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A short review of studies on cynodonts

Bernard BATTAIL[1]

Abstract. The cynodonts, a diversified group of advanced therapsids which appeared in the fossil record at the end of the Permian, constitute an important component of many Triassic and Early Jurassic terrestrial ecosystems. It seems now generally accepted that the cynodonts are the sister-group of the therocephalians, and that they include the mammals as a derived subgroup, but many aspects of their phylogeny still remain a matter of debate. The problem of the relationships of the various families of advanced cynodonts to mammals, in particular, is far from being solved. Progress in the knowledge of the group, though very significant, has also been very unequal: many small forms, in particular, are known up to now only by rare and often incomplete specimens. A better understanding of the group will require more field work and new discoveries. This paper is a short account of studies on the phylogeny of cynodonts; it is an attempt to point out what has already been clearly established, and what remains obscure or controversial.

Key words. Cynodontia. Therapsida. Triassic. Phylogeny.

Introduction: what is a cynodont?

The Cynodontia were erected in 1860 by Richard Owen as a subdivision of the order Anomodontia, which included, at that time, all kinds of therapsids. Originally, the cynodonts accomodated only *Galesaurus* and *Cynochampsa laniaria* Owen, the latter form being represented by a badly preserved specimen, now considered as a probable *Diademodon*.

Later, in his "Description of the fossil Reptilia of South Africa in the collection of the British Museum", published in 1876, Owen clearly separated the forms with reduced dentitions, still called the Anomodontia, from the forms with dentitions of the carnivorous type, called the Theriodontia; the Cynodontia were no longer kept as a distinct group within the Theriodontia, to which Owen attributed various forms known today as gorgonopsians, therocephalians and cynodonts, and also, obviously by mistake, the parareptile *Procolophon*.

As early as 1890, Seeley pointed out the heterogeneous nature of the theriodonts as defined by Owen, and, in 1895b, he gave the first modern definition of the cynodonts, then understood as a subgroup of the theriodonts: "This name was originally used, by Sir R. Owen, for the division of the Anomodontia of which *Galesaurus* is the type. Subsequently, Theriodontia was defined, so as to be co-extensive with the older Cynodontia, both groups being based upon a type of dentition, which approximates to that of Carnivorous Mammalia. The name Theriodontia, hence, has some appearance of being a synonym of Cynodontia. The group Theriodontia is obviously a larger group than the original Cynodontia, since its type, *Lycosaurus*, has simple pointed molar teeth, and it also includes *Nythosaurus* and *Scaloposaurus*, in which the molar teeth are laterally cuspidate. The Theriodontia include the Cynodontia, because the cynodont genera were grouped in this way by sir R. Owen, and because there is no evidence of ordinal difference in the skull. The Cynodontia is conveniently distinguished from the Lycosauria by dental, and other minor characters of the skull; and I propose to use the name Cynodontia for animals which resemble *Galesaurus* in skull structure, and resemble *Nythosaurus* in the type of molar teeth. The crowns of the cheek teeth not being preserved in, I take *Cynognathus*, the genus now to be described, as the type of the group, which will be thus defined and limited. (...)" (Seeley, 1895b, p. 59).

However, as Seeley had put special emphasis in the definition of the cynodonts, on their carnivorous dentition, he erected another group, called the Gomphodontia, to accomodate such forms like *Diademodon*, *Trirachodon* and *Tritylodon*, in which the postcanine teeth are expanded transversely. He admitted, nevertheless, that the Cynodontia and the Gomphodontia were closely related. "So far as is known, there is no fundamental difference in the

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[1] Laboratoire de Paléontologie, Muséum national d'Histoire naturelle. 8 rue Buffon, 75005 Paris, France.

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skeleton to separate the Gomphodontia from the Cynodontia, which may be regarded as related in the same way as are groups of Marsupials with similarly differing dentitions." (Seeley, 1895a, p. 2).

The next major contributor to the knowledge of cynodonts is Robert Broom, who wrote a number of papers on mammal-like reptiles during the end of the nineteenth century and the first half of the twentieth century. In his well known book, "The mammal-like reptiles of South Africa and the origin of mammals", published in 1932, Broom gave a detailed account of the anatomical features of the cynodonts, understood as including the gomphodonts. From the cynodonts, however, Broom excluded what he had called the Ictidosauria, represented by poorly known, very advanced theriodonts, and *Tritylodon*, which he considered to be an early mammal.

By 1950, a considerable number of specimens had already been collected and described from the Karoo beds, and progress had been made in the knowledge of similar faunas in Russia and in South America (Argentina and Brazil); a few tritylodonts had been discovered in Europe and in China; therefore, the time had come for general syntheses. In 1954, Haughton and Brink published "A bibliographic list of Reptilia from the Karoo beds of Africa", in which the ictidosaurians of Broom as well as *Tritylodon* were considered to be advanced cynodonts. However, two years later, in 1956, Watson and Romer presented "A classification of therapsids" where the ictidosaurians had reappeared, but with a broader definition, as they included also *Tritylodon*.

The two specimens of "ictidosaurians" which had been only briefly mentionned, and not named, by Broom, became better known after their detailed description by Crompton in 1958 and 1963. Crompton called them *Diarthrognathus*, as he believed that they had a double cranio-mandibular articulation, reptilian and mammalian; he made a comparison between *Diarthrognathus* and the tritylodonts, and pointed out many differences between the two groups. At that time, Crompton considered that *Diarthrognathus* might have evolved from scaloposaurians, whereas the tritylodonts were specialised cynodonts, and should therefore be excluded from the ictidosaurians.

During the sixties and seventies, many new cynodonts were found in South America (Argentina and Brazil); they were described mainly by Bonaparte, by Barberena and by Romer. Among the new forms, three very advanced ones can be mentioned: *Probainognathus*, a carnivorous form which was thought by Romer (1969c, 1970) to have a double cranio-mandibular articulation, *Chaliminia* Bonaparte, 1978, apparently very close to the South African genus *Diarthrognathus*, and *Therioherpeton* Bonaparte et Barberena, 1975, presented as a possible mammalian ancestor. A few new forms were also found in Russia and in China. In the Lower Triassic beds of Antarctica several cynodont specimens which could be attributed to species already known from South Africa were discovered. During the same period new studies dealing for example with functional anatomy of the jaws were also developed (Crompton, 1963a, Barghusen, 1968), tooth replacement (Crompton, 1963b), anatomy of the postcranial skeleton (Jenkins, 1971), growth series and intraspecific variability (Grine *et al.*, 1978).

At the beginning of the eighties came a major change in phylogenetic concepts with the development of cladism. Kemp is, I think, the first person who published cladograms of therapsids, in his book " Mammal-like reptiles and the origin of mammals", dated 1982. Kemp's cladograms were however not accompanied with detailed lists of characters, and were therefore difficult to analyse and to criticize. Soon afterwards, in 1986, Hopson and Barghusen, in their "Analysis of therapsid relationships", gave a diagnosis of the cynodonts based on 28 synapomorphies. In my opinion, some of the apomorpies listed by Hopson and Barghusen are debatable ("incisors spatulate", for example), and some others are difficult to take into consideration, as they deal with bone proportions rather than with anatomical structures ("reflected lamina of angular greatly reduced in size", for example); most of them, however, seem very reliable, particularly the following ones (non-exhaustive selection): fossa on dorsolateral surface of coronoid region of dentary for insertion of portion of *musculus adductor mandibulae externus*; posterior half of nasal bone expanded at expense of facial portion of prefrontal so that nasal contacts lacrimal and excludes prefrontal from contact with maxilla; lateral flange of prootic expanded anteroposteriorly and contacts quadrate ramus of epipterygoid; postorbital and prefrontal bones meet on orbital margin and exclude frontal bone from orbital rim; occipital condyles double; supraoccipital bone narrow, excluded from posttemporal fossa by expanded tabular bone; well-developed palatal processes formed by palatines as well as by maxillae; jugular foramen faces ventrally rather than posteriorly; frontal contacts epipterygoid; posterior part of dentary elongated to broadly overlap the surangular; postfrontal bone lost; teeth on pterygoid bone lost.

As defined by Hopson and Barghusen, the cynodonts include the mammals and the ictidosaurs, considered as sister-groups, on the one hand, and the tritylodonts, classified with the gomphodont cynodonts in a superfamily Tritylodontoidea, on the other hand. Indeed, without the mammals, the cynodonts would become a paraphyletic group. And consequently, in all subsequent works, no clear-cut limit is drawn between cynodonts and mammals: in Rowe (1988) and in Wible (1991), a clade called the Mammaliamorpha includes the tritylodonts and a clade Mammaliaformes, the latter being composed of various forms formerly considered as early mammals, and of a clade Mammalia restricted to the Monotremata and Theria.

Cynodont origins

The cynodonts are the last major group of therapsids to appear in the fossil record, as their first known representatives are from the uppermost Permian of South Africa and Russia. In precladistic times, it was a common attitude to look for direct ancestors, and, quite naturally, most scientists considered that such ancestors could be found within earlier groups of theriodonts, either the gorgonopsians, or the therocephalians. This point of view is well summarized by Romer (1969b), who wrote: "In earlier decades, the Gorgonopsia were rather generally thought to be cynodont ancestors. Such ancestry was long favored by Watson (1920, 1951). In a number of regards, the gorgonopsians represent a primitive morphological stage antecedent to that of the cynodonts (and, as a minor point, are the only therapsid group apart of the cynodonts in which the primitive 2.3.4.5.3 phalangeal formula is known to have been retained). But there are few indications among gorgonopsians of any trend toward a cynodont condition; the gorgonopsians seem to have been, so to speak, 'frozen' in a primitive theriodont morphological pattern, and, in addition, universally retain such gorgonopsian 'trademarks' as a preparietal bone and a reduced cheek tooth series".

"If the gorgonopsians are excluded, where can we turn? In recent decades the Therocephalia, or rather that advanced series of therocephalians termed the 'scaloposauroids' (which Watson and I preferred to group with their Triassic descendants, the Bauriamorpha), have been favored as cynodont ancestors. The scaloposauroids show various advanced characters. The skull is lightly built, there is a trend toward a secondary palate, the dentary is well developed, and so on. These trends lead toward the advanced condition seen in *Bauria*; but, it has been suggested, may there not have been a second advanced line leading to the cynodonts? To be sure, most scaloposauroids tend to be long-snouted forms with a long tooth row, with, in general, little differenciation of canines, and with the characteristic therocephalian-bauriamorphan 'trademark' of large palatal vacuities. However, reversal in such features might have occured and if transitional forms were to be found, belief in a scaloposauroid ancestry of the cynodonts would attain credibility". (Romer, 1969b, p. 19-20).

Indeed, in 1961, Brink had described, under the name *Scalopocynodon gracilis*, a form which he considered as a primitive cynodont with therocephalian-like features. But, as pointed out by Romer, 1969b, the therocephalian-like features listed by Brink are in fact archaic therapsid characters also retained in therocephalians, and not proper therocephalian characters. It must be added that the type and only specimen of *S. gracilis* was studied by serial grinding, and cannot consequently be re-examined.

In 1972, Kemp made a comparative analysis of cranial anatomical characters in various groups of therapsids (eotheriodonts, pristerognathids, scaloposaurs, whaitsiids and cynodonts). In his conclusions, he expressed the hypothesis that "cynodonts arose from therocephalians, and that among the latter the whaitsiids are the closest known forms to the actual cynodont ancestor (...)." But, he wrote, "... despite the similarities between whaitsiids and cynodonts, the known whaitsiids themselves cannot be seriously considered as cynodont ancestors because of their possession of several peculiarities which in no way anticipate the cynodont structure." And that is, indeed, the main weakness of Kemp's hypothesis, a weakness which he himself perceived, as he wrote ten years later: "Among the known therocephalians, the whaitsiids are possibly the closest to the cynodonts for they have a very broad, cynodont-like epipterygoid involved in the side wall of the braincase, and reduction of the suborbital vacuity. However, more primitive whaitsiids such as *Moschowhaitsia* (Tatarinov, 1963, 1964) still have a suborbital vacuity, and therefore this character at least may have changed independently in cynodonts and advanced whaitsiids. Certainly, the whaitsiids have a number of specialisations indicating that a common ancestor between them and cynodonts could not have advanced much beyond a fairly generalised therocephalian-like form". (Kemp, 1982, p. 182).

In other words, the quest for the missing link had failed again. Soon afterwards, however, with the development of cladism, ancestors were no longer actively sought; instead, attempts were made to determine sister-groups on the basis of synapomorphies, which in turn could be considered as the essential features of the unknown common ancestor.

In their analysis of therapsid relationships, published in 1986, Hopson and Barghusen consider the cynodonts as the sister-group of the therocephalians. Their view is supported by a rather convincing list of eleven synapomorphies. They note: "Kemp (1972) has presented a detailed argument for the sister-group relationship of cynodonts and whaitsiids. The present analysis indicates that of the seven apomorphies shared by cynodonts and whaitsiids, only two are unique to these groups: (1) epipterygoid greatly expanded anteroposteriorly, and (2) sagittal crest extending far forward to incorporate the parietal foramen. (...) For cynodonts to be considered the sister-group of whaitsiids, the seven presumed synapomorphies would have to be balanced against a total of ten to twelve convergences of whaitsiids with other therocephalian groups, or reversals in the ancestral cynodont to a pretherocephalian condition (...). Derivation of cynodonts from baurioids (as suggested by Brink, 1961), or from any other therocephalian group, would involve equally great numbers of convergences or reversals relative to synapomorphies. Parsimony dictates that cynodonts be regarded as having a sister-group relationship with the Therocephalia as a whole rather than with any subgroup of therocephalians" (Hopson and Barghusen, 1986, p. 98, 100).

Cynodont diversity

Cynodont diversity can be appreciated at two different levels, systematic and phylogenetic.

Indeed, many -and certainly, too many- genera and species were created by ancient authors: in South Africa, for example, Broom described almost every newly collected specimen, whether well preserved or not, as the type of a new species. In their "Bibliographic list of Reptilia from the Karroo beds of Africa", published in 1954, Haughton and Brink had listed seventy species of cynodonts, belonging to forty-three genera. Among these taxa, only fourteen species and thirteen genera were still acknowledged as valid by Hopson and Kitching (1972). A similar trend occurred also in the rest of the world, and particularly in South America: "splitters" had been succeeded by "lumpers". The new tendency could easily be justified: many of the ancient type specimens were very incomplete or badly preserved, and therefore did not display diagnostic features; in addition, intraspecific variability had often been ignored, so that, for example, juvenile and adult individuals of the same species had sometimes be described as separate taxa. It must be added, however, that some of the synonymies that have been proposed in recent years are weakly supported, and, consequently, debatable.

The fact remains that cynodonts are remarkably variable in sizes, skull proportions, postcanine tooth structure, etc., which led to the definition of a large number of families, the phylogenetic relationships of which remain, to a certain extent, open to discussion.

For the sake of convenience, we shall examine here the various groups of cynodonts following the stratigraphic order of their first appearence.

Early cynodonts (Late Permian)

Early cynodonts are known mainly from South Africa (procynosuchids) and from Russia (dviniids). One of the major questions regarding the early cynodont families could be the following: which one is the plesiomorphous sister-group of all other cynodonts? According to Kemp (1982), Hopson and Barghusen (1986), Kemp (1988), and Hopson (1991), the dviniids are the sister-group of all other cynodonts. However, it seems to me that the four characters which Hopson and Barghusen (1986) retain as primitive features are all related to the light build of the skull, and are not necessarily plesiomorphous features. It must be stressed, in addition, that the known cranial material of dviniids is limited to two poorly preserved skulls (one of them only with its lower jaw), and an isolated maxilla, all attributed to *Dvinia prima* Amalitzky: many features of *Dvinia* remain unclear, and can be diversely interpreted.

Most specimens of procynosuchids are known from southern Africa. However, remains of *Procynosuchus* have been found in Germany (Sues and Boy, 1988), and a form closely related to *Procynosuchus* has been described from Russia (Tatarinov, 1987).

One word must be said also of the "silphedestids" *Silphedestes* Broom, 1949 and *Silphedocynodon* Brink, 1951, known by tiny, poorly preserved specimens from South Africa. They are considered by Hopson and Kitching (1972) as juvenile individuals of the procynosuchid *Procynosuchus*. One can however notice the absence of lingual cingula on the postcanines of *Silphedestes*, whereas lingual cingula are developed on the postcanines of *Procynosuchus*. Hopson (1991) argues that it can be considered a juvenile feature. I have examined a series of indisputable procynosuchids, and noticed that lingual cingula are relatively better developed in the smaller specimens; that makes me doubt very much that the "silphedestids" are juvenile procynosuchids. But better material would be needed to express a reliable hypothesis about what they really are!

Unspecialized cynodonts of the Late Permian-Early Triassic

These are represented by small forms which are slightly more advanced than the early cynodonts: the precanine teeth are lost, the number of incisors is reduced, the coronoid process of the dentary is higher and the masseteric fossa is larger, the quadrate is smaller and the interpterygoid vacuity is reduced or absent. Sometimes all have been attributed to only one family, either called the thrinaxodontids (*sensu lato*) (Watson and Romer, 1956, for example), or the galesaurids (*sensu lato*) (Kemp, 1982, for example). They are now usually split into two families, the galesaurids (*sensu stricto*) and the thrinaxodontids (*sensu stricto*). The galesaurids retain a plesiomorphic feature, a cleft in the secondary palate, and are characterized by the loss of cingulum cusps on the postcanine teeth. The thrinaxodontids have a complete osseous secondary palate.

Galesaurids and thrinaxodontids are essentially represented in southern Africa; however, *Thrinaxodon* is also known from Antarctica, and *Nanocynodon seductus* Tatarinov, 1968, from Russia, is probably a thrinaxodontid. In my opinion, the South American forms *Cromptodon mamiferoides* Bonaparte, 1972, and "*Thrinaxodon*" *brasiliensis* Barberena, Bonaparte et Texeira, 1987, should not be referred to the thrinaxodontids, but to the chiniquodontids (Battail, 1991a, 1991b).

Advanced cynodonts (Late Early Triassic, Middle and Late Triassic, Early Jurassic)

These include the cynognathids, the gomphodont cynodonts, and the chiniquodontids and probainognathids. Late, highly specialized cynodonts will be considered in the next section, dealing with the origin of mammals. Advanced cynodonts, called "post-thrinaxodontid cynodonts" by Hopson and Barghusen (1986), and named Eucynodontia by Kemp (1982), are characterized, according to Hopson (1991), by the following cranial synapomorphies: 1. Dentary greatly enlarged so that it closely approaches the jaw articulation and also forms a distinct posteroventral angular region. 2. Vertical portion of surangular and angular reduced in height, and postdentary series becomes more rodlike and obliquely oriented. 3. Reflected lamina of the angular further reduced in size from the primitive cynodont condition. 4. Quadrate ramus of the pterygoid greatly reduced or absent. 5. Secondary jaw articulation formed between the surangular and a flat facet on the descending flange of the squamosal. 6. The dentaries fused at the symphysis. 7. The pterygoids and basisphenoid forming an elongate ventral basicranial girder. 8. The paroccipital process with a posteroventral ridge behind the jugular foramen (forming a posterior wall to the middle-ear cavity).

Cynognathids

The cynognathids include only one genus, *Cynognathus*. They are mostly represented in southern Africa, but are also known in Argentina (Bonaparte, 1969); a fragmentary lower jaw of *Cynognathus* has also been recovered from Antarctica (Hammer *et al.*, 1990). Two main hypotheses have been expressed regarding the phylogenetic relationships of the cynognathids within the eucynodonts: they are usually considered either as the sister-group of all other eucynodonts (Kemp, 1982, 1988; Rowe, 1993) or as the sister-group of the gomphodonts (Hopson and Barghusen, 1986; Hopson, 1991). Hopson and Bargusen found only one synapomorphy of the cynognathids + gomphodonts: "jugal with descending flange on the anterior root of the zygomatic arch". I do not think that this character is of much value: it is only induced by an important development of the superficial masseter, and, as such, can appear independently in various forms; in addition, it is not known in small traversodontids such as *Rusconiodon* or *Massetognathus*. Later, Hopson (1991) introduced new synapomorphies of the cynognathids+gomphodonts, one of them being the specialized condition of the costal plates on the lumbar ribs, and three of them concerning the skull:

-"The posteroventral part of the zygomatic arch expanded laterally at, or behind, the level of the quadrate, giving the skull a triangular appearence in dorsal view and creating a broad anteroventral margin to the groove for the external auditory meatus". I think that this feature is rather a character of heavily built forms, not observed, for example, in the small traversodontid *Rusconiodon*;

-"The jugal portion of the zygomatic arch dorsoventrally expanded". This is equally true of many non-gomphodont eucynodonts, the chiniquodontids for example.

-"The internal carotid foramina absent". This character is difficult to deal with, as these foramina, when they exist, are always extremely small. I have observed, on several *Cynognathus* skulls, what could be tiny carotid foramina.

To sum up, I consider the hypothesis of the cynognathids as the sister-group of the gomphodonts as weakly supported.

Kemp (1982, 1988) interpreted the cynognathids as the sister-group of all other eucynodonts, based on the presumed synapomorphic status of the following characters of the latter: (1) the posterior part of the squamosal (lambdoidal crest) deeply incised to give a strong W-shaped occiput; (2) emarginated posterior edge of the coronoid process of the dentary; (3) snout constricted in front of the orbits, so the orbits tend to face more anteriorly; (4) ventrolateral edges of the parasphenoid slightly flared to produce parasphenoid alae (Kemp, 1988, p. 16).

In 1991a, I expressed yet another view regarding the phylogenetic relationships of the cynognathids: I considered them as the sister-group of the galesaurids, on the basis of two supposed synapomorphies: 1. Regression or disappearance of the incisure in the dorsal border of the squamosal between the occiput and the posterior root of the zygomatic arch. 2. Loss of the lingual cingula of the postcanines. This hypothesis presents however a major inconvenience: it implies that many characters (the development of the dentary, the reduction of the post-dentary bones, etc.) evolved independently, as convergences, in cynognathids and in other advanced cynodonts, which is improbable.

Gomphodont cynodonts

The gomphodont cynodonts (if restricted to the diademodontids, trirachodontids and traversodontids), appear as a relatively homogeneous group of herbivorous eucynodonts with laterally expanded, occluding postcanines. The families have been diagnosed on the basis of postcanine structure.

The diademodontids are essentially represented by the southern African genus *Diademodon*; many other genera were described in the past, but they can all be regarded as junior synonyms of *Diademodon*, with the exception of a giant form from Namibia, *Titanogomphodon* Keyser, 1973.

The trirachodontids include three genera, *Trirachodon* and *Cricodon* from southern Africa, and *Sinognathus* from China. The latter genus was described by Young (1959) as an early cynodont, but reinterpreted as a trirachodontid by Sun Ailing (Sun Ai-lin, 1988; Sun Ailing *et al.*, 1992).

The traversodontids are by far the most diversified family of gomphodont cynodonts, and they have also a very wide stratigraphic range, from the end of the Early Triassic to the end of the Late Triassic. Most taxa have been described from South America, Argentina and Brazil, initially by Huene, later by Cabrera, and then, by Bonaparte, Romer, and Barberena; a synthesis, with complete references, will be found in Bonaparte (1978); in more recent times, a number of papers, mostly dealing with early traversodontids, have been published by Goñi, Goin and Abdala (Goñi, 1986, Goñi and Abdala, 1988; Goñi and Goin, 1987, 1988, 1990). In Africa, traversodontids are known from South Africa, Lesotho, Zambia and Tanzania (Crompton, 1955; Crompton and Ellenberger, 1957; Brink, 1963; Kemp, 1980; Gow, 1993). A few forms have also been described from India (Chatterjee, 1982), from North America (Hopson, 1984; Sues and Olsen, 1990; Sues *et al.*, 1992, 1999), and from Europe (Tatarinov, 1973, 1974; Hahn *et al.*, 1988; Godefroit and Battail, 1997).

One of the problems concerning the traversodontids is their relationships to the highly specialized tritylodontids; as it will be seen below, three different hypotheses have been put forward: 1. The tritylodonts are not closely related to the traversodontids; 2. The tritylodontids are the sister-group of the traversodontids; 3. The tritylodonts are the sister-group of part of the traversodonts; and in that case, the traversodontids would no longer be a valid family, as they would become a paraphyletic group.

There is another puzzling question concerning the traversodontids; at first glance, they seem to evolve rather regularly from small forms (*Pascualgnathus, Andescynodon, Rusconiodon*, for example) to giant forms such as *Scalenodontoides, Exaeretodon* or *Ischignathus*. But, at the very end of the Triassic, tiny forms seem to appear suddenly in North America and in western Europe. They are unfortunately known by quite poor material: one maxilla in North America (the type-specimen of *Boreogomphodon jeffersoni* Sues et Olsen, 1990), and minute isolated postcanines in western Europe; their phylogenetic relationships to other traversodontids are still unclear.

Chiniquodontids and probainognathids

A close relationship between the chiniquodontids and the probainognathids is generally accepted, mainly on the basis of the long secondary palate characteristic of both. The probainognathids include only the genus *Probainognathus*, from Argentina. The chiniquodontids, more numerous and diversified, are considered, depending on the authors, either as exclusively south american, or as mainly South American (in the latter case, one or several southern African forms are included).

"Chiniquodontids are eucynodonts possessing sectorial postcanine teeth but retaining more primitive skull form than *Cynognathus*. They are characterized most readily by having a secondary palate that is broad posteriorly and extends behind the level of the last postcanine. However, the unique distinguishing feature of the family is the distinct angulation between the ventral edge of the zygomatic process of the maxilla and the anteroventral margin of the zygomatic arch" (Hopson, 1991, p. 673).

The main studies about chiniquodontids include: Huene (1935-1942: description of *Chiniquodon theotonicus* and *Belesodon magnificus*), Romer (1969a: new description of *Belesodon* and *Chiniquodon;* 1969b: description of *Probelesodon lewisi*; 1973: description of *Probelesodon minor*), Teixeira (1982: description of *Probelesodon kitchingi*), Martínez and Forster (1996: description of *Probelesodon sanjuanensis*), Abdala (1996: a synthesis on the systematics of chiniquodontids). The family is understood as composed only of South American forms with strictly sectorial postcanines by Abdala and Giannini; it is extended to *Aleodon*, from Tanzania, by Hopson and Kitching (1972), Hopson and Barghusen (1986), Hopson (1991) and Battail (1991a); to *Cromptodon*, by Hopson (1991) and Battail (1991a, 1991b); to "*Thrinaxodon*" *brasilien-*

sis and, with reservations, to *Cistecynodon* from South Africa by Battail (1991a, 1991b).

Probainognathus, initially described as a chiniquodontid by Romer (1969c), was attributed later to a distinct family, the Probainognathidae (Romer, 1973). Indeed, *Probainognathus* displays many progressive features; however, the mammal-like jaw articulation described by Romer is in fact an articulation between surangular and squamosal, as shown by Crompton, 1972.

The affinities of the chiniquodontids and probainognathids have been very diversely interpreted. Probainognathids are more often considered in phylogenetic reconstructions, probably because they are more "mammalian". The chiniquodontids and probainognathids have often be regarded as sister-groups (Hopson and Barghusen, 1986, and Kemp, 1988, for example). But Hopson (1991) writes: "I have not found any synapomorphies of Probainognathidae plus Chiniquodontidae and so no longer recognize the Chiniquodontoidea as a monophyletic taxon " (Hopson, 1991, p. 675).

Among the many hypotheses which have been proposed in the past fifteen years concerning the phylogenetic position of the chiniquodontids and probainognathids, one can select a few very different ones:

-The sister-families Chiniquodontidae and Probainognathidae are united in a superfamily Chiniquodontoidea; the Chiniquodontoidea are the sister-group of the Cynognathia (Cynognathidae+Tritylodontoidea, the latter including the gomphodonts and the tritylodontids) (Hopson and Barghusen, 1986).

-The sister-families Chiniquodontidae and Probainognathidae are the sister-group of a clade which includes the Tritheledontidae and the mammals, and perhaps also the Tritylodontidae (as the sister-group of the clade Tritheledontidae+mammals) (Kemp, 1988).

-The Chiniquodontidae (including *Probainognathus*) are the sister-group of the gomphodont cynodonts (including the Tritylodontidae) (Battail, 1991a).

-There is an unresolved trichotomy of the Chiniquodontidae, the Probainognathidae and a clade composed of the Tritheledontidae+Mammalia (Hopson, 1991).

-*Probainognathus* is the sister-taxon of a clade comprising the Tritheledontidae and the Mammaliamorpha, the latter including the Tritylodontidae as the sister-group of all others; the Chiniquodontidae are not analyzed (Wible, 1991).

-*Probainognathus* could be the sister-taxon of a clade comprising the Tritheledontidae and an unnamed clade which has essentially the same content as the Mammaliamorpha, but the position of the Tritylodontidae is considered as unresolved: the Tritylodontidae could be linked to the gomphodonts, or be part of the sister-group of *Probainognathus*; in the latter case, two possibilities are considered, with branching off either before or after the Tritheledontidae (Zhang Fakui *et al.*, 1998).

Cynodonts and the origin of mammals

The important question of the origin of mammals is indeed beyond the scope of this short paper, as it would involve detailed comments on the definition of the Mammalia as well as considerations on the Mammaliamorpha and Mammaliaformes. Consequently, this chapter is only intended to point out, in broad lines, the main problems, and to provide a few bibliographic references.

Two families of highly specialized cynodonts, the tritylodontids and the tritheledontids, need to be considered here, as they are the most often regarded as being very closely related to mammals.

Tritylodontids

This family of herbivorous cynodonts is known almost worldwide. Most tritylodontids are Early or Middle Jurassic in age, but one form has recently been recorded from the Lower Cretaceous of Siberia (Tatarinov and Mashchenko, 1999). The tritylodontids are well characterized by their postcanine teeth, broadened, composed of longitudinal rows of crescent shaped cusps, and provided with several roots. There is no canine; the postorbital bar is absent, and both the prefrontal and the postorbital bones are lost.

The phylogenetic position of the tritylodonts is particularly puzzling. For many authors, they are specialized gomphodont cynodonts, and are not particularly close to the ancestry of mammals. They could then either be derived from advanced traversodontids (Crompton and Ellenberger, 1957; Crompton, 1972; Hopson, 1984, 1991; Sues, 1985), or be the sister-group of the traversodontids (Battail, 1991a). Another hypothesis, expressed as one out of several possibilities by Gow (1991), consists in considering the Tritylodontoidea (gomphodont cynodonts+tritylodontids) as "the sister clade of another middle Triassic to lower Jurassic cynodont clade which includes Mammalia, but several key members of which are not represented in the known fossil record" (Gow, 1991, p. 144). Yet another view consists in regarding the cranial resemblances of tritylodontids to gomphodonts as convergences, and the many resemblances between tritylodontids and mammals as synapomorphies: the tritylodontids would then be phylogenetically distant from the gomphodonts, but closely related to mammals, or rather to a clade consisting of the Tritheledontidae+mammals *sensu lato* (Kemp, 1982; Rowe, 1988; Wible, 1991; Luo and Crompton, 1994). Finally, the difficulties in sorting out the synapomorphies and the homoplasies also led some authors to admit that the position of the tritylodontids is still not clear (Kemp, 1988; Zhang Fakui *et al.*,1998).

Tritheledontids

In sharp contrast to the tritylodontids, the tritheledontids are poorly known, being represented in collections by rare, incomplete and often badly preserved specimens. It is a family of specialized carnivorous cynodonts, including three South African genera, *Tritheledon*, *Diarthrognathus* and *Pachygenelus*, and one South American genus, *Chaliminia* (see Crompton, 1958, 1963; Bonaparte, 1978, 1980; Gow, 1980). Like the tritylodontids, they have lost the postorbital bar and the prefrontal and postorbital bones; they display many resemblances to mammals, and, being carnivorous, are more often accepted than tritylodontids as the sister-group of the mammals *sensu lato*. However, in many cranial and dental structures, they differ very much from other advanced cynodonts, and, unexpectedly, they display also a few characters which are lost in all other advanced cynodonts, but which recall what one observes in early cynodonts: they have kept an interpterygoid vacuity, and the quadrate ramus of their pterygoid is developed. Therefore, the question of the relationships of the tritheledontids to other cynodonts is difficult, and subject to diverse interpretations, the main recent ones being summarized as follows:

-Clade Tritheledontidae+mammals sister-group of the Tritylodontidae (preferred hypothesis of Kemp, 1988; Luo and Crompton, 1994).

-Clade Tritheledontidae+mammals closely related to the Chiniquodontidae and to the Probainognathidae, the trichotomy being unresolved (Hopson, 1991).

-Tritheledontidae sister-group of a clade Tritylodontidae+mammals (Wible, 1991).

As can be seen from this brief analysis, the question of the origin of mammals is still a matter of considerable controversy. And in my opinion, there are still a number of weaknesses in the different hypotheses, for the following reasons:

-The tritheledontids, though always taken into consideration in phylogenetic reconstructions, are still very inadequately known, and might even be a relatively heterogeneous group, judging from the diversity in their tooth structure, clearly shown by Gow (1980).

-Many advanced cynodonts, and in particular the Therioherpetidae (Bonaparte and Barberena, 1975) and the Dromatheriidae, are totally ignored in recent phylogenies: indeed, the available material is poor, and many taxa display too few undisputable characters to be reliably included in phylogenetic schemes. Small forms have seldom been found, and usually only very incomplete material has been recovered, as is the case for the tiny Late Triassic cynodonts from western Europe (Belgium, France and Luxemburg), as yet known almost exclusively by isolated teeth (Hahn *et al.*, 1984, 1987, 1988; Godefroit and Battail, 1997; Godefroit, 1999). The fossil record needs definitely to be improved.

-A comparative analysis of the published phylogenetic hypotheses leads to the conclusion that extensive parallel evolution in cranial and dental characters occurred among cynodonts, and especially in the most advanced ones, obscuring their real phylogenetic relationships.

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