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PROVISIONAL CLASSIFICATION OF EXTINCT SOUTH AMERICAN HOOFED MAMMALS¹

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Since their discovery by Darwin over a century ago, the native ungulates of South America have enjoyed, or suffered, an unusually checkered taxonomic career. This distinction was guaranteed them by their puzzling morphological dualism. On one hand, they are remarkably exotic in comparison with the fossil or recent mammals of any other continent, and on the other they parallel these mammals in many features, now considered largely adaptive or secondary, in a way often amazing. Ameghino, the greatest authority, came to consider the resemblances as of prime importance, and his later classifications reflect these almost exclusively; but if his discussions are read it will be found that in most cases he also recognized and interpreted, on the whole correctly as now appears, those characters peculiar to the South American beasts. Most other students emphasize these more aberrant characters and base classification primarily on them. This now seems to be correct and necessary, but it places taxonomists in the embarrassing position of having to leave most South American groups hanging in the middle of the world classification with no visible means of support. The Ameghinoan method is intellectually more satisfying, but unfortunately it seems almost certainly to be farther from the truth.

No classification yet presented is very satisfactory, and none has any good chance of surviving very long. The same is true of the present attempt. But each brought out some new and useful feature. In the present case, aside from the effort to embody new discoveries in this field and new viewpoints in the general science, the principal feature is the consideration of the light cast on these problems by pre-Santa Cruz fossils. Except Ameghino, no one has previously been able to study these in detail and at first hand, and their evidence is of crucial importance in many if not most points. A great deal remains to be done, even with the material now in hand (especially that of the Scarritt Expeditions of 1930-31 and 1933-34), but already enough is known to demand some revision, and to invite its prompt publication in the hope of criticism and discus-

¹Publications of the Scarritt Expeditions, No. 22.

sion. An attempt has also been made to digest the alarmingly extensive literature of the groups and incorporate the results in this trial sheet classification.

The groups here considered are those ungulate in the broadest sense which occur in South America previous to the Late Tertiary incursion of surely Holarctic types. Of this great assemblage not one trace survives. Every family and every order is extinct. The consensus is that only two groups are known from outside South America, the condylarths being typically Holarctic but also (I believe) present in the Eocene of South America, and the notoungulates of the new suborder Notioprogonia typically South American but, although scantily, indubitably represented also in North America and in Asia.

Renewed thanks are due to the authorities of the Museo Argentino de Ciencias Naturales¹ in Buenos Aires, and particularly to its director, Dr. M. Doello Jurado, for access to the Ameghino Collection and facilities for its study², and also to H. S. Scarritt, E. S. Riggs and the Field Museum, and several others whose cooperation has incidentally been of great value in the present study although primarily granted in connection with the faunal revisions and other researches now in progress.

PREVIOUS CLASSIFICATIONS

From the many previous classifications of the groups here considered, those of Lydekker (1894), Ameghino (in its definitive form, 1906), Gregory (and Osborn, in Osborn 1910), Scott (in its definitive form, 1913), and Schlosser (1923) are selected to give some idea of typical opinions and taxonomic trends. Lydekker's classification represents essentially a broad European viewpoint, based on much personal study, progressive at the time but dating from near the beginning of the full flood of discovery, essentially the first modern classification. Ameghino's classification, one of the fruits of a life-time of excellent work, represents the mature opinion of the authority whose first-hand knowledge has not been equalled before or since, but also reflects a peculiarly narrow and personal point of view not shared by any other student. The Gregory system (edited and accepted by Osborn) represents a highly competent synthesis adapting the concrete data of Ameghino, and others, to the broad views more generally held, then and now, by European and North American students. Scott's classification, unquestionably the best available and in general here modified only as far as made necessary by

¹Formerly the Museo Nacional de Historia Natural.

²A descriptive catalogue of the two earliest faunas is nearly completed.

subsequent extension of knowledge, represents first-hand study of the most typical forms from this broader point of view and with new data unknown to Ameghino. Schlosser's work, while including some unacceptable and peculiar personal points, is a widely used and relatively modern synthesis, which also involves some first hand acquaintance with the fossils.

LYDEKKER, 1894.

Order UNGULATA

Suborder TOXODONTIA

Pachyrucidae

Typotheriidae

Toxodontidae

Suborder ASTRAPOTHERIA

Homalodontotheriidae

Astrapotheriidae

Suborder LITOPTERNA

Proterotheriidae

Macrauchiidae

AMEGHINO, 1906.

*PROSIMIAE

Archaeopithecidae

Notopithecidae

Henricosborniidae

*HYOPSODONTIDAE

Clenialetidae

Eudiastatidae

*HYRACOIDEA

Acoelodidae

Archaeohyracidae

TYPOTHERIA

Eutrachytheriidae

Hegetotheriidae

Protypotheriidae

Typotheriidae

TOXODONTIA

Nesodontidae

Xotodontidae

Haplodontidae

Toxodontidae

*HIPPOIDEA

Colpodontidae

Notohippidae

†CONDYLARTHRA

Pantostylopidae

*Phenacodontidae

*Catathleidae

- *Pantolambdidae
- *Arctocyonidae
- *PERISSODACTYLA
 - *Hyracotheriidae
 - *Palaeotheriidae
 - Protherotheriidae
 - Macraucheniiidae
 - Adiantidae
- *PROBOSCIDEA
 - Carolozitteliidae
 - Pyrotheriidae
- *AMBLYPODA
 - Trigonostylopidae
 - Albertogaudryidae
 - Astrapotheriidae
- *LOPHIODONTIDAE
- *ANCYLOPODA
 - Isotemnidae
 - Homalotheriidae
 - Leontiniidae
- *TILLODONTA
 - Notostylopidae

[The classification is compiled from all Ameghino's separate faunal lists, but the grouping and succession are his. Groups marked * are Holarctic and not now believed to occur in the early Tertiary of South America. That marked † is Holarctic, principally, but I agree that it does appear in South America.]

OSBORN, 1910. This arrangement was published by Osborn but is by him credited to Gregory. The classification published by Gregory (1910) in the same year differs, however, in considering the Notoungulata as an order, with the other super-family groups as suborders, in uniting the Toxodontia and Typotheria under the former name, and in recognizing the families Henricosborniidae (doubtful, in the "Homalodotheria"), Nesodontidae, and Prototypotheriidae. Presumably these differences are due to Osborn's editing of the classification here copied.

Order CONDYLARTHRA

Fam. *Inc.*

Didolodus, etc.

Superorder NOTOUNGULATA

Order TOXODONTIA

Suborder HOMALODOTHERIA

Notostylopidae

Homalodotheriidae

Suborder ASTRAPOTHERIA

Inc. sed. Albertogaudryidae

Inc. sed. Isotemnidae

Astrapotheriidae

- Suborder TOXODONTIA
 - Inc. sed.* Archaeohyracidae
 - Toxodontidae
- Suborder TYPOTHERIA
 - Interatheriidae
 - Hegetotheriidae
 - Typotheriidae
- Order LITOPTERNA
 - Proterotheriidae
 - Macraucheniidae
- Order PYROTHERIA
 - Pyrotheriidae

SCOTT, 1913. This nearly represents the present views of this authority, as his later work (e.g., 1932) changes a few details but in the main confirms his earlier opinions.

- Order TOXODONTIA
 - Suborder TOXODONTA
 - Toxodontidae
 - Notohippidae
 - Leontiniidae
 - Suborder TYPOTHERIA
 - Typotheriidae
 - Interatheriidae
 - Hegetotheriidae
 - Notopithecidae
 - Archaeopithecidae
 - Archaeohyracidae
 - Suborder ENTELONYCHIA
 - Notostylopidae
 - Isotemnidae
 - Homalodontotheriidae
 - Suborder PYROTHERIA
 - Pyrotheriidae
- Order ASTRAPOTHERIA
 - Astrapotheriidae
 - Trigonostylopidae
- Order LITOPTERNA
 - Macraucheniidae
 - Proterotheriidae
 - Didolodidae

SCHLOSSER, 1923.

- Order UNGULATA
 - Suborder LITOPTERNA
 - Bunolitopternidae¹
 - Macraucheniidae

¹A curious and invalid emendation of Didolodidae Scott. There is no generic name on which this family name could be based.

- Proterotheriidae
- Adiantidae
- Suborder AMBLYPODA
- Pyrotheria¹
- Order NOTOUNGULATA
- Suborder TYPOTHERIA
- Notopithecidae
- Interatheriidae
- Hegetotheriidae
- Typotheriidae
- Archaeopithecidae
- Archaeohyracidae
- Suborder TOXODONTIA
- Notohippidae
- Nesodontidae
- Toxodontidae
- Suborder ENTELONYCHIA
- Arctostylopidae
- Notostylopidae
- Isotemnidae
- Leontiniidae
- Homalodontotheriidae
- Suborder ASTRAPOTHERIOIDEA
- Trigonostylopidae
- Albertogaudryidae
- Astrapotheriidae

NEW CLASSIFICATION

The following proposed classification is based on all those given above, and many others, as well as on study of original specimens. Of previous classifications, while each has its peculiar merits and marks a progressive step, that of Scott is worthy of special note, as it combines a first hand knowledge of the material equalled only by Ameghino with a broader and less biased viewpoint as well as the progress of science since Ameghino completed his work on this subject.² Any departure from Scott's arrangement requires special defense. The considerations on which the new arrangement is based are given below under the name of each major group.

Order CONDYLLARTHA Cope, 1881.

Didolodontidae Scott, 1913.³

¹Given in this form as a family, an invalid procedure.

²Although Ameghino continued work until his death in 1911, his classification had reached its definitive form in all essentials by 1904.

³Emended from Didolodidae. I do not consider such an orthographic change as altering the authorship of the name.

- Order LITOPTERNA Ameghino, 1889.
 - Macraucheniidae Gill, 1872.
 - Protheroetheriidae Ameghino, 1887.
- Order NOTOUNGULATA, Roth, 1903.
 - Suborder NOTIOPROGONIA, new.
 - Arctostylopidae Schlosser, 1923.
 - Henricosborniidae Ameghino, 1901.
 - Notostylopidae Ameghino, 1897.
 - Suborder ENTELONYCHIA Ameghino, 1893.
 - Isotemnidae Ameghino, 1897.
 - Homalodotheriidae Ameghino, 1889.
 - Suborder TOXODONTA Owen, 1858.
 - Notohippidae Ameghino, 1894.
 - Toxodontidae Gervais, 1847.
 - ?Leontiniidae Ameghino, 1895.
 - Suborder TYPOTHERIA Zittel, 1893.
 - Notopithecidae Ameghino, 1897.
 - Interatheriidae Ameghino, 1887.
 - Typotheriidae Lydekker, 1886.
 - Hegetotheriidae Ameghino, 1894.
 - ?Archaeohyracidae Ameghino, 1897.
 - ?Acoelodidae Ameghino, 1901.
- Order ASTRAPOTHERIA Lydekker, 1894.
 - Suborder ASTRAPOTHERIOIDEA¹ Ameghino, 1894.
 - Astrapotheriidae Ameghino, 1887.
 - Suborder TRIGONOSTYLOPOIDEA, new.
 - Trigonostylopidae Ameghino, 1901.
- Order PYROTHERIA Ameghino, 1895.
 - Pyrotheriidae Ameghino, 1889.

CONDYLARTHRA

Ameghino believed that many of his Casamayor and a few of his Musters and Deseado fossils represented the Condylarthra. While he was almost surely mistaken as regards some of these (e.g., the whole family Pantostylopidae, which I consider synonymous with the Henricosborniidae and true notoungulates), others are so like condylarthrs as to lend at least a strong suspicion that he was right. This resemblance has been recognized by most later students, but with few exceptions² they have more strongly emphasized the also real resemblance to the litopterns and have placed these genera in the Litopterna. After re-studying all of Ameghino's material and a number of other specimens, practically all that are known, I can find no definite characters which exclude *Didolodus* and its close allies from the Condylarthra. It is

¹Emended from Astrapotherioidea.

²Roth, for instance, placed these genera in a distinct group Didolodia and denied litoptern affinities.

quite possible that they represent approximately an ancestral stage through which the litopterns passed, but in themselves they have no diagnostic litoptern characters. As knowledge of them is not very good, it is possible that the condylarth resemblance is not conclusive, but on the evidence now available it must be concluded that Ameghino was right and that this group must be classified in the Condylarthra. Their reference to the Phenacodontidae, however, seems to overemphasize the resemblance to Holarctic forms, and it seems best to retain the distinctive South American family Didolodontidae.

LITOPTERNA

Ameghino proposed the name Litopterna for an order (or suborder—the intention is not clear) of the group Perissodactyla, with approximately the contents now accepted except that the Homalodotheriidae were at first included. The latter surely extraneous element was later removed by Ameghino. Later (e.g., 1906) he abandoned the name Litopterna and simply referred the litoptern families Proterotheriidae and Macrauchiidae to the Perissodactyla. Other students, however, notably Scott in his definitive revision of the Santa Cruz forms (1910), did not accept the reference to the Perissodactyla and so retained the name Litopterna for an order or suborder sometimes placed with the notoungulates, and sometimes as a separate group of uncertain affinities. That the litopterns are a distinctive natural group with no near affinities with perissodactyls is now universally recognized, but there are many shades of opinion as to their nearness of relationship to the notoungulates. Some (e.g., Gregory 1910, Loomis 1914) place them within the Notoungulata. Others follow Scott (1910) in retaining them as a separate order, but one of common origin with the Notoungulata (his Toxodontia). Still others (e.g., Schlosser, 1923) reject any close connection with the notoungulates and emphasize the evidence of derivation from the condylarths.

As a matter of practical taxonomy, these forms should surely be placed in a separate Order Litopterna. As a matter of opinion, I do not see how their relationship with the notoungulates can be closer than through a condylarthran or condylarth-like, very remote common ancestor, which means little more than that they are all ungulates or “subungulates.”

The families Proterotheriidae and Macrauchiidae are certainly valid and universally recognized. The Didolodontidae have been removed to the Condylarthra, as stated above. The fourth supposed

family, *Adiantidae*, is so badly known as to have no real value and I prefer to follow Scott in tentatively uniting it with the *Macraucheniidae* at least until better known. In the *Casamayor*, especially, there are a few genera, most of them based on single teeth, which are of doubtful affinities and may eventually warrant family separation, but at present it seems better to distribute them tentatively in the *Proterotheriidae* and *Macraucheniidae*.

NOTOUNGULATA

The appropriate name *Notoungulata* ("Southern ungulates") was proposed by Roth (1903) on the basis of the peculiar structure of the temporal region especially noted in toxodonts and typotheres. *Litopterns*, *astrapotheres*, and *pyrotheres* were clearly excluded by the definition and intention of the author, and the *notostylopids* and *homalodontotheres* were explicitly included. As proposed, therefore, the group *Notoungulata* had exactly the same scope as that here given it, including *Notioprogonia* (hitherto part of the *Entelonychia*), *Entelonychia*, *Toxodonta*, and *Typotheria*. Scott (1904) preserved Roth's grouping, but applied to it the name *Toxodontia*, distinguished from the smaller group *Toxodonta*, and he also proposed to extend Roth's name *Notoungulata* to include the *Toxodontia* (in the *sensu lato* of Scott), the *Litopterna*, and the *Astrapotheria*. Later (see 1913), Scott dropped the name *Notoungulata*, made his Order *Toxodontia* include the suborders *Toxodonta*, *Typotheria*, *Entelonychia*, and *Pyrotheria*, and made separate orders of the *Astrapotheria* and *Litopterna*.

In this I cannot follow Scott. The use of *Toxodontia* and *Toxodonta* for two groups of different rank is not strictly invalid, but is inconvenient and is to be avoided if possible without confusion and without coining new names unnecessarily. *Toxodontia*, as proposed by Scott, was really an exact synonym of *Notoungulata* Roth, and I see no reason for rejecting the latter much less confusing and very appropriate name. Whether it is to be extended to include also groups at first excluded by Roth seems to be beside the point, and in any event there is no strong evidence for such extension at present. It is also beside the point that the group is now defined on a broader basis than used by Roth and that he may have overemphasized and to some extent misunderstood the ear and temporal region characters.¹

¹Scott (1932) recently suggests that if Order *Toxodontia* be raised to superordinal rank, Roth's name *Notoungulata* should be adopted. It is difficult for me to follow the logic of this proposal. No change of contents is proposed. It might be argued that a change of rank in itself warrants change of name (with which I strongly disagree), but Roth did not propose *Notoungulata* as a superorder, but explicitly as a suborder of the *Ungulata*, fully corresponding in usage with an order of ungulates in all modern classifications.

In the Notoungulata I include the now classical groups Entelonychia, Toxodonta, and Typotheria, as well as the new Notioprogonia, defined below.

Suborder **NOTIOPROGONIA**¹ new

DISTRIBUTION.—Paleocene, Mongolia. Eocene, North and South America.

DIAGNOSIS.—An early suborder of Notoungulata, including some primitive, rather generalized forms and a few ancient divergent lines superficially specialized but basically primitive.

Dentition complete or with $I\frac{3}{2}$ $C\frac{1}{1}$ $P\frac{1}{1}$ variously reduced. All cheek teeth brachydont, without cement. Upper premolars progressively complicated, but all triangular or nearly so, with protocone at least on $P^{2,4}$ and hypocone very feeble or absent. Upper molars transverse, with strong parastyle, well formed ectoloph and oblique protoloph, but metaloph variable and often imperfect. Crochet present, anteroposterior when elongated, and generally free of ectoloph. Other secondary folds or crests slight or absent. M^{1-2} quadrate, with strong hypocones, nearly or quite equal to protocones. M^3 large but triangular, hypocone small or unrecognizable as such. Lower premolars essentially bicrescentic, with subequal trigonid and talonid. Lower molars with very short trigonids and long talonids. Trigonid essentially a single transverse lophid, anterior wing reduced, paraconid inconspicuous and median or relatively external. Talonids with a strong, elongate, crescentic lophid and simple, transverse, crested entoconid pillar, without secondary connections or crests.

Rostrum, as far as known, short, deep, and rather narrow. Nares terminal. Zygomata arising opposite anterior molars. Cranium (Notostylopidae, unknown in other families but probably similar) markedly triangular between squared zygomata. Strong postorbital constriction. Endocranial cast much in as typotheres, but more primitive. Ear region of generalized notoungulate type, epitympanic sinus relatively small, porus low, ossified meatus short and nearly horizontal, tympanic crested, hypotympanic sinus large and globular, extending far ventral to basisphenoid, cranio-facial flexion slight.

Mandible rather elongate and slender, tooth series nearly straight.

Although reluctant to add to an already burdensome nomenclature, the considerations given below and the more detailed data bearing on the structure and relationships of the several early groups of notoungulates lead to the conclusion that the creation of a fourth suborder of Notoungulata, here named Notioprogonia, is necessary for greatest clarity and simplicity of expression. The Notostylopidae are the best known of the notioprogonians, but here should also be included the families, still less specialized at least in the dentition, Henricosborniidae and Arctostylopidae. These seem to form a natural, varied group, on present evidence,

¹*υόριος*, southern, *πρόγονος*, ancestor, to suggest the primitive character of the group and its more or less archetypal relationships with the typically southern Notoungulata. There seems no possibility of confusion with *Notoprologonia*, which is a generic name, invalid (a synonym), and different in spelling, pronunciation, and derivation (*υόριος*, south, *πρώτος*, first, *γωνία*, angle). Schlosser does list a "*Notoprogonia*," but even aside from derivation, spelling, and the question as to whether a generic name can preoccupy one of higher rank, this was an obvious misprint or error for *Notoprologonia* (itself invalid) and has no standing in nomenclature.

and in general the Notioprogonia may at least tentatively include such early, primitive or only superficially specialized, short lived groups of notoungulates as have no clear and special relationships to one of the three other suborders, Toxodonta, Typotheria, and Entelonychia.

The affinities of the Arctostylopidae, aside from casual mention, have been discussed only by Matthew (1915) and by him only in a preliminary and brief way, without the benefit of the much richer material now at hand. Although referring *Arctostylops* to the Entelonychia, and even questionably to the family Isotemnidae, this was merely taxonomic conservatism and does not represent his expressed views as to general affinities. He compared this form chiefly with *Notostylops* and placed *Arctostylops* (and later *Palaeostylops*) in the Entelonychia largely because he accepted the common view that *Notostylops* belongs there. He held that the relationship to the Entelonychia was probably similar to that of *Metacheiromys* to the Loricata. In other words, as is clear from his other work and general usages, he believed that the arctostylopids were subordinally distinct but did not wish to make them so until better known. The view thus rather vaguely adumbrated is similar to that to which I have now come, quite independently and on the basis of a very large body of evidence not available to Matthew.

The Henricosborniidae (with the Pantostylopidae, etc.) have hitherto been studied only by Ameghino (see final conclusions in 1906), who places some of them in the "Prosimiae" as primates and some in Condylarthra. When they mention them at all, other writers have rejected these views, on general principles, and without restudy have placed this group in various notoungulate suborders. Thus both Scott (1913) and Schlosser (1923) placed some or all of them in the Typotheria probably because of a quite natural confusion with the Notopithecidae, which are typotheres but are quite distinct from the henricosborniids. It now appears probable that these very primitive forms, while they might be structurally ancestral to any of the three previously recognized suborders, are not definitely referable to any one of them. They do seem to be fairly close to the notostylopids and placing them in this new suborder, Notioprogonia, is a simple solution of the taxonomic and phylogenetic difficulties as now visualized.

The group Entelonychia was founded by Ameghino on the basis of the Homalodotheriidae, and especially of *Homalodotherium* itself, and defined on foot characters. He always considered the homalodotheres as related to chalicotheres (another case of convergence mistaken for affinity) and finally (e.g., 1906) he abandoned the name of Entelony-

chia and placed the Homalodotheriidae in the Ancylopoda. The other groups considered entelonychian by other authors were distributed in various orders. Although abandoned by its author, the name Entelonychia has been revived or continued in use by others and is now a generally accepted and quite necessary name in the taxonomy of notoungulates.

From this history it is clear that the name Entelonychia is principally based on *Homalodotherium* and is properly applicable only to include relatives of that genus. The propriety of placing *Notostylops*, *Henricosbornia*, *Palaeostylops*, etc., in the Entelonychia depends on the degree of their relationship to *Homalodotherium*, also taking into account, of course, the earlier forms ancestral or clearly allied to that genus. The reference of these groups to the Entelonychia depends on the statement or clear implication that they are more nearly related to the homalodotheres than to any typotheres or toxodonts. Although this is the common, almost traditional, expression, the actual evidence does not warrant such unanimity.

If a group Entelonychia is to be defined so as to include the Notostylopidae and still more primitive families, it must be based on the following characters, which are about the only important ones shared by homalodotheres and notostylopids:

1. Dentition brachyodont, rooted.
2. Cement absent.
3. Molars broader than long.
4. Premolars less complex than molars.
5. Auditory region of generalized notoungulate type, epitympanic sinus and related occipital exposure of pars serialis relatively small, porus rather low.
6. Skull orthocephalic, with long basicranial region.

Every one of these characters and apparently all the features that could be included in such a diagnosis are primitive and not really distinctive. They exclude the more specialized, later toxodonts and typotheres, but do not exclude the earlier members of those groups. All these characters do occur in the Toxodonta and Typotheria and are either known or with high probability inferred to have been universal in their early forms.

Even though *Notostylops*, *Henricosbornia*, *Palaeostylops*, and related genera resemble the homalodotheres only to the extent that both retain some primitive characters, some degree of special affinity might be suggested if the forms mentioned retained these characters after they had disappeared in the other suborders, but this is not the case. So far

as they are known, contemporaneous or even some later typotheres and toxodonts are not significantly more advanced in these respects than are the forms here placed in the Notioprogonia.

The homalodotheres are distinguished to a degree usually and reasonably considered subordinal, by the retention of certain primitive characters, such as the complete brachyodont dentition and pentadactyl feet, accompanied by the development of certain remarkable specializations not closely paralleled in other notoungulates, progressive or variable in the group, such as the canine tusks, retracted nasals, and extraordinary skeletal developments. The notioprogonians have been placed with this group largely because comparison was made mainly or only with much later forms, and was confined to a few primitive characters which were normal if not universal in the notoungulates of Casamayor age but were later lost except in the homalodotheres.

The notostylopids had, in fact, already lost some of the primitive characters, such as the closed tooth series, still present in the much later *Homalodotherium* and they did not have any of the peculiar specializations of the homalodotheres, early or late. The dentition gives no evidence of affinity beyond the fact that all are notoungulates. The general adaptive type and trend are different. The molar pattern also is distinctive. There is, for instance, more resemblance between the earliest typotheres and entelonychian molars than between either and *Notostylops*. The skulls are similar in so far as both are primitive. That of *Notostylops* seems to be very generalized, but it has some specialization, and this is not at all in the direction of the homalodotheres. As pointed out elsewhere (Simpson, 1933B), the braincasts, even in forms in comparable stages of development, indicate different lines of descent, and indeed tend to bring *Notostylops* closer to the typotheres than to the homalodotheres. The evidence of the skeletal parts, so far as the imperfect data go, is similar.

The almost inevitable conclusion is that the notostylopids are an early offshoot of the Notoungulata which shows no evidence of closer affinities to the Entelonychia (*sensu stricto*) than to other groups of notoungulates. They are a side branch, appearing as a minor and less distinctive group chiefly because of their early extinction and lack of more highly specialized Miocene or later descendants.

The general problem involves also the other early forms, less well known than *Notostylops*, which are also primitive and related in a general way to the various suborders of more long-lived and specialized notoungulates but not to any particular one of these suborders.

The broad nature of the phylogenetic relations indicated is, of course, subject to much possible modification from further discovery but as a theory on present evidence this is well founded and fairly clear and comprehensible. Its formulation and necessary taxonomic expression, however, are a difficult problem.

This problem is not unique and similar situations frequently arise in dealing with early mammals of any group or region. There seem to be three general types of solutions, none thoroughly satisfactory except as a working compromise, but each supported by good precedent and authority:

1. The later taxonomic group (suborder in this case) that is, on the whole, the most conservative might be broadened to include the ancestry of the whole larger unit (Order Notoungulata) and its early lines (such as the Notostylopidae, Henricosborniidae, etc.) regardless of whether the latter have any special affinity with the later members of this particular taxonomic group (suborder).

2. Each of these early lines, if it cannot be shown to be more closely related to one of the later groups than to another, or if it can be shown not to be, might be given a separate taxonomic position (necessarily subordinal in this case). Strict "vertical" or so-called phyletic classification demands this procedure and admits no alternative.

3. The undifferentiated ancestry of the whole larger unit (Notoungulata) and its relatively little modified early and sterile offshoots (including the Notostylopidae) might be placed in a unit (suborder) separate from the more long-lived and, eventually, more strongly modified and distinctive lines.

As a more or less analogous example of the first solution, may be cited the use of Insectivora to cover not only the relatively specialized recent representatives of that order but also many primitive and early mammals which have little or nothing in common with the modern insectivores except characters primitive for most or all placentals. In recent classifications there seems to be a drift away from this method and some tendency to place these early forms in distinct orders as they become better known, but this practice still holds to a certain extent.

Somewhat analogous examples of the second method are numerous. On a smaller scale, the separation of the hyracodonts from the true rhinoceroses as a non-ancestral group (family) of equal rank is an example. Because of the stressing of the more phyletic ideal in taxonomy and also, perhaps, because of some tendency to split hairs in such phyletic research, this has become probably the commonest course to follow in such cases.

A very closely analogous example of the third type of solution is the currently accepted classification of the Order Carnivora, the Suborder Creodonta including the ancestors of all later carnivores and also various highly distinctive but relatively short-lived early side branches, such as the hyaenodonts or mesonychids.

Of these practices, the last seems to me applicable to the present case with greatest convenience and least confusion. If, as has usually been done in the immediate past, the name Entelonychia be extended to include these early side branches, much confusion must result, as already suggested in part. The later and typical Entelonychia are not really generalized but in most respects very highly specialized. Whether they retain more primitive characters than contemporaneous members of other suborders, as has been implied, is really very debatable. Study of the recently discovered skeleton of *Homalodotherium* (Scott 1930), for instance, certainly will lead to great hesitance in accepting this view. From the Casamayor to post-Santa Cruz, the Entelonychia in a limited sense are a varied but quite distinct group. To include *Henricosbornia*, *Notostylops*, etc., in that group is in itself highly anomalous, and if the present views as to the real affinities of these genera are accepted, this would necessarily lead to the further anomaly of making the Entelonychia ancestral to all other notoungulates—an arrangement hardly less peculiar and unsatisfactory than would be the inclusion of the ancestral perissodactyls in the Chalicotherioidea, for instance.

The Suborder Notioprogonia is, therefore, named and defined to solve the present problem. The creation of this fourth suborder makes the differentiation of the other three much easier and renders it possible to make an arrangement of all the adequately known notoungulates which is relatively free of anomalies and confusion. The suborder is largely, but not exclusively, defined on primitive and negative characters. This does not necessarily make the group less distinctive, even verbally, since it includes no strongly aberrant forms which need to be considered as exceptional within it and since the other groups include no adequately known forms which are readily confused with notioprogonians. Like any taxonomic division the character of which is in part "horizontal," this suborder may prove to be unnatural to the extent of including phyla which may later prove to be more decisively separable, but as a whole it does now appear to be a natural unit and, furthermore, to be justified if on no other basis than that of convenience in dealing with various waifs and strays in the most practical and least misleading way.

The relationships of the Notioprogonia to the other notoungulates are probably similar to those of the creodonts to the other carnivores.

As a composite, or as an abstraction of the characters common to its various numbers, it probably nearly represents the structural ancestry of the other notoungulates, and if that actual common ancestry were found it would probably be notioprogonian by definition. There are also included various ancient and relatively archaic side lines that did not survive long enough to have major and separate deployments.

ENTELONYCHIA

This group was founded by Ameghino on the basis of the Homalodotheriidae and especially of *Homalodotherium*.¹ Ameghino later abandoned the name Entelonychia and referred these animals to the Ancylopoda (=Chalicotherioidea). Most other authors, however, probably impressed by the comparative conservatism in the dentition of *Homalodotherium*, retained the name Entelonychia and extended it to include a number of primitive forms with other notoungulates. This has been discussed under "Notioprogonia." On the evidence at hand, I confine the name Entelonychia to the Homalodotheriidae and the closely related, perhaps synonymous, Isotemnidae.

TOXODONTA

Toxodontia was proposed by Owen for an order or suborder of ungulates, with *Toxodon* and *Nesodon* given as examples of the group. With subsequent discovery, the marked differences between these animals and some others, especially the typotheres, were not recognized, or were less emphasized than the resemblances. Thus, for instance, Lydekker (1894) includes the typotheres in the Suborder Toxodontia, although Zittel in the same year placed them apart in the Typotheria and confined Toxodontia to the true toxodonts plus the astrapotheres and homalodotheres (both placed in the Astrapotheria by Lydekker). Ameghino at first also included both toxodonts and typotheres in the Toxodontia, but he later separated them, using the names Typotheria and Toxodontia (the only names of more than family rank in his definitive classification which are exclusively applied to South American groups). Gregory (1910) returned to Lydekker's system of placing both toxodonts and typotheres in one group, but almost all other recent authors have recognized them as forming two distinctive units of equal rank. Scott's proposal to use the form Toxodonta for the toxodonts

¹Many authors (particularly Scott and later workers) have used the emendation *Homalodontotherium*. It is true that *Homalodotherium* Huxley, 1870, is a *nomen nudum* with no standing in nomenclature and that Flower in his definitive description of 1874 used the spelling *Homalodontotherium*, but Flower published a brief, valid description in 1873 under the name *Homalodotherium*. The genus is therefore *Homalodotherium* Flower, 1873. I am indebted to Patterson for calling my attention to this history.

proper and giving the name *Toxodontia* to a group of even wider scope than that of Lydekker and of Gregory has already been mentioned, and the reasons for rejecting it given.

In order to avoid confusion with Scott's variant usages, I tentatively retain his spelling *Toxodonta* for this group (suborder in this system). No one now denies its general character and distinction. One dubious point is the reference here of the *Leontiniidae*, in which I follow Scott although further study of this point seems essential. It is curious that no representative of this very important suborder has yet been surely recognized previous to the *Deseado*. The *Archaeohyracidae* were tentatively placed here by Gregory, and this may be correct although pending more detailed study it seems more probable that this family belongs in the *Typotheria*. There is also the family *Acoelodidae* which might be of toxodont affinities, but is also tentatively placed in the *Typotheria* pending further study. These forms are so near the point of divergence of typotheres, toxodonts, and homalodotheres that their subordinal position is still difficult to define.

I follow Scott in uniting the *Nesodontidae* and *Toxodontidae*, which are closely related and perhaps only progressive stages of the same rather limited group, and Patterson (personal communication, paper in press) in uniting the *Rhynchippidae* and *Notohippidae*.

TYPOTHERIA

Previous to 1893, the typotheres and toxodonts were confused and were commonly united in the *Toxodontia*, but in that year Zittel established the ungulate Suborder *Typotheria* with the families *Protypotheriidae* (= *Interatheriidae*) and *Typotheriidae*. The addition of the family *Hegetotheriidae* by Ameghino brought the suborder into essentially its present form, and there is little question as to its validity and general character. The Casamayor and Musters *Notopithecidae* are certainly typotheres, and perhaps could be united with the *Interatheriidae*, which they closely resemble in skull structure although the dentition is much more primitive. *Archaeohyracidae* and *Acoelodidae* are placed here only tentatively, pending more detailed study. One or both might prove to be toxodonts.

ASTRAPOTHERIA

This name was proposed by Lydekker (1894) for a suborder of the Order *Ungulata*, to include the *Astrapotheriidae* and *Homalodotheriidae*. In the same year, however, Ameghino placed the homalodotheres in the distinct group *Entelonychia*, and almost all later workers have followed

this step of Ameghino's.¹ In 1894 Ameghino placed the astrapotheres in a suborder Astrapotherioidea. In his definitive work, Ameghino referred the astrapotheres to the Amblypoda, but this has been thoroughly controverted (see especially Scott, 1932 and earlier papers) and requires no further comment. The present questions are (1) the degree of relationship between the astrapotheres and the typical notoungulates, and (2) the placing of the family Trigonostylopidae.

Both of these questions have been considered in a preliminary paper of this series (Simpson 1933A). On the data there given, and other facts to be more fully discussed elsewhere, it is concluded (1) that the astrapotheres are not closely related to the typical Notoungulata and probably should not be included in that order, (2) that litopterns, astrapotheres, and trigonostylopids probably had a common, possibly condylarth, ancestry, (3) that these three groups represent three distinct and divergent lines from that ancestry, and (4) that the trigonostylopids may be nearer to the astrapothere line than to the litoptern line, or possibly diverged from the ancestral astrapotheres after their origin as such, but are nevertheless very distinctive from any true astrapotheres.

The taxonomic expression of these views seems most simply accomplished by retaining a separate Order Astrapotheria, reviving Ameghino's Suborder Astrapotherioidea for the true or typical astrapotheres, and placing the Trigonostylopidae in a second suborder, Trigonostylopoidea, defined below.

ASTRAPOTHERIOIDEA

This suborder is redefined as follows:

Extinct South American ungulates, typical of the Order Astrapotheria. Three pairs of strongly bilobed lower incisors. Upper incisors lost, at least in later genera. Canines very large and becoming rootless tusks. Premolars becoming reduced to $\frac{2}{3}$. Cheek teeth becoming moderately hypsodont, always rooted. Upper molars trapezoidal, without distinct metacone fold, protoloph strong, hypocone not excluded from trigon and tending to merge into a metaloph, crista incipient to strong. Lower molars fully lophiodont and bicrescentic, anterior wing of trigonid crescent strong, secondary internal pillar arising at anterior end of talonid crescent. Infraorbital foramen single. Palate and choanae normal. Sagittal crest short, temporal crests very strong. Auditory region deeply embedded and exposure small, auditory notch deep and narrow, tympanic loosely attached, post-tympanic process strong, no occipital exposure of mastoid. Condylar foramen large and independent. Skeleton (unknown in Trigonostylopoidea or earliest Astrapotherioidea) becoming graviportal, feet retaining five digits. Scaphoid resting on trapezium and trapezoid, not reaching magnum,

¹Gregory (1910) did suggest that Lydekker had some basis for his grouping. Gregory's classification did not place the Homalodotheriidae in the Astrapotheria, but did so place the Isotemnidae, a family so near the Homalodotheriidae as to be possibly synonymous.

lunar overlapping unciform. No fibulo-calcaneal or naviculo-cuboid contacts. Astragalus short, broad, very short neck, cuboid facet rather on neck than on head. Proximal end of cuboid covered by astragalus, calcaneal facet on fibular side. Second and third digits of pes reduced, first and fourth large.

Suborder **TRIGONOSTYLOPOIDEA**, new

DISTRIBUTION.—Casamayor and (?) Musters Formations, Patagonia.

DIAGNOSIS.—Extinct South American ungulates of very isolated and doubtful position, but perhaps related to the Astrapotheria. Two pairs of one-lobed lower incisors. $P\frac{1}{1}$ present (vestigial) or absent, $P\frac{2}{2}=\frac{4}{4}$ present. Tusks somewhat like those of true astrapotheres, but always rooted, relatively low-crowned, and smaller. Cheek teeth brachyodont. Upper molars usually triangular, metacone fold present but may be very weak, protoloph continuous but feeble, hypocone rudimentary and excluded from trigon, no true metaloph, no crista, trigon basin closed, broad, shallow. Lower molars imperfectly lophodont, anterior wing of trigonid poorly developed and short, ending at midline, no talonid pillar. Infraorbital foramen multiple. Palate with posterior median process. Choanae divided by bony partition. Sagittal crest very long and powerful, temporal crests little developed. Auditory region broadly expanded and well exposed. Auditory notch broad and open, post-tympanic process practically absent. Tympanic nearly horizontal, attached suturally, thick and scale-like, not inflated, with deep notch beneath meatus and round carotid evagination on inner side. Mastoid exposed on occiput. Condylar foramen far from condyle and opening into pit or gap between tympanic and basioccipital.

PYROTHERIA

This group was named by Ameghino in 1895, but as in many other cases he abandoned it under the growing influence of his belief in an Argentine origin for all mammalian orders, and in his definitive classification (1906) the word Pyrotheria does not appear and the pyrotheres are placed in the Proboscidea. Loomis (1914) agreed that they are proboscideans, but retained the Pyrotheria as a suborder. I believe no more recent authority definitely accepts this view of relationships (now abandoned even by Loomis) and the question now is whether the pyrotheres are related to the notoungulates.¹

Scott at first (1904) excluded the pyrotheres from the Notoungulata (his Toxodontia) but later (1913) placed them there. Still more recently (1932) he seems to incline slightly, but not definitely, back to the idea of proboscidean relationships. Gaudry (1909) concluded that *Pyrotherium* is not clearly related to any known order. Gregory (1910) argues for a somewhat remote connection with the Entelonychia ("Homalodotheria"), and doubtfully includes the Suborder Pyrotheria in the Notoungulata.

¹Schlosser (1923) places the pyrotheres in the Amblypoda. Perhaps a case could be made out for this, but Schlosser adduces no important evidence, nor am I acquainted with any.

Much new skeletal material has been collected by Riggs, and this will presumably give a better basis for judgment. My own restudy of the early dental remains, hardly considered by other students, and of the published data on *Pyrotherium* itself, strongly opposes union either with the Proboscidea or with the Notoungulata. The group seems to be a very distinctive one of unknown sub- or proto-ungulate origin, and can at present only be classified as an independent order. I see no good reason for placing the little known and probably merely ancestral early forms in a separate family, Carolozitteliidae, as did Ameghino, and place all pyrotheres in the Pyrotheriidae.

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