

The Systematic Position of Monotremes Reconsidered (Mammalia)

Walter G. Kühne

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Summary. By reinterpretation of the tooth formula of *Ornithorhynchus* as $dp/P M_{1-4}$ a synapomorphy with Marsupials has been discovered. Monotremes and Marsupials are sister groups, together derived from Theria of the Middle-Cretaceous.

The systematic position of the Monotremes is up to now problematical. The consensus, now ably expressed by Hopson and Crompton (1969), allocates Monotremes and Multituberculata, Docodontia and Triconodontia to a nontherian group, stemming from *Morganucodon*, and the Theria proper, stemming from *Kuehneotherium*. The date of the cladistic dichotomy, the “terminus post quem non”—according to Hennig—is before the Upper Rhaetic, when *Morganucodon* and *Kuehneotherium* live side by side in Glamorgan, Wales.

An unfortunate squabble over a nomenclatorial question has resulted that among the few authors writing on Rhaetic mammalia one and the same thing is called by Crompton, Jenkins, Parrington and Hopson *Eozostrodon* (Parrington, 1941) and by Kermack, Musset, Mills and Kühne *Morganucodon* (Kühne, 1949). The writer has emphasized in 1958 (p. 214) that for a number of good reasons *Morganucodon* ought to be used, the name of *Eozostrodon* being used for sentimental reasons only or because of ignorance. The reasons for my choice are the following:

1. Of *Morganucodon* an enormous hypodigm is now available.
2. In the hypodigm of *Eozostrodon* no molar—which holds the typical character—is available. The specimen *E. problematicus* does not contain the Kuehnecone (Parrington, 1967).
3. The hypodigm of *Eozostrodon* comes from one fissure in Holwell, Somerset. The hypodigm of *Morganucodon* comes from several fissures in Glamorgan.
4. The 3 roots originally present in the hypodigm of *Eozostrodon* are long and tapering.

The roots of *Morganucodon* show thaurodontism.

5. Measured on the hypodigm of *Morganucodon*, the “hypodigm” of *Eozostrodon* is indeterminate. It is my firm conviction that in order not to cloud the issue, it is advisable to let fall into oblivion the name *Eozostrodon*. It is obvious that I am not going to fight a legalistic battle on this issue. It is—to me—irrelevant whether, from a formal taxonomic point of view, one or the other name is justified, as long as for the use of one name rational reasons are available.

The consensus has been formed by opinions, expressed at various times by Crompton, Hopson, Jenkins, Kermack, Kühne, MacIntyre, Mills, Simpson, and others.

Gregory (1947) maintained—against the consensus—that Monotremes have their nearest phylogenetic relationship with Marsupials, both taxa constituting the Marsupionta.

The Marsupionta and the Placentalia constitute the Mammalia of Gregory. Though Gregory does not write it, his paper implies a cladistic dichotomy between Monotremes and Marsupialia after the common ancestors of these two groups parted from the Placentals. Hence the terminus post quem non for Monotremes and Marsupials according to Gregory cannot be earlier than Middle Cretaceous. Recently the paper by Gregory has hardly been discussed. Gregory's arguments however have not been refuted and a reconsideration of the problem is attempted with regard to the methodological principles of modern theory of phylogenetic systematics (Hennig, 1950, 1966). To give the result before I present the evidence: Monotremes have their nearest phylogenetic relation with Marsupials. The terminus post quem non of the two taxa concerned, is later than Middle Cretaceous. The presented evidence will reveal a clear cut case. I can prove my point with a single argument.

In order to state plainly the kind of argumentation, I quote van Valen (1965, p. 147): "It should be axiomatic that retention of the same primitive characters is of no use whatever in establishing vertical relationship. Only characters modified from the primitive condition in the same or different direction (preferably unusual directions) provide valid evidence one way or the other."

The sentences epitomize what Hennig (1950) called Synapomorphy contrary to Sympleisiomorphy, which is useless, when establishing the sister group relation of two monophyletic taxa. Synapomorphy is the common heritage of a derived character in two phylogenetically related taxa in respect to their ancestral taxa. The latter has the character in the "primitive" (plesiomorphic) form. In Fig. 1, B, differs inter alia from A by the possession of this derived character which A and A₁ lack. C and D as contemporaries of A₁ are nearer related to each other than either is to A₁. As an example A are therian mammals with tooth replacement in 3 or 4 postcanines. B are Marsupials with tooth replacement in only one postcanine. C and D are Polyprotodontia and Diprotodontia respectively. A₁ are Placentals. Plesiomorphic is the replacement of 3 or 4 postcanines in "Theria" and in Placentals. These two groups are sympleisiomorphic with respect to this character. Apomorphic is the replacement of only one postcanine. Hence Diprotodontia and Polyprotodontia are synapomorphic with respect to this character. Apomorphic is the diprotodont condition, derived from the polyprotodont condition. Therefore Polyprotodontia cannot be shown to be a monophyletic group on the basis of this plesiomorphic character (polyprotodonty).

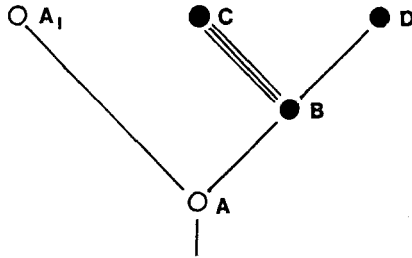


Fig. 1. For explanation see p. 60

To be precise: I am not going to weigh a number of similarities against a number of differences. But I will give weight to the characters on which I base my argument. A “single-parameter-character”, for instance absence of the jugal, is more likely to develop in parallel evolution—without indicating phylogenetic relationship—than a multi-parameter-character, for instance the sound-conducting chain of the bones Malleus, Incus and Stapes. I regard it as very unlikely for a multi-parameter-character to develop in parallel evolution. Expressed in the abstract way: historicity is proportional to the number of parameters involved. Uniqueness of a historic event is realized only when many parameters are involved. Another point: The amount of parallelism in two phylogenetically related lineages decreases with increasing time from the terminus post quem non.

By bringing forward arguments which I regard as crucial or which have been brought forward only by Gregory, I am not going to refute all arguments on which the consensus depends. I would claim in such cases that the relevance of the character in question has not convincingly been proven—or that the relevance of the respective character is still subjudice. Finally: if only one synapomorphy is found and recognized as such, and generally acknowledged, the problem is solved, in spite of a number of other characters, which are not synapomorphic but plesiomorphic, dubious or—under the present state of knowledge—cannot rationally be discussed.

The crucial argument runs as follows: polyprotodont Marsupials have four molars in the non-reduced dentition; for instance in *Didelphys*, *Perameles*, *Caenolestes*, *Phascolarctos* etc. The fifth tooth counted from the posterior end of the dentition is the last “premolar” or correctly expressed the only deciduous premolar, which is the only tooth in upper and lower jaw of the marsupial dentition which is shed and replaced by a replacement tooth.

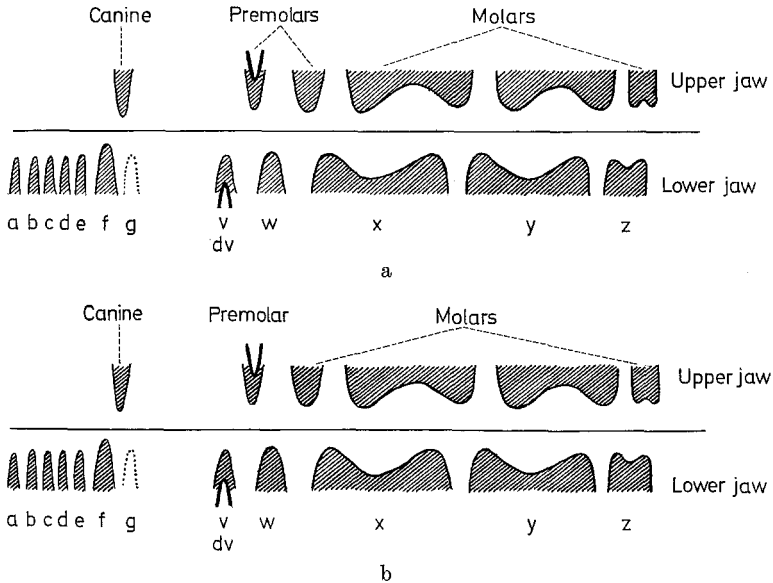


Fig. 2a and b. Dentition of *Ornithorhynchus*. a Interpretation of Green (1937).
b Reinterpretation

Green (1937) has analyzed the functional and the abortive dentition of *Ornithorhynchus*. Not all of the molars are functional during a short period; the last upper molar is never functional, this is Green's "upper Z". The fourth upper tooth counted from the posterior end of the dentition is likewise nonfunctional. Both fifth tooth-anlagen counted from behind are nonfunctional, and both have a replacement tooth-anlage.

Green (p. 392), by designating the fourth tooth from behind—his tooth *W*—as a premolar, does so with the following words: "It is probable that *W* is the last premolar tooth". Green's reason for this designation is not given; a probable reason might be the morphology and the size of *W*, which—compared with the next member of the dentition—*X*—, is significantly smaller. But Green's designation has been crucial; on it depends his tooth formula— $P_2 M_3$ —and with the tooth formula, the identity of tooth replacement in *Ornithorhynchus* and the Marsupialia became obscured, it became hidden, it was not noticed. We write it now as $P_1 M_4$!

Conversely one can state: as Green did not see the profound significance of his evidence, he had no reason to emphasize it, hence his evidence, neutral, sober and not touched on by interpretation can be taken at its face value.

An essential point: a proven synapomorphy cannot be counter-balanced by other arguments; if it cannot be refuted it has to be accepted as evidence.

It is indeed a lucky accident that one character of the Monotreme—(that is *Ornithorhynchus*) dentition has been preserved—in spite of the vestigial nature of it—which is of the kind van Valen requires for the establishment of vertical relationship and which has been quoted above. Reduction of tooth-replacement in Marsupials is highly apomorphic. The tenor of the evolution of the mammalian dentition has been—among other features—the reduction of tooth-replacement: the Marsupialia have exceeded the Placentalia, only one tooth in the upper and lower jaw being replaced. The picture given by Green of tooth replacement of *Ornithorhynchus* matches exactly the condition in Marsupials. This is synapomorphy proven for the two taxa concerned and the end of the argument.

As Gregory claimed in 1947, Monotremes have their nearest relation with the Marsupials, the terminus post quem non for them is after the cladistic dichotomy of Placentals and Marsupials; hence not earlier than the Middle Cretaceous. The triad Malleus-Incus and Stapes cum the Tympanic, holding the tympanic membrane, is thus present only in a narrow group of late mammals, phylogenetically intimately related. When the triad evolved, we cannot say for certain. The event took place before the age of the Trinity-fauna, that is Lower Aptian. The event took place after the Upper Rhaetic where both *Morganucodon* and *Kuehneotherium* still possess the sulcus cartilagineus meckeli, fide Kermack (1968 p. 418), and the event never took place in the lineage leading from *Morganucodon* to *Docodon*.

Lack of the prespinal part of the scapula has been proven by McKenna (1961) in Tertiary Multituberculata. The lack of the prespinal part of the scapula is symplesiomorph in Tertiary Multituberculata, Monotremes and for instance Cynodonts. The earliest absence of the coronoid in Dryolestids and in the *Amphitherium-Pappotherium*-lineage is found in the Dryolestid *Crusafontia* from the Hauterivian of Una, Spain (Henkel and Krebs, 1969). Here is proof for the slowness of the evolution of those items concerning the lower jaw and the middle ear.

If it would be true the ancestors of Monotremes and Theria parting company in the Middle Triassic and both lineages arriving somewhere in the Cretaceous with the triad as the sound conducting apparatus, a severe blow to evolution as a historical process would have been delivered. This blow has been averted.

It is significant and discouraging that Gregory's arguments, some of which could have been derived from fossils, did not gain acceptance; that those workers concerned with the relevant fossils and with the

recent taxa, did not find the synapomorphy which is crucial for our case, viz. the marsupial tooth replacement in Monotremes, and finally, that the valid synapomorphy—unless some other, equally valid are found—is the result of a morphological study by Green, performed on recent material and on ontogenetic stages, which are unavailable to the palaeontologist.

It is fitting to express admiration for William King Gregory who, into the face of the phalanx of the consensus, maintained an independent opinion, which has been confirmed 33 years later.

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Prof. Dr. W. G. Kühne
Lehrstuhl für Paläontologie
der Freien Universität Berlin
D-1000 Berlin 33
Schwendenerstr. 8
Germany