MONOPHYLIA AND POLYPHYLIA IN THE ORIGIN OF MAMMALS

L. P. TATARINOV

PALAEONTOLOGICAL INSTITUTE, USSR ACADEMY OF SCIENCES, MOSCOW

ABSTRACT

In the history of views concerning the origin of mammals monophyletic and polyphyletic concepts replaced each other many times. Division of mammals into two main groups—*Prototheria* and *Theria*—is quite common in recent works. Both groups trace their origin from archaic cynodonts, and this makes it possible to speak of the monophyletic origin of mammals in the broad sense of word. At the same time, the wide-spread parallelism and the onset of divergent evolution of mammals prior to the complete formation of the specific traits of the class, add certain polyphyletic traits to the picture of mammalian evolution. Strictly monophyletic concept at species level is not applicable to high-rank taxons, having no rigidly defined boundaries.

Analysis of the processes that have led to the formation of mammals is of great importance for solving the problem of mono- and polyphylia. In our times we know a great deal more about the origin of mammals than about the origin of all other classes of vertebrates including amphibians. In the history of views concerning the origin of mammals we may observe a frequent replacement of monophyletic conceptions by polyphyletic ones and vice versa. The transition from one system of concepts to another appeared to be connected not with the finding of obvious errors in the works of predecessors, but with the discovery of new facts that necessitate the revision of earlier concepts. The evolution of the views concerning the origin of mammals is very instructive in this respect.

Soon after the publication of the "Origin of Species", there appeared "General Morphology" of Haeckel, who hypothesized the monophyletic origin of mammals from primitive reptiles (Haeckel, 1866). The main argument in favour of Haeckel's concept was based on the presence of amnion both in mammals and reptiles. The results of anatomic study of *Hatteria*, which showed its extremely archaic structure (Gunter, 1868), led to a wide-spread belief about close connection between *Hatteria* and primary reptiles. Accordingly, Osborn (1903) considered the only zygomatic arch of mammals to originate from both arches of *Hatteria*-like diapside reptiles grown together, in his opinion, in mammal ascendants. Concurrently with Osborn, Th.Huxley (1871) suggested the origin of mammals directly from amphibians, and, hence, the polyphyletic origin of *Amniota*. As to mammals Huxley was in favour of their monophylia, but he strongly defended

the idea of polyphyletic origin of *Placentaria* as a result of parallel development from different marsupials (Huxley, 1880).

The discovery and the first investigations of fossil theromorph reptiles (subclass *Theromorpha*) in the second half of the 19th century made it possible to date the origin of mammals from the beginning of the palaeontological era. E. Cope (1878) was the first who formulated the idea of the origin of mammals from theromorphs, although already Owen (1856) had noted that it was possible to derive the mammalian organization from that of theromorphs (or dicynodonts). Up to the 1920's we knew practically nothing of the Mesozoic mammals, and all the achievements scored in the elucidation of the mammal origin were based on the results obtained in the study of theromorphs, particularly theriodonts, which are especially close to mammals. Almost every work on theriodonts showed their well-grounded resemblance to mammals and the enhancements of this resemblance in later Triassic theriodonts, that have acquired in particular the secondary palate, differentiated dentition, mammal constitution (Fig. 1), etc. In the late twenties of the present century the problem seemed to be solved, when the ictidosaurs, in which R. Broom (1929) found a double mandicular joint and considerably reduced rear madibular bones, were discovered. Broom considered the ictidosaurs, or diarthrognaths, as they are called now to be the true transitional forms between reptiles and mammals, and had no doubts as to the monophyletic origin of mammals from reptiles.

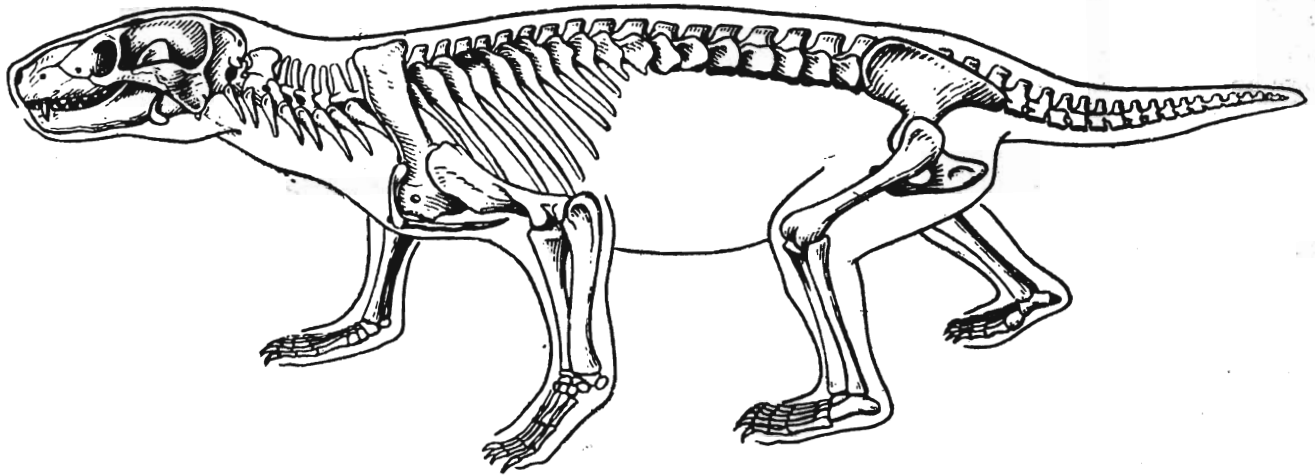Along with this success, there began a considerable progress in studying the Mesozoic mammals. In the 1920's

Fig. 1. Reconstruction of a Lower Triassic Thrinaxodon *Liorhieus* cynodont from South Africa (Crompton, Jenkins, 1973).

Fig. 2. Scheme of relationships between the theriodonts and the Mesozoic mammals based on the studying of their molar teeth (Kuhn-Schneider, 1968).

this progress was connected almost exclusively with the name of H. Simpson. A majority of Mesozoic mammal groups, specialized herbivorous *Multitugerculata* excluded, is known by teeth and jaw fragments. Naturally the analysis of molar teeth building takes an important place in discussing the Mesozoic mammals phylogeny. Cope (1883) included all the non- *Multituberculata* Mesozoic mammals into the *Trituberculata* order, Osborn (1888) singled the *Triconodonta* out of the *Trituberculata*, and Simpson distinguished several more groups among the *Trituberculata-Symmetrodonta*, *Docodonta* and *Pantotheria* (Simpson, 1928, 1929). Cope and Osborn considered the tritubercular teeth to be ancestral to those of recent marsupials and *Placentaria* and to derive from triconodontal teeth as a result of mutual displacement of tubercles, development of talon (talonide), etc. (Osborn 1907)*. But Simpson came to the conclusion that in some groups of Mesozoic mammals complex molar teeth developed from haplodont reptile teeth independently. In 1928 Simpson suggested that the evolution of mammals followed four independent stems (1—*Prototheria*, 2—*Multituberculata*, 3—*Triconodonta*, 4—*Symmetrodonta* and all "true" *Theria*). In later works (Simpson, 1959, 1960, 1961) hs postulated a possibility of mammalian evolution along six parallel stems (Fig. 2).

The hypothesis of the polyphelytic origin of mammals was considerably supported by the results of theriodonts studies which showed that various mammal traits developed in parallel to different branches (Broom, 1932; Olson, 1944, 1959; Brink, 1957; Tatarinov, 1965, 1970, 1972). This parallelism embraces the whole complex of differences between primitive thermorph reptiles and mammals, as they are seen in the osteological material. The process of theriodonts "mammalization" is shown in Fig. 3, where the curves indicate the moment when these reptiles acquired upper olfactory conches (VI), tritubercular postcanine teeth (V), moderately widened great cerebral hemispheres (IV), soft lips (III), additional mandibular joint between the dental and squamose bones (III). These curves cross almost all the groups of theriodonts, but they concentrate particularly on cynodonts, the direct ancestors of mammals. Cynodonts, as well as baurimorphs, also acquire the complete osseous palate, their postedental bones are reduced, their limbs are more or less turned under the body, giving them "near-mammal" bearing, a long neck (of seven vertebrae) is formed, and the lumbar spine becomes differentiated. On the other hand, the archaic Late Triassic

mammals still preserved the rudimentary madibular bones with the square-articular joint, the mammal middle-ear with three acoustic bones formed it higher organized mammals (I).

The conception of the polyphyletic origin of mammals came to its peak at the end of the 1950's, when the ictidosaurs, the most mammal-like of the theriodonts, were shown to be a mixed group, having rather diverse ancestors (Crompton, 1958). The discovery mixed up the whole picture of the relationships between mammals and theriodonts for some time. Almost every researcher published his original scheme of the origin of mammals at that time, the same mammal groups were derived from different groups of theriodonts—ictidosaurs (diarthrognaths), tritylodonts, cynodonts and baurimorphs (Brink, 1957; Kuhne, 1958; Olson, 1959; Simpson, 1960). All the authors remained unanimous only in their belief in wide polyphylia of mammals. Later it was also shown that the additional mandibular joint of mammal type was being formed in ictidosaurs and higher cynodonts in parallel.

The new change of conception was connected with the beginning of a deeper investigation of the remains of archaic Upper Triassic and, partly, of Jurassic mammals (Kuhne, 1958; Kermack, Mussett, 1958; Parrington, 1967, 1971, 1973; Crompton, Jenkins, 1967, 1968, 1973; Hopson, Crompton, 1971, 1973; Kermack, Mussett, Rigney, 1973). First of all, it was found that the teeth of all mammals could be derived from one type of theriodont teeth peculiar to the most primitive (but not the most mammal-like) cynodonts. The postcanine teeth in these primitive cyno-
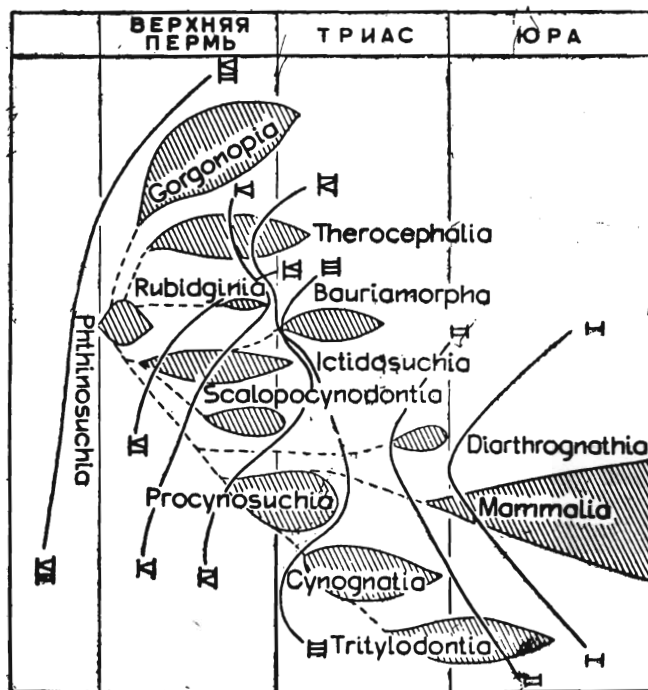

Fig. 3. Scheme of phylogeny and the process of mammalization theriodont (Tatarinov, 1972).

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*For several years the Cope-Osborn theory was bitterly criticized. Specifically, the opponents of the theory were of the opinion that no "rotation" of tubercles took place in mammal molar teeth evolution, and that it was paracone, and not the protocone, that corresponded in the mammalian upper molars to the main peak of the reptile teeth (Gregory, 1934; Butler, 1939). Later studies of the Upper Triassic partially rehabilitated the Cope-Osborn theory. (See below.)

donts are very much similar to those of triconodonts, they also have three main peaks and a well-developed lingual cyngulum with additional tubercles on it (Fig. 4). The determination of the character of teeth occlusion in Late

Fig. 4. Teeth of a Late Triassic mammal Eozostrodon (A) and of an Early Triassic cynodont Thrinaxodon (B). (Hopson, Crompton, 1969).

Triassic mammals was even more important, it required thorough investigation of many dozens of single teeth and mandibular fragments and scrupulous comparison of abrasion facets of single teeth. It appeared that the Late Triassic mammals can be clearly subdivided into two groups, and that both the establishment of teeth occlusion and replacement of the double mandibular joint by the single one went on in parallel. To the first group belong the morganucodontides (=eozostradontides) and synoconodontides, in which the main peak of the lower molar teeth comes between the two front peaks of the upper ones. The second group includes kuhneotheriides, in which the main peak of the lower molars comes in between the two contiguous upper molars (Fig. 5). Teeth of *Symmetrodonta* and *Pantotheria* and of recent marsupials and *Placentaria* can be derived from kuhneotheriide teeth, and teeth of triconodonts and docodonts can be derived from those or morganucodontides (Fig. 6). The triconodonts are distinct from typical mammals in the preauricular part of endocranium, which is formed in them, like in morganucodontides, not by the alisphenoid, but by a periotic process (Kermack, 1963); it is interesting, that this feature also
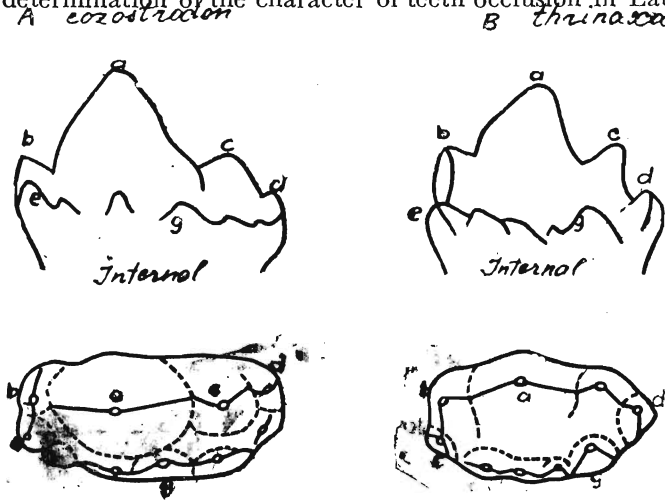

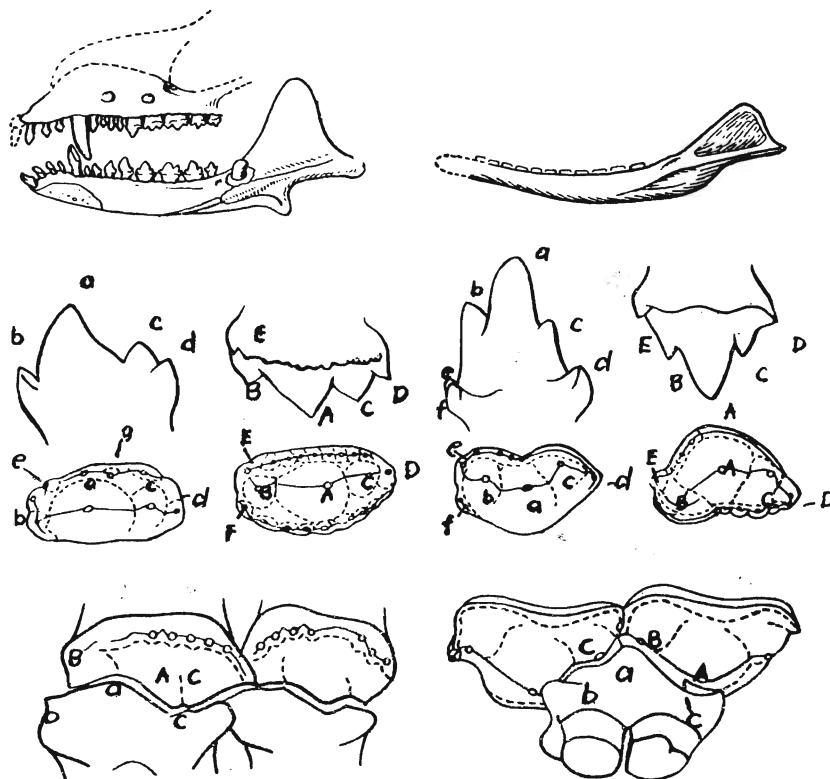Fig. 5. Teeth building and occlusion in Late Triassic mammals Morganucodon (A) and Kuhneotherium (B). (Crompton, Jenkins, 1973).

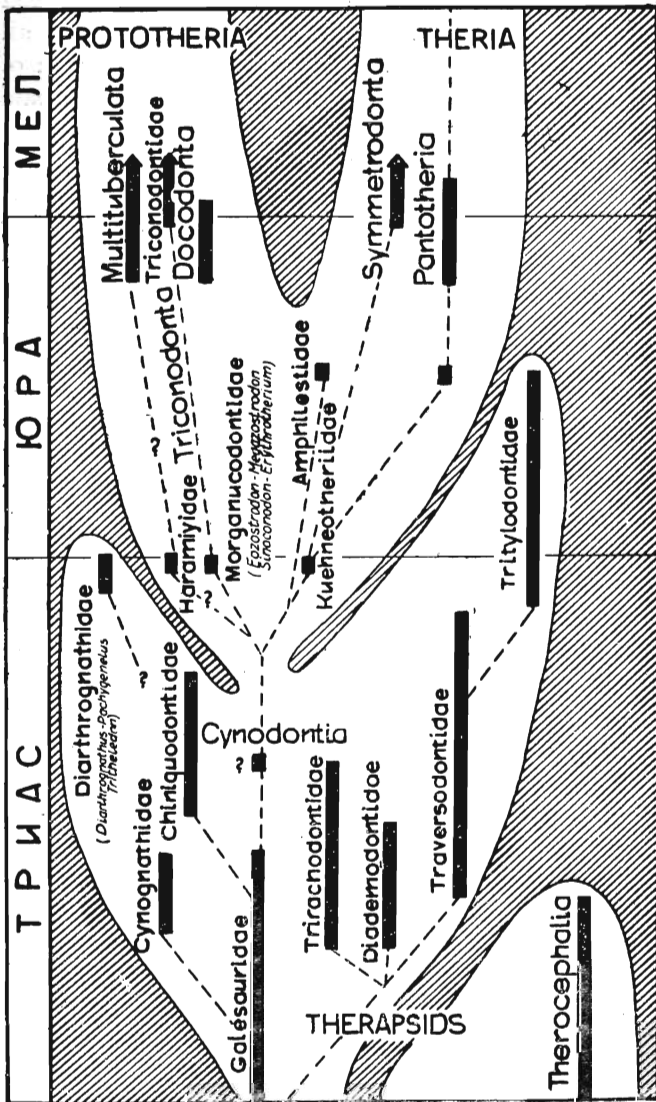Fig. 6.   Phylogenetic relationships of the Mesozoic mammals
(Crompton, Jenkins, 1973).

Monotremata and other mammals another position in relation to the mandibular depressor (Fig. 8).

It is on the basis of all these data that the division of mammals into two main groups (subclasses)—*Prototheria* and *Theria*—has widely spread in recent works (Hopson, 1970; Kermack, Mussett, Rigney, 1973; Crompton, Jenkins, 1973). Thus the latest findings have led to rejection of Simpson's hypothesis of polyphylia of mammals. One may speak of the common origin of all the mammals from archaic cynodonts with prototriconodont teeth. The most mammal-like of cynodonts appeared to be not the mammals' ancestors, but only a side branch of theriodonts, developing in parallel with those ancestors. However, the time of mammal ancestors division into *Prototheria* and *Theria* remains unknown, although, beyond any doubts, this process took place at an early date, prior to the commencement of mammal organization. There remain some doubts as to generic unity of *Prototheria*, because the roots of *Multituberculata* and *Monotremata* are still uncertain, and the periotic process, the main argument in favour of their being included into the same subclass, is moderately represented practically in all cynodonts (Tatarinov, 1974a).

For solving the problem of mono- or polyphylia of mammals the question of the character of transition from theriodonts to mammals, the question whether it was continuous or not, is of utmost importance. The mammal-like changes, especially characteristic of theriodonts, were peculiar to the whole subclass of theromorph reptiles *Synapsida*, or *Theromorpha*) beginning from their first appearance at the end of the Middle Carboniferous up to the boundary between the Triassic and Jurassic periods, where the appearance of first mammals dates from. The process of mammalization is most typical of the higher thermorphs, the theriodonts.

Thus, it is difficult to give the general morpho-physiological characteristics of theromorphs. Their lower representatives in the Middle Carboniferous slightly differed from *Captorhynomorpous Cotylosauria*, belonging to the most archaic vertebrates, while the higher theriodonts were close to Mesozoic mammals. In earlier theriodonts we note already progressive changes in locomotor apparatus, followed by the increase of cerebellum, its floccular lobes in particular. Along with it, even the higher cynodonts, apparently, were not capable of typically mammal locomotion with asymmetric paces, which is evident from the lack of differentiation in spinal bone processes length. The well-developed lumbar spine suggests the presence of the mammal-type diaphragm in higher theridonts, and, hence, of the mammal-type lungs ventilation mechanism. The diaphragm has been apparently acquired by the *Captorhynomorpha Cotylosauria*, having only a vestigial neck, that can account for the connection between the embrionic formation of diaphragm muscle and the formation of front cervi-

brings here the *Multituberculata* and the recent *Monotremata* (Fig. 7). which cannot be connected with any group of archaic mammals (Kermack, Kielan-Jaworowska, 1971). The *Monotremata* differ distinctly from the other recent mammals also by non-homologous mandibular depressor (m. detrahens mandibulae), which has derived from the mandibular adductor (Adams, 1919); and we must remember that the mandibular depressor of the mammals (m. digastricus) consists of two abdoments, of which the front one is derivative from m. mylohyoideus and the rear one, innerved by the facial nerve, appears to be a newly developed feature. The distinct origin of the mandibular depressor in *Monotremata* definitely shows that they have lost reptile mandibular joint independently and acquired in parallel the mammal middle-ear with three acoustic bones (Hopson, 1956); by the way, the external auditory meatus takes in
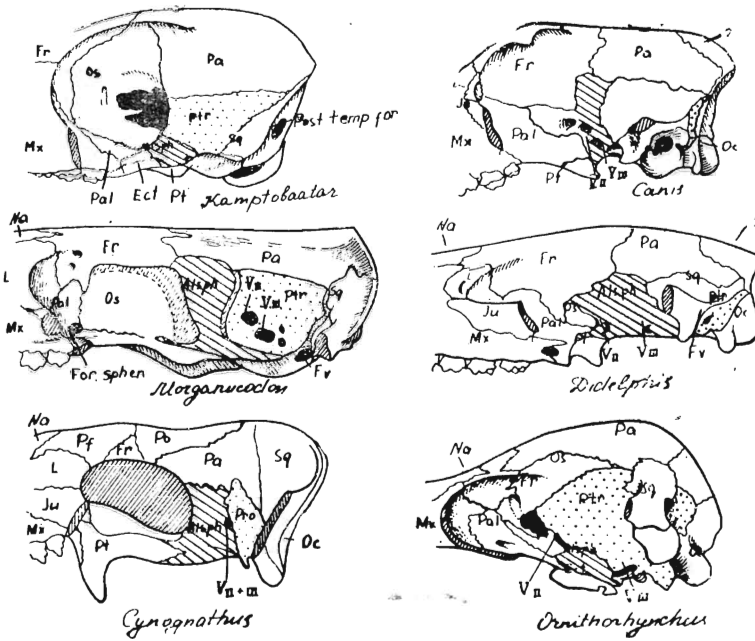
Fig. 7. Preauricular cranium building in different mammals and in cynodonts Cynognathus (Crompton, Kielan-Jaworowska, 1972).
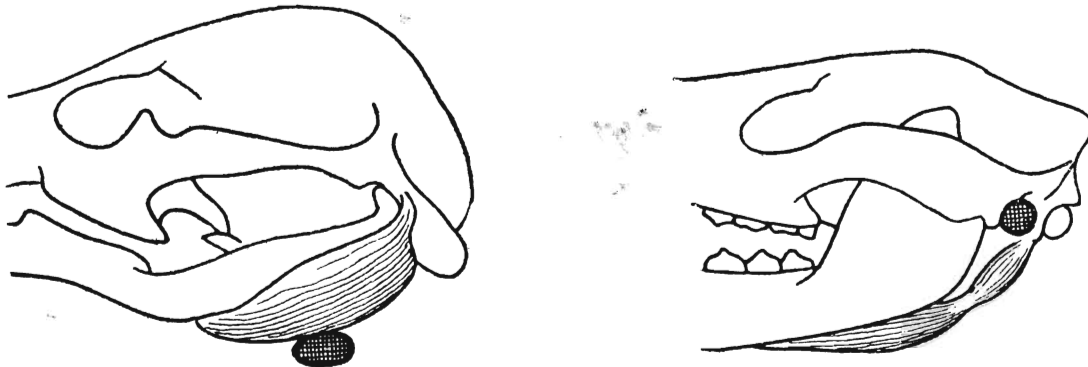

Fig. 1. The external auditory meatus in the Monotremata and in Eutheria (B). (Hopson, 1966).

cal muscles, and also its innervation with cervical nerves III-V.

The higher theriodonts had acquired a completely formed secondary osseous palate. Its initial function was, apparently, not so much the separation of the respiratory truct from the mouth cavity as the strengthening of the mandibular apparatus. The vestigial secondary palate is formed simultaneously with the tritubercular postcanine teeth more or less capable of food grinding. Teeth occlusion was forming in hervivorous gomphodont cynodonts, tritylodonts, diarthrognaths and bauriides, which made mastication possible. In some lower cynodonts (*Dvinia*) the extremely complex lower postcanine teeth were used to grind the food on the surface of the secondary palate (Tatarinov, 1974b).

The reduction of the postdental bones of the lower jaw along with the development of the mammal-type masseter muscles took place only in higher cynodonts. There also formed in their angle bone an incisure, similar to the incisure for the membrane in the tympanic bone of the mammal embryons (Fig. 9), which shows that the mammal ancestors had acquired the tympanic membrane independently.

Despite their increased activity even the higher theriodonts apparently had not become homeothermal animals, which is confirmed by the lack of maxillary conch in the nose cavity, in mammals this conch is covered with respiratory epithelium, and its function is warming and moistning the inhaled air. At the same time the upper olfactory conches (nasoturbinalia) were present practically in all theriodonts.

Therefore even the higher theriodonts were not likely to have hairy cover. Hairs that theriodonts developed in the labial area fulfilled apparently sensor functions forming
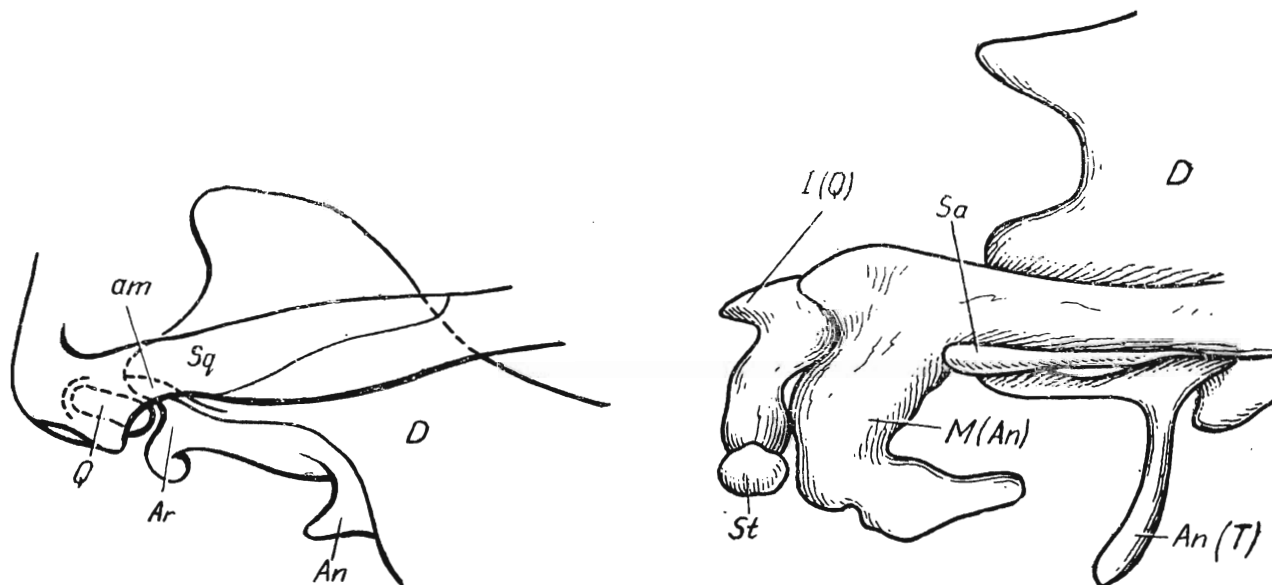
Fig. 9. The rear part of the lower jaw in a Didelphis embryo (A) and in Diarthrognathus (B).

the vestigial vibrissae (Tatarinov, 1967). The higher theriodonts—baurimorphs and cynodonts—show signs of developing vestigial soft lips, which made suckling and milk feeding possible. The presence of marsupial bones in tritylodonts (Fourie, 1963) suggests the presence of the pouch, where the eggs and the young could be borne. It is quite possible that the initial function of the lactiferous gland, having developed of the sweat glands in the pouch, was to moist the new-born "babys" and the eggs to maintain the optimal microclimate in the pouch (Hopson, 1973).

The newly acquired mammal features were combined in theriodonts with extremely archaic ones. Even the recent mammals in some peculiarities of water metabolism (glomerular kidney, urea being the final product of the albumin metabolism) are closer to the amphibians than to the recent reptiles (Smith, 1953). The mammal heart is derived not from the reptile one but from the amphibian one (Goodrich, 1919). There still preserved numerous glands in theromorph skin (Tchudinov, 1970). The greater hemispheres in the lower theriodonts remained vestigial; in gorgonopsian Sauroctonus, for example, the both hemispheres are 6 mm wide, while the cranium is 25 cm long (Tatarinov, 1974b). The greater hemispheres became considerably wider in the progressive theriodonts, but even in the Jurassic triconodonts they remained extremely undeveloped (Fig. 10).

The slow and gradual character of the change, the widespread parallelism and the commencement of divergent evolution in particular, gives the pictures of the mammal formation certain polyphyletic traits. At the same time, the mammal roots belonging to a single ancestral group (archaic cynodonts) makes it possible to speak of their monophyletic origin in the broad sense of the word. The for-

mal solving of the problem in favour of strict mono- or polyphylia depends on where we place the nearest ancestral species for the both subclasses—to the theriodonts or to the mammals. The continuous transition from the theriodonts to the mammals makes the boundaries of the latter classes uncertain at the species level. Therefore the relation of the mammals' nearest common ancestor either to the reptiles or to the mammal class may be arbitrary to some extent.

I believe that the strictly monophyletic concept (at the species level) is in general not applicable to taxons of high systematic rank, because of their having no sharp boundaries. The most consistent with the strictly monophyletic concept of the higher taxons would be discontinuous
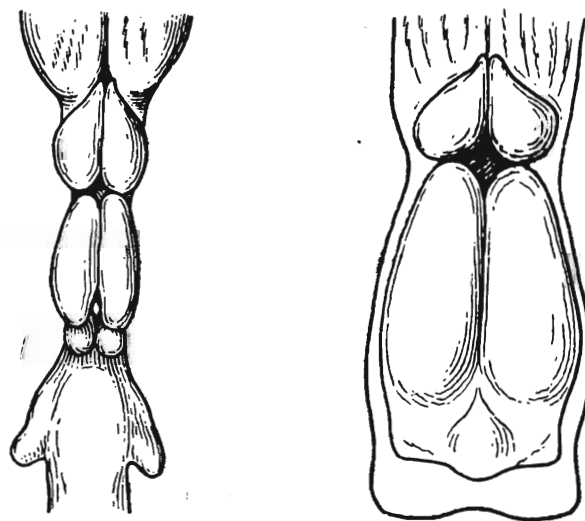
Fig. 10. A mould of the cranium cavity in a Lower Triassic cynodont Nythosaurus (A) and in a Jurassic mammal Triconodon (B). (Simpson, 1927).

evolution, which gave rise, for example, to an ancestral species belonging to reptiles, that originated, in its turn, a mammal species, which becomes the initial point of all the branching of a new taxon. It would be a gross error to consider the general continuous and divergent evolutionary process to be wholly inconsistent with the mono phyletic concept. There is a certain contradiction between the modus of evolution and the hierarchical principle of Linney's classification of organisms. According to this principle, all the taxons are separated, and the higher the rank of the taxon, the greater the separation. Sometimes only such taxons are called the "true" systematic groups (Lookin, 1968). The hierarchism of taxons is not set in advance, but it is resulting from divergent evolution and extinction of the transitional forms. Now the chains of transitional forms connnect the far-separated taxons in time. Therefore the inclusion of the extinct organisms in the system together with the recent ones makes it impracticeable to establish the hierarchism of the systems.

Similar difficulties have led Pia (1921) and Simpson (1960) to the idea that it was necessary to alter the content of the "monophylia" concept when applied to the taxons of super-secies rank. These writers suggest to consider any taxon as monophyletic when it traces its origin by one or several trunks from ancestral taxon of a lower or even equal rank. The only advantage of this definition, from our point of view, is that it makes possible to count as monophyletic the majority of the groups, whose origin is at present being discussed. According to this definition, it would be possible, for example, to consider the amphibians as a monophyletic class, even if we could prove their origin by different trunks from the *Teleostomi*, the *Acipencer*, the *Dipneusti* and the *Crossopterygii*. The Pia-Simpson definition is not successful also because the rank attributed to this or that taxon is determined to some extent by the investigator's individual approach. Thus, all the *Crossopterygii* are usually attributed the rank of superorder or subclass, and the origin of the amphibians from the Crossopterygii by any number of trunks will be monophyletic according to Simpson. Stensio (1963) counts the porolepimorphid and osteolepimorphid *Crossopterygii* as separate classes, and in this case the origin of the amphibians from the Crossopterygii by two trunks only will become polyphyletic. In some cases the application of the Pia-Simpson criteria may give paradoxal and even absurd results. One and the same evolutionary transit in, e.g. the origin of terrestrial vertebrates, we may regard from the point of view of taxonomy, as the origin of the *Ichthyostegalia* suborder. As a result of this, accepting, for example, Stensio's system and the phylogenetic concept we could speak of the monophylia of tetrapods and of the polyphylia of amphibians at one time.

Thus, we can say that it is impossible to answer the question, whether the mammal origin is mono- or polyphyletic,. The formally logical definition of "monophylia" and "polyphylia" concepts seems to be too narow to describe the actual history of events, that have led to the formation of mammals. Such contradictions between the immobility of the logical categories and the mobile phenomena they define, occur rather frequently. Between the cases of extreme polyphylia and strict monophylia there is a wide range of transitions which contribute to the formation of a new taxon due to parallelisms. The term "paraphylia" could be used to define these transitional cases.

It is often suggested that for practical purposes it is necessary to observe the principle of strict monophyletism of all the taxons (Davitashvili, 1968). But this recommendation is easy and necessary to fulfil only when we deal with an obviously mixed taxon, having derived from divergent roots. But it is difficult to give exact recommendations for the paraphyletic taxons having close roots. The appliction of the strictly monophyletic principle to the mammals would lead, for example, to the mammals being put together with cynodonts, or the *Prototheria* mammals being united with theriodonts, or to the main group of *Protothria*—the *Triconodonta*, the *Multituberculata* and the *Monotremata*,—being regarded as separate classes. Neither of these decisions may be considered satisfactory; the last one divides the Mesozoic mammals into several parallel groups slightly divergent and therefore being attributed too high a rank. Let us remind again, that it is impossible to represent the actual phylogeny by means of hierarchical classifiction (especially, when including both recent and fossil forms into the system). In practice one always has to balance the consistent genetic principle of classification and the "horizonal" one, in which the taxons are determined according to the achieved organization level.

The peculiarities of the material under investigation give the work of the paleontologists in the field of phylogenetic classification a specific character. Discoveries of new transitional forms and the enlargement of our knowledge about the earlier evolution of a taxon make its boundaries more and more diffuse. Thus, the paleontologist while improving the phylogenetic classification, at the same time destroys it. This partly accounts for the fact that on the whole the paleontologists are more, than the neontologists, inclined to accept the hypothesis of the polyphyletic origin of large taxons.

Neontologists investigate the final results of the evolution. The hierarchism of forms, as it is represented in zoological systems, is given to them as a prior. In their scrutiny of the data on the recent forms morphology, neontologists tend to reconstruct the stages in the morphoecological evolution of taxons. In doing so, emphasis is inevitably laid on those moments when the organisms acquire certain features. The sources of divergence as such fall out of researcher's attention, because we have no

reason to expect the main grades of phyletic evolution to coincide with lines branching. But they coincide as often as not (Mayr, 1963). As a result of this, opinion of the phylogeneticist-neourtologist is often gradational as far as taxonomy is concerned.

Paleontologists, investigating the forms dating back to the onset of divergence, become convinced that many of the most characteristic features of a higher taxon are not inherited from the common ancestral species, but have been acquired or, in any case, developed in parallel with related forms. Thinking of the palentologists is more cladistic than that of the neontologists. The work of the paleontologists is to a great extent handicapped by the incompleteness of the fragments and, in particular, by the fact that the ancestral forms, even belonging to different phylogenetic branches, often appear to be very much alike, as they have not yet diverged. As a result, the paleontologists inevitably pay more attention to the earlier specialization of ancestral forms.

The one-sidedness of both purely neontological investigation of the evolutionary process may lead to serious errors. The neontologists are usually inclined to raise the grades of the moments of divergence, substituting in the phylogenetic schemes the extremely complex bundles of slightly divergent relationships for simple, linear ones. The paleontologists, in their turn, often connect the forms, with relation to lines having specialized only in a few skeleton features. Evidently, a deeper investigation into the phylogenesis requires consolidation of both neontologists' and paleontologists' efforts. An example of such a comprehensive approach may be found in the recent works by I. I. Schmalhausen who has noted in his preface to "The Origin of Terrestrial Vertebrates that he never intended to consider in his book "all those questions that can be solved only by means of comparison with fossil material" (Schmalhausen, 1964). Along with it, having turned to more thorough investigation of the morphology of the fossil specimens, paleontologists became more dependent on the knowledge of the recent organisms morphology. While solving particular phylogenetic problems, both paleontological and neontological material may either appear to be incomplete, or sometimes it may be of greatest importance.

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