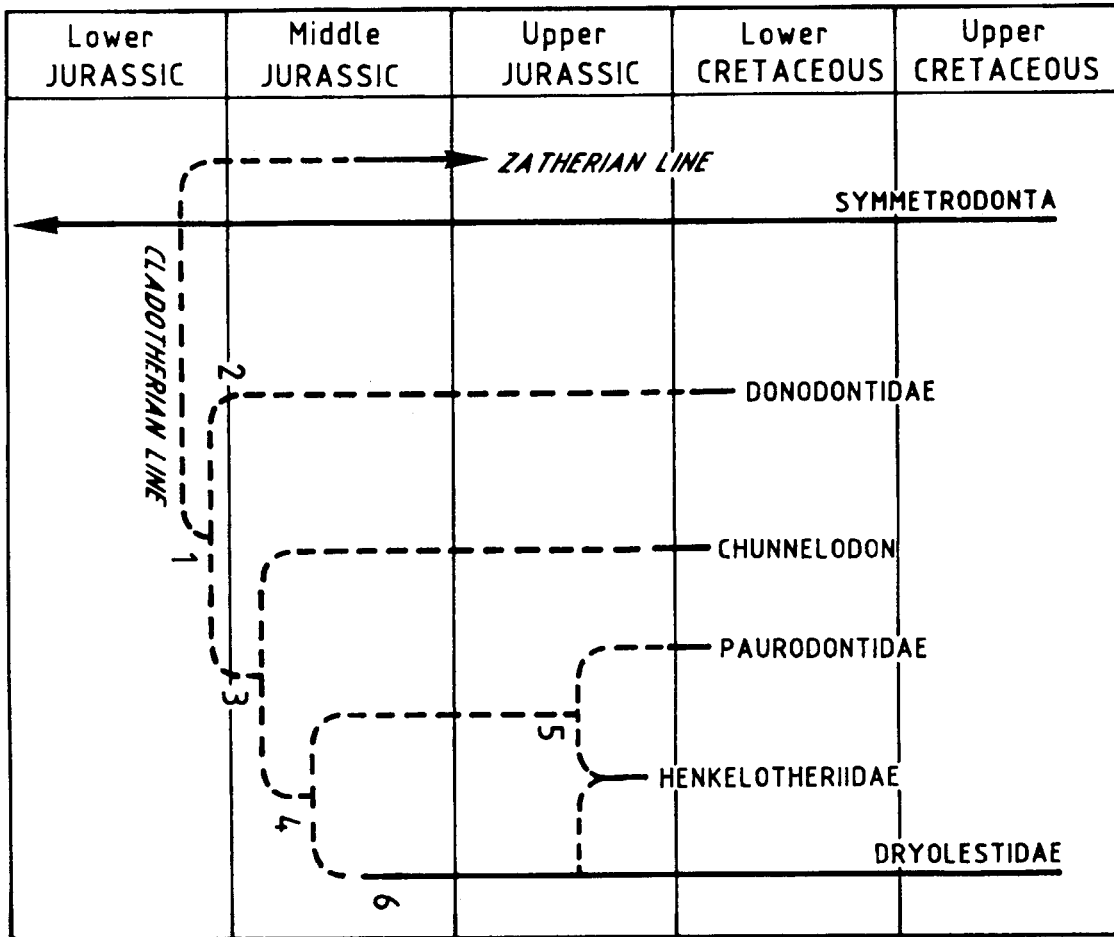
TEXT-FIG. 14. Cladogram of paurodontids, after Prothero (1981), modified. 1. transverse metacristid shear, strongly procumbent paraconid, reduced to four premolars. 2. reduction to two premolars, broad shelf-like paraconid and talonid, reduced paraconid and talonid cusps, metaconid slightly shorter than protoconid. 3. metaconid much shorter than protoconid, jaw short and stout with short symphysis, last lower premolar loses anterior cingulum. 4. talonid semicircular in crown view. 5. anterior molar root much larger than posterior root, trigonid and talonid anteroposteriorly compressed, lingual alveolar border lower than labial border, angular process slender and dorsally deflected.

by the number of premolars; but it has already acquired the short symphysis of *Araeodon* and the semicircular talonid of *Paurodon* and *Archaeotrigon*, both characters considered, probably justly, as derived. *Foxraptor* also possesses a relatively high protoconid, again considered to be a shared derived character of the last three genera; but this feature is apparently variable along the jaw. We must admit that, when we know too little to even ascertain the polarity of some characters, it becomes very 'acrobatic' to evaluate relationships between the relevant taxa. Finally, we note again that phylogenetic relationships cannot be as simplistic as our two-dimensional dichotomic cladograms would imply. These are necessarily based on very incomplete specimens as well as on the serendipitous discoveries of particularly small specimens; such limitations are inescapable, but the value of such cladograms should not be overestimated, nor their presentation be dogmatic.

Position of Chunnelodon

The morphology of the crown and the proportions of the roots separate *Chunnelodon* from Dryolestidae, and the non-shelf-like paraconid ensures that these molars are not paurodont-henkelotheriid teeth. They might evoke Amphitheriidae, but the Dorset molars differ by the absence of a metacristid (the hypoconulid is not offset labially as in *Amphitherium*, hence there is no differentiation of a metacristid directed toward a labial hypoconulid); they also differ from Amphitheriidae by the wide U separating para- and metaconid, and by the lesser labial convexity of the trigonid; by a much smaller talonid and the asymmetry of the para- and metaconid. The same asymmetry and the shape of the talonid distinguish the new genus from Donodontidae (Sigogneau-Russell 1991). Thus *Chunnelodon*, on the morphology of the lower molars, stands apart from the cladotherian (Dryolestidae plus Zatheria in Prothero 1981) families so far known from lower teeth, while at the same time probably belonging to that group, on the basis of the presence of four derived characters: loss of lower molar lingual cingulum, trigonid angle less than 100° , talonid better defined than that of Symmetrodonta, transverse shear. However, such uncertainties as those concerning the angular region of the lower jaw, the structure of the premolars, not to mention the corresponding upper molars, leave some doubt as to this attribution.

Within Cladotheria and as mentioned above, the non-procumbent paraconid would exclude *Chunnelodon* from Dryolestidae *sensu* Prothero 1981; the same is true for *Donodon*. This character-state would justify either the position of these two latter taxa as a common sister-group to Dryolestidae, or more likely, the isolation of both from that 'sublegion', according to the tentative scheme given below (Text-fig. 15).



TEXT-FIG. 15. Proposed relationships of the various cladotherian families considered in this paper, based on lower molars only. 1. loss of lingual cingulum on molars; trigonid angle < 100°; expanded talonid; transverse shear. 2. antero-posterior compression. 3. loss of symmetry; paraconid decreases; loss of anterior cuspule; slightly unequal roots. 4. shelf-like paraconid; procumbent paraconid. 5. decrease in number of molars; paraconid low relative to protoconid. 6. increase in number of molars; antero-posterior compression; strongly asymmetrical roots; talonid decreases.

Poor though our knowledge is of these two new forms from the Purbeck, their discovery opens a small window on a much richer and more varied world of Mesozoic mammals than hitherto suspected.

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