THE MARSUPIAL FAUNA OF THE SANTA CRUZ BEDS.

(Plates I and II.)

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(*Read April 13, 1905.*)

The Patagonian marsupials of the Santa Cruz epoch are of peculiar interest from the relationship which they bear to certain Australian and Tasmanian forms. This relationship establishes the reality of a former land connection between the Australian region and South America, so plainly indicated by the distribution of the Tertiary marine mollusks, fishes, land shells, decapod crustacea and plants.[1]

These marsupials are referable to three families, remnants of which survive in widely separated parts of the world. The Thylacynidæ are represented by at least four genera in the Santa Cruz fauna, where they occupy the place of the placental carnivora. The Didelphyidæ include the genus *Microbiotherium* and several other imperfectly known forms, comparable in size to some of the smaller South American opossums. The Santa Cruz diprotodonts belong to a third family which may be called the Cænolestidæ. A single representative of this family, *Cænolestes*, survives in Ecuador and Colombia.

The Thylacynidæ.

This family is sharply separated from the Dasyuridæ and all other existing carnivorous marsupials by the absence of the metaconid in the lower molars and by the great reduction of the outer cingulum

[1] Ortmann, A. E., *Reports of the Princeton University Expeditions to Patagonia, 1896–1899*, Vol. IV, pp. 299–302, 1902.

Ortmann, A. E., "The Geographical Distribution of Freshwater Decapods and its Bearing upon Ancient Geography," *Proc. Amer. Phil. Soc.*, Vol. XLI, pp. 267–400, 1902.

Pilsbry, H. A., "Distribution of Helices in Time and Space," *Manual of Conchology*, Series 2, Vol. IX, pp. xxxviii *et seq.*, 1894.

Lydekker, R., "A Geographical History of Mammals."

Hedley, C., "Considerations on the surviving refugees in Austral lands of ancient Antarctic life," *Proc. Roy. Soc. N. S. Wales*, August, 1895, p. 3, footnote 1.

and styloid cusps in the upper teeth. In the Dasyuridæ, these styles are almost as high as the outer cusps of the trigon. The family name, based on the Tasmanian marsupial wolf *Thylacynus*, was proposed by Buonaparte in 1838, and may very properly be extended to include the related South American forms.

The Santa Cruz thylacynes were predatory carnivores. An indication of their pugnacious habits is afforded by the traces of wounds received in fighting, which are found occasionally on the skull and mandible.

These carnivores have been placed by Ameghino in a sub-order named by him the Sparassodonta, a group which he regards as referable neither to the creodonts, the placental carnivores, nor the carnivorous marsupials. That the so-called Sparassodonta are true marsupials, and not worthy of sub-ordinal rank, is fully apparent from the following characters, which they possess in common with existing marsupial carnivores:

1. A typical marsupial dental formula, $\frac{4-3}{3}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{4}{4}$.

2. The number of successional teeth is reduced below that characteristic of the placentals.

3. The nasals are broad posteriorly, excluding from contact the frontals and maxillæ. There is usually a small contact in existing carnivorous marsupials. A similar broadening of the nasals is observable in *Mesonyx*, *Harpagolestes* and *Dromocyon* among the Creodonta.

4. Anteroposterior shortening of basis cranii.

5. Lachrymal spreading out on the face; lachrymal duct within the orbit. An internal opening of the lachrymal duct is observable in *Thylacynus*.

6. Inflected mandibular angle.

7. Excavation of the premaxillæ for reception of the tips of the lower canines as in the dasyures, *Thylacynus* and the opossums.

8. Basisphenoid and alisphenoid ridged as in existing marsupial carnivores and unlike the structure of this region in the placentals.

9. Posterior extension of the malar bar to form the pre-glenoid process.

10. Posterior border of palate thickened. This structure is observable also in certain creodonts.

11. Posterior border of palate perforated by a large foramen on either side of the posterior nares.

12. An alisphenoid bulla present in some genera, absent in others. Tympanic annular and unfused with the adjacent elements in the former, unknown in the latter.

13. Basisphenoid perforated by internal carotid artery.

14. Presence of a vascular foramen (the post-zygomatic of Cope) perforating anteriorly the base of the zygoma below or within the lip of the post-glenoid foramen.

15. Presence of a large vascular foramen (the sub-squamosal of Cope) perforating the squamosal on or above the crest which connects the base of the zygoma with the inion. This is absent in the placental carnivores.

16. Sutures of the skull distinct. Not strictly a marsupial character, but indicative of marsupial affinities when considered in connection with the other characters presented.

The four best known genera may be arranged as follows:

A. Skull brachycephalic. Alisphenoid not dilated to form an auditory bulla.

1. Dental formula $\frac{3}{3}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{4}{4}$. Protocone on upper molars reduced. M^4 biscuspidate with paracone and antero-external style. Posterior premolars greatly enlarged. Talonid of $M_{\overline{4}}$ with single conical cusp. Terminal phalanges round, blunt, and broadly fissured at the tips.

B. Skull dolichocephalic. *Borhyæna.*

(*a*) Alisphenoid bulla absent.

1. Dental formula $\frac{4}{3}$?, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{4}{4}$. Protocone well developed on M^{1} and M^{2}, reduced on M^{3}. M^4 with vestigial protocone and metacone. Posterior premolar not greatly enlarged; in the inferior series not exceeding the median premolar in size. Talonid of $M_{\overline{4}}$ small and basin-shaped. Terminal phalanges laterally compressed, sharply pointed, and slightly cleft at tips. *Prothylacynus.*

(*b*) An alisphenoid bulla.

1. Dental formula $\frac{4}{3}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{4}{4}$. Protocone well developed on M^{1-3}. M^4 with small conical protocone, large paracone and antero-external style; metacone reduced to the merest vestige or absent. Premolars increasing regularly in size posteriorly in both upper and lower series. Talonid of $M_{\overline{4}}$ enclosing a small basin-shaped area, unicuspidate. Terminal phalanges uncleft, laterally compressed and pointed. *Cladosictis.*

2. Dental formula $\frac{4}{3}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{4}{4}$. Protocone well developed on all the upper molars. M^4 with protocone enclosing a basin-shaped area; paracone and antero-external style large; metacone vestigial or absent. Upper premolars increasing regularly in size posteriorly; median and posterior lower premolars subequal. Talonid in $M_{\overline{4}}$ large and strongly bicuspidate. Terminal phalanges laterally compressed and pointed without clefts. *Amphiproviverra.*

The Santa Cruz thylacynes are short-legged animals with large heads, long necks and heavy tails. These characters are well shown in the accompanying restorations of *Prothylacynus patagonicus* and *Cladosictis lustratus* (Plates I and II) reproduced from the forthcoming Volume IV of the Reports of the Princeton University Expeditions to Patagonia. In addition to the characters already mentioned, the following are worthy of notice :

1. The facial region of the skull is short in proportion to the length of the cranium. The brain case is small and greatly constricted postorbitally. The orbits are placed much further forward than in the Dasyuridæ, opossums, or *Thylacynus*. The jugal arches are robust and broadly expanded, and the sagittal and lambdoidal crests well marked but not very high. The palate lacks the vacuities present in all existing carnivorous marsupials, but is perforated by a number of accessory palatine foramina. Between the molars, the margin of the palate is depressed into deep hemispherical fossæ for reception of the tips of the lower teeth when the mouth is closed. The occiput is semicircular in outline in contrast with its triangular shape in the dasyures, *Sarcophilus* and *Thylacynus*. The lachrymal canal opens well within the orbital rim. In the majority of living marsupials, the opening of the lachrymal duct is placed either on or external to the orbital rim. *Thylacynus* is transitional between these two types of structure in that it possesses a double lachrymal perforation, one branch of the canal opening without and the other within the orbit. *Borhyæna* and *Prothylacynus*, resemble *Sarcophilus* in the fusion of the mandibular symphysis. In the remaining genera the symphysial union is ligamentous.

2. The molars are of the same type as in *Thylacynus*, differing principally in the greater reduction of M^4, the loss of all the styloid cusps except the antero-external, and the character of the heel of the last lower molar, which may be either small and conical, basin-shaped or bicuspidate. The premolars are unreduced in number, and usually increase in size posteriorly in both series. The canines are long, sharply pointed and slightly curved in the smaller genera. In *Borhyæna* the fang is swollen and the point short and blunt. The incisors in *Borhyæna* are reduced to $\frac{3}{3}$, an exceptional formula among marsupials in that the number above and below is the same. In *Amphiproviverra* the median pair are conical and approximated at the tips as in *Dasyurus* and *Didel-*

phys. The posterior premolar is preceded, in *Cladosictis*, by a deciduous tooth resembling the first molar. According to Ameghino, the median premolar and canine in this genus also have deciduous predecessors, and in *Borhyæna* the canine is said to displace a deciduous tooth.

3. The atlantal intercentrum is unfused with the base of the neural arch in *Borhyæna* and *Amphiproviverra*, as it is also in *Thylacynus*. In *Prothylacynus* and *Cladosictis* complete fusion has taken place with obliteration of the sutures. An atlantal foramen for the transmission of the spinal nerve and vertebral artery is present in all the genera except *Borhyæna*, which resembles *Phascolomys* in transmitting the nerve and artery through a groove in the anterior margin of the neural arch. The axis carries a large hatchet-shaped neural spine. The bases of the transverse processes of the second to the seventh cervicals are perforated for the transmission of the vertebral artery. The dorso-lumbar vertebral formula was probably nineteen as in *Thylacynus:* thirteen dorsals and six lumbars. As in that genus, the anticlinal vertebra is the tenth dorsal. Two vertebræ are coössified in the sacrum. The tail was undoubtedly long, very heavy and greatly thickened at the base.

4. The limbs are short in proportion to the length of the body and the feet small with spreading toes. The trochlear surface of the astragalus is short and flat with feebly differentiated facets for the tibia and fibula which latter articulates with the calcaneum. In *Prothylacynus*, the hallux is reduced to a deformed metatarsal, which carries no phalanges and terminates distally in a blunt rounded knob. In *Cladosictis*, the hallux is small, judging from the size of its articulation on the entocuneiform. It may have supported phalanges. The hallux in *Amphiproviverra* is large and opposable indicating that this genus was probably arboreal. The pollex is known in *Amphiproviverra* and *Cladosictis*. In these genera, the phalanges of the pollex are deflected toward the inner side of the foot as a result of the enlargement of the outer condyle of the metacarpal of the thumb. In gait, the Santa Cruz thylacynes were probably plantigrade. In striking contrast with these extinct genera the pes of *Thylacynus* shows a peculiar cursorial modification. Not only is the gait of this animal digitigrade, and the hallux entirely obliterated, but the ectocuneiform has shifted toward the outer side of the foot until it is supported almost entirely by the

cuboid. In the Santa Cruz forms, this shifting has progressed to about the same extent as in *Sarcophilus*. There is no trace of syndactyly. The manus and pes are pentadactyl in *Amphiproviverra* and *Cladosictis*. The manus is pentadactyl in *Borhyæna* and probably also in *Prothylacynus*. The hallux is reduced to a vestige in the latter genus. Its condition in *Borhyæna* is unknown.

5. The pelvis is without trace of epipubic ossifications in *Cladosictis*. The pubes are not preserved in the only specimen of *Prothylacynus* in the Princeton collection, and the pelvis of *Borhyæna* and *Amphiproviverra* is unknown. The patella is ossified in *Amphiproviverra* and *Prothylacynus*. The radius and ulna are capable of some degree of pronation and supination. The tibia and fibula are unfused. The inner humeral epicondyle is perforated by a large foramen in *Prothylacynus* and *Cladosictis;* imperforate in *Amphiproviverra*. The supinator ridge terminates in a hook-shaped extremity in *Prothylacynus*. This is wanting in *Amphiproviverra* and *Cladosictis*.

THE DIDELPHYIDÆ.

The Didelphyidæ are represented in the Santa Cruz fauna by several genera of which *Microbiotherium* is the best known. In dental formula and the structure of the lower molars *Microbiotherium* agrees with *Didelphys*, differing from all the opossums in the greater reduction of the outer cingulum, styloid cusps, and metacone spur in the upper molars. The posterior premolar is enlarged in both the upper and lower dental series. The premolars are double-rooted in the majority of the species and decrease in size anteriorly. The molars in both series decrease in size posteriorly as in the existing didelphyd genus *Caluromys*.

THE CÆNOLESTIDÆ.

This family, better known as the Epanorthidæ, includes all the Santa Cruz diprotodont marsupials. As the genus *Palæothentes*, defined by Ameghino in 1887, has priority over *Epanorthus*, proposed by him two years later, necessitating the rejection of the latter, the family has been renamed after its best known representative, *Cænolestes*. All the members of this family are small animals and are very incompletely known.

Three subfamilies may be recognized. The more primitive members of the first of these, the Cænolestinæ, form a connecting

link between the polyprotodont and diprotodont marsupial suborders in possessing, in the lower jaw, the tuberculo-sectorial type of molar characteristic of the polyprotodonts combined with a diprotodont modification of the median incisors. One of the minute Santa Cruz forms has the same inferior dental formula as the opossums. Unfortunately, nothing is known of the upper dentition, skull and feet of this important transitional form.

The second subfamily, the Palæothentinæ, contains the largest of the Santa Cruz diprotodonts. The upper molars of the Palæothentinæ resemble closely those of certain bunodont phalangers. The first is fully quadritubercular. The second has a rudimentary hypocone. The third and fourth are tritubercular. The lower molars are lophodont. The posterior upper premolar and first lower molar are modified as sectorial teeth. The dental formula varies in the different genera but there are always four molars above and below. The members of this subfamily form a regular progressive series in the shortening of the anterior portion of the mandible and the reduction of the posterior lower premolar from a double-rooted fully functional tooth to a single-rooted more or less vestigial condition.

The Abderitinæ, the third subfamily, are the most specialized of the Santa Cruz diprotodonts. The first lower molar is greatly enlarged, vertically grooved, and notched along the cutting edge of the crown, resembling in some respects the peculiar sectorial teeth of the multituberculate Plagiaulacidæ. The sectorial in *Abderites*, however, possesses a large bicuspidate heel, which is lacking in the Plagiaulacidæ, and the remaining molars are quadritubercular.

The Cænolestidæ are examples of the restrictive influence of competition on adaptive radiation. During the Santa Cruz epoch they were crowded into obscurity by a horde of placentals, sloths, rodents, and ungulates, and had no opportunity to attain the high degree of adaptive specialization shown by the Australian diprotodonts, although so far as can be judged, they possessed as much latent capacity toward variation as do their nearest living allies, the phalangers.

RELATIONSHIPS OF THE SANTA CRUZ MARSUPIALS.

The Patagonian thylacynes do not represent the main line of descent which ended in *Thylacynus*. In all the Santa Cruz genera

the last upper molar has undergone greater reduction and the styloid cusps have decreased in number, the antero-external alone being represented. Apart from these advanced characters in the dentition, the Santa Cruz thylacynes are of a distinctly more primitive type than their surviving Tasmanian relative, which has progressed in the lengthening of the face and posterior shifting of the orbit, the increased brain capacity, the acquisition of palatal vacuities, the prenatal shedding of the deciduous teeth, the external shifting of the outer cuneiform, and the loss of the hallux. With the exception of the reduced hallux in *Prothylacynus*, transitions to these advanced types of structure do not appear in the Santa Cruz members of the family.

The marsupial faunas of those formations in Patagonia older than the Santa Cruz are still too imperfectly known to afford a secure basis for phylogenetic speculation, but it may confidently be expected that the common ancestor of *Thylacynus* and the extinct Santa Cruz types will be found among them. In fact, certain large carnivorous marsupials from the Pyrotherium beds named by Ameghino, *Proborhyæna* and *Pharsophorus* retain the metaconid in the lower molars as in the Dasyuridæ, while the premolar formula is unreduced as in the Thylacynidæ.

The affinities of *Microbiotherium* are unquestionably didelphyd. The genus can not be regarded as ancestral to any of the existing South American opossums as the degree of reduction of the external cingulum and styloid cusps in the upper molars is greater.

The most primitive of the Cænolestidæ, the genus *Halmarhiphus*, is transitional to the Polyprotodontia and represents, with little or no modification, a type which is not only ancestral to the Palæothentinæ but agrees perfectly with the "minute insectivorous forms which, apart from the diprotodont modification of the antemolar teeth, possessed a full antemolar formula," indicated by Bensley's[1] studies as the ancestors of the Phalangerinæ. Unfortunately this interesting transitional genus is known only from the lower jaw. The Palæothentinæ are important in retaining constructive stages in the evolution of the bunodont type of molar characteristic of the more primitive of the existing phalangers. The Abderitinæ are highly specialized diprotodonts which appear

[1] Bensley, B. A., "The evolution of the Australian marsupials, etc.," *Trans. Linn. Soc., London*, ser. 2 (Zoöl.), vol. 9, p. 139, 1903.

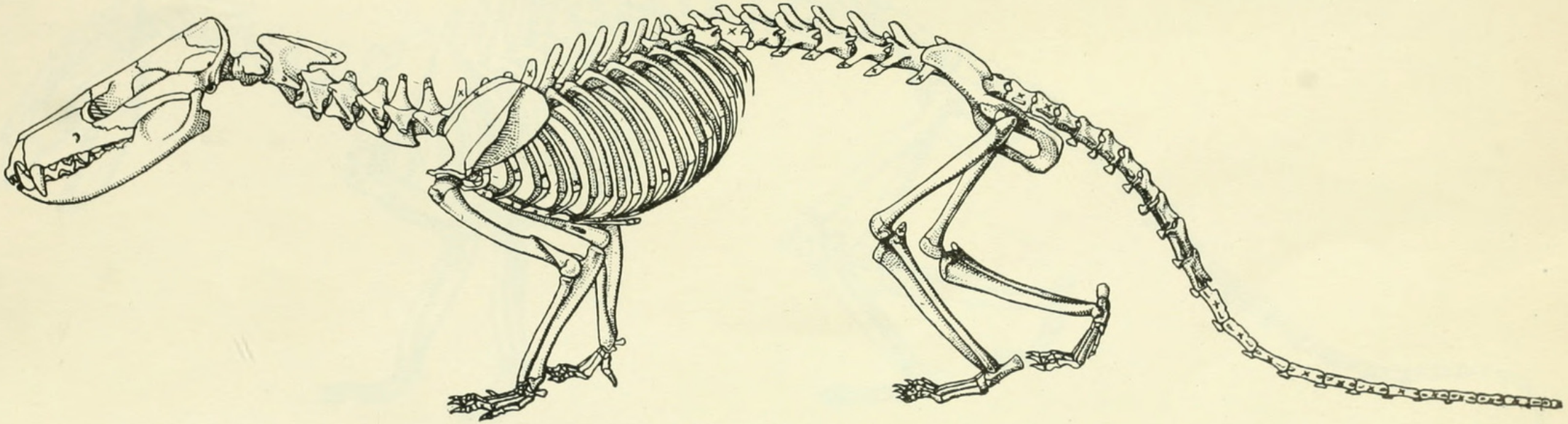

PLATE I. Cladosictis lustratus, × about $\frac{1}{4}$.