Early Cretaceous “symmetrodont” mammal *Gobiotheriodon* from Mongolia and the classification of “Symmetrodonta”

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Averianov, A.O. 2002. Early Cretaceous “symmetrodont” mammal *Gobiotheriodon* from Mongolia and the classification of “Symmetrodonta”. *Acta Palaeontologica Polonica* 47 (4): 705–716.

The “symmetrodont” mammal, *Gobiotheriodon infinitus* (Trofimov, 1980), from the Early Cretaceous (Aptian–Albian) of Mongolia, is redescribed. The species is restricted to the holotype only (dentary with three last molars), the referred maxillary fragment with M3? is considered here as cf. *Gobiconodon* sp. The dental formula of *G. infinitus* is reinterpreted as i1–3 c1 p1–3 m1–4. *G. infinitus* is characterized by a short dentary symphysis; long, well-developed Meckel’s groove; small, triangular-shaped pterygoid fossa; weakly developed pterygoid crest; i3 enlarged; p1–3 two-rooted; lower molars acute- to obtuse-angled, labial cingulids lacking, lingual cingulids very short, well developed mesial and distal cingulid cuspules (“e” and “d”) and prominent wear surface on the paracristid. *Gobiotheriodon* is similar to *Tinodon* (Late Jurassic, USA; Early Cretaceous, Great Britain and Portugal) in postcanine dental formula and structure of the pterygoid fossa; it is provisionally assigned to Tinodontidae Marsh, 1887. Some taxa previously assigned to (or suggested as possible relatives of) “Symmetrodonta” are reviewed. Amphidontidae Simpson, 1925 is considered as *nomen dubium*. A new classification for “Symmetrodonta” is proposed.

Key words: *Gobiotheriodon*, “Symmetrodonta”, systematics, Höövör, Mongolia, Early Cretaceous.

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Introduction

The “symmetrodont” mammal *Gobiotheriodon infinitus* (Trofimov, 1980) was based on a single dentary with the last three molars (holotype) and a referred maxilla with a single molar from the Early Cretaceous (Aptian–Albian) Höövör (according to the recent transliteration of Mongolian place-names, see Benton 2000) locality in Mongolia (Trofimov 1980, 1997), previously referred to as Khoboor. Trofimov (1980) placed *Gobiotheriodon* in the Amphidontidae, a poorly known family referred by Simpson (1929) to “Symmetrodonta”, and otherwise represented (omitting questionable referrals) by a single, poorly preserved holotype of *Amphidon superstes* Simpson, 1925.

Fox (1984a: 1205) criticized Trofimov’s interpretation of *Gobiotheriodon*. He expressed doubt that the upper and lower dentitions attributed to *G. infinitus* actually belong to the same species, because of different occlusal angles in upper and lower molars. Moreover, he thought that the upper molar could not belong to an amphidontid because the latter are interpreted to have upper molar crowns longer than broad, based on the lower dentition only known. According to Fox’s opinion, the lower molars of *Gobiotheriodon*, which have an obtuse trigonid angle and unicuspid talonid, are equally attributable to an amphilestid or amphitheriid as to an amphidontid. Possible amphilestid affinities of *Gobiotheriodon* can be immediately excluded, because amphilestids, *contra* Fox’s opinion, have trigonid cusps aligned longitudinally (Kielan-Jaworowska and Dashzeveg 1998 and references therein). In molars of *Amphitherium* de Blainville, 1838 (Mills 1964; Fox 1975; pers. obs.) the talonid is keeled and is much better developed than in *Gobiotheriodon*, taking up to one-third of the crown length, so that a close relationship between these taxa seems improbable.

Sigogneau-Russell and Ensom (1998: 461) considered *Gobiotheriodon* as a possible “late member of the tinodontids”, based on structure of the referred upper molar. Cifelli and Madsen (1999: 206) retained *Gobiotheriodon* within Amphidontidae without comment or study.

Kielan-Jaworowska et al. (2000: 596–597, fig. 29.15) accepted Trofimov’s interpretation of *Gobiotheriodon* and published a slightly different figure of the holotype of *G. infinitus*, based on Trofimov’s illustration.

My examination of the published figures and original materials of *Gobiotheriodon* reveals that the original description and interpretation of this taxon by Trofimov (1980, 1997) is incorrect in some respects. In this note I redescribe *G. infinitus* and restrict the species to the holotype only, for which new illustrations are provided herein. I discuss the possible phylogenetic position of *Gobiotheriodon*, and take this opportunity to discuss also some problems of the systematics of “Symmetrodonta”. Usage of this group name in quotes reflects the strong possibility that it is a paraphyletic assemblage, as discussed below.

Institutional abbreviations. — MAE, Mongolian Academy of Sciences–American Museum of Natural History Expeditions; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; PSS, Paleontological and Stratigraphy section (Geological Institute), Mongolian Academy of Sciences, Ulaanbaatar; USNM, United States National Museum, Washington, D.C.; YPM, Yale Peabody Museum, Yale University, New Haven; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Measurements.—L, length; W, width. All measurements are in mm.

Systematic paleontology

"Symmetrodonta" Simpson, 1925

?Tinodontidae Marsh, 1887

Gobiotheriodon Trofimov, 1997, new assignment

Gobiotheriodon infinitus (Trofimov, 1980)

Figs. 1, 2B.

Gobiodon infinitus Trofimov, 1974 [*sic*, *nomen nudum*]: Belyaeva et al. 1974: 20.

Gobion [*sic*, *l.c.*] *infinitus* Trofimov [*nomen nudum*]: Belyaeva et al. 1974: 364.

Gobiodon infinitus [*nomen nudum*]: Cassiliano and Clemens 1979: 156.

Gobiodon infinitus sp. n. [*partim*]: Trofimov 1980: 211, fig. 2a, b, v.

Gobiondon [*sic*, *l.c.*] *infinitus*: Yadagiri 1985: 412.

Gobiotheriodon infinitus (Trofimov, 1980) [*comb. n.*] [*partim*]: Trofimov 1997: 496

Gobiotheriodon infinitus (Trofimov, 1980) [*partim*]: Kielan-Jaworowska et al. 2000: 596, fig. 29.15

Holotype: PIN 3101/80, right dentary lacking the coronoid and condylar processes, with m2–4 and alveoli of i1–3, c1, p1–3, and m1. Höövör (Khoboor), Mongolia; Aptian–Albian, Early Cretaceous.

Material.—Holotype only. In the original description the holotype was designated as PIN 3101/50 in the text, but as PIN 3101/80 in the figure caption (Trofimov 1980: 212); the latter is the proper collection number for this specimen. Trofimov (1980: 212) cited "two upper teeth (M3)" as referred specimens, but figured only one maxillary fragment with M3 (PIN 3101/81; Trofimov 1980: fig. 2g). I could not locate in the PIN collection "one more M3 (not figured)" referred to this species by Trofimov (1997: 496). The figured maxillary fragment, PIN 3101/81, is herein excluded from *G. infinitus* (see discussion).

Two isolated petrosals from the Höövör locality (PSS-MAE-104: Wible et al. 1995: figs. 1–2; Rougier et al. 1996a: fig. 5F; and PSS-MAE-119, not figured), assigned to a prototribosphenidan therian (Wible et al. 1995; Rougier et al. 1996a), may belong to *Gobiotheriodon*.

Description.—The dentary is almost complete, except for the coronoid process (broken off at the alveolar level) and the condylar process. The horizontal ramus, especially its anterior part, is considerably curved in a parasagittal plane and is relatively shallow, exceeding only some 1.5 times m2 crown height posteriorly, and gradually tapers anteriorly. There are four mental foramina. They are situated under i3, c1, between c1 and p1, and the anterior root of p2, respectively. There is no considerable diastema, but rather short diastemata separate a few teeth. The masseteric fossa is bounded ventrally by a strong ridge, starting at mid-height of the dentary. Just above the beginning of this ridge there is a shallow but marked depression. The posteroinferior border of the dentary is considerably deflected laterally. The symphysis is rather short compared to the condition in *Tinodon*, terminating at the level of c1 (extending up to the middle of p2 in *Tinodon*, Simpson 1925: fig. 2), and placed at an angle of ~23° to the long axis of the dentary (a line parallel to the molar alveolar border), and apparently was not fused. On the medial side of the dentary there is a distinct Meckel's groove, which starts as a narrow slit close to the ventral border of the dentary below m1, then runs almost parallel to this border toward a level slightly below the mandibular foramen, gradually increasing in height and flattening posteriorly. The postdentary trough is missing and there is no clear evidence for attachment of postdentary bones. The mandibular foramen is placed relatively high and opens into the pterygoid fossa, which is rather deep, triangle-shaped, and well delimited, but occupies a relatively small space compared to, e.g., spalacotheriids, dryolestids and more advanced therians: its dorsal border can be seen on the dentary fragment preserved. The anterior end of the pterygoid fossa is placed far posterior to the last molar. The pterygoid crest is rather short and does not extend anteriorly beyond the mandibular foramen. It is a thick shelf along the ventral border of the dentary, and may be continued all the way to the condylar process, based on its considerable thickness at the level of breakage.

I interpret the dental formula of *G. infinitus* as i1–3 c1 p1–3 m1–4, rather than i1–3 c1 p1–4 m1–5, as was suggested by Trofimov (1980, 1997; see discussion). The alveoli for i1 and i2 are subequal and quite large. The alveolus for i3 is even larger, being as large as the alveolus for c1. Judging from their alveoli, p1 and p2 were of roughly similar size, but the roots of p2 were more spread. The alveoli for p3 are labiolingually larger than those of p2, but mesiodistally shorter. The inferred length of m1 is similar to that inferred for p3 and known for m2.

The known molars gradually decrease in length from m2 to m4. The m2 and m3 have a similar morphology, but the tips of the trigonid cusps are missing from m3. The trigonid is dominated by the protoconid; paraconid and metaconid are roughly subequal in height and are lingually placed. The trigonid angle is ~85° on m2 and ~95° on m3 (a similar gradient of posteriorly increasing triangulation is also present in *Tinodon*: see Crompton and Jenkins 1967). There is no distinct labial cingulid and a very short lingual cingulid confined to the base of protoconid. There is only one mesial cingulid cuspule ("e") preserved in m2–3, but the more labial cingulid cuspule "f" might be eliminated by wear. In m3 both cusps "e" and "f" are present, but weakly separated. The distal cingulid cuspule ("d") is well developed in m2–3 and smaller in m4. Cusps "e" and "d" abut between adjacent molars. The m4 differs from the preceding molars in having a more obtuse trigonid angle (~133°) and relatively narrower distal portion.

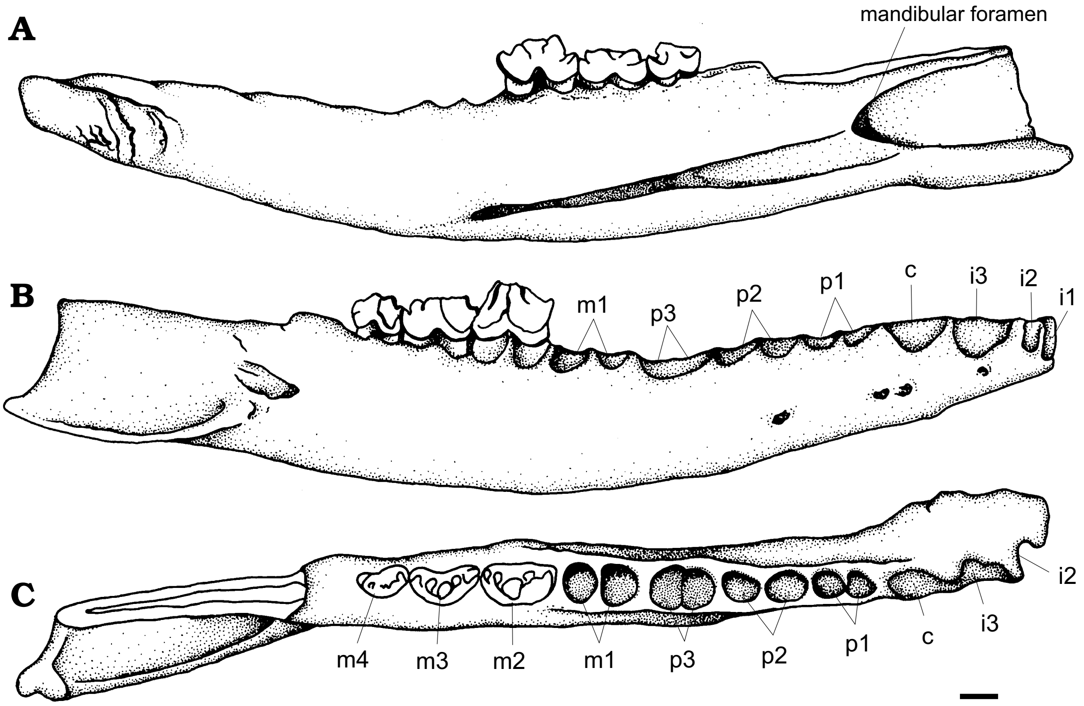

Fig. 1. *Gobiotheriodon infinitus* (Trofimov, 1980). PIN 3101/80, holotype, right dentary with m2–4 in lingual (**A**), labial (**B**), and occlusal (**C**) views. Höövör (Khoboor), Mongolia; Early Cretaceous, Aptian or Albian. Scale bar 1 mm.

Each of the three known molars bears a prominent, continuous wear facet 2+A+B along the paracristid, which occupies almost the whole anterolabial part of the crown, anterior to the protoconid midline and extending onto the mesial cingulid cuspule “e” (m2–3) or “f” (m4). Strong, but much narrower wear facet 1 is present along the labial side of the metaconid and cuspule “d” in m2 and along the metaconid in m3.

Measurements.—PIN 3101/80: m2: L = 2.3, W = 1.3; m3: L = 2.2, W = 1.1; m4: L = 1.5, W = 0.8.

Discussion.—PIN 3101/81, previously referred to *G. infinitus*, is a right maxillary fragment with M3? and alveoli of M2? and M4–5? (Fig. 2A; not a left maxillary fragment with M3 and alveoli for M2 and posterior alveolus for M1, as was stated by Trofimov 1980: 212; 1997: 496). The posterior portion of the maxilla is intact and clearly shows the end of the bone. The interpretation of this specimen as posterior part of a right maxilla is evident also from the position of the maxillary zygomatic process, which starts opposite to M3? and widens posteriorly. The position of this process in PIN 3101/81 is very similar to that seen in *Gobiconodon* spp. (e.g., Kielan-Jaworowska and Dashzeveg 1998: figs. 4c, 5). Moreover, PIN 3101/81 is similar to *Gobiconodon* in molar structure and in the fact that molar roots are anteroposteriorly strongly compressed, differing mainly in the wider stylar shelf, deeper ectoflexus, and more pronounced cusps D and E. The molar in PIN 3101/81 bears two cusps in position B (B1 and B2). The similar vestigial cusp B2 can be seen in some specimens of *Gobiconodon* (Kielan-Jaworowska and Dashzeveg 1998: figs. 4C, 5). PIN 3101/81 shows also deep rounded palatal fossae medial to the upper molars (Fig. 2A_1), which are also characteristic for *Gobiconodon* (Kielan-Jaworowska and Dashzeveg 1998). Although the attribution of PIN 3101/81 to *Gobiotheriodon* cannot be dismissed completely, it seems unlikely on the current state of our knowledge. For these reasons, I herein restrict *G. infinitus* to the holotype alone. PIN 3101/81 could be currently attributed to as cf. *Gobiconodon* sp.

Trofimov (1980, 1997) interpreted the lower dental formula of *G. infinitus* as i1–3, c1, p1–4 and m1–5. He did not give any formal explanation for this interpretation. However, as he referred *Gobiotheriodon* to Amphidontidae, he may have assumed the lower premolar formula (p1–4) of *Amphidon* Simpson, 1925, and possibly in *Manchurodon* Yabe and Shikama, 1938, in assessing the cheek tooth formula in *Gobiotheriodon*.

The alveolus of the fifth tooth from the back, interpreted by Trofimov (1980, 1997) as m1, has a very thin and apparently not fully formed septum between the anterior and posterior roots. This suggests that the tooth at this locus was relatively recently erupted. With few exceptions, m1 is the first molar to be erupted in mammals, and for this reason the tooth locus in question probably pertains to the ultimate premolar, which is replaced relatively late in ontogeny, usually after eruption of the anterior molars. The same pattern of the ultimate premolar (p3) eruption after m1 had been in place is documented for *Tinodon* (Cifelli 1999: 265). The balance of evidence thus suggests that *Gobiotheriodon* had only four lower molars, not five as was suggested by Trofimov (1980, 1997).

Interpretation of the more anterior premolars is less clear, but some inference may be made. The two first postcanine al-

Fig. 2. **A**. Cf. *Gobiconodon* sp., PIN 3101/81, right maxillary fragment in occlusal view, with M3?, and alveoli for M2? and M4–5? (A_1); enlarged M3? of the same in occlusal view (A_2); the same in anterior view (A_3). **B**. *Gobiotheriodon infinitus* (Trofimov, 1980), PIN 3101/80, holotype, right dentary fragment with m2-m4 in occlusal view (B_1); the same in lingual and slightly posterior view (B_2). All SEM micrographs, A_1, A_2 and B_1, stereopairs. All from Early Cretaceous (Aptian or Albian) at Höövör (Khoboor) in Mongolia. Scale bars 1 mm.

veoli likely represent a single tooth locus: the bone partition between them is thin and compressed, shorter than the diastemata preceding and succeeding the respective alveoli. This pattern would be expected for a bone septum between a two-rooted therian tooth with closely spaced anterior and posterior roots. Given this, and the foregoing interpretation of the fourth postcanine tooth as a two-rooted ultimate premolar, the two alveoli interceding between p1 and the last premolar are most reasonably interpreted as belonging to a two-rooted p2. This yields a premolar formula of p1–3 for *Gobiotheriodon.* In all known "symmetrodonts", except *Kuehneotherium* Kermack et al., 1968 and *Manchurodon*, lower premolars are two-rooted. This is consistent with the interpretation that *Gobiotheriodon* had three two-rooted premolars instead of four single-rooted premolars, as was suggested by Trofimov (1980, 1997).

The continuous wear facet along the paracristid on lower molars of *Gobiotheriodon* apparently represents united wear facets 2+A+B (terminology after Crompton 1971), which remain separate in young individuals of *Kuehneotherium* and *Tinodon* (Crompton and Jenkins 1967, 1968; Crompton 1971). A similar oblique or transverse, continuous shear surface is present in spalacotheriids (e.g., Sigogneau-Russell and Ensom 1998: fig. 11). Continuity of the crests seems to be related to intensification of molar shearing function. The condition appears to have arisen independently in the two.

Phylogenetic position of *Gobiotheriodon*

Gobiotheriodon is a holotherian: it shares the fundamental apomorphy of triangulated principal molar cusps (e.g., Hopson 1994), wherein paraconid and metaconid are placed lingually with respect to the protoconid. *Gobiotheriodon* lacks the derived characters of Cladotheria (Dryolestoidea + Peramura + Tribosphenida [Boreosphenida]), such as an expanded talonid and development of hypoconid shear against metacone; it also possibly lacks a true angular process (Prothero 1981; Cifelli and Madsen 1999; Martin 1999). Hence, known evidence places *Gobiotheriodon* among plesiomorphic Holotheria, and the genus would traditionally be referred to "Symmetrodonta".

Mesozoic mammals with a symmetrodont molar pattern were first grouped taxonomically by Simpson (1925), whose Symmetrodonta was conceived to ally Spalacotheriidae (then including *Tinodon*) with Amphidontidae. The group was later expanded to include geologically older taxa, such as Late Triassic–Early Jurassic *Kuehneotherium* (e.g., Cassiliano and Clemens 1979). However, few (if any) characters can be cited as unambiguous synapomorphies for a monophyletic "Symmetrodonta". Prothero (1981: 321) cited reduction of premolars to four, greatly reduced talonids, and strong internal pterygoid crest as synapomorphies for his "Symmetrodonta" (excluding *Kuehneotherium*). The first two characters may be in fact plesiomorphic for Holotheria; in any case, the number of premolars is highly problematic for most "symmetrodonts". The count in *Kuehneotherium*, for example, is not known with certainty, though it may have been 5–6 (Kermack et al. 1968) or six (Gill 1974); a wide range is known for spalacotherioids: *Zhangheotherium* was thought to have two (Hu et al. 1997, 1998), but actually has three (Luo et al. 2002), *Spalacotherium* has three (Clemens 1963), and a North American member of the family has five (Cifelli et al. 2000). The last character—a strong pterygoid crest—is distinctly a derived character, but its distribution is ambiguous: the pterygoid crest reaching the dentary condyle via a low crest is characteristic for some "triconodonts", amphilestids, and "symmetrodonts" (Luo et al. 2002). The integrity of a broad-based "Symmetrodonta"—including all mammals differing from "triconodonts" in having the reversed-triangle molar pattern, but lacking specializations seen in more derived taxa (e.g., "eupantotheres")—has been challenged in recent years (see discussions by Rougier et al. 1996a, b; Luo et al. 2002). Even if archaic forms such as *Kuehneotherium* are excluded, there exists doubt as to whether the best known remaining taxa (Spalacotheriidae and Tinodontidae) share an exclusive ancestor with respect to various other early mammals (Luo et al. 2002). These problems cannot be resolved herein. Recognizing the uncertainties regarding monophyly of "Symmetrodonta", the affinities of *Gobiotheriodon*—which has only three premolars, molars with very small talonids, and a distinctly developed pterygoid crest—appear to lie among mammals generally placed in "Symmetrodonta".

Specific relationships of *Gobiotheriodon* among "symmetrodonts" are problematic. In terms of cusp pattern, it appears to be intermediate between typical "obtuse-angled" and "acute-angled" taxa, the trigonid angle on known molars varying from 85° (m2) to 133° (m4). A proposed relationship (Trofimov 1980) with the Late Jurassic *Amphidon* can be rejected: *Gobiotheriodon* has molars with well-developed paraconid and metaconid, and thus cannot be considered as "functionally monocuspid". Moreover, the concept of Amphidontidae is considered here as not valid (see below) and this taxon is regarded as a *nomen dubium. Gobiotheriodon* differs from Kuehneotheriidae in that postdentary bones appear to have been detached (as indicated by lack of a postdentary trough and overlying ridge, together with other scars on the dentary; see Kermack et al. 1968) and in very short and faint lingual cingulid. *Gobiotheriodon* differs from *Zhangheotherium* Hu et al., 1997 in having fewer molars (four *versus* six or more: the holotype of *Z. quinquecuspidens* Hu et al., 1997 represents a juvenile animal and not all of the molars are erupted) and structure of dentary (lacking of the massive and strongly curved condylar process of *Zhangheotherium*). *Gobiotheriodon* is similar with Spalacotheriidae in having laterally deflecting posteroinferior border of the dentary, but evidently lacks dental specializations of that group (Cifelli and Madsen 1999). Other possible "symmetrodonts" have been described from the Berriasian of Morocco (Sigogneau-Russell 1989, 1991;

Sigogneau-Russell and Ensom 1998), Campanian–Maastrichtian of Argentina (Bonaparte 1990), and Campanian of Canada (Fox 1984a). These are represented by isolated teeth only and "symmetrodont" affinities are problematic (see discussion of some of these taxa below); for present purposes, they can be omitted from comparison. The only "symmetrodont" remaining for comparison is *Tinodon* Marsh, 1879, known by several dentaries from the Kimmeridgian–Tithonian Morrison Formation of the USA (Simpson 1925, 1929), one isolated lower molar from the Tithonian–Berriasian of Portugal (Krusat 1989), and by some isolated teeth from the Berriasian of England (Ensom and Sigogneau-Russell 2000). Indeed, *Tinodon* has at least two characters similar to those in *Gobiotheriodon*: the postcanine dental formula is p1–3 m1–4 and the pterygoid fossa is relatively small and triangle-shaped (Prothero 1981: fig.7B). However, *Tinodon* differs from *Gobiotheriodon* in having a longer dentary symphysis (terminating between p1 and p2), a more obtuse-angled m2 (115° *versus* 85°; Crompton and Jenkins 1967: 1006), and somewhat more prominent lingual cingulid. The mesial cingulid cusp "f" is not preserved (obliterated by wear?) in m2–3 of *Gobiotheriodon*. This cusp is present in *Tinodon bellus* Marsh, 1879 (YPM 13644; Crompton and Jenkins 1967: fig. 1A). In *T. lepidus* Marsh, 1879 (USNM 2131; personal observation of a cast; synonym of *T. bellus* according to Cifelli, pers. comm. 2002) and in the Cretaceous *T. micron* Ensom and Sigogneau-Russell, 2000 (Ensom and Sigogneau-Russell 2000: 774, fig. 8) cusp "f" is absent. Similarly, multiple, separate wear facets along the paracristid and protocristid are present in *Tinodon*, as they are in *Kuehneotherium* (see Crompton and Jenkins 1967). In *Gobiotheriodon* the paracristid is occupied by a single, prominent wear surface (facets 2+A+B) and there is a smaller wear facet (1) along the protocristid. All of these characters distinguishing *Tinodon* from *Gobiotheriodon* may be considered as plesiomorphic for the former; loss or modification in *Gobiotheriodon* is unsurprising, considering its geologically younger age. These data seem to be sufficient to provisionally place *Gobiotheriodon* within the Tinodontidae.

Comments on some taxa assigned or possibly related to "Symmetrodonta"

Woutersia Sigogneau-Russell, 1983, from the Late Triassic (Rhaetian) of France was based on several isolated teeth and was originally referred to Kuehneotheriidae (Sigogneau-Russell 1983). When additional material become available, it was transferred to the monotypic Woutersiidae within "Symmetrodonta" and "a certain parallelism" between this family and Docodonta was noted (Sigogneau-Russell and Hahn 1995: 245). Subsequently, Butler (1997) referred *Woutersia* to Docodonta. In my opinion, molars of *Woutersia* could be structurally antecedent to Docodonta, but *Woutersia* itself should not be formally included in that group (see Martin and Averianov in press). *Woutersia* molar morphology is structurally intermediate between those in morganucodontids and docodonts, and this taxon is better maintain in the monotypic Woutersiidae. Dental synapomorphy for Morganucodontidae, Woutersiidae, and Docodonta would be presence of the cusp "g" ("kuhneocone") on the lower molars. Woutersiidae and Docodonta form a more inclusive clade, sharing lingual shift of the cusp "c" (semitriangulation). The idea about similarity of *Morganucodon* Kühne, 1949 with docodonts was first proposed by Butler (in Kühne 1950) and later supported by Crompton and Jenkins (1968) and Crompton (1974), who, however, referred Morganucodontidae to the "Triconodonta", a point of view shared by most of the recent authors (but see McKenna and Bell 1997: 512, who retain *Megazostrodon* Crompton and Jenkins, 1968 within the Docodonta).

The possibility of docodont affinities for *Woutersia* suggests that the "reversed triangle" pattern, postulated as synapomorphy for Holotheria (e.g., Prothero 1981; Hopson 1994 and references therein), was derived at least twice: once in "holotherians" ("symmetrodonts", "eupantotherians", and boreosphenidans), and again in docodonts, possibly related to Australosphenida (*Asfaltomylos* Rauhut et al., 2002, *Ambondro* Flynn et al., 1999 + *Ausktribosphenos* Rich et al., 1997 + Monotremata), which independently acquired a tribosphenic molar pattern (Luo et al. 2001, 2002; Rauhut et al. 2002). However, the recent cladistic analyses of Mammalia (Luo et al. 2001, 2002) supported the old believe that docodont molar pattern evolved from the linear, not triangulated cusp configuration. Pascual et al. (2000) and Pascual and Goin (2001) argued for the close affinities of Docodonta and Australosphenida, but their interpretation for the origin of "triangulated" molars and the cusps homologies in docodonts is radically different.

Docodonts retain a primitive, *Morganucodon*-like mandible with a trough for postdentary bones and anteriorly placed angular process (see Kermack and Mussett 1958; Lillegraven and Krusat 1991). These mandibular features were retained in primitive australosphenidans, such as *Asfaltomylos*, *Ausktribosphenos*, and *Bishops* Rich et al., 2001, but reduced in living monotremes (an angle is still present in the fossil monotremes *Teinolophos* Rich et al., 1999 and *Obdurodon* Woodburne and Tedford, 1975, see Musser and Archer 1998 and review by Luo et al. 2002). In "symmetrodonts" the angular process is lacking; a posteriorly placed angular process, present in "eupantotheres" and more advanced therians, therefore appears to be secondarily derived. Summing up, among Mesozoic mammals the combination of an angular process with the trough for the postdentary bones is found only in Morganucodontidae, Docodonta, and Australosphenida and close relationship between these group should be seriously considered. *Shuotherium* lacks an angular process and in molar appearance more reminiscent that of primitive holotherian ("symmetrodont") mammals and should be included to that group (see below). Although these ideas are not in line with the current parsimony analysis (Luo et al.

2002), we should remember that this analysis is based on limited data and could be affected greatly by numerous dental parallelisms between two main non-allotherian mammal groups: Morganucodontidae–Docodonta–Australosphenida and Holotheria. These parallelisms include development of both "normal" (posterior) and "pseudo" (anterior) talonid in two groups: Australosphenida *versus* Boreosphenida and derived Docodonta (Tegotheriidae) *versus Shuotherium*.

Kotatherium haldanei Datta, 1981, based on single upper molar from the Early Jurassic Kota Formation, India, is usually placed in "Symmetrodonta" without attribution to a particularly family (Datta 1981: 308; McKenna and Bell 1997: 44; Sigogneau-Russell and Ensom 1998: 457), or in Tinodontidae (Prasad and Manhas 1997: 565). It is generally similar to *Kuehneotherium*, especially in the presence of a small, "extroverted" "metacone" [cusp C], but differs in having a much smaller stylocone. Sigogneau-Russell and Ensom (1998: 458) hint about "a possibly affinity [of *K. haldanei*] with the Moroccan "peramurids", but in the subsequent revision of the Moroccan peramurids (Sigogneau-Russell 1999) this question was not discussed. A second species, *Kotatherium yadagirii* Prasad and Manhas, 1997, from the same formation and also based on an isolated upper molar (Prasad and Manhas 1997), is probably not congeneric with the type species (Sigogneau-Russell and Ensom 1998: 458). *Kotatherium* is restricted herein to the type species and is referred to Kuehneotheriidae. "*Kotatherium*" *yadagirii* may be an archaic amphilestid rather than a "symmetrodont".

Delsatia Sigogneau-Russell and Godefroit, 1997, from the Rhaetian of France was originally referred to Docodonta (Sigogneau-Russell and Godefroit 1997). I agree with Butler (1997: 439) that *Delsatia* is not a docodont, but rather a "symmetrodont". Except for the facts that paracristid and protocristid break at almost a right angle, and that the lingual cingulid is discontinuous, *Delsatia* is very similar to *Kuehneotherium*, and I refer it herein to Kuehneotheriidae.

Shuotherium Chow and Rich, 1982, from the Middle Jurassic of China and England (Chow and Rich 1982; Sigogneau-Russell 1998; Wang et al. 1998), is similar to *Kuehneotherium* in retaining primitive dentary structure, with a trough for postdentary bones. *Shuotherium* may be derived from a kuehneotheriid such as *Delsatia*, from the Late Triassic of France (Sigogneau-Russell and Godefroit 1997), with which it shares a characteristic trigonid structure, wherein the paracristid and protocristid break at a right angle toward the paraconid and metaconid, respectively. *Delsatia* also has somewhat enlarged mesial cingulid cuspules ("e" and "f"), which appear to be incipient to the "pseudotalonid" of *Shuotherium*.

Amphidon Simpson, 1925 from the Upper Jurassic (Kimmeridgian–Tithonian) Morrison Formation, Wyoming, USA, is based on a single dentary with five cheek teeth (Simpson 1925). The postcanine formula is usually interpreted as p1–4 m1–4 (e.g., Simpson 1925, 1929; Cassiliano and Clemens 1979). However, the supposed p4 has essentially the same morphology as m1 and other molars. The molars are "functionally monocuspid" (Cassiliano and Clemens 1979: 155), having weak paraconid and metaconid, although this weakness may be caused at least partly by the considerable wear on the only known specimen (Cassiliano and Clemens 1979: 155). The occlusal view is "reconstructed" only for m1 (Simpson 1929: fig. 17): it has an obtuse-angled crown with a trigonid angle of ~145°. This is the only feature that would place *Amphidon* within "Symmetrodonta". However, it is equally plausible that *Amphidon* may be an aberrant amphilestid with a postcanine formula of p1–3 m1–5. Given these ambiguities, the genus is herein considered Mammalia *incertae sedis*. The concept of Amphidontidae is dubious and this taxon is regarded here as a *nomen dubium*.

Manchurodon Yabe and Shikama, 1938, from the Middle Jurassic Wafangdian Formation (see Zhang 1984; Zhou et al. 1991; Wang et al. 2001) of eastern China, is based on a single specimen now lost, including a scapula and a dentary fragment with p1–3 m1–5 (Yabe and Shikama 1938). *Manchurodon* has generally been referred to Amphidontidae, because of its "functionally unicuspid" molars (Yabe and Shikama 1938: 355; Cassiliano and Clemens 1979: 155; McKenna and Bell 1997: 44). However, the dentition of *Manchurodon* was figured only in the labial view, and in this view molars of spalacotheriids may also look "functionally unicuspid" because of their acute-angled cusp pattern, in which paraconid and metaconid may be concealed by protoconid. Importantly, *Manchurodon* has a labial cingulid on lower molars (Yabe and Shikama 1938: 355, fig. 1), characteristic for the majority of spalacotheriids (e.g., Cifelli and Madsen 1999), whereas in *Amphidon* the labial cingulum seems to be lacking (Simpson 1929: fig. 17). At least one premolar (p1) in *Manchurodon* is single-rooted, which differentiates this taxon from *Zhangheotherium* and Spalacotheriidae, where all lower premolars are double-rooted. Patterson (1956: 29) considered the dental formula of *Manchurodon* as being p1–4 m1–4 because of "a noticeable break in size between the first four and the last four teeth". This size break, however, does not necessarily reflect the premolar-molar boundary because of differing size relationships in the molar series. Whereas Spalacolestinae have an m1 that is nearly twice as long as m2 (Cifelli and Madsen 1999), m1 is only 87% the length of m2 in the "symmetrodont" *Zhangheotherium* (calculated from Hu et al. 1998: fig. 1). In *Manchurodon*, the fourth cheek tooth is 82% the length of the fifth. By analogy with *Zhangheotherium*, these teeth are thus reasonably interpreted as m1–2. These homologies are supported by the fact that a distinct metaconid (lacking, so far as known, on premolars of "symmetrodonts") is present on the fourth cheek tooth. Hence, the postcanine formula of *Manchurodon* appears to be p1–3 m1–5. Beyond this, little more can be said. The dental formula is not, in itself, particularly diagnostic. It is possible that the molar paraconids and metaconids were unreduced and there also exists significant doubt as to whether paraconid and metaconid of *Amphidon* are reduced or simply obliterated by wear. There is insufficient basis to posit a special relationship between the two genera, and *Manchurodon* is considered herein as "Symmetrodonta" *incertae sedis*.

Nakunodon Yadagiri, 1985 from the Early Jurassic Kota Formation, India, is based on a single upper molar, possibly lacking a considerable part of the anterior crown (not only a "small portion", as was stated in the original description, Yadagiri 1985: 415). *Nakunodon* was referred to Amphidontidae because of its "monodont [monocuspid] type" (Yadagiri 1985: 415; McKenna and Bell 1997: 44; Prasad and Manhas 1997: 570). The tooth is indeed monocuspid: the metacone is absent and the stylocone is not present on the preserved crown, *contra* the description by Yadagiri (1985); the metastyle is very small. The most striking feature of *Nakunodon* is a complete cingulum, especially thick and robust lingually, with a protocone-like eminence at the junction of the pre- and postcingula. The affinities of *Nakunodon* remain problematic, but there exists no basis to classify it with *Amphidon*. *Nakunodon* is considered here as Holotheria *incertae sedis*.

Liaotherium Zhou et al., 1991, from the Middle Jurassic of Liaoning Province, China, was originally referred to ?Amphilestidae (Zhou et al. 1991); McKenna and Bell (1997: 42) referred the genus to Amphilestidae without question. *L. gracile* Zhou et al., 1991, the only known species, is represented by a nearly complete dentary preserving only one tooth, a crushed last molar, which is said to have had "three cusps arranging in a line" before suffering postmortem damage (Zhou et al. 1991: 174). This was obviously the main (only?) reason for attribution of *Liaotherium* to Amphilestidae. However, a nearly linear arrangement of cusps can be observed on the last molar in some obtuse-angled "symmetrodonts", such as *Gobiotheriodon*. There is no clear basis for dividing the postcanine tooth series of *Liaotherium* into premolars and molars by the alveoli preserved. Zhou et al. (1991) interpreted the postcanine tooth formula of *Liaotherium* as p1–3 m1–5 or p1–4 m1–4, but the interpretation p1–2 m1–6 is equally possible. This would give a postcanine formula similar to that of the spalacotherioid "symmetrodont" *Zhangheotherium*, from the Early Cretaceous of the same region, Liaoning Province, China (Hu et al. 1997). More important, *Liaotherium* is similar to *Zhangheotherium* in having a long, thin, plate-like coronoid process, not exceeding the condylar process in width. In the amphilestids *Phascolotherium* and *Amphilestes* (Simpson 1928: fig. 19), the coronoid process is much wider, considerably exceeding the condylar process in width. *Liaotherium* should be considered as Mammalia *incertae sedis*, because attribution to Amphilestidae or "Symmetrodonta" is equally possible.

Thereuodon Sigogneau-Russell, 1989, based on isolated upper teeth from the Early Cretaceous (Berriasian) of Morocco and England, was originally described as a "symmetrodont" (Sigogneau-Russell 1989; Sigogneau-Russell and Ensom 1998). However, this taxon may be based on the milk dentition of a dryolestid or a stem-group zatherian, as was recently suggested by Martin (2002) based on new materials from the Jurassic of Portugal. *Thereuodon* and the similar *Atlasodon* Sigogneau-Russell, 1991 from Morocco are herein excluded from "Symmetrodonta". Similarly, *Mictodon simpsoni* Fox, 1984, based on a single tooth from the early Campanian of Canada (Fox 1984a), may represent milk dentition of the spalacolestine symmetrodont *Symmetrodontoides canadensis* Fox, 1976, known from the same formation (Fox, 1972, 1976, 1985) (R. Cifelli personal communication 2002). This tooth is similar by almost aligned ("obtuse"-angled) cusp arrangement, low lateral cusps, well separated from the main cusp, and slender roots with the deciduous teeth of the mid-Cretaceous and Turonian spalacolestines (Cifelli 1999; Cifelli and Gordon 1999).

Bonaparte (1990) described five "symmetrodont" taxa from the Late Cretaceous (Campanian) Los Alamitos Formation of Argentina: *Bondesius* Bonaparte, 1990 (Bondesiidae), *Casamiquelia* Bonaparte, 1990 (family indet.), *Brandonia* Bonaparte, 1990 (?Spalacotheriidae), *Barberenia* Bonaparte, 1990, and *Quirogatherium* Bonaparte, 1990 (both Barbereniidae). Later (Bonaparte 1994) the four latter taxa were referred to the Dryolestida and only *Bondesius* was left within the "Symmetrodonta". In spited of this, McKenna and Bell (1997) kept Barbereniidae within the "Symmetrodonta", considered *Casamiquelia* as "Symmetrodonta" *incertae sedis*, and placed *Bondesius* to the Tinodontidae; only *Brandonia* was referred to the Dryolestida. Sigogneau-Russell and Ensom (1998: 465) noted the great similarity between upper molars of *Barberenia* and *Thereuodon* and decided that the former taxon "could still be considered a symmetrodont". Indeed, the similarity between these two taxa is great and *Barberenia* may represent the milk dentition of one of the dryolestid known from the Los Alamitos fauna. *Casamiquelia* and *Brandonia* with the typical median ridge between the paracone and stylocone on the upper molars are best placed within the Dryolestida. The systematic position of *Quirogatherium* is less certain, it also could be based on upper milk tooth of a dryolestid. The lower molar, the holotype of *Bondesius ferox* Bonaparte, 1990 (Bonaparte 1990: fig. 3A–F), by its almost transverse protocristid and transverse talonid crest is more approximating condition of dryolestids (Ensom and Sigogneau-Russell 1998; Martin 1999) than any of "symmetrodonts". Its slender roots, enlarged talonid, and anteriorly projecting paraconid suggest that it is rather deciduous than permanent tooth (compare with Martin 1999: taf. 12A–C). Consequently, *Bondesius* is removed here from the "Symmetrodonta" and placed within the Dryolestida. Currently there is no unambiguous record of "symmetrodonts" in the Late Cretaceous of South America.

Microderson Sigogneau-Russell, 1991, based on a single upper molar from the Early Cretaceous (Berriasian) of Morocco, was originally attributed to the Spalacotheriidae (Sigogneau-Russell 1991; followed by McKenna and Bell 1997: 45), but later (Sigogneau-Russell and Ensom 1998) considered family *incertae sedis* within "Symmetrodonta". However, presence of three roots and a vestigial metacone at the lingual base of the cusp "C" (Sigogneau-Russell and Ensom 1998: 461, fig. 9) clearly set this taxon apart of "Symmetrodonta" and allow us to compare it with the Peramura, which are well diversified in the Anoual fauna (Sigogneau-Russell 1999). *Microderson* is a stem-group zatherian, more primitive by the metacone development than *Nanolestes* Martin, 2002 from the Late Jurassic of Portugal (Martin 2002).

Donodon Sigogneau-Russell, 1991, from the Early Cretaceous (Berriasian) of Morocco, was originally referred to the monotypic Donodontidae within Dryolestoidea (Sigogneau-Russell 1991), and later transferred to a new sublegion within Cladotheria (Ensom and Sigogneau-Russell 1998). The holotype of *Donodon perscriptoris* Sigogneau-Russell, 1991, an isolated upper molar, seems to belong to a dryolestoid, but the referred specimen, a dentary fragment with the two ?last molars (Sigogneau-Russell 1991: pl. 1, fig. 4), certainly does not belongs to this group. These lower molars have acute-angled trigonids (trigonid angle ~65° and ~72°) with small, roughly equal paraconid and metaconid, quite small talonid, and apparently unreduced posterior root. From their origin at the protoconid, the paracristid and protocristid extend almost anteriorly and posteriorly, respectively, then abruptly turn inwards towards the paraconid and metaconid respectively. It appears that a transverse shearing surface, characteristic for Cladotheria, was lacking. Ensom and Sigogneau-Russell (1998: 43) were fully aware that "the characteristics of the protoconid and of the roots of the attributed lower molars [of *Donodon*] are not those of dryolestoids", but preferred to retain the upper and lower molars in the same taxon. I think that the dentary specimen referred to *D. perscriptoris* should be attributed to "Symmetrodonta". The reduction of the lingual cingulid and mesial cingulid cuspule "f" are similarities shared with *Gobiotheriodon*.

Excluding *Zhangheotherium*, Cretaceous Spalacotheriidae form a well-supported monophyletic group, within which are placed the more inclusive Spalacolestinae, containing endemic taxa of a North American radiation (Cifelli and Madsen 1999). The main trend of spalacotheriid evolution is toward development of an acute-angled molar pattern, bringing mesial (prevallum) and distal (postvallum) shearing surfaces into a more transverse position, which considerably increases the total length of the shearing surface for the same molar series length. Correspondingly, the molar formula increases to M1–6 (or 7) m1–6 (or 7), which also increases the total shearing surface length. The dentary was quite derived, eventually lacking the Meckel's groove and having an hypertrophied pterygoid crest or process and efflected postero-inferior border of dentary for m. pterygoideus medialis and m. masseter attachment respectively, which provide lateral translation and rotation of the dentary during the masticatory cycle (Cifelli and Madsen 1999). This lateral translation and rotation was responsible for development of continuous prevallum and postvallum shearing surfaces on molars (Crompton 1971). An additional wear surface was formed along the enlarged and somewhat transversely (obliquely) oriented, crest-like distal stylar cusp on upper molars (Fox 1985: 22, fig. 1, 1 and 2), which apparently sheared against food particles. In the development of transversely oriented continuous shearing surfaces, spalacotheriids are analogous to tribosphenic and dryolestoid mammals. Evidently, spalacotheriids were highly specialized; an untestable speculation explaining their long survival in the Cretaceous of North America is that they were able to consume food resources not readily available to other mammals in the ecosystem. To speculate further, it is possible that progressive evolution and specialization of Spalacolestinae was permitted by the rarity of eutherian mammals: eutherians are not known from Cenomanian–Santonian faunas of North America, and do not become abundant on the continent until the early Campanian (Fox 1984b; Cifelli 1990, 2000). Radiation of eutherian mammals in North America at this time may have led to the rapid extinction of endemic Spalacolestinae, which are "not known in North America later than about the early late Campanian" (Cifelli and Gordon 1999: 11).

The Chinese *Zhangheotherium*, having rounded, conical molar cusps that lack connecting crests (Hu et al. 1997), apparently did not achieve the dental specialization characteristic for Spalacotheriidae, described above, and should be excluded from this taxon, although it may be a sister taxon to Spalacotheriidae (Cifelli and Madsen 1999: fig. 19).

Shalbaatar Nessov, 1997 was based on single specimen (an edentulous dentary fragment) from the lower Bissekty Formation at Dzharakuduk, Uzbekistan. *Shalbaatar* was originally referred to Multituberculata (?Plagiaulacoidea), because of the "relatively anterior position of the coronoid process" (Nessov 1997: 162). Nessov (1997: 162–163) also noted prominent "hystricognathy" of this specimen; i.e., lateral deflection of the posteroventral border of the dentary. He thought that *Shalbaatar* belongs to a peculiar group of multituberculates, retaining a primitive posterior position of the masseteric fossa and unenlarged p4, but derived in "hystricognathy" of the mandible (in parallel with some rodents). According to Z. Kielan-Jaworowska (personal communication 2000), the posteriorly placed masseteric fossa excludes *Shalbaatar* from Multituberculata, because this indicates absence of the "backward masticatory power stroke" that is characteristic of the group (Gambaryan and Kielan-Jaworowska 1995).

My investigation of ZIN 82622, the holotype of *Shalbaatar bakht* Nessov, 1997, reveals several features characteristic of spalacotheriid (or, even, spalacolestine: Cifelli and Madsen 1999) "symmetrodonts": molars small, less than 1 mm in length; the last molar is smaller than the penultimate molar; the molar alveoli are obliquely set on the dentary, canting labially; molar roots anteroposteriorly short and transversely wide; prominent pterygoid crest, placed relatively high and extending anteriorly to the alveolar border; a pocket posterior to the mandibular foramen and above the pterygoid crest; and strong lateral deflection of the angular region. The extraordinary structure of the dentary, found only in some spalacotheriids and in *Shalbaatar*, unambiguously places the latter taxon within the "symmetrodont" family Spalacotheriidae, at least. If possible attribution to Spalacolestinae is corroborated by further specimens, *Shalbaatar* would be the only non-American member of this subfamily. It is quite possible, because the Bissekty vertebrate fauna,

Table 1. Classification of “Symmetrodonta”*

- Holotheria Wible, Rougier, Novacek, McKenna, and Dashzeveg, 1995
  - “Symmetrodonta” Simpson, 1925
    - Kuehneotheriidae D. Kermack, K. Kermack, and Mussett, 1968
      - *Kuehneotherium* D. Kermack, K. Kermack, and Mussett, 1968 (?=*Kuehneon* Kretzoi, 1960, *nomen dubium*)
      - *Delsatia* Sigogneau-Russell and Godefroit, 1997
      - *Kotatherium* Datta, 1981
    - Shuotheriidae Chow and Rich, 1982
      - *Shuotherium* Chow and Rich, 1982
    - Tinodontidae Marsh, 1887
      - *Tinodon* Marsh, 1879 (=*Menacodon* Marsh, 1887; =*Eurylambda* Simpson, 1929)
      - ?*Gobiotheriodon* Trofimov, 1997
    - Spalacotheroidea Prothero, 1981
      - *Zhangheotherium* Hu, Wang, Luo, and Li, 1997
    - Spalacotheriidae Marsh, 1887
      - *Spalacotherium* Owen, 1854 (=*Peralestes* Owen, 1871)
      - *Shalbaatar* Nessov, 1997
    - Spalacolestinae Cifelli and Madsen, 1999
      - *Spalacotheroides* Patterson, 1955
      - *Spalacolestes* Cifelli and Madsen, 1999
      - *Spalacotheridium* Cifelli, 1990
      - *Symmetrodontoides* Fox, 1976 (=?*Mictodon* Fox, 1984)
  - “Symmetrodonta” *incertae sedis*
      - *Manchurodon* Yabe and Shikama, 1938

*taxa excluded from “Symmetrodonta”: *Amphidon* Simpson, 1925 (Mammalia *incertae sedis*), *Nakunodon* Yadagiri, 1985 (Holotheria *incertae sedis*), *Woutersia* Sigogneau-Russell, 1983 (Woutersiidae, sister group for Docodonta), *Thereuodon* Sigogneau-Russell, 1989 (Dryolestida, or Zatheria indet., milk dentition), *Bondesius* Bonaparte, 1990 (Dryolestida indet., milk dentition), *Casamiquelia* Bonaparte, 1990 (Dryolestida), *Brandonia* Bonaparte, 1990 (Dryolestida), *Barberenia* Bonaparte, 1990 (Dryolestida indet., milk dentition), *Quirogatherium* Bonaparte, 1990 (Dryolestida indet., ?milk dentition), *Atlasodon* Sigogneau-Russell, 1991 (Dryolestida, or Zatheria indet., milk dentition), *Microderson* Sigogneau-Russell, 1991 (stem-group zatherian), “*Kotatherium*“ *yadagirii* Prasad and Manhas, 1997 (?Amphilestidae).

Uzbekistan, is rather similar to that from the coastal plains of the North American Late Cretaceous. Several taxa are shared; including, notably, the eutherian mammal *Paranyctoides* (see Archibald and Averianov 2001).

Classification of “Symmetrodonta”

Though I do not ascribe to the view that a classification must be isomorphic with a single cladogram, a classification must clearly not contradict the prevailing phylogenetic hypothesis (e.g., Fox 1985: 24; Sigogneau-Russell and Ensom 1998: 455). In the case of “symmetrodonts”, available data are extremely scarce and limited, so that a reliable, robust hypothesis of relationships is presently unattainable. Among “symmetrodonts”, a reasonably well-corroborated phylogeny can only be established for the specialized spalacotheriids; the relationships of the remaining taxa remain problematic. In this case a conventional classification, based on some degree of similarity between taxa, appears to be the most reasonable and stable approach. As discussed above, monophyly of a broadly conceived “Symmetrodonta” is poorly corroborated and has been contradicted by recent studies: while continuing to use the group name mainly for the purposes of convenience, I tend to agree with other authors who consider this group as paraphyletic, if not polyphyletic (see review by Luo et al. 2002). The classification of “Symmetrodonta” proposed herein is presented in Table 1.

Acknowledgements

I thank Dr. Evgeny N. Maschenko for access to PIN specimens in his care and for preparing of the SEM micrographs in PIN (Fig. 2). I thank Profs. Richard L. Cifelli, Zhe-Xi Luo, Denise Sigogneau-Russell, and Zofia Kielan-Jaworowska for reading of the manuscript and their comments. My work was supported by the Russian Fund of Basic Research (RFBR) grants 00-15-99355 and 01-04-49548.

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Addendum

While this paper was in press, Kielan-Jaworowska et al. (2002) published a paper with reinterpretation of the dental formula of *Shuotherium*. They argued that it has three instead of four molars, and a molariform ultimate premolar (px). The latter character, found also in *Ausktribosphenos* and *Ambondro*, is a synapomorphy indicating the sister group relationships of *Shuotherium* and Australosphenida. Indeed, m1 ("px") in *Shuotherium* differs from the remaining molars by two important features: it has a more antero-posteriorly expanded trigonid and lacks a pseudotalonid. None of these features, however, indicates that this tooth is a premolar. An antero-posteriorly expanded m1 trigonid is found in other symmetrodonts, e.g., in *Tinodon* and *Zhangheotherium*, and is quite characteristic for spalacotheriids. As in other "holotherians", m1 in *Shuotherium* should occlude with the ultimate upper premolar anteriorly and M1 posteriorly. The three known lower premolars of *Shuotherium* are not molariform and there is no basis to assume that upper premolars would be molariform. Consequently, the ultimate upper premolar would not have a pseudoprotocone and thus there is no need for the pseudotalonid in m1. This is a disadvantage of an anterior talonid-like structure, four molars produce only three pseudotalonid-pseudoprotocone contacts, whereas in a posterior talonid construction four molars (e.g., in marsupials) produce four talonid-protocone contacts. I see no basis for a special relationships between *Shuotherium* and Australosphenida. The former has an essentially *Kuehneotherium*-like dentary apparently without an angular process. In australosphenidians the dentary is a morganucodontid-docodont-like, with a peculiar angular process and an anterior prolongation of Meckel's groove (reduced in *Bishops*).

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