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ONTOGENY AND TAXONOMY OF *PAURODON VALENS* (MAMMALIA, CLADOTHERIA) FROM THE UPPER JURASSIC MORRISON FORMATION OF USA

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ABSTRACT

Several basal cladotherian taxa previously referred to the “Paurodontidae” (Dryolestida) from the Upper Jurassic Morrison Formation of Wyoming, U.S.A. represent ontogenetic and individual variation of one single taxon, *Paurodon valens* Marsh, 1887 (= *Archaeotrigon brevimaxillus* Simpson, 1927, syn. n.; = *Pelicopsis dubius* Simpson, 1927, syn. n.; = *Archaeotrigon distagmus* Simpson, 1929, syn. n.; = *Araeodon intermissus* Simpson, 1937, syn. n.; = *Foxraptor atrox* Bakker et Carpenter, 1990, syn. n.). *P. valens* is characterized by prolonged dental replacement, including late eruption of m4 (and m5 as individual variation) and a time gap between shedding of dp2 and eruption of p2, which can be lost in aged individuals. By a shortened dentary and mandibular symphysis, two-three simple premolariform teeth, and four molariform teeth with tall trigonid and small talonid, *P. valens* is strinkingly similar to the modern golden moles (Chrysochloridae), particularly to *Amblysomus hottentotus*. This similarity suggests that *P. valens* was specialized on consuming earth worms in contrast to a more insectivorous diet characteristic for other dryolestidans.

Key words: Cladotheria, Dryolestida, Jurassic, Mammalia, Morrison Formation, ontogeny, *Paurodon*, taxonomy

ОНТОГЕНЕЗ И ТАКСОНОМИЯ *PAURODON VALENS* (MAMMALIA, CLADOTHERIA) ИЗ ВЕРХНЕЮРСКОЙ ФОРМАЦИИ МОРРИСОН В США

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РЕЗЮМЕ

Несколько таксонов базальных кладотериев из верхнеюрской формации Моррисон в Вайоминге, США, отнесенных ранее к “Paurodontidae” (Dryolestida), представляют собой онтогенетическую и индивидуальную изменчивость одного вида, *Paurodon valens* Marsh, 1887 (= *Archaeotrigon brevimaxillus* Simpson, 1927, syn. n.; = *Pelicopsis dubius* Simpson, 1927, syn. n.; = *Archaeotrigon distagmus* Simpson, 1929, syn. n.; = *Araeodon intermissus* Simpson, 1937, syn. n.; = *Foxraptor atrox* Bakker et Carpenter, 1990, syn. n.). *Paurodon valens* характеризуется

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длительной сменой зубов, включая позднее прорезывание m4 (и m5 у некоторых особей) и временной промежуток между выпадением dp2 и прорезыванием p2, который может быть утрачен у старых особей. По укороченной зубной кости и нижнечелюстному симфизу, двум-трем простым премоляриформным зубам и четырем моляриформным зубам с высоким тригонидом и маленьким талонидом *P. valens* удивительно похож на современных златокротов *(*Chrysochloridae), особенно на *Amblysomus hottentotus*. Это сходство свидетельствует о том, что *P. valens* был специализирован на поедании земляных червей, а не насекомых, что характерно для других дриолестид.

Ключевые слова: Cladotheria, Dryolestida, юра, Mammalia, формация Моррисон, онтогенез, *Paurodon*, таксономия

INTRODUCTION

Paurodontidae Marsh, 1887 was originally proposed for *Paurodon* Marsh, 1887, "a peculiar genus <...> widely different from any form hitherto found in this country [U.S.A.] or Europe" (Marsh 1887: 341). *Paurodon valens* Marsh, 1887 was based on a single dentary fragment with canine and six postcanine teeth from the famous Quarry 9 (Como Bluff) locality within the Upper Jurassic (Kimmeridgian-Tithonian) Morrison Formation in Wyoming, U.S.A (Carrano and Velez-Juarbe 2006). Marsh (1887) did not specify to which suprafamiliar group Paurodontidae should be attributed, but he divided all known Mesozoic mammals into two orders: Pantotheria and Allotheria (Marsh 1880). Only multituberculates were referred to Allotheria by Marsh and thus he apparently regarded Paurodontidae to belong to Pantotheria. Osborn (1888) and Gregory (1922) considered *Paurodon* to be related to Amphitheriidae Owen, 1846.

Simpson (1927) revised Marsh's Pantotheria and added to Paurodontidae two new monotypic genera: *Archaeotrigon* Simpson, 1927 and *Tanaodon* Simpson, 1927 (a preoccupied name replaced by *Tathiodon* Simpson, 1929). Both new taxa were based on dentary fragments from Quarry 9. Later Simpson (1928a) added to Paurodontidae also *Peramus* Owen, 1871 from the Lower Cretaceous (Berriasian) Lulworth Formation (Purbeck Limestone Group) of England. Two additional paurodontid taxa were subsequently described based on dentary fragments from Quarry 9: *Archaeotrigon distagmus* Simpson, 1929 and *Araeodon intermissus* Simpson, 1937. Butler (1939) pointed to the similarity of lower molars of *Amphitherium* de Blainville, 1838 from the Middle Jurassic (Bathonian) Sharps Hill Formation of England and of Paurodontidae sensu Simpson, 1929. He also suggested that *Peramus* is not closely related to the North American Paurodontidae. Subsequently *Peramus* was placed in a distinct family Peramuridae Kretzoi, 1946 and now it is considered as a basal member of Zatheria McKenna, 1975, a clade comprising modern tribosphenic mammals and their ancestors (Kielan-Jaworowska et al. 2004).

Simpson (1928b) noted a close similarity of *Brancatherulum tendagurense* Dietrich, 1927, known from a single edentulous dentary from the Late Jurassic (Kimmeridgian-Tithonian) Tendaguru Beds in Tanzania to *Peramus*. As *Peramus* at that time was considered by Simpson to be a paurodontid, *Brancatherulum* Dietrich, 1927 was also referred to that family in Simpson's (1945) influential classification of mammals. Kraus (1979) referred *Brancatherulum* to ?Peramuridae and restricted Paurodontidae to the four Morrison lower dentition genera (*Paurodon*, *Archaeotrigon*, *Tathiodon*, and *Araeodon*). *Brancatherulum* has been assigned to the Paurodontidae again, albeit with a question mark, in the monograph on Mesozoic mammals by Kielan-Jaworowska et al. (2004), mostly because of its low postcanine dental count.

Kraus' concept of Paurodontidae was accepted in a cladistic classification of "pantotheres" by Prothero (1981), who added to this group also the upper dentition taxon *Pelicopsis* Simpson, 1927, a proposition made previously by Simpson (1929: 83). Two other upper dentition taxa from Quarry 9, *Euthlastus cordiformis*, Simpson, 1927 and *Comotherium richi* Prothero, 1981, are now also assigned to the Paurodontidae (Martin 1995, 1999; Kielan-Jaworowska et al. 2004).

Engelmann and Callison (1998) referred to *Araeodon intermissus* two isolated lower molars from the Morrison Formation at Dinosaur National Monument in Utah, U.S.A. A distinct paurodontid taxon, *Foxraptor atrox* Bakker et Carpenter, 1990 has been established based on a single dentary with incisors, canine, and seven postcanine teeth from a locality close to Quarry 9 within the Morrison Formation.

Three taxa referred to Paurodontidae are known from Europe (Kielan-Jaworowska et al. 2004). *Henkelotherium guimarotae* Krebs, 1991 and *Drescheratherium acutum* Krebs, 1998 come from the Upper Jurassic (Kimmeridgian) Guimarota coal mine in Portugal. The first taxon is represented by a unique almost complete skeleton while the second is known by upper jaws with dentition (Krebs 1991, 1998). *Dorsetodon haysomi* Ensom et Sigogneau-Russell, 1998 from the Lower Cretaceous (Berriasian) Lulworth Formation of England is based on isolated lower molars.

For a long time the family Paurodontidae was considered as a monophyletic sister taxon of Dryolestidae Marsh, 1879; both are referred to the monophyletic Dryolestida Prothero, 1981, a member of Dryolestoida Prothero, 1981, a group paraphyletic to Zatheria (Kielan-Jaworowska et al. 2004). Kielan-Jaworowska et al. (2004:388) noted that there are only minute differences between several of the paurodontid genera that are based on lower dentitions and on single type specimens, and that the group requires a revision. In more recent phylogenetic analyses the monophyly of Paurodontidae has not been supported and the genera included there form a paraphyletic array of basal cladotherians (Rougier et al. 2011, 2012; Averianov et al. 2013). In this report we revise the alpha-level taxonomy of paurodontids from the Morrison Formation.

Paurodontidae Marsh, 1887 is a senior homonym for the nematode family Paurodontidae Thorne, 1941 based on *Paurodontus* Thorne, 1941.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, U.S.A.; CM, Carnegie Museum, Pittsburgh, U.S.A.; DINO, Dinosaur National Monument, Utah, U.S.A.; UCM, University of Colorado Museum, Denver, U.S.A.; USNM, United States National Museum, Washington DC, U.S.A.; YPM, Yale Peabody Museum, Yale University, New Haven, U.S.A.

METHODS

The coefficient of variation (CV) is defined as the ratio of the standard deviation to the mean value multiplied by 100%. The mean values and standard deviations for dental measurements (Table 1) were calculated using the basic statistic module of STATISTICA 7.1 © StatSoft, Inc. The CV values for the lower postcanine dentition of the paurodontid specimens from the Morrison Formation (Table 2) were compared with the values of these measurements for a sample of *Dryolestes leiriensis* Martin, 1999 from the Upper Jurassic Guimarota coal mine. Altogether there are 42 specimens of *D. leiriensis* with lower postcanine teeth, but because most specimens have the dentition incompletely preserved, the sample size of measurements varies from 7 to 30. The geometric mean of the molar measurements was calculated as the square root of the molar length multiplied by the molar width.

SYSTEMATICS

Mammalia Linnaeus, 1758

Cladotheria McKenna, 1975

Dryolestida Prothero, 1981

Paurodon Marsh, 1887

Paurodon Marsh, 1887: 342 (original description)
Archaeotrigon Simpson, 1927: 410 (new synonym)
Pelicopsis Simpson, 1927: 414 (new synonym)
Araeodon Simpson, 1937: 2 (new synonym)
Foxraptor Bakker and Carpenter, 1990: 4 (new synonym)

Type species. *Paurodon valens* Marsh, 1887

Differential diagnosis. As for the type and only known species.

Paurodon valens Marsh, 1887

(Figs. 1–4)

Paurodon valens Marsh, 1887: 342, pl. 10, figs. 7–8 (original description).
Archaeotrigon brevimaxillus Simpson, 1927: 410 (new synonym).
Pelicopsis dubius Simpson, 1927: 414 (new synonym).
Archaeotrigon distagmus Simpson, 1929: 52, pl. 6, fig. 1 (new synonym).
Araeodon intermissus Simpson, 1937: 3, fig. 1 (new synonym).
Foxraptor atrox Bakker et Carpenter, 1990: 4, figs. 6, 7J (new synonym).

Holotype. USNM 2143, left dentary fragment with c, p2-3, and m1-4.

Type locality and horizon. Quarry 9, Como Bluff, Albany County, Wyoming, U.S.A.; Morrison Formation, Late Jurassic (Kimmeridgian-Tithonian).

Referred specimens. Type locality: YPM 13754, right maxillary fragment with three posterior molars, holotype of *Pelicopsis dubius* Simpson, 1927; AMNH

27775, right dentary fragment with p1-2 and m1, holotype of *Araeodon intermissus* Simpson, 1937; USNM 2793, right dentary fragment with c, p2-3, and m1-2, holotype of *Archaeotrigon brevimaxillus* Simpson, 1927; YPM 13641, right dentary fragment with m3, holotype of *Archaeotrigon distagmus* Simpson, 1929; YPM 13648, left dentary fragment with p2-3 and m2-3, "badly crushed," attributed to *Archaeotrigon brevimaxillus* (Simpson 1929: 51); YPM 13642, right dentary fragment with one molar attributed to *Archaeotrigon* sp. (Simpson 1929: 53); YPM 13640, right lower molar attributed to *Archaeotrigon* sp. (Simpson 1929: pl.7, fig. 2); AMNH 101142, right dentary fragment with a molar (identified here as dp4) referred to an indeterminate dryolestid (Prothero 1981: tab. 1); USNM 442636, left dentary fragment with the last molar.

"Breakfast Bench" (UCMP Locality 80001), Albany County, Wyoming, U.S.A.: UCM 59089, right dentary fragment with i3-4, c, p1-3, and m1-4, holotype of *Foxraptor atrox* Bakker et Carpenter, 1990.

Dinosaur National Monument, Utah, U.S.A.: DINO 10726, left lower molar (Engelmann and Callison 1998: fig. 19). Possible also DINO 10712, isolated lower molar mentioned but not figured by Engelmann and Callison (1998: 374).

The "Breakfast Bench" locality is geographically very close to Quarry 9 but stratigraphically higher, near the top of the Morrison Formation (Carpenter 1998). The Dinosaur National Monument locality in Utah is within the same Upper Brushy Basin Member of the Morrison Formation as the Quarry 9 locality in Wyoming (Engelmann and Callison 1998).

Butler (1939: 334, fig. 3d) reported two additional paurodontid specimens from Quarry 9: YPM 13775 and 13778. According to Prothero (1981: 305) the first specimen has been lost and the second specimen was heavily damaged. Now both specimens are missing in the YPM collection (AA personal observation, 2005).

Differential diagnosis. Differs from stem zatherians by the following characters: fewer lower premolars (2–3 instead of 5), last lower premolar taller than m1, D-shaped paracristid-protocristid, cingulid cusps e and f absent, distal metacristid absent, dentary twice deeper than the highest molar, Meckelian groove extended between mandibular symphysis and mandibular foramen and convergent to the ventral border of the dentary. Differs from *Henkelotherium*, *Drescheratherium*, *Tathiodon*, and stem zatherians by absence of postmetacrista cusp. Differs from *Henkelotherium* and Dryolestidae by fewer lower molars (4 instead of 7 or 8–9), a mandibular ramus that is sub-uniform in height, and an angular process that is divergent from the medial pterygoid crest. Differs from *Tathiodon* and Dryolestidae by the following characters: upper molars less wide transversely, stylocone smaller than metacone, paraconid about twice shorter than metaconid, distal metacristid absent, and heel-like talonid. Differs from Dryolestidae by long labial cingulum on upper molars, caniniform lower canine, fewer lower premolars (2–3 instead of 4), short mandibular symphysis, lower molars that are longer than wide and lack of unilateral hypsodonty, equal roots of lower molars, and equal alveolar borders of dentary.

DESCRIPTION AND INTERPRETATION

Maxilla. There is a single maxillary fragment referable to *P. valens* (YPM 13754), containing three posterior molars. The anterior origin of the zygomatic process is placed at the level of the first preserved molar (likely M2, see below; at M3-4 in Morrison dryolestids). The posterior origin of the zygomatic process is placed at the distal end of last molar.

Upper molars. The upper dentition is known only from YPM 13754, a maxillary fragment with the three last molars. Based on proportions of the preserved teeth, Simpson (1929: 83) suggested that this specimen possessed probably only four or five molars. The typical number of lower molars in *P. valens* is four and thus four upper molars is the most likely estimation for this specimen. Indeed, the change in proportions between these three molars is drastic when compared with the gradual change of proportions in longer molar series of Dryolestidae. M2 is a nearly equilateral triangle in shape with a pronounced parastyle. M3 has the shape of an isosceles triangle, with relatively smaller parastyle. The last molar is asymmetrical, with reduced metastylar region and large parastyle. There is a strong labial cingulum between stylocone and metastyle. The paracrista is a strong crest between paracone and labially placed poorly individualized stylocone. In occlusal view, this crest is slightly convex mesially. On M2-3 the metacone is large and crest-like; it is placed on the metacrista almost equidistant from the paracone and metastyle. At the last molar the metacone is absent. The ectoflexus is very shallow

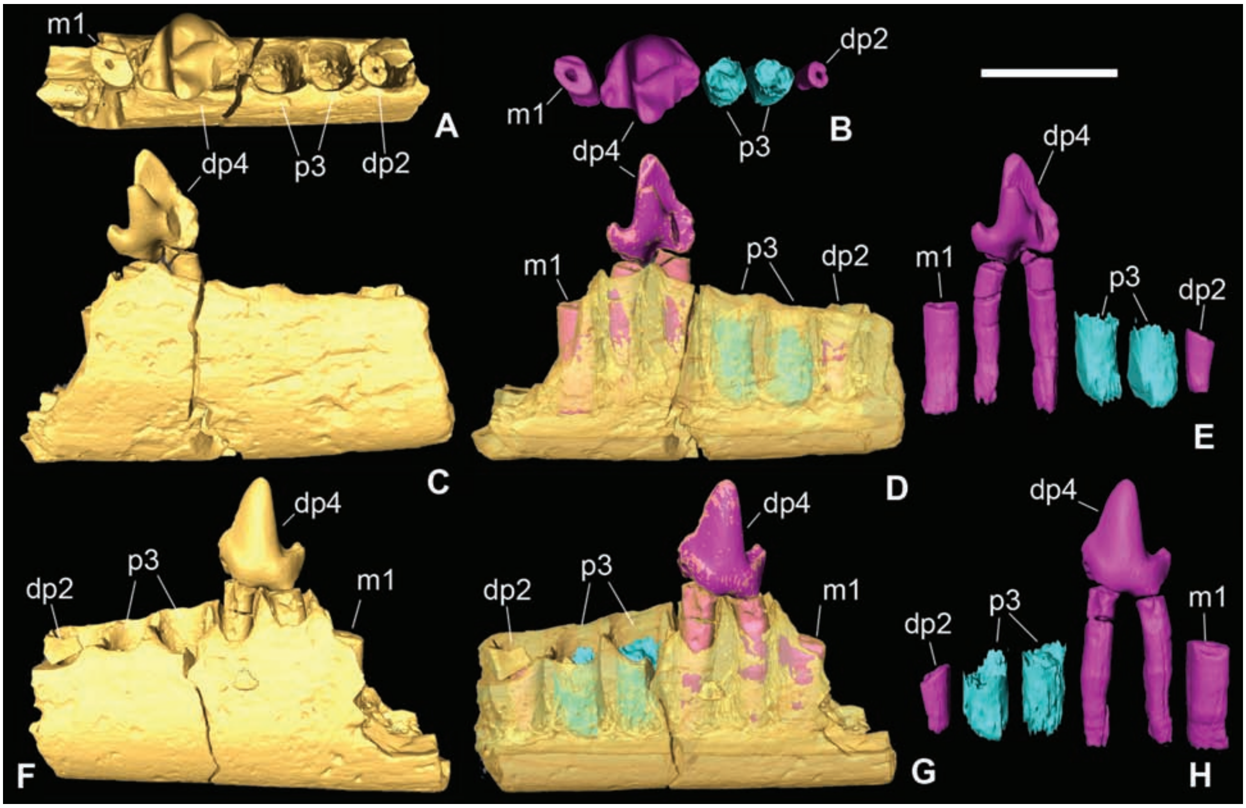

Fig. 1. *Paurodon valens* Marsh, 1887, µCT scans of AMNH 101142, right dentary fragment with dp4 (pink), roots of dp2 and m1 (pink), and alveoli of p3 (blue), in occlusal (A, B), lingual (C–E), and labial (F–H) views. Quarry 9, Como Bluff, Albany County, Wyoming, U.S.A.; Morrison Formation, Upper Jurassic (Kimmeridgian – Tithonian). Scale bar = 1 mm.

on M2-3 and absent on the last molar. The paracone is relatively larger on the penultimate molar. The trigon basin is voluminous and quite deep. On the last molar there is a short median ridge extending from the paracone into the trigon basin.

Dentary. The dentary is relatively short and deep, about twice the height of the molars. The ventral profile of the mandibular body is slightly convex. The dorsal profile is straight or slightly concave; in senile specimen USNM 2143 it is convex. The mandibular symphysis is deep and terminates between c and p2. The Meckelian groove extends between the mandibular foramen and the mandibular symphysis, approximating the ventral margin in the middle. In juvenile specimens the Meckelian groove is parallel and very close to the ventral border of the dentary (Figs. 1D, 4). In USNM 2143 there are a rugosity at the base of the coronoid process and a short flat facet below the posterior end of the Meckelian groove (Marsh 1887: pl. 10, fig. 8) suggesting the presence of paradentary bones (coronoid and splenial). The angle between the alveolar border and the coronoid process varies between 150° in immature AMNH 27775 and USNM 2793 and 135° in senile USNM 2143. In immature AMNH 27775 m4 is placed at the base of the coronoid process, above the alveolar border. In adult specimens USNM 2143 and UCM 59089 there is a considerable space between m4 and the coronoid process. An anterior mental foramen, beneath the canine, is preserved only in USNM 2793 (Fig. 2C, D; Simpson 1929: 52). A posterior mental foramen is located between p2-3 in AMNH 27775 and below p2 in USNM 2793 (Fig. 2C, D; Simpson 1929: 52). For USNM 2143 the position of this foramen was described differently: below diastema between c and p2 (Marsh 1887: 342) or below p2 (Simpson 1929: 50; p2 is the tooth traditionally designated as p1, see below). It is actually positioned below the mesial root of p2. The coronoid crest is low and the masseteric fossa is shallow, extending anteriorly up to m4

(AMNH 27775 and USNM 2143), or posterior to m4 (UCM 59089). Simpson (1929: 53) described the angular process in YPM 13642 as small, triangular, and projecting posteroventrally. He noted that its structure is "quite unlike that in Dryolestidae and has much resemblance to *Peramus*" (Simpson 1929: 53). Apparently, this specimen (Kühne 1968: fig. 8) was the base for the reconstruction of the angular process in *Paurodon* (Simpson 1929: fig. 23).

Lower incisors. The incisors are known only in UCM 59089. This specimen preserves the two posterior incisors (i3-4) and part of the alveoli of the two anterior incisors (i1-2; Carpenter 1998). The posterior incisors are closely spaced and separated by a short diastema from the anterior incisors. The incisors are relatively large and only slightly inclined anteriorly. The last incisor (i4) is larger than i3, a quite unusual feature. The crowns of i3-4 are spatulate, with excavated lingual side and lingually curved apices. The alveoli of four incisors are preserved in USNM 2793 (Simpson 1929: 51), but apparently this part of the dentary was damaged since Simpson's description (Fig. 2). In contrast to dryolestids and the majority of other Mesozoic mammals, the row of incisors is not in line with the longitudinal axis of the dentary but curved medially towards the symphysis (Simpson 1929: 51). In USNM 2793 the alveolus for i1 suggests that it was a procumbent tooth, and the alveolus for i4 is smaller than that for i3 (Simpson 1929: 51).

Lower canine. The canine is known in USNM 2793, USNM 2143 and UCM 59089 (Figs. 2–4). It is high-erect and closely spaced with the incisors, and has a single root (in USNM 2793 the root is subdivided by a vertical groove on the labial side; Fig. 2D). The canine is about twice higher than i4. The crown shape is similar to that of the incisors: it is spatulate, with lingually recurved apex. There are distinct mesial and distal carinae in both specimens and a lingual cingulid in USNM 2893 and USNM 2143. In USNM 2793 the apex of the canine is missing but the remaining part is "much like that of *Paurodon* [USNM 2143]" (Simpson 1929: 51).

Lower deciduous premolars. There is a single specimen preserving deciduous premolars, AMNH 101142 (Figs. 1, 3, 4). The interpretation of the dentition in this specimen is based on comparison with *Dryolestes*, where lower premolars have alternate replacement, with dp1 and dp3 being replaced in a first wave (Martin 1997). According to this interpretation, AMNH 101142 preserves the distal root of dp2, alveoli for p3, dp4, and the mesial root of m1 (Fig. 1). The dp4 in AMNH 101142 (crown length 0.63 mm, crown width 0.51 mm) is considerably smaller than the molars in *Paurodon* (Table 1). This specimen is not referable to Dryolestidae because its metaconid is much lower than its protoconid while in Dryolestidae the protoconid and metaconid on dp4 are of similar height (Martin 1997, 1999). The paraconid is almost completely broken. The talonid is small and hook-like. The roots of dp4 (Fig. 1E, H) are distinctly thinner compared with the roots of m1, while in p4 the roots are equal or even more robust than the roots of m1 (Fig. 2D, F).

Lower permanent premolars. The number of premolars varies from two (USNM 2143 and USNM 2793) to three (AMNH 27775, YPM 13648, and UCM 59089). These premolars are usually termed p1-2 when two premolars and p1-3 when three premolars are present. But evidently the last premolar is homologous in all specimens. Moreover, these teeth are likely corresponding to p2-4 of dryolestids, and here

Table 1. Measurements of postcanine lower dentition in the type specimens referred to "Paurodontidae".

Specimen	Taxon	Measurements													
		Lp1	Wp1	Lp2	Wp2	Lp3	Wp3	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm4	Wm4
USNM 2143*	*Paurodon valens*			0.83	0.53	1.01	0.68	1.1	0.75	1.14	0.95	1.08	0.86	0.95	0.69
AMNH 27775*	*Araeodon intermissus*	0.57	0.31	1.11	0.59			1.05	0.66						
UCM 59089**	*Foxraptor atrox*	0.47	0.36	1.01	0.54	1.06	0.54	1.17	0.93	1.17	0.93	1.22	0.78	1.33	0.9
USNM 2793	*Archaeotrigon brevimaxillus*			0.9	0.57	1.2	0.67	1.2	0.82	1.6	0.99				
YPM 13641	*Archaeotrigon distagmus*									1.5		1.3	0.85		

*Measured from the cast.

**After Carpenter (1998).

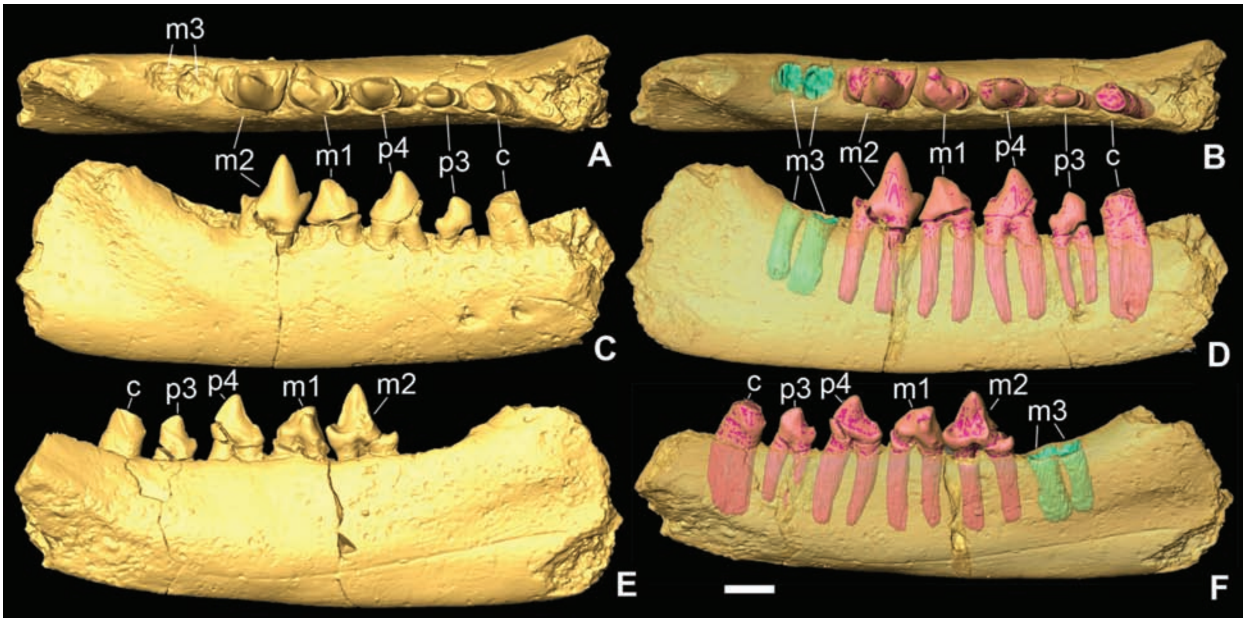

Fig. 2. *Paurodon valens* Marsh, 1887, µCT scans of USNM 2793, holotype of *Archaeotrigon brevimaxillus* Simpson, 1927, right dentary fragment with c, p2-3, and m1-2 (pink) and alveoli of m3 (blue), in occlusal (A, B), labial (C, D), lingual (E), and occlusolinual (F) views. Quarry 9, Como Bluff, Albany County, Wyoming, U.S.A.; Morrison Formation, Upper Jurassic (Kimmeridgian-Tithonian). Scale bar = 1 mm.

they are termed p3-4 when two premolars are present and p2-4 when three premolars are present. In USNM 2793 p2 was possibly not yet erupted because it is an immature specimen and in USNM 2143 is was possibly already shed and its alveolus plumbed because it is a senile specimen. An alternative explanation for the different number of premolars could be individual variation with p2 missing in some specimens.

The p2 is the smallest premolar. This tooth is about half the size of p3 (AMNH 27775, YPM 13648), or much smaller than p3 (UCM 59089), partially because of heavy abrasion. The p2 is single-rooted in YPM 13648 and AMNH 27775; in the latter specimen its root is slightly subdivided by a vertical groove on the labial side. In UCM 59089 all premolars were described as having two roots but our study of this specimen cannot confirm presence of two roots in p2. The crown is elongated with a main cusp and distal heel. In AMNH 27775 there is a rudimentary mesial cuspule. The lingual side is swollen at the base but there is no distinct cingulid. In AMNH 27775 and YPM 13648 the long axis of p2 is in line with the other check teeth, while in UCM 59089 it is oblique to the latter. A diastema between p2 and p3 in AMNH 27775 is likely caused by postmortem displacement of p2 from its original position.

The p3-4 are double-rooted and have a similar crown shape. In USNM 2793 p3 has half the height of p4 while in UCM 59089 it is only 20% lower than p4. In USNM 2143 the crown of p3 is heavily damaged. The crowns of p3-4 are dominated by the main cusp. In p4 of USNM 2143 the apex of the main cusp is slightly recurved distally; in the other premolars it is more vertical. The mesial margin of the main cusp is variously convex. The distal end of the crown is extended into the prominent heel, with the distal cusp most individualized in p3 of AMNH 27775. Both p3-4 have a well-developed lingual cingulid. There is a short diastema between p3 and p4.

Lower molars. There are four molars in USNM 2143 and AMNH 27775. In USNM 2793 there are two molars and alveoli for m3. The last molar, m4, was apparently not yet erupted in this immature specimen. In UCM 59089 there is a small alveolus posterior to m4 separated by a distinct diastema. It could be an alveolus for a single rooted rudimentary m5 or just a hole housing the protoconid of the erupting m5 of normal size. The first possibility seems to be more likely because a single-rooted last molar is known in a number of dryolestids.

The structure of the lower molars is basically similar, with slight variations between tooth positions

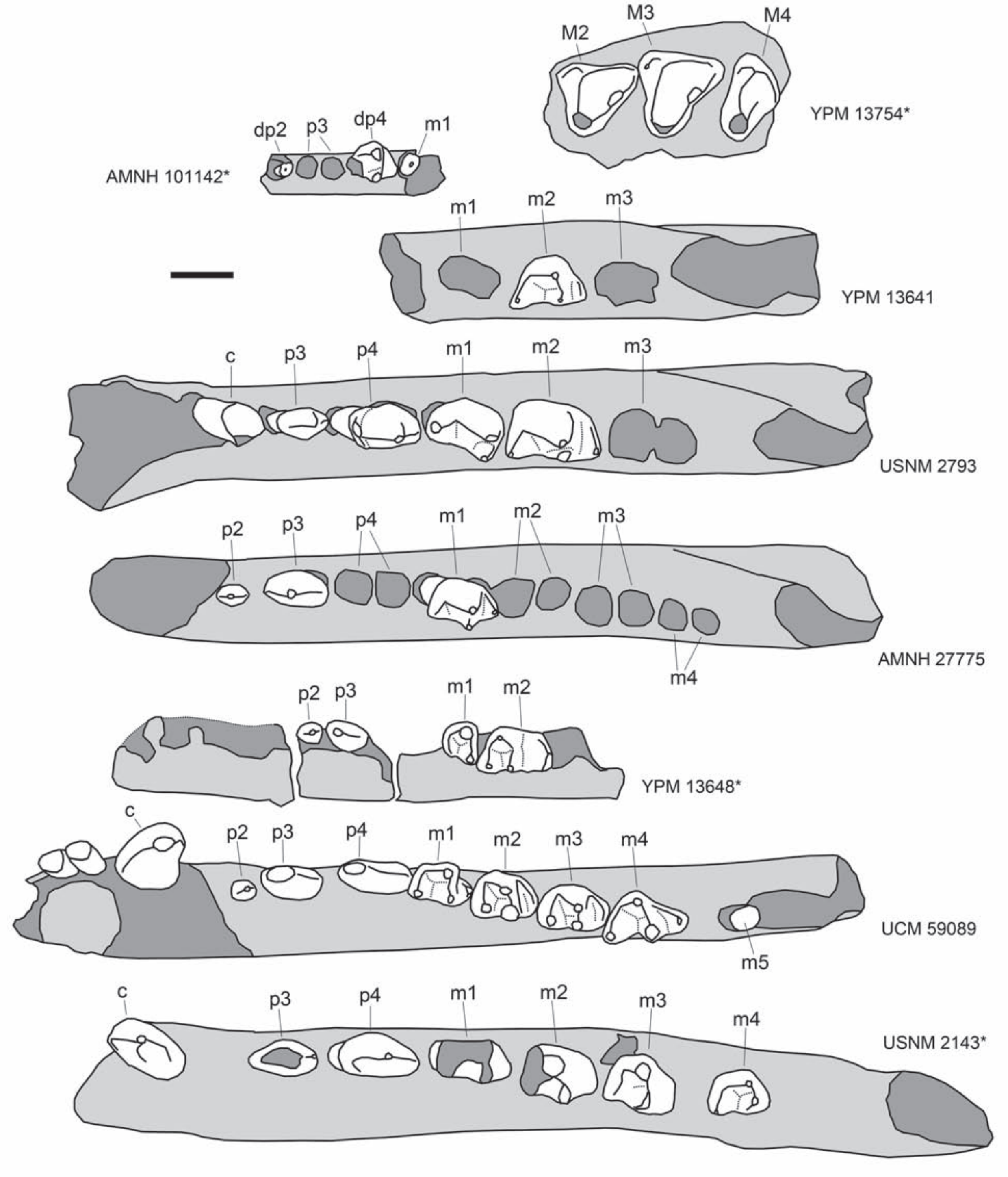

Fig. 3. The more complete specimens of *Paurodon valens* Marsh, 1887 (Morrison Formation, Upper Jurassic; U.S.A.) drawn at the same scale in occlusal view, with interpretation of preserved teeth and alveoli. Reversed images are marked by an asterisk. Scale bar =1 mm.

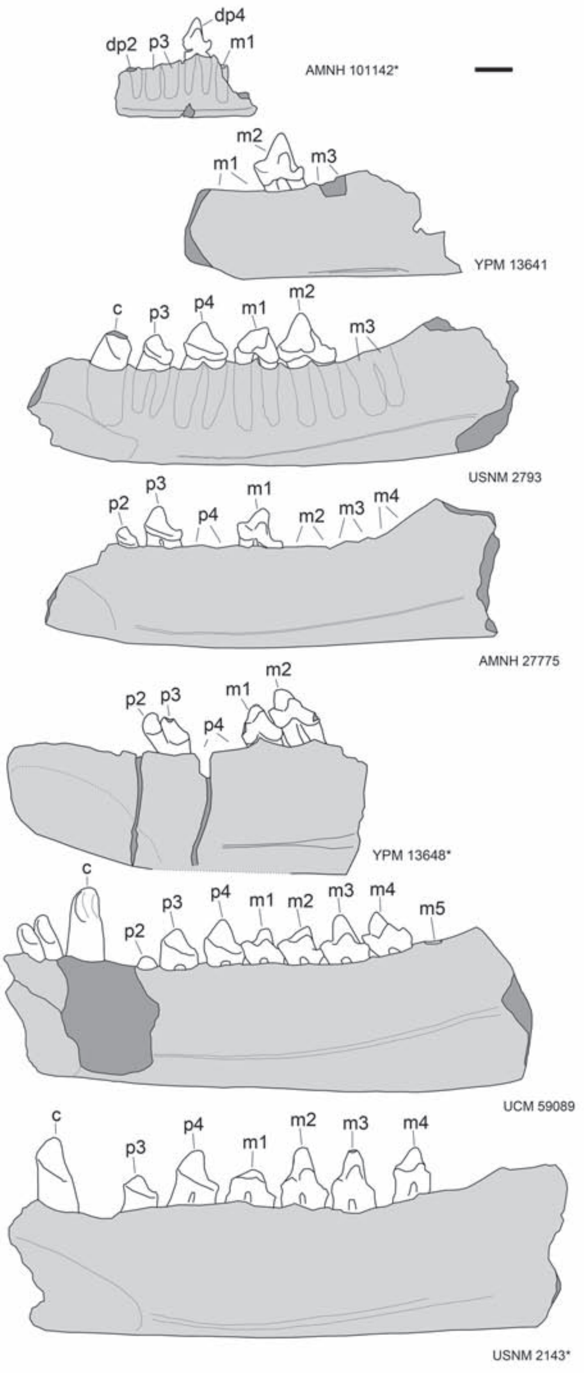

Fig. 4. The more complete specimens of *Paurodon valens* Marsh, 1887 (Morrison Formation, Upper Jurassic; U.S.A.) drawn at the same scale in lingual view, with interpretation of preserved teeth and alveoli. Reversed images are marked by an asterisk. Scale bar = 1 mm.

and specimens. The lower molars have two roots of roughly similar size. Butler (1939: 334) noted two specimens with the distal root smaller than the mesial root, but both specimens are missing now and their attribution to *Paurodon* cannot be tested. The crown is formed by the large three-cusped trigonid and small heel-like talonid. The mesiodistal length of the trigonid is larger than its labiolingual width, in contrast to the mesiodistally shortened trigonids of the Dryolestidae. The protoconid is the highest trigonid cusp. The metaconid is largely confluent with the protoconid and placed lingually to the protoconid, with the transverse protocristid present in most specimens. The protocristid is oblique in m4 of UCM 59089 and in the isolated molar DINO 10726 (Engelmann and Callison 1989: fig. 19). In all specimens with undamaged protoconid, the height of the metaconid is less than half of the protoconid height. The paraconid is a little smaller than the metaconid and varies in structure. It is more or less procumbent anteriorly. In USNM 2793 it is almost horizontal and shelf-like (Ensom and Sigogneau-Russell 1998: fig. 10). Prothero (1981: 307) noted that in *P. valens* (represented at that time by the holotype only) "the paraconid is completely flat without a cusp." This is a preservation artifact as on all molars of the holotype specimen the paraconid is heavily worn. The bases of the paraconid and metaconid are well separated on the lingual side of the trigonid. The talonid is a small heel-like projection highly variable in structure. Usually it is located near the middle of the posterior trigonid side, but in USNM 2793 it is approximated to the lingual side, as in dryolestids (Fig. 2A, B; Ensom and Sigogneau-Russell 1998: fig. 10). The talonid cusp or crest is poorly individualized.

Ontogenetic stages. The known dentary fragments of *P. valens* can be assigned to four ontogenetic stages (Figs. 3, 4).

I) The earliest known stage is documented by AMNH 101142 which has deciduous premolars in place (dp2 and dp4), dp3 replaced by p3, and m1 fully erupted.

II) This stage is represented by YPM 13641 and USNM 2793. Here dp2 is shed but p2 is not yet erupted (USNM 2793) and m4 has not begun to form (both specimens; there is no cryptic alveolus for m4 in USNM 2793; Fig. 2).

III) At this stage p2 and m4 are fully erupted (AMNH 27775, UCMP 59089, and YPM 13648; m4 is not preserved in the last specimen). As an individ-

Table 2. Coefficient of variation (cv) of postcanine lower dentition measurements in *Dryolestes leiriensis* (calculated after data presented in Martin 1999) and in Morrison paurodonts (calculated after Table 1): n—number of measured specimens. Note: the only three premolars of paurodontids are usually considered to be p1-3. Here they are designated as p2-4 to facilitate the comparison with three last premolars in *Dryolestes*.

Measurement	*Dryolestes leiriensis*		Morrison paurodonts	
	n	cv, %	n	cv, %
Lp1	16	13.69		
Wp1	16	16.29		
Lp2	18	10.59	2	13.60
Wp2	18	8.83	2	10.55
Lp3	22	8.67	4	12.79
Wp3	22	12.92	4	4.94
Lp4	25	9.65	3	9.04
Wp4	25	17.28	3	12.40
Lm1	20	11.76	4	6.00
Wm1	21	10.00	4	14.43
Lm2	29	9.67	4	17.15
Wm2	30	9.59	3	3.19
Lm3	28	8.77	3	9.28
Wm3	28	7.19	3	5.25
Lm4	29	8.64	2	23.57
Wm4	29	4.93	2	18.68
Lm5	28	8.67		
Wm5	28	7.35		
Lm6	23	8.26		
Wm6	24	7.56		
Lm7	14	9.78		
Wm7	17	10.15		
Lm8	7	16.07		
Wm8	7	30.52		

ual variation, a rudimentary m5 is present in UCMP 59089). All molars are closely spaced.

IV) The final stage is characterized by USNM 2143. Here p2 is lost and its alveolus is plugged by bone and the molars are separated by short diastemata.

This ontogenetic series is unusual because there is a delay in replacement of dp2 by p2: Some specimens have shed dp2 but p2 is not yet erupted (e.g., USNM 2793). An alternative interpretation of the observed pattern is that the tooth identified as dp2 in AMNH 101142 is actually a double-rooted deciduous canine and the first premolar, identified here as p2, is actually a late erupting dp2 which has no replacement. However, alveoli for dp2 and p3 are of similar size while the canine alveolus should be somewhat larger.

Size variation. The size variation of the lower postcanine dentition of the paurodontid specimens from the Morrison Formation is similar to that in a sample of *Dryolestes leiriensis* from Portugal (Table 2; Fig. 5). In *D. leiriensis* there are three most variable regions with CV exceeding 15%: 1) p1 (specifically width of p1); 2) p4 (width of p4); and 3) the last molar (m8, length and width). The width of the last molar is the most variable measurement, with CV greater than 30%. In the Morrison paurodontids there are only two highly variable regions with CV exceeding 15%: 1) m2 (length of m2) and 3) the last molar (m4, length and width). In the whole, the size variation of the paurodontid sample from the Morrison Formation is not larger than in the sample of *D. leiriensis* from the Guimarota coal mine. This suggests attribution of all paurodontid specimens from the Morrison Formation to a single species, *Paurodon valens*.

Sexual dimorphism. A sexual dimorphism is likely pronounced in *P. valens*. AMNH 27775, with erupted p2 and m4, is more gracile than younger specimen USNM 2793 with unerupted p2 and m4. The first specimen may belong to a female.

Association of upper and lower dentitions. In his revision of the Morrison mammals Simpson (1929) assigned upper and lower dentition specimens to different taxa because none of them were found in clear association. He noted that *Pelicopsis dubius*, known by a single maxillary fragment, is more likely paurodontid than dryolestid (Simpson 1929: 83). This idea was supported by Prothero, who figured *Pelicospis* associated with *Paurodon* but did not put the former genus in synonymy of any lower dentition taxon of the Morrison paurodontids (Prothero 1981: fig. 7G). Krebs (1991: 96) and Martin (1999: 63) advocated that *Pelicopsis* would be better associated with the lower dentition represented by *Tathiodon agilis* and the synonymy of these two taxa was formally recognized by Kielan-Jaworowska et al. (2004). Wang et al. (1998) combined *Paurodon* and *Euthlastus* into a single terminal taxon for their phylogenetic analysis. Because upper and lower molars of dryolestidans do not have a pronounced overlap

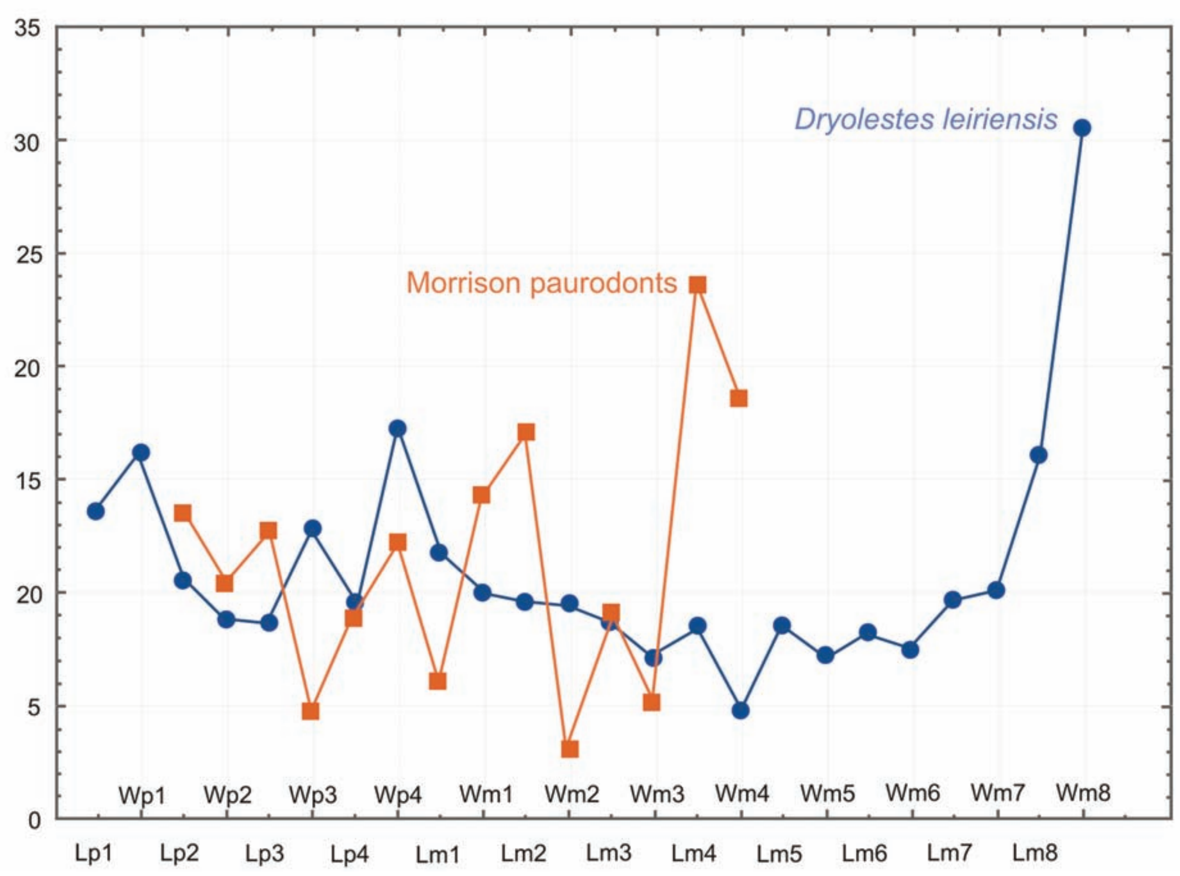

Fig. 5. Coefficient of variation (CV, %) of postcanine lower dentition measurements in *Dryolestes leiriensis* and Morrison paurodonts (Table 2). Note: the only three premolars of paurodontids are usually considered to be p1-3. Here they are designated as p2-4 to facilitate the comparison with three last premolars in *Dryolestes*.

during occlusion (Simpson 1929; Schultz and Martin 2010), it is difficult to combine isolated upper and lower dentitions by crown morphology alone. This difficulty can be overcome by size comparison of the questionable dentitions. In *D. leiriensis* (Fig. 6) the geometric mean value of the upper molars appears as a parabolic graph with a maximum value in the middle of the series (M4-5). The graph for the lower dentition is quite similar, but displaced down and to the right, so the two graphs are crossing between M6 and M7. In the anterior lower molars the geometric means are about one quarter smaller than these means for the corresponding upper molars. This size difference gradually decreases and becomes lowest at M6. At the position of M7 the geometric mean for the lower value is larger than for the upper. In *Tathiodon* the geometric mean for m1 (1.212) is already larger than in M2 of *Pelicopsis* (1.196). The fitting size for the upper dentition of *Tathiodon* is apparently represented by *Comotherium*. *Euthlastus* is too small to be the upper dentition of either *Paurodon* or *Tathiodon*. But the graph relationships between *Paurodon* and *Pelicospis* are similar to those of the lower and upper dentitions of *D. leiriensis*. In *Paurodon*, the mean geometric values are mesially lower for the lower molars and converge distally. The orientation of the shearing cristae of trigon and trigonid and the size of the interdental embrasures between these two taxa are also very similar. These similarities make it very probable that *Pelicopsis dubius* represents the upper dentition of *Paurodon valens*.

Diet of *Paurodon*. Bakker and Carpenter (1990) noted that “paurodontids” differ from the contemporaneous dryolestids in having tall, piercing protoconids, increased length of the paracristid, reduced cheek-tooth count, shortened dentary, ver-

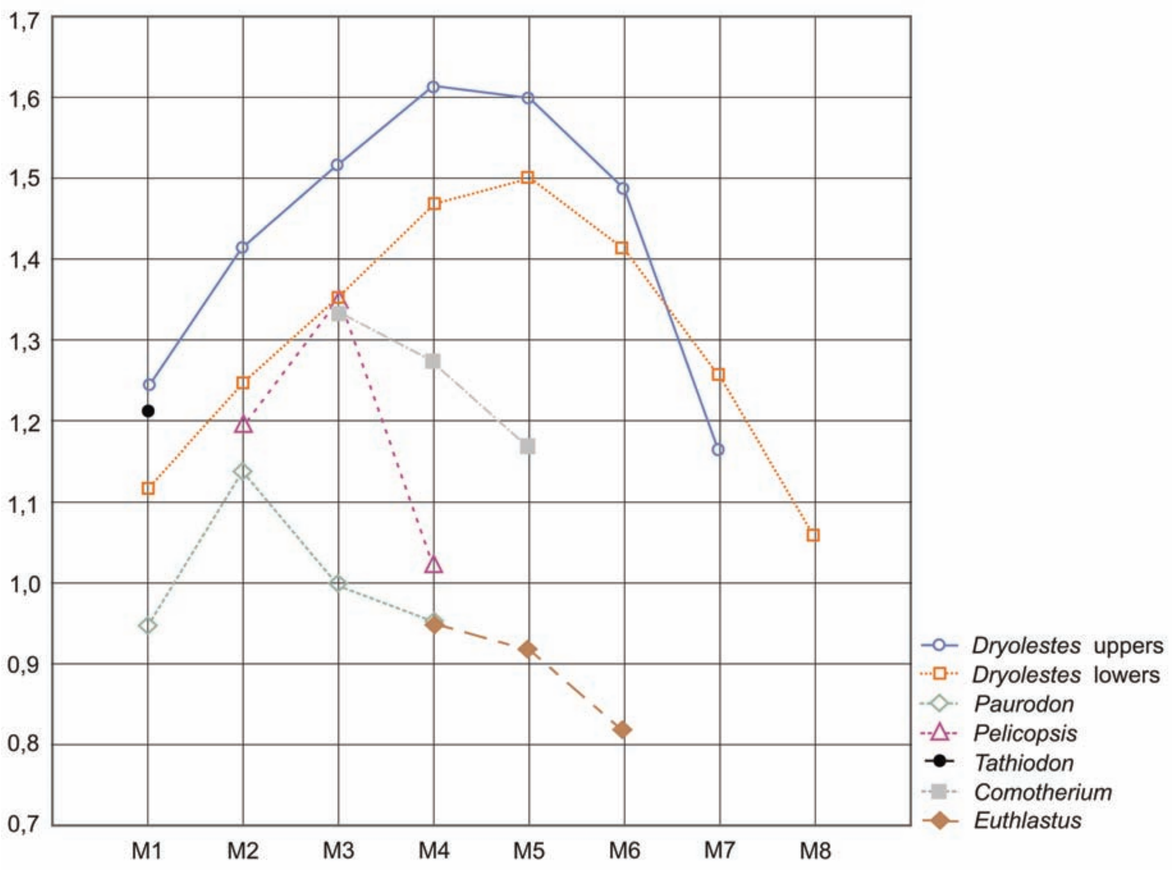

Fig. 6. Geometric mean values for the molars in *Dryolestes leiriensis* and Morrison paurodonts.

tical symphysis, and nearly vertical canine. These features indicate, according to these authors, more emphasis on a canine bite and more carnivorous diet compared to dryolestids. Bakker and Carpenter (1990) suggested that derived "paurodontids" were possible termite-eating, like modern numbat (*Myrmecobius*) or falanouc (*Eupleres*). However, the diet of the falanouc consists of almost exclusively small-sized, soft invertebrates, such as earthworms (Nowak 1999). Both *Myrmecobius* and *Eupleres* have a slender dentary with long incisor section and widely spaced molars (Thenius 1989; Cooper 2010) which contrasts greatly with the shortened jaw in *Paurodon*. Among modern mammals, the best analogues of the paurodontid jaw and dentition is represented in golden moles (Chrysochloridae). In the Hottentot golden mole (Fig. 7) the jaw is short with a short symphysis, the incisors are large and semiprocumbent, the canine is premolariform, the two anterior premolars are simple and the last premolar is molariform which gives four molariform teeth, as in *Paurodon*. The difference from *Paurodon* is that the enlarged anterior tooth is an incisor rather than a canine. The molariform teeth are somewhat spaced, as in USNM 2143. The structure of the molariform teeth, with tall trigonid and reduced talonid, is also very similar to that in *Paurodon*. The diet of the Hottentot golden mole

Fig. 7. *Amblysomus hottentotus* Smith, 1829, CM 40782, left dentary in lingual view. Scale bar = 5 mm.

consists of worms, larvae, pupae, and insects (Nowak 1999). It is likely that *Paurodon* was more specialized on consuming earth worms in contrast to the more insectivorous dryolestids.

COMMENTS ON OTHER TAXA REFERRED TO "PAURODONTIDAE"

Tathiodon agilis (Simpson, 1927) is based on a single dentary fragment from Quarry 9 with two molars, interpreted originally as m2-3 (YPM 13649; Simpson 1927, 1929). The dentary is clearly juvenile: it is very slender and houses posteriorly a cryptic alveolus for an unerupted molar (Simpson 1929: 54). The first preserved tooth is the fourth postcanine tooth according to Simpson's description, and thus it is likely dp4 rather than m1. This type of lower dentition can be associated with the upper dentition taxon *Comotherium* (see above). According to the phylogenetic analysis by Averianov et al. (2013), *Tathiodon* is a dryolestidan.

Euthlastus cordiformis Simpson, 1927 is represented by the holotype (YPM 13755), a maxillary fragment with four last molars from Quarry 9. This taxon was originally referred to Dryolestidae (Simpson 1927, 1929; Prothero 1981), but Engelmann and Callison (1998) and Martin (1995, 1999) considered it as a paurodontid. Engelmann and Callison (1998: 376, fig. 20) referred a well preserved isolated upper molar from Dinosaur National Monument to that taxon and mentioned an undescribed skull from Fruita with similar upper dentition. *Euthlastus* is one of the smallest cladotherians in the Morrison assemblage, much smaller than the estimated size of the upper dentition for *Paurodon*. This taxon could be a non-dryolestid dryolestidan (Averianov et al. 2013).

Comotherium richi Prothero, 1981 is an upper dentition taxon from Quarry 9 represented by the holotype maxilla with three molars (AMNH 101132) and a referred upper molar (AMNH 104826). It is generally similar to *Euthlastus* but about twice larger. Engelmann and Callison (1998) suggested referral of both species to a single genus. Here it is considered as a junior synonym of *Tathiodon agilis* (Simpson, 1927).

Henkelotherium guimarotae Krebs, 1991 and *Drescheratherium acutum* Krebs, 1998 were described from the Late Jurassic (Kimmeridgian) Guimarota coal mine in Portugal. The first is known from a rather complete skeleton (Krebs 1991) and a maxillary fragment now lost (Kühne 1968: fig.6; "*Simpsonodon splendens*" nomen nudum), while the second is based on two isolated maxillae (Krebs 1998). Both taxa are a non-dryolestid dryolestidans (Averianov et al. 2013).

Brancatherulum tendagurense Dietrich, 1927 is based on a single edentulous dentary fragment from the Upper Jurassic (Kimmeridgian-Tithonian) Tendaguru Beds in Tanzania (Heinrich 1991: fig.1). Because of its incompleteness, interpretation of this taxon has always been difficult (see introduction). According to the alveoli, at the two penultimate teeth the mesial root was wider than the distal root but the disparity in root size is not so pronounced as in dryolestids. These teeth are likely m1-2, and the lower dentition of this taxon could be interpreted as comprising more than two incisors, a large double-rooted canine, three double-rooted premolars, and three molars with the last molar reduced in size. The roots of the postcanine teeth are quite robust resembling the condition in Dryolestidae. The angular process is *Peramus*-like, but this shape could be ancestral for Dryolestida. *Brancatherulum* could be either a dryolestidan or stem zatherian.

Dorsetodon haysomi Ensom et Sigogneau-Russell, 1998 from the Lower Cretaceous (Berriasian) Lulworth Formation of England is known from several lower molars. The shape of the lower molars is similar to those of *Paurodon* but the size is somewhat smaller. Ensom and Sigogneau-Russell (1998: fig.13) figured a maxillary fragment with the two last molars which may belong to *Dorsetodon*. These teeth are similar in proportions to the last molars of *Pelicopsis* but differ in having no parastyle, a deeper ectoflexus, and the lack of the metacone at the penultimate molar. If this specimen really belongs to *Dorsetodon*, a generic distinction of this taxon from *Paurodon* would be well justified. Because of its incompleteness, *Dorsetodon* was not included into the formal phylogenetic analysis by Averianov et al. (2013), but its position as a non-dryolestid dryolestidan is the most likely assumption.

CONCLUSION

The concept of Paurodontidae as a monophyletic sister taxon of Dryolestidae (Simpson 1928a, b, 1929 and subsequent workers) is not valid. All lower dentition taxa of paurodonts from the Morrison Formation that have been previously classified within five species of four genera (*Paurodon*, *Archaeotri-*

gon, *Araeodon*, and *Foxraptor*) can be attributed to a single species, *Paurodon valens*. *Pelicopsis dubius* from the Morrison Formation is based on the upper dentition of the latter species. *Paurodon* and other taxa referred to the "Paurodontidae" from the Morrison Formation and Guimarota coal mine (*Tathiodon* [= *Comotherium*], *Euthlastus*, *Henkelotherium*, and *Drescheratherium*) are basal dryolestidans (Averianov et al. 2013). *Dorsetodon* from the Purbeck beds is close to *Paurodon* and may be a basal dryolestidan as well. The phylogenetic position of *Brancatherulum* from Tendaguru is not yet resolved; this taxon could be either a basal dryolestidan or stem zatherian.

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