New Early Cretaceous spalacotheriid "symmetrodont" mammal from Japan

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We describe a new spalacotheriid (acute-angled) "symmetrodont" (Mammalia, Trechnotheria), *Symmetrolestes parvus* gen. et sp. nov., from the Lower Cretaceous, likely Barremian, Kitadani Formation of the Tetori Group, central Japan. The specimen consists of a fragmentary right lower jaw with first incisor and five preserved postcanine teeth (interpreted as p5–m4). *Symmetrolestes* has acute-angled molariforms with complete shearing surfaces on the para- and protocristids, and relatively tall crowns, features that are referable to Spalacotheriidae. *Symmetrolestes* is more derived than zhangheotheriids in having complete shearing surfaces, taller crowns, and more complete cingulids. It differs from other spalacotheriids in having fewer molariforms (m1–4), higher number of premolariforms (p1–5), and gradual transition between premolariforms and molariforms. Our cladistic analysis of 29 characters shows *Symmetrolestes* as the sister group of the remaining Spalacotheriidae. This node is supported by only one character (Bremer support: 1) and therefore not particularly stable. The remaining spalacotheriids are arranged in a fully pectinated tree conforming to the topology of the previous researchers, in which Spalacolestinae occupy an apical position. The combination of the occurrences of a primitive spalacotheriid, *Symmetrolestes*, in Japan and of Zhangheotheriidae, which is the sister taxon of Spalacotheriidae, in China suggests a possibility for an East Asian origin of Spalacotheriidae, although it implies long ghost lineages for the latest Jurassic to Early Cretaceous East Asian "symmetrodonts".

Key words: Spalacotheriidae, "symmetrodonts", *Symmetrolestes*, Early Cretaceous, Tetori Group, Japan.

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Introduction

"Symmetrodonta" is a basal group of Mesozoic mammals characterized by the triangular aspect of the molars in occlusal view and the absence of a well-developed talonid (Simpson 1925; Cassiliano and Clemens 1979). The traditional group of "symmetrodonts" ranges in age from the latest Triassic to the Cretaceous and fossils are to be found in North America, South America, Europe, Africa, and Asia (Simpson 1928, 1929; Crompton and Jenkins 1967; Fox 1976, 1984, 1985; Fraser et al. 1985; Bonaparte 1990; Sigogneau-Russell and Ensom 1998; Cifelli and Madsen 1999; Cifelli and Gordon 1999; Ensom and Sigogneau-Russell 2000; Averianov 2002; Rougier, Ji, and Novacek 2003; Rougier, Spurlin, and Kik 2003). Despite the loosely defined nature of the group, the expansive temporal record, and the relatively wide geographic distribution, "symmetrodonts" form a small part of most faunas where they are represented (Cassiliano and Clemens 1979; see Cifelli and Madsen 1999 for an exception). Most recent studies question the monophyly of the group (Rougier et al. 1996, 1999, 2001; Rougier, Ji, and Novacek 2003; Sigogneau-Russell and Ensom 1998; Cifelli and Madsen 1999; Ji et al. 1999; Averianov 2002; Luo et al. 2002). The inclusion of the Rhaeto-Liassic *Kuehneotherium praecursoris* and its relatives (Crompton and Jenkins 1967, 1968, 1973; Kermack et al. 1968; Sigogneau-Russell 1983; Hahn et al. 1991) in a group which also includes Spalacotheriidae is in particular problematic. Not only the dentition in "symmetrodonts" seems to illustrate successive stages in the development of more complex occlusal relationships, but the lower jaw of *Kuehneotherium* shows a very primitive morphology with a prominent postdentary groove for the attachment of well-developed postdentary elements (Gill 1974; Prothero 1981), which are unknown in the more derived spalacotheriids. Because of these uncertainties with regard to the naturalness of "Symmetrodonta", we use double quotes for this term and its vernacular derivatives in this paper.

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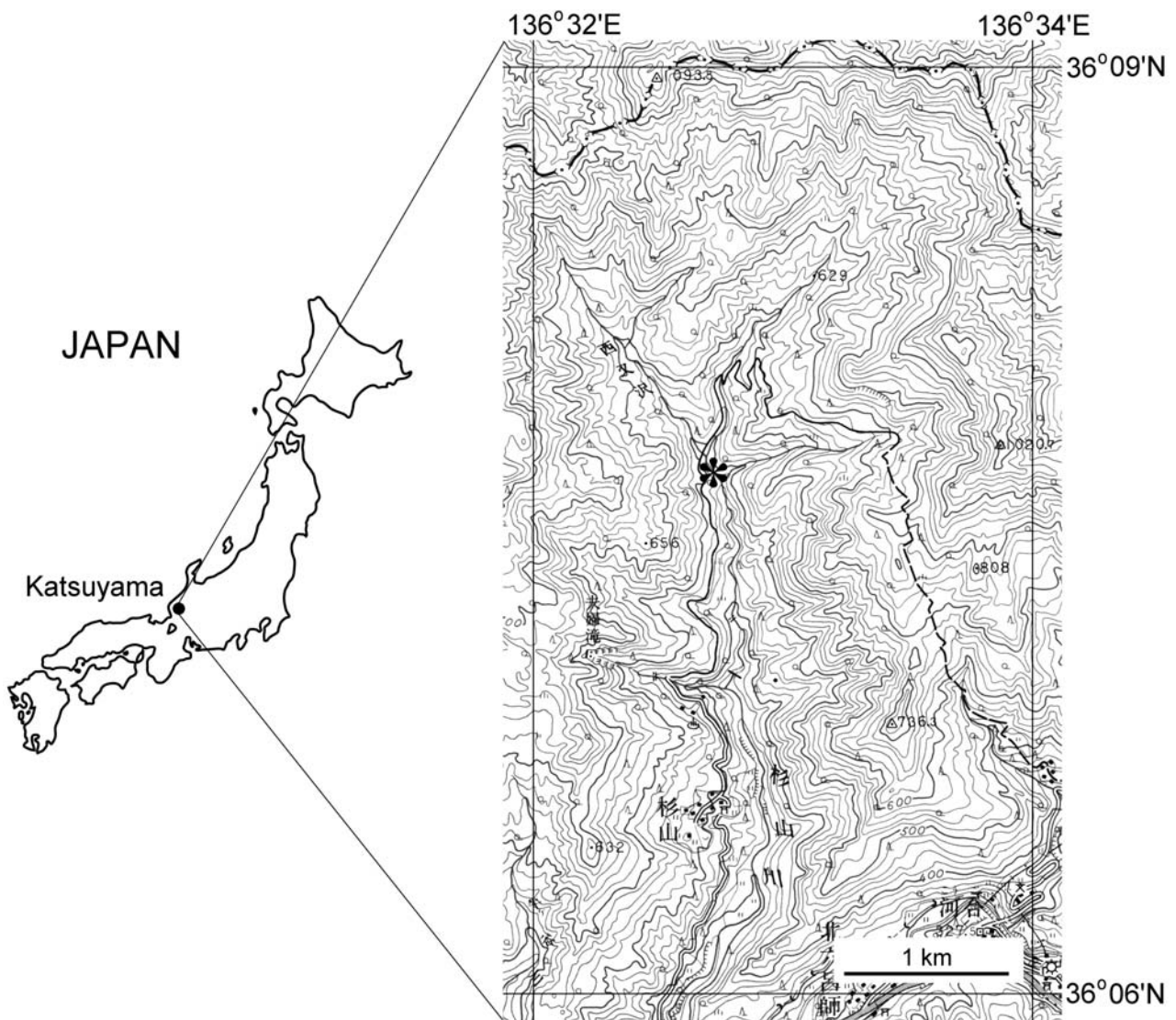http://app.pan.pl/acta49/app49-329.pdf

Fig. 1. Topographic map showing the fossil locality (asterisk), in the valley of the Sugiyama-gawa River, Kitadani-cho, Katsuyama City, Fukui Prefecture, central Japan (topographic map "Echizenkatsuyama", Geographical Survey Institute of Japan).

However, uncertain the arrangement and interrelationships of "symmetrodonts" may be, the monophyly of particular sub-groups is well-supported. Spalacotheriidae, which has acute-angled molariform teeth, strongly reduced talonids, and conspicuous anterior and posterior cingulids, is widely supported (Cifelli and Madsen 1999; Rougier et al. 2001). This family had been recorded only in Lower Cretaceous of Western Europe and Cretaceous of North America (Cassiliano and Clemens 1979; Krebs 1985; Cifelli and Madsen 1986, 1999; Cifelli 1990), and has been considered to have originated in Western Europe (Cifelli and Madsen 1999). On the other hand, a few spalacotheriids and/or spalacotheriid-like mammals have recently been reported from eastern Eurasia (Hu et al. 1997, 1998; Averianov 2002; Rougier, Ji, and Novacek 2003).

In this work, we describe a new spalacotheriid "symmetrodont" discovered in the Lower Cretaceous Kitadani Formation of the Tetori Group, Katsuyama City, Fukui Prefecture, central Japan. This is the first discovery of a "symmetrodont" and the second oldest mammalian fossil record in Japan (Setoguchi et al. 1999b; Rougier et al. 1999; Takada et al. 2001).

Abbreviations.—NSM PV, National Science Museum (Tokyo, Japan) Paleontology Vertebrate; I/i, upper/lower incisors; C/c, upper/lower canines; P/p, upper/lower premolars/premolariforms; M/m, upper/lower molars/molariforms.

Geologic setting and age

The isolated right lower jaw of the mammal described here was recovered from a rock block discovered at the valley of the Sugiyama-gawa River (Katsuyama City, Fukui Prefec-

ture, central Japan), where the upper part of the Kitadani Formation (= Kitadani alternation of sandstone, shale and tuff in Maeda 1958) of the Tetori Group is distributed (Fig. 1). This rock block was made up of gray-colored and fine-grained sandstone, and when splitted was found to contain in addition to the mammalian specimen described here, an indeterminate vertebral fragment, egg shell fragments, and a iguanodontid tooth. The lithology of the rock block was identical to that of the outcrops of the Kitadani Formation exposed at the locality, and the edges of the block were rather sharp, indicating that it was not transported from very far away. Therefore, we believe that the rock block including the fossil comes from the upper part of the Kitadani Formation.

The Mesozoic Tetori Group is broadly distributed in central Japan. It is subdivided into three subgroups, Kuzuryu, Itoshiro, and Akaiwa Subgroups in ascending order (Maeda 1961). The Kuzuryu Subgroup is composed mainly of marine deposits, yielding ammonoid species indicative of Tithonian to Berriasian (uppermost Jurassic to lowermost Cretaceous) age (Sato et al. 2003). The Itoshiro Subgroup is composed mainly of brackish to fresh-water deposits, yielding many vertebrate, molluscan, and plant fossils (e.g., Geyler 1877; Maeda 1958, 1961; Hasegawa et al. 1995; Cook et al. 1998; Evans et al. 1998; Evans and Manabe 1998, 1999a, b; Manabe 1999; Setoguchi et al. 1999a; Rougier et al. 1999; Manabe et al. 2000; Takada et al. 2001; Matsumoto et al. 2002). The Akaiwa Subgroup which is the uppermost of the three subgroups within the Tetori Group is composed mostly of sandstones representing fresh-water and brackish environments.

The Kitadani Formation is the uppermost formation of the Akaiwa Subgroup (i.e., the topmost of the Tetori Group). It conformably overlies the Akaiwa Formation (= Akaiwa sandstone) and is unconformably overlain by the Upper Cretaceous Omichidani Formation (= Omichidani alternation) (Maeda 1958, 1961). The Kitadani Formation consists of alternating beds of sandstones and shales, with many greenish gray tuffaceous beds, and yields fresh-water molluscs and many vertebrate fossils (e.g., Maeda 1961, 1962, 1963; Isaji 1993; Azuma and Tomida 1997; Kobayashi 1998; Azuma and Currie 2000; Goto et al. 2002; Hirayama 2002; Kobayashi and Azuma 2003).

The Kitadani Formation yields two fresh-water trigonioidid bivalve species, *Nippononaia ryosekiana* and *Trigonioides tetoriensis*, which also occur in other deposits dated indirectly based on their interfingering relationships with marine deposits in Japan (Maeda 1961, 1963; Isaji 1993). *Nippononaia ryosekiana* also occurs in the lower part of the Sebayashi Formation in the Sanchu area, which is distributed about 200 km east from the locality of the present material (Hayami and Ichikawa 1965; Matsukawa 1977). The Sebayashi Formation conformably overlies the Ishido Formation, which yields late Barremian ammonite assemblages, while the upper part of the Sebayashi Formation yields late Aptian ones (Matsukawa 1983; Matsukawa et al. 1997: fig. 2). Therefore, the lower part of the Sebayashi Formation is cor-

related to somewhere within the upper Barremian to upper Aptian. *Trigonioides tetoriensis* also occurs from the upper part of the Tatsukawa Formation in the Katsuuragawa area, which is distributed about 300 km southwest from the locality of the present material (Tashiro and Okuhira 1993). The Tatsukawa Formation is conformably overlain by the Hanoura Formation, which yields early Barremian ammonite indices in its basal part (Matsumoto et al. 1982; Tashiro and Okuhira 1993; Matsukawa et al. 1997: fig. 2). Although the Tatsukawa Formation unconformably overlies the pre-Cretaceous, the *T. tetoriensis*-bearing horizon of the Tatsukawa Formation is just below the early Barremian ammonite-bearing horizon (basal part) of the Hanoura Formation, implying that the age of the *T. tetoriensis*-bearing horizon is probably not very different from that of the basal part of the Hanoura Formation and probably not older than the late Hauterivian (Tashiro and Okuhira 1993). Therefore, the *T. tetoriensis*-bearing horizon of the Tatsukawa Formation can be correlated to somewhere within the upper Hauterivian to lower Barremian. On the other hand, the Sebayashi Formation has not yielded *T. tetoriensis* and the Tatsukawa Formation has not yielded *N. ryosekiana*.

Therefore, the co-occurrence of *N. ryosekiana* and *T. tetoriensis* in the Kitadani Formation suggests that this formation can be correlated between the Tatsukawa and Sebayashi Formations, that is, within the upper Hauterivian to upper Aptian. Despite the temporal bracketing provided by the paleontological evidence, the precise geologic age of the Kitadani Formation is still somewhat ambiguous, because the above correlation of the Kitadani Formation is based only on the occurrence of fresh-water bivalves, which are traditionally less precise age indicators than marine index fossils. Nevertheless, there is consensus in attributing an Early Cretaceous Age, likely Barremian to the Kitadani Formation (Matsumoto et al. 1982; Matsukawa and Obata 1992; Isaji 1993; Tanase et al. 1994; Matsukawa and Ito 1995; Matsukawa et al. 1997).

Material and method

The specimen described here is a fragmentary right lower jaw preserved in two little blocks. The alveolar process, teeth, and the root of the coronoid process are in the main block and are exposed mainly in lingual view; the condyle, masseteric fossa, parts of the coronoid process, and tiny fragments of broken teeth are in the second block and are exposed mainly in buccal view. The two pieces have been kept separated because they have been prepared from opposite sides and contact surface is minimal, making re-assembly of the fossil difficult.

Dental measurements are shown in Table 1. Measurements were taken from the Scanning Electronic Microscope (SEM) photos of the epoxy cast of the material. We followed the measurement convention and dental and dentary terminologies by Cifelli and Madsen (1999).

Table 1. Dental measurements (in mm) of NSM PV 20562 (the holotype of *Symmetrolestes parvus* gen. et sp. nov.). L, mesiodistal length; ANW, anterior width (greatest width of lower teeth) (Cifelli and Madsen 1999: fig. 2A); *, estimate.

	L	ANW
p5	1.07	0.67
m1	0.67	0.78
m2	0.69	0.82*
m3	0.67	0.62*
m4	0.57	0.29

Morphology alone is an unreliable criterion to determine if a postcanine is a molar or a premolar (which in a strict sense is defined based on the presence/absence of replacement) particularly for Mesozoic mammals (Owen 1868; Clemens and Lillegraven 1986). We therefore use the terms "premolariform" and "molariform" to refer to morphology only, and without any implications with regard to replacement or lack thereof in a given tooth position. Premolariforms are simple-shaped postcanine teeth located mesial to complex-shaped molariforms.

Systematic paleontology

Mammalia Linnaeus, 1758
Trechnotheria McKenna, 1975
Superfamily Spalacotherioidea Marsh, 1887

Included families.—Spalacotheriidae Marsh, 1887; Zhangheotheriidae Rougier, Ji, and Novacek, 2003.

Family Spalacotheriidae Marsh, 1887

Type genus: *Spalacotherium* Owen, 1854 (including *Peralestes* Owen, 1871).

Included genera.—*Spalacotheroides* Patterson, 1955; *Symmetrodontoides* Fox, 1976; *Spalacotheridium* Cifelli, 1990; *Shalbaatar* Nessov, 1997; *Spalacolestes* Cifelli and Madsen, 1999; *Symmetrolestes* gen. nov. Tsubamoto and Rougier.

Revised diagnosis.—Acute-angled "symmetrodonts" which differ from other "symmetrodonts" in having a strong pterygoid crest of the dentary, broad and erect coronoid process, laterally deflected posteroinferior border of dentary, buccal alveolar margin of dentary much lower than lingual margin, continuous prevallum and postvallum shearing crest, high crown (twice as or more than the mesio-distal length), reduced talonid on lower molariforms, and continuous or almost continuous buccal and lingual cingulids on lower molariforms (the last character is lost in *Spalacotheroides*). Also characteristic of the family is the presence of upper molariforms with reduced, or very small, stylocones, and two roots strongly mesiodistally compressed. Differs from more basal zhangheotheriids in the presence of complete shearing surfaces on the para- and protocristids, taller crowns, and more complete cingulids.

Comment on taxa content and synonymy.—Many workers (e.g., Simpson 1928, 1929; Clemens, 1963; Cassiliano and Clemens 1979; Prothero 1981; Hu et al. 1997, 1998; McKenna and Bell 1997; Sigogneau-Russell and Ensom 1998; Averianov 2002) consider *Peralestes* to be a junior synonym of *Spalacotherium*. Sigogneau-Russell (1991) described *Microderson* from the Lower Cretaceous of Morocco and assigned it to Spalacotheriidae. However, Sigogneau-Russell and Ensom (1998) and Averianov (2002) excluded *Microderson* from Spalacotheriidae. Averianov (2002) considered *Microderson* to be a stem-group zatherian, a group that includes peramurans and tribosphenidans (McKenna and Bell 1997). Hu et al. (1997) described *Zhangheotherium* from the Lower Cretaceous of China, and assigned it to Spalacotheriidae. However, Cifelli and Madsen (1999), Rougier et al. (2001), Rougier, Ji, and Novacek (2003), and Averianov (2002) suggested that *Zhangheotherium* seems to be a sister taxon of Spalacotheriidae. We follow here this concept of Spalacotheriidae. Nessov (1997) described *Shalbaatar* from the Upper Cretaceous of Uzbekistan and assigned it to the Multituberculata. However, Averianov (2002) has considered *Shalbaatar* to be a spalacotheriid. Bonaparte (1990) described *Brandonia* from the Upper Cretaceous of Argentina and with doubts assigned it to Spalacotheriidae. Later, Bonaparte (1994) and Averianov (2002) consider *Brandonia* to be a dryolestoid.

Genus *Symmetrolestes* nov. Tsubamoto and Rougier

Type and only known species: *Symmetrolestes parvus* gen. et sp. nov. Tsubamoto and Rougier.

Etymology: From Greek *symmetros*, symmetric, in reference to the symmetric aspect of the molars of most members of the "Symmetrodonta"; from Greek *lestes*, hunter, a common ending of the names of Mesozoic mammals despite that the hunting habits of these miniscule critters are dubious.

Diagnosis.—Small and primitive spalacotheriid, with only four molariforms and at least four (probably five) premolariforms. Differs from other spalacotheriids in the small number of molariforms, the high number of premolariforms, and the more gradual transition between premolariforms and molariforms (the last premolariform has triangular outline in occlusal view).

Symmetrolestes parvus sp. nov. Tsubamoto and Rougier

Figs. 2–6.

Holotype and only specimen: NSM PV 20562, a fragmentary right lower jaw with a incisor and five postcanine teeth found in two blocks.

Repository: National Science Museum, Tokyo, Japan.

Type locality: 36˚07'41"N, 136˚32'44"E; in the valley of the Sugiyama-gawa River, Kitadani-cho, Katsuyama City, Fukui Prefecture, central Japan (Fig. 1).

Type horizon: Upper part of the Kitadani Formation (= Kitadani alternation of sandstone, shale and tuff in Maeda 1958), Akaiwa Subgroup, Tetori Group; Early Cretaceous (late Hauterivian to Aptian).

Etymology: From Latin *parvus*, small.
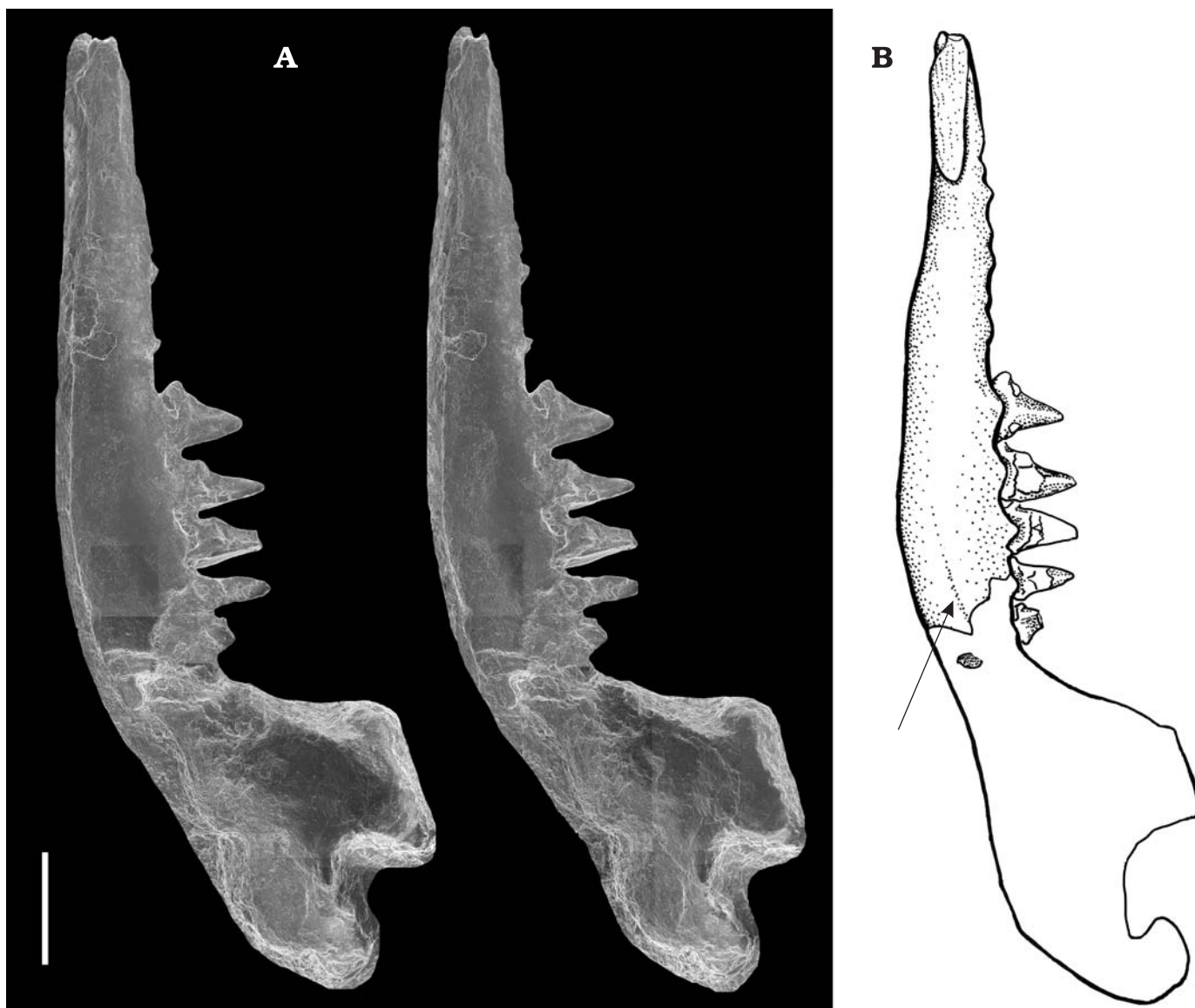
Diagnosis.—As for genus.

Fig. 2. S*ymmetrolestes parvus* (NSM PV 20562, holotype). **A**. Lingual stereo view of the dentary. Note the ledge of matrix left along the ventral edge of the jaw, which continues toward the back bearing impressions of the condyloid and coronoid processes. **B**. Drawing of the jaw in approximately the same position as in A. The back of the coronoid process has been reconstructed from impressions left in the main block and the fragments preserved in the smaller block (Fig. 6). Scale bar 2 mm. The arrow indicates the position of Meckel's sulcus. The dark circle towards the back of the jaw is the mandibular foramen.

Description

The jaw preserves the first incisor and five postcanine teeth, which represent the ultimate premolariform and the whole molariform series (m1–m4). In front of these postcanine teeth, there are nine complete alveoli and somewhat ambiguous evidence for three more (Figs. 3, 4). At the very tip of the jaw is the procumbent i1, whose root is exposed in dorsal view by breakage of the alveoli. Its crown is partially covered by bone but can be seen along the ventral edge of the jaw (Figs. 2, 4).

The posterior six alveoli show distinctive interradicular septa, which typically are higher than the intermolar septa. This implies the presence of three double-rooted teeth in front of the ultimate premolariform. Given the monotonic change in size and shape of these alveoli whose sizes diminish anteriorly, it is very likely that all of them represent premolariform loci. There are three further alveoli mesial to those considered (i.e., seventh–ninth from the most posterior alveolus preserved) that are also complete. The most posterior of these (seventh) is subequal in size and similar in shape to the alveolus of the premolariform behind it. In front of the seventh alveolus there are two smaller and subequal alveoli arranged at a small angle to the alveolar process of the jaw. This change in orientation suggests that there is a change in tooth family. The likely interpretation of these alveoli would suggest that a small double-rooted canine occupied the front two alveoli and that a single-rooted first premolariform followed it. Small double-rooted canines are present among
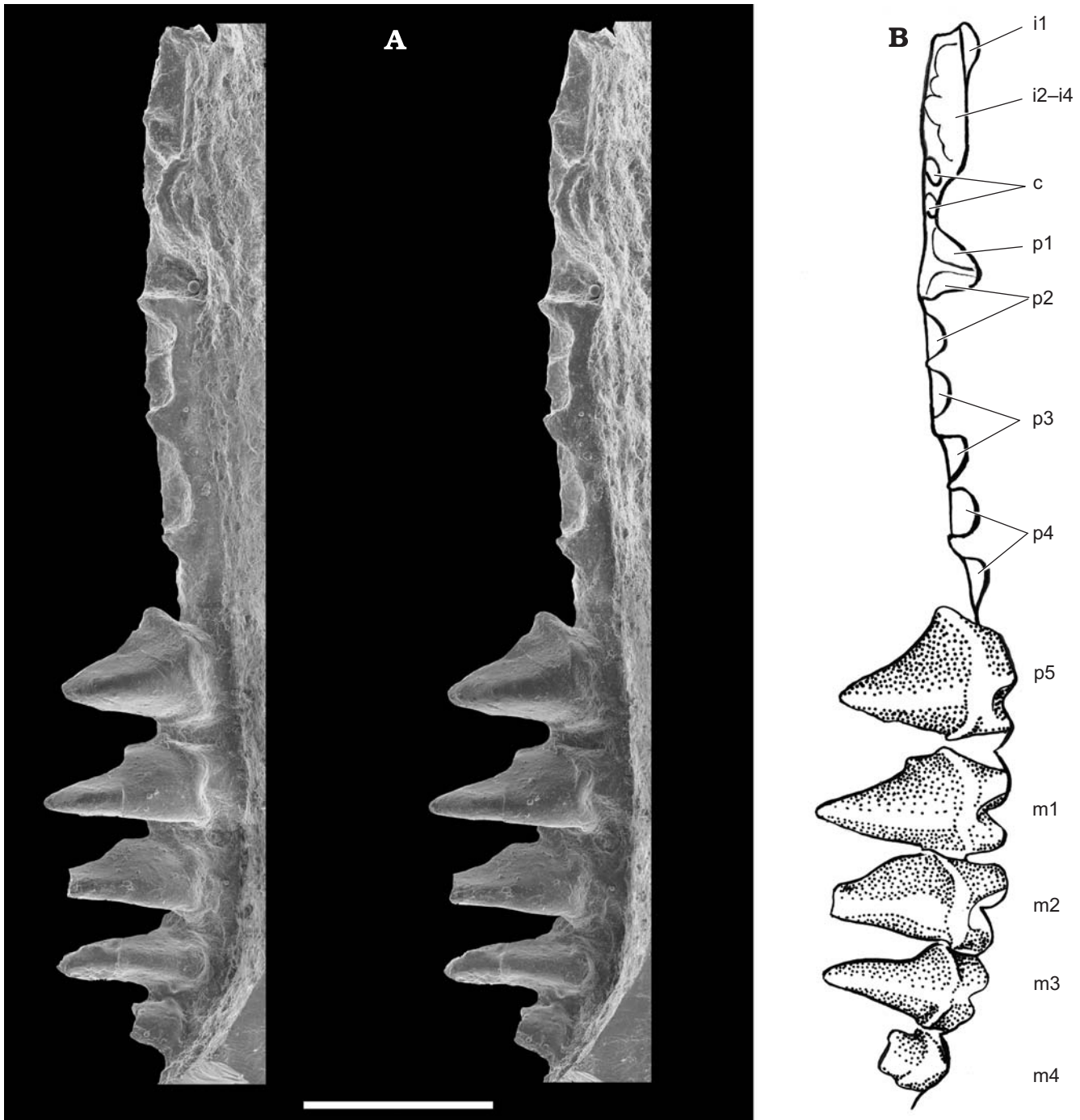
Fig. 3. S*ymmetrolestes parvus* (NSM PV 20562, holotype). **A**. Buccal stereo view of the dentition and alveolar margin of the jaw. **B**. Interpretation of tooth positions and alveoli. Abbreviations follow those in the main text. Scale bar 2 mm.

basal forms of trechnotheres and cladotheres, making this interpretation plausible. Regardless of alternative interpretations of the three mesial alveoli, we are certain of a count of four or more premolariforms. The minimum number of incisors is three and if our suggestions were accepted, there would be at least four lower incisors.

In short, the dental formula can be conservatively postulated as i3+, c1, p4+?, m4, and if the outline put forward above is followed, the likely formula is i4, c1, p5, m4.

Dentition.—The fist incisor (i1) is complete, strongly procumbent and with a long root that extends back at least up to the level of the first completely preserved alveolus, which is interpreted here as the likely anterior root of a two-rooted canine (Figs. 3, 4). The crown is rather featureless with a convex mesial surface devoid of accessory cusps and a fairly flat distal surface. No wear facets are visible and the enamel of the crown does not extend back towards the root. Given the position of the tooth on the extreme ventral edge of the jaw

and the lack of wear, it is likely that this tooth was as yet unerupted and has been exposed by breakage of the anterior-most portion of the jaw.

The first preserved postcanine tooth is the ultimate premolariform and here we will assume it to be the p5 for the purpose of description (Figs. 2–5). The p5 is the best-preserved tooth, although it shows some damage. The crown is buccolingually compressed and dominated by a single cusp, the sharp and trenchant protoconid, made even more prominent by the lack of a metaconid, which is lost due to breakage. The tall protoconid is in the confluence of three main crests. The mesial one is the paracristid, on the lingual aspect of which the broken base of a minute cuspule, likely the paraconid is shown. The second crest reaches the lingual surface of the protoconid and bisects this surface in two fairly equal areas. The third and last crest, the protocristid, bears a flat and distally oriented wear facet near the apex and a small cusp midway between the protoconid and the base of the now missing metaconid. A shallow groove descends on the lingual surface of the protoconid from the cuspule on the protocristid. The paraconid, as deduced from its broken base, amounted to little more than a conical cusp on the lingual end of the paracristid. The substantially more robust metaconid, as deduced from its broken base, was removed from the protocristid and much smaller than the protoconid. There are small anterior and posterior cingular cusps. The lingual surface of the crown is distinctly delimited from the roots by a thickened edge reminiscent of a cingulid. In the buccal side of the tooth the cingulid is complete and fully encircles the base of the crown from one cingular cusp to the other. The cingulid has small crenulations or cuspules along its length. The roots are somewhat transitional between the slightly oval or circular roots deduced for the premolariforms or their alveoli, and the distinctively mesiodistally compressed roots of the molariforms of spalacotheriids. The condition, however, is much closer to that of the molariforms than to the circular roots present in the alveoli for the premolariforms.

Despite severe damage to m1–m3 the main features can be described, and these elements will be treated together here because a composite of all of them has to be made in order to describe the molar morphology (Figs. 2–5). The m4 will be described separately because it is morphologically distinct form more mesial molariforms. The protoconid is the dominant cusp and is mesiodistally compressed with flat paracristid and protocristid implying prevallum-postvallum shearing surfaces. The teeth reduce the size of the protoconid in the mesial to distal direction. At the same time, the protoconid becomes more compressed and the paraconid and metaconid approach each other more closely. Both para- and metaconids are heavily damaged in all teeth but fragments of them are preserved on the smaller of the two blocks. Both cusps are connated and subequal in size. The paraconid is slightly procumbent and the metaconid inclined slightly posteriorly. The lingual bases of these two cusps are connected with distinct anterior and posterior cingular cusps, which can be seen on the fragment of the m3 on the smaller of two
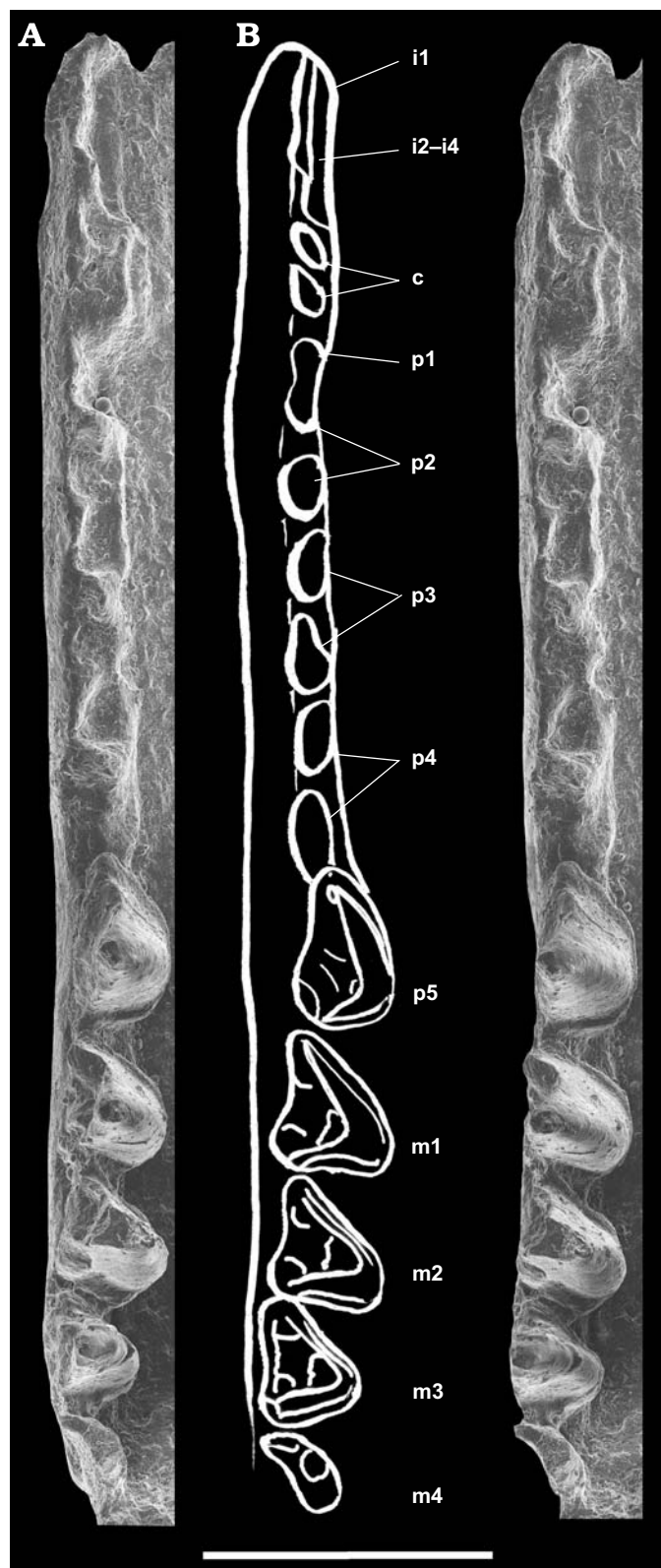

Fig. 4. S*ymmetrolestes parvus* (NSM PV 20562, holotype). **A**. Occlusal view of the dentary as preserved in the main block. **B**. Outline drawing of the dentition in occlusal view. Scale bar 2 mm.

blocks. As in the case of the last premolar, the lingual margin of the crown is indicated by a thickened ridge that connects
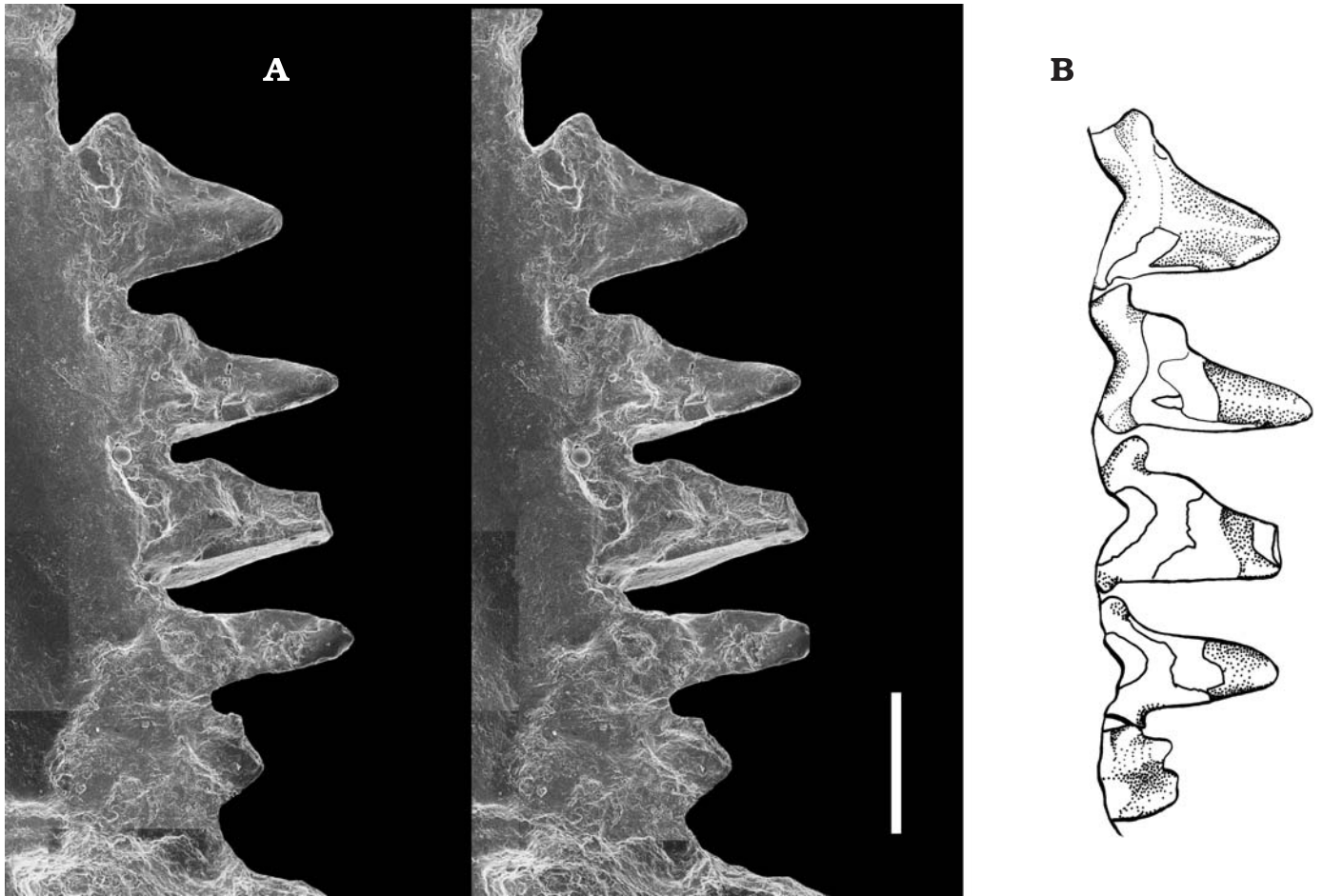
Fig. 5. S*ymmetrolestes parvus* (NSM PV 20562, holotype). **A**. Detail stereo view of p5–m4 in lingual view. **B**. Drawing of the dentition in lingual view. Scale bar 1 mm.

both cingular cusps. The main feature on the buccal surface is the prominent cingulid that runs on the base of the crown. It is strong mesiodistally but it becomes weaker in the buccal edge of the protoconid. It is interrupted in the m2 but likely continuous as a feeble ridge on m1 and m3. Therefore, the cingulid is continuous or almost continuous in *Symmetrolestes*. The m3 has the para- and metaconids much lower than the same cusps of the preceding molariform; this difference is not present between m1 and m2. The molariform roots are strongly compressed mesiodistally as other spalacotheriids. The interlocking between succeeding teeth is typical of spalacotheriids involving a single cusp mesially and distally.

The m4 is the smallest molariform (Figs. 2–5). The m4 is also damaged, missing the apex of the protoconid. The paraconid is tall and trenchant, united lingually to a robust anterior cingular cusp. The metaconid was not present on the m4, and has a skewed outline typical of a last molariform. The buccal cingulid is fairly complete and formed by a blunt crest. It is likely that a single root supported the tooth. There is a prevallid surface (for shearing against the distal surface of M3) but no postvallid surface, suggesting the lack of functional M4. Therefore, *Symmetrolestes* probably has only three upper molariforms, or a very reduced M4.

Dentary.—Although the dentary is divided between two blocks, much of the anatomy of the jaw can be described (Figs. 2, 6). The corpus (alveolar process) of the jaw is gracile, slender, never reaching more than 1.5 times the height of the teeth. The dentary becomes progressively more robust posteriorly up to the level of m3; from there back, the jaw margin is slightly upwardly turned to become continuous with the condylar process. In dorsal view, the corpus of the jaw is relatively straight anterior and posterior to the level between p4 and p5, where it slightly curves medially. On the lingual surface of the jaw, the more prominent feature is the long and narrow mandibular symphysis that is only moderately rugose and extending back to the level of the tooth we interpret as p1 (Fig. 2). More posteriorly and about mid-height of the corpus there is a sulcus from the level of m1 that extends back through the preserved portion of the jaw. The groove represents a poorly developed Meckel's sulcus (Meckel's groove). Further back, the mandibular foramen and canal can be seen through the broken bone of the dentary. It is a proportionally large foramen. The coronoid process was extensive and erect; the anterior coronoid crest is blunt and broad, demarcated by a prominent ventral masseteric ridge and a deep masseteric fossa. At the anteroventral corner

Fig. 6. *Symmetrolestes parvus* (NSM PV 20562, holotype). **A**. Stereo view of the posterior portion of the jaw in buccal view, as preserved in the smaller of the two blocks. **B**. Drawing of the preserved portion of the jaw. Scale bar 2 mm.

of this fossa is the masseteric (buccal mandibular) foramen. The dorsalmost portion of the coronoid process is lost. The ventral masseteric ridge is sharp and continuous with the ventral edge of the jaw anteriorly and with the condylar process posteriorly. The condylar process is broken and slightly downwardly reflected. There is no distinct angular process, and the condyle itself is small, mostly dorsally facing, and of triangular cross-section. The condyle is dorsal to the level of the alveolar edge. In ventral view, a strong pterygoid crest can be seen projecting medially; however, the morphological details of its lingual view are not accessible.

Identification of the first preserved postcanine tooth in *Symmetrolestes*

The primary homologies of the first molariform postcanine tooth in many Mesozoic mammal groups are problematic, as there is a difficulty in determining the boundary between premolars and molars, the criteria for molar recognition, and ultimately, tooth formula. One peculiar feature of *Symmetrolestes* is the predicted high premolariforms count and the reduced number of molariforms, which is opposite to what would be expected in a spalacotheriid (Cassiliano and Clemens 1979; Prothero 1981; Cifelli and Madsen 1999). This problem could be mitigated if the first preserved postcanine tooth in NSM PV 20562 is interpreted as the m1. We consider, however, this option unlikely (see below).

Among basal mammaliaforms, *Tinodon*, and spalacotheriids there is an abrupt change in morphology between the premolariforms and the molariforms (Crompton 1974; Clemens 1963; Cifelli and Madsen 1999). This is not the case in

Symmetrolestes where the last premolariform had at least a fairly well-developed metaconid. Certainly, the tooth in question was not fully molarized and lacked a paraconid, as indicated by small size of its broken base. In spalacotheriids, the premolariforms are trenchant with a main central cusp, a posterior metaconid in line and taller than the first molariform. This is not the case in *Symmetrolestes* where the premolariform is lower or subequal in height to the m1, and the crown has a distinct triangular outline. This tooth position in *Symmetrolestes* resembles the tooth interpreted as m1 in *Zhangheotherium* (Zhangheotheriidae) in these likely primitive features. However, the m1 in *Zhangheotherium* also has well-developed paraconid and metaconid, and the preceding tooth is premolariform, which is much simpler-shaped and buccolingually-compressed with small metaconid and lacking paraconid, suggesting that the tooth of *Zhangheotherium* in question can be interpreted as the m1. Because of the lack of well-developed paraconid, we feel justified in interpreting this somewhat complex tooth in *Symmetrolestes* not as a somewhat simplified m1 but as a somewhat complicated last premolariform.

On the other hand, the tooth interpreted as first molar in *Zhangheotherium* by Hu et al. (1997, 1998) is a premolar, as indicated by the much less worn condition of this tooth with respect to the following molariform. This interpretation recently has been confirmed by an additional specimen of *Zhangheotherium* that shows replacement actually occurring at this locus (Luo et al. 2001; Rougier, Ji, and Novacek 2003). Additionally, Rougier, Ji, and Novacek (2003) described a new zhangheotheriid from Liaoning, *Maotherium sinensis*, which also shows a peculiar wear pattern that can only be explained if the first molariform is actually a premo-

lar. Therefore, it is possible that the tooth interpreted as m1 in spalacotheriids might be in fact a permanent premolar.

If the tooth traditionally interpreted as the m1 in amphilestids, zhangheotheriids, and other Mesozoic mammals can be instead interpreted as a complex premolar (in strict sense of this term), then the complex posterior premolars of some derived stem group Theria such as *Arguimus*, *Arguitherium*, peramurids, and relatives would not show such a surprising and unique morphology. From a purely theoretical point of view, the presence of a deciduous predecessor of a fully molarized element is just the retention of a primitive pattern present in the mammalian sister groups. In light of the seemingly widespread occurrence of replacement of the first molariform in several Mesozoic lineages, determination of tooth formula and tooth positions depend on the correct assessment of the premolar-molar boundary. Until a better understanding of this dynamic interface in Mesozoic groups is reached, attributing much importance to tooth formula may be unwarranted.

Comparisons

The dentary of *Symmetrolestes* is smaller than that of other spalacotheriids (*Spalacotherium* and *Spalacolestes*) and zhangheotheriids (*Zhangheotherium* and *Maotherium*). Morphologically, it is similar to that of *Spalacotherium* in being gracile and slender with no distinct angular process. As in both *Spalacotherium* and zhangheotheriids, the small and mostly dorsally faced condyle is above the level of the alveolar edge and the dentary has a shallow Meckel's groove. We believe the condition of the condyle in *Zhangheotherium*, reconstructed by Hu et al. (1997: fig. 2, 1998: fig. 1) as below the alveolar edge of the dentary is incorrect; see the photos of the specimen by Hu et al. (1997: fig. 1). *Symmetrolestes* differs from *Zhangheotherium* in having a more slender alveolar process of the dentary, more dorsally located condyle and condylar process, less posteriorly-tilted coronoid process, and weaker Meckel's groove. In general, differences between zhangheotheriids on one hand and spalacotheriids on the other (even basal taxa as *Symmetrolestes*) are related to the expansion of the temporal and pterygoid musculature and refinements of mastication involving a larger degree of bucco-lingual movement. *Symmetrolestes* and other spalacotheriids differ from cladotherians in lacking a distinct angular process, in having complete buccal cingulids, and extensive lingual ones. The extreme reduction of the talonid of spalacotheriids could potentially be a diagnostic feature depending on how the dryolestoids (which also have extremely reduced talonids) are placed on the accepted phylogenetic tree. *Symmetrolestes* has a strong pterygoid crest, which seems to be as well-developed as that of *Spalacotherium* but better-developed than that of zhangheotheriids. The North American Cretaceous *Spalacolestes* and *Symmetrodontoides* (Cifelli and Madsen 1999) show a remarkably strong system of masseteric and pterygoid crests, which are far more promi-

nent than those of *Symmetrolestes*. Relatively short and blunt pterygoid ridges are also present in triconodontids (Simpson 1928, 1929; Cifelli et al. 1998) and amphilestids-gobiconodontids (Simpson 1928; Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Rougier et al. 2001), possibly representing a structural model from which the spalacotheroid pterygoid morphology would develop.

Symmetrolestes has masseteric (buccal mandibular) foramen, as do many basal mammals (e.g., Dashzeveg and Kielan-Jaworowska 1984; Marshall and Kielan-Jaworowska 1992; Cifelli et al. 1998; Rougier et al. 2001; Luo et al. 2002); the known dentaries of *Spalacolestes* and zhangheotheriids lack this foramen (Hu et al. 1997, 1998; Cifelli and Madsen 1999; Rougier et al. 2001; Rougier, Spurlin, and Kik 2003). This character might bear a phylogenetic signal but at present its distribution and nature are not well understood. The masseteric foramen likely represents a vascular structure transversing the dentary from the masseteric fossa to the mandibular canal. The only modern model for this structure is *Ornithorhynchus* (Monotremata), where the deep mandibular fossa has a small connection with the mandibular canal (Zeller 1989: 70).

The lower first incisor (i1) of *Symmetrolestes* is relatively large and procumbent with a long root. This condition is similar to that of *Zhangheotherium* and seems common among Mesozoic mammals, such as gobiconodontids (Trofimov 1978; Jenkins and Schaff 1988) and triconodontids (Simpson 1925, 1928, 1929; Hu et al. 1998), although the i1 in *Symmetrolestes* is proportionally much smaller than that in these groups.

The lower canine of *Symmetrolestes* is interpreted here as double-rooted; this is also the condition in some triconodonts, amphilestids, *Tinodon*, and *Spalacotherium*, and is fairly widespread among cladotherians, most dryolestoids and therian stem-groups (see Clemens and Lillegraven 1986 for a review of older specimens). On the other hand, zhangheotheriids have single-rooted canines (Hu et al. 1997, 1998; Rougier, Ji, and Novacek 2003). If our interpretation of the dentition in *Symmetrolestes* is correct, the canine would be a very small tooth, not unlike the tooth interpreted as a canine in *Tinodon* (Simpson 1925, 1929; Prothero 1981). This condition is radically different in spalacotheriids where the canine is tall, trenchant, and substantially larger than the first premolariform. Regardless of the position identified as a canine, the extremely slender symphysis of *Symmetrolestes* indicates a small-sized canine.

The postcanine lower dentition of *Symmetrolestes* is formed by acute-angled molariforms with complete shearing surfaces on the para- and protocristids, relatively tall crowns, and very much reduced talonids. These characteristics are closely comparable to those present among other members of Spalacotheriidae. If our interpretation of the alveoli in the front of the jaw is correct, *Symmetrolestes* differs from *Spalacotherium* in having a single-rooted p1 (*Spalacotherium* has double-rooted p1). *Symmetrolestes* differs from the derived spalacolestines in having broader, less acute

molariforms. It also differs from zhangheotheriids, which is the sister taxon of Spalacotheriidae (see Rougier et al. 2001; Rougier, Ji, and Novacek 2003), in having complete shearing surfaces on the para- and protocristids, taller crowns, more complete sharper cingulids, weaker cingular cusps, and single-rooted p1 (zhangheotheriids have double-rooted p1).

Symmetrolestes, zhangheotheriids (Hu et al. 1997, 1998; Rougier, Ji, and Novacek 2003), and *Gobiotheriodon* (Trofimov 1980; Averianov 2002) retain the likely primitive condition of four to five molariforms. *Zhangheotherium* was originally described as having six lower molars, but if our interpretation of the homologies of the first molariforms are followed, it implies that only five molariforms are present in *Zhangheotherium* (misprinted in Rougier, Ji, and Novacek 2003 as p3 m3 instead as p3 m5). It should be noted that there is still a remaining problem: the closely related zhangheotherid *Maotherium* (Rougier, Ji, and Novacek 2003) has one extra molariform and therefore even under the revised homologies proposed here there is at least one zhangheotherid with six molariforms. It is possible that the type of *Zhangheotherium* is a juvenile and further molariforms were to erupt at a later stage (the sixth molar in *Maotherium* is extremely reduced).

Derived spalacotheriids, on the other hand, increase the number of molariforms up to seven (Simpson 1928; Prothero 1981; Cifelli and Madsen 1999), a trend further developed by dryolestoids, which can have as many as eight molariforms. The acquisition of a high number of molariforms in spalacotheriids and dryolestoids, however, is likely to have been achieved independently because most phylogenetic proposals do not cluster them as a monophyletic entity to the exclusion of more derived stem-therian taxa such as peramurids or *Vincelestes* (see Luo et al. 2002 for a recent iteration).

In contrast, the number of premolariforms is higher in *Symmetrolestes* (likely five) than in other spalacotheriids, where a count of three is accepted as representing the generalized condition for the group. In this regard, the condition among zhangheotheriids, which have either two or three premolariforms, pose a problem, implying either an independent reduction of the premolariform number in zhangheotheriids and latter spalacotheriids, or an independent acquisition of five premolars in *Symmetrolestes*.

In the basal mammaliaforms, the common ancestor of *Morganucodon*, therians, and its descendents (Rowe 1988, 1993), the numbers of premolariforms and molariforms are variable. For example, different species of *Morganucodon* have four or five lower premolariforms (p4–5) and a variable number of molariforms ranging form three to five (m3–5) depending of the species (Mills 1971; Kermack, et al. 1973, 1981; Luo and Wu, 1994); *Megazostrodon* has p5/m4; *Kuehneotherium* has p6/m4–5 (Gill 1974); *Triconodon* has p4/m4; *Priacodon* and *Tinodon* have p3/m4 (Simpson 1928, 1929); *Paurodon* has p2/m4 (Simpson 1929); and *Laolestes* has p4/m8 (Simpson 1929). Most of triconodonts and obtuse-angled "symmetrodonts" have three to five lower premolariforms and also three to five lower molariforms (Simpson 1928, 1929; Jenkins and Crompton 1979), so that this

condition seems to be primitive for mammals. If it is true, the condition of *Symmetrolestes*, with five lower premolariforms and four lower molariforms, can be seen as retention of the primitive, generalized dental formula, which would be also primitive for Spalacotheriidae in general.

The more gradual transition between premolariforms and molariforms present in *Symmetrolestes* (whether the tooth interpreted as p5 here is a true premolar or molar), is also a feature present in the Zhangheotheriidae, but absent in most spalacotheriids, where the distinction between the two tooth morphologies is sharp. Assuming the tooth positional identifications proposed here, the condition in *Symmetrolestes*, with a gradual increase in complexity from last premolariform to m1 is probably the primitive condition at this level of mammalian tree. Last lower premolariform is longer than m1 in zhangheotheriids, *Symmetrolestes*, and possibly also in *Gobiotheriodon* (Trofimov 1980; Averianov 2002) if the alveolar length can be used as a predictor of tooth length. The complex last premolariform in zhangheotheriids, *Symmetrolestes*, peramurids, and other cladotheres (Clemens and Mills 1971; Dashzeveg 1979, 1994; Hu et al. 1997, 1998) raises the possibility that a molarized or intrinsically complex last premolar may be primitive for Theria. A direct consequence of this would be the recognition of the metatherian condition, where the premolar-molar transition is abrupt, as the derived condition, and the retention of complex last premolars occurring in eutherians as primitive. It should be noted, however, that there is substantial variation on what a "complex last premolar" is: in *Symmetrolestes* the p5 is triangular with a prominent cingulid, a tall protoconid, remnants of what must have been a fair sized metaconid, but only traces of a minute paraconid; on the other hand, the last lower premolar (m1 interpreted by Hu et al. 1997, 1998) in zhangheotheriids has subequal paraconid and metaconid approaching the condition of the molars in development (Hu et al. 1997, 1998; Rougier, Ji, and Novacek 2003). Among more derived cladotheres and therian stem groups, the last lower premolariform may have complete trigonid and a small talonid (Clemens and Mills 1971; Clemens 1989; Sigogneau-Russell 1999; Butler and Clemens 2001).

The last lower molariform (m4) of *Symmetrolestes* is very reduced in size, is diagonally oriented in occlusal view, and lacks a metaconid. In this point, *Symmetrolestes* resembles *Maotherium*, *Spalacolestes*, and *Symmetrodontoides*, which have a last molariform without a metaconid or with such a cusp reduced to a bare remnant. On the other hand, the last lower molariform of *Symmetrolestes* is more reduced than that of most spalacotheriids and *Zhangheotherium*, which preserves a triangular outline of the anterior molariforms in occlusal view, with all three trigonid cusps, including a metaconid.

An important difference between *Symmetrolestes* and zhangheotheriids is the presence of well developed flat wear facets in the molariforms of *Symmetrolestes* and other spalacotheriids but not in the zhangheotheriids. Flat wear facets develop by the use of the dentition, therefore they are better

individualized in adults than in juveniles. Both zhangheotheriids, *Zhangheotherium* and *Maotherium*, are subadults, *Maotherium* being relatively older because of the greater fusion of the epiphysis. The discontinuous wear facets are still clearly present in *Maotherium*, despite the heavy wear on some of the anterior molariforms, therefore we believe that this difference between zhangheotheriids and spalacotheriids may diminish functionally with age but it is still significant. The acquisition of precise occlusal surface that does not require a lot of wear to produce a continuous cutting edge in *Symmetrolestes* and allies seems to represent a sophistication of the more loose occlusal relationship present among more basal mammaliaforms.

Phylogenetic analysis

We compiled a data matrix, which is based on the information in Cifelli and Madsen (1999) with modifications and additions. A parsimony analysis to determine the phylogenetic position of *Symmetrolestes* among Spalacotheriidae was performed on this matrix. The data matrix includes a total of eight terminal taxa (six spalacotheriid genera with *Zhangheotherium* and *Kuehneotherium* as outgroups) and 29 morphological (23 dental and 6 dentary) characters (Appendices 1, 2). Most characters were treated as unordered with the exception of two characters, molar shape (character number 5) and development of the pterygoid crest (character number 24). We believe that a reasonable morphocline can be postulated for the different conditions in these characters and have therefore ordered them here.

We have kept this study centered on spalacotheriids, and despite the fact that some other groups may bring to bear information important for the resolution of internal nodes of spalacotheriids, they are out of the scope for placing the new taxon on the spalacotheriids cladogram. The two most obvious stem groups that are not included are *Gobiotheriodon* Trofimov, 1980 (see also Averianov 2002) and *Maotherium* Rougier, Ji, and Novacek, 2003. Both of them lack the continuous wear facets of the derived spalacotheriids and are similar in most respects to *Zhangheotherium* (Averianov 2002; Rougier, Ji, and Novacek 2003) and, therefore, we believe these stem-"symmetrodonts" are adequately represented by the better-known *Zhangheotherium*. A probable spalacotheriid genus, *Shalbaatar*, was not included in our phylogenetic analysis because the only material of *Shalbaatar* does not preserve teeth and introduces much missing data, especially because several of the taxa included in the matrix are known exclusively by isolated teeth (see review by Cifelli and Madsen 1999).

The data matrix was analyzed using PAUP 4.0b10 (Swofford 1998) with the branch and bound search option. The result of the PAUP analysis was exported to MacClade 4.0 (Maddison and Maddison 2000) and examined for patterns of character evolution. Preliminary searches were also performed with Pewee and Nona (Goloboff 1993) and results managed with Winclada (Nixon 1999).
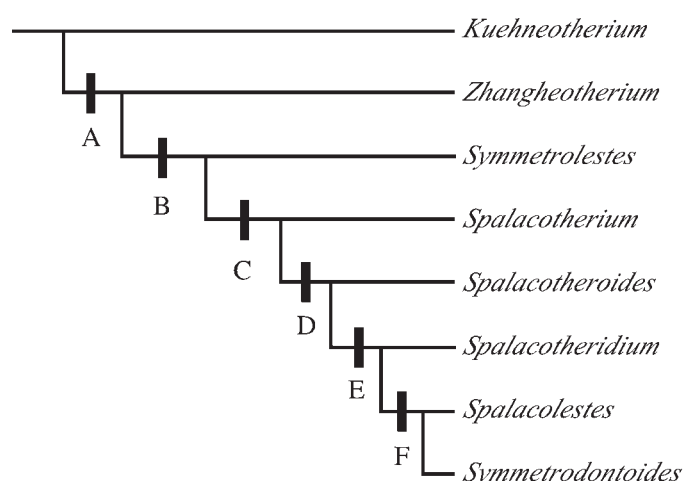

Fig. 7. Most parsimonious tree recovered by the analysis of our 29 character data-matrix (Appendices 1, 2). Diagnosis of the nodes: Node A: 5(1) Acutely angled molariforms; 8(1) single mesial cingular cusp in lower molariforms; 9(1) highly reduced talonid (cusp-like); 10(1) lower molar cingular cusp d lingual to cingular cusp e (molar interlocking); 16(1) cusp B1 present on upper molariforms; 23(1) roots mesiodistally compressed; 29(1) mandibular condyle above the alveolar margin. Node B: Spalacotheriidae: 1(1) Continuous prevallum and postvallum (prevallid-postvallid) shearing surfaces; 2(1) two canine roots; 7(1) complete, or almost complete buccal cingulum on lower molariforms; 13(1) crown height twice mesiodistal length; 24(1) strongly developed pterygoid crest; 25(1) posteroventral edge of the jaw efflected; 28(1) broad coronoid process. Node C: 6(1) Six or more molariforms. Node D: Spalacolestinae: 5(2) Very acutely angled molariforms; 14(1) Pre- and postparacrista present; 19(1) hook-like parastyle; 20(1), distal stylar cusp present; 24 (2) strong pterygoid crest extending to near the alveolar level. Node E: 17(1) Cusp C absent; 20(2) enlarged distal stylar cusp; 21(1) ultimate upper molariforms reduced (missing one of the main cusps). Node F: 11(1) Paraconid and paracristid lower than metaconid and protocristid; 12 (1) paraconid lingually placed in distal molariforms; 15 (1) deep trigon basin on upper molariforms.

Our analysis recovered only one most parsimonious tree of 36 steps long. Figure 7 shows the unrooted parsimonious tree-rooted using a default outgroup. This tree has a consistency index (excluding uninformative characters) of 0.8966, homoplasy index (excluding uninformative characters) of 0.1034, retention index of 0.9091, and rescaled consistency index of 0.8333. Our cladistic analysis shows a tree topology basically unaltered from that presented by Cifelli and Madsen (1999), with the addition of *Symmetrolestes* as sister-group to the previously known spalacotheriids. *Spalacotherium* is the basal member of the previously known Spalacotheriidae and the derived Spalacolestinae form the apical group in the tree. The overall stability of the tree is poor, especially at the node supporting Spalacotheriidae with the exclusion of *Symmetrolestes*, which has a Bremer support of 1. We have chosen to include *Symmetrolestes* within Spalacotheriidae despite the more primitive features shown (premolariform and molariform count in particular) because it does not seem to warrant the creation of a new higher level taxon based on such incomplete material with such tenuous links to later spalacotheriids. We prefer at this point to expand our

understanding of Spalacotheriidae to include *Symmetrolestes* as an expedient solution until the diversity of the Spalacotheriidae is better documented.

Spalacotheriidae are supported by seven unambiguous characters (Bremer support 5) and is therefore a relatively well-supported clade. Spalacolestinae are supported by five unambiguous traits (Bremer support 3). Our tree supports the distinctiveness of Spalacolestinae as proposed by Cifelli and Madsen (1999) and adds a likely ancestral structural pattern for Spalacotheriidae, as represented by *Symmetrolestes*.

The general trends for morphological evolution within the family would be the increase of molariform numbers, decrease of premolariform numbers, and development of more acute molariforms with sharper continuous wear facets developed in taller crowns. The molariforms become progressively more acute and the lower jaws develop more extensive coronoid and pterygoid process related to an increased bucco-lingual component in mastication. Remnants of primitive developmental features, such as Meckel's cartilage, are progressively less conspicuous.

Paleobiogeography and origin of Spalacotheriidae

With the removal of *Zhangheotherium* from the family (Averianov 2002; Rougier, Ji, and Novacek 2003), members of Spalacotheriidae had been recorded only in Lower Cretaceous Western Europe and Cretaceous North America (Table 2). The European spalacotheriids are represented by a single genus, *Spalacotherium*. The English Purbeck beds bearing *Spalacotherium tricuspidens* and *Spalacotherium evansae* were traditionally regarded as Upper Jurassic, but they have recently been reallocated to the Berriasian (lowermost Cretaceous) (Cassiliano and Clemens 1979; Allen and Wimbledon 1991; Kielan-Jaworowska and Ensom 1994; Sigogneau-Russell and Ensom 1994; Ensom and Sigogneau-Russell 1998, 2000; Cifelli and Madsen 1999). *Spalacotherium* is also recorded from the Valanginian (Lower Cretaceous) of England (Clemens and Lees 1971) and the Barremian (Lower Cretaceous) of Spain (Krebs 1985). It is likely, however, that this apparent low diversity of the European spalacotheriids is artificial; several of the specimen described are too poorly preserved as to be diagnostic at a higher level. The North American forms represent a monophyletic subfamily, Spalacolestinae Cifelli and Madsen, 1999, which includes four genera (*Spalacotheroides*, *Symmetrodontoides*, *Spalacotheridium*, and *Spalacolestes*) (Cassiliano and Clemens 1979; Cifelli 1990; Cifelli and Madsen 1999). *Spalacotherium* is more generalized in its dental morphology and much older in geologic age than the North American genera, so that this family had been considered to have originated in Western Europe (Table 2; Cifelli and Madsen 1999).

A few spalacotheriids and/or spalacotheriid-like mammals have recently been reported from eastern Eurasia. Hu et al. (1997) have described a new spalacotheriid, *Zhangheotherium*, from the upper Valanginian or mid-Barremian

Table 2. Temporal and geographic distribution of Spalacotheriidae and relatives (Krebs 1985; Cifelli 1990; Hu et al. 1997; Nessov et al. 1998; Cifelli and Madsen 1999; Swisher et al. 1999; Ensom and Sigogneau-Russell 2000; Wang et al. 2000; Averianov 2002; Rougier, Ji, and Novacek 2003). Abbreviations: Al, Albian; Ap, Aptian; As, Asia; Be, Berriasian; Ca, Campanian; Ce, Cenomanian; Co, Coniacian; Eu, Europe; M-Cret, Mid-Cretaceous; NA, North America; Tu, Turonian; Va, Valanginian.

	Early Cretaceous			M-Cret	Late Cretaceous	
	Be	Va-Ap	Al	Al-Ce	Tu	Ca
Zhangheotheriidae						
Zhangheotherium quinquecuspidens		As				
Maotherium sinensis		As				
Spalacotheriidae						
Symmetrolestes parvus		As				
Spalacotherium tricuspidens	Eu					
Spalacotherium evansae	Eu					
Spalacotherium taylori		Eu				
Spalacotherium henkeli		Eu				
Shalbaatar bakht					As	
Spalacolestinae						
Spalacotheroides bridwelli			NA			
Spalacotheridium noblei				NA		
Spalacotheridium mckennai					NA	
Spalacolestes cretulablatta				NA		
Spalacolestes inconcinnus				NA		
Symmetrodontoides oligodontos					NA	
Symmetrodontoides canadensis						NA
Symmetrodontoides foxi						NA

(Lower Cretaceous) Jianshangou Bed of the Yixian Formation of the Jehol Group in northeastern China (Swisher et al. 1999; Wang et al. 2000). More recently, however, Averianov (2002), Rougier et al. (2001), Rougier, Ji, and Novacek (2003), and Rougier, Spurlin, and Kik (2003) considered *Zhangheotherium* to be not a spalacotheriid but a sister taxon to Spalacotheriidae. Rougier, Ji, and Novacek (2003) erected a new family Zhangheotheriidae for *Zhangheotherium* and the closely allied *Maotherium*, which was recovered also from the lower part of the Yixian Formation. Averianov (2002) considered *Shalbaatar* (Nessov, 1997) from the upper Turonian (Upper Cretaceous) of the lower part of the Bissekty Formation in Uzbekistan (Nessov et al. 1998: 44; Averianov 2002) to be a spalacotheriid on the basis of the structure of the dentary. This form, likely a Spalacolestinae (Averianov, 2002), would represent the only record for the group outside North America.

The discovery of a new spalacotheriid, *Symmetrolestes*, in the Lower Cretaceous of Japan lets us reconsider the origin of Spalacotheriidae. Our phylogenetic analysis indicates that *Symmetrolestes* is a basal spalacotheriid and likely the sister group of the remaining Spalacotheriidae: it is more primitive than *Spalacotherium* and spalacolestines, and is more derived than zhangheotheriids, the sister taxon of Spalacotheriidae (Fig. 7). The combination of the occurrences of a primitive spalacotheriid (*Symmetrolestes*) in Japan, of the sister taxon of the Spalacotheriidae (i.e., Zhangheotheriidae) in the adjacent China, and of the basal generalized "tinodontid" *Gobiotheriodon* from Mongolia (Averianov 2002), advocate for Spalacotheriidae originating in East Asia, or at least for an early diversification of the Spalacotheriidae and its immediate relatives in East Asia.

However, a chronological problem still remains, implying long "ghost lineages" for the spalacotheriid stem-groups. *Symmetrolestes*, zhangheotheriids, and the generalized *Gobiotheriodon* have been found in the Lower Cretaceous (Valanginian to Aptian) of East Asia. These supposedly basal taxa are chronologically intermediate between *Spalacotherium tricuspidens* and *Spalacotherium evansae* from the lowermost Cretaceous of Europe and spalacolestines from the Albian to Upper Cretaceous of North America (Table 2). Therefore, if the East Asian taxa are near the root of Spalacotheriidae, we are missing a host of Jurassic representatives of these lineages in East Asia. This is in fact not surprising given the paucity of the Jurassic mammalian record in East Asia. An East Asian origin hypothesis for Spalacotheriidae implies relatively long ghost lineages: from the latest Jurassic to the Early Cretaceous for the missing East Asian "symmetrodonts".

Conclusions

Symmetrolestes parvus, which was discovered from the Lower Cretaceous Kitadani Formation of Japan and described here, is a close relative of traditional spalacotheriid "symmetrodont" such as *Spalacotherium*, but retains basal mammalian characters lost in the more derived members of the group. *Symmetrolestes* confirms early impressions by other authors that a smaller number of molariforms and higher number of premolariforms are primitive for Spalacotheriidae (Prothero 1981; Cifelli and Madsen 1999). The intermediate complexity of the element identified here as p5 illustrates that complex last premolariform is likely to be a generalized condition for the successive therian-stem groups, which has the potential to help us better understand the controversial tooth homologies of the premolar-molar boundary in metatherians and eutherians. The evidence from *Symmetrolestes* (and by implication of Spalacotheriidae) adds to the growing number of therian stem taxa showing a blurry morphological premolar-molar boundary arguing in favor of considering this a primitive feature preserved in eutherians. Metatherians on the other hand would acquire as a derived feature a clear-cut premolar-molar transition, possibly produced by the incorporation of the ultimate premolariform to the molar series by suppressing replacement of deciduous premolar or by loss of the deciduous eruption altogether (Owen 1868; Archer 1974, 1975; Luckett 1993).

Spalacotheriidae as a group is defensible as a monophyletic entity and relatively well supported. At least the subgroup formed by *Spalacotherium* and later Spalacolestinae is dentally conspicuous. With the demise of Amphitheriidae as "symmetrodonts" (Rougier et al. 2001; Averianov 2002) and the loose affinities of *Kuehneotherium* and tinodontids with other "symmetrodonts" (Rougier et al. 1996; Cifelli and Madsen 1999; Ensom and Sigogneau-Russell 2000), spalacotheriids are the only monophyletic "symmetrodonts" that show a moderately successful history, with representatives present in the Cretaceous of the Laurasian continents.

The repeated occurrence of East Asian taxa at the very base of Spalacotheriidae or among the immediate outgroups raises the possibility of an East Asian origin for the group. This consideration must be tempered, however, by the dismal Jurassic record in East and Central Asia and continental Europe.

Acknowledgments

References

Allen, P. and Wimbledon, W.A. 1991. Correlation of NW European Purbeck-Wealden (nonmarine Lower Cretaceous) as seen from the English type-areas. *Cretaceous Research* 12: 511–526.

Archer, M. 1974. The development of the cheek-teeth in *Antechinus flavipes* (Marsupialia, Dasyuridae). *Journal of the Royal Society of Western Australia* 57 (2): 54–63.

Archer, M. 1975. Abnormal dental development and its significance in dasyurids and other marsupials. *Memoirs of the Queensland Museum* 17 (2): 251–265.

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

Azuma, Y. and Currie, P.J. 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences* 37: 1735–1753.

Azuma, Y. and Tomida, Y. 1997. Japanese dinosaurs. *In*: P. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*, 375–379. Academic Press, San Diego.

Bonaparte, J.F. 1990. New Late Cretaceous mammals from the Los Alamitos Formation, northern Patagonia. *National Geographic Research* 6: 63–93.

Bonaparte, J.F. 1994. Approach to significance of the Late Cretaceous mammals of South America. *Berliner geowissenschaftliche Abhandlungen E* 13: 31–44.

Butler, P.M. and Clemens, W.A. 2001. Dental morphology of the Jurassic holotherian mammal *Amphitherium*, with a discussion of the evolution of mammalian post-canine dental formulae. *Palaeontology* 44 (1): 1–20.

Cassiliano, M.L. and Clemens, W.A. 1979. Symmetrodonta. *In*: J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens (eds.), *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, 150–161. University of California Press, Berkeley.

Cifelli, R.L. 1990. Cretaceous mammals of southern Utah. III. Therian mammals from the Turonian (early Late Cretaceous). *Journal of Vertebrate Paleontology* 10 (3): 332–345.

Cifelli, R.L. and Gordon, C.L. 1999. Symmetrodonts from the Late Cretaceous of southern Utah and distribution of archaic mammals in the Cretaceous of North America. *Brigham Young University Geology Studies* 44: 1–15.

Cifelli, R.L. and Madsen, S.K. 1986. An Upper Cretaceous symmetrodont (Mammalia) from southern Utah. *Journal of Vertebrate Paleontology* 6: 258–263.

Cifelli, R.L. and Madsen, S.K. 1999. Spalacotheriid symmetrodonts (Mammalia) from the medial Cretaceous (upper Albian or lower Cenomanian) Mussentuchit local fauna. Cedar Mountain Formation, Utah, USA. *Geodiversitas* 21: 167–214.

Cifelli, R.L., Wible, J.R., and Jenkins, F.A., Jr. 1998. Triconodont mammals from the Cloverly Formation (Lower Cretaceous), Montana and Wyoming. *Journal of Vertebrate Paleontology* 18: 237–241.

Clemens, W.A., Jr. 1963. Late Jurassic mammalian fossils in the Sedgwick Museum, Cambridge. *Palaeontology* 6: 373–377.

Clemens, W.A. 1989. The primitive therian dental formula, evidence from *Amphitherium. Journal of Vertebrate Paleontology* 9 (Suplement to no. 3): 17A.

Clemens, W.A., Jr. and Lees, P.M. 1971. A review of English Early Cretaceous mammals. *In*: D.M. Kermack and K.A. Kermack (eds.), Early Mammals. *Zoological Journal of the Linnean Society of London* 50 (Supplement 1): 117–130.

Clemens, W.A. and Lillegraven, J.A. 1986. New Late Cretaceous, North American advanced therian mammals that fit neither the marsupial nor eutherian molds. *Contributions to Geology, University of Wyoming, Special Paper* 3: 55–85.

Clemens, W.A. and Mills, J.R.E. 1971. Review of *Peramus tenuirostris* Owen (Eupantotheria, Mammalia). *Bulletin of the British Museum (Natural History) Geology* 20 (3): 87–113.

Cook, E., Isaji, S., and Manabe, M. 1998. Preliminary results of a taphonomic study of a vertebrate accumulation from the Tetori Group (Lower Cretaceous) of Japan. *Paleontological Research* 2 (1): 47–52.

Crompton, A.W. 1974. The dentitions and relationships of the southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae*. *Bulletin of the British Museum (Natural History) Geology* 24 (7): 397–437.

Crompton A.W. and Jenkins, F.A., Jr. 1967. American Jurassic symmetrodonts and Rhaetic "pantotheres". *Science* 155: 1005–1009.

Crompton A.W. and Jenkins, F.A., Jr. 1968. Molar occlusion in Late Triassic mammals. *Biological Reviews* 43: 427–458.

Crompton A.W. and Jenkins, F.A., Jr. 1973. Mammals from reptiles: a review of mammalian origins. *Review of Ecology and Earth Planetary Sciences* 1: 131–155.

Dashzeveg, D. 1979. *Arguimus khosbajari* gen. n., sp. n. (Peramuridae, Eupantotheria) from the Lower Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 24 (2): 199–203.

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

Dashzeveg, D. and Kielan-Jaworowska, Z. 1984. The lower jaw of an aegialodontid mammal from the Early Cretaceous of Mongolia. *Zoological Journal of the Linnean Society of London* 82: 217–227.

Ensom, P.C. and Sigogneau-Russell, D. 1998. New dryolestoid mammals from the basal Cretaceous Purbeck Limestone group of southern England. *Palaeontology* 41: 35–55.

Ensom, P. and Sigogneau-Russell, D. 2000. New symmetrodonts (Mammalia, Theria) from the Purbeck Limestone Group, Lower Cretaceous, southern England. *Cretaceous Research* 21: 767–779.

Evans, S.E. and Manabe, M. 1998. Early Cretaceous frog remains from the Okurodani Formation, Tetori Group, Japan. *Paleontological Research* 2 (4): 275–278.

Evans, S.E. and Manabe, M. 1999a. A choristoderan reptile from the Early Cretaceous of Japan, Palaeontology. *Special papers in Palaeontology* 60: 101–119.

Evans, S.E. and Manabe, M. 1999b. Early Cretaceous lizards from the Okurodani Formation of Japan. *Geobios* 32 (6): 889–899.

Evans, S.E., Manabe, M., Cook, E., Hirayama, R., Isaji, S., Nicholas, C.J., Unwin, D., and Yabumoto, Y. 1998. An Early Cretaceous assemblage from Gifu Prefecture, Japan. *Bulletin of New Mexico Museum of Natural History and Science* 14: 183–186.

Fox, R.C. 1976. Additions to the mammalian local fauna from Upper Milk River Formation (Upper Cretaceous), Alberta. *Canadian Journal of Earth Sciences* 13: 1105–1118.

Fox, R.C. 1984. A primitive, obtuse-angled symmetrodont (Mammalia) from the Upper Cretaceous of Alberta, Canada. *Canadian Journal of Earth Sciences* 21 (10): 1204–1207.

Fox, R.C. 1985. Upper molar structure in the Late Cretaceous symmetrodont *Symmetrodontoides* Fox, and a classification of the Symmetrodonta (Mammalia). *Journal of Paleontology* 59 (1): 21–26.

Fraser, N.C., Walkden, G.M., and Stewart, V. 1985. The first pre-Rhaetic therian mammal. *Nature* 314: 161–162.

Geyler, H.T. 1877. Über fossile Pflanzen aus der Juraformation Japans. *Palaeontographica* 24: 221–232.

Gill, P.G. 1974. Resorption of premolars in the early mammal *Kuehneotherium praecursoris. Archives of Oral Biology* 19: 327–328.

Goloboff, P.A. 1993. *NONA*. Computer programs and documentation. New York. Free download at www.cladistics.org.

Goto, M., Yabe, A., and Sano, S. 2002. The research report of the Dinosaur Fossil Exploratory Excavation held by Fukui Prefecture in 2001 [in Japanese with English abstract]. *Memoirs of the Fukui Prefectural Dinosaur Museum* 1: 102–118.

Hahn, G., Sigogneau-Russell, D., and Godefroit, P. 1991. New data on *Brachyzostrodon* (Mammalia; Upper Triassic). *Geologica et Palaeontologica* 25: 237–249.

Hasegawa, Y., Manabe, M., Isaji, S., Ohkura, M., Shibata, I., and Yamaguchi, I. 1995. Terminally resorbed iguanodontid teeth from the Neocomian Tetori Group, Ishikawa and Gifu Prefecture, Japan. *Bulletin of National Science Museum, Tokyo C* 21: 35–49.

Hayami, I. and Ichikawa, T. 1965. Occurrence of *Nippononaia ryosekiana* from the Sanchu Area, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan (New Series)* 60: 145–155.

Hirayama, R. 2002. Preliminary report of the fossil turtles from the Kitadani

Formation (Early Cretaceous) of the Tetori Group of Katsuyama Prefecture, Fukui Prefecture, Central Japan [in Japanese with English abstract]. *Memoirs of the Fukui Prefectural Dinosaur Museum* 1: 29–40.

Hu, Y., Wang, Y., Li, C., and Luo, Z. 1998. Morphology of dentition and forelimb of *Zhangheotherium*. *Vertebrata PalAsiatica* 36 (2): 102–125.

Hu, Y., Wang, Y., Luo, Z., and Li, C. 1997. A new symmetrodont mammal from China and its implications for mammalian evolution. *Nature* 390: 137–142.

Isaji, S. 1993. *Nippononaia ryosekiana* (Bivalvia, Mollusca) from the Tetori Group in Central Japan. *Bulletin of National Science Museum, Tokyo C* 19: 65–71.

Jenkins, F.A., Jr. and Crompton, A.W. 1979. Triconodonta. *In*: J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens (eds.), *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, 74–90. University of California Press, Berkeley.

Jenkins, F.A. and Schaff, C.R. 1988. The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana. *Journal of Vertebrate Paleontology* 8 (1): 1–24.

Ji, Q., Luo, Z., and Ji, S. 1999. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature* 398: 326–330.

Kermack, D.M., Kermack, K.A., and Mussett, F. 1968. The Welsh pantothere *Kuehneotherium praecursoris*. *Journal of the Linnean Society (Zoology)* 47 (312): 407–423.

Kermack, K.A., Mussett, F, and Rigney, H.W. 1973. The lower jaw of *Morganucodon*. *Zoological Journal of the Linnean Society* 53: 87–175.

Kermack, K.A., Mussett, F, and Rigney, H.W. 1981. The skull of *Morganucodon*. *Zoological Journal of the Linnean Society* 71: 1–158.

Kielan-Jaworowska, Z. and Dashzeveg, D. 1998. Early Cretaceous amphilestid ('triconodont') mammals from Mongolia. *Acta Palaeontologica Polonica* 43: 413–438.

Kielan-Jaworowska, Z. and Ensom, P.C. 1994. Tiny plagiaulacoid mammals from the Purbeck Limestone Formation of Dorset, England. *Palaeontology* 37: 17–31.

Kobayashi, Y. 1998. A new goniopholid from the Early Cretaceous Kitadani Formation, Fukui Prefecture, Japan. *Journal of Vertebrate Paleontology* 18 (3): 56A.

Kobayashi, Y. and Azuma, Y. 2003. A new iguanodontian (Dinosauria: Ornithopoda) from the Lower Cretaceous Kitadani Formation of Fukui Prefecture, Japan. *Journal of Vertebrate Paleontology* 23 (1): 166–175.

Krebs, B. 1985. Theria (Mammalia) aus der Unterkreide von Galve (Provinz Teruel, Spanien). *Berliner geowissenschaftliche Abhandlungen A* 60: 29–48.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, reformata.* 824 pp. Laurentii Salvii, Stockholm.

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

Luo, Z.-X., Ji, Q., and Ji, S.-A. 2001. New evidence on dental replacement in symmetrodonts and its implications for mammalian evolution. *Journal of Morphology* 248: 256–257.

Luo, Z.-X., Kielan-Jaworowska, Z., and Cifelli, R.L. 2002. In quest for a phylogeny of Mesozoic mammals. *Acta Palaeontologica Polonica* 47 (1): 1–78.

Luo, Z.-X. and Wu, X.-C. 1994. The small tetrapods of the lower Lufeng Formation, Yunnan, China. *In*: N.C. Fraser and H.-D. Sues (eds.), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 251–270. Cambridge University Press, Cambridge.

Maeda, S. 1958. Stratigraphy and geological structure of the Tetori Group in the Hakusan District (Part. 1 Stratigraphy) [in Japanese with English abstract]. *Journal of the Geological Society of Japan* 64 (758): 583–594.

Maeda, S. 1961. On the geological history of the Mesozoic Tetori Group in Japan. *Japanese Journal of Geology and Geography* 32 (3–4): 375–396.

Maeda, S. 1962. Some Lower Cretaceous pelecypods from the Akaiwa Subgroup, the upper division of the Tetori Group in central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan (New Series)* 48: 343–351.

Maeda, S. 1963. *Trigonioides* from the Late Mesozoic Tetori group, central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan (New Series)* 51: 79–85.

Maddison, W.P. and Maddison, D.R. 2000. *MacClade Version 4.0*. Sinauer Associations, Inc., Sunderland, Massachusetts.

Manabe, M. 1999. The early evolution of the Tyrannosauridae in Asia. *Journal of Paleontology* 73 (6): 1176–1178.

Manabe, M., Barrett, P.M., and Isaji, S. 2000. A refugium for relics? *Nature* 404: 953.

Marsh, O.C. 1887. American Jurassic mammals. *American Journal of Science* 33: 326–348.

Marshall, L.G. and Kielan-Jaworowska, Z. 1992. Relationships of the dog-like marsupials, deltatheroidans and early tribosphenic mammals. *Lethaia* 25: 361–374.

Matsukawa, M. 1977. Cretaceous system in the eastern part of the Sanchu "Graben", Kwanto, Japan. *Journal of the Geological Society of Japan* 83 (2): 115–126.

Matsukawa, M. 1983. Stratigraphy and sedimentary environments of the Sanchu Cretaceous, Japan. *Memoirs of Ehime University, Natural Science (D)* 9: 1–50.

Matsukawa, M. and Ito, M. 1995. Evaluation of nonmarine bivalves as index fossils based on those from the Japanese Lower Cretaceous [in Japanese with English abstract]. *Journal of the Geological Society of Japan* 101 (1): 42–53.

Matsukawa, M. and Obata, I. 1992. Correlation of nonmarine and marine formations in the Lower Cretaceous of Japan: a contribution to nonmarine formations in Asia. *In*: N.J. Mateer and P.J. Chen (eds.), *Aspects of Nonmarine Cretaceous Geology*, 78–93. Chinese Ocean Press, Beijing.

Matsukawa, M., Takahashi, O., Hayashi, K., Ito, M., and Konovaloy, V.P. 1997. Early Cretaceous paleogeography of Japan, based on tectonic and faunal data. *Memoirs of the Geological Society of Japan* 48: 29–42.

Matsumoto, R., Evans, S.E., and Shimojima, S. 2002. The dentary of a choristodere (Reptilia: Archosauromorpha) from the Okurodani Formation, Tetori Group (Lower Cretaceous) of Japan. *Bulletin of National Science Museum, Tokyo C* 28: 43–48.

Matsumoto, T., Obata, I., Tashiro, M., Ohta, Y., Tamura, M., Matsukawa, M., and Tanaka, H. 1982. Correlation of marine and non-marine formations in the Cretaceous of Japan [in Japanese with English abstract]. *Fossils (Palaeontological Society of Japan)* 31: 1–26.

McKenna, M.C. 1975. Toward a phylogenetic classification of the Mammalia. *In*: W.P. Luckett and S.S. Frederick (eds.), *Phylogeny of the Primates: a Multidisciplinary Approach*, 21–46. Plenum Press, New York.

McKenna, M.C. and Bell, S. K. 1997. *Classification of Mammals, Above the Species Level*. xii + 631 pp. Columbia University Press, New York.

Mills, J.R.E. 1971. The dentition of *Morganucodon*. *In*: D.M. Kermack and K.A. Kermack (eds.), Early Mammals. *Zoological Journal of the Linnean Society of London* 50 (Supplement 1): 29–63.

Nessov, L.A. 1997. *Cretaceous Nonmarine Vertebrates of Northern Eurasia* [in Russian with English summary]. 218 pp. (Posthumous paper ed. by L.B. Golovneva and A.O. Averianov). University of Sankt Petersburg, Institute of Earth Crust, Sankt Petersburg.

Nessov, L.A., Archibald, J.D., and Kielan-Jaworowska, Z. 1998. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. *Bulletin of Carnegie Museum of Natural History* 34: 40–88.

Nixon, K.C. 1999. *Winclada (BETA) ver. 0.9.9*. Published by the author, Ithaca, NY.

Owen, R. 1854. On some fossil reptilian and mammalian remains from the Purbecks. *Quarterly Journal of the Geological Society of London* 10: 420–433.

Owen, R. 1868. *On the Anatomy of Vertebrates. Vol. III. Mammals*. 768 pp. Longmans, Green and Co., London.

Owen, R. 1871. Monograph of the fossil Mammalia of the Mesozoic formations. *Palaeontological Society* 24: 1–115.

Patterson, B. 1955. A symmetrodont from the Early Cretaceous of northern Texas. *Fieldiana (Geology)* 37: 689–693.

Prothero, D.R. 1981. New Jurassic mammals from Como Bluff, Wyoming,

and the interrelationships of no-tribosphenic Theria. *Bulletin of the American Museum of Natural History* 167: 277–326.

Rougier, G.W., Isaji, S., and Manabe, M. 1999. An Early Cretaceous Japanese triconodont and a revision of triconodont phylogeny. *Journal of Vertebrate Paleontology* 19 (3): 72A.

Rougier, G.W., Ji, Q., and Novacek, M. 2003. A new symmetrodont mammal with fur impressions from the Mesozoic of China. *Acta Geologica Sinica* 77 (1): 7–14.

Rougier, G.W., Novacek, M.J., McKenna, M.C., and Wible, J.R. 2001. Gobiconodonts from the Early Cretaceous of Oshih (Aisle), Mongolia. *American Museum Novitates* 3348: 1–30.

Rougier, G.W., Spurlin, B.K., and Kik, P. 2003. A new specimen of *Eurylambda aequicrurius* and considerations of "symmetrodont" dentition and relationships. *American Museum Novitates* 3398: 1–15.

Rougier, G.W., Wible, J.R., and Novacek, M.J. 1996. Middle-ear ossicles of the multituberculate *Kryptobaatar* from the Mongolian Late Cretaceous: implications for mammaliamorph relationships and the evolution of the auditory apparatus. *American Museum Novitates* 3187: 1–43.

Rowe, T. 1988. Definition, diagnosis and origin of Mammalia. *Journal of Vertebrate Paleontology* 8: 241–264.

Rowe, T. 1993. Phylogenetic systematics and the early history of mammals. *In*: F.S. Szalay, M.J. Novacek, and M.C. McKenna (eds.), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*, 129–145. Springer, New York.

Sato, T., Hachiya, K., and Mizuno, Y. 2003. Latest Jurassic–Early Cretaceous ammonites from the Tetori Group in the Shokawa, Gifu Prefecture [in Japanese with English abstract and systematic description]. *Bulletin of the Mizunami Fossil Museum* 30: 151–167.

Setoguchi, T., Matsuoka, H., and Matsuda, M. 1999a. New discovery of an Early Cretaceous tritylodontid (Reptilia, Therapsida) from Japan and the phylogenetic reconstruction of Tritylodontidae based on the dental characters. *In*: Y. Wang and D. Teng (eds.), *Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology*, 117–124. China Ocean Press, Beijing.

Setoguchi, T., Tsubamoto, T., Hanamura, H., and Hachiya, K. 1999b. An early Late Cretaceous mammal from Japan, with reconsideration of the evolution of tribosphenic molars. *Paleontological Research* 3 (1): 18–28.

Sigogneau-Russell, D. 1983. Nouveaux taxons de mammefères rhétiens. *Acta Palaeontologica Polonica* 28 (1–2): 233–249.

Sigogneau-Russell, D. 1991. Nouveaux Mammifères thériens du Crétacé inférieur du Maroc. *Comptes Rendus de l'Académie des Sciences, Paris, Série II* 313: 279–285.

Sigogneau-Russell, D. 1999. Réévaluation des Peramura (Mammalia, Cladotheria) sur la base de nouveaux spécimens du Crétacé inférier d'Angleterre et du Maroc. *Geodiversitas* 21 (1): 93–127.

Sigogneau-Russell, D. and Ensom, P.C. 1994. Découverte, dans le Groupe de Purbeck (Berriasian, Angleterre), de plus ancien témoinage de l'existence de mammifères tribosphéniques. *Comptes Rendus de l'Académie des Sciences, Paris, Série II* 319: 833–838.

Sigogneau-Russell, D. and Ensom, P. 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. 1925. Mesozoic Mammalia. II: *Tinodon* and its allies. *American Journal of Science (Series 5)* 10: 451–470.

Simpson, G.G. 1928. *A Catalogue of the Mesozoic Mammals at the Geological Department of the British Museum*. x + 215 pp. British Museum (Natural History), London.

Simpson, G.G. 1929. American Mesozoic Mammalia. *Memoirs of the Peabody Museum of Yale University* 3 (1): 1–235.

Swisher, C.C., III, Wang, Y.-Q., Wang, X.-L., Xu, X., and Wang, Y. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* 400: 58–61.

Swofford, D.L. 1998. *PAUP: Phylogenetic Analysis Using Parsimony (4.0)*. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Takada, T., Matsuoka, H., and Setoguchi, T. 2001. The first multituberculate from Japan. *In*: T. Deng and Y. Wang (eds.), *Proceedings of the Eighth Annual Meeting of the Chinese Society of Vertebrate Paleontology*, 55–58. China Ocean Press, Beijing.

Tanase, A., Yamada, N., and Wakita, K. 1994. Hayashidani Andesite— 100 Ma calc-alkaline andesite in the uppermost reaches of Kuzuryu River, central Japan [in Japanese with English abstract]. *Journal of the Geological Society of Japan* 100 (8): 635–638.

Tashiro, M. and Okuhira, K. 1993. Occurrence of *Trigonioides* from the Lower Cretaceous of Shikoku, and its significance [in Japanese with English abstract]. *Geological Reports of Shimane University* 12: 1–9.

Trofimov, B.A. 1978. The first triconodonts (Mammalia, Triconodonta) from Mongolia [in Russian]. *Doklady Akademie Nauk SSSR* 243: 213–216.

Trofimov, B.A. 1980. Multituberculata and Symmetrodonta from the Lower Cretaceous from Mongolia [in Russian]. *Doklady Akademie Nauk SSSR* 251: 209–212.

Wang, X.-L., Wang, Y.-Q., Zhou, Z.-H., Jin, F., Zhang, J.-Y., and Zhang, F. 2000. Vertebrate faunas and biostratigraphy of the Jehol Group in western Liaoning, China. *Vertebrata PalAsiatica* 38 (Supplement): 41–56.

Zeller, U. 1989. Die Entwicklung und Morphologie des Schädels von *Ornithorhynchus anatinus* (Mammalia: Prototheria: Monotremata). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 545: 1–188.

Appendix 1

List of characters and character definition used in the phylogenetic analysis.

1. Molariform shearing surfaces: 0) interrupted, 1) continuous.
2. Number of lower canine roots: 0) one, 1) two.
3. Lower canine shape: 0) caniniform, 1) premolariform/incisiviform.
4. Number of premolariforms: 0) Four or more, 1) three or less.
5. Molariform shape: 0) broad, 1) molars acutely angled, 2) more acutely angled, 3) M1–2 more acutely-angled. (*ordered*)
6. Number of lower molariforms: 0) fewer than six molariforms, 1) six or more upper and lower molariforms.
7. Labial cingulid on lower molariforms: 0) absent or restricted to the lingual portion of the crown, 1) complete.
8. Mesial cingular cusp on lower molariforms: 0) bifid mesial cingular cusp, 1) a single mesial cingular cusp.
9. Distal cingular cusp (talonid) on lower molars: 0) large, ridge like, 1) reduced, cusp like.
10. Lower molar interlocking: 0) fits in an embayment between b and cingular cusp d, 1) cingular cusp d lingual to cingular cusp e.
11. Paraconid and paracristid lower than height: 0) higher than metaconid and protocristid, 1) lower than metaconid and protocristid.
12. Paraconid position on distal lower molariforms: 0) in line with metaconid, 1) lingually placed.
13. Height of the crown: 0) low, 1) high.
14. Preparacrista and postparacrista (anterior loci): 0) absent, 1) present.
15. Trigon basin on upper molariforms: 0) unreduced, or reduced but with three main cusps, 1) reduced, missing one of the main cusps.

16. Cusp B1 (CAC, B'') on upper molariforms: 0) absence, 1) presence. [This character is scored different than in Cifelli and Madsen (1999) following interpretation of homology of cusps in Rougier, Spurlin, and Kik (2003). According to this interpretation, the neomorphic cusp is the parastyle. So the distribution of the character is equivalent to the presence of stylocone.]
17. Cusp C: 0) present, 1) lost.
18. Stylocone: 0) large, 1) reduced.
19. Parastyle on upper molariforms: 0) absent or not protruding mesially, 1) hook-like.
20. Distal stylar cusp: 0) cingulid, cusp absent, 1) present, 2) enlarged.
21. Ultimate upper molariform: 0) unreduced with all three main cusps, 1) reduced.
22. Cingulid on upper molariforms: 0) incomplete lingually, 1) complete lingually.
23. Shape of molariform roots: 0) circular or oval in cross section, 1) strongly mesiodistally compressed.
24. Pterygoid crest: 0) weakly developed, not forming shelf, 1) strongly developed in region of mandibular foramen, 2) strong and extending anterodorsally to near occlusal margin of dentary. (*ordered*)
25. Posteroinferior border of dentary: 0) in line with main jaw body, 1) effected.
26. Meckel's groove: 0) present, 1) absent.
27. Coronoid facet: 0) present, large, 1) reduced, absent.
28. Coronoid process: 0) narrow or small, 1) broad.
29. Position of the dentary condyle with regard to the alveolar margin: 0) below or at level of the alveolar margin, 1) above.

Appendix 2

Character matrix employed in this paper for assessing the phylogenetic relationship of *Symmetrolestes* with traditional spalacotheriids. Characters are listed in Appendix 1. Missing or unknown characters are represented by "?".

Taxon	Character 1–10										Character 11–20										Character 21–29								
Kuehneotherium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zhangheotherium	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1
Spalacotherium	1	1	0	1	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	1	1
Spalacotheroides	1	?	?	?	2	?	0	1	1	1	0	0	1	1	0	1	0	?	1	1	0	0	1	2	?	?	?	?	?
Spalacotheridium	1	?	?	?	2	1	1	1	1	1	0	0	1	1	0	1	1	1	1	2	1	?	1	?	?	?	?	?	?
Spalacolestes	1	?	?	?	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	0
Symmetrodontoides	1	?	?	?	3	?	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	?	?	1	?	?	?
Symmetrolestes	1	1	?	0	1	0	1	1	1	1	0	0	1	?	?	?	?	?	?	?	?	?	1	1	1	0	0	1	1