

*THE EDENTATA OF THE SANTA CRUZ
BEDS.**

IN the Santa Cruz fauna the edentates form one of the most conspicuous elements, both in the abundance of individuals and in the number and variety of the genera and species. As a whole, they are strikingly different from those of recent times, for of the three orders which are represented among the fossils, armadillos, glyptodonts and ground-sloths, only the first-named persists to the present day, the other two being extinct. On the other hand, no trace has yet been found in the Santa Cruz beds of the true sloths or of the anteaters. It can hardly be doubted that both of these orders had already become differentiated and were in existence as such. If so, however, they must have originated in some other part of the South American continent, and were prevented by climatic or other barriers from extending their range into Patagonia. One fact which clearly justifies this assumption is the relatively small degree of structural change that took place between the edentates of the Santa Cruz and those of later periods, such as the Pampean. There are many differences of detail between the earlier and the later forms, but nothing comparable to what would be implied in the derivation of the sloths or anteaters from any known Santa Cruz fossils.

As will be shown more at length in a later section, much the same statement applies to the armadillos of the Santa Cruz beds, with reference to their connection with those of modern times. Speaking broadly, the latter would appear not to have been derived from the former, which suggests that Miocene Patagonia was rather an outpost of the South American

fauna than the main area of its development.

The Santa Cruz glyptodonts are, on the whole, markedly more primitive than those of the Pampean, and in many structural details show a closer connection with the armadillos than do the latter; but for the most part, the Santa Cruz genera do not appear to be directly ancestral to those of the Pampean. Like the armadillos, they seem to be aside from the main lines of descent which terminated in the giant types of the Pleistocene.

On the other hand, the *Gravigrada* appear to be more directly ancestral to the great Pampean forms, and representatives, if not the actual ancestors, of almost all the genera may be observed in this fauna. However, no entirely convincing solution of these problems can be obtained until the fossils intermediate in time between the Santa Cruz and the Pampean are more fully known.

A remarkable feature of the Santa Cruz edentates is their variability within certain well-defined limits. As a rule, the genera may be readily identified, but the species, especially of the *Glyptodontia* and *Gravigrada*, present extraordinary difficulties to the systematist. This variability, however, confines itself to comparatively unimportant details, and the characteristics of the three orders and of the families and genera within those orders are already, for the most part, firmly established, though transitional forms from species to species and, less commonly, from genus to genus abound.

1. The Santa Cruz edentates are relatively small animals and a few of them are really minute. As compared with the ground-sloths and glyptodonts of the Pampean, they are pygmies, but the armadillos have a greater number of large species than exist at present, though none of them

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is gigantic, or comparable to such a form as *Macroeuphractus*.

2. Fully developed carapaces are found in all of the armadillos and glyptodonts of the period, but as yet no dermal ossifications have been found in connection with any of the ground-sloths. This is the less surprising, because very little is known of the skeleton of the Santa Cruz *Mylodontidae*, the only family in which these ossifications could be expected to occur.

3. The teeth are in all cases devoid of enamel, rootless and tubular, though they may be lobate, examples of which occur in all three of the orders. No trace of a milk-dentition has been observed. Premaxillary teeth and the corresponding mandibular teeth have been definitely found only in the armadillos, though rudimentary traces of such teeth are apparent in some of the glyptodonts and they may also occur in a few of the ground-sloths.

4. The skull has few common features throughout the series, each order having its own characteristic type of structure. The difference is largely in the relative development of the cranial and facial regions, which varies from the extremely elongate skull, with long, slender rostrum, of the armadillos, to the short, broad, deep and almost cubical skull of the glyptodonts. Sagittal and occipital crests are never very strongly marked, but they are present in most genera of all three orders, and there is no such development of cranial air-sinuses as took place at a later period. In all of the known genera from this formation, except *Peltephilus*, there is a more or less prominent descending, suborbital process given off from the zygomatic arch; it may be formed by the jugal alone or by the jugal and maxillary, and in position it may be at the anterior or the posterior end, or in the middle of the arch. The arch itself is always complete, never rudi-

mentary, though in the *Gravigrada* the jugal is usually loosely attached, and has been lost from most of the specimens.

5. The neck has never more or less than seven vertebræ, though in all of the armadillos and glyptodonts the apparent number is much reduced by coossification. In the same two groups the trunk is short and the number of trunk-vertebræ small, and in the glyptodonts these vertebræ are coossified into long 'tubes,' one thoracic, the other lumbo-sacral. In the *Gravigrada*, on the contrary, the trunk is very long and the trunk-vertebræ numerous. In both armadillos and ground-sloths the lumbar and posterior thoracic vertebræ have very complex accessory zygapophyses, which in the former are as fully developed as at the present time, but in the latter are somewhat less so than they became at a later period. The sacrum may be long (*Dasy-poda*, *Glyptodontia*) or short (*Gravigrada*), but always articulates with both ilia and ischia. The tail is sometimes of moderate length and sometimes very long, but always heavy and always has a complete series of chevron-bones.

6. The limbs and feet differ greatly in the three orders, and have comparatively little in common. The scapula is broad and has an extremely prominent spine and acromion; the coracoid is very large in the ground-sloths, reduced in the glyptodonts and armadillos, except *Peltephilus*. In all three orders the humerus has a similar general appearance, having small tuberosities, extremely prominent deltoid and supinator ridges and internal epicondyle, while the foramen is large. Ulna and radius are separate and, except in the ground-sloths, the former has a very large olecranon. All the carpals are free, but no genus has been found which has the centrale. The manus is pentadactyl and plantigrade, though it is not improbable

that the Gravigrada had already begun to rest the ulnar edge of the hand upon the ground; the metacarpals are free and, except in one species of armadillo, none of the phalanges are coossified. The unguals are generally longer and more pointed than in the pes.

The pelvis differs much in the three groups, but always the ischia are extensively connected with the sacrum. The femur is long and has prominent trochanters, and in some of the armadillos the great trochanter reaches extraordinary proportions. Tibia and fibula are free in the Gravigrada, coalesced at both ends in the glyptodonts and armadillos. The pes is pentadactyl and, except in the glyptodonts, is plantigrade, while in the latter group it is semidigitigrade. No coossification occurs in tarsus, metatarsus or phalanges, and the unguals, which in the ground-sloths are large claws, in the other two orders are more or less hoof-like, completely so in the glyptodonts.

DASYPODA.

The Santa Cruz armadillos form a peculiar assemblage of types, very unlike, as a whole, the modern representatives of the suborder, for only one, or possibly two, species would appear to be directly ancestral to existing forms, while the majority belong to extinct lines. Some of these lines, like that of *Proeutatus*, for example, persisted till a much later period than the Santa Cruz, and reached their culmination in the Pampean, but have no representatives in the recent fauna, while other series, like *Stegotherium* and the extraordinary *Peltephilus*, are not known to pass beyond the limits of the Santa Cruz formation. At the same time, there is a very notable diversity among these armadillos, and no less than three families and seven genera have been described, most of

the genera having each several species. The discovery of more complete material may reduce these numbers, but the variety will continue to be remarkable.

Attention has already been called to the difference between the Santa Cruz and the recent armadillos, a difference which can be made clear in a few words. No probable forerunner of *Dasypus*, *Priodontes*, *Tolypeutes*, *Chlamydomorphus* or *Tatu*, has been found in these beds, though some one of the species of *Prozaedius* was almost certainly an ancestor of the recent *Zaedyus*—it is possible, though far from certain, that some species of *Stenotatus* stood in the same relation to the modern *Cabassous*. In view of the stage of differentiation attained by the Santa Cruz armadillos, it is most improbable that all of these modern types should have originated since that period. This confirms the conclusion indicated by several other mammalian series, that in Miocene times Patagonia was not the principal theater of evolution of the South American fauna. This would explain the entire absence from the Santa Cruz beds of many types which would naturally be expected to occur there.

In general, the armadillos of this period may be said to have attained nearly the modern degree of specialization, though, in many details, primitive characteristics have been retained. As Ameghino has pointed out, the carapace never has an anterior buckler, but is made up of movable, imbricating bands, except posteriorly, where a larger or smaller number of plates are joined together by their edges to make the pelvic buckler. In one genus, *Præuphractus* (*vide* Ameghino) there is no pelvic buckler, all the plates being movable, and it is uncertain whether this was not also true of *Stegotherium*. In *Peltephilus* the pelvic buckler would appear to have been very loosely formed, the plates merely

touching one another, though in this region they are not imbricating. The cephalic shield is usually composed of numerous small, non-imbricating, irregularly polygonal and rather heavy plates, which are finely pitted, but display no regular sculptural pattern, but in the altogether exceptional genus *Peltephilus* these plates are large, very thick and coarsely sculptured. A further remarkable peculiarity of the head-shield in this genus is the presence of one or two pairs of pointed, horn-like scutes upon the rostrum. It is a curious fact that no plates of the tail-sheath have been found in association with any of the genera, except *Peltephilus*. It seems most unlikely that all the other genera had unarmored tails, and yet, in view of the large number of well-preserved specimens, including the caudal vertebræ, that have been collected, it is possible that such may have been the case.

Considerable variety is displayed in the dentition, though in no species has any trace of enamel or of the milk-teeth been observed. The marked diphyodontism of the modern *Tatu* makes this fact somewhat surprising. Premaxillary teeth and the corresponding mandibular teeth occur in two genera, *Proeutatus* and *Peltephilus*, and in the latter they are so closely approximated that the teeth of both upper and lower jaws form a continuous series. *Prozaëdius* and *Stenotatus* have teeth like those of most recent armadillos, while in *Proeutatus* the teeth show an incipient division into lobes and have a complex masticating surface, produced by layers of dentine of different hardness and color, and with some resemblance to the teeth of the glyptodonts. In *Peltephilus* the teeth are sharply pointed and form what appears to have been a formidable lacerating apparatus, while, finally, in *Stegotherium*

the dentition is in such an extreme state of reduction that the animal must have been functionally all but edentulous.

In all the known genera, except *Peltephilus*, the skull has a very elongate and usually a slender rostrum, and, with the same exception, the zygomatic arch has a prominent descending, suborbital process, which is generally from the jugal, but sometimes from the zygomatic process of the maxillary also.

The cervical vertebræ closely resemble those of the modern armadillos, one or two vertebræ coalescing with the axis. The trunk is short, and in those genera in which the number is known does not contain more than eleven thoracic and four lumbar vertebræ; in the lumbar and the posterior part of the thoracic regions the vertebræ have the same complex mode of articulation, by means of accessory zygapophyses, as is found in recent genera. The sacrum is long and always has an extensive union with the ischia. The tail varies considerably in the different genera; it is usually quite elongated, but in some of the genera, as *Proeutatus*, it is of only moderate length, though very heavy; in *Stegotherium* the caudal vertebræ are remarkable for the great development of their transverse process. The ribs, both costal and sternal, and the sternum, differ in no important respect from those of the recent armadillos.

The shoulder-girdle is practically the same as in the existing genera, but the humerus is noteworthy for the great size and prominence of the deltoid ridge, and the epicondylar foramen is always present. The ulna has a very large olecranon, which in most of the species terminates proximally in a prominent, incurved hook. The manus is always pentadactyl and all the digits bear claws; in all known species

the second digit is the longest of the series. In only one genus, *Stenotatus*, are any of the phalanges coossified. The ungual phalanges are always long, heavy, decurved and pointed, and were evidently well adapted to burrowing habits.

The pelvis varies considerably in the different genera, but does not depart widely from the modern type. The femur is elongate and has a very prominent great trochanter, which in *Proeutatus* reaches remarkable proportions; the third trochanter is also well developed in all cases. As in the recent armadillos, the tibia and fibula are invariably coossified at both the proximal and the distal ends. Like the manus, the pes is always pentadactyl, though in some of the genera, and especially in *Peltephilus*, the lateral digits are much reduced. The ungual phalanges are usually much shorter and broader than those of the manus, and are often more like hoofs than claws.

In size, there is much variety among the Santa Cruz armadillos, ranging from the minute *Prozaëdius* to *Proeutatus*, some species of which are larger than any existing armadillo, except *Priodontes*, while the very incompletely known *Peltephilus grandis* may have equaled or even surpassed the latter.

To sum up: The Santa Cruz armadillos differ comparatively little in appearance or in structure from the modern ones, and yet it is apparent that they do not, as a whole, represent the main line of descent which ended in the recent genera. That evolution must have taken place in some other region of the South American continent, doubtless the same region as that which gave rise to the true sloths and the anteaters.

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SCIENTIFIC BOOKS.

The Constructive Development of Group-theory; with a Bibliography. By B. S. EASTON. Boston, Ginn & Co. 1902. Pp. iv + 89. Cloth, \$0.75. (Publications of the University of Pennsylvania, series of mathematics, No. 2.)

This monograph aims to present in continuous form, but omitting all proofs, the main concepts and results of abstract and substitution group theory. While the theory of linear groups is expressly excluded, some of its results are tabulated on pages 83 and 84 under 'systems of simple groups.'

Employing a set of abbreviations for the journals, the author has succeeded, in the short space of thirty-four pages, in giving an exhaustive bibliography of the subject. In it appear 157 names of authors. To further indicate its extent, we note that it gives 97 titles by G. A. Miller, 35 by L. E. Dickson, 33 by C. Jordan, 23 by W. Burnside, 21 by Cayley, 20 by Cauchy and 16 by Kronecker.

The treatise proper extends over 39 pages, the successive headings being as follows: substitutions, groups, substitution groups, conjugacy, multiple isomorphism and quotient-groups, composition series, commutators, Abelian groups, groups of order a power of a prime, Sylow's theorem and its extensions, Hamiltonian groups, transitivity, intransitivity, primitivity, regular groups, imprimitivity, multiple transitivity, class of a group and degree of transitivity, automorphism, representation, index notation.

The tables give the numbers of distinct abstract groups of each order as far as 63; the number of substitution groups of each degree as far as 18, classified as multiply transitive, other primitive, imprimitive, and intransitive; the types of group of orders p^2 , pq , p^3 , pq^2 , pqr , $8p$ ($p > 2$), 16, p^4 ($p > 2$), p^3q , 32, p^5 ($p > 2$); simple groups of low orders; orders of composite and soluble groups; systems of simple groups.

Some minor remarks or corrections are here in order. In § 21, for 'class' read 'degree.' In § 44, for 'product of two elements' read 'product of any two elements.' In § 26, add alternative designation 'commutative