

I I. Notes on the horns of the *Merycodontini*.

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Since the discovery of the peculiar horns of the *Merycodontini* various opinions have been expressed regarding the true nature of these horns. A review of the most important statements on this subject is found in FRICK's monograph of 1937. Briefly, the following possibilities have been discussed: The horns were

A. deciduous

B. non-deciduous

a. covered with normal skin

b. covered with a deciduous horn-sheath

c. naked above the burr in the adult

(RUSSELL 1936, p. 80.)

Personally, I am convinced that the alternative *Ba* is the right one and that one ought to be able to prove this beyond doubt. It even seems as though the problem were a comparatively simple one, if only all evidence furnished by the fossils is taken into consideration. MATTHEW (1924, p. 202) mentions the following facts to prove that the horns were persisting: 1. the burrs are only loosely attached to the beam. 2. multiple burrs frequently occur and must be regarded as something normal. 3. the total absence of skulls or antlers on which a shedding can be demonstrated; — this evidence would seem quite sufficient. But yet as late as in 1937 (FRICK, p. 280—283) the alternative *A* has been defended in opposition to the other ones, and therefore it might be appropriate to put forth still some facts in support of MATTHEW's view. The observations discussed in the present paper were made during a visit to Berkeley in 1938. The material preserved there is important, although it is dwindling small when compared with the one at Mr. FRICK's disposal. My paper is written in the hope that someone with access to the larger material would undertake a study along the lines here proposed, and I do not claim to have definitely settled the dispute regarding the horns.

My sincere thanks are due to Dr. R. A. STIRTON and Dr. G. GREGORY for all their efforts to facilitate my work.

As noted by FURLONG (1927, p. 154) and FRICK (1937, p. 281) the tips of the tines are very often polished and sometimes distinct facets have been formed, for instance Berkeley Mus. 26781 (cfr. FURLONG l. c.; the facet on the front tine of the left horn is 15×4 mm; for another specimen, Berk. Mus. 33959, a polishing extending 35 mm below the tip on the fore side of the anterior tine was noted). This shows, as FRICK rightly suggests, that the wear has »taken place in life and when that portion, at least, was unprotected by covering». But it does not allow us to go any farther. A systematical study of a great number of horns with polished tips might even give positive evidence that the rest of the horn was protected — a tolerably sharp line of demarcation between the polished surfaces and the unpolished ones may be taken as such. — Strange as it may seem, such unprotected bone does not necessarily bring with it a necrosis which would spread and endanger the life of the animal. Two evidently male skulls of *Palaeotragus microdon* in the Uppsala collection show on their horns beautiful facets indicating a long period of wear, and an unmistakable polishing is seen on a slenderer probably female horn (BOHLIN 1926, pp. 10 and 11). In this case a shedding is entirely out of question. Further, there is not the slightest trace of a necrosis: the beautifully preserved and carefully prepared specimens show no irregularities whatever on the surface of their horns which could indicate that the bone was diseased. Evidently the polishing also stopped up all channels which could have served as inlets for germs; there might also have occurred processes analogous to the retreat of the pulp cavity of a tooth during the wear — in fact the naked tips of the horns do not seem to imply a greater danger for the animal than the exposed dentine. A recent form with the tips of the horncores exposed and polished is the Okapi. A deciduous sheath of horn can under such circumstances not have occurred (and would have been quite meaningless). The compact structure of the horns of the *Merycodontini*, resembles that one in the antler of the deer and is quite different from the loose structure of the horn cores of *Sphenophalus*, *Ilingoceros* and the recent pronghorn in which a sheath gives a well needed addition to the solidity of the horn.

FRICK remarks (1937, p. 280) that »our inability to understand how such hardened structures went through the necessary changes attendant on increase of size except by some process of periodic shedding and replacement as in the deer, seem to indicate their necessarily deciduous character». It may suffice to state that it seems almost equally difficult to understand how the compact bone of the skeleton can grow. Also the horns of the

gazells are compact almost to the same degree as the horns of the *Merycodontini* and yet they increase in size.

For the question if the horns were shed or not (and also for other problems connected with the horns) the nature of the burr has its great interest. Most authors are aware of the profound difference between the deer and the *Merycodontini* in this regard. Already COPE (1877, p. 347) made sections of this region of the horn in order to find out if there was any discontinuity in the bony tissue of the beam underneath the burr which could indicate a healed fracture, but he found that »both the denser and coarser central tissues are uninterrupted». This has been confirmed

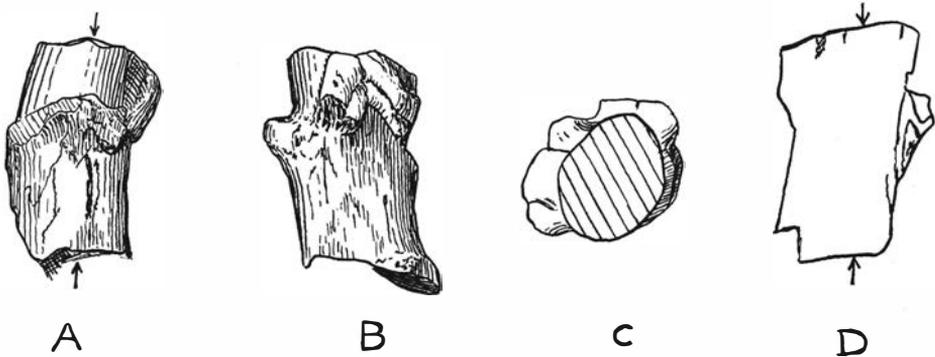


Fig. 1. Fragment of horn with burrs. (Fig. 1 D section at + in fig. 1 A.) Nat. size.

by FURLONG in 1927. Several authors have pointed out that the burr is loosely attached to the beam and can be removed without leaving a perceptible scar (MATTHEW 1924, p. 201, FURLONG 1927, p. 153). This latter statement might be true for some specimens and it might even be the rule. On a fragment in the Uppsala Museum (fig. 1 A—C) with two burrs only partially preserved, the connection seems to have been more intimate as splinters of the beam have come out together with the missing portions of the burrs. It is however evident from FURLONG's study of longitudinal and transverse sections that the tissues of the burr and beam are not continuous. On several specimens in Berkeley I could, however, state that distally the burr is marked off from the beam by a kind of a »suture», whereas proximally the surface of the burr is continuous with the surface of the beam (several specimens figured in the literature seem to show the same, for instance FRICK fig. 33, F: A. M. 31271, and fig. 38 A, F.: A. M. 31153). It thus seems as though the burr formed the thick upper rim of a socket surrounding the base of the horn (fig. 2). I tried in vain to trace the line of demarcation in the region below the burr on the sectioned specimen figured by FURLONG, but it might have been obliterated or be indistinct for some reason or other. The burr and its continuation downwards would thus have grown up from below; by far the strongest

deposition of bone was concentrated to the burr, the lamella below was thin, possibly very thin and even incomplete. Measurements taken below and above the burr show that the cross section below often is the larger one, which also would seem to indicate that something has been added to the volume of the beam below the burr (a greater number of measurements are desirable to settle if this is the rule or if the cases when the sections are equal or the upper one the larger, are the more frequent ones).

The measurements in the following table were taken on specimens in the Berkeley Museum (in millimeter):

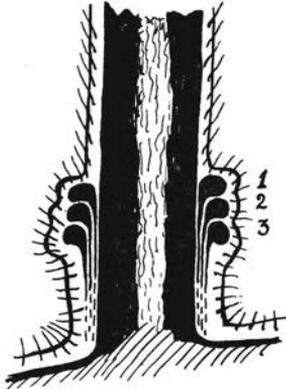


Fig. 2. Hypothetical section through the base of a *Merycodontini* horn. 1—3 order in which the burrs are supposed to have been formed.

	above the burr	below the burr
22495	14.8	19.5
26784	12.5 × 19.	14.8 × 16.
27243	16.3 × 16.7	14 × 16.4
28799	14.9 × 16.3	15.2 × 17.5
2056/28799	18.9 × 16.7	16.6 × 16.8
29625	17.4	20
33959	15.2 × 15.8	17.8 × 18.2

In 32308 the cross section is the same above and below.

It must be noted that the calipers used was not very good and that the tenths of the millimeter are at most relatively correct in so far as I tried my best to always use the instrument in the same way.

When several burrs are present it must be possible to determine on sectioned specimens the order in which they have come into existence. One thing seems to be certain: the burrs must have been added successively in order either from above downwards or from below upwards, and thus a burr has never been formed between two burrs already present. This naturally is valid only for multiple burrs belonging to the same group — and does not necessarily concern all the burrs present on the same horn. So, for instance, the burr on a tine in COPE's Pl. 80, fig. 3. (1877) might be an independent structure, and when widely separated groups of burrs are present as in FRICK's fig. 37, F.: A. M. 32895 (l. c. p. 306) each group might have its own history (in the case quoted they most probably also have). Further, I am inclined to believe that only one of the alternatives mentioned has been realized inside the family i. e. in all representatives which possess burrs, new burrs have been added in the same way. If my opinion about the structure of the burrs is correct the succession must have been from above downwards.

This in its turn must mean that the burrs cannot have had any close relation to periodical changes in the integument of the horn proper. That they should represent »the seasonal stoppage of growth and lime supply

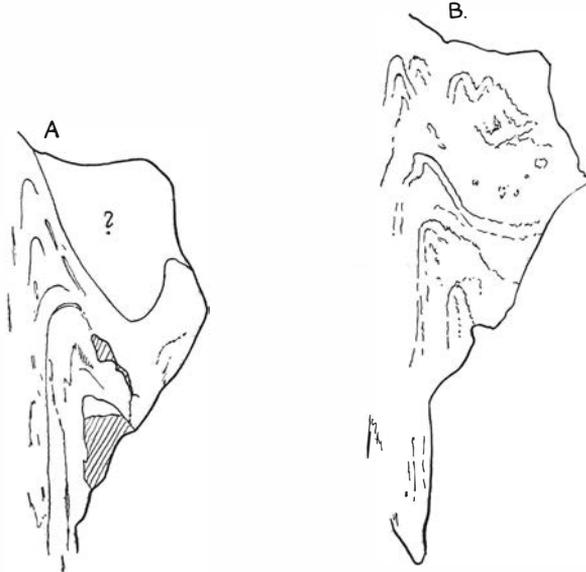


Fig. 3. Details from fig. 1 D, compare text. $\times 6$

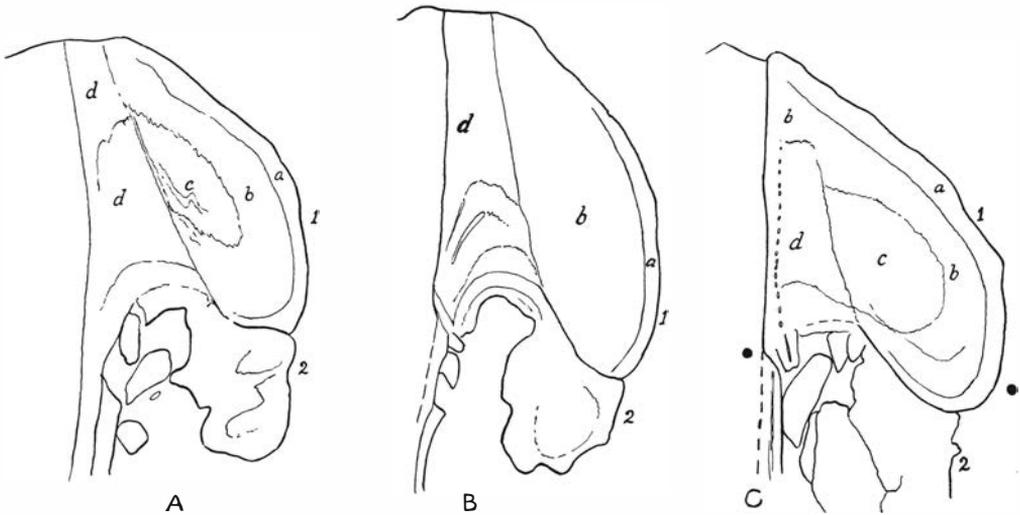


Fig. 4. Details of section at + in fig. 1 D, compare text. $\times 6$.
In C the parts above and below ●● are not in the same plane.

after the new growth of horn and horncase had been completed» as suggested by MATTHEW in 1924 would thus be impossible as one then would expect the burr, last in contact with the covering of the horn proper, to be the last one to have appeared. FRICK's suggestion (1937, p. 281), that »multiple burrs might be accounted for through periodical retreat of the velvet and encroachment of the head covering» requires the same succession of the burrs. The opinion expressed by RUSSELL (1936) that

with the degeneration of the covering of the horn »a burr might develop at the upper margin of the still living skin» on the contrary fits perfectly well with a succession of the burrs from above downwards. — In spite of this I am not quite willing to accept RUSSELL's theory *in extenso* and prefer to start out from the more indifferent statement made by FURLONG (1927, p. 154) that »the burrs may be regarded as the terminal point of the heavier skin covering of the head, and the initial point of growth of the lighter covering of the antlers». The difference between these two types of covering evidently did not exist before the appearance of the first burr and the further burrs were then formed as ossifications in the supposedly heavier skin covering the base of the horn below this first burr.

The order suggested above for the formation of the burrs of course precludes every thought of the horns having been deciduous. An arrangement for shedding leaving the burr on the beam does not seem less feasible than the possibility realized in the deer, but to make sense the burr connected with the last shedding would need to be the one nearest to the shed portion of the horn, i. e. a succession of burrs from below upwards must be postulated.

So far facts seem to speak a fairly plain language. When it comes to the question about the meaning of the burrs our statements must naturally be less positive. Firstly we must lay stress on the fact that the »burrs» in the *Merycodontini* are formations so profoundly different from the burrs of the deer, that the term »burr» should perhaps better not be used for them. It is evident that we here meet a quite unique device invented by nature to provide for needs not met with in any living species, or a new way to solve problems present also in other animals. The burrs, added one by one, would mark the seasonal changes of growth of the horns in the same way as the rings at the base of a cow's horn. — The burrs might have been quite of no importance. Or the addition of rings of bone at the base might have served the purpose to solidify the attachment of the horn to the skull — an attachment which perhaps was largely accomplished by a heavier covering of skin in this region. The function of the »burrs» might have been that of an upper fixed attachment for this skin.

Evidently the formation of »burrs» was a way which the *Merycodontini* used to respond to various outer influences: regeneration or at least healing of broken ends of the tines (FRICK 1937, fig. 37, F: A. M. 32895) — evidently not in all cases, however (COPE 1877, p. 352, Pl. LXXX, fig. 4 a).

Peculiar is the case figured by FRICK (l. c. fig. 37 a, F: A. M. 32902) showing burrlike formations without any connection with the horns (»ossification from an evident injury» FRICK l. c. p. 342). It is probably a scar of some kind but the healing has taken place in a way peculiar to the *Merycodontini*. The most important impulse for the formation of burrs was,

however, the physiological changes at the rutting season and it would seem that, whereas in the deer a whole new antler was formed, in the *Merycodontini* only the formation of a burr at the base of the horn resulted (possibly plus an increase in size of the horn).

It appears from FRICK's paper that the horns without a burr belong to adolescent individuals and that individuals with burrs were mature. It seems natural to assume that the number of burrs has some relation to the age of the individual, one burr having been added at each rutting season. The material with associated horns and dentition seems too scarce to allow a statement as to the relation between the number of burrs and the amount of wear on the teeth. The highest number of burrs in FRICK's figures seems to be four (individuals 5 or 6 years old?). The problem is complicated by the fact that also the females were horned and probably did not develop their horns exactly like the males (a hornless (?) female skull has been described by GAZIN 1930, p. 74).

Remarks to the figures.

When I visited Berkeley Dr. STIRTON kindly presented me with some fragments of merycodont horns, one of them with two burrs. The preparator of the Palaeontological Museum of Uppsala, Mr. N. HJORTH, has made sections for me of this fragment, but on account of the hard and brittle bone these did not turn out as well as could have been desired. Further, fissures occurred in the fragment at critical points and therefore my studies of the bone structure on polished surfaces did not give all I had expected. In figs 3 and 4 I have indicated the structures as I have seen them and it seems as though the tissue of the burr was continuous with the one of the adjoining layer of the beam and the structures bent around and went downwards when entering the beam. After one drawing was made the surface was ground down 0.5 a 1 mm. In fig. 3 evidently only one of the burrs (the upper one) is preserved, in fig. 4 both burrs. In the latter figure the letters indicate zones of different colour: *a*. almost white (evidently through weathering), *b*. dark brown (in *A* and *C* with a core of a lighter shade = *c*); *d*. light reddish brown. The structure of *b* (and *c*) is very irregular, in 4 *C* the portion marked *d* has a similar structure and evidently the line of demarcation between zones *b* and *d*, although rather sharp in 4 *A* and *B*, has no greater importance. The question-mark in fig. 3 *A* indicates a portion well separated from the adjoining portion through a fissure (possibly *post-mortem*).

A more detailed analysis of the sections is out of place, as this single, somewhat maltreated specimen hardly alone can be accepted as norm. I may only say that they seem to give support to my interpretation of

the burrs in the *Merycodontini*, and I hope that a future study will be made of a great number of specimens — there is evidently no lack of material that could be sacrificed for this purpose.

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