2. The function of the malar processes in the Entelodonta.

By

Birger Bohlin.

———

At first sight one would be inclined to interpret the malar processes in the *Entelodonta* as muscular attachments, without even a thought that there could be any doubt. So they have been apprehended for instance by MARSH 1873, by PETERSON (to judge from the reconstruction made under his direction; 1909 pl. 62), and finally by TROXELL (1920) who puts forth good evidence in support of his view. But the doubters have been equally well represented (SINCLAIR 1921, MARINELLI 1924), and among them SCOTT (1898, p. 281) states that »these processes are, so far as is yet known, quite unique among hoofed mammals, and it is difficult to form even a conjecture as to what their functional significance may have been». (Cfr. also SCOTT 1937: function entirely unknown).

The present paper is based exclusively upon observations made on figures in various publications, and I am aware that for a definite solution of the problem a renewed study of the originals is necessary to state the occurence and extension of muscular attachments etc. I am, however, convinced that TROXELL is right in his suppositions and will test the objections raised against them and see what new evidence can be added.

SINCLAIR (1921) has proved, as it seems beyond doubt, that the anterior border of one of the malar processes in a skull of *Archaeotherium scotti* must have been damaged (evidently partially bitten off) and the wound healed again during life. He concludes (p. 493) rejecting TROXELL's hypothesis that the processes have given origin to the masseter: »It seems to me equally probable that the process in question extended over the masseter without giving origin to it, and projected sufficiently beyond the outer surface of the cheek to afford a handy grip to an antagonist». But TROXELL's views are by no means incompatible with these observations of SINCLAIR's. If the masseter was attached to the processes, these were almost certainly not deeply imbedded in the mass of the muscle. On the contrary, the anterior margin of the bone must have been in contact with

the skin as the muscle extended backwards from the process, and must have protruded in the same way as the margins of the pelvic bone in a cow, where it would be an easy thing for an animal with strong jaws and teeth to get a firm hold and break out a piece of the bone. Teeth marks at the lower end of one of the flanges in a skull of *Archaeotherium marshi* have been figured by TROXELL (p. 382); these evidently can be explained in a similar way.

MARINELLI, in his interesting study on the mechanical relations between the teeth and the skull structure, does not take the malar processes into consideration: »TROXELL meint, er sei eine verbreiterte Ansatzstelle für den M. masseter, doch scheint mir sowohl Form wie auch Lage gegen diese Annahme zu sprechen; auch ist er wohl als Muskelansatz viel zu schwach. Eher möchte ich mich der Ansicht SINCLAIRs anschliessen, dass er als eine Art Flankenschutz des Schädels aufzufassen sei» (p. 30). — The process may have been weak (in *Megachoerus zygomaticus* »for most of its extent it is not thicker than 20 mm», its maximum length 200 mm [TROXELL, p. 434], which seems to make a fairly strong piece of bone) but it was at least not weaker (comparatively) than the similar processes in *Bradypus* and other edentates in which the masseter is attached to it (MACKINTOSH 1873, p. 518: »Masseter arises from the anterior and posterior surfaces of the descending jugal process and runs backwards to the usual mandibular insertion»). Otherwise the malar is comparatively weak below the orbit as noticed by LEIDY, but »this comparative weakness of the connection of the zygoma with the side of the face is duly compensated for in the additional abutment to the zygoma, in the strong postorbital arch» (1869, p. 177). The stress on the malar must of course have been great when a massive muscle acted upon the lever formed by the depending process, and it then seems reasonable to assume that the development of the postorbital bar to support the malar had some mechanical relation to the increased stress on the bone. In fact, in some of the figured species, the postorbital bar bends forward above the eye towards its attachment to the frontal in a way which would make it fit to resist a pressure at least if the lever was pulled straight backwards, the fix point assumed to be at the attachment of the malar at the anterior lower corner of the orbit. This occurs even just in the species where the malar process is inclined forwards (*e. g. Archaeotherium marshi*) and the torsion thus must have been more pronounced than in others in which the process extends in the direction of the pull of the masseter and a tension is more likely to have resulted than a torsion. MARINELLI is quite aware that the malar with its two attachments in front forms a solid structure, but he gives another explanation (pp. 39—40) which is not excluded by the one proposed here.

In *Bradypus* the orbit is open behind, and the malar is attached to

the skull only by means of the weak suborbital bar. The movements of the lower jaw must, however have been different in the entelodonts as compared with *Bradypus*. *Mylodon, Grypotherium, Scelidotherium* etc. are all of the *Bradypus* type: the masseter pulled backwards and the suborbital connection only had to withstand a tension. *Glyptodon,* on the other hand, has a very high skull; the depending process, to which I suppose no one would deny that the masseter was attached, acted as a lever, and here we also find a postorbital bar.

Of the authors who have dealt with the *Entelodonta,* WINGE (1906, pp. 141—142) seems to be the only one who has tried to see in the malar processes an adaption necessitated by the extraordinary development of the skull as a whole. As his paper is written in Danish, I will give the passage which is of interest for the present paper in translation (p. 142): »In their dentition it is obvious how the incisors, the canines, and the premolars more and more take the form of a grasping apparatus and of weapons in a similar way as in the carnivores and become large and strong, whereas at the same time the molars gradually lose there ungulate characters and comparatively decrease in size. In comparison with what is found in other ungulates the masticatory muscles obtain a remarkable strength; in order to give due force to the anterior teeth in the jaws the temporalis muscle increases considerably in size, forms a long crista sagittalis and presses the zygomatic arch outwards posteriorly; the masseter muscle grows in a more peculiar way; in order to permit a wider gape, it cannot as usual in the ungulates extend forwards, it produces instead an immense downward directed outgrowth from the lower border of the zygomatic arch on which its origin is extended and the processus angularis of the lower jaw is enlarged by its attachment.»

The demand for a wider gape but at the same time for greater muscular strength must evidently have caused changes in the region where the masticatory muscles had their insertion, and WINGE's discussion at least provides a motive for the formation of the malar processes. It is interesting to compare WINGE's conclusions with the ones reached by MARINELLI. According to the latter the lower jaw with its large canines was used in a way which required some shock-absorbing device to prevent the jaw from getting dislocated. The masticatory muscles were made use of for this purpose and therefore their attachments to the skull moved forwards and those to the lower jaw backwards. »So wandert denn auch der M. masseter vom Jochbogen nach vorn an den Schädel selbst und gibt seinen ursprünglichen Insertionspunkt am Jochbogen auf: am Unterkiefer aber wird das hintere Ende der beiden Kinnladen nach unten und rückwärts verbreitert» (pp. 37—38).

It is, however, doubtful whether an attachment of the masseter to the malar process really would permit a wider gape, at least would the per-

centage of stretching of the muscle be about three times as great as if the muscle were attached to the face above the molars. For points indicated with a $\times$ in fig. 7:

Mouth opening 18°   80 %   and   25 % respectively
             33° 140 »   49 »

of which at least the figures in the first column are impossibilities. In *Hippopotamus* the mouth can be opened at least 45° but this does not involve a stretching of the foremost portion of the masseter amounting to more than 28 %. The corresponding figure for *A. marshi* according to MARINELLI's interpretation would be 72 %. The computed values are of course rough approximations as they do not take the third dimension into consideration, and, furthermore, the points at which the measurements were taken are arbitrarily chosen. From my point of view the conclusion would be that the gape was not very wide, at most as wide as indicated in fig. 7 (10°; cfr the reconstruction in MATTHEW 1923, p. 368), and even if the masseter inserted on the face, the gape cannot have been by far as wide as in *Hippopotamus*. (Cfr. TROXELL, p. 255: »The condyles of the ramus permitted an unusual freedom of movement to the jaws in nearly every direction including the opening to a wide angle ...»).

If WINGE and those who share his opinion that the masseter was inserted on the process are right, then one would expect to find some structural conformity between the parts of the skull and the lower jaw which were under the influence of the same muscle, and this also seems to be the case. Three types can be distinguished (figs. 1—4):

A. The processes are distinctly bent forwards — in the lower jaw the anterior free border of the angular flap correspondingly bends forwards. This condition is found in *Archaeotherium marshi* (figs. 4 and 7); evidently also in *A. ingens* (SCOTT 1898, pl. 17), and *A. wanlessi* (SINCLAIR 1921 fig. 5).

B. The processes are directed backwards — in the lower jaw the »hook» at the anterior end of the angular process is very little pronounced, the lower border of the horizontal ramus bending downwards at a wide angle. *Archaeotherium mortoni* (fig. 2) and *Daeodon (Elotherium) calkinsi* (SINCLAIR 1905, pl. 15) are of this type. In both this species the angle of the jaw is obliquely truncated in a peculiar way.

B a. An extreme development of type B. *Choerodon caninus* (fig. 1) and evidently also *Megachoerus zygomaticus* (SINCLAIR 1921, fig. 18; cfr. TROXELL, p. 255: »In the enormously developed jugal of *M. zygomaticus* it is important to notice that the process extends backward so that its outer, posterior edge almost parallels the border of the angle of the ramus.

Whatever may have been the original purpose of this dependent process it is evident that these animals profited by its use until it reached the enormous size shown in this species, probably the last of its race.»

C. Finally in *Dinohyus* the processes are short and directed downwards — in the lower jaw the angle is regularily rounded off. A similar intermediate condition is suggested by TROXELL in his reconstruction of the missing parts in *Archaeotherium clavus darbyi* (p. 367: fig. 4).
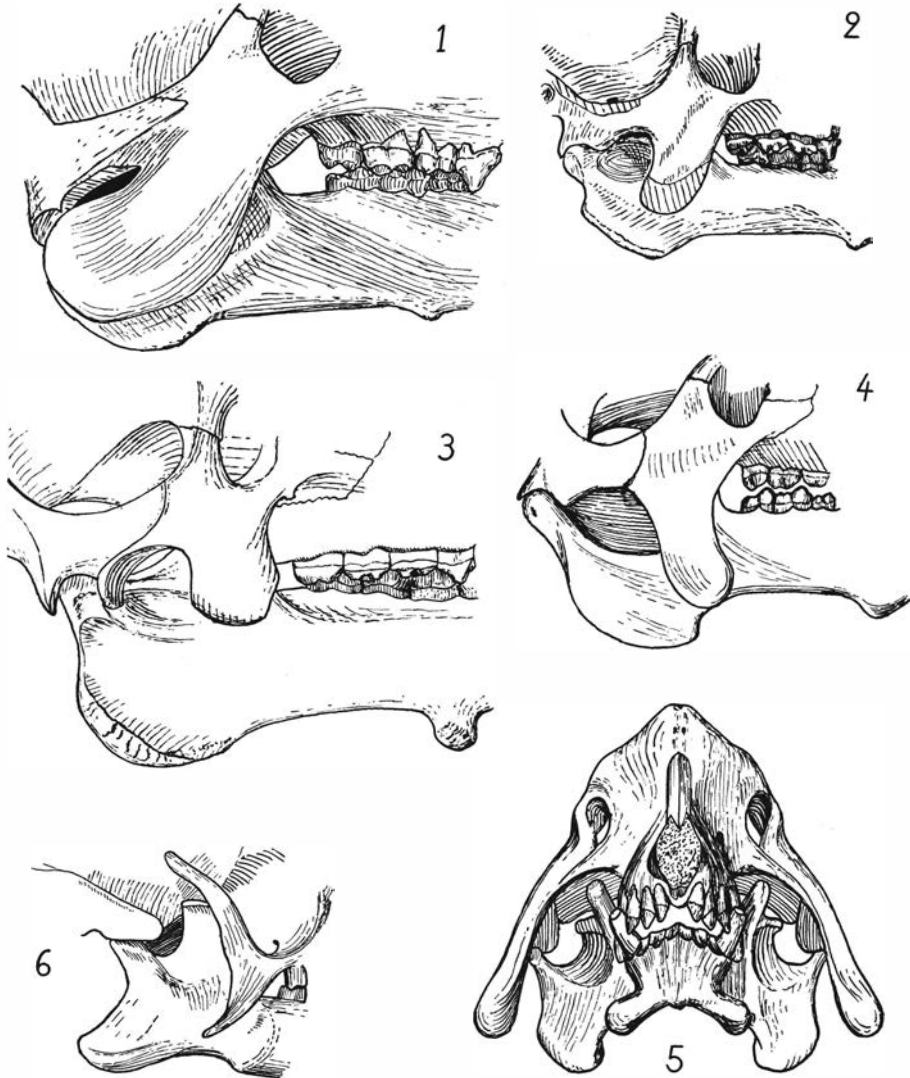

Fig. 1. *Choerodon caninus* (after TROXELL). Fig. 2. *Archaeotherium mortoni* (after PETERSON). Fig. 3. *Dinohyus hollandi* (after PETERSON). Fig. 4 & 5. *Archaeotherium marshi* TROXELL (after MARSH 1893). Fig. 6. *Bradypus tridactylus*.

The correspondence between the process and the angle of the lower jaw is too complete to be merely coincidental. The only explanation is evidenty that the same force must have acted on both, and the only force that can be thought of is the contraction of the masseter. In *Bradypus* we find a corresponding backward sweep of the malar process and the angle of the lower jaw (fig. 6).

Apart from their deviation forwards and backwards the processes are usually not directed straight downwards but more or less outwards. The angle of the lower jaw is, however, also turned outwards (TROXELL, p. 383: fig. 12; SINCLAIR 1921, fig. 14).

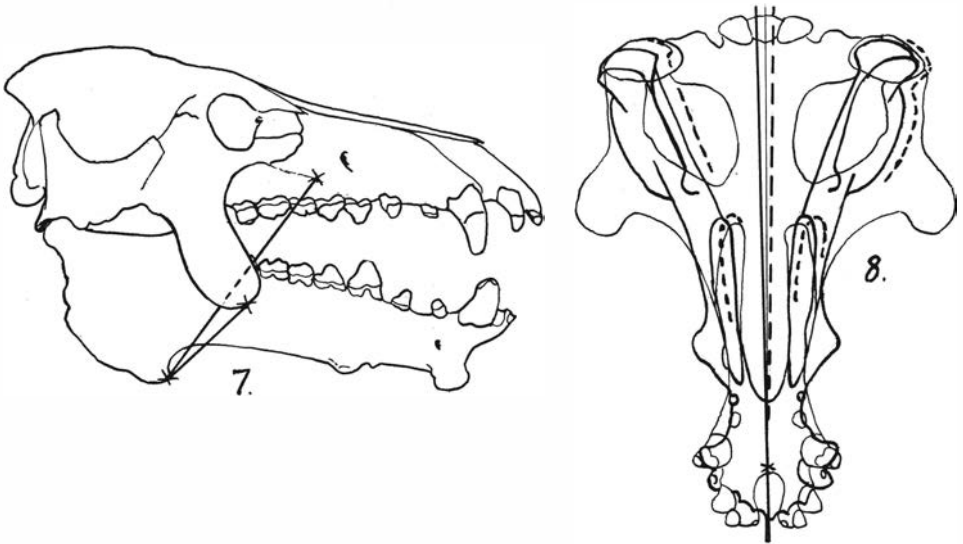If SINCLAIR were right, that the processes protruded freely and acted

Fig. 7 & 8. *Archaeotherium marshi* (after the holotype, TROXELL 1920).

as some kind of protection of the flanks (»Flankenschutz», »Schutz der Augen», according to MARINELLI) one would expect to find all kinds of excesses in their development, not only in size but also in shape and direction. Among horned mammals we find several examples of such excesses (*Protoceratidae, Sivatheriinae, Ovibovinae* etc.) — it almost seems to be a rule that inside a group processes which are not altogether under the control of the mechanical system formed by the muscles and the surrounding bones sooner or later produce monstrosities. In the entelodonts the malar processes differ in different species, and they are also heavier in the males than in the females of the same species; further, they are more prominent in the later forms than in the earlier ones (*Dinohyus* forms an exception). But, they never grow out of harmony with the, in many other respects peculiar skull in which they are implanted. It may perhaps be worth noticing that when the processes are enlarged they extend

backwards over the angle of the lower jaw (= type B a), and we do not up till now know any case of extreme development corresponding to types A and C. — SCOTT (1937, pp. 390—391) figures a male and a female skull of *Archaeotherium mortoni* from behind; it is true that the processes are heavier in the former, but the skull of the male is as a whole con- siderably broader and heavier than the female skull (posterior width ap- proximately as 4 : 3). — As protections for the eye the processes must have been very ineffective as it would have been a protection almost only from below, and attaks from that direction would evidently least of all have endangered the eyes.

Brachyhyops described by COLBERT (1938) has a malar which suggests the one of the entelodonts and which could very well represent a first stage in the development of real processes. The relationships of *Brachy- hyops* seem to be far from settled, but COLBERT means that the genus »is probably fairly close to the ancestors of the achaenodonts and the entelodonts» (l. c. p. 99). About the function of the process in the en- telodonts COLBERT expresses himself very cautiously: »Whether this is entirely an adaption for an enlarged masseter may be questioned».

If now the masseter, or part of it, had its origin on the malar process, the question arises: What special function of the masseter depended on this peculiar arrangement for its insertion? According to MARINELLI the most important parts of the dentition were the large canines and the molars. (The premolars are in *Archaeotherium*, on which genus MARI- NELLI's analysis is chiefly based, of less importance, but their develop- ment in *Scaptohyus* [SINCLAIR 1921, fig. 15] seems to indicate that they took part in the functions of the canines). »Die eigentliche Beisstätigkeit beginnt erst im Molarenabschnitt, doch dürften so ausgiebige Seitwärts- bewegungen der Kiefer, wie wir sie bei Wiederkäuern beobachten können, hier nicht möglich gewesen sein, da bei geschlossenem Maule die Zähne des Vordergebisses zu sehr ineinandergriffen. Dadurch ist der Fixpunkt der Bewegung nach vorn verlegt, eine ausgiebige Mahlbewegung nur in der hintersten Gebissregion möglich.» That lateral movements of the lower jaw really were possible seems to be evident from a statement in TROXELL's paper (p. 255): »From the tip of the process the fibres of the muscle might have given the forward, the backward, and even a sideward movement to the mandible, for, judging from the wear on the teeth and the form of the molars, there was a definite transverse motion.»

The answer to the question would then be: As the lower jaw, when the mouth was closed, was locked in front by the heavy interlocking canines, some other way had to be found to make a transverse motion possible. To enable the masseter to assist in the sideward movements of the lower jaw its attachment to the malar was lowered to a position laterally to the attachment to the mandibular angle. How the chewing

under such circumstances was done, I have tried to make clear in fig. 8.
The position of the fix point must have been sowewhere between the
canines (indicated by a ×). As stated by TROXELL the articulation
between the lower jaw and the skull permitted an unusual freedom of
movement; I have assumed that the condyles were free to move from
side to side in the glenoid fossae and this would correspond to a trans-
verse movement in the region of the molars amounting to about half of
the breadth of these teeth. The knob-like coronoid process evidently
goes well with the assumption of a rotational movement, whereas a higher,
flattened process might have constituted a hinder.

It thus seems as if all evidence were in favour of the interpretation
proposed by TROXELL.

A reconstruction of the jaw muscles of the entelodonts would of course
be incomplete if the mental processes were disregarded. These TROXELL
has discussed at some length and as far as I can find he has considered
all possibilities. We must, however, assume that the muscles which
possibly were attached to these processes were the same ones which in
other mammals occupy a corresponding position, and thus any attempt
to introduce new muscles must be rejected. Therefore I do not think
that TROXELL's suggestion in addition to the »natural» alternatives, that
there was a muscular connection between one or both of the mental pro-
cesses and the dependent process of the malar is very fortunate. — To
me the mental processes are more of a puzzle than the malar process.
They have the same position in all genera, their extension seems to be
in accordance with the general mechanical trends of the lower jaw (very
obvious in Scaptohyus, SINCLAIR 1921, fig. 15); when small, as for in-
stance in *Dinohyus*, they can without hesitation pass as rugosities for the
attachment of muscles, and from there to the development of the processes
in *Archaeotherium* it is not so exceedingly far — but then come the
immense anterior processes in *Pelonax*, which may, however, seem less
fantastical when once the whole skull will be known.

References.

COLBERT, E. H. (1938): *Brachyhyops*, a new bunodont Artiodactyl from Beaver Divide, Wyoming. Ann. Carnegie Mus. Vol. XXVII, Art. IV. Pittsburgh, Pa.

LEIDY, J. (1869): The extinct Mammalian Fauna of Dakota and Nebraska. Journ. Acad. Nat. Sci. Ser. 2, Vol. VII. Philadelphia.

MACKINTOSH, H. W. (1873): On the myology of the genus *Bradypus*. Proc. Royal Irish Acad. Ser. 2, Vol. I — Science. Dublin.

MARINELLI, W. (1924): Untersuchungen über die Funktion des Gebisses der Entelodontiden. Palaeontol. Zeitschr. Bd. VI. Berlin.

MARSH, O. C. (1873): Notice of new Tertiary Mammals. Amer. Journ. Sci. Ser. 3, Vol. V. New Haven.

—— (1893): Description of Miocene Mammalia. Amer. Journ. Sci. Ser. 3, Vol. 46. New Haven.

MATTHEW, W. D. (1923): Fossil Bones in the rock. Natural History, Vol. XXIII, No. 4. New York.

PETERSON, O. A. (1909): A revision of the *Entelodontidae*. Mem. Carnegie Mus. Vol. IV, No. 3. Pittsburgh.

SCOTT, W. B. (1898): The osteology of *Elotherium*. Trans. Amer. Philos. Soc. Ser. 2, Vol. XIX, Philadelphia.

—— (1937): A history of Land Mammals in the Western Hemisphere. 2. Ed. New York.

SINCLAIR, W. J. (1905): New or imperfectly known Rodents and Ungulates from the John Day series. Univ. Calif. Publ., Bull. Dept. Geol. Vol. IV, No. 6. Berkeley.

—— (1921): Entelodonts from the Big Badlands of South Dakota. Proc. Amer. Philos. Soc. Vol. LX. Philadelphia.

TROXELL, E. L. (1920): Entelodonts in the Marsh Collection. Amer. Journ. Sci. Ser. 4, Vol. L. New Haven.

WEBER, M. (1927—28): Die Säugetiere. 2. Ed. Jena.

WINGE, H. (1906): Jordfundne og nulevende Hovdyr. E Museo Lundi 3: 1. Köbenhavn.