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NEW STEM-LINEAGE REPRESENTATIVES OF ZATHERIA (MAMMALIA) FROM THE LATE JURASSIC OF PORTUGAL

THOMAS MARTIN
Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Malteserstrasse, 74-100, 12249 Berlin, Germany, tmartin@zedat.fu-berlin.de

ABSTRACT—*Nanolestes drescherae*, new genus and species, a stem-lineage representative of Zatheria, is represented by 48 isolated teeth, a dentary with p2 only, and an anterior dentary fragment with p3–p5 from the Kimmeridgian of the Guimarota coal mine, Portugal. Lower molars of *N. drescherae* have an enlarged, unicuspid talonid and a small additional cuspule on the cristid obliqua not referable to any of the standard talonid cusps. No trace of an incipient talonid basin is present. Tooth formula is I?/4, C?/1, P?/5, M?/5; all lower teeth except for incisors and m5 are double-rooted. The dentary has a well developed angular process, an internal groove extending beyond m3, and a mandibular foramen in an anterior position. Upper molars have a comparatively large stylocone; cusp ''C'' is present, stylar cusps are well developed, and additional cusps on the paracrista are present. The former attribution of these specimens to the peramurids cannot be corroborated. The ''Porto Pinheiro Molar'' from the latest Jurassic/earliest Cretaceous of Porto Pinheiro (or Dinheiro) is referred to *Nanolestes* as *N. krusati*, new species. There are no autapomorphies for Arguimuridae Dashzeveg, 1994. The teeth preserved in the holotype of *Arguitherium cromptoni* Daszheveg, 1994 are p3–p5 and not p4–m1 as assumed in the original description. The teeth described as upper molars of the symmetrodont *Thereuodon* Sigogneau-Russell, 1989 are posterior upper deciduous premolars (DP?3–5) of holotherians (probably zatherians).

INTRODUCTION

The Guimarota coal mine near Leiria in west-central Portugal is one of the most important localities for Late Jurassic (Kimmeridgian) small vertebrates, such as mammals, small dinosaurs, crocodiles, lizards, amphibians, and fishes (e.g., Kühne 1961, 1968a, b; Krebs, 1967, 1988, 1991; Hahn, 1969; Seiffert, 1973; Thulborn, 1973; Krusat, 1980; Weigert, 1995; Kriwet, 1997; Zinke, 1998; Martin, 1999). The Guimarota fossil lagerstätte has produced more than 800 dentaries and skull fragments of Docodonta, Multituberculata, and Dryolestida. *Henkelotherium guimarotae*, discovered in 1976 (Henkel and Krebs, 1977), is the only Jurassic holotherian mammal (Paurodontidae) for which an almost complete postcranial skeleton is known (Krebs, 1991). A partial skeleton of the docodont *Haldanodon exspectatus*, discovered in 1979 (Henkel and Krusat, 1980), indicates a fossorial lifestyle (Krusat, 1991). In addition to *H. guimarotae*, the Dryolestida is represented by a second paurodontid with a strongly elongated upper canine (Krebs, 1998) and at least three genera and species of Dryolestidae (Martin, 1999).

In a preliminary report on the mammals of the Guimarota mine, Kühne (1968a:121) briefly mentioned a very delicate, fragmentary ''pantothere'' dentary which he tentatively designated as ''cf. *Peramus*.'' Unfortunately, the dentary lacks all teeth except for p2. In the same report, Kühne noted a left and right isolated lower molar with two roots of equal size which fit the alveoli of ''cf. *Peramus*'' and which he provisionally attributed to this dentary. Sigogneau-Russell (1999:99–100) discussed the two isolated molars and came to the conclusion that one of them does not belong to a peramurid and that the attribution of the other specimen to the pretribosphenic lineage remains doubtful. However, the talonid is broken off in this specimen which leads to a more symmetrodont-like appearance.

The described holothere dentary and skull material from Guimarota (Krebs, 1998; Martin, 1999) was recovered through splitting coal chunks. No further specimens referable to ''cf. *Peramus*'' were apparently found in this fashion. However, numerous isolated teeth were recovered by using other methods in the field investigations, which spanned 1973–1982. After splitting coal chunks, about 100 kg of the resulting lignitic debris was processed each day, first by dissolution with caustic potash solution, and then by screenwashing with the Henkel process (Henkel, 1966). Teeth were picked out and instantly put in small sample boxes in the field; for every day a separate box was used for possible reconstruction of the distribution of fossils in the sediment body. The sorting of more than 10,000 teeth kept in about 2000 micro-cellules in 1997 yielded 25 lower and 23 upper isolated postcanine teeth and an anterior dentary fragment of this peculiar holothere taxon. In one single box three upper teeth and in another two lower teeth of ''cf. *Peramus*'' were found. They very probably derive from a single upper and lower jaw, respectively. Apparently the very small jaws or jaw fragments were overlooked by the workers splitting the coal. The jaw fragments were destroyed during screenwashing but the teeth survived the procedure almost undamaged. Although all teeth are isolated and no upper and lower teeth have been found in association, their small size and peculiar morphology make identification unambiguous. The discovery of the new teeth from the Guimarota coal mine also allows formal redescription and reinterpretation of the ''Porto Pinheiro Molar'' (Krusat, 1969) and an additional tooth from the uppermost Jurassic of Porto Pinheiro (or Dinheiro) near Lourinhã, Portugal.

MATERIALS AND METHODS

The teeth from Guimarota were collected in 1959–1962 (old collection) and from 1973–1982 (new collection) by the staff of the Institut für Paläontologie of the Freie Universität Berlin. In the Guimarota mine, two coal seams were commercially mined (upper and lower seam) until 1961 (Krebs, 2000). The material from the old collection derives from the period when the Guimarota mine was still commercially worked. Samples were taken from coal heaps and mining debris on the surface (Kühne, 1961a, b) so that an attribution to the upper or lower coal seam is not possible. In the second and main collecting period (new collection), the Guimarota mine was worked for paleontological purposes only and all samples were taken from the lower coal seam. The teeth from Porto Pinheiro (or Dinheiro) were collected in 1967 from fluvio-lacustrine beds by screenwashing with the Henkel process. The material studied here is currently housed at the Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität Berlin (**IPFUB**) under the collection numbers given (**Gui** = Guimarota, **Mam** = Mammalia and subsequent number, **PP** = Porto Pinheiro); **BMNH** = Natural History Museum, London. A camera lucida was used for the drawings. Measurements were taken with a high-precision reflex microscope (theoretical measuring accuracy, 2 μm). All measurements are given in millimeters; **L** = anteroposterior length; **W** = labiolingual width.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Infraclass HOLOTHERIA Wible, Rougier, Novacek, McKenna, and Dashzeveg, 1995
Superlegion TRECHNOTHERIA McKenna, 1975
Legion CLADOTHERIA McKenna, 1975
Sublegion ZATHERIA McKenna, 1975

Remark—Prothero (1981:321) defined Zatheria as Cladotheria which reduce to three molars and which possess a basined talonid exhibiting a hypoconulid and entoconid. Using this definition, which excludes the stem-lineage (Ax, 1984, 1985) of Zatheria [above node 11 and below node 17 in Prothero (1981: fig. 12)], the new genus described in this paper is not a member of Zatheria. However, McKenna and Bell (1997) included *Arguitherium* Dashzeveg, 1994 and *Arguimus* Dashzeveg, 1979 in Zatheria as incertae sedis. As in the new genus described here, both of these have a somewhat enlarged talonid which is not yet fully basined. Therefore, they are considered as representatives of the stem-lineage that is included in Zatheria, following the stem-lineage concept proposed by Ax (1984, 1985).

Infralegion indet.
Family indet. (''Arguimuridae'' Dashzeveg, 1994)

Remark—The family ''Arguimuridae'' Dashzeveg, 1994 differs only by a plesiomorphic character from the Peramuridae Kretzoi, 1946 respectively Peramura McKenna, 1975 [which itself lacks autapomorphic characters (Sigogneau-Russell, 1999: 96)]: the absence of a talonid basin, even though a comparatively large hypoconid is present. There are no autapomorphic characters present that would justify the erection of a family Arguimuridae. Consequently, members of ''Arguimuridae'' are here instead considered stem-lineage representatives of Zatheria McKenna, 1975.

Genus *NANOLESTES*, gen. nov.

Etymology—*νανος*, (Greek) dwarf, refers to the small size of the animal, and λεστης, which means predator. *Nanolestes* (male), small predator.

Diagnosis—Plesiomorphic stem-lineage representative of Zatheria with enlarged but basinless talonid on the double-rooted lower molars. Trigonid comparatively short (angle 50°), proto-, para-, and metaconid slender and acute. Metaconid in line with the protoconid, not shifted posteriorly. The talonid consists of a main cusp (hypoconid) and a small additional cuspule on the cristid obliqua. No cusps or crests are developed lingual to the cristid obliqua. Last premolar (p5) not molarized. Dentary very slender with well developed angular process and Meckel's groove extending below m2 anteriorly. Mandibular foramen at an anterior position near the origin of the coronoid process. Tooth formula I?/4, C?/1, P?/5, M?/5.

Upper molars with three roots and trigon basin [''trigon'' is here used to mean the ''primary trigon'' (Patterson, 1956) of pretribosphenic mammals] flat without any crest or bulge. Stylocone comparatively large and paracrista and metacrista separated into cusps and cuspules. Large cusp ''C'' between metacone and double-cusped metastyle. Additional cusp with two tips at the anterior border of the trigon near the base of the paracone. Trigon angle 65°.

Differential Diagnosis—On the lower molars, *Nanolestes* differs from *Peramus*, *Palaeoxonodon*, *Arguitherium*, *Magnimus*, and *Minimus* by the basinless talonid and more slender trigonid cusps. *Nanolestes* differs from *Abelodon* by the much narrower angle of the trigonid, the high paraconid and metaconid, the longer talonid, and smaller size. *Nanolestes* differs from *Arguimus* by the p5, which shows almost no tendency towards molarization, and by the more strongly developed anterolabial cuspule(s) on the lower molars. *Amphitherium* differs from *Nanolestes* by the greater number of molars (6 to 7), larger size, and a longer talonid. On the dentary, *Nanolestes* differs from *Peramus* and *Tendagurutherium* by the length of Meckel's groove. In *Nanolestes*, it extends below m2 anteriorly, but in *Peramus* it ends slightly posterior to p4 and in *Tendagurutherium* it does not reach the ultimate molar. *Nanolestes* differs from *Peramus*, *Tendagurutherium*, and *Brancatherulum* by the mandibular foramen, which is at an anterior position near the origin of the coronoid process.

On the upper molars, *Nanolestes* differs from *Peramus*, *Palaeoxonodon*, *Abelodon*, *Magnimus*, and *Afriquiamus* by the paracrista and metacrista, which are separated into cusps and cuspules. *Abelodon* differs from *Nanolestes* by its larger size and a much sharper ectoflexus. *Magnimus* differs from *Nanolestes* by its larger size, missing ectoflexus, very long (anteroposteriorly) parastyle, and very small stylocone. *Afriquiamus* differs from *Nanolestes* by the low paracone, double-cusped stylocone, very short (anteroposteriorly) parastylar region, and presence of only two roots.

Chronologic and Geographic Distribution—Late Jurassic (Kimmeridgian) of Guimarota (Portugal) and latest Jurassic/earliest Cretaceous (Tithonian–Berriasian) of Porto Pinheiro (or Dinheiro) near Lourinhã (Portugal).

Type Species—*Nanolestes drescherae*, sp. nov.

Referred Species—*Nanolestes krusati*, sp. nov.

NANOLESTES DRESCHERAE, sp. nov.
(Figs. 1, 2A–C)

Diagnosis—Differs from *Nanolestes krusati* by the presence of a smaller molar talonid and an anterobasal cingulum labial to the paraconid at the crown base. Molar talonid with only two cusps, lacking an additional cusp on the labial side of the hypoconid (present in *N. krusati*).

Etymology—*drescherae*, after Mrs. Ellen Drescher, Berlin, who prepared all the Guimarota specimens with great expertise and diligence.

Holotype—Gui Mam 1002, right lower molar from the middle of the tooth row (Figs. 1, 2A–C). A molar is designated as the holotype because many Mesozoic mammals are known only by isolated teeth and their systematics is mainly based on molar morphology.

Hypodigm—The holotype and the following specimens: lower teeth (molars if not otherwise indicated): Gui Mam 1000 (left); 1001 (left); 1003 (left); 1004 (left); 1005 (dp?2–3, left); 1006 (right); 1007 (sectioned for enamel analysis); 1008 (left); 1009 (left); 1010 (left); 1011 (left); 1012 (right); 1013 (dp?3–5, right); 1014 (left); 1015/1 (right) and 1015/2 (right), most probably from the same individual; 1016 (right); 1017 (right); 1018 (right); 1019 (dp?3–5, right); 1020 (right); 1021 (left); 1022 (left); 1040 (left); anterior dentary fragment with p3–5, broken roots of p2 and alveoli for i1–4, c, and p1 (Gui Mam 66/79); right dentary with p2 and alveoli for i1–4, p1–5, and m1–5 (Guimarota 19; ''cf. *Peramus*'' of Kühne, 1968a); upper

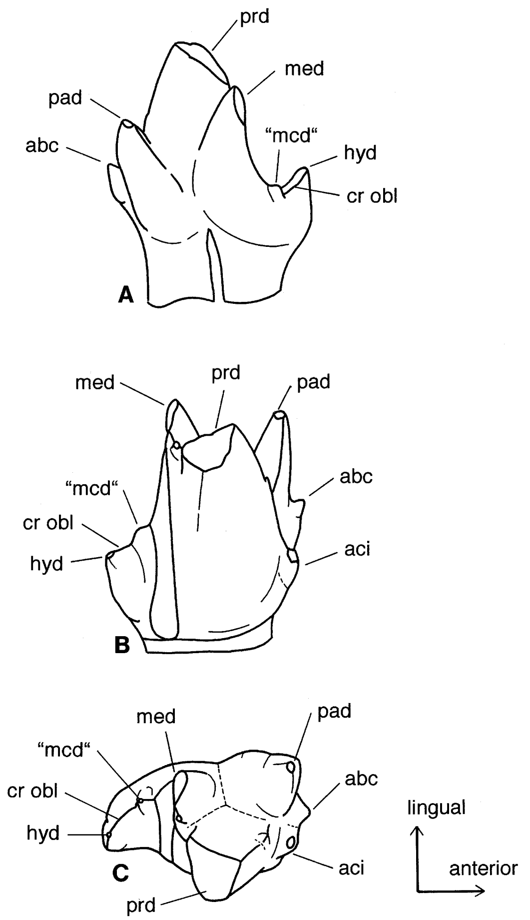


FIGURE 1. Lower molar of *Nanolestes drescherae*, sp. nov. with explanations of cusps (after Gui Mam 1002, holotype; protoconid broken). **A**, lingual view; **B**, labial view; **C**, occlusal view. **Abbreviations**: **abc**, anterobasal cuspule; **aci**, anterobasal cingulum; **cr obl**, cristid obliqua; **hyd**, hypoconid; **"mcd"**, "mesoconid"; **med**, metaconid; **pad**, paraconid; and **prd**, protoconid.

teeth (molars if not otherwise indicated): Gui Mam 1023/1 (P4 or 5, left), 1023/2 (left), 1023/3 (left), most probably from the same individual; 1024 (left); 1025 (left); 1026 (left); 1027 (DP? 3–5, left); 1029 (left); 1030 (left); 1031 (right); 1032 (right); 1033 (right); 1034 (DP? 3–5, right); 1035 (right); 1036 (left); 1037 (right); 1038 (right); 1039 (DP? 3–5, right, double-rooted, roots broken, tooth was not shed); 1041 (left); left maxilla fragment consisting of two maxillary fragments and five isolated teeth (C, P1–P4) and a possible molar fragment (Gui Mam 176/75).

Type Locality and Horizon—Guimarota coal mine in Leiria, central Portugal. Lower coal seam, "Guimarota-beds" (Schudack, 2000), Alcobaça Formation, Kimmeridgian, Late Jurassic.

NANOLESTES KRUSATI, sp. nov.
(Fig. 10A–C)

Etymology—For the late Dr. Georg Krusat, Berlin, who described the holotype in 1969 without naming it.

Diagnosis—Talonid slightly larger than in *Nanolestes drescherae* and with three cusps. Small cuspule on the middle of the cristid obliqua. Additional cusp on the labial side of the hypoconid. Small cuspule labial to the paraconid at the crown base ("vorderer Basalhöcker" of Krusat, 1969).

Holotype—PP 29/67, left lower molar with para- and metaconid broken (Fig. 10A–C).

Hypodigm—The holotype and PP 1000/67, right upper molar (Fig. 10D–E) from Porto Pinheiro (or Dinheiro), attributed to *N. krusati*.

Type Locality and Horizon—Top of southern cliff at Porto Pinheiro (or Dinheiro) near Lourinhã, Portugal. Tithonian-Berriasian (Mohr, 1989).

DESCRIPTION OF *NANOLESTES DRESCHERAE*, sp. nov.

Lower Molars

The lower molars have two well separated roots which are of equal size. In the holotype (Gui Mam 1002; Figs. 1, 2A–C), the terminal portions of both roots are broken off. The crown consists of three main cusps, protoconid, paraconid, and metaconid. All three are pointed and slender. The tallest cusp is the protoconid, followed by meta- and paraconid. The trigonid is comparatively short (anteroposteriorly) and the metaconid is aligned with the protoconid (not shifted posteriorly). Trigonid angle of molars is 50°.

The protoconid is bent somewhat posteriorly and has a triangular cross section with a broadly rounded labial side. The upper part of the protoconid is broken in the holotype, but is completely preserved in Gui Mam 1011 (Fig. 2G–I), an almost unworn lower molar. In this specimen, the unworn posterior cutting edge of the protoconid (posterior metacristid) bears a very small cuspule. The lingual side of the protoconid is slighly concave. The anterior cutting edge (paracristid) of the protoconid, which is slightly worn in the holotype, bears a tiny cuspule in its lower part. In the holotype, the anterolingual flank of the protoconid does not show any trace of wear. In Gui Mam 1002, only few tiny wear scratches are visible in the upper part of this area, no wear facet is present; it regularly occurs in Dryolestida from Guimarota. In Gui Mam 1000 (Fig. 2D–F), a large attrition facet is present at the anterobasal part of the protoconid; in the lower part of this facet the base of the anterobasal cuspule is visible (now nearly completely worn away). The anterobasal cuspule is completely preserved in the holotype and other lower molars which are less worn (e.g., Gui Mam 1011). In the holotype, a bulbous cingulum extends from the anterobasal cuspule to the buccal side of the protoconid where it fades.

The second highest cusp is the metaconid. In the holotype, it appears erect with a slender conical shape; on its posterior side it is deeply worn and a wear facet has cut part of its tip. In almost unworn lower molars, such as Gui Mam 1001, the metaconid has a sharply pointed tip which is slightly bent posteriorly. A deep V-shaped valley separates the metaconid from the protoconid; both cusps are labiolingually aligned.

The lowest of the main cusps is the paraconid. It is nearly erect and only slightly bent anteriorly. Its shape is not shovel-like but rather conical (somewhat flattened anteroposteriorly). In the holotype, the sharply pointed tip of the paraconid is preserved and bears a small wear facet; in Gui Mam 1000, the tip of the paraconid is removed by wear. Between the paraconid and protoconid is a narrow V-shaped valley. A fine cutting edge runs down the labial side of the paraconid; it does not contact the paracristid of the protoconid. Between the paraconid and metaconid is a wide V-shaped valley, opening the trigonid basin widely on the lingual side. In Gui Mam 1000, the paraconid has a small anterolingual cuspule near its base. It is in a more lingual position than the slightly larger anterobasal cuspule of the holotype.

The talonid is comparatively large and has one well developed cusp which sits near the lingual side of the crown. The posterior side of the talonid is rounded and its lingual flank is flat and does not protrude lingually. In the holotype, the talonid

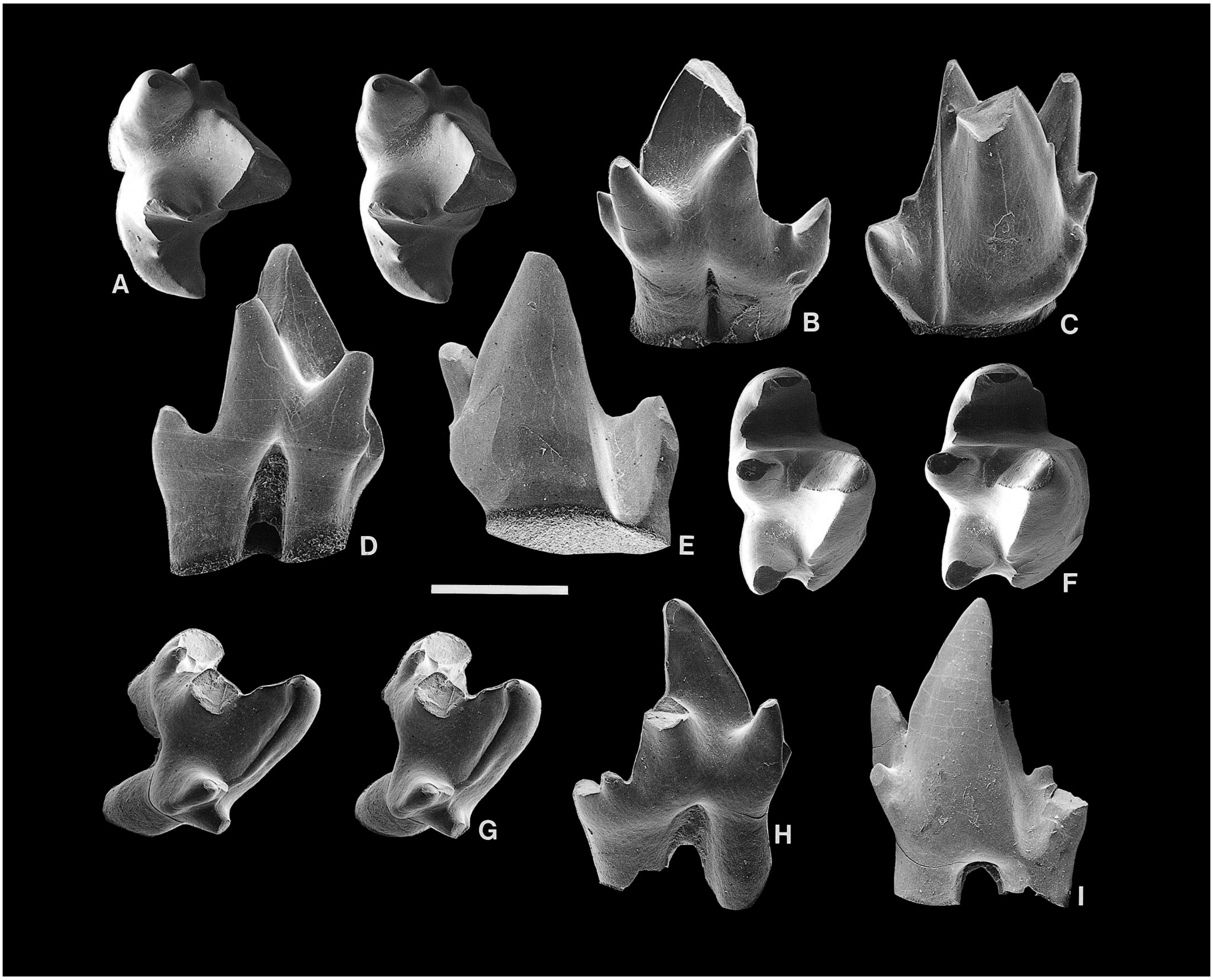


FIGURE 2. Lower molars of *Nanolestes drescherae*, sp. nov. Scale bar equals 0.5 mm. **A–C**, right molar, Gui Mam 1002 (holotype); **A**, occlusal view, anterior side pointing upwards (stereopair); **B**, lingual view; **C**, labial view. **D–F**, left molar, Gui Mam 1000; **D**, lingual view; **E**, labial view; **F**, occlusal view, anterior side pointing downwards (stereopair). **G–I**, left molar, Gui Mam 1011; **G**, occlusal view, anterior side pointing downwards (stereopair); **H**, lingual view; **I**, labial view.

is worn only near the contact with the metaconid. In other specimens, such as Gui Mam 1000, the talonid is more heavily worn and a deeply worn groove is present between the posterior side of the protoconid and metaconid and talonid which results from the paracone of the upper molar.

The talonid has a broad base with a pointed tip approximately in the middle of the posterior flank of the molar. This tip is worn away in some specimens (e.g., Gui Mam 1000) and therefore the position of the talonid appears somewhat shifted lingually. In the holotype, a very faint ridge runs downwards from the posterior flank of the metaconid to the tip of the talonid (also very clearly visible in Gui Mam 1001) which is the cristid obliqua. In the holotype and some almost unworn lower molars (Gui Mam 1004, 1011, and 1014), a small cuspule is located in the middle of the cristid obliqua which corresponds to the cuspule interpreted erroneously as an ''entoconid'' in the ''Porto Pinheiro Molar'' by Krusat (1969) and as a hypoconid in *Arguimus* by Dashzeveg (1979). According to Butler (1990: 535), this cuspule ''does not correspond with any of the standard talonid cusps present in tribosphenic molars but rather with the ''mesoconid'' of *Procerberus*, *Mixodectes*, etc.''

Lower Molar Enamel Microstructure

A fragmentary lower molar (Gui Mam 1007) was sectioned for enamel microstructure analysis. The enamel of *Nanolestes drescherae* is extremely thin. At the labial side of the protoconid it measures only 17 μm. A longitudinal section of the protoconid enamel exhibits indistinct prisms embedded in interprismatic matrix (Fig. 3). The indistinct prisms are most probably the result of the thin enamel; prism diameter usually lies between 3 and 5 μm, which corresponds to nearly one third of the entire enamel thickness of *Nanolestes*. Apart from therians, prismatic enamel is present in the Guimarota Dryolestidae (Martin, 1999), in the paurodontid *Henkelotherium*, and spalacotheriids (Wood and Stern, 1997), all of which have much thicker enamel, however. The Guimarota mammals have the oldest known prismatic enamel.

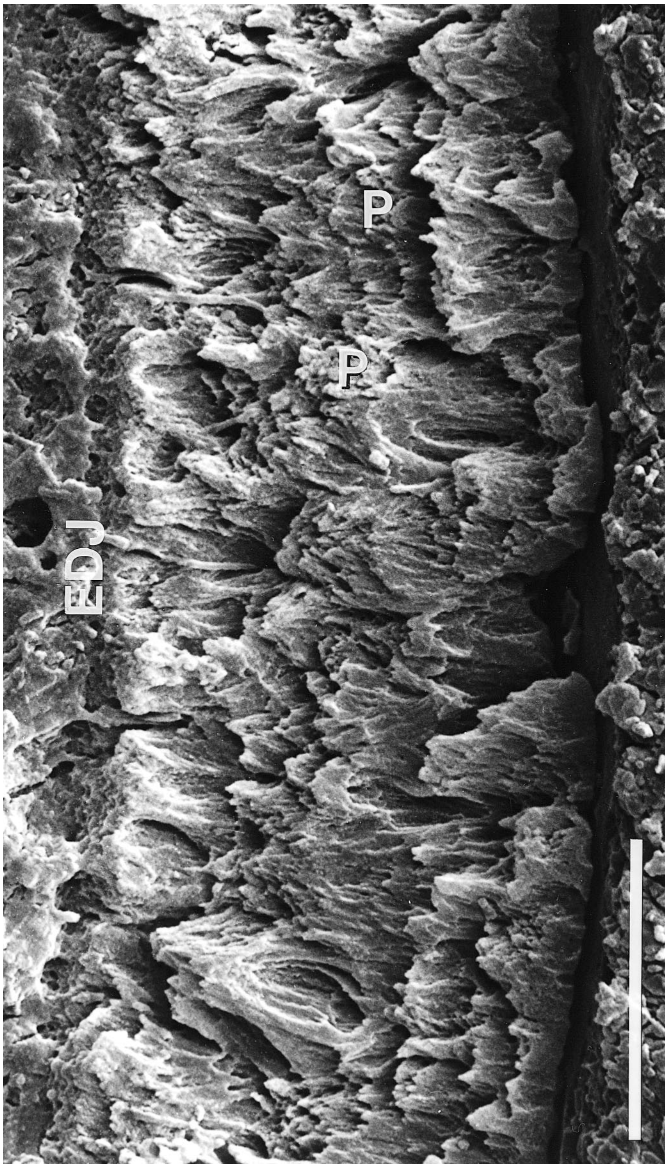


FIGURE 3. Enamel microstructure of lower molar (protoconid) of *Nanolestes drescherae*, sp. nov. (Gui Mam 1007). Enamel dentine junction (**EDJ**) to the left, outer enamel surface to the right; tip of protoconid pointing upwards. Prisms (**P**) are only very indistinctly visible. Scale bar equals 10 μm.

Lower Deciduous Premolars

Three lower molariform teeth (Gui Mam 1005, 1013, 1019) have strongly separated roots and somewhat different morphology from the molars. The crown is elongate in all three and the trigonid basin very widely open lingually, all characters which are typical for deciduous premolars. Complete juvenile dentitions of the Guimarota Dryolestidae were described by Martin (1997) with premolariform dp1 and dp2 and molariform dp3 and dp4. Therefore, Gui Mam 1013 and 1019 are interpreted as either dp3, dp4, or dp5. The less molarized Gui Mam 1005 (Fig. 4A–C) is likely from a more anterior position.

The highest cusp of the trigonid is the protoconid, followed by the metaconid and paraconid. The protoconid is broken in Gui Mam 1013 (Fig. 4G–I). The paraconid is less pointed than in a true molar and more shovel-like. Because it is less erect and much more procumbent than in a permanent molar, the trigonid appears longer and more open lingually. Two small additional cuspules are present on the lingual border of the trigonid, a larger one half way between para- and metaconid and a smaller one at the base of the metaconid. The accessory cuspule on the anterolabial side of the crown base is much smaller than in a permanent molar and the second cuspule is missing.

In Gui Mam 1013, the talonid is less pointed and exhibits more a rounded rim than a cusp; it appears slightly worn. The cristid obliqua runs from the metaconid at the lingual border of the talonid to the hypoconid. From the hypoconid a rim runs first labially and then turns anteriorly to the protoconid. This rim circumscribes a basin-like structure; at the posterolabial turning point is a small wear facet which has been caused by the paracone of an upper tooth. A small cuspule may have been present where the wear facet is now as is evident from a small cusp base; this cuspule does not correspond to the additional cusp which is also present in the ''Porto Pinheiro Molar'' (Butler, 1990:fig. 3). The anterior root of Gui Mam 1013 is broken at the base and the distal end of the posterior root is missing. Judging by the orientation of the anterior root base the roots were clearly separated. The broken anterior root gives view to a wide pulp cavity as is typical for deciduous teeth.

In Gui Mam 1019 (Fig. 4D–F), the crown is complete and generally resembles that of Gui Mam 1013. On the lingual border of the trigonid, there is only one additional cuspule present halfway between para- and metaconid. As in Gui Mam 1013, the talonid consists of the hypoconid at the lingual border of the talonid; the cristid obliqua between metaconid and talonid is weakly developed but clearly visible. A faint rim extends from the hypoconid forming the labial side of the talonid and fades at the labial base of the protoconid. The basin-like structure bears a large wear facet which is oriented labially. The roots are missing and most probably had been resorbed in vivo as evident from the pitted crown base, indicating that this is a shed milk tooth. The tooth crown has a wide pulp cavity.

Gui Mam 1005 (Fig. 4A–C) is less molarized than the other two, but all cusps are present. The trigonid basin is much more narrow (labiolingually) and the talonid basin structure is less developed. The highest cusp is the protoconid, followed by meta- and paraconid. The paraconid is less shovel-shaped than in the other deciduous premolars and more pointed. However, the roots are strongly separated giving the tooth a typical appearance of a dp. The talonid consists of the hypoconid and bears a strong labially oriented wear facet which has removed part of the hypoconid. The cristid obliqua is interrupted before reaching the metaconid and ends in a very small cuspule; another small cusp is at the base of the metaconid. Anterolabially at the base of the paraconid is a small anterior cuspule. Because of the less molarized shape, this tooth might be a dp2 or dp3. This interpretation is made somewhat uncertain by the fact that no complete milk dentitions of *Nanolestes* are known and that it has five premolars instead of four as in Dryolestidae.

Dentary ''cf. *Peramus*'' (Guimarota 19)

The dentary is preserved in three parts, the main slab with partial plastic cast, the posterior part of the dentary, and a small fragment with two alveoli in original bone preservation (Fig. 5). Only the anterior and posterior part of the right dentary are preserved in original bone on the main slab; the middle portion is preserved as a plastic cast of the bone impression in the coal. The anterior part contains the only preserved tooth, the p2; all other teeth had fallen out before fossilization as evident from the coal-filled alveoli. In the anterior section there are four alveoli for single rooted incisors; the lateral wall of the dentary bone is broken off which reveals the orientation of the alveoli. The alveolus for i1 is almost horizontal, indicating that i1 was procumbent. The alveoli of the following incisors are increas-

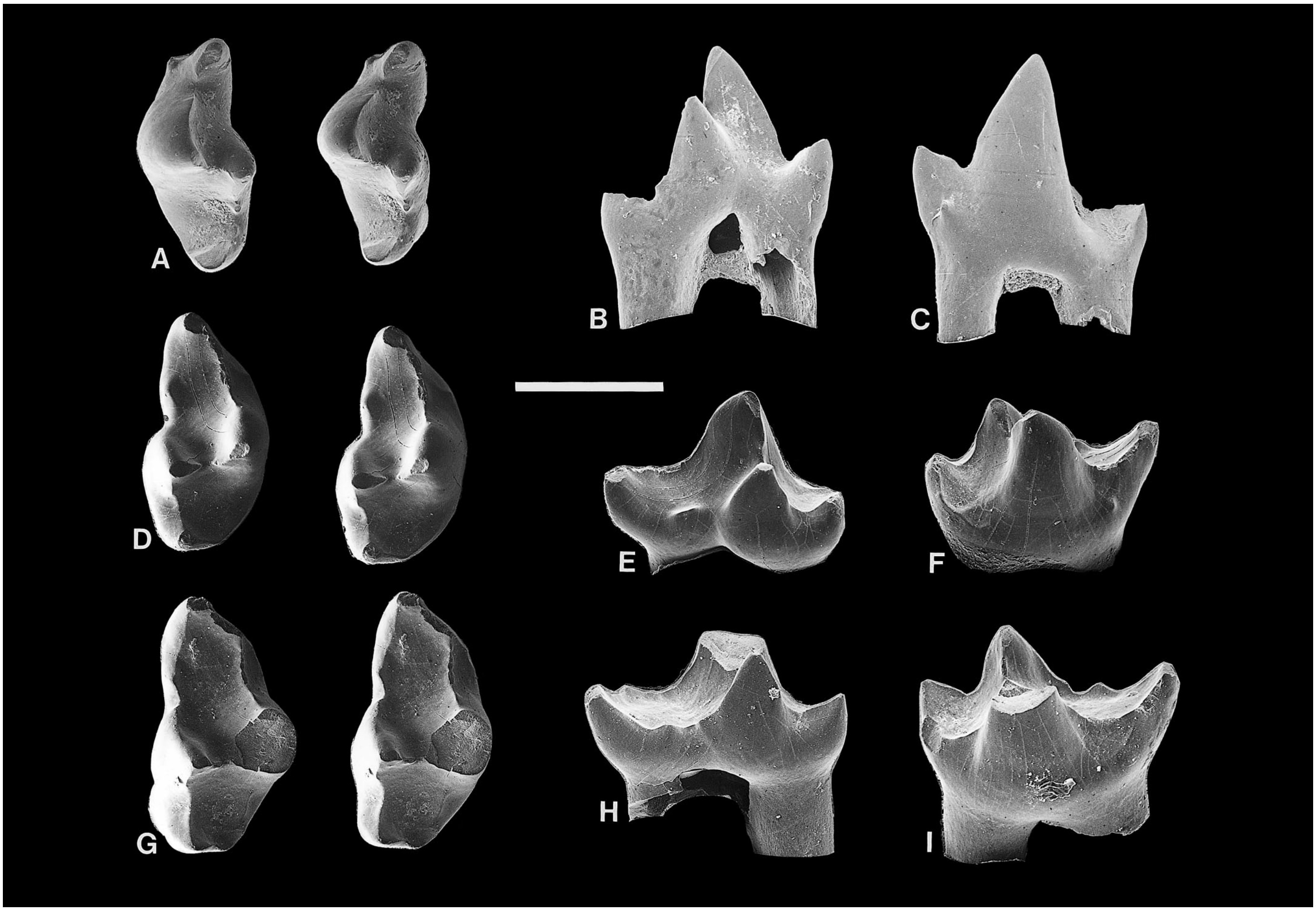


FIGURE 4. Lower deciduous premolars of *Nanolestes drescherae*, sp. nov. Scale bar equals 0.5 mm. **A–C**, left deciduous premolar (dp?2–3), Gui Mam 1005; **A**, occlusal view, anterior side pointing upwards (stereopair). **D–F**, right deciduous premolar (dp?3–5), Gui Mam 1019; **D**, occlusal view, anterior side pointing upwards (stereopair); **E**, lingual view; **F**, labial view. **G–I**, right deciduous premolar (dp?3–5), Gui Mam 1013; **G**, occlusal view, anterior side pointing upwards (stereopair); **H**, lingual view; **I**, labial view.

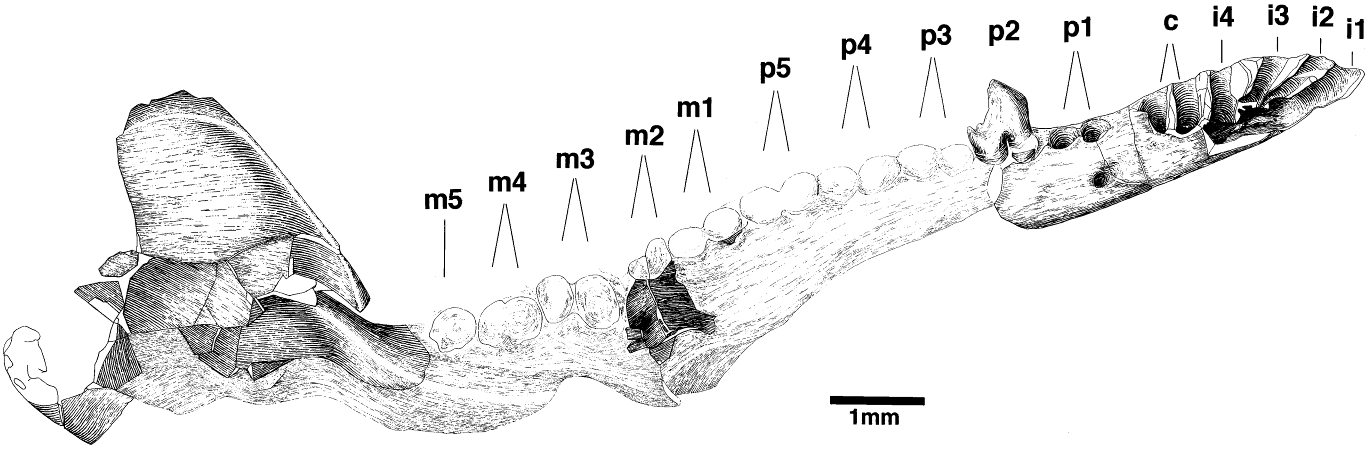


FIGURE 5. *Nanolestes drescherae*, sp. nov., right dentary (''Guimarota 19'') in labial view. Lightly drawn areas with alveoli for p3 to m5 are preserved as plastic cast of natural mold. At the position of alveoli for m2 the dentary is broken and slightly distorted.

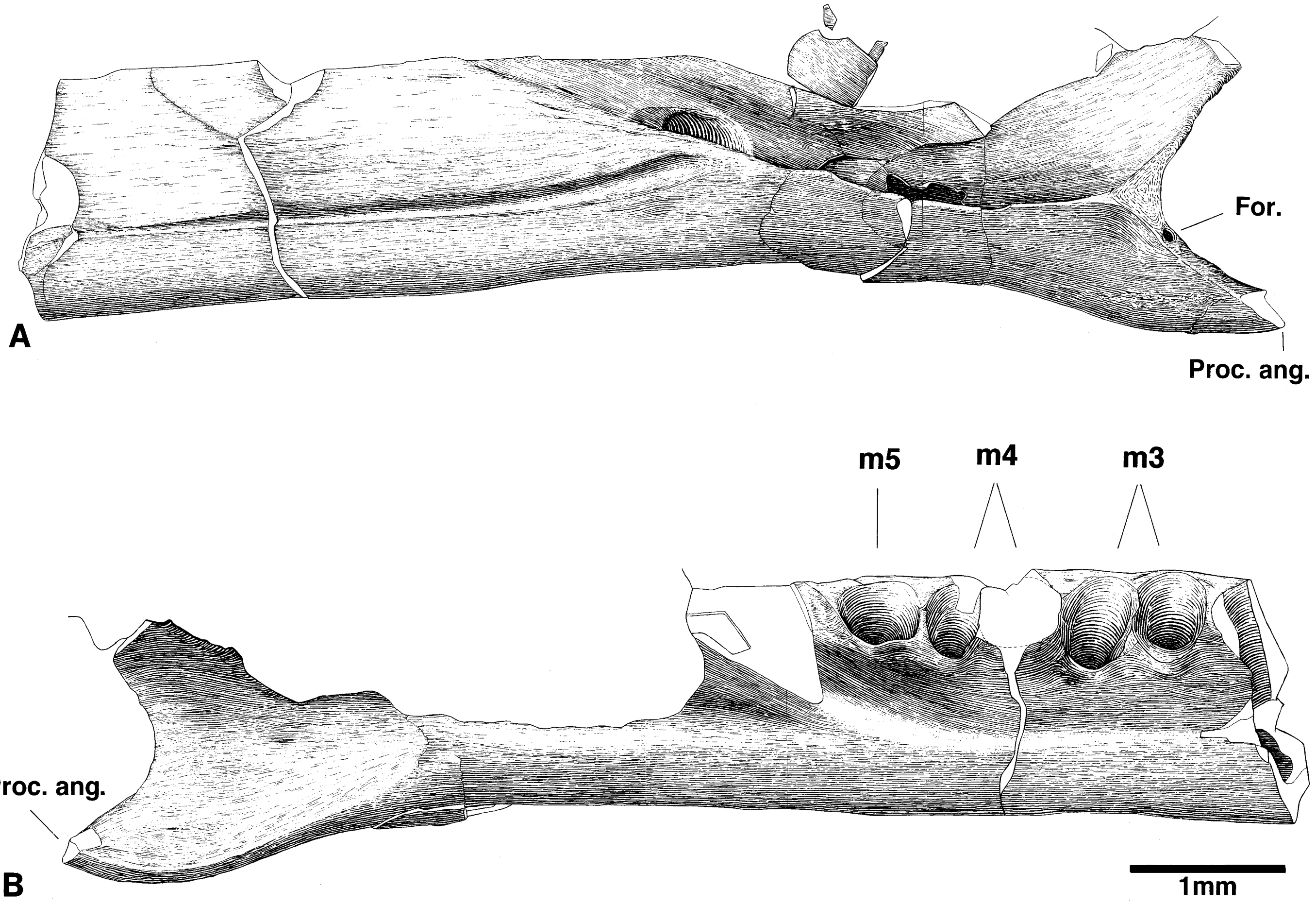


FIGURE 6. *Nanolestes drescherae,* sp. nov., posterior part of right dentary (''Guimarota 19''). **A**, lingual view with internal groove for the persisting Meckel's cartilage starting at the position of the mandibular foramen. Note the small foramen (**For.**) at the base of the angular process (**Proc. ang.**). **B**, labial view with alveoli for double-rooted m3 and m4 (anterior alveolus of m4 damaged) and single-rooted m5.

ingly more steeply inclined: i2 about 25°, i3 about 45°, and i4 about 70°.

Next to the alveolus of i4 are the alveoli of the double-rooted canine, of which the anterior is slightly wider than the posterior. The partially broken lingual wall of the dentary reveals that the canine was slightly bent anteriorly. The alveoli for the canine are separated from those of the double-rooted p1 by a short diastema. The alveoli of the p1 are slightly smaller than those of the canine and both of equal size. Immediately behind the alveoli for p1 follows p2 which is the only preserved tooth in the dentary. Its alveoli are about the same size as those of the p1. The following section of the dentary is only preserved as a plastic cast of the natural bone impression in the coal but the alveoli of the following teeth are easily recognizable. The alveoli of eight teeth can be detected behind p2. All except for the last one are double-rooted with both roots of equal size. The alveoli of the three teeth behind p2 are slightly increasing in size and are interpreted as alveoli of p3, p4, and p5.

The four paired alveoli behind those of the premolars are all larger and each pair is of equal size. The first pair is well preserved. In the region of the next pair, the dentary was broken and somewhat distorted; therefore the cast of the double-rooted alveolus is somewhat compressed. The double-rooted alveoli of the next two molars are clearly visible as impressions in the plastic on the main slab. In the isolated posterior dentary fragment those alveoli are present plus the posterior alveolus of m2. The last alveolus on the main slab is smaller than the anterior ones and single-rooted. The lower dental formula of *Nanolestes drescherae* can be reconstructed as 4/1/5/5 (m5 single-rooted).

As in *Peramus*, the corpus mandibulae is very slender and narrow. This clearly distinguishes Zatheria from Dryolestida, where the dentary is of considerable height. The dentary has an oval cross section with the ventral side rounded. The border of the alveoli is higher on the lingual side than on the labial side. A large mental foramen is visible on the labial side below the anterior root of p1.

A depression runs below the five preserved alveoli on the labial side of the isolated posterior dentary fragment and ends at the base of the coronoid process (Fig. 6B). The posterior dentary fragment has a well developed angular process which extends somewhat ventrally. The angular process is pointing backwards and tapers.

The coronoid process is preserved on the main slab and is visible in lateral aspect (Fig. 5). The bone material is fixed on plastic but partially broken and distorted. The coronoid process rises straight at about 45° from the dentary and has a smooth lateral surface. At the top it is rounded and on its posterior edge it runs downwards with only very slight indention. The origin of the condyle is preserved, but the condylar region is broken and deflected about 90° from its original position. Apparently a distinct transversely oriented condyle was present. The lingual side of the coronoid process is hidden in the plastic.

The lingual side of the dentary can be studied on the posterior dentary fragment (Fig. 6A). On this side, the dentary is flat and bears a well developed groove for Meckel's cartilage. The groove begins at the edge of the pterygoid fossa, runs slightly ventrally and then anteriorly parallel to the long axis of the dentary. The groove rapidly becomes shallow and has nearly disappeared at the broken edge of the dentary fragment (below m3); apparently it did not extend much further anteriorly. No detectable depressions or slight parallel grooves indicate the insertion of a splenial bone in contrast to the Guimarota Dryolestidae.

The pterygoid fossa is well developed and bordered lingually by a sharp edge. Anteriorly this edge runs smoothly onto the surface of the dentary where it fades. No trace of an insertion place for a coronoid bone is visible in the triangular area anterior to the pterygoid fossa. The large mandibular foramen has an anterior position and opens just below this triangular area into the pterygoid fossa; the bottom of the pterygoid fossa is damaged due to breakage. The angular process slopes somewhat on its lingual side. It points backwards with a slight ventral deflection and bears a small foramen at the posterior end. Above the origin of the angular process there is a triangular area with a cancellous bone surface; a small foramen is present at the ventromedial corner of this triangle.

Lower Premolar (p2)—The only tooth preserved in the right dentary assigned to ''cf. *Peramus*'' by Kühne (1968a) is the p2 (Fig. 5). The tooth is comparatively long (anteroposteriorly; Table 1) and double-rooted. The posterior root is somewhat stronger than the anterior one. The crown consists of an acutely triangular main cusp with slightly recurved tip and an elongated posterior heel. This heel bears two small cuspules which are arranged in an anteroposterior line with the main cusp. The labial flange of the crown is slightly rounded and the lingual side is flat. The anterior cutting edge is rounded and rises steeply. After having reached one third of the crown height it curves posteriorly towards the tip of the crown. The tip bears a small oval wear facet which is oriented in posterolingual direction. The posterior cutting edge is comparatively sharp and runs steeply down towards the posterior heel.

TABLE 1. Measurements of teeth (mm) of *Nanolestes drescherae*, sp. nov. and *Nanolestes krusati*, sp. nov. from Portugal.

Specimen	Length	Width
''Guimarota 19'', p2	0.72	0.27
Gui Mam 66/79, p3	0.75	0.33
Gui Mam 66/79, p4	0.83	0.37
Gui Mam 66/79, p5	0.81	0.41
Gui Mam 1000, m	0.89	0.59
Gui Mam 1001, m	0.89	0.56
Gui Mam 1002, m	0.90	0.56
Gui Mam 1003, m	0.96	0.57
Gui Mam 1004, m	0.99	0.56
Gui Mam 1006, m	0.99	0.52
Gui Mam 1008, m	0.76	0.49
Gui Mam 1009, m	0.68	0.49
Gui Mam 1010, m	0.89	0.50
Gui Mam 1011, m	0.90	0.49
Gui Mam 1012, m	0.95	0.57
Gui Mam 1014, m	0.80	0.48
Gui Mam 1015/1, m	0.68	0.47
Gui Mam 1015/2, m	0.76	0.60
Gui Mam 1016, m	0.84	0.55
Gui Mam 1017, m	0.79	0.54
Gui Mam 1018, m	0.74	0.54
Gui Mam 1021, m	0.70	0.62
Gui Mam 1022, m	1.07	0.59
Gui Mam 1040, m	0.94	0.55
PP 29/67, m	0.80	0.50
Gui Mam 1005, dp	0.84	0.44
Gui Mam 1013, dp	0.92	0.51
Gui Mam 1019, dp	0.88	0.46
Gui Mam 176/75, C	0.31	0.55
Gui Mam 176/75, P1	0.61	0.23
Gui Mam 176/75, P2	0.67	0.23
Gui Mam 176/75, P3	0.54	0.24
Gui Mam 176/75, P4	0.58	0.22
Gui Mam 1023/1, P4	1.07	0.49
Gui Mam 1023/2, M	1.09	1.01
Gui Mam 1023/3, M	1.02	0.82
Gui Mam 1024, M	0.56	0.81
Gui Mam 1025, M	0.79	0.62
Gui Mam 1026, M	0.68	0.78
Gui Mam 1029, M	0.95	0.96
Gui Mam 1030, M	0.84	0.84
Gui Mam 1031, M	0.87	0.86
Gui Mam 1032, M	0.63	0.54
Gui Mam 1033, M	0.84	0.84
Gui Mam 1035, M	0.94	0.58
Gui Mam 1036, M	0.72	0.52
Gui Mam 1037, M	0.66	0.70
Gui Mam 1038, M	0.64	0.84
Gui Mam 1041, M	0.85	0.83
PP 1000/67, M	0.83	0.94
Gui Mam 1027, DP	1.10	0.58
Gui Mam 1034, DP	1.06	0.53
Gui Mam 1039, DP	1.25	0.56

Anterior Dentary Fragment (Gui Mam 66/79)

Dentary—Gui Mam 66/79 is a left anterior dentary fragment (Fig. 7) with three preserved teeth (p3–p5); p2 is broken off, and all other teeth anterior to p2 fell out before fossilization as is evident from the coal-filled alveoli. The dentary fragment is strikingly slender and differs from all other lower holotherian dentaries from Guimarota except for ''Guimarota 19''. Therefore and based on the premolar morphology, this dentary fragment can be attributed to *Nanolestes drescherae*.

The dentary contains alveoli for four single-rooted incisors. As in ''Guimarota 19,'' the alveolus for the first incisor is oriented almost horizontally in the dentary; due to breakage, this alveolus is visible only in anterior aspect. Alveoli for subsequent incisors are increasingly more steeply inclined. A large mental foramen is visible on the labial side of the dentary just below the alveolus for i2.

Directly behind the alveolus for i4 follow the alveoli for the double-rooted canine; both sockets are of equal size and slightly smaller than the incisor alveoli. After the alveoli for the canine, separated by a small diastema, follow the somewhat smaller alveoli for the double-rooted p1; the anterior socket is slightly larger than the posterior. Both root fragments of the following broken p2 are still in place and are separated from p1 and p3 by small gaps. As judged from the diameter of its alveoli, p2 was slightly smaller than p1. The double-rooted, premolariform p3 is still in place and p4 is separated by a comparatively wide gap from p3. Morphologically it resembles p3 but is slightly larger. Immediately behind p4 follows a fifth premolariform tooth of the same general morphology which is interpreted as p5.

The dentary has a high-oval diameter with a more rounded labial and a flat lingual side; no trace of a groove for Meckel's cartilage is present. The rough bone surface of the symphyseal suture extends backwards below the alveoli for p1. The suture apparently was not co-ossified. Six mental foramina are visible on the labial side of the mandibular fragment. Large foramina open just below the alveolus of i2 and below the anterior root

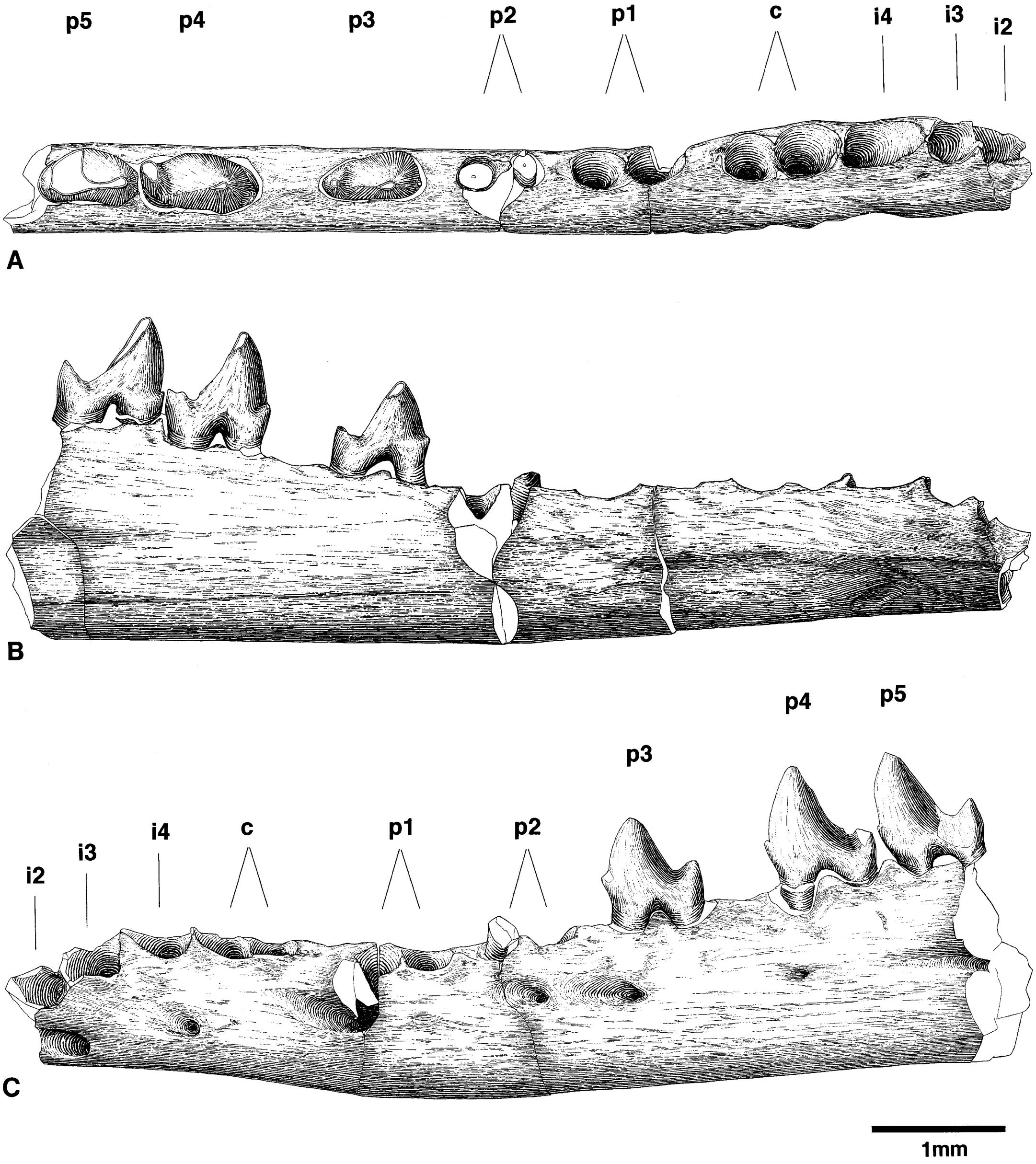


FIGURE 7. *Nanolestes drescherae*, sp. nov., anterior fragment of left dentary (Gui Mam 66/79) with alveoli for i1–4, c, p1, roots of p2, and p3–5 in place. **A**, occlusal; **B**, lingual; **C**, labial views. Note the large mental foramen below anterior root of p1; smaller foramina below i4, p2, p3, and p5. Small gaps anteriorly and posteriorly of p3.

of p1 (partially destroyed due to breakage); smaller foramina are present below the i4, p2, p3, and p5 (partially broken off).

Lower Premolars—All premolars are of typical premolariform shape with a triangular main cusp, small basal anterior cuspule and somewhat larger posterior basal cuspule. They are double-rooted with nearly equally sized anterior and posterior roots.

The main cusp of p3 is slightly recurved with a gently rounded labial and a flat lingual flank; the tip is cut by wear and bears a posterolingually oriented teardrop-shaped wear facet (Fig. 7). The anterior basal cuspule is not more than a small enamel bump; the posterior cuspule is well developed and bears a wear facet on its tip. On the anterior part of the labial side near the crown base, the main cusp bears a bulge-like structure; a lingual cingulum is not developed.

The p4 generally has a similar morphology as p3 but it is higher and its main cusp is more slender; apically it bears a posterolingually oriented oval wear facet. The anterior basal cuspule is better developed than that of p3 and slightly shifted lingually. From this anterior cuspule a bulge extends on the labial side and a much weaker bulge-like structure on the lingual side. The posterior basal cuspule is well developed, but its tip is missing due to wear. The cusp sits on a heel-like prolongation of the base of the tooth crown. If one follows the posterior cutting edge of the main cusp from the tip downwards, near the base a small accessory cuspule on the cutting edge is developed. The cuspule bears a very small wear facet and corresponds to the small accessory cuspule of p2 in ''Guimarota 19.''

The p5 is about the same size as p4 and more worn. The

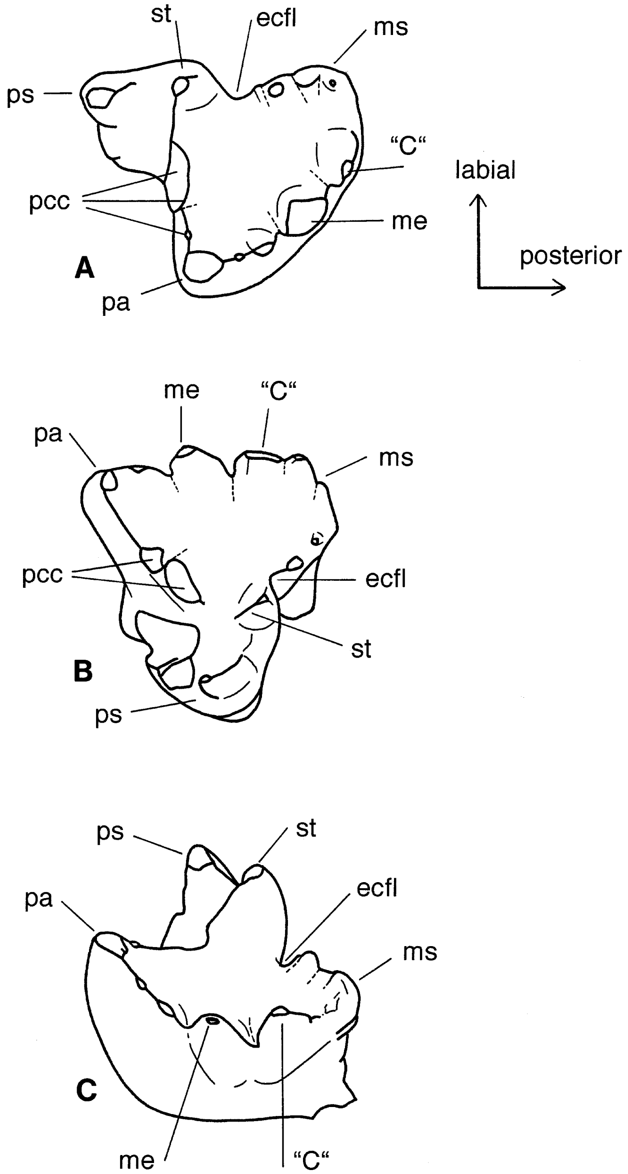


FIGURE 8. Upper molars of *Nanolestes drescherae*, sp. nov. with explanations of cusps. **A** and **B**, Gui Mam 1023/2, left molar; **C**, Gui Mam 1033, right molar. **A**, occlusal view; **B**, occlusoposterior view; **C**, occlusoanterior view. **Abbreviations**: **"C"**, cusp "C"; **ecfl**, ectoflexus; **me**, metacone; **ms**, metastyle; **pa**, paracone; **pcc**, paracrista cusps; **ps**, parastyle; and **st**, stylocone.

anterior basal cuspule is considerably smaller than on the p4, but the posterior accessory cusp is higher than its p4 equivalent. Bulge-like structures extend on the labial and lingual side of the crown base from the anterior basal cuspule. The tip of the main cusp is worn away and the whole posterior cutting edge bears an elongated wear facet which extends into the notch between posterior accessory cusp and main cusp. The anterior half of the accessory posterior cusp is worn away and the wear facet extends on the labial flank of the main cusp. If any cuspule on the posterior cutting edge was present, it would have been removed by wear.

Upper Molars

This description is primarily based on Gui Mam 1033 and 1023/2 (Figs. 8, 9A–D). The upper molars have three roots of nearly equal size, supporting the paracone, parastyle, and metastyle. In Gui Mam 1033 (left upper molar from middle tooth position, Figs. 8C, 9A, B) all roots are broken. The crown of the upper molar looks very different from that of all other holotherians. At first glance the large number of cusps and cuspules which surround the trigon basin is rather confusing. The anterior and posterior cutting edges, paracrista and metacrista, are separated into cusps and cuspules. Seen from occlusal view, the tooth crown has the shape of an equilateral triangle with the base facing lingually. The labial border of the trigon is not straight but sharply indented (ectoflexus) just posterior to the stylocone (Figs. 8, 9C). The trigon basin is completely flat without any ridges or bulges.

The highest cusp is the paracone at the lingual corner of the trigon basin. It is erect, but shifted somewhat anteriorly and is pointed. The paracone is comparatively small and slender and has a triangular cross section with rounded labial side. A very faint median ridge runs down the middle of the labial flank, which disappears before reaching the flat trigon basin. The stylocone is comparatively high and slender and is situated in the anterolabial corner of the trigon. It has a conical shape and is somewhat compressed labiolingually.

The interpretation of the cusps on the posterior border of the trigon seems difficult at first glance. Immediately labial to the paracone is a cusp of about the same height as the stylocone. It is compressed anteroposteriorly and separated from the stylocone by a narrow V-shaped notch. It is interpreted as the metacone because of its large dimensions and position. The metacone bears an oval attrition facet on its linguoposterior side. Labial to the metacone and separated from it by a deep V-shaped notch are three additional cusps. The most lingually positioned large cusp is interpreted as cusp "C"; both more labially sitting smaller cusps belong to the metastyle. The interpretation of the large cusp as cusp "C" is based on its position labial to the metacone and does not imply homology with similarly placed, tiny cuspules on the metacristae of some primitive tribotheres.

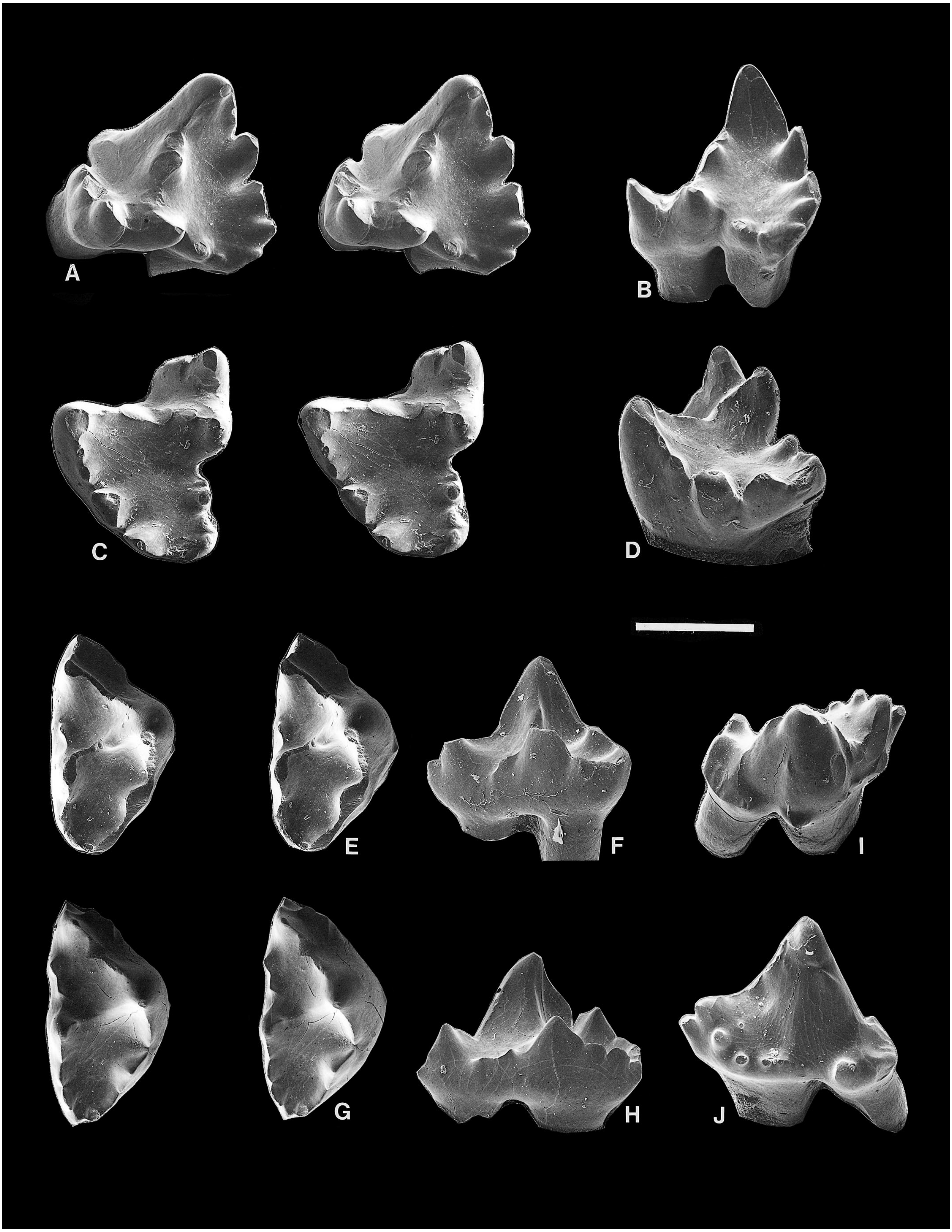
Cusp "C" is larger than the metastylar cusps and probably had the same original height as the metacone. Now its tip is worn away and the wear facet is oriented occlusoposteriorly. Labial to the larger metastylar cusp is a much smaller cuspule which shows only a very small wear facet. The smaller metastylar cusp is located in the labial corner of the metastyle and represents not much more than an enamel swelling. The metastyle is bounded by a slight notch on the lingual side.

At the labial border of the trigon, between metastyle and stylocone, is a small bulge with a tiny enamel cuspule. On the anterior border of the trigon, near the base of the paracone, is a cusp with two tips. The bigger, labial tip has a larger and the lingual one has a smaller wear facet; both wear facets are oriented anteriorly. These cusps cannot be attributed to one of the regular trigon cusps and are regarded as additional paracrista cusps.

The parastyle is well developed and bears two large and one very small cusps forming its anterior border. The surface of the parastyle rises occlusally from the lingual to the labial side. The labial cusp is the largest cusp and lies on a line with the labial metastylar cusp and the stylocone. It is slender and comparatively high and slightly compressed anteroposteriorly. The second parastylar cusp is broken and only its anterior wall is partly present; judged from the remaining parts, it was somewhat smaller than the more labial one. The third cusp is a small bud with a ridge forming the anterior border of the parastyle; the ridge ends near the base of the anterolabial root.

Upper Canine and Premolars

The box containing the teeth picked from the washing concentrate of the lignite sample processed on March 12, 1977


A
B
C
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E
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I
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yielded two left upper molars of *Nanolestes drescherae*. A left upper premolariform tooth of comparative size and with similar morphological characters such as the pronounced development of all cusps and cuspules was found in the same box (probably P4 or P5; Gui Mam 1023P, Fig. 9I, J). It is very probable that these teeth belong to the same individual, particularly because they have the same honey-golden color (the majority of the teeth from the Guimarota locality are black).

The premolar is double-rooted with the posterior root much stronger than the anterior one. The crown is formed by a large, acutely triangular main cusp (=paracone) with a rounded labial and a flat lingual flank. The paracone has no sharp cutting edges. The anterior edge is rounded and forms in the upper third a small enamel-ledge. The posterior cutting edge is rounded in the upper third and further downwards forms an irregular running edge.

On the labial side, the main cusp bears a broad ledge with a number of cuspules. On the anterolingual side, there is a comparatively large cuspule which is separated from the ledge by a notch. The ledge broadens posteriorly and the enamel cuspules become larger. At its posterior end, the ledge bears two comparatively large cusps which are situated one upon another.

The premolar exhibits a large wear facet on the anterior side near the base; apparently there was a large anterior cuspule which is now almost worn away. The labial side of the crown lacks a cingulum but has a number of enamel bumps. The notch which separates both roots is continued as a groove on the tooth crown and fades toward the tip of the tooth. The apex of the crown bears a wear facet facing posterolingually and on the lingual flank of the tooth an oval wear facet is visible. If one follows the posterior cutting edge posteriorly, there are small and large semilunar wear facets extending on the labial flank.

Gui Mam 176/75 is a badly crushed maxilla fragment which had fallen to pieces when it was isolated from the coal. It comprises two small maxillary bone fragments and five tiny teeth and a tooth fragment (labial portion of paracone from a molar). The teeth can be interpreted as C and P1–P4, and after their small size they correspond well with *Nanolestes drescherae*. The canine has an acutely triangular main cusp which is slightly recurved. It is double-rooted with the posterior root broken; apparently, the anterior root was slightly stronger than the posterior one.

The premolars are much smaller than P5 described above, which is similar to the dryolestid condition where only the last premolar (P4 in Dryolestidae) is enlarged. The determination of tooth loci was made after comparison with dryolestid upper dentitions from Guimarota. All premolars are double-rooted and have a triangular main cusp which is labiolingually flattened except for one premolar; they differ somewhat in size and presence of additional cusps. The smallest premolar (possibly P2) has a low main cusp and a comparatively large posterior heel with a well developed cuspule. The second largest premolar (possibly P1) has a more slender, higher main cusp and anterior and posterior cuspules of which the posterior is slightly larger. The third largest premolar (possibly P3) has an even higher acutely triangular main cusp which is slightly recurved. It has a posterior basal cuspule and a tiny anterior enamel bump. The roots and posterior portion are broken on the largest premolar; preserved are a triangular main cusp which is less flattened labiolingually than in the other premolars and an anterior basal cuspule. This tooth is interpreted as P4 because of the more conical shape of the main cusp.

Upper Deciduous Premolars

Among the upper cheek teeth, three molariform teeth (Gui Mam 1027, 1034, 1039) with only two roots differ somewhat from true molars (Fig. 9E–H). They are strikingly long and narrow which is typical for deciduous premolars. After comparison with upper deciduous dentitions of dryolestids from Guimarota, the teeth in question are either DP3, DP4, or DP5 because DP1 and DP2 are premolariform in Dryolestidae. The tooth crown of the molariform deciduous premolars consists of paracone, stylocone, metacone, parastyle, and metastyle. The largest cusp is the paracone and the second largest is the tetrahedron-shaped stylocone which is much smaller; both cusps are connected by a median ridge. The metacone is slightly smaller than the stylocone and labiolingually compressed; it is well distinct and separated from the paracone by a deep notch. The metastylar region consists of two labial and two posterolingual tiny cuspules which are separated by a posterior notch; the posterolingual cuspules are rather indistinct swellings on the posterolingual margin of the trigon basin border than clearly developed cuspules. The parastyle is large and well distinct from the trigon. It consists of a labiolingually compressed main cusp separated from the paracone by a V-shaped valley. There is a faint edge connecting the parastylar cusp and the paracone; it follows the V-shaped valley and is slightly worn. Labially to the main cusp are two small accessory cuspules and lingually to it a small ledge-like structure.

Gui Mam 1034 (Fig. 9E, F), an upper right DP3 or DP4, generally exhibits the same morphology but is more worn. The posterolingual flank of the metacone is strongly worn as is the whole metastylar region, where individual cuspules are no longer present. The tips of paracone, stylocone, and parastylar cusp bear wear facets and the edge between parastylar cusp and paracone is likewise worn.

DESCRIPTION OF *NANOLESTES KRUSATI*, sp. nov.

Lower Molar (PP 29/67)

A full description of the holotype, PP 29/67 (Fig. 10A–C), was given by Krusat (1969). It corresponds in size and morphology to the lower molars of *Nanolestes drescherae*. As in *N. drescherae*, an anterobasal cuspule is present. A major difference are the three cusps in the talonid of PP 29/67 (Fig. 10C). Following Butler (1990), the largest cusp is considered the hypoconid. The small cuspule on the cristid obliqua corresponds to that observed in *N. drescherae*, but the small cusp on the buccal side of the talonid is an accessory cusp not present in *N. drescherae*.

Upper Molar (PP 1000/67)

Among the isolated teeth from Porto Pinheiro (or Dinheiro), a right upper molar (Fig. 10D, E) compares closely to the upper molars of *Nanolestes drescherae* from Guimarota. The paracone is broken off, but the remaining cusps exhibit the same pattern as the upper molars of *N. drescherae*. The large metacone is separated from cusp ''C'' by a notch. Both cusps are

←

FIGURE 9. Upper teeth of *Nanolestes drescherae*, sp. nov. Scale bar equals 0.5 mm. **A** and **B**, right molar, Gui Mam 1033; **A**, occlusoanterior view, lingual side pointing upwards (stereopair); **B**, occlusolabial view. **C** and **D**, left molar, Gui Mam 1023/2; **C**, occlusal view, lingual side facing to the left (stereopair); **D**, occlusoposterior view. **E** and **F**, right deciduous premolar (DP?3–5), Gui Mam 1034; **E**, occlusal view, anterior side pointing upwards (stereopair); **F**, labial view. **G** and **H**, right deciduous premolar (DP?3–5), Gui Mam 1039; **G**, occlusal view, anterior side pointing upwards (stereopair), **H**, labial view. **I** and **J**, left premolar (P4 or 5), Gui Mam 1023/1; **I**, occlusolingual view, **J**, occlusolabial view.

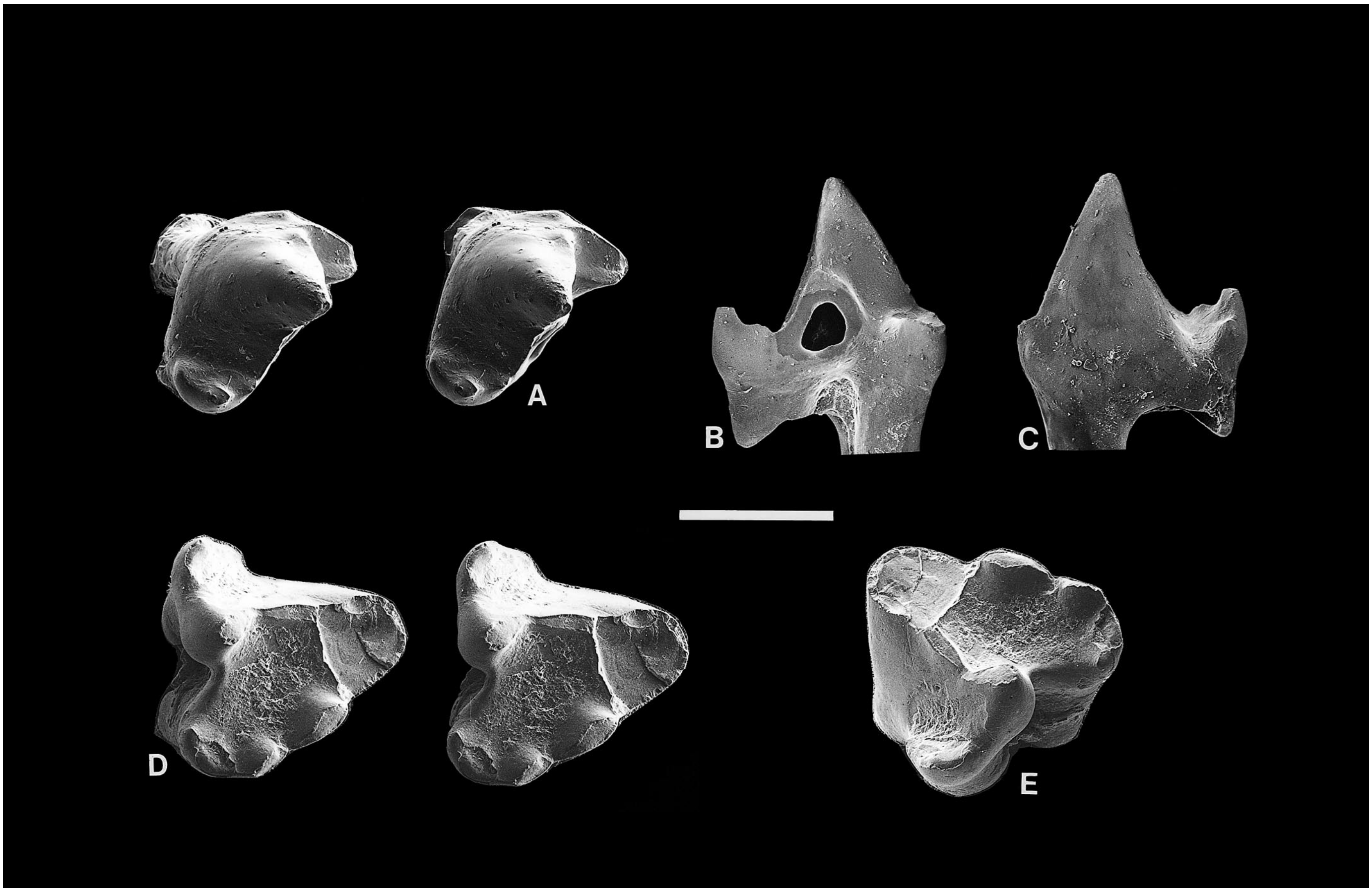

FIGURE 10. Teeth of *Nanolestes krusati*, sp. nov. from Porto Pinheiro (or Dinheiro). Scale bar equals 0.5 mm. **A–C**, lower left molar, PP 29/67 (holotype), ''Porto Pinheiro Molar''; **A**, occlusal view, anterior side pointing upwards; **B**, lingual view; **C**, labial view. **D–E**, upper left molar, PP 1000/67; **D**, occlusal view, labial side pointing to the left; **E**, occlusoanterior view.

considerably worn. The metastyle is broken and therefore it is difficult to say how many metastylar cusps were present. As in *N. drescherae*, a small cuspule is present on the labial side of the trigon close to the metastyle. The stylocone is slightly higher than the metacone and somewhat worn. The anterior cutting edge (paracrista) bears an elongate wear facet; apparently there were no cuspules present on the paracrista, such as occur in *N. drescherae*. The parastyle has a very similar shape to those of the upper molars from the Guimarota locality; however, the parastylar cusps are less strongly developed. As in *N. drescherae*, the trigon basin is completely flat, and the labial border of the tooth crown has a distinct ectoflexus. Due to its great resemblance to the upper molars from Guimarota, PP 1000/67 is referred to *Nanolestes krusati*.

DISCUSSION

Comparisons

Dentary—The well developed angular process on the dentary clearly indicates that *Nanolestes* is a member of the Cladotheria. The dentary of *Nanolestes* differs from that of *Peramus tenuirostris* from the Berriasian (Mills, 1964; Clemens and Mills, 1971) and the possible peramurids *Tendagurutherium* and *Brancatherulum* from the Upper Jurassic of Tendaguru, Tanzania (Dietrich, 1927; Simpson, 1928; Heinrich, 1991, 1998) by the anterior position of the mandibular foramen. This plesiomorphic condition is shared with other non-peramurid holotheres such as Dryolestidae and Paurodontidae (Simpson, 1928; Prothero, 1981; Krebs, 1991; Martin, 1999).

Meckel's groove (internal groove) ends in *Peramus* slightly posterior to m4 (Clemens and Mills, 1971:fig. 1A), and in *Tendagurutherium* it also does not reach the position of the ultimate molar (Heinrich, 1998:figs. 4, 5). It extends at least to the position of m3 in *Nanolestes* and probably further anteriorly (dentary fragment Gui Mam 66/79 is broken anterior to the alveolus of m3). Meckel's groove extends to the symphysis in *Amphitherium*, Dryolestidae, and Paurodontidae, the primitive condition. The presence or absence of a rudimentary coronoid bone in *Nanolestes* remains unknown because this part of the dentary is not preserved in internal aspect.

Lower Molars—The lower molars of *Nanolestes* exhibit the typical synapomorphies of Holotheria. The tooth crown consists of three main cusps, protoconid, metaconid, and paraconid. The protoconid is the highest cusp and the paraconid is lower than the metaconid, but the size difference between the protoconid and the two other cusps is not very strong. The equal-sized roots, the lack of an anteroposterior compression of the tooth crown, the pointed and not procumbent paraconid, as well as the enlarged talonid cusp exclude *Nanolestes* from Dryolestidae and Paurodontidae. The angle of the trigonid in *N. drescherae* (50°) is close to *Amphitherium* (45–55°) but considerably narrower than in *Peramus* (60°).

Amphitherium (Amphitheriidae) has an enlarged unicuspid talonid (larger than in *Nanolestes*). It differs from *N. drescherae* by greater number of molars (6 to 7) and larger size (Mills, 1964). Anterior basal cuspules are lacking in the lower molars of *Amphitherium*, but an anterolabial cingulum is present which was considered a primitive character by Sigogneau-Russell (1999). Sigogneau-Russel (1999) interpreted the crest running from the metaconid to the talonid cusp as the metacristid and in the lower molar BMNH M 36822 observed a faint entocristid. These characters were interpreted as synapomorphic with Zatheria, and Sigogneau-Russell (1999) considered *Amphitherium* the sister group of Zatheria.

The main talonid cusp of *Nanolestes* is here interpreted as a hypoconid following Butler (1990:fig. 3) who compared the molars of peramurids and their relatives. Following Butler (1990), the hypoconid and hypoconulid are united in one cusp in *Nanolestes krusati* (''Porto Pinheiro Molar'') and in *Arguimus khosbajari*. Both *N. krusati* and *Arguimus* (and the peramurids *Peramus* and *Palaeoxonodon* except for some specimens of *Peramus tenuirostris*) show a small cuspule on the middle of the crista obliqua which does not correspond with any of the standard talonid cusps of tribosphenic molars (Butler, 1990:535). This cuspule was erroneously homologized with the hypoconid in *Arguimus* (Dashzeveg, 1979) and with the entoconid in the ''Porto Pinheiro Molar'' (Krusat, 1969). This additional cusp is also clearly visible in some lower molars of *Nanolestes drescherae* (Gui Mam 1002, 1004, 1011, 1014) and is possibly a synapomorphy for peramurids, *Arguimus*, and *Nanolestes*. *Peramus* is distinct from *Arguimus* and *Nanolestes* by the development of a hypoconulid posterolingually from the hypoconid and an incipiently basined talonid. Butler (1990) proposed that the area lingual to the cristid obliqua in *Peramus* (Mills, 1964; Clemens and Mills, 1971) and *Palaeoxonodon* from the Middle Jurassic of Kirtlington (Freeman, 1976, 1979) is homologous with the talonid basin of tribosphenic molars. This lingual area with an incipient basin is absent in *Nanolestes* and *Arguimus*; they therefore are excluded from the ''Peramura.'' *Nanolestes* is interpreted as an early stem-lineage representative of Zatheria with a somewhat enlarged (anteroposteriorly elongated) talonid which does not yet show any basin development.

Upper Molars—In the upper molars, *Nanolestes* can easily be distinguished from members of the Dryolestidae by the following plesiomorphic characters: the trigon is not shortened, the stylocone is not enlarged, and the metacone is not reduced. *Nanolestes* lacks any median ridge (present in *Laolestes*) or bulge (present in *Drescheratherium* and *Krebsotherium*) in the trigon basin which distinguishes it from Dryolestidae and Paurodontidae. The general resemblance of the upper molars of *Nanolestes*, *Palaeoxonodon*, and *Peramus* is based on plesiomorphic characters such as a small (compared to Dryolestidae) stylocone, obtuse trigon angle and flat trigon basin. However, the metacone is not shifted in one line with the paracone as in *Peramus*; in this regard, *Nanolestes* remains more primitive. Unfortunately, the upper teeth of *Amphitherium* are not known; judging by the resemblance of the lower molars, it can be assumed that they resembled the morphotype of *Nanolestes*. As in *Peramus* and *Palaeoxonodon*, a sharp ectoflexus is present on the labial side of the trigon in *Nanolestes* which is considered a synapomorphic character.

A very striking autapomorphic character of *Nanolestes* is the enlargement and/or elongation of the metacone, cusp ''C,'' and para- and metastylar cusps. Furthermore, a number of accessory cusps are developed, of which the cusps on the paracrista are most bizarre. This cusp pattern has never been observed in Dryolestoidea or any other Zatheria. The paracrista is no longer a blade-like cutting edge as in *Peramus* and *Palaeoxonodon*, but divided into a number of separate cups with individual wear facets.

Reinterpretation of the Questionable Symmetrodont *Thereuodon* Sigogneau-Russell, 1989

Sigogneau-Russell (1989) erected a new symmetrodont genus and species, *Thereuodon dahmanii*, based on an upper cheek tooth from the Early Cretaceous of Anoual (Morocco). The tooth which is rather long (anteroposteriorly) and narrow (labiolingually) was interpreted as a left upper molar. The discovery of deciduous premolars of *Nanolestes drescherae* from Guimarota suggests a reinterpretation of the tooth from Anoual. The holotype of *T. dahmanii* (Sigogneau-Russell, 1989:figs. 1, 2) shows striking similarities to the DP?3–5 of *N. drescherae* (Fig. 9E, F), notably the obtuse trigon angle (giving the tooth a long and narrow shape), a comparatively low and recurved paracone, and subdivison of the trigon basin by a crest running from the paracone to the stylocone. Sigogneau-Russell and Ensom (1998) described five upper teeth from the Lower Cretaceous Purbeck Limestone Group in southern England and created a new species, *Thereuodon taraktes*. Both species of *Thereuodon* were included in the new symmetrodont family Thereuodontidae. Although the upper teeth attributed to *T. taraktes* differ slightly from the specimens from Anoual, they exhibit the same characters that are typical for holotherian upper deciduous premolars, such as the labiolingual narrowness of the tooth crown and the median ridge. Therefore the upper cheek teeth attributed to *Thereuodon* by Sigogneau-Russell (1989) and Sigogneau-Russell and Ensom (1998) are reinterpreted as deciduous posterior upper premolars (DP?3–5) of holotherians (probably zatherians). Currently it is not possible to attribute these teeth to a specific genus because several holotherian (and zatherian) genera have been described from both localities (e.g., *Minimus* and *Afriquiamus* from Anoual; *Magnimus* and *Peramus* from the Purbeck Limestone Group). The overall similarity between these upper deciduous premolars and the upper cheek teeth from the Upper Cretaceous Los Alamitos Formation (Patagonia) that were assigned to a new genus *Barberenia* (and new family Barbereniidae) by Bonaparte (1990) is because the latter are also deciduous upper premolars (possibly of the ?spalacotheriid *Brandonia* Bonaparte, 1990). This was suggested by Martin (1999) after comparison with deciduous upper dentitions of Guimarota dryolestids.

Reinterpretation of Tooth Loci in the Dentary of *Arguitherium cromptoni* Dashzeveg, 1994

Dashzeveg (1994) described the new ''eupantotherian'' *Arguitherium cromptoni* based on an anterior dentary fragment containing three teeth and eight alveoli. The teeth were interpreted by Dashzeveg as p4, p5, and m1, and the alveoli anterior to p4 as those of c (double-rooted), single-rooted p1, and double-rooted p2. Behind m1, the alveoli of the double-rooted m2 and part of the alveolus for the anterior root of m3 are visible. Comparison with the dentition of *Nanolestes drescherae* casts doubt on this interpretation of tooth positions. The mental foramina in the dentary can be used as landmarks for defining tooth loci. In the dentary fragments of *N. drescherae* (''Guimarota 19'' and Gui Mam 66/79), a large foramen is present below the anterior root of the double rooted p1, and a second, smaller foramen below the anterior root of p3. In the dentary fragment figured by Dashzeveg (1994:fig. 1A), a foramen below the first preserved premolar is present; anterior to this foramen another mental foramen is visible below the second and third alveolus (counting from the anterior root of the first preserved premolar). The position of the anterior mental foramen in *Nanolestes* corresponds well with the situation in *Peramus*, where a mental foramen is present between double-rooted p1 and p2; a second foramen is located below the posterior root of p4 (Clemens and Mills, 1971:fig. 1C), which differs from the situation in *Nanolestes*. The first preserved premolar in the dentary fragment of *Arguitherium* is probably not p4, but is instead p3. If this is the case, the alveoli anterior to the first preserved premolar belong to p2 and p1 (both double-rooted); from the canine only a fragment of the posterior alveolus is preserved at the broken anterior end of the dentary. This interpretation is in accordance with the observation that p2 in dryolestids is generally the smallest premolar. The alveoli in front of p3 (following the new interpretation) are indeed slightly smaller than those of p1. According to Dashzeveg's (1994) interpretation, p1 is single-rooted in *Arguitherium*. Among Jurassic–early Cretaceous holotherians, a single-rooted p1 has been observed only in the Early Cretaceous *Crusafontia cuencana* (Henkel and Krebs, 1969; Martin, 1998) from Uña (Spain) which represents the last European representative of the Dryolestidae. The p1 is double-rooted in all other Dryolestida, *Amphitherium* (Mills, 1964), *Peramus* (Clemens and Mills, 1971), and *Nanolestes*. As mentioned above, if any tendency towards size reduction in premolars occurs, it is in p2 rather than p1. The posterior preserved tooth in the dentary of *Arguitherium*, interpreted by Dashzeveg (1994) as m1, does not look like a molar. It has a main cusp (protoconid), but it lacks para- and metaconids. Therefore it has the typical shape of a premolar with only a single molar-like character, the elongated talonid heel, which is, however, unicuspid. This tooth is here interpreted as a slightly molarized p5. This interpretation of tooth loci in *Arguitherium* is in accordance with Sigogneau-Russell (1999:98).

Number of Premolars in Early Stem-Lineage Representatives of Tribosphenida

Judging by tooth morphology, *Nanolestes* clearly has five premolars in the dentary. All are double-rooted and premolariform (p1 is not preserved in any of the dentaries studied). The shape of the premolars of *Nanolestes* resembles that of the premolars in *Arguitherium* and *Peramus*, except for p5, which is semimolariform in *Peramus* but premolariform in *Nanolestes*. Therefore, *Nanolestes* supports the hypothesis forwarded by McKenna (1975) and Novacek (1986) that five premolars represent the primitive condition for Tribosphenida, if no premolar was lost in the tribothere-lineage after *Nanolestes* had split off from it. The number of premolars in the Guimarota Dryolestidae is four, as was shown by morphological comparison and mode of tooth replacement (Martin, 1997, 1999). Apparently, Dryolestidae is derived in this regard; the tendency to reduce the number of premolars is even stronger in Paurodontidae from Guimarota (Krebs, 1998) and North America (Simpson, 1929). Cifelli (2000) discussed the premolar count in early eutherian mammals. He noted that in early eutherians with five premolars, the middle (third) premolar is probably a retained deciduous premolar, as was proposed by Luckett (1993). There is no morphological evidence in *Nanolestes* that the third premolar is a deciduous premolar, because it does not differ from the other premolars. In Dryolestidae, dp3 and dp4 are semimolariform or molariform, and isolated deciduous premolars (possibly dp3–5) of *Nanolestes* are also molariform. This supports the interpretation of the middle lower premolar of *Nanolestes* as p3 instead of dp3.

CONCLUSIONS

With the improvement of the fossil record for early mammals the number of pretribosphenic holotherians described in the literature increases steadily. As is the case for peramurids (Sigogneau-Russell, 1999), unambiguous autapomorphic characters are missing for most of these pretribosphenids, due to their plesiomorphic nature and the fragmentary condition of the fossils (mostly isolated teeth and jaw fragments). This creates problems for their suprageneric classification. As demonstrated for *Nanolestes*, these plesiomorphic taxa are best placed in the stem-lineage of Zatheria. The stem-lineage of a taxon is defined as the lineage between the last common ancestor of this taxon and its sister-taxon (Ax, 1984, 1985). The stem-lineage of Zatheria lies between the separation of Dryolestoidea and the last common ancestor of *Peramus* and Tribosphenida. Other stem-lineage representatives of Zatheria are *Arguimus* Dashzeveg, 1979, *Arguitherium* Dashzeveg, 1994, *Abelodon* Brunet et al., 1991, *Magnimus* Sigogneau-Russell, 1999, *Minimus* Sigogneau-Russell, 1999, *Afriquiamus* Sigogneau-Russell, 1999, and *Amphitherium* de Blainville, 1838.

The description of *Nanolestes drescherae* from Guimarota finally makes possible the systematic affiliation of the enigmatic ''Porto Pinheiro Molar,'' which has puzzled researchers for over three decades. Having lost its pivotal position for the evolution of the tribosphenic molar (Butler, 1990), the ''Porto Pinheiro Molar'' nevertheless plays an important role for the discussion of ''talonid experiments'' at the pretribosphenic stage. Completely tribosphenic molars were recently described from the Middle Jurassic (Barremian) of Madagascar (Flynn et al., 1999), which sets the evolution of the tribosphenic molar back to the Middle or probably even Early Jurassic. If this Gondwanan lineage did not evolve in parallel with Laurasian Tribosphenida (Luo et al., 2001), *Nanolestes* and the other pretribosphenic stem-lineage representatives of Zatheria from the Northern Hemisphere and northwestern Africa were already ''old timers'' in the Late Jurassic and Early Cretaceous.

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LITERATURE CITED

Ax, P. 1984. Das Phylogenetische System. Gustav Fischer Verlag, Stuttgart, 349 pp.

——— 1985. Stem species and the stem lineage concept. Cladistics 1: 279–287.

Blainville, H. M. D. de. 1838. Doutes sur le prétendu Didelphe de Stonesfield. Comptes Rendus de l'Académie des Sciences, Paris 7: 402–418.

Bonaparte, J. F. 1990. New Late Cretaceous mammals from the Los Alamitos Formation, Northern Patagonia. National Geographic Research 6:63–94.

Brunet, M., Y. Coppens, J. Dejax, L. Flynn, E. Heintz, J. Hell, L. Jacobs, Y. Jehenne, G. Mouchelin, D. Pilbeam, and J. Sudre. 1991. Nouveaux mammifères du Crétacé inférieur du Cameroun, Afrique de l'Ouest. Comptes Rendus des Séances de l'Acadmeémie des Sciences Paris 310:1139–1146.

Butler, P. M. 1990. Early trends in the evolution of tribosphenic molars. Biological Reviews 65:529–552.

Cifelli, R. L. 2000. Counting premolars in early eutherian mammals. Acta Palaeontologica Polonica 45:195–198.

Clemens, W. A., and J. R. E. Mills. 1971. Review of *Peramus tenuirostris* Owen (Eupantotheria, Mammalia). Bulletin of the British Museum (Natural History) Geology 20:89–113.

Dashzeveg, D. 1979. *Arguimus khosbajari* gen. n., sp. n., (Peramuridae, Eupantotheria) from the Lower Cretaceous of Mongolia. Acta Palaeontologica Polonica 24:199–204.

——— 1994. Two previously unknown eupantotheres (Mammalia, Eupantotheria). American Museum Novitates 3107:1–11.

Dietrich, W. O. 1927. *Brancatherulum* n.g., ein Proplacentalier aus dem obersten Jura des Tendaguru in Deutsch-Ostafrika. Centralblatt für Mineralogie, Geologie und Paläontologie 1927(B):423–426.

Flynn, J. J., J. M. Parrish, B. Rakotosamimanana, W. F. Simpson, and A. R. Wyss. 1999. A Middle Jurassic mammal from Madagascar. Nature 401:57–60.

Freeman, E. F. 1976. Mammal teeth from the Forest Marble (Middle Jurassic) of Oxforshire, England. Science 194:1053–1055.

——— 1979. A Middle Jurassic mammal bed from Oxfordshire. Palaeontology 22:135–166.

Hahn, G. 1969. Beiträge zur Fauna der Grube Guimarota Nr. 3. Die Multituberculata. Palaeontographica A, 133:1–100.

Heinrich, W.-D. 1991. Über *Brancatherulum tendagurense* Dietrich, 1927 (Mammalia: Eupantotheria) aus dem Oberjura von Tendaguru, Tansania. Eine vorläufige Mitteilung. Mitteilungen des Zoologischen Museums Berlin 67:97–104.

——— 1998. Late Jurassic mammals from Tendaguru, Tanzania, East Africa. Journal of Mammalian Evolution 5:269–290.

Henkel, S. 1966. Methoden zur Prospektion und Gewinnung kleiner Wirbeltierfossilien. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1966:178–184.

———, and B. Krebs. 1969. Zwei Säugetier-Unterkiefer aus der Unteren Kreide von Uña (Prov. Cuenca, Spanien). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1969:449–463.

———, and ——— 1977. Der erste Fund eines Säugetier-Skelettes aus der Jura-Zeit. Umschau Wissenschaft und Technik 77:217–218.

———, and G. Krusat. 1980. Die Fossil-Lagerstätte in der Kohlengrube Guimarota (Portugal) und der erste Fund eines Docodontiden-Skelettes. Berliner geowissenschaftliche Abhandlungen A, 20:209–216.

Krebs, B. 1967. Der Jura-Krokodilier *Machimosaurus* H.v. Meyer. Paläontologische Zeitschrift 41:46–59.

——— 1988. Mesozoische Säugetiere—Ergebnisse von Ausgrabungen in Portugal. Sitzungsberichte der Gesellschaft naturforschender Freunde Berlin (n. F.) 28:95–107.

——— 1991. Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. aus dem Oberen Jura von Portugal. Berliner geowissenschaftliche Abhandlungen A, 133:1–110.

——— 1993. Das Gebiss von *Crusafontia* (Eupantotheria, Mammalia)—Funde aus der Unter-Kreide von Galve und Uña (Spanien). Berliner geowissenschaftliche Abhandlungen E, 9:233–252.

——— 1998. *Drescheratherium acutum* gen. et sp. nov., ein neuer Eupantotherier (Mammalia) aus dem Oberen Jura von Portugal. Berliner geowissenschaftliche Abhandlungen E, 28:91–111.

——— 2000. The excavations in the Guimarota mine; pp. 9–20 *in* T. Martin and B. Krebs (eds.), Guimarota—a Jurassic Ecosystem. Verlag Dr. Friedrich Pfeil, München.

Kretzoi, M. 1946. On Docodonta, a new order of Jurassic Mammalia. Annales Historico-Naturales Musei Nationalis Hungarici 39:108–111.

Kriwet, J. 1997. Beitrag zur Kenntnis der Fischfauna des Oberjura (unteres Kimmeridgium) der Kohlengrube Guimarota bei Leiria, Mittel-Portugal: 2. Neoselachii (Pisces, Elasmobranchii). Berliner geowissenschaftliche Abhandlungen E, 25:293–301.

Krusat, G. 1969. Ein Pantotheria-Molar mit dreispitzigem Talonid aus dem Kimmeridge von Portugal. Paläontologische Zeitschrift 43:52–56.

——— 1980. *Haldanodon exspectatus* Kühne & Krusat 1972 (Mammalia, Docodonta). Contribuiçao para o Conhecimento da Fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal) IV Parte; VIII. Memórias dos Serviços geológicos de Portugal, (nova Sér.) 27:1–79.

——— 1991. Functional morphology of *Haldanodon exspectatus* (Mammalia, Docodonta) from the Upper Jurassic of Portugal. Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota. Extended abstracts. Contributions from the Paleontological Museum, University of Oslo 364:37–38.

Kühne, W. G. 1961a. A mammalian fauna from the Kimmeridgian of Portugal. Nature 192:274–275.

——— 1961b. Eine Mammaliafauna aus dem Kimeridge Portugals. Vorläufiger Bericht. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1961:374–381.

——— 1968a. Kimeridge mammals and their bearing on the phylogeny of the Mammalia; pp. 109–123 *in* E. T. Drake (ed.), Evolution and Environment. Yale University Press, New Haven, London.

——— 1968b. History of discovery, report on the work performed, procedure, technique, and generalities. Contribuiçao para o Conhecimento da Fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal) I Parte, I. Memórias dos Serviços geológicos de Portugal, (nova Sér.) 14:7–20.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum caracteribus, differentiis, synonymis, locis. Editio decima reformata. Tom I. Laurentii Salvii, Holmiae, 824 pp.

Luckett, W. P. 1993. An ontogenetic assessment of dental homologies in therian mammals; pp. 182–204 *in* F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny, Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials. Springer Verlag, New York.

Luo, Z., R. L. Cifelli, and Z. Kielan-Jaworowska. 2001. Dual origin of tribosphenic mammals. Nature 409:53–57.

Martin, T. 1997. Tooth replacement in Late Jurassic Dryolestidae (Eupantotheria, Mammalia). Journal of Mammalian Evolution 4:1–18.

——— 1998. The premolars of *Crusafontia cuencana* (Dryolestidae, Mammalia) from the Early Cretaceous (Barremian) of Spain. Berliner geowissenschaftliche Abhandlungen E, 28:119–126.

——— 1999. Dryolestidae (Dryolestoida, Mammalia) aus dem Oberen Jura von Portugal. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 550:1–119.

McKenna, M. C. 1975. Toward a phylogenetic classification of the Mammalia; pp. 21–46 *in* W. P. Luckett and F. S. Szalay (eds.), Phylogeny of the Primates. Plenum Press, New York.

——— and S. Bell. 1997. Classification of Mammals Above the Species Level. Columbia University Press, New York, 631 pp.

Mills, J. R. E. 1964. The dentitions of *Peramus* and *Amphitherium*. Proceedings of the Linnean Society of London 175:117–133.

Mohr, B. A. R. 1989. New palynological information on the age and environment of Late Jurassic and Early Cretaceous vertebrate localities of the Iberian Peninsula (eastern Spain and Portugal). Berliner geowissenschaftliche Abhandlungen A, 106:291–301.

Novacek, M. J. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. Bulletin of the American Museum of Natural History 183:1–112.

Patterson, B. 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana:Geology 13:1–105.

Prothero, D. R. 1981. New Jurassic mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic theria. Bulletin of the American Museum of Natural History 167:281–325.

Schudack, M. E. 2000. Geological setting and dating of the Guimarota-beds; pp. 21–26 *in* T. Martin and B. Krebs (eds.), Guimarota—a Jurassic Ecosystem. Verlag Dr. Friedrich Pfeil, München.

Seiffert, J. 1973. Upper Jurassic lizards from Central Portugal. Contribuiçao para o Conhecimento da Fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal) III Parte, VI. Memórias dos Serviços geológicos de Portugal, (nova Sér.) 22:7–85.

Sigogneau-Russell, D. 1989. Découverte du premier Symmétrodonte (Mammalia) du continent africain. Comptes Rendus des séances de l'Académie des Sciences Paris 309:921–926.

——— 1999. Réévaluation des Peramura (Mammalia, Cladotheria) sur la base des nouveaux spécimens du Crétacé inférieur d'Angleterre et du Maroc. Geodiversitas 21:93–127.

———, and P. Ensom. 1998. *Thereuodon* (Theria, Symmetrodonta) from the Lower Cretaceous of North Africa and Europe, and a brief review of symmetrodonts. Cretaceous Research 19:445–470.

Simpson, G. G. 1928. Mesozoic Mammalia. XI. *Brancatherulum tendagurense* Dietrich. American Journal of Science 15:303–308.

——— 1929. American Mesozoic Mammalia. Memoirs of the Peabody Museum of Yale University, New Haven 3:1–235.

Thulborn, R. A. 1973. Teeth of ornithischian dinosaurs from the Upper Jurassic of Portugal. Contribuiçao para o Conhecimento da Fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal) III Parte, VI. Memórias dos Serviços geológicos de Portugal, (nova Sér.) 22:89–134.

Weigert, A. 1995. Isolierte Zähne von cf. *Archaeopteryx* sp. aus dem

Oberen Jura der Kohlengrube Guimarota (Portugal). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1995:562–576.
Wible, J. R., G. W. Rougier, M. J. Novacek, M. C. McKenna, and D. Dashzeveg. 1995. A mammalian petrosal from the Early Cretaceous of Mongolia: implications for the evolution of the ear region and mammaliamorph interrelationships. American Museum Novitates 3149:1–19.
Wood, C. B., and D. N. Stern. 1997. The earliest prisms in mammalian and reptilian enamel; pp. 63–83 *in* W. v. Koenigswald and P. M. Sander (eds.), Tooth enamel microstructure. Balkema, Rotterdam.
Zinke, J. 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). Paläontologische Zeitschrift 72:179–189.

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