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COMMUNICATIONS

REMARKS ON THE PHYLOGENY AND THE CLASSIFICATION OF THE XENARTHRAL EDENTATES (MAMMALIA) EXTANT AND FOSSIL

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During the last few years, diverse modifications have been proposed to the classification of the Xenarthral Edentates, notably by PATTERSON & PASCUAL (1963) ROMER (1966) and PATTERSON (The Fossil Record, Mammalia, Edentata, 1967). Some of them concern essentially the nomenclature; others have a deeper meaning, calling into question the phylogenetic relationships of certain fossils or groups. Unfortunately the very nature of the publications in question has not permitted the authors to explain their opinion, so that it is sometimes difficult to take a position in this regard.

A thorough discussion cannot take place until after the aforementioned authors have made their arguments known. Here and now, and without intending to propose a definitive classification, I believe will be useful to consider and to discuss below a certain number of points.

DIVISION OF THE XENARTHRALS INTO THREE SUB-ORDERS
CHOICE OF CORRESPONDING NAMES

The division of the Xenarthrals into three sub-orders, today represented respectively by the armadillos, the anteaters and the sloths (HOFFSTETTER 1954 – 1958) seems to have received

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general acceptance. It is evident that the regrouping (under the name of Pilosa) of the Tardigrades (Sloths and Gravigrades) and the Anteaters, proposed by FLOWER (1883), rests on an erroneous phylogeny. It is impossible, indeed, to accept with this author (FLOWER, 1882) that the anteaters could have descended from the gravigrades. As I have already stated, there are two major objections to it: firstly the primitive foot, and above all the dasyspondyl astragalus of the tamanoas could not have derived from those of the gravigrades, which were much more specialised; secondly the myrmecophagous diet appears to be a specialisation of the primitive regime of the Edentates and does not permit the supposition of an intermediate phytophagous phase.

It is still difficult to be more specific about the phylogenetic relationships of the three sub-orders. The palaeontological literature seems to indicate that the armadillos appeared first and that the differentiation of the gravigrades (unknown before the Mustersan) and of the anteaters (unknown before the Miocene) was later.

If the primitive armadillos constitute a common trunk, it then becomes necessary to accept that the two other groups represent independent branches.
Nevertheless, even if there is agreement regarding their separation, the names of the three sub-orders varies from one author to another; if only for reasons of convenience, it would be desirable for an agreement to be reached.

1˚ - The armadillos, which have been joined by the glyptodonts, have received the following collective names: *Sclerodermata* (partim) Blumenbach, 1779, pp. 72-73; *Loricati* Vicq d'Azyr, 1792, p. ciii; *Cingulata* Illiger, 1811, p. 110; *Loricata*, Owen, 1842, p. 167 (nec Merrem, 1820); *Hicanodonta* Ameghino, 1889, p. 653, 758. The third name (Cingulata) has been generally adopted, although ROMER (1966) went back to Loricata. In fact SIMPSON (1945, p. 193) has already underlined the inconvenience of this last term which, with the same ending, has already been applied to the crocodiles (MERREM, 1820, pp. 7, 34).

2˚ - The Anteaters have been designated as : *Myrmecophagi* Vicq d'Azyr, 1792, p. ciii; *Vermilinguia* Illiger, 1881, p. 112; *Pilosa* (partim) Flower, 1883, p. 184; *Anicanodonta* (partim)

Ameghino, 1889, pp. 653, 657; *Vermilingua* Simpson, 1931, p. 273. The second has been adopted, but SIMPSON has amended it to the form Vermilingua.

3˚ - The sloths, which were attached to the gravigrades following their discovery, have received these names: *Tardigradi* Brisson 1756, p. 33, 1772, p. 20; *Pigri* Vicq d'Azyr, 1792, p. ciii; Tardigrades Geoffroy & Cuvier, 1795, p. 188; *Tardigrada* (partim) Latham & Davies, 1795, p. 3; *Phyllophaga* Owen, 1842, p. 168; *Phytophaga* Huxley, 1871, pp. 330-331; *Pilosa* (partim) Flower, 1883, p.184; *Anicanodonta* (partim) Ameghino, 1889, pp. 653, 657.

It is apparently BRISSON, who first, in his "Regnum Animale" (Paris edition, 1756, p. 33; Leyde edition, 1762, p. 20) applied the name Tardigradi to the Sloths. The form 'Tardigrada', more in keeping with usage for a name of an infra-order, was published for the first time by LATHAM & DAVIES (1795), with an excessively broad sense. However, this name, in either the Latin or vernacular form, was in use for more than a century (Geoffroy & Cuvier, 1795; ILLIGER, 1811; DOYÈRE, 1840*b*; OWEN, 1842; HUXLEY, 1871; GILL, 1872, 1910; GERVAIS, 1873; TROUESSART, 1898-1905; etc.) either applied to the sloths alone, or to the group sloths + gravigrades. Note that the latter extension was proposed (CUVIER 1799-1800, *Leçons d'Anatomie comparée*, first chart) following the discovery of the first *Megatherium*. It was formally adopted by GILL (1872, 1910), and it corresponds to current ideas in different languages (tardigrades or *Paresseux*; Sloths; *faultiere*; etc.). It is, then, by the priority of its usage, the term which should be legitimately applied to the group in question.

It is worth pointing out for clarification, the fact that the same name (Tardigrada) is also applied to a group of invertebrates. It is advisable to recall that at this level homonymy need not lead to the rejection of the same name used in different branches of classification, (thus, the term Decapoda is accepted as just as valid in the cephalopods as in the crustaceans). Furthermore, the term Tardigrada (Invertebrates) is recent enough. It is sometimes (PASCUAL, 1960, note 1, p. 143) incorrectly attributed to SPALLANZANI (1776): this last author contented himself with describing an organism which he named "il tardigrado"; the true author of the name of this group is DOYÈRE (1840 *a*, *Memoire sur les Tardigrades*) and the Latinised form 'Tardigrada' only appeared later AGASSIZ, 1842-46: Nomenclator Zoologicus, Rotaria, p. 5), it was around half a

century later that the same term was adopted for the sloths (or even near to a century if one accepts BRISSON'S proposal).

The other names applied to the sloths or to the group sloths + gravigrades present many drawbacks.

Bradypoda (which groups sloths and anteaters) and Pigri (Sloths) have been forgotten. There is still the Phyllophaga, which has anyway been utilised earlier for two genera of insects. It is equally the case with Phytophaga, which has besides served to designate groups of Coleoptera (DUMÉRIL, 1806), molluscs (GRAY, 1840) and marsupials (A. WAGNER, 1844).

Concerning 'Pilosa', which is still preferred by some authors, it must be remembered that it was proposed by FLOWER (1883) to group together the Tardigrada and Vermilingua of GILL (1872). The term introduced by FLOWER (which, incidentally, is equivalent to the Bradypoda of BLUMENBACH, 1779, and to the Anicanodonta of AMEGHINO, 1889) has been generally adopted with this understanding, and its inclusion in the classification of SIMPSON (1931, 1945) has established its use. Only GILL (1910) held himself above such a usage, declaring: "I cannot consider the combination of sloths and anteaters in a group distinct from armadillos as an improvement in the taxonomy of the Xenarthra, and therefore the name Pilosa seems to me to be superfluous. Flower himself virtually confesses as much. The suborders Tardigrada and Vermilinguia, recognised by me in 1872, appear to be at least as distinct as are the 'Loricata' from the Tardigrada". When, beginning in 1954, and in support of new arguments, I returned to GILL'S position, it seemed to me that I should also adopt his nomenclature (this in response to the question posed by R. PASCUAL, 1960, p. 143). Other authors have preferred to substitute for 'Tardigrada' the term 'Pilosa' of FLOWER, while restricting its application. I can well see the drawbacks there. It becomes necessary, each time that the term is used, to clarify the new sense of the term. On the other hand, 'Pilosa' (and even more its translations: *poilus* or *velus*, *peludos o velludos*, 'hairy', *haarige*) might be difficult to use alone, not being sufficiently evocative to designate a group of mammals. In order to make it intelligible to non-specialists, one is led either to replace it with a vernacular name (tardigrades, sloths, *faultiere*), or to use it as an adjective, as in *Edentate Pilosa*; this expression is acceptable in the sense proposed by FLOWER, but not in a more limited sense. It appears to me, indeed, absurd to apply that designation to a group from which are excluded the only mammals which are really lacking in teeth and covered with hair,

namely the anteaters! In fact, if one wishes to limit the understanding of the term 'Pilosa', it is necessary just as rightfully to apply the term to the anteaters alone, which fall within the synonymy of Vermilinguia = Vermilingua.

SYSTEMATIC POSITION OF *Palaeopeltis*

The genus *Palaeopeltis* Ameghino, 1895, is only known from some large dermal plates, the type specimen (*P. inornatus* Ameghino), found in the "*Pyrotherium* layer" (Deseadan) of Patagonia; another species is based on a fragment of carapace from the Mustersan. These plates from the Deseadan are illustrated by plenty of examples, some of which are figured by AMEGHINO (1897, fig. 83, p. 102 of the off-print), GAUDRY (1908, fig. 71, p.57) and HOFFSTETTER (1958, fig. 41, p. 595); they show a distinctive type, which fit neither with those of the armadillos nor with those of the glyptodonts.

A. TOURNOUËR, who has collected over twenty of these, claimed to have found them in association with jawbones of *Octodontotherium*, (and of *Orophodon*, which he does not separate); from this he concludes that it must come from a type of armoured gravigrade. This opinion appears plausible enough, all the more so since, in the Deseadan of Patagonia, no other animal is known to which these plates could be attributed; and the argument has some force if it is recalled that it must concern an animal which was powerful and (according to AMEGHINO) relatively common.

Like GAUDRY, I have therefore adopted (HOFFSTETTER, 1954*a*, *b*; 1958) the same interpretation, while expressing elsewhere serious reservations (see HOFFSTETTER, 1956*b*, pp. 26-28), which will not be removed until a verifiable relationship is seen.

PATTERSON & PASCUAL (1963, p. 143) and PATTERSON (Fossil Record, Mammalia, 1967, p. 772) restate the problem, but think that these plates relate to the genus *Pseudorophodon* Hoffstetter, 1954*b* (type species *Ps. kraglievichi* Hoffstetter, 1954 = "*Orophodon*" cf. *hapaloides* Kraglievich & Rivas, 1951) of which is known only the rostral part of the cranium and several plates, from the Laguna Carri-Laufquén Chica (Territ. of Río Negro). PATTERSON & PASCUAL (1963) concluded that this genus should be named *Palaeopeltis* (= *Pseudorophodon*) and that it represents a group of Cingulata which is distinct from both the armadillos and the glyptodonts. This interpretation is defensible, but it would be dangerous to accept it as proven. The Deseadan

of Patagonia, where the plates of *Palaleopeltis* came from, has not yet yielded anything more which could relate to *Pseudorophodon*. On the other hand, the several plates associated with the skull of *Pseudorophodon* are far from being identical to those of *Palaeopeltis*, with which they have in common above all negative characteristics. Finally, the geological age of the deposit of the Laguna Carri-Laufquén is not precise, this is because it is believed that a genuine *Orophodon* has been found there, which KRAGLIEVICH & RIVAS have assigned to the Deseadan.

ROMER (1966, p. 392) adopts a third position. He places *Palaeopeltis* in its own superfamily (Palaeopeltoidea) of the Cingulata, while he classifies *Pseudorophodon* in the Dasypodoidea and places the genera *Orophodon* and *Octodontotherium* in the Mylodontidae.

This last position, which rejects first one then the other of the preceding hypotheses, is equally debatable. In fact, until the new elements have been sorted out, the wisest solution would be to consider *Palaeopeltis* (which has practically, for now, the character of a parataxon) as a genus *incertae sedis* within the Xenarthra.

SYSTEMATIC POSITION OF THE GENERA *Orophodon* and *Octodontotherium*

Since 1954, I have come to regard the genera *Orophodon* and *Octodontotherium* as constituting a separate branch (Paragravigrada or Orophodontoidea), distinct from all the other gravigrades, although curious parallels can be seen with the Mylodontidae.

A completely contrary opinion is expressed by PATTERSON & PASCUAL (1963, p. 143), according to whom "*Octodontotherium* is certainly, and *Orophodon* possibly, a mylodontid". PATTERSON (1967, p. 772) expresses practically the same words. Following them, ROMER (1966) places the two genera in the Mylodontidae. These assertions call for some reservations. In effect, even if (which is quite possible) the plates from *Palaeopeltis* do not relate to either of the two genera considered here, it does not necessarily follow that these belong to the Mylodontidae. For my part, I continue to consider them as a distinct group which has at least the grade of a family (Orophodontidae).

As announced by AMEGHINO (1895, 1897) from the first description of these fossils, and as has been underlined by L. KRAGLIEVICH (1931) and by myself (1954-1958), the teeth of *Orophodon* and those of *Octodontotherium* are made up almost exclusively of compact dentine, covered with a thin bed of cement, and surrounding an extremely reduced nucleus of vascular dentine. This

structure is reminiscent of that known to be found in the armadillos (and this explains why KRAGLIEVICH & RIVAS were able confuse the teeth of *Pseudorophodon* with those of *Orophodon*). It puts the two genera under consideration against all the classical gravigrades. It entails, moreover, wear facets different from those shown by the latter, more similar to those which the armadillos show. It follows that from this that one can recognise a tooth from the Orophodontidae, even when it belongs to a novel genus (this is the case of isolated teeth which I have been able to observe in the Deseadan of Salla-Luribay, in Bolivia). This dental structure strongly suggests a true relationship between the two genera under consideration : this was, on the same criteria, the opinion of AMEGHINO after 1897; on the other hand SIMPSON, 1945, placed *Orophodon* in the Nothrotherinae and *Octodontotherium* in the Mylodontidae; for their part, PATTERSON & PASCUAL again hesitated to treat the two genera jointly, thereby showing that they accord greater significance to the morphology of the teeth than to their structure.

Compared to the true Mylodontidae (unknown before the Miocene), the Orophodontidae are more ancient. They appear to be confined to the Oligocene, and especially to the lower Oligocene (Deseadan). From this epoch, they show an advanced evolutionary stage, especially in *Octodontotherium*: great height, (easily superior in this to all the Santacrucian gravigrades; astragalus comparable to that of the Pleistocene Mylodontidae; clear/ distinct bilobation affecting the two last teeth of each half-jaw, that is to say more advanced than any true Mylodontidae.

Taking into account these observations, it appears to me to be impossible to envisage a direct affiliation of the Orophodontidae to the Mylodontidae of the Santacrucian (*Nematherium, Analcitherium*) and therefore to the later forms of the same family.

I remain convinced that the Orophodontidae (whether or not they possessed dermal armour) constitute a side branch, which split off early from the common trunk of the Gravigrada. They have, like the armadillos, retained the primitive dental structure of the edentates. If the observation of TOURNOUËR is confirmed, they have also conserved another characteristic of the Dasypodoidea: the osteogenic potential of the dermis. Their radiation is virtually limited to the Oligocene. They comprise the genera *Orophodon* and *Octodontotherium*, both Deseadan, respectively the types of two sub-families; a neighbouring form which lived in Bolivia in the same epoch (HOFFSTETTER, 1968); perhaps also one can include the genus *Chubutherium* Cattoi, from the Colhuéhuapien, of equally great height, but of which the teeth are unfortunately not

known. They became extinct before the Santacrucian, leaving a vacant ecological niche which allowed the later development of the true Mylodontidae.

It remains possible that they constitute a distinct superfamily (Orophodontoidea), but this point cannot be usefully discussed until we have at our disposal more complete information on the constituent genera, and in particular on the temporal region (see below).

PHYLOGENY AND SUBDIVISIONS OF THE TARDIGRADES

ROMER (1966) introduced profound modifications in the classification of the tardigrades. He recognised two superfamilies: 1) the Megalonychoidea combined the Megalonychidae, the Megatheriidae (incl. Nothrotheriinae) and the Bradypodidae; 2) the Mylodontoidea, comprising the Mylodontidae (incl. *Orophodon, Octodontotherium* and *Chubutherium*) and, with reservations, the Entelopsidae.

Several preliminary remarks can be made:

- Megatherioidea Cabrera, 1929, p.426, has priority over Megalonychoidea Simpson, 1931, p.272, be it in the original sense (the two terms had been formally created, with an identical meaning), or in the limited sense adopted by ROMER (since the superfamily still includes the genera *Megatherium* and *Megalonyx*. This priority appears still clearer if one applies to it article 36 of the International Code of Zoological Nomenclature; the authors and dates valid for all the divisions are then: Megatherioidea Grey, 1821 (family Megatheriadae) and Megalonychoidea Ameghino, 1889 (family Megalonycidae).
- *Entelops* is too incompletely known to be interpreted with certainty. There is in any case no reason to group it especially with the Mylodontidae. If it is truly a tardigrade, as admitted by PASCUAL (1960), I think, with this author, that there are grounds for interpreting it as the survivor of an archaic group which merits its own superfamily (Entelopsoidea). Let us recall that AMEGHINO (1889, pp. 653-654) had created for them the group Pleiodonta.
- Concerning the genera *Orophodon, Octodontotherium* and possibly *Chubutherium*, I have already stated the reasons which led me to interpret them as an early branch, becoming extinct without any descendants towards the end of the Oligocene, and which has at least the grade of a family (Orophodontidae) or perhaps even a superfamily (Orophodontoidea).

For the rest of the tardigrades, it is necessary to recognise that the traditional classification is far from being satisfactory, and does not adequately take into account their phylogenetic relationships. For example, it exaggerates the importance of the separation between the sloths and the gravigrades. It does not admit the possibility of diphyly of the earliest forms. For the most recent, it regroups in the same sub-family (Nothrotheriinae) all the pre-Santacrucian forms (with the exception of the Orophodontidae). Now these forms certainly include the direct ancestors of the later individual branches, and in which one can distinguish, according to the importance of their divergence, tribes, sub-families, or families proper. But it is equally evident that at the beginning of their differentiation, the divergences are very weak and difficult to detect (this is not a problem unique to the tardigrades, it can be found in all groups at the beginning of their radiation).

The many anatomical studies, moreover, can give contradictory indications. PATTERSON has not yet clarified the criteria which he has used. But I shall mention here the observations of GUTH (1962, 1962) on the temporal region of the edentates. He unfortunately only studied a few fossil genera, which did not represent all the classical sub-families, but his studies already contribute several useful things. According to him, the temporal region, and more precisely the endotympanic, allows the distinction of two principal types, which characterise respectively the two existing sloths, and which can be designated as type *Bradypus* and type *Choloepus*. The former, which GUTH considered primitive because it is known from the Deseadan, was found by him with "*Hapalops*" *antistis* (Deseadan), with certain Santacrucian *Hapalops* (*H. adteger, H. elongatus, H. indifferens, H. rectangularis*) with *Eucholoepus* and also, although modified, with *Megatherium*. The second, unknown before the Santacrucian, is observed with other species of *Hapalops* (*H. brachycephalus, H. robustus*) with *Pelecyodon*, with *Nothrotherium*, with *Pliomorphus* (Ortotheriinae) and also with all the true Mylodontidae (*Nematherium, Analcitherium, Scelidotherium, Scelidodon, Glossotherium, Lestodon* and *Mylodon*).

Of course, it is not only about one criterion, which one must take into account (the temporal region is reputed to have great phyletic significance), but it would be futile to attempt to construct a genealogical tree on this alone.

This criterion in any case confirms the real heterogeneity of the Nothrotheriinae, in the traditional understanding, and even that of certain "*genres fagots*" (bundled groups) like *Hapalops*.

Besides, he brings some indications which do not entirely agree with the views of PATTERSON or with the classification of ROMER. I do not conclude from this that these views and this classification are wrong, since, once again, it is necessary to confront arguments drawn from diverse criteria, but it is certain that the debate is still open, at least on certain issues.

Concerning the sloths, *Bradypus* is grouped with the Megatheriinae as much by GUTH as by PATTERSON; on the other hand *Choloepus*, which PATTERSON puts in the Megalonychidae (limited sense), presents, according to GUTH, an endotympanic of the Mylondontid type.

Nothrotherium, which PATTERSON links to the Megatheriidae (wider sense) also presents (according to GUTH), an endotympanic of the Mylodontid type.

With regard to the true Mylodontidae, PATTERSON makes them derive from the Orophodontidae (of which, it should be stressed, we unfortunately do not know the temporal region). If it was thus, it is not well understood (unless there are parallels to show) how the endotympanic of the Mylodontid type appeared, after the Santacrucian, in diverse sub-families: Nothrotheriinae, Orthotheriinae, Cholœpodinae. On the other hand, the facts are much more clear if one admits that these sub-families, as well as the true Mylodontidae, are well established within the bushy assemblage constituted by the pre-Santacrucian Nothrotheriinae. But of course, that leads to taking again the classic concept of the Megatherioidea (Megalonychidae, Megatheriidae and Mylodontidae) in including also the Sloths (Bradypodidae or Bradypodidae + Choloepodidae if one accepts the diphyly).

Let us return to the classification of Romer (1966) and consider the interpretation given by him to the various families.

The Megalonychidae of Romer comprise the classical sub-families of the Megalonychinae (incl. *Valgipes*), Megalocninae, Ortotheriinae and Ocnopodinae. The only diagnostic characters indicated in the text (absence of symphyseal fossa) and differentiation of the canines) are not always checkable and do not permit a satisfactory definition. Above all, it seems that the constituent sub-families are in fact late branches (Pliocene - Pleistocene), probably derived from a common trunk and excluded from the family (sub-family Nothrotheriinae, re-attached by Romer to the Megatheriinae). In this interpretation, then, the Megalonychidae constitute a polyphyletic assemblage. To make them into a natural group, it is necessary to include the common ancestor (a poorly defined part of the Nothrotheriinae) from

which the constituent branches have derived. It appears, moreover, that this is the goal aimed at by PATTERSON, since he (1967, table p. 771), contrary to ROMER, raised the Megalonychidae to the Upper Eocene, and possibly to the Middle Eocene. (Let it be noted on this subject a contradiction, since according to the text, the presence of "Pilosa" is only proved from the Lower Oligocene).

The Megatheriidae of ROMER groups together the Megatheriinae, the Planopsinae and the Nothrotheriinae (classical sense). We have already seen that the latter are heterogeneous, and that it is improper to attribute them in their entirety to the Megatheriidae (classification of ROMER, 1966). It seems moreover that PATTERSON, in proposing to re-attach the "Nothrotheres" (PATTERSON & PASCUAL, 1963, p.142) or the "Nothrotheriines" (PATTERSON, 1967, p.772) to the Megatheriidae, did not envisage, as did ROMER, all of the Nothrotheriinae in the classical sense of the term. Indeed, in his table (PATTERSON, 1967, p. 771) he makes the Megatheriidae start at the Higher Oligocene, while the Megalonychidae are earlier.

The Mylodontidae, in my sense and as already stated, must be brought back to their classical understanding while excluding the Orophodontidae. They are not known before the Santacrucian, and are probably rooted in the common trunk of the "Nothrotheriinae". They divided early on into two sub-families, Scelidotheriinae and Mylodontinae. Let us note on this subject, that according to the cranial architecture, the form of the teeth and also, according to GUTH, the characteristics of the temporal region, the first known genera (*Nematherium, Analcitherium*) go better with the Scelidotheriinae than with the Mylodontinae. On the other hand, their astragalus no longer presents a concave facet to receive the cuboid (a character gained secondarily by the Scelidotheriinae, and often considered as diagnostic for the sub-family). Perhaps one approaches more of a natural classification in modifying the diagnoses so as to include the two genera considered in the Scelidotheriinae (see HOFFSTETTER, 1962, p.359).

The sloths are probably diphyletic, this must logically lead to the recognition of the two families (Bradypodidae and Choloepodidae) and the abandoning of the term 'Bradypodoidea'. Unfortunately, no fossils are known. But, if one takes account of the indications of PATTERSON and the observations of GUTH, one can suppose that *Bradypus* is the successful realisation of a branch which fits into the common trunk ("Nothrotheriinae") in the proximity of the point of separation of the Megatheriinae. The Choloepodidae derive from another branch which equally

gave rise to the Ortotheriinae (Megalonychidae according to all authors) and the Mylodontidae (see HOFFSTETTER, 1962, pp. 359-360).

These several reflections still leave out some obscure points. In particular the necessary fragmentation of the "Nothrotheriinae", and the delimitation between Megalonychidae and Megtheriidae can only be envisaged after a precise study of the various genera, some of which are unfortunately known only by pieces which are much too incomplete.

PHYLOGENY AND CLASSIFICATION OF THE CINGULATA

The armadillos (Dasypodoidea) constitute a natural group, relatively homogenous, in spite of their apparent bushiness. They comprise numerous branches, descended from an axial group leading to the extant banded armadillos. The most divergent branches were considered at first as families, then as simple sub-families. Finally, PATTERSON (1967) recognised no more than one sole family (Dasypodidae) and included in it the Peltephilinae. In fact the class accorded to each branch still presents a conventional character, and, in the present case, the divergences do not translate into phylogenetic concepts.

It is more difficult to decide on the Pseudorophodontidae (*Pseudorophodon*), which ROMER (1966) places in the Dasypodoidea, acknowledging in them the rank of family. With good reason, and under another name, KRAGLIEVICH & RIVAS (1951) thought of them as a distinct super-family ("Orophodontoidea") distinct at the same time from the armadillos and the glyptodonts; this is also the opinion of PATTERSON & PASCUAL (1963). If it is recognised, this super-family should receive the name of Pseudorophodontoidea.

A closely related problem is posed by the Palaeopeltidae (*Palaeopeltis*), which perhaps merge with the previous (opinion of PATTERSON & PASCUAL, 1963), and for which ROMER has created the super-family Palaeopeltoidea. I have already urged caution, about a group of which we know only elements of the carapace. For my part, I prefer to consider *Palaeopeltis* as a Xenarthra *incertae sedis*.

The glyptodonts (Glyptodontoidea) appeared in the Mustersan (Middle or Upper Eocene), and diversified up to the Deseadan (a new genus, distinct from *Glyptatelus*, has been gathered by R. PASCUAL at El Pajarito, Chubut).

The origin of the group is still problematical. PATTERSON (1967, p. 722) thinks that it probably derives from the "chlamytheriine dasypodids", in other words, the Pampatheriinae. This

is not very probable, for these are only known for certain from the Upper Miocene (Argentina and Colombia). It is true that STIRTON (1953, p. 611) reports some plates from a "large chlamythere" from the Coyaima (Upper Oligocene or Lower Miocene) of Colombia, though without figuring them; one may therefore suppose that the group is more ancient in the intertropical zone, but it is doubtful if it had been established from the Eocene.

For my part, I envisage above all a derivation of the glyptodonts being from the close forms *Pseudorophodon* (of which the age is not known), and *Machlydotherium* (Eocene genus poorly known, of which the mobility of the dorsal plates is in decline in relation to those of the primitive armadillos, which, it can be said in passing, rules it out of consideration as a possible ancestor of the Pampatheriinae: see HOFFSTETTER, 1956*b*, p.58). But nothing precise can be suggested until we have a better knowledge of these two genera or their related forms.

Two final remarks, concerning generic nomenclature:

- The Pampatherine from the Pleistocene of the Carolina (Ecuador), described under the name *Chlamytherium occidentale* Hoffstetter, 1952, has been attributed by others (HOFFSTETTER, 1953) to the genus *Holmesina*. On the same species, CASTELLANOS, (1957) has founded the genus *Hoffstetteria*, which is evidently synonymous with *Holmesina*. The latter, very definitely, can be conserved as a true genus, or admitted as a sub-species of *Pampatherium*.

- Along with all other authors at that time, AMEGHINO believed that *Hoplophorus euphractus* Lund, from Brazil, and *Glyptodon ornatus* Owen, from Argentina, were co-generic; furthermore he considered (incorrectly according to the existing rules) that *Hoplophorus* Lund, 1838, was not valid because of homonymy with *Hoplophora* Perty, 1830, *Oplophorus* Milne-Edwards 1837, etc. As a replacement, he has therefore created the genus *Sclerocalyptus*, in which he placed both species, while expressly designating *ornatus* as type species of the genus (AMEGHINO, 1891, p.251). It is not, therefore, a simple name substitution such as apparently admitted by ROMER (1966) after PAULA COUTO. In fact, since PAULA COUTO has demonstrated that the two species belong to distinct genera, which should receive the names respectively *Hoplophorus* Lund, 1838 (type *H. euphractus* Lund) and *Sclerocalyptus* Amegh., 1891 (type *G.*

ornatus Owen). The name *Neosclerocalyptus* Paula Couto, 1957, equally based on the species *ornatus*, falls into synonymy with *Sclerocalyptus* (see HOFFSTETTER, 1963, note 1, p.128).

Too much uncertainty remains for me to be able to give, in a new outline, the actual state of our knowledge of the phylogeny of the xenarthran edentates. All in all, with some minor modifications, the table which I have published in the Treatise of Palaeontology (*Traité de Paléontologie*) (HOFFSTETTER, 1958, fig. 2, p. 537) still conveys in a satisfactory manner my ideas on the reciprocal relationships of the various groups. It is sufficient to delete the name *Protobradys* (which has not yet been figured and which SIMPSON has just rejected from the edentates); to replace the sloths (recognised as diphyletic) by two branches (Bradypodidae and Choloepodidae), separate lines from the pre-Santacrucian "Nothrotheriinae" stock; to place *Machlydotherium* to the left of the tree of the armadillos to indicate that it could be at the origin of the glyptodonts; and to figure, in the vicinity of the previous, the genus *Pseudorophodon* (wrongly dated) which also illustrates a group intermediate between the armadillos and the glyptodonts. As for the rest, the grouping together or the splitting can be viewed as being driven by the modifications in our understanding of the families, without having indicated any profound changes in the phyletic relationships found between the different branches.

Translation: Philip Adds, Queen Mary University of London, 2001.