

Article XVII.—A ZALAMBODONT INSECTIVORE FROM THE BASAL EOCENE.

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PLATES LX AND LXI.

In Madagascar, Cuba, South Africa and West Africa there are found living today certain rare little Insectivores with a peculiar type of teeth, fundamentally different from those of all other mammals. The Cape Golden Moles (*Chrysochloridæ*) of South Africa, the Tenrecs (*Centetes*) and smaller relatives in Madagascar, the *Solenodon* of Cuba and Hayti and the

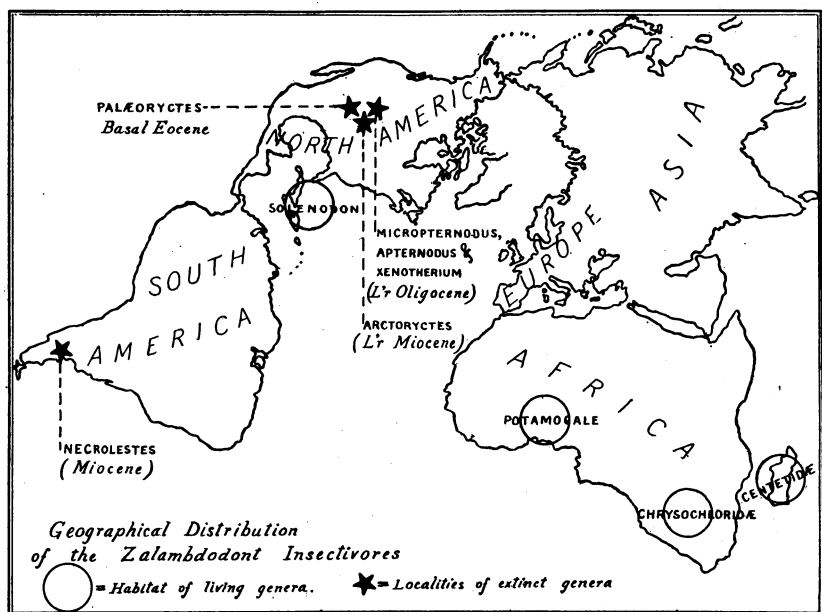


Fig. 1. Distribution of Zalambdodonta, shown on North Polar projection. This gives the true geographic relations more nearly correct than does the usual Mercator projection.

“Ottershrew” (*Potamogale*) of West Africa, are not closely related—they are usually placed in four distinct families, but they all have this peculiar type of cheek teeth, and were on this account associated by Gill in 1872 as a section of the order Insectivora under the name Zalambdodonta.

Their peculiar teeth, separating them off from other mammals, made them of especial interest in morphology, as they appeared to represent

an intermediate stage between the tritubercular pattern of tooth (from which all the various kinds of mammalian teeth appear to be derived) and the simpler conical teeth of the lower vertebrates. Teeth of somewhat similar type were known among the Jurassic mammals, but until the last few years they were unknown from the Tertiary. In 1891, a fossil species of this group was found in the Miocene of Patagonia by Ameghino, and described as *Necrolestes*. It was related to the Cape Golden Mole; a better specimen subsequently found by the Princeton Expedition and described by Scott showed that the relationship was not very close and it was placed in a fifth family Necrolestidae. But the geographical distribution of these Zalambdodont Insectivores limited entirely to the Ethiopian and Neotropical regions, was considered to be strong evidence for a former union of those two continents. On the fact that they had not been found fossil in the northern world was based the conclusion that they had never inhabited it.

The incorrectness of this conclusion has been shown during the last decade by a series of discoveries (1903-1910) in the Tertiary of North America, proving that several kinds of Zalambdodonta inhabited this continent in the Oligocene and Lower Miocene.¹ All of them were new additions to well known faunæ; they had not previously been discovered because they were rare, and of minute size. They were not closely related to any of the living forms, nor to *Necrolestes*; and the evidence is insufficient to say whether they were directly or approximately ancestral to any of them. What they prove is that this group of Insectivora inhabited a portion of the Holarctic region in Mid Tertiary.

During last summer's work in the Eocene of New Mexico, Mr. Walter Granger of the American Museum Expedition secured a very interesting specimen of a Zalambdodont from the Torrejon formation, Basal Eocene. It consists of the under surface of the skull with lower jaws, the upper and lower cheek teeth excellently preserved. The specimen is of minute size and its extraction from a hard silico-calcareous matrix is a remarkable feat of preparation due to the skill and patience of Mr. A. E. Anderson, who has also made enlarged photographs of the prepared specimen.

¹ *Apternodus* Matthew, 1903, Lower Oligocene, Montana.

Micropternodus Matthew, 1903, Lower Oligocene, Montana.

Xenotherium Douglass, 1906, Lower Oligocene, Montana.

Arctoryctes Matthew, 1907, Lower Miocene, S. Dakota.

Apternodus was described from the lower jaw; a well preserved skull with lower jaws was referred to it by Matthew in 1910 and it was placed as a subfamily under the Centetidae. *Micropternodus* was described from a lower jaw; it is regarded by Osborn and Gregory (I think justly so) as related to *Solenodon*. *Xenotherium* was described by Douglass from a skull and referred to the Monotremata; its affinity to the Chrysochloridae was stated by Matthew in 1906. The generic name is preoccupied by *Xenotherium* Ameghino 1904. *Arctoryctes* was described but not named by Matthew in 1906, and is based upon a humerus.

This discovery extends the known geological range of the Zalambdodonta back to the Basal Eocene. It shows that this type of tooth is a very ancient one, and supplies direct evidence as to the probable evolution of the several variants displayed by the different modern families. The genus and species are new, the family reference is provisionally to the Centetidae. It is worthy of note that if this reference is correct, the Centetidae are the oldest living family of placental mammals.

***Palaeoryctes puerensis* gen. et sp. nov.**

Dentition $\frac{7.1.3.3}{7.1.3.3}$ upper molars sharply triangular, very wide transversely, with a high sub-crescentic outer cusp slightly twinned at the tip, strongly compressed crescentic inner cusp, and broad external shelf raised into crests at postero-external and antero-external angles. Last upper molar unreduced, transverse, without metastyle. Lower molars with very high trigonid, protoconid overtopping metaconid, paraconid

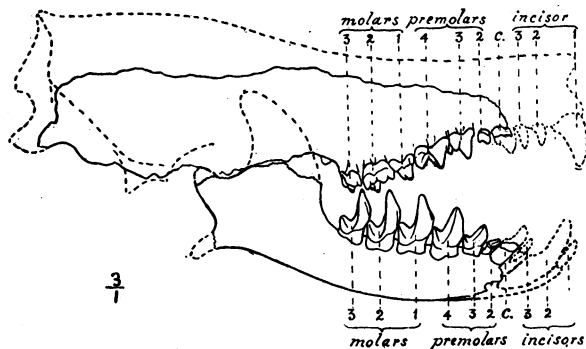


Fig. 2. *Palaeoryctes puerensis*. Side view of skull and jaws, with outlines conjecturally restored. Enlarged three diameters. Am. Mus. No. 15923, type. Torrejon formation, Basal Eocene, New Mexico.

antero-internal, smaller than metaconid, heel small, deeply basined, hypoconid and entoconid prominent. Premolars progressively reduced in size and complexity, the second very small and the first absent. Upper premolars non-molariform, P² very small, simple, somewhat compressed with minute posterior basal cusp. P³ a high compressed cusp, with imperfectly separated posterior and no internal cusp. P⁴ with high subtrigonal central cusp, large compressed postero-external, and large, well separated compressed-triangular internal cusp, set somewhat anteriorly; a minute rudiment of the antero-external cusp is also present. A small part of the alveolar border of c¹ is preserved, indicating that there was no spacing behind it. Upper incisors unknown. Lower premolars simple, p₂ minute, all with high, simple, moderately compressed principal cusp, and trenchant heel. No internal or anterior cusp on p₄. Lower canine with single oval root, the crown not preserved, but apparently the tooth was as large as p₂ and had a small heel-cusp. In front of the canine

is an alveolus for a large procumbent or semi-procumbent tooth presumably i_2 ; i_3 if present must have been very small; there are no indications in regard to the development of i_1 . The muzzle is comparatively short, the middle portion of the skull of moderate length and the basicranial region broad and flat. There are no palatal vacuities, and the posterior border of the palate is a little behind m_3 . The presence or absence of zygomatic arches cannot be determined. The palatal and basicranial axes are approximately parallel.

The otic region is well preserved, and by the skill and care of Mr. Anderson has been extracted from its hard matrix without injury. Its construction is as follows:

The auditory prominence is a round eminence rising considerably above (properly below) the level of the basioccipital and separated from it and from the basisphenoid by a well defined suture. Its anterior end is prolonged alongside the basioccipital and basisphenoid in a short ridge sharply crested, but the crest is not extended to take any considerable part in the bulla. On the postero-external face of the prominence is the fenestra ovalis, well marked, but not lying in a depression. The mesotympanic fossa lies anterior and external to the prominence, and on one side a

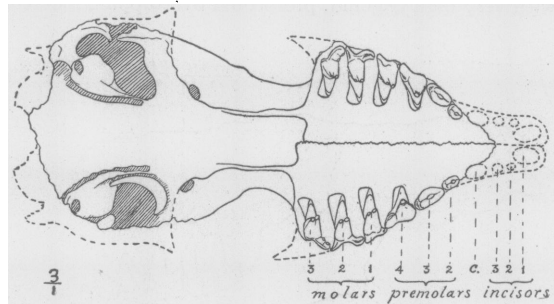


Fig. 3. *Palaeoryctes puercensis*, palatal view of type skull, enlarged three diameters.

considerable part of the bulla has been preserved; it roofs over the antero-internal portion of the mesotympanic fossa extending posteriorly alongside the ridge of the auditory prominence just within it and quite distinct from either petrosal or alisphenoid. This is apparently a true tympanic ring, and constitutes apparently the whole of the osseous bulla, the petrosal and alisphenoid taking no part in it, although the ridges described above represent in form and position the petrosal and alisphenoid portion of the bulla as developed in other insectivora.

The alisphenoid crest is continuous with the post-glenoid crest of the squamosal and with the pterygoid crest, and the foramen ovale lies close in front of it. The posterior lacerate foramen lies behind and somewhat external to the auditory prominence, while the carotid canal apparently occupies the deep furrow internal to the prominence and does not perforate the basisphenoid. The alisphenoid canal was apparently not present, a deep groove, incompletely bridged for a short distance, occupying its place.

The above data indicate a primitive and generalized Insectivore construction, with no indication of Marsupial affinities. In many respects it approaches *Microgale* which is regarded by Leche and Gregory as the most

primitive modern representative of the Zalambdodonta. But the basicranial structure appears to be more primitive and is more nearly in accord with that of the early Creodonts. This is true also of the dentition, if the principal cusp be interpreted as the united metacone and paracone. But if Gregory's interpretation of this cusp as the protocone be followed, the resemblance to such insectivora as *Ictops* is convergent and not indicative of any real approach. Unquestionably the evidence of this specimen appears to support the view advocated by Mivart and more recently supported by Gidley, that the principal cusp of Zalambdodonts is the united paracone and metacone, and that *Potamogale* is the most primitive living genus in this respect, although highly specialized in others.



Fig. 4. *Palæictops bicuspis* Cope. Upper teeth, enlarged two diameters. No. 4802, type, Lost Cabin beds (Lower Eocene), Wind River Basin, Wyoming.

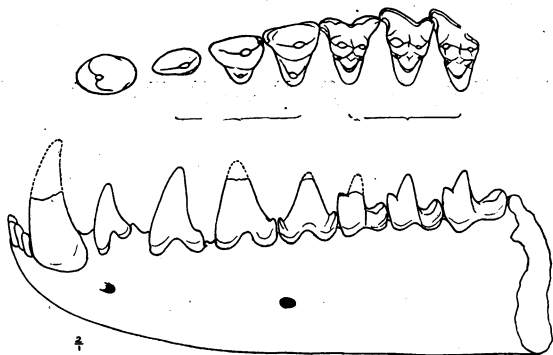


Fig. 5. *Didelphodus absaroka* Cope. Crown view of upper, and outer view of lower teeth, enlarged two diameters. No. 4228, type, Wasatch formation (Lower Eocene), Big Horn Basin, Wyoming. The lower teeth completed from a New Mexico specimen.

A comparison of the molar construction in *Palæoryctes* with that of such typical trituberculates as *Didelphodus* and *Ictops*, shows a correspondence that it is difficult to believe deceptive except upon very convincing evidence.

In my description of the skull of *Apternodus* (1910), I pointed out the apparent homology of the molar and premolar cusps in that genus, the oldest Zalambdodont then known, and suggested that the peculiar type of molar of the Zalambdodonts had been independently evolved without passing through the typical "tritubercular" stage from which most types of mammalian molars have been derived. According to the view there expressed the evolution of the molars in Zalambdodonts is exactly illustrated in its

successive stages by the progressive complication of the premolars. The principal central cusp of the upper molars is the primary cusp; the inner cusp is a later development and those genera like *Chrysochloris* which have it not, are more primitive in this respect, while *Potamogale* which approaches nearest to the tritubercular type is the latest development.

Leche (1907) and Gregory (1910) had come to much the same conclusion upon different grounds. They showed that *Microgale*, in which the inner crescent of the upper and heel of the lower molars are very small, is in most respects a very central and primitive type of the group, while *Potamogale*, in which the inner crescent is large and the central cusp is partly divided into two, is a very specialized and aberrant type. The inference that *Microgale* and others with inner crescent and heel very slightly developed represented the primitive type of Zalambdodont dentition, seemed well founded.

These conclusions are not supported by the present specimen. It is by far the most ancient of Zalambdodonts, and so far as the evidence goes it is in every respect a central and generalized type from which the diverse



Fig. 6. Upper molar construction (m^2 , right side) in: 1, *Chrysospalax* (Chrysochloridæ); 2, *Potamogale*, and 3, *Palaeoryctes* (Centetidæ); 4, *Didelphodus*, and 5, *Palaeictops* (Leptictidæ); 6, *Tritemnodon* (Hyænodontidæ). *Hy*, hypocone; *me*, metacone; *ml*, metaconule; *ms*, metastyle; *pa*, paracone; *pl*, paraconule; *ps*, parastyle; *pr*, protocone.

modern types are derivable. But the molar construction is nearest to that of *Potamogale*, and even more than *Potamogale* it approaches clearly and in all details to the normal tritubercular type, especially that of such early Eocene Insectivora as *Didelphodus* or *Palaeictops*. The peculiarities that separate it from these types are partially paralleled among the Creodonta, especially the Mesonychidæ and Hyænodontidæ, in which groups the evidence is conclusive that the normal tritubercular molar with large heels on the lower series and well separated and distinct paracone and metacone on the upper series, is the primary type, from which the various other modifications have arisen.

The conclusion seems to be very strongly supported that the main cusp of the Zalambdodont upper molar is the connate paracone and metacone of the normal tritubercular molar, and the inner crescent is the protocone.

It is by no means so certain whether the Zalambdodont type of molar has been derived from the normal tritubercular, or vice versa, but the evi-

dence at hand favors the former view. The oldest Tertiary representative of the group approaches nearest to the trituberculates, while the oldest Tertiary trituberculates are most typical and there are certain partial parallels to the zalambdodont type which are clearly specializations from tritubercular ancestry. There is sufficient morphologic evidence for the unity of origin of the Insectivora and most if not all other placental mammals, to make it very improbable that the *Palæoryctes* teeth represent an arrested development of a pre-tritubercular stage distinct since the Jurassic from the normally tritubercular Jurassic and Cretaceous mammals.

The ultimate origin of the tritubercular molar is not here under discussion. The conclusions emphasized are (1) that the Zalambdodont molar has not been independently evolved from the reptilian cone, and (2) that it has probably although not certainly passed through a normal tritubercular stage in its evolution.

The construction of the otic bulla is comparable with that in the more primitive Centetidæ (*Oryzorictes* and *Microgale*) and with *Solenodon*. The crest on the petrosal is suggestive of *Oryzorictes* as figured by Leche; this is absent in *Solenodon*; but in all the Centetidæ there is more or less development of a tympanic wing on the alisphenoid, lacking in *Solenodon* and apparently lacking in *Palæoryctes*. The supposed true tympanic ring, somewhat displaced inwards in our specimen, accords with *Solenodon* much better than any other Zalambdodont. But the genus is best interpreted as a central type from which the several modern specializations have arisen; and the considerable approach to the Creodonta already noted, is in accord with this view. In the Chrysochloridæ the basifacial axis has been sharply bent downwards upon the basicranium, the bulla is complete, the teeth more specialized.

In the construction of the molars this genus approaches nearest to *Potamogale*, but the central cusp is much higher, its twinning is less marked and the inner cusp more compressed. In *Potamogale* the premolars are not so simply constructed and the muzzle is more elongate. The form of the molars is more like that in some species of Chrysochloridæ, but in this family the molars are progressively reduced from first to third, the last is not transverse, and p^4 is fully molariform.

In *Solenodon* the characters of the internal cusp of the upper molars are quite different, p_4 is fully and p^4 more nearly molariform and the muzzle is elongate.

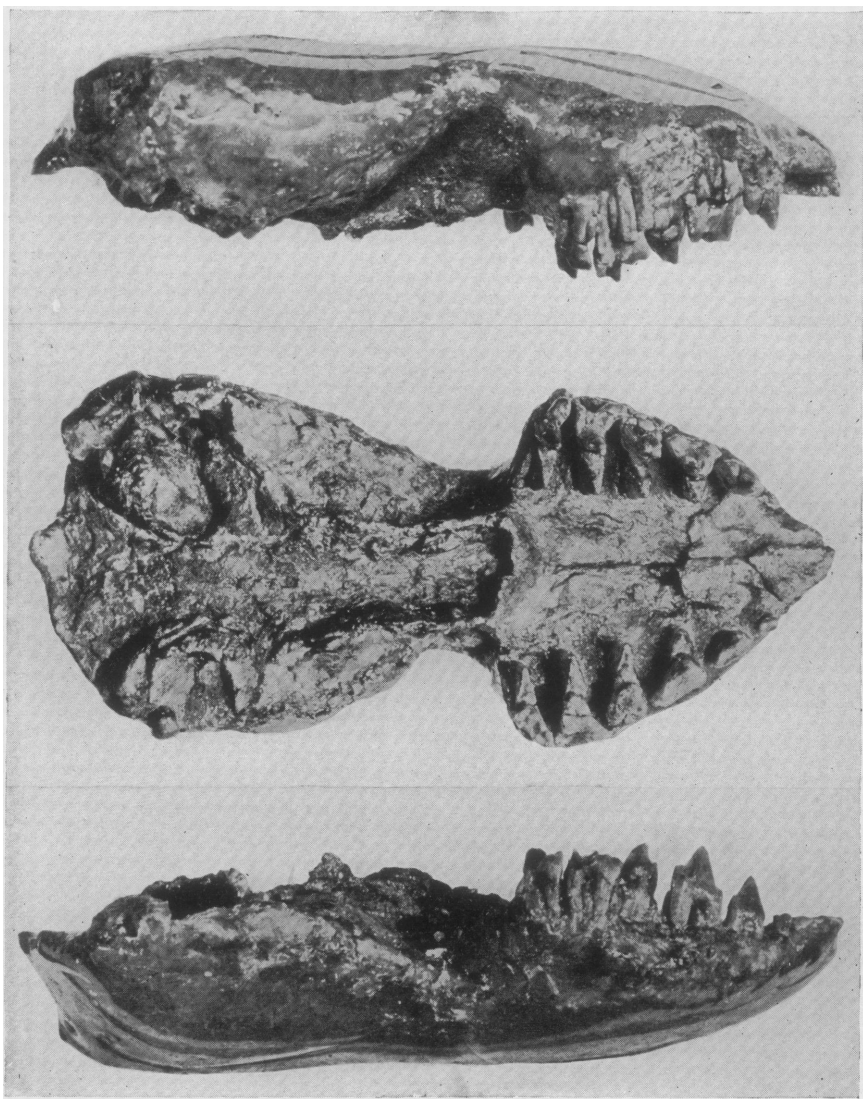
In the Centetidæ the crowns of the teeth are to a varying degree lower, the inner crescent of the upper molars smaller, the central cusp is not twinned and the premolars are more complex, p^4 more or less completely molariform. The position of the posterior mental foramen under the middle of p_4 consti-

tutes an approximation to the conditions in the Centetidæ, and in *Solenodon* and *Potamogale*, in which it is under m_1 . In the Chrysochloridæ it has the normal position under p_3 .

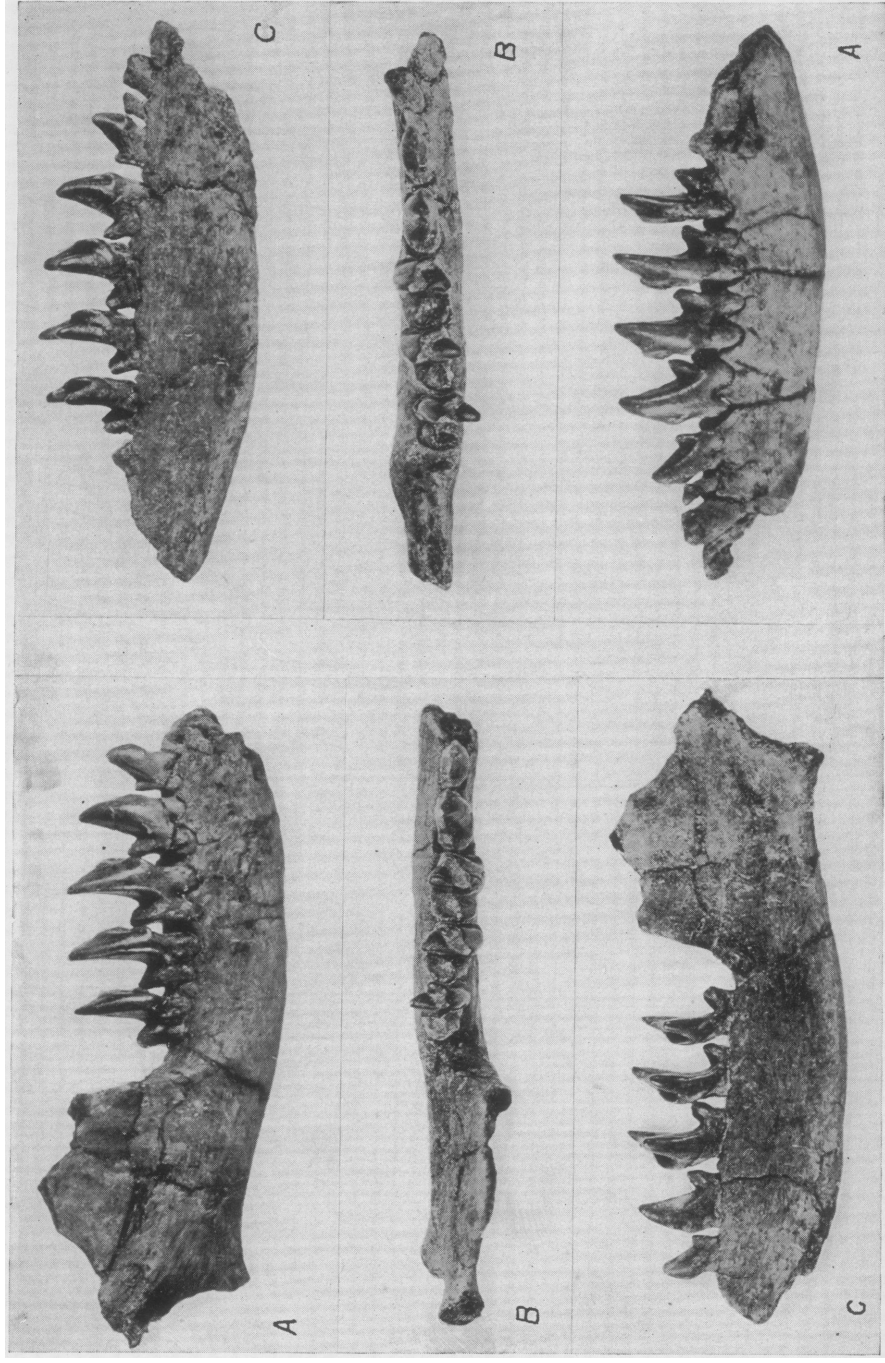
Family reference: *Palæoryctes* appears from the preceding data to be a primitive ancestral type from which any or all of the later Zalambdodonts may be derived. The genus might be placed, according as more weight were laid upon one or another character, in any of the four modern families. There does not seem to be warrant for the erection of a distinct ancestral family; and on the whole the Centetidæ afford the most convenient resting place for the genus.

The question whether the principal cusp of the Zalambdodonts represents the paracone-plus-metacone, or the paracone only, of ordinary trituberculates is apparently rather nominal than real. So at least I judge from Broom's remark ¹ in discussing this point that "*Potamogale* seems to me to show not a fusion, but a dwindling of the posterior triangle." To my mind when the bases of two cones are almost coincident it is more proper to say that they are fused than that the lesser one has dwindled away. But the difference, such as it is, is purely a matter of phrasing, the condition described is not different. The reverse process might be described either as unequal twinning or as budding off of a new cusp. The difference is one of concept of individuality, not of anything real or material. But in such cases as that of *Palæoryctes* or *Tritemnodon* the conditions can hardly be described otherwise than as a fusion of the two cusps.

¹ *Annals Natal Gov't Museum*, 1909, Vol. II, p. 135.



Palaeoryctes puercensis, skull, palatal and side views, enlarged five diameters. No. 15923, type. Photo by A. E. Anderson.



Palaeoryctes puericensis, lower jaws, outer, top and inner views, enlarged six diameters. No. 15923, type. Photo. by A. E. Anderson.

