A New Specimen of *Eurylambda aequicrurius* and Considerations on "Symmetrodont" Dentition and Relationships

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ABSTRACT

A new specimen of the tinodontid "symmetrodont" *Eurylambda* (Simpson, 1925a, 1929) from the Late Jurassic Como Bluff Quarry, Morrison Formation, is described. The specimen, a complete upper left molariform, is probably an M1.

The major crown cusps of *Eurylambda* show similarities to those of triconodontids on the one hand and to spalacotherioids on the other. Cusp B of basal mammaliaforms is tentatively proposed as homologous with the cusp traditionally described as a stylocone in *Eurylambda* and with cusp B′ of *Peralestes*. These homologies imply that the stylocone is ancestrally a small cusp in the lineage leading to Theria and that the development of a parastylar lobe or "hook" is a derived feature of post-tinodontid mammals. If accepted, this scenario results in a more complex origin for the therian upper molar than previously recognized. Wear facet 1 (Crompton, 1971) of holotherians would not be homologous between *Kuehneotherium–Eurylambda–Zhangheotherium*, on the one hand, and the therians, on the other.

INTRODUCTION

Information on the upper molars of early Mesozoic mammals is sparse, due largely to the mechanical fragility of the maxilla when compared with the mandible, which results in a bias favoring the preservation of lower teeth and jaws. Therefore, our knowledge of dental evolution during the Mesozoic relies heavily on mandibular and lower molar morphology (Crompton, 1971; Prothero, 1981). Discovery of upper molariforms is always a

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welcome addition because it allows the evaluation of models of evolutionary transformation that have been based primarily on lower teeth, with occluding upper teeth being based on hypothetical reconstructions (Mills, 1964; Kermack et al., 1964; Crompton, 1971).

We report here on an isolated upper left molariform of *Eurylambda aequicrurius* (Simpson, 1925a, 1929). This is only the second specimen known for this taxon originally described as *Amphidon aequicrurius* (Simpson, 1925a) from the Late Jurassic Morrison Formation in Wyoming. The new specimen was collected at Como Bluff Quarry in 1883 by members of the O.C. Marsh expedition and catalogued at the National Museum of Natural History as an undetermined Mesozoic mammal tooth with the number USNM 2846. Como Bluff is also the locality where the Yale University party collected the type specimen of *Eurylambda*.

Discovery of a second specimen of *Eurylambda* is important because the type, a fragmentary maxilla with one tooth, has previously been the only model for the upper dentition of basal or obtuse angled "symmetrodonts" (Crompton and Jenkins, 1967, 1968; Crompton, 1971; Ensom and Sigogneau-Russell, 2000). Furthermore, the incomplete type is missing the parastylar region of the tooth. *Eurylambda* has been suggested to be a junior synonym of *Tinodon* (Prothero, 1981; Fox, 1985; McKenna and Bell, 1997; Sigogneau-Russell and Ensom, 1998; Ensom and Sigogneau-Russell, 2000) and we tentatively follow this interpretation here (see below), although for convenience we continue to use the name *Eurylambda* for the upper molars.

SYSTEMATIC PALEONTOLOGY

TINODONTIDAE FOX, 1985

Tinodon bellus Marsh, 1879 (*Amphidon aequicrurius* Simpson, 1925a; *Eurylambda* Simpson, 1929).

DESCRIPTION
(Figures 1, 2)

MATERIAL: The specimen (USNM 2846) is an isolated complete left upper molar pos-

sessing the bases of both roots. The crown was broken into halves at the base of the paracone and has been previously repaired. The crown of the new specimen is more buccolingually compressed than the type specimen and is slightly longer mesiodistally, with the major cusps forming an obtuse angle of about 171° (with the type specimen forming an angle of about 168°). These features suggest that the new specimen is a more anterior tooth than is the type. If tooth variance in other symmetrodonts is used as a model (Cifelli, 1999; Cifelli and Gordon, 1999; Cifelli and Madsen, 1999; Hu et al., 1997, 1998; undescribed specimen in prep.), the new tooth probably represents the position directly mesial to the type, which was originally regarded as M1 (Simpson, 1925a, 1929) but is here interpreted as a probable M2. However, USNM 2846 has a slightly more pronounced ectoflexus than does the type. This becomes more pronounced in distal elements of other "symmetrodonts", that is zhangheotheriids (Hu et al., 1997, 1998; undescribed specimen in prep.), spalacotheriids (Cifelli and Gordon, 1999; Cifelli and Madsen, 1999) and *Peralestes* (Owen, 1871; Simpson, 1928; Clemens, 1963). This latter consideration introduces some doubts about the more mesial position of USNM 2846 proposed here.

The crown has the shape of an elongated "D", with the straight side oriented buccally and slightly excavated by the shallow ectoflexus. Six cusps are fairly regularly placed on the outline of the "D". The largest of them is the centrally placed paracone (cusp A in terminology of Crompton and Jenkins, 1968). Three cusps are distal to the paracone: the metacone (cusp C), cusp D, and a small metastyle (following the terminology of Crompton and Jenkins (1967) and subsequent modifications) forming the extreme distolabial corner of the crown. Mesial to the paracone is the fairly lingual cusp B′ (as interpreted by Hu et al. (1997, 1998) or "cusp on anterior crest" of Patterson (1956), and a small stylocone in the mesiobuccal corner of the crown (see discussion below). The stylocone is joined to cusp B′ by a sharp crest that descends abruptly from the mesial slope of B′. The small stylocone extends distally as a fairly robust crest that reaches the mid-

dle of the buccal surface of B′. The area buccomesial to cusp B′ is raised and forms a small platform which sets off a small thickening of the mesial slope of the stylocone.

Cusp B′ is a main cusp of the crown and is not connected to a cingulum of any kind. It has a concave mesial face and a teardrop-shaped wear facet that truncates its apex. Distal to its apex, cusp B′ is connected to the massive face of the paracone by a short, nearly horizontal ridge. A shallow notch is formed at the intersection of the distal crest of cusp B′ and the mesial edge of the paracone.

The paracone is the largest and tallest cusp, being twice as high as the next highest cusp in the crown, the metacone. The paracone is slightly asymmetrical mesiodistally, with a blunter, more vertical mesial edge and a sharper, longer, and more gently sloping distal crest. The lingual side of the paracone is almost flat while the buccal side is strongly convex. These differences give the paracone a conspicuous hooklike shape.

The metacone (cusp C) is separated by deep notches from both the paracone and cusp D. It is a fairly symmetrical cusp, although the distal ridge is somewhat longer and less vertical. Its lingual face is grooved by a distinctive wear facet, which covers not only cusp D, but extends to the metastyle.

Cusp D (which may be interpreted as the larger of two metastylar cusps) is separated by a relatively shallow embrasure from the metacone (C) and by a deep notch from the metastyle. The wear facet mentioned above flattens its lingual surface while its labial aspect is strongly convex. The distal metastyle is a poorly differentiated small cuspule that forms a small, sharp posterior edge for interlocking with the following molar. All of these cusps, with the exception of those in the parastylar area (this portion is missing in YPM 13639, the type specimen of *Eurylambda aequicrurius*), can be seen in YPM 13639 with similar proportions. A shallow, buccally-concave stylar shelf extends between the stylocone and the metastylar portion of the tooth. A low crest, the buccal cingulum, demarcates the outer margin of the stylar shelf.

There is no clear demarcation between the crown and the roots. Both roots are buccolingually compressed, set obliquely with regard to the main axis of the tooth, and subequal in size. They differ markedly from the condition in *Spalacotheroides* (Cifelli and Madsen, 1999), whose roots are mesiodistally compressed and parallel to each other.

DISCUSSION

The importance of *Eurylambda* in our understanding of early ''symmetrodont'' relationships has recently been stressed by Ensom and Sigogneau-Russell (2000). *Eurylambda*, putatively a junior synonym of *Tinodon*, represents one of the few examples of upper tooth morphology among ''symmetrodonts'' and it has played a crucial role in the study of dental occlusion (Crompton and Jenkins, 1967, 1968; Crompton, 1971). *Eurylambda* represents the archetype for basal nontribosphenic holotheres (Hopson, 1994; Wible et al., 1995).

Ensom and Sigogneau-Russell (2000) recently described a new species of *Tinodon*, *Tinodon micron*, from the Purbeck Limestone Group, Lower Cretaceous of England. The type specimen is a lower molar that agrees quite closely with the American species of *Tinodon*. In addition to lower molars, Ensom and Sigogneau-Russell (2000) attributed an isolated upper molar to the same species and compared it to *Eurylambda*. We concur with their analysis in noting the close similarities between the two North American specimens of *Eurylambda* and the English specimen, DORCM GS 694, referred to *T. micron*. The main difference between the American specimens of *Eurylambda* and that from the Purbeck is the presence of a well-developed cusp B′ in the former, which is vestigial in the latter. The mesial lobe of the crown is also broader and proportionally larger in the English specimen than in the American specimens. The latter also lack the small labial cingulum (or have it extremely reduced) that is seen on the upper molar referred to *T. micron* (Ensom and Sigogneau-Russell, 2000: fig. 9C). Ensom and Sigogneau-Russell (2000) wondered if the differences they noted between their specimen and the American *Eurylambda* specimens were due to different positions on the dental series or to individual variation. The two American specimens agree with each other very close-
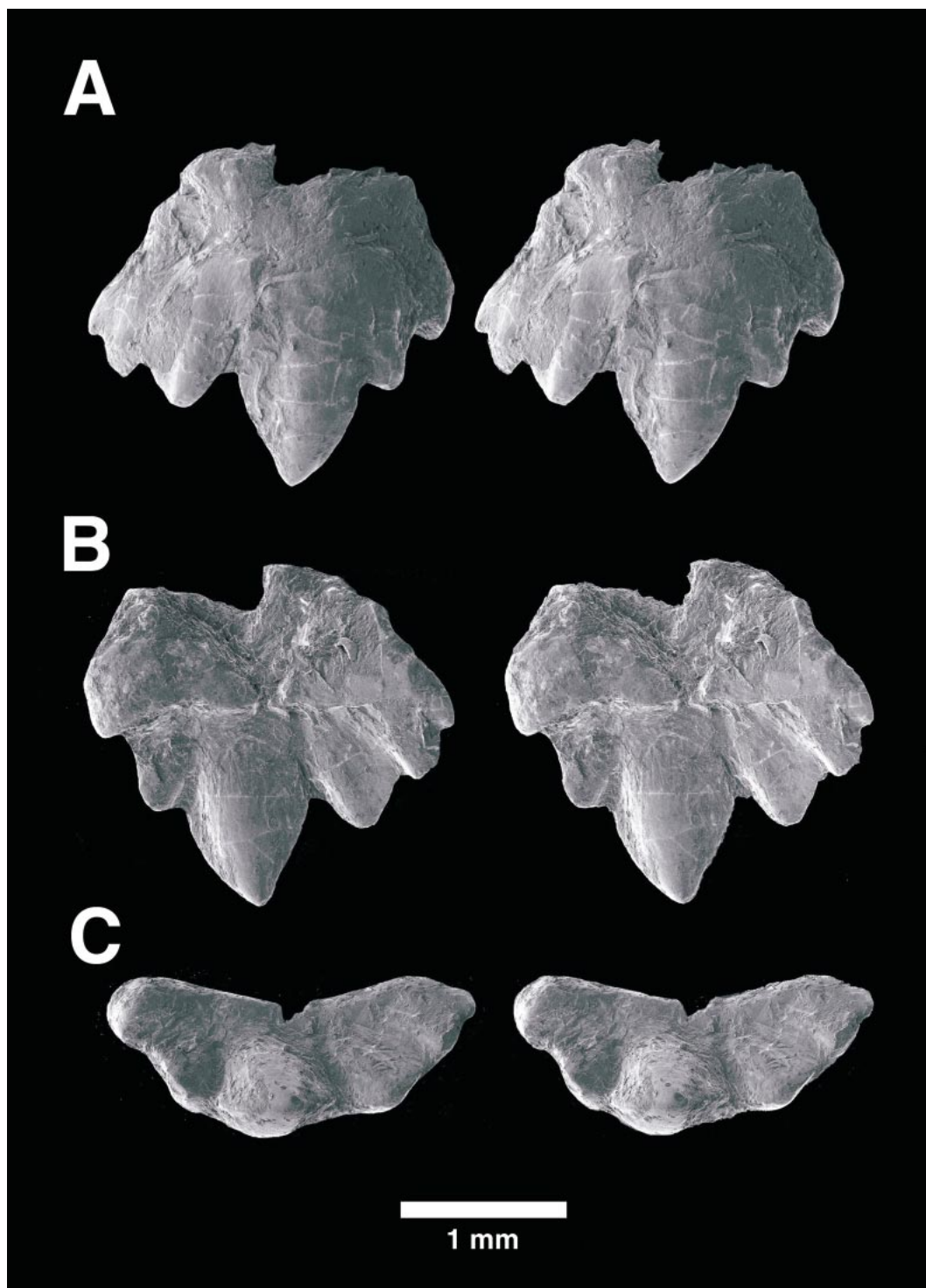
Fig. 1. USNM 2846, *Eurylambda aequicrurius*, left upper molariform (M1?), in lingual (A), labial (B) and occlusal (C) views.
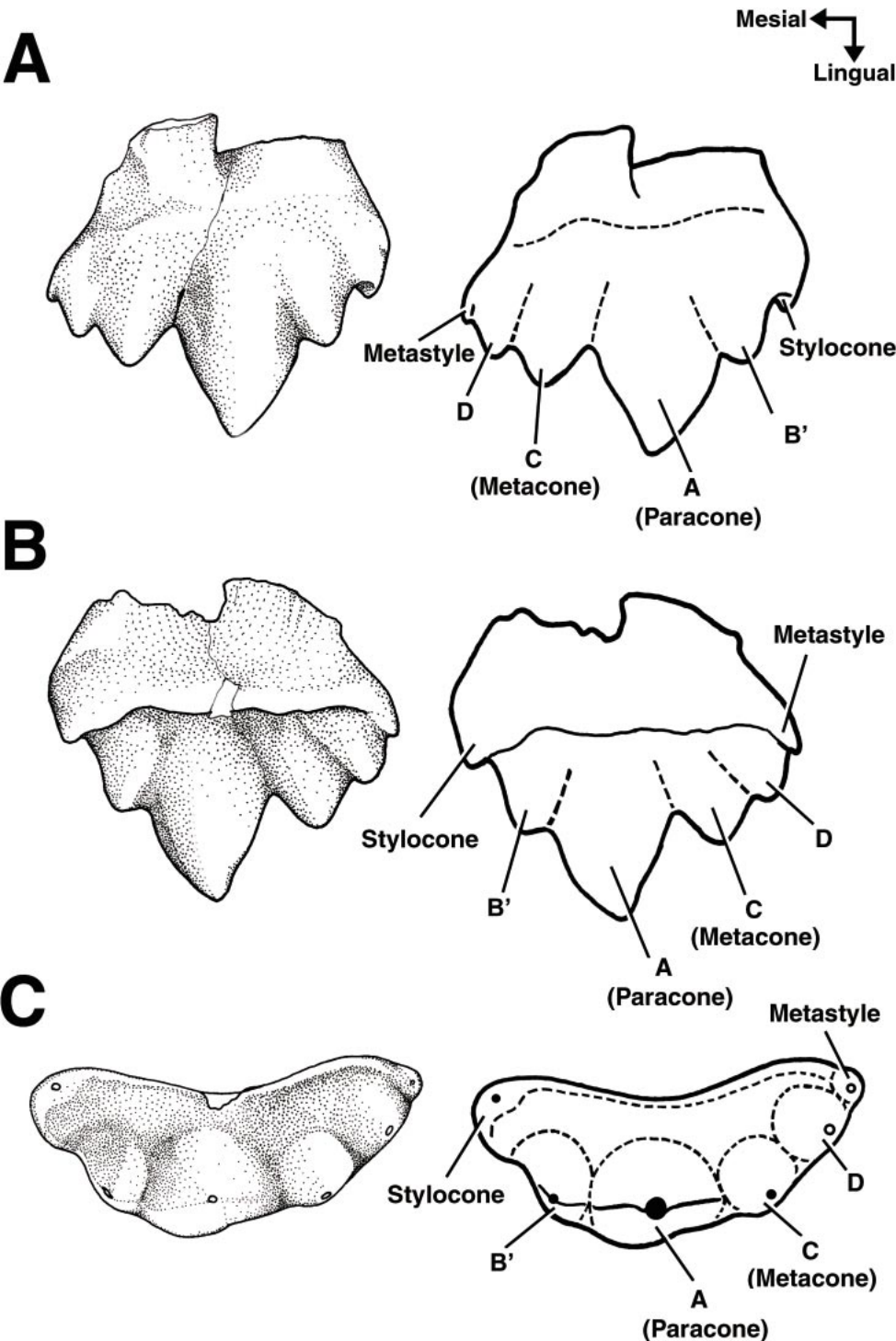
Fig. 2. USNM 2846, *Eurylambda aequicrurius*, drawings of the left upper molariform, in lingual (A), labial (B) and occlusal (C) views. Cusp nomenclature follows Hu et al. (1997, 1998) which in turn is a modification of that employed by Hopson and Crompton (1969) and Crompton (1971). Arrows refer to B and C.
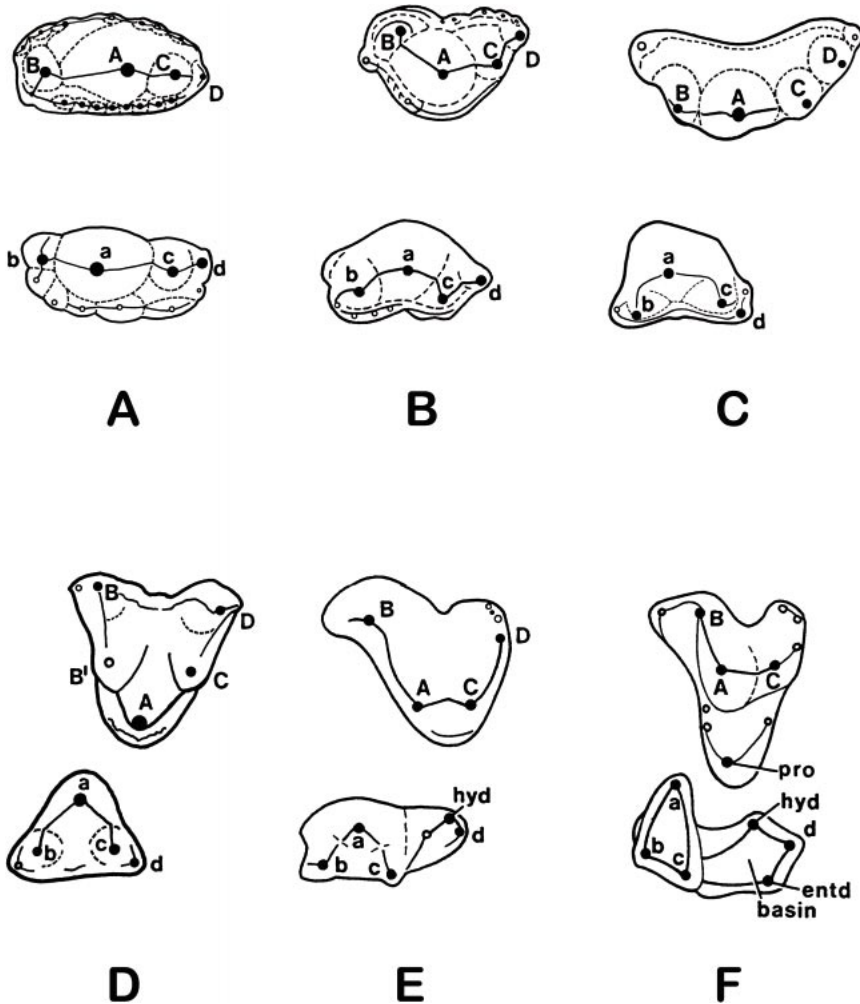
Fig. 3.   Traditional interpretation of the homologies of the main cusps among mammaliaformes (occlusal views): (A) upper and lower molariforms of *Morganucodon*; (B) upper and lower molariforms of *Kuehneotherium*; (C) upper and lower molariforms of *Tinodon* (*Eurylambda*); (D) upper and lower molariforms of an undescribed zhangheotherid mammal; (E) upper and lower molariforms of *Peramus*; (F) upper and lower molariforms of *Pappotherium*. Drawings are not at the same scale. (A, lower), (B), (E), and (F) taken with modifications from Hopson (1994). Represented in black are the main cusps of upper and lower molariforms. Abbreviations: entd= entoconid, hyd= hypoconid, pro= protocone.

ly, which suggests that the very reduced cusp B′ (see below) of the English specimen reflects a taxonomic difference more than variation within a single species of *Tinodon/Eurylambda*.

   Ideas on cusp homologies among basal holotheres, including *Kuehneotherium*, *Tinodon/Eurylambda*, and spalacotherioids, go back to the original proposals by Patterson (1956), Crompton and Jenkins (1967, 1968),

Hopson and Crompton (1969), as well as the latter modifications by Crompton (1971) and somewhat revised ideas by Prothero (1981) (fig. 3). Ensom and Sigogneau-Russell (2000) doubted the identification by Crompton and Jenkins (1967) of the large cusp mesial to cusp A in *Eurylambda* as the stylocone (= cusp B of basal mammaliaforms such as *Morganucodon*). Ensom and Sigogneau-Russell (2000) thought it possible that

this cusp was in fact the homologue of cusp B′ present in *Peralestes* (Patterson, 1956; Sigogneau-Russell and Ensom, 1998; Cifelli and Madsen, 1999) and zhangheotheriids (fig. 3; Hu et al., 1997, 1998), a possibility also considered by Simpson (1929) when noting similarities between *Eurylambda* and *Peralestes* (although he used a different cusp nomenclature).

Resolution of this controversy is important because if the above proposal by Crompton and Jenkins is accepted, we would have essentially a structural continuity within holotheres for all the major cusps and wear facets (excluding the protocone) on the upper tooth crown. On the other hand, if Ensom and Sigogneau-Russell are correct and the very lingual, large anterior cusp of *Eurylambda* is homologous with cusp B′ of the spalacotherioids, then either the parastyle or the stylocone has disappeared in *Tinodon/Eurylambda* and obtuse-angled symmetrodonts (Fox, 1972, 1984; Cifelli and Madsen, 1999; Sigogneau-Russell and Ensom, 1998) or the stylocone and the traditional cusp B is not homologous with that of cladotheres. Basing this debate on cusp and crown morphology is problematic because without relative position (and its concomitant functional implications), we are left with no other criteria on which to base homology (Simpson, 1961). Relative position is generally accepted as highly variable among cusps thought to be homologous, and is therefore not the best criterion to be used as the sole determinant of cusp homology. Although the phylogenetic relationships of nontribosphenic mammals are currently in a state of flux, the general framework, as presented by Wible et al. (1995); Hu et al. (1997), and Luo et al. (2001, 2002) can be used to address this problem.

Symmetrodonta, as considered by Simpson (1928, 1929) and Cassiliano and Clemens (1979), is not supported as a monophyletic group in any of the recent analyses of mammaliaform relationships (Hu et al., 1997; Ji et al., 1999; Luo et al., 2001, 2002; Rougier et al., 1999, 2001). In spite of numerous small disagreements among these analyses, the taxa traditionally included in Symmetrodonta (i.e., kuehneotheriids, tinodontids, and spalacotherioids) generally form a paraphyletic series leading to Theria. In all of these studies, groups traditionally included in "Triconodonta" (Jenkins and Crompton, 1979), such as Triconodontidae and amphilestids, form a succession of paraphyletic groups leading to some of the groups traditionally included in Symmetrodonta. Upper teeth of traditional amphilestids, such as *Amphilestes* (Owen, 1871; Simpson, 1928) and *Phascolotherium* (Owen, 1838, 1871; Simpson, 1928) are not known at present, although the occlusal pattern as deduced from the morphology and wear facets of the lower dentition suggest that three main cusps were present on the upper teeth and that they were arranged to form a broadly obtuse-angled triangle (Mills, 1964, 1971; Crompton, 1974; Kielan-Jaworowska and Dashzeveg, 1998).

Gobiconodon from the Early Cretaceous of Mongolia (Trofimov, 1978; Kielan-Jaworowska and Dashzeveg, 1998) has been variously interpreted as an amphilestid (Trofimov, 1978; Kielan-Jaworowska and Dashzeveg, 1998) or as a member of a monotypic family Gobiconodontidae (Chow and Rich, 1984; Jenkins and Schaff, 1988). Recent analyses weakly link *Gobiconodon* with triconodontids (Luo et al., 2001; Rougier et al., 2001; Wang et al., 2001). Regardless of the ultimate affinity of gobiconodontids (either with amphilestids or triconodontids), they show enough similarity to amphilestids to use their upper molariform morphology as the general pattern expected for the upper molars of amphilestids which represent a grade instead of a clade (Rougier et al., 2001).

As noted by Kielan-Jaworowska and Dashzeveg (1998), *Gobiconodon* shows an incipient triangular arrangement of the cusps of the upper molariforms. In *Gobiconodon*, the degree of triangulation of the main cusps is 140 degrees, averaged for the M3–M5, whereas it is 168° for the type specimen of *Eurylambda aequicrurius* from Como Bluff. Note that this is somewhat different from the crown outline angles measured by Crompton and Jenkins (1967) and Prothero (1981) for the type specimen of *Eurylambda*. The angle is 154° in the upper molariform attributed to *Tinodon micron* (from Ensom and Sigogneau-Russell, 2000). Therefore, the somewhat triangular arrangement of the main

cusps is likely to be a primitive feature shared by symmetrodonts and at least some of their "triconodont" outgroups.

Gobiconodontids and the more basal mammaliaforms, including Triconodontidae and *Dinnetherium* (Jenkins et al., 1983; Crompton and Luo, 1993), have three main cusps on the crown. These are a central cusp A (paracone), a distal cusp C (generally accepted as the metacone, but see Crompton (1971) and comments in Prothero (1981) for opposing views), and a mesial cusp B (generally thought to be homologous with the stylocone).

By comparing the upper teeth of *Eurylambda* with those of *Gobiconodon*, triconodontids, *Dinnetherium*, and *Jeholodens* (personal obs.), a fairly simple case of positional homology can be defended for a correspondence of cusp B of triconodonts (Simpson 1925b, 1925c; Patterson, 1956; Crompton, 1974) with the stylocone of *Eurylambda* as identified by Crompton and Jenkins (1967) or cusp B′ above (fig. 4). In all of these forms, the three main cusps are placed lingually, forming a broad triangle with a dominant cusp A, and flanking cusps B and C of similar size. From this, it also follows that the large cusp on the paracrista in spalacotherioids (such as *Peralestes*) is in fact cusp B of basal mammaliaforms; therefore, the use of B′ to designate it is unnecessary. We should refer to it simply as cusp B, reflecting the homology between the cusps of upper molariforms across precladothere mammaliaforms. In our description of the new specimen of *Eurylambda*, we used B′ to describe this cusp so as not to introduce the unfamiliar B without justification. However, if the above proposal is accepted, the names should be interchangeable. This proposal supports Ensom and Sigogneau-Russell's (2000) interpretation of the homologies of the cusps in *Tinodon micron* and *Zhangheotherium–Peralestes*. Cusp B would be lost among dryolestoids and later mammals. Patterson (1956) illustrated the occurrence of a small cuspule occupying a similar position to cusp B in the Jurassic dryolestoid *Melanodon*, but a similar cusp is not known in other dryolestoids (Ensom and Sigogneau-Russell, 1998; Martin, 1999). A well developed cusp B is however present in the stem zath-

erian *Nanolestes* (Martin, 2002) from the Jurassic of Portugal.

If cusp B of triconodonts and other basal mammaliaforms is homologous with B′ of spalacotheriids, which also have a stylocone, it follows that B and the stylocone are not the same cusp (figs. 3, 4). What, then, is the homologue of the stylocone among basal mammaliaforms and later cladotheres? In *Gobiconodon*, *Jeholodens*, and triconodonts there is a small cusp occupying the mesiobuccal corner of the crown. All of these forms also lack a distinct parastylar lobe, a feature also absent in *Eurylambda*. Therefore, we deduce the mesiobuccal cusp of triconodonts, *Gobiconodon*, and other basal mammaliaforms to be the homologue of the stylocone of later mammals. If this proposal is accepted, the small stylocone of symmetrodonts, *Peramus* (Clemens and Mills, 1971), basal tribosphenic mammals, and their relatives such as *Vincelestes* (Bonaparte and Rougier, 1987; Rougier, 1993) and *Comanchea* (Jacobs et al., 1989) would be a retained primitive feature.

As a corollary of the homologies proposed above, the parastylar hook would be a derived feature diagnosing all post-tinodontid mammals, because it is lacking in basal mammaliaforms. A parastyle as an individual cusp seems also to be absent in all, or most, of these basal forms. A distinctive parastylar hook and parastyle are likely associated with the increased transverse development of molariforms in more derived mammals by providing an interlocking mechanism between successive teeth.

A possible and noteworthy exception to the proposals above is *Kuehneotherium*, known from isolated teeth and jaws from the Early Jurassic Welsh fissure fillings (Kühne, 1950; Kermack et al., 1968; Parrington, 1971; Gill, 1974). The upper molariforms of *Kuehneotherium* have three main cusps in the crown traditionally interpreted as a somewhat centrally positioned paracone, an anterior stylocone, and a posterior metacone. Despite some obvious similarities between *Eurylambda* and *Kuehneotherium* (Crompton and Jenkins, 1967), there are differences, notably the very lingual position of the cusp here identified as B (or B′) in *Eurylambda* and the far more buccally located cusp tra-
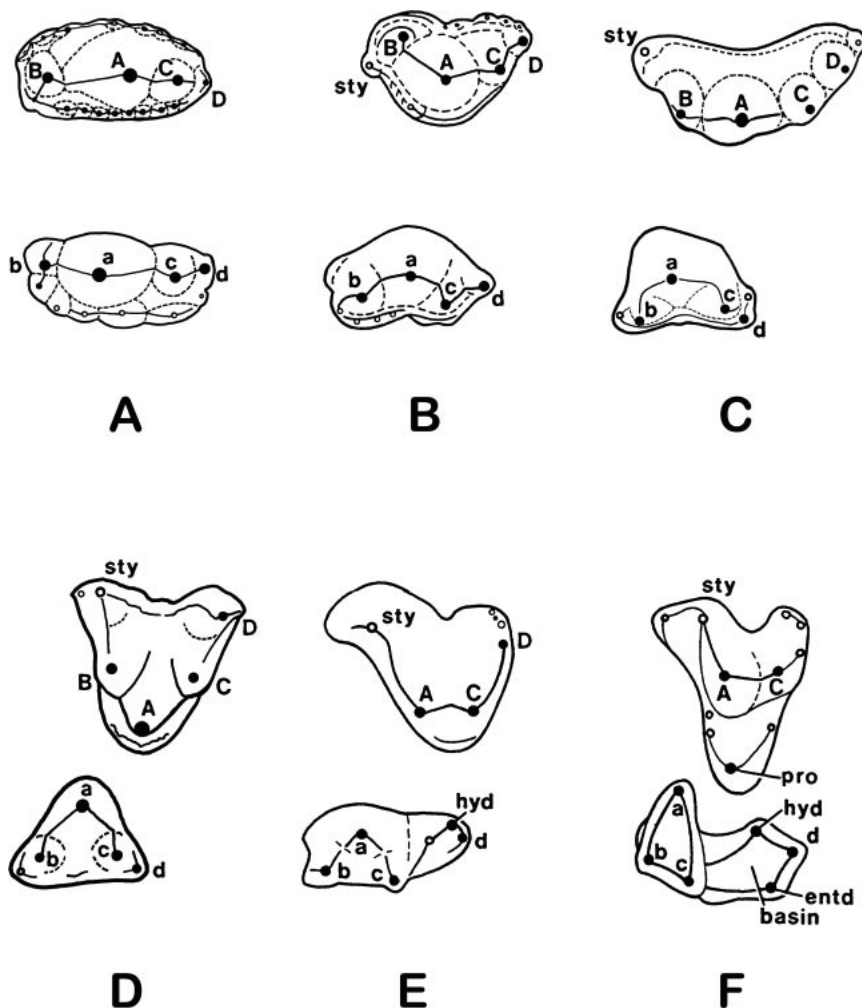
Fig. 4. Interpretation of the homologies of the main cusps among mammaliaformes postulated in this paper: (A) upper and lower molariforms of *Morganucodon*; (B) upper and lower molariforms of *Kuehneotherium*; (C) upper and lower molariforms of *Tinodon* (*Eurylambda*); (D) upper and lower molariforms of an undescribed zhangheotherid mammal; (E) upper and lower molariforms of *Peramus*; (F) upper and lower molariforms of *Pappotherium*. Drawings are not at the same scale. (A, lower), (B), (E), and (F) taken with modifications from Hopson (1994). Represented in black are the main cusps of upper and lower molariforms. Abbreviations: entd= entoconid, hyd= hypoconid, pro= protocone, sty= stylocone.

ditionally identified as the stylocone in *Kuehneotherium*. As noted by Ensom and Sigogneau-Russell (2000), cusp B of *Eurylambda* is more lingual than in any other symmetrodont and even in *Kuehneotherium*. Recent phylogenetic analyses place *Kuehneotherium* as a basal mammaliaform outside the common ancestor of triconodontids, "symmetrodonts", and therians (Luo et al., 2001; Rou-

gier et al., 2001). This basal position for *Kuehneotheium* and its lack of affinities with later cladotheres has been proposed early on by Rougier et al. (1996) as an expression of the contradiction posed by the primitive mandibular morphology and the supposed derived triangular dentition. In numeric phylogenetic analyses the basal position for *Kuehneotherium* is determined mostly by the

plesiomorphic dentary, which retains a broad postdentary groove with a medial ridge, a mandibular angle located very far forward, and a small, backward-sloping coronoid process. Considering that several groups with nontriangular dentitions are intercalated between *Kuehneotherium* and *Tinodon* (including triconodontids, amphilestids, and possibly multituberculates), it is likely that the triangular arrangement of the cusps in *Kuehneotherium* and the stem group Theria is convergent. *Kuehneotherium* may represent an early and independent acquisition of the reversed triangles occlusal pattern (Rougier et al., 1996, 2001; Luo et al., 2002). The cusp identified as the stylocone in *Kuehneotherium* is arguably homologous with the mesialmost large cusp in the crown of triconodonts, *Gobiconodon*, *Eurylambda*, and spalacotherioids, where it is called B (or B′). The minute cusp identified as the parastyle in *Kuehneotherium* can be either homologous with the stylocone of *Eurylambda* or simply a neomorph. We think that these issues are irresolvable at present.

The possibility that cusp B of a basal mammaliaforme (e.g., *Morganucodon*) and the stylocone of a therian are not homologous also raises the issue about the homology of the wear facets purported to connect these cusps. Facet 1 (Crompton, 1971; Crompton and Kielan-Jaworowska, 1978) constitutes one of the most primitive features of the triangular molariforms thought to be precursors of the therian tribosphenic molar. However, facet 1 as identified by Crompton (1971) would not be homologous between *Kuehneotheriu–Eurylambda–Peralestes* and the nontriangular mammaliamorphs, on the one hand, and the cladotheres, on the other. In the first group it would extend between the stylocone and B (B′) and the paracone in the second. Changes in occlusal relationships among major cusps are, of course, possible. Furthermore, it is feasible to imagine that the functional difference might not be very substantial between a facet that stops at a poorly developed cusp B or one that continues (after the disappearance of the cusp B) to the paracone. This change, however, is of the same magnitude as those used to argue in favor of or in opposition to therian affinities for amphilestids. In light of the above, the use of

functional features (such as wear facets) as independent characters in phylogenetic analyses seems best approached with caution. Inferring the presence of cusps based on the facets present in an opposite element (e.g., upper molar cusps predicted by wear facets on a lower molar) seems risky and subject to too many idiosyncrasies (reflecting mostly the favored morphology of the person reconstructing the missing element).

Along the posterior crest of the tooth of *Eurylambda* there are two major and one minor cusp, referred to here as paracone, metacone, and cusp D, respectively. We are fairly confident that the cusp immediately posterior to the paracone is homologous with cusp C of triconodonts and *Zhangheotherium*; we are less certain, however, that the same cusp is homologous with the metacone of therians. Crompton (1971) argued that the metacone of therians was a neomorph absent in primitive Mesozoic mammals (citing as supporting evidence an accessory cusp C′ that in his view would be homologous with cusp C of more basal forms). Prothero (1981) and Hopson (1997) refuted the presence of accessory cusps C′ in *Peramus* (Clemens and Mills, 1971), and Hopson (1997) also denied its presence in *Amphitherium* although no upper teeth are known. In *Eurylambda* there are clearly three cusps distal to the paracone, two of them large. The two more distal (cusp D and the metastyle here) can be viewed as a bifid metastyle, and the more mesial cusp (C) as the metacone. It is equally plausible, in our opinion, that these three cusps represent the metacone (C), cusp C′ of Crompton (1971), and the metastyle. Cusp C′ is widespread among cladotheres, being present in taxa basal to Theria, including *Vincelestes* (Rougier, 1993), *Comanchea* (Jacobs et al., 1989), and some basal tribosphenic forms, including *Pappotherium* (Patterson, 1956; Butler, 1978). We believe that it is difficult to resolve if the metacone is indeed the homologue of cusp C in triconodonts and more basal mammals as traditionally defended (Patterson, 1956; Prothero, 1981; Hopson, 1997); however, we also view the evidence marshaled by Crompton (1971) to challenge this as being insufficient. Until new specimens bearing on this problem are discovered and studied, we choose to follow the tradi-

tional interpretation that equates cusp C and metacone, thus preserving a very general statement of homology spanning from basal nonmammalian cynodonts to modern therians.

AMPHIDON AND ''SYMMETRODONTS''

Simpson (1929) considered the possibility that the type of *Eurylambda* (YPM 13639) was, in fact, an upper molar of *Amphidon*, instead of *Tinodon*, and was his original attribution. These caveats were his main reasons for erecting a new genus for YPM 13639. Crompton and Jenkins (1967), however, determined that the wear facets of *Eurylambda* and *Amphidon* did not match, rendering Simpson's 1929 attribution unlikely.

The type and only known specimen of *Amphidon superstes* seems to be better interpreted as an amphilestid with worn-down molars rather than a typical ''symmetrodont'' (Rougier et al., 2001). There are five molariforms preserved in the type and only specimen (YPM 13638) traditionally interpreted as p–last m1–4. The first preserved tooth shows little wear in contrast with the heavily worn posterior molariforms, indicating that this element had a deciduous predecessor and that it erupted later than the more distal teeth. A deciduous predecessor would make this tooth, by definition, a premolar (Clemens and Lillegraven, 1986; Luckett, 1993). The morphology of this tooth, however, agrees closely with that of the first molariform of *Amphilestes* and *Phascolotherium* in showing five cusps that are fairly symmetrically arranged, as well as a faint basal cingulum (the smaller cusp b is damaged). Replacement of molariforms is known in the putative amphilestid gobiconodonts *Gobiconodon* and *Hangjininia* (Jenkins and Schaff, 1988; Godefroit and Guo, 1999); additionally, the tooth identified as m1 in zhangheotheriids has a deciduous predecessor (personal obs). Therefore, the dentition preserved in *Amphidon* can be interpreted as m1–m5, which agrees well with the almost universal presence of five molariforms among amphilestids. The somewhat triangular aspect of the crown of *Amphidon* is, in our opinion, caused by the extreme wear of cusps b and c, and by the labial bulging of the base of cusp a. A few

other mammals have been included in Amphidontidae (Yabe and Shikama, 1938; Trofimov, 1980; Yadagiri, 1985; Krusat, 1989), with *Manchurodon* (Yabe and Shikama, 1938) and *Gobiotheriodon* (Trofimov, 1980, 1997) based on the most complete specimens. These materials, however, do not shed additional light on the morphology of the Amphidontidae, if there is such a group at all. *Manchurodon* has been lost since the brief original description. It is unclear if the dental morphology described really corresponds to a full buccal view or simply to the exposed labial surface of the molariforms. In the published source, there is very little to link *Manchurodon* with *Amphilestes*. The affinities of *Manchurodon* are at present better left unresolved.

Gobiotheriodon (Trofimov, 1980, 1997) is known by a fairly complete lower jaw with three molariforms and an attributed upper tooth in a fragment of maxilla. We had the opportunity to study this specimen at the Paleontological Institute, Moscow. *Gobiotheriodon* is indeed a symmetrodont, but it resembles more closely the recently discovered *Zhangheotherium* from Liaoning (Hu et al., 1997, 1998) than *Amphidon*. As in *Zhangheotherium*, the lower jaw is very slender with multiple mental foramina (four or more), and the molar cusps have their bases separated, forming individual cones. The presence of individualized cusps contrasts with the condition in spalacotheriids where the main molariform cusps are united by crests at the time of eruption. In zhangheotheriids, and presumably also in *Gobiotheriodon*, wear removes substantial parts of the crown to obtain matching surfaces between upper and lower molariforms. We think, therefore, that Amphidontidae as a distinct family of Mesozoic mammals is probably unwarranted, and that it is based on an artificial grouping of badly preserved and poorly known fossils.

In addition to *Amphidon*, there are two other amphilestids described from the Morrison Formation, *Phascolodon* (Simpson, 1925a) and *Aploconodon* (Simpson, 1925a). Both of these are known by the type specimens only, in both cases partial lower dentitions. We cannot rule out that *Eurylambda* represents the uppers of an amphilestid, al-

though the poor matching of wear facets between *Amphidon* and *Eurylambda* makes it unlikely (Crompton and Jenkins, 1967). Based on the orientation of the wear facets on these amphilestids and their crown outline we would expect the upper molariforms to be similar to those of *Gobiconodon*, with the main cusps forming a broad triangle, the teeth somewhat broad buccolingually, and the parastylar hook absent. Thus, we support the traditional view that *Eurylambda* is likely the upper dentition of *Tinodon*.

CONCLUSIONS

Eurylambda (Simpson, 1925a, 1929) is likely to be a junior synonym of *Tinodon* (Marsh, 1879) as previously argued by Crompton and Jenkins (1967). The molar described here seems to correspond to a more mesial position than the corresponding one in the type. The type of *Eurylambda* is likely an M2, which would make the new specimen a probable M1.

It is likely that the most mesial of the three large cusps of the crown in *Eurylambda* is homologous with cusp B of triconodonts, including triconodontids and amphilestids; in turn, this cusp is also likely to be homologous with cusp B′ of *Peralestes* (Simpson, 1928; Clemens, 1963; Cifelli and Madsen, 1999; Cifelli and Gordon, 1999) and *Zhangheotherium* (Hu et al., 1997, 1998). If these homologies are accepted, cusp B would be lost in most, if not all, cladotheres, while the parastylar hook and likely the parastyle would be a derived feature of post-tinodontid mammals. If the homologies outlined above were followed, the history of the upper molariforms would be somewhat more complex than previously assumed in the therian stem lineage. This would imply the loss of a major crown cusp (B) and the derived acquisition of the parastylar area, instead of a somewhat continuous elaboration of the primitive holotherian pattern of triangulated cusps. The homology of the ancestral wear facet 1 (Crompton, 1971) across Holotheria would be compromised by the likely involvement of nonhomologous cusps. Basal forms have facet 1 spanning from the stylocone to cusp B (B′) (e.g., *Kuehneotherium*, *Tinodon*, *Zhangheotherium*); therian forerunners have, instead, facet 1 stretching from stylocone to the paracone (A).

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