

# INTERRELATIONSHIPS OF MESOZOIC MAMMALS

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*(Received October 16, 1991)*

Polyphyletic or monophyletic origins of mammals have been subjects of considerable controversy for a century. Late Triassic–Early Jurassic mammals are more diverse than previously thought. The stumbling block in establishing mono- or polyphyletic origins of mammals is the uncertain position of the Haramiyidae (the oldest Multituberculata, and possibly the oldest mammals), known only from isolated teeth. Triconodonta and Theria probably shared an unknown common ancestor, while Monotremata possibly branched from early Eupantotheria at the end of the Early Jurassic, before the Dryolestoidea did, from the forms in which the cochlea started to coil and small cerebellar hemispheres developed. Aegialodontia gave rise to Metatheria but not to Eutheria. Deltatheroidea belongs to Metatheria. A group of Cretaceous therian mammals with tribosphenic molars informally classified as “Tribotheres” cannot be assigned either to Metatheria or Eutheria.

KEY WORDS: Mammalia, Multituberculata, Haramiyidae, Theria, Triconodonta, Mesozoic, phylogeny.

## INTRODUCTION

The interrelationships of Mesozoic mammals cannot be discussed without touching on the problem of their origins. Until the mid-sixties, mammals were regarded by almost all students as a group of polyphyletic origin (Simpson, 1928, 1959, 1960; Olson, 1944, 1959; Patterson, 1956, Kermack, 1963). The polyphyletic concept resulted from the limited knowledge of the evolution of mammals in Rhaeto-Liassic times, from the diversity of teeth of Late Jurassic mammals, and from the parallel development of mammalian characters in various therapsid groups.

Beginning in the mid-sixties various authors advocated indirectly or directly diphyletic (Mills, 1964; Kermack, 1967; Kermack and Kielan-Jaworowska, 1971) or monophyletic (Hopson, 1967; Hopson and Crompton, 1969; Parrington, 1971; Crompton and Jenkins, 1968, 1973, 1979) origin for mammals.

The diphyletic concept was primarily based on studies of the braincase structure in Mesozoic mammals (Kermack 1963; Kielan-Jaworowska 1971), leading to the division of the class Mammalia into non-therian and therian mammals. These terms, illogical as they are (the first implying *contradictio in adiecto*, the second tautology), were often used as informal units (e.g. Lillegraven *et al.*, 1979 and references therein). Other authors (e.g. McKenna 1975; Hopson, 1970; Crompton and Jenkins, 1973) regarded these groups as formal taxa: the subclasses Prototheria Gill, 1872 and Theria Parker and Haswell, 1897, although Kermack *et al.* (1973) advocated that the name Prototheria is inappropriate for non-therian mammals and proposed the name Atheria instead.

The main difference between the two subclasses was said to be laid in the structure of the lateral wall of the braincase, which in Theria is formed by the alisphenoid and the squamosal while in Prototheria (or Atheria) by the anterior

lamina of the petrosal. It soon became evident that this difference is not a valid one. Presley (1981) demonstrated on embryological evidence that the part of the alisphenoid and the anterior lamina of the petrosal are partly homologous, both being membrane bones that later in ontogeny fuse either with the cartilaginous ala temporalis (to form the alisphenoid) or with the cartilaginous otic capsule (to form the anterior lamina of the petrosal). Kermack *et al.* (1981) showed that *Morganucodon*, a Rhaeto-Liassic triconodont, possesses a large alisphenoid in addition to the anterior lamina, the same holds for the Paleocene multituberculate *Lambdopsalis* (Miao, 1988). Some therians such as the Early Cretaceous eupantothere *Vincelestes* (Rougier and Bonaparte, 1988) has a large anterior lamina in addition to the alisphenoid. It is now generally accepted (e.g. Clemens, 1986; Kemp, 1983, 1988b; Lillegraven *et al.*, 1987; Miao, 1991 and many others) that the concept of the dichotomy separating mammals into therian and non-therian groups should be abandoned.

The monophyletic concept was based mainly on studies of the dentition. Hopson and Crompton (1969), Crompton (1974), and Crompton and Jenkins (1973, 1979) demonstrated close similarity in the dentition of morganucodontids and kuehneotheriids (Rhaeto-Liassic, oldest known representatives of the Theria) and suggested their (Hopson and Crompton, 1969, p. 67): "... relatively recent separation from a common ancestor". Crompton and Jenkins (1968) and Hopson and Crompton (1969) also suggested the probable derivation of the Docodonta from the Triconodonta. Butler (1988, p. 339) argued that the docodonts and therians: "... were probably derived from a form with triconodont molars, having occlusal relations like those of *Megazostrodon*".

The phylogenetic position of multituberculates somewhat obscured the relatively clear picture of mammalian monophyly, as the apparent oldest multituberculates (Haramiyidae), known only from isolated teeth, appear in beds older than those yielding the morganucodontids and kuehneotheriids and are very different from them. In spite of this Hopson (1970) tentatively suggested that the multituberculates may have developed from the triconodonts (morganucodonts), while Crompton (1974, p. 430) stated that: "... the haramiyid molars could have been derived from a form ancestral to the Morganucodontidae by enlargement and modification of cingular cusps".

New fossil discoveries in the eighties, discussed below, showed that some conclusions about the relationships of the Rhaeto-Liassic mammals based on teeth (e.g. the origin of the Docodonta, see Lillegraven and Krusat, 1991) are not valid.

The tortuous course of the debate concerning mammalian origins was longer and more complex than it may appear from the summary above. As this problem was recently reviewed in an historical perspective by Miao (1991), I refer the reader to his paper and references therein.

It is obvious that the answer to the question whether mammals are polyphyletic or monophyletic depends on how they are defined. The character states listed recently by Crompton and Sun (1985), Hopson and Barghusen (1986), Kemp (1988b), Lillegraven and Krusat (1991), and Miao (1991) are often regarded as mammalian synapomorphies (although there are some differences among the above mentioned authors). The most important of these synapomorphies (as summarized by Miao, 1991) are: establishment of squamosal-dentary jaw articulation; loss of "alternate" tooth replacement of postcanine teeth; postcanine teeth with divided roots; and development of a bony floor to the cavum epiptericum. If not stated otherwise, in this paper mammals are regarded as having the above apomorphies (*contra* Rowe, 1988 and Wible, 1991).

Recently Clemens (1986), Miao (1991) and Lillegraven and Krusat (1991) concluded that the class Mammalia is polyphyletic. Incidentally the same set of data led other authorities (e.g., Crompton and Sun, 1985; Hopson and Barghusen, 1986; Kemp, 1988b) to conclude that mammals are monophyletic. Hopson and Barghusen (1986, p. 103) state: "Mammals possess a number of unique features that strongly indicate they are strictly monophyletic. A well developed articulation between the dentary and squamosal is known with certainty only in mammals." The possession of an articulation between the squamosal and dentary (and some other characters cited by Hopson and Barghusen) in groups traditionally classified as mammals cannot be taken as a proof of mammalian monophyly, as this character could develop in parallel, as many other features did, e.g. three ear ossicles (Miao and Lillegraven, 1986; Allin, 1986).

If, however, one accepts e.g.: (1) that only Theria should be called mammals (MacIntyre, 1967); either (2) that Mammalia comprises the most recent common ancestor of living Monotremata and Theria, and all its descendants, including Multituberculata (Rowe, 1988); or (3) excluding Multituberculata (Wible, 1991)—then the dwarfed class Mammalia, very different from traditional view, would be monophyletic.

Other attempts of maintaining mammalian monophyly were earlier proposals of Van Valen (1960) and Reed (1960) to include respectively the Therapsida, or all the Synapsida into Mammalia, the latter more recently adopted by Ax (1987). Miao (1991) reviewed definitions of Ax (1987) and Rowe (1988), while Wible (1991) reevaluated craniodental characters employed by Rowe in his cladogram and refuted a part of them. Therefore I do not discuss the papers of Ax and Rowe, referring the reader to Miao's and Wible's reviews, which does not imply that I necessarily agree with all the conclusions of these two latter authors.

In the account that follows I will discuss only the most important discoveries of Mesozoic mammals in the years since the publication of *Mesozoic Mammals: The First Two-Thirds of Mammalian History* (Lillegraven *et al.*, 1979) that are relevant for their relationships.

## RHAETIAN AND LIASSIC MAMMALS

### *The Oldest Mammal-Bearing Localities*

Some of the important localities of the world yielding mammals previously regarded as of Rhaeto-Liassic age are now thought to be of Liassic age (Lillegraven *et al.*, 1979; Clemens, 1980, 1986). The so-called "Rhaetic fissure fillings" of England and Wales were deposited at various times and most of them are of Liassic, probably Sinemurian age (Kermack *et al.*, 1981; Clemens, 1986). As summarized by Clemens (1986), the Kayenta Formation of North America (Jenkins *et al.*, 1983); the upper part of the Stromberg group of South Africa; the Kota Formation of India (Datta, 1981), and the Lufeng beds of China are now also thought to be of Early Jurassic age.

Other European localities: Württemberg bonebeds of Germany and Hallau in Switzerland are probably of Rhaetian age, while the site at Saint-Nicolas-de-Port (France) and Gaume (Belgium) (Hahn, 1973; Clemens, 1980, 1986; Sigogneau-Russell, 1983 and references therein, 1989; Wouters *et al.*, 1984) are possibly older than the bonebeds of Germany and Switzerland being of Upper Norian or Lower Rhaetian age (Hahn *et al.*, 1989). Lastly Emborough fissure filling of

England yielding *Kuehneotherium*, was referred to originally as Norian (Fraser *et al.*, 1985), but Whiteside and Marshall (1985) argued that it is rather of the Upper Rhaetian age.

### *Major Groups of Rhaetian and Liassic Mammals*

Mammals that occur in Rhaetian, Rhaeto-Liassic or Liassic beds belong to three major lines: Morganucodontidae (Triconodonta); Kuehneotheriidae (Symmetrodonta, Theria) and Haramiyidae (Multituberculata). Also occurring are some poorly known groups such as *Sinoconodon*, regarded by Crompton and Sun (1985) as the sister group of all other mammals, and the Theroteinidae, known from the dentition only, assigned by Sigogneau *et al.* (1986) to Mammalia *incertae sedis* and subsequently by Hahn *et al.* (1989) to the Allotheria. Docodonta, as suggested by Lillegraven and Krusat (1991), "represent a cladistically earlier stage of synapsid evolution than morganucodontids". Although the oldest record of Docodonta is from the Bathonian (Middle Jurassic), they had to exist in Liassic or Rhaetian times, but have not been found as yet. The Docodonta, *Sinoconodon*, and possibly the Theroteinidae (but see discussion below), and *Dinnetherium*, an aberrant triconodont from the Kayenta Formation of Arizona (Jenkins *et al.*, 1983), may represent other (blind) lines of early mammals.

It follows that the Rhaetian and Liassic mammals were more diverse than previously thought and can no longer be classified simply within the three families Morganucodontidae, Kuehneotheriidae and Haramiyidae.

Of these families, the Morganucodontidae are by far the best known not only from the dentition, but also from skulls, lower jaws and postcranial skeleton (Parrington, 1971; Mills, 1971; Crompton, 1974; Kermack *et al.* 1973, 1981; Jenkins and Parrington, 1976). The Kuehneotheriidae are known from isolated teeth and jaw fragments (D. M. Kermack *et al.*, 1968), which allows a reconstruction of the mandibular jaw joint. Although comparison between the two families must be limited to the dentition and the lower jaw, there are no doubts that they are more closely related to each other than either of them is to the Haramiyidae. The comparison of the morganucodontid and kuehneotheriid dentition by Crompton and Jenkins (1968), and Hopson and Crompton (1969) still holds.

### *Problem of the Multituberculata*

The most controversial of the three families occurring in Rhaetian and Liassic beds is the Haramiyidae (assigned by most to Multituberculata), known only from isolated teeth. It is interesting that in the Liassic of Europe (e.g. in England) the Morganucodontidae and Kuehneotheriidae dominate and the Haramiyidae are rare, whereas in older (Lower Rhaetian or Upper Norian—see Hahn *et al.*, 1989) beds such as those of Saint-Nicolas-de-Port, the Haramiyidae dominate (Sigogneau-Russell, 1983). Although the exact age of the Late Triassic mammal-bearing beds is still controversial (Clemens, 1980, 1986), this observation of Sigogneau-Russell is of importance. Haramiyids are common in Rhaetian beds of Europe, less common in younger Liassic European and North American strata (where so far only one possible haramiyid tooth has been found in the Kayenta Formation, see Jenkins *et al.*, 1983), and are unknown from other parts of the world.

The oldest known haramiyid is a single tooth of *Thomasia* (Hahn, 1973), possibly a junior synonym of *Haramiyia* (Sigogneau-Russell, 1989) from the

Middle Keuper rocks (Norian) of Württemberg. If *Thomasia* is indeed a haramiyid, and haramiyids are multituberculates, then it is the oldest known mammal, some 5–10 million years older than the oldest known morganucodontids (triconodonts).

The works of Hahn (1973) and Sigogneau-Russell (1989) convinced most paleontologists that the Haramiyidae belongs to the multituberculates. It is currently classified as a multituberculate suborder Haramiyoidea. In the newly described haramiyid material from the Lower Rhaetian of France, Sigogneau-Russell (1989) recognized two types of incisors and four types of cheek teeth, suggesting that the latter may correspond to two upper and two lower teeth. The wear facets and striations suggest that the movement was essentially rotatory, with oral and longitudinal components and some transverse laxity.

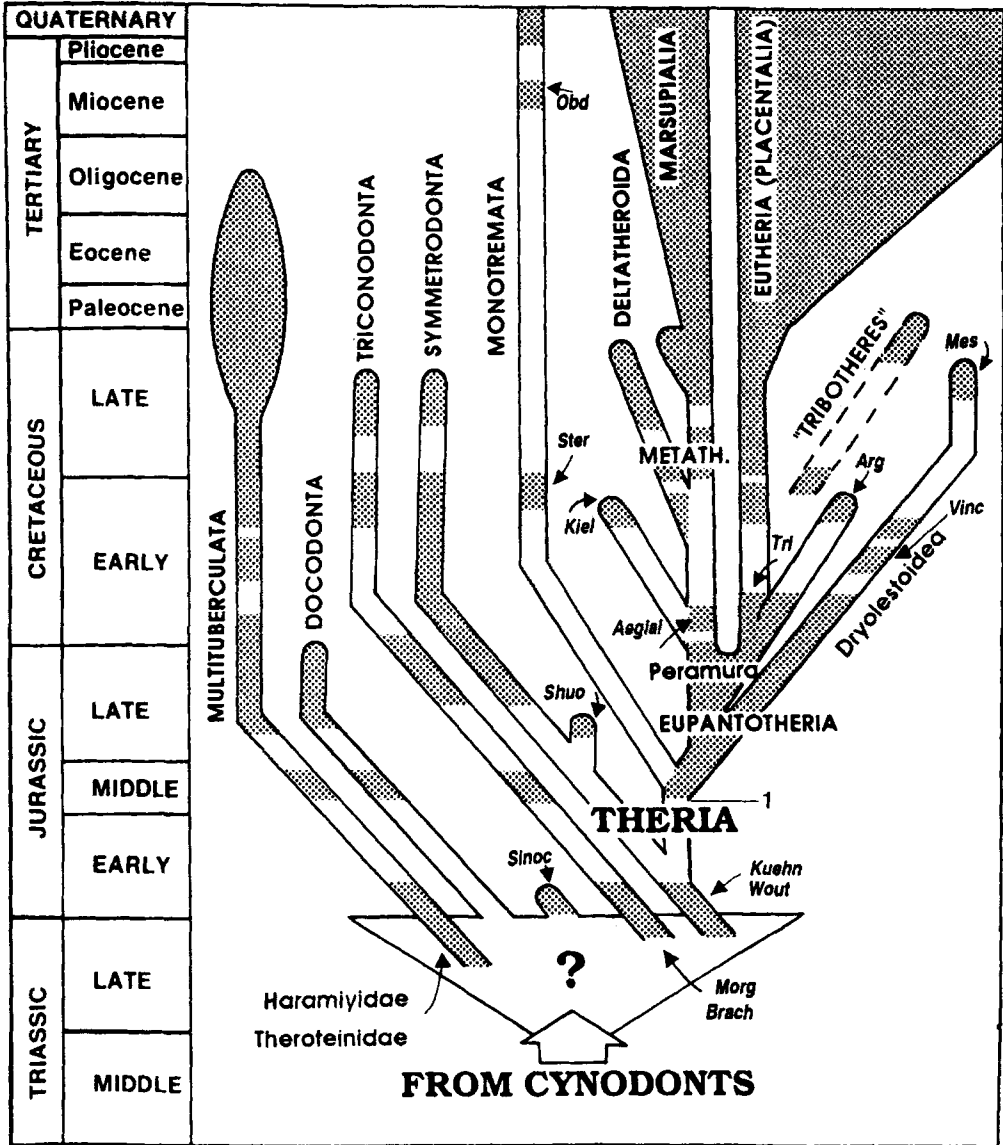
If the Haramiyoidea belongs to the Multituberculata, then the temporal distribution of the multituberculates is strongly punctuated (Fig. 1): while apparently flourishing at the end of the Triassic, they are rare in the early Early Jurassic, and almost absent from the fossil record in the late Early and Middle Jurassic, appearing again in abundance in Late Jurassic rocks. The first "true" multituberculates made their appearance (although being very rare) in the Bathonian, unless a part of a single tooth, *Mojo usuratus*, from the Lower Rhaetian of Belgium assigned by Hahn *et al.* (1987) tentatively to the Paulchoffatiidae belongs indeed to this family. If it were shown that *Mojo* is rather a haramiyid, it would serve as another proof for the multituberculate affinities of the Haramiyoidea.

Recently Wible and Hopson (in press) reached an impressive insight into the structure of the mammalian braincase. Using the computer program PAUP (Phylogenetic Analysis Using Parsimony), they placed (Fig. 4) Multituberculata as a sister group of the Monotremata, between the Triconodontiadae below and *Vincelestes* (Dryolestoidea) above. This work was based exclusively on studies of the basicranium. Wible and Hopson (in press) explained: "Our exclusive use of basicranial characters in this analysis is not a reflection of a belief in the basicranium as a taxonomic touchstone. We do not advocate phylogenies produced from a single anatomical (or biochemical) system. Our purpose here is to identify characters to be included in analyses of the entire anatomy and to detail how the basicranium evolves relative to other systems."

In spite of this explanation, I am of the opinion that construction of cladograms on the basis of a single anatomical system, before the entire anatomy is studied, may be misleading. Although I was unable to find in any textbooks of phylogenetic systematics (e.g., Wiley, 1981) a recommendation that in phylogenetic reconstructions as many different characters as possible should be used, such a corollary appears obvious if one accepts that there is only one phylogeny of any group of organisms. Cladograms based on a single anatomical system create different phylogenies of the same group and may obscure the true relationships. They also lead to an unusual situation that the same author may have *at the same time* two or more different views on the phylogeny of the studied group (e.g. Wible, 1991; and Wible and Hopson, in press).

Twenty years ago, when describing the first well preserved braincases of multituberculates (Kielan-Jaworowska, 1971) I was impressed by the similarity of some details of the multituberculate and monotreme braincase (confirmed recently by Wible and Hopson, in press) and I advocated a close relationship of these groups. However, the discoveries of the past twenty years have induced me to revise my opinion on this relationship. Prime among these discoveries were the

teeth of the Early Cretaceous monotreme *Steropodon* (Archer *et al.*, 1985; Kielan-Jaworowska *et al.*, 1987) and those of the Late Triassic Haramiyidae (Sigogneau-Russell, 1989). As discussed in the next section, the structure of the *Steropodon* teeth allies Monotremata with early Eupantotheria. On the other hand, the teeth of



**Figure 1** Tentative family tree of Mesozoic mammals. *Aegial*—*Aegialodon*, *Arg*—*Arginbaatar*, *Brach*—*Brachyzostrodon*, *Kiel*—*Kielantherium*, *Kuehn*—*Kuehneotherium*, *Mes*—*Mesungulatum*, *METATH*—*Metatheria*, *Morg*—*Morganucodon*, *Obd*—*Obdurodon*, *Shuo*—*Shuotherium*, *Ster*—*Steropodon*, *Tri*—*Tribotherium*, *Vinc*—*Vincelestes*, *Wout*—*Woutersia*, *1*—level in eupantotherian evolution showing the beginning of development of the cerebellar hemispheres and coiling of the cochlea. The question mark implies doubts on the monophyletic versus polyphyletic origin of mammals and interrelationships of earliest mammals.

the Haramiyidae are very different from those of earliest Theria. The other line of evidence against multituberculate-monotreme relationship comes from studies of the brain structure. New, mostly unpublished as yet, data on the monotreme cerebellum discussed in the next chapter, allies the monotreme brain to that of the modern Theria, while the cerebellum (and the brain as a whole) of multituberculates is very different from that of the earliest known therians. Another line of evidence is the postcranial skeleton, which is very different in monotremes and multituberculates. The extremely narrow multituberculate pelvis with the pubes and ischia fused into a strong ventral keel characteristic of *Kryptobaatar* (Kielan-Jaworowska, 1979) has been found in Paleocene North American multituberculates (Krause and Jenkins, 1983) and in several Asian genera (Kielan-Jaworowska and Gambarian, in preparation). I regard this type of pelvis, unknown in other groups of mammals, as a multituberculate apomorphy; it is very different from the pelvis of monotremes, where in relation to the oviparity the pelvis is very wide and the ischial arch is U-shaped. The multituberculate pectoral girdle (Serenio and McKenna, 1990; Kielan-Jaworowska and Gambarian, in preparation) is also specialized and very different from that of monotremes.

Incidentally Wible (1991, Fig. 4) in the paper published coeval with that of Wible and Hopson (in press), using a PAUP analysis of craniodental characters, no longer united the Multituberculata and Monotremata, but placed the Multituberculata and the Haramiyidae at a separate node between the Morganucodontidae, *Dinnetherium* and *Kuehneotherium* below and Monotremata and *Vincelestes* above.

A third manually produced cladogram of early mammals was published about the same time by Mjao (1991, Fig. 1). Here Multituberculata is placed between the advanced triconodonts below and the Kuehneotheriidae above, while Monotremata is placed between the Eupantotheria below and "tribotheres" above. This agrees generally with my idea on the relationships between the early mammals presented in Fig. 1, although the position of Multituberculata requires additional comments.

The problem is that the relationship of the oldest Multituberculata (Haramiyidae) to other early mammals has become even more controversial due to the discovery of the Theroteinidae (Sigogneau *et al.*, 1989), placed by Hahn *et al.* (1989) in Allotheria. The conclusion from this discovery was summarised by Lillegraven and Krusat (1991) as follows: "Hahn and others (1989), for example, suggested origin of the subclass Allotheria (order Multituberculata) from a lineage that has been distinct from other mammals at least since the Late Triassic. The dentition of the basal members of the lineage (Theroteinidae), which Hahn and others (1989) consider mammalian, is dramatically different in its arrangement of parallel rows of anteroposteriorly aligned cuspules from other, approximately contemporaneous, early mammals. The possibility exists, therefore, that allotherians had quite a different phylogenetic source from the group that we herein designated as 'mammals'."

It is interesting that such a conclusion was not drawn by the authors who placed the Theroteinidae in the Allotheria (Hahn, Sigogneau-Russell and Wouters, 1989), as Sigogneau-Russell (1989) admits that four of the haramiyid teeth in her collection support the opinion of Crompton (1974) that the Haramiyidae might have originated from the ancestral forms of the Morganucodontidae.

It follows that the following alternative should be considered: either the Theroteinidae are the earliest Allotheria and then this group must have originated separately from all other mammals, and thus mammals are polyphyletic; or the Haramiyidae might have originated from the ancestral forms of the

Morganucodontidae, and if so, there exists a possibility that mammals might be monophyletic.

## MIDDLE-LATE JURASSIC AND CRETACEOUS MAMMALS

### *Multituberculata and Triconodonta*

With regard to the multituberculates the most significant discovery from the phylogenetic point of view was the occurrence of three ear ossicles in the Paleocene multituberculate *Lambdopsalis* (Miao and Lillegraven, 1986). Numerous new Laurasian multituberculates have been described (see Kielan-Jaworowska and Ensom, 1992, for references concerning Late Jurassic and Early Cretaceous forms), but more important are the discoveries of the first multituberculates in Gondwanaland (Bonaparte, 1990; Sigogneau-Russell, 1991a). However, important as they are from the paleogeographic and taxonomic points of view, they do not contribute to a better understanding of the relationships of multituberculates with other mammals.

As far as triconodonts are concerned, the most important discovery appears to be the replacement of molariform teeth in the triconodont *Gobiconodon* from the Early Cretaceous Cloverly Formation of North America. As put by the authors of the discovery (Jenkins and Schaff, 1988, p. 21): "The surprising occurrence of replacing molariform teeth in *Gobiconodon ostromi* might be construed as evidence that this form was derived separately from all other known Mesozoic mammals, and in particular represents a survivor of that stage in the reptilian-mammalian transition in which primitive tooth replacement still occurred." Coeval with earlier mentioned findings of Early Jurassic mammals (Clemens, 1980; Jenkins *et al.*, 1983; Sigogneau-Russell, 1983; Datta, 1981; Crompton and Sun, 1985) the new finding led Jenkins and Schaff to conclude (1988, p. 21): "As a consequence, the previously held interpretation that the initial radiation of mammals involved a simple dichotomy between morganucodontids and kuehneotheriids no longer appears plausible." However, in the present state of knowledge no reconstruction of a detailed phylogeny of Triconodonta has been attempted.

### *Early Theria, Monotremata and Dryolestoidea*

Many discoveries of the last decade dramatically changed the picture of therian phylogeny (Fig. 1). Chow and Rich (1982) described from the Jurassic of China *Shuotherium*, a lower jaw with primitive therian-like teeth, with a "talonid" situated in front of the trigonid, and regarded it as a fairly advanced, although aberrant therian. Kermack *et al.* (1987) described *Simpsonodon*, a docodont that possesses a talonid-like structure placed anteriorly in the lower molars, and concluded tentatively on this basis that *Shuotherium* might also be a docodont. Although inconclusive, it seems to me more probable that the molars of *Shuotherium* may have developed from those of the symmetrodonts, and I place *Shuotherium* in Fig. 1 as a side branch of symmetrodonts.

Most important among the new findings of the therians are: the discovery of a partial lower jaw with teeth of an Early Cretaceous monotreme *Steropodon* from Australia (Archer *et al.*, 1985; Kielan-Jaworowska *et al.*, 1987) and the discovery of a diversified mammalian fauna, including among others specialized



dryolestoids (eupantotheres) in the Late Cretaceous of Argentina (Bonaparte, 1990 and references therein; Rougier and Bonaparte, 1988).

The teeth of *Steropodon*, although similar to those of Miocene *Obdurodon* and modern juvenile *Ornithorhynchus*, possess a distinct trigonid similar to that known only in Theria and a specialized, two-cusped talonid. On this basis Kielan-Jaworowska *et al.* (1987) suggested that the monotreme line diverged from the main therian line at an eupantothere level of evolution during the Late Jurassic. In the present paper I place (Fig. 1) the point of monotreme-eupantothere divergence earlier, somewhere at the boundary between the Early and Middle Jurassic for reasons discussed below. (Regarding eupantotheres: though McKenna, 1975 and Prothero, 1981 suggested that Eupantotheria is a paraphyletic group and should not be used, I continue to refer to eupantotheres in the present paper, since introducing in a review paper, as the present one, new names proposed by these authors and not generally accepted may only add to the confusion.)

The Multituberculata, Triconodonta and Docodonta differ from extant Theria in having a straight (uncoiled) cochlea. In monotremes the cochlea is bent, but not coiled. In remarkably well preserved skulls of the dryolestoid eupantothere *Vincelestes* from the early Late Cretaceous of Argentina the cochlea is coiled through 270° (Rougier, 1990) and appears to be intermediate between that of the monotremes and therians. As the oldest dryolestoids are known from the Bathonian (Lillegraven *et al.*, 1979), they had to branch off from pre-peramuran eupantotheres sometime at the boundary between the Early and Middle Jurassic. In the common ancestor of the Dryolestoidea and Peramura (or other non-tribosphenic Eupantotheria) the cochlea possibly started to coil. As it is bent but not coiled in Monotremata, it appears that the Monotremata possibly diverged from the main therian line before the dryolestoids did.

Kemp (1982, 1983) cited several synapomorphies of Monotremata and modern Theria. To this I would add data on brain structure, supporting a relationship between monotremes and therians. Two types of brains occur in Mesozoic mammals (Kielan-Jaworowska, 1986), designated: the cryptomesencephalic type, characteristic of Multituberculata and Triconodonta (very large vermis, no dorsal midbrain exposure, and no cerebellar hemispheres); and eumesencephalic type, characteristic of Cretaceous Tribosphenida (wide cerebellum, cerebellar hemispheres and large dorsal midbrain exposure).

The brain of modern monotremes is specialized, and there is no midbrain exposure, as in most extant Theria. However, in spite of statements in classical textbooks of neuroanatomy (e.g. Ariëns Kappers *et al.*, 1960) that the monotreme cerebellum differs notably from that of other mammals, the difference is smaller than previously thought. The lateral parts of cerebellum in *Tachyglossus* are currently identified as cerebellar hemispheres (although they are poorly demarcated from the vermis); there is a large paraflocculus and very small flocculus. In *Ornithorhynchus*, the brain of which differs from that of *Tachyglossus*, there are still clear cerebellar hemispheres, paraflocculus and flocculus (Holst, 1986, and personal communication from Prof. Wally Welker—letter of 25 May, 1990). It follows that brains of monotremes, especially *Tachyglossus*, are more therian-like than multituberculate-like.

#### *Metatheria, Eutheria and Related Forms*

A recent discovery helped to clarify the systematic position of the group of carnivorous Cretaceous mammals with tribosphenic dentition, the Delatheroidea,

known from Asia and North America. Kielan-Jaworowska and Nessov (1990) demonstrated that the Deltatheroidea have at least incipient allsphenoid bulla, which is a metatherian apomorphy, and placed the Deltatheroidea in Metatheria, as the sister group of the Marsupialia.

Until recently *Aegialodon* from the Early Cretaceous (Wealden) of Great Britain (Kermack *et al.*, 1965) was regarded as the earliest known mammal with tribosphenic molars and as a common ancestor of both the Metatheria and Eutheria. New studies (Marshall and Kielan-Jaworowska, in preparation) induced us to believe that Aegialodontia (*sensu* Butler, 1990) may be the ancestors of Metatheria, but not of Eutheria (Fig. 1). We also believe that the South American Borhyaenoidea are closely related to Deltatheroidea. If deltatheroids are metatherians, then the differentiation of the stocks which gave rise to metatherians and eutherians apparently occurred in Late Jurassic or Early Cretaceous time, as also suggested by Lillegraven *et al.* (1987), but *contra* an earlier, elegant hypothesis of Lillegraven (1974).

The eupantotherian ancestor of Eutheria is still to be found. Recently Sigogneau-Russell (1991b), reported the discovery of a tribosphenic molar *Tribotherium* in the earliest Cretaceous (Berriasian) of Morocco. *Tribotherium* is thus the oldest known tribosphenic molar, older but more advanced than *Aegialodon*, and is in my opinion possibly a eutherian. This discovery supports an earlier division of the Metatheria and Eutheria than previously thought.

Aegialodontia, Deltatheroidea and several other Cretaceous mammals with tribosphenic molars were often placed together in an informal unit "Theria of metatherian-eutherian grade" (e.g. Lillegraven *et al.*, 1979). If we remove Aegialodontia and Deltatheroidea from this informal unit, there remains a large group of Early and Late Cretaceous "tribotheres" (Fig. 1), whose relationships with the Metatheria and Eutheria remain unclear (Butler, 1978, 1990; Fox, 1975, 1980; Clemens and Lillegraven, 1986).

Knowledge of the evolution of Cretaceous Eutheria recently increased due to collection of Cenomanian, Turonian, Judithian and Campanian mammals from Utah assembled by Cifelli and Eaton (see Cifelli, 1990 for references), and especially due the collection of Early and early Late Cretaceous mammals accumulated from Uzbekistan and Kazakhstan (Nessov, 1987 and references therein; Nessov and Kielan-Jaworowska, 1991). Only a small part of this latter collection has been described so far. In most Cretaceous localities in the Northern Hemisphere the multituberculates dominate. In contrast, in Uzbekistan and Kazakhstan, in sections ranging from Late Albian through Late Santonian or ?Early Campanian, the multituberculates were found only in Late Turonian and Coniacian and are extremely rare (four specimens in a collection of over 400 mammal specimens).

#### *Laurasia/Gondwana Connections*

As may be seen in Fig. 1, the Dryolestoidea survived until the Late Cretaceous (Campanian). The Campanian dryolestoids are known from the Argentinian Los Alamitos Formation. In contrast to the conditions in Laurasia, there are no mammals with tribosphenic molars in the pre-Maastrichtian Cretaceous of Argentina. These mammalian faunas are dominated by dryolestoids, triconodonts, symmetrodonts, rare multituberculates, and a hypsodont family Gondwantheriidae recently assigned also to the multituberculates (Krause and Bonaparte, 1990). The comparison of mammalian and dinosaurian Late Cretaceous faunas of Laurasia

and Gondwana led Bonaparte and Kielan-Jaworowska (1987, p. 24) to conclude that: "... Cretaceous tetrapods from Laurasia and Gondwana evolved in isolation, thus giving rise to vicariant adaptive types on both supercontinents."

The earliest mammals with tribosphenic molars known until recently from Gondwanaland (Peru and Bolivia—see Marshall *et al.*, 1985 and Van Valen, 1988 for references, and from India, see Prasad and Sahni, 1988) were of Maastrichtian or Paleocene age. Bonaparte (1986) suggested that they may represent Latest Cretaceous immigrants from Laurasia. However, the above mentioned discovery of a tribosphenic molar *Tribotherium* in Berriasian of Morocco changes this paleobiogeographic picture. As put by Sigogneau-Russell (1991b), there must have existed at least occasional paleogeographic connections between Laurasia and Gondwana during the Late Jurassic.

### *Molecular Clock*

Attempts at reconstructing mammalian phylogeny using a molecular clock (see, e.g., McKenna, 1987 and references therein) cannot be of a great help in reconstructing the relationships of Mesozoic mammals most of which belong to extinct groups.

## MAMMALIAN ANCESTRY

It is not known which cynodont family was ancestral to mammals, or whether all the mammals originated from the same group (family) of cynodonts. In the vast literature concerning mammalian origins, it is easier to find suggestions that one or the other therapsid or cynodont family cannot be ancestral to the Mammalia, rather than to find a positive answer.

An exception is Hopson and Crompton paper (1969, p. 67) in which it is stated: "... the close resemblance between cheek teeth of the early cynodont *Thrinaxodon* and the molars of *Eozostrodon* [=*Morganucodon*] suggests derivation of mammals from persisting members of the Family Galesauridae." The discovery of *Probainognathus* (Romer, 1970) induced, however, Crompton to change his opinion, as in the paper with Jenkins (Crompton and Jenkins, 1979, p. 72) they state: "The earliest mammals were cynodonts' descendants, very probably from a form allied to *Probainognathus*". Similarly Hopson, in his later papers, was more reluctant in pointing out the direct cynodont ancestor of the Mammalia. Hopson and Barghusen (1986, Fig. 12) placed Mammalia as a sister group of the Ictidosauria, originating from an unknown ancestor, characterized by a suit of characters common to both groups. In his thorough review of synapsid relationships Hopson (1991) stated: "On the basis of the total information available (both published and unpublished) on tritheledontids [=Ictidosauria], especially that on the postcranial skeleton, the most parsimonious conclusion as to their relationship is that they are closer to mammals than is any group of 'typical' Triassic cynodonts. However, when the tritylodontids are brought into the picture, a tritheledontid-mammal clade indeed must be considered tentative as Kemp and Rowe pointed out. ... In other words, I believe it possible that a sister-group relationship between *any* of two of these three taxa might be given an equally convincing defense." See also Hopson's review of earlier opinions on this subject, especially of Kemp (1982, 1983, 1988a, 1988b) and Rowe (1988).

Recently Shubin *et al.* (1991) on the basis of new tritheledontid material from

the Early Jurassic of Nova Scotia (Canada) provided additional arguments that the Tritheledontidae is a sister group of Mammalia. They claimed that the Tritheledontidae shares with mammals the dentary-squamosal jaw joint, and if this is true the latter feature cannot be regarded any more as a mammalian apomorphy.

It should be pointed out that Crompton and Jenkins (1979) and many other students when discussing mammalian origins excluded the Haramiyidae from consideration, as a poorly known group of unknown affinities, while Kemp (1982, Fig. 104) was unable to place this taxon in a cladogram of cynodonts and early mammals with any certainty and merely located the Haramiyidae with a question mark near his cladogram.

Hahn (1973) demonstrated that the teeth of the Haramiyidae are very different from those of the Traversodontidae. Sigogneau-Russell (1989) discussed the idea of Kemp (1982) that the ancestral forms of the Haramiyidae and Moganucodontidae may be close to the Tritheledontidae (Ictidosauria). However, she pointed out that such ancestral form cannot originate from the Ictidosauria, as ictidosaurians acquired a more advanced prismatic enamel than that of the Haramiyidae (Grine *et al.*, 1979; Frank *et al.*, 1984). It is now accepted by many authors (e.g. Kemp, 1982, but not 1988a; Jenkins, 1984; Hopson and Barghusen, 1986; Hopson, 1991, but see the quotation from Hopson's paper above) that mammals are a sister group of the Ictidosauria. It is still, however, to be demonstrated which cynodont family (families?) was (were) ancestral to mammals.

## CONCLUSIONS

In Fig. 1, an attempt to reconstruct the temporal distribution and relationships of Mesozoic mammals is presented. I should make it clear that this family tree should not be read as a cladogram and the placement of the particular mammalian lines from left to right does not imply a phylogenetic relationship between them.

It appears from the summary presented in previous sections that at the present state of our knowledge on Late Triassic mammals, it is impossible to demonstrate unequivocally whether mammals as traditionally defined are monophyletic or polyphyletic. The question mark at the bottom of the family tree in Fig. 1 implies this doubt as well as the uncertainty concerning the interrelationships of the earliest mammals. Much depends on the positions of the Haramiyidae and Therapsididae and their relationships to the Morganucodontidae and Kuehneotheriidae.

Most students of multituberculates believe now that the Haramiyidae belongs to the Multituberculata. If so, the multituberculates branched off very early from the main mammalian stock and acquired many characters in parallel to the triconodonts and therians, including the acquisition of three ear ossicles (Miao and Lillegraven 1986; Allin, 1986) and of viviparity shared with modern Theria (Kielan-Jaworowska, 1979).

If the characters cited above as mammalian apomorphies (most important of which appears to be an acquisition of the dentary/squamosal joint) were acquired by the common ancestor of the multituberculates, triconodonts and therians somewhere in the Norian time (if *Thomasia* as discussed above is a multituberculate), and if such an ancestor was already a mammal, then mammals are monophyletic. If, however, such a common ancestor would not have mammalian synapomorphies and would turn out to be a cynodont, then the

characters cited above as mammalian synapomorphies had to be acquired independently at least twice (in multituberculates and in the triconodont/therian lineage), and mammals are polyphyletic (at least diphyletic).

One might also foresee a less probable possibility, that if more haramiyid material is accumulated, and complete skulls are found, it may appear that the haramiyoids are not multituberculates, but specialized cynodonts, and if so, the ancestors of multituberculates are to be sought among, e.g. the triconodonts or early therians. In such a case it would probably be possible to demonstrate that mammals are monophyletic, as there are no doubts that Theria are monophyletic, and a close relationship of the earliest Theria and earliest triconodonts has not been questioned.

In the last decade several papers concerning origins of mammals and interrelationships of early mammals were published, many of them including cladograms (e.g. Kemp, 1982; Crompton and Sun, 1986; Hopson and Barghusen, 1986; Rowe, 1988; Hopson, 1991; Miao, 1991; Lillegraven and Krusat, 1991; Wible and Hopson, in press; Wible, 1991).

It is interesting that in the lists of character states used to construct all these cladograms the brain structure has (with one exception) not been used. Rowe (1988) used a character of midbrain size that Wible (1991) subsequently eliminated from his analysis due to the ambiguity in the character description. I strongly believe that brain structure has been overlooked by previous researches. Studies on endocranial casts of Mesozoic mammals, may, in fact, bring important information on their relationships and it would be desirable if such research would be performed in the future on a larger scale than hitherto done.

## EPILOGUE

As may be seen in Fig. 1 there are still many blank spaces and question marks concerning the phylogeny and relationships of Mesozoic mammals. Nevertheless the data accumulated since the last summary of knowledge on Mesozoic mammals (Lillegraven *et al.*, 1979) have changed dramatically our understanding of early mammal evolution.

In the era when desk and computer palaeontology became more and more fashionable, I still regard among the most important achievements of the discussed period the accumulations of new collections, assembled by industrious and determined colleagues searching over the years for early mammals, studies of which have already changed or will change in the future our picture of early mammal evolution.

I consider of most significance: a very important collection of Late Triassic mammals from France and Belgium collected by Dr Denise Sigogneau-Russell and co-workers, during several years of meticulous work; a rich collection of Cretaceous mammals from Argentina (the first significant collection of Cretaceous mammals from Gondwanaland) assembled by Dr Jose F. Bonaparte with great drive during years of field work in Patagonia; and the first collection of Mesozoic mammals from the territory of the Soviet Union, assembled with great effort under very difficult field conditions by Dr Lev A. Nessov in desert regions of Uzbekistan and Kazakhstan.

### Acknowledgements

I thank Drs Desui Miao, Denise Sigogneau-Russell and John R. Wible for reading the manuscript and providing useful comments. W. A. Hopson, J. A. Lillegraven, D. Miao, D. Sigogneau-Russell and J. R. Wible sent manuscripts of their unpublished papers and allowed me to cite them. M.-C. Holst and W. Welker provided important information on the structure of cerebellum in extant mammals. This study was supported by Norges Allmenvitenskapelige Forskningsråd, grant no. ABC/RL 441, 91/003.

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## ADDENDUM

After the present paper was submitted for publication I read the paper by Lucas and Hunt (1990), in which the authors describe the braincase of an apparent mammal *Adelobasileus cromptoni* (order and family *incertae sedis*), from the

Late Carnian of Western Texas. If *Adelobasileus* is indeed a mammal, then one should agree with the authors that mammals are 5–10 million years older than previously suspected.

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