8. Food habit of the machaerodonts, with special regard to *Smilodon*.

By

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When preparing some lectures on the fossil Carnivora early in 1939 I had the occasion to enlarge my knowledge on the machaerodonts beyond what can be found in the text-books, and what induced me to pry still somewhat deeper into the literature was a reaction against the way in which the enlarged canines and bloodthirstiness or fierceness usually are coupled and the combination raised almost to the rank of an axiom. I readily admit that this reaction primarily was dictated by a spirit of contradiction, but after having considered the question in a calmer mood there remains a conviction that the strong development of the tusks must not necessarily have been accompanied by an extremely pronounced rapacity.

I have not been able to get hold of everything that has been published on the biology of these carnivors. Much that perhaps would add to the collection of possibilities proposed on the subject has been published in popular weekly and monthly magazines. Further, I have, above all, had difficulties to get hold of papers which have not appeared in scientific periodicals. In about 60 papers I have found at least something that is of interest in this connection. In my list of literature I have chiefly entered those which deal with the subject at some length.

My intention is not to give an entirely new *Lebensbild*. The ideas which turned up when I read the first part of the literature I have been able to find in one form or another when I continued my studies. But it is evident that no unity of opinion has yet been reached, and even the interesting results arrived at by American scientists after a careful study of the muscular attachments on the skull and the lower jaw, have been rejected by such a prominent authority as Professor ABEL (for instance in 1927 and 1939)[1]. I have therefore thought it worth while to let the various contributions to the discussion undergo a reconsideration and to

[1] Compare MATTHEW 1910, p. 305.

try to combine the pieces of the puzzle which I find useful for a possible, if not the only possible picture. As the biology usually has been treated in passing in papers chiefly dealing with systematical or anatomical problems or as parts of a general treatise on palaeobiology, I have thought that a special paper could have its interest. First after I had entered on this task MARINELLI's paper (published in 1938) reached me, but, as far as I can find, it has not made the present treatise entirely superfluous.

The incisors and lower canines.

I first have to take up a position in reference to various opinions on the function of the dentition and certain parts of the skeleton which in some way or other are functionally connected with the teeth.

The incisors and the lower canines must have functioned together; on this point there seems to be general agreement. These teeth gradually increase in size in the direction of the canines and C_{inf} falls well into the lower series (WEBER 1927, I, fig. 176). An antagonism between upper and lower canines has never been assumed as far as *Smilodon* is concerned (MATTHEW 1901, p. 386: »lack of use of the lower canines (used against the upper ones by other carnivores, but useless in this way to the Sabre-tooth)»[1]. In some species of machaerodonts things may have been different as is evident from SCHAUB's remarks on *Machaerodus crenatidens* (1925, p. 264): »Dazu kommt noch, dass beide untere Caninen deutliche, durch die obern Eckzähne verursachte Usuren besitzen, dass also, wiederum im Gegensatz zu den 3 genannten Arten» (i. e. *Machaerodus aphanistus*, *M. cultridens* and *Smilodon*) »ein normaler Antagonismus zwischen den Caninen möglich war».[2]

The incisors (and C_{inf}) must have been of more use than in the true cats. They are proportionally larger, and their rows protrude in front of the large upper canines, which latter otherwise would have interferred seriously with any kind of grasping, gnawing or similar function. In the true cats the comparatively week upper and lower incisors come to stand between the large lower canines when the mouth is closed, although the stand well in front of the upper ones (but they still can add to the efficiency of the grasping apparatus of which, however, the canines form the most important part).

That the incisors of *Smilodon* have been used is evident from the fact that they are worn (see for instance BURMEISTER 1868, p. 189: »Jeder einzelne Schneidezahn von *Machaerodus*[3] geht in eine einfache, durch Ab-

[1] The Spacing of parts of the quotations is mostly mine.

[2] See also POMEL 1843, p. 33. — FABRINI remarks, evidently with reference to machaerodonts in general (1890, p. 126) »... mascella inferiore, il cui dente canino serviva di contrafforte, di punto d'appoggio al canino superiore».

[3] i. e. *Smilodon neogaeus*.

nutzung etwas abgerundete Spitze aus»). BRANDES (1900, p. 106) points out that the conical shape of the incisors make them less fit to gnaw off the flesh from bones, a statement which ABEL (1908, p. 209) transcribes as »weit weniger leistungsfähig ... als bei den lebenden Tigern und Löwen»[1]. In the second edition of his »Lebensbilder» (1927, p. 161) ABEL states, however, that to judge from the impressions of teeth on bones found at Pikermi »sich an diesen Mahlzeiten nicht nur die aasfressenden Hyänen und Ictitherien, sondern auch Machairodus und sogar Nagetiere beteiligt haben», which possibly refers to marks of the incisors(?). MERRIAM & STOCK lay stress upon the large size of the incisors in proportion to the week lower jaw as an evidence of some special function, and they suggest that *Smilodon* used its incisors when it »shook or worried its prey (p. 25), or (p. 46) »the grasping and holding of prey was accomplished largely with the aid of the strong penetrating incisor teeth». In 1936 SCOTT & JEPSEN write about *Drepanodon* (p. 127): »The lower canine and third upper incisor together form an efficient secondary grasping apparatus, which might be used when the mouth was not open so far as to free the points of the great upper tusks».

In my opinion the incisors must have been very inefficient against the thick hide of a struggling elephant or any other heavy-bodied animal. The distance between the points of the upper median incisors and the front of the large canine tusks is only about 3 cm, for the lower incisors the distance is much less (measured on frontispiece in MERRIAM & STOCK 1932). The effect would sooner be pinching and irritating than shaking and worrying, and it seems very unlikely that *Smilodon* with such a limited »free bite» would have attacked a prey with its incisors, mouth only moderately opened. Even if the prey were comparatively slow, the sabre-tooth must aim and bite quickly and would thereby risk the shock of the body of the victim against its upper canines. It would be different if the prey were already slain and *Smilodon* could at its ease press its muzzle into the soft parts, take a firm hold with the incisors of a strip of flesh, and tear. The occlusion of the incisors — the points of the upper ones between the points of the lower ones — seems to be ideal for this purpose. In principle the teeth ought to have functioned like a pair of clawed pincers, a function which also seems to be reflected in the symphyseal portion of the lower jaw.

MARINELLI (1938, p. 263) speaks of a »Fortfall der Greiffunktion im Vordergebiss» which should be reflected in the development of the temporalis muscle (»nicht die nach hinten ziehenden, sondern die senkrecht wirkenden Fasern überwiegen». This I cannot unreservedly subscribe to. I may quote a sentence from THORPE 1922 (p. 281; comparison of *Neo-*

[1] BRANDES means that, except for the upper canines, the dentition of *Smilodon* expresses the carnivore type in a very imperfect way.

hyaenodon with *Smilodon*): »of the three sets of muscles, temporalis, masseter, and internal pterygoid, each alone was relatively weak in the power of closing the jaw, but the three acting in unison were powerful.» They were powerful enough, anyhow, if *Smilodon* did not with its incisors hang on with the whole weight of its own body to a prey which did its very best to escape, but the work of the incisors was restricted to the tearing of the flesh of a dead animal.

The main point is, however, that shape, size, and position of the incisors of *Smilodon* indicate a specialisation not found in the contemporary *Felis atrox* (MERRIAM & STOCK 1932: e. g. Plates 1 and 13; 26 and 33), and that this specialisation must have had its meaning and must not be neglected in a treatise on the food-habit of *Smilodon*. The interpretation adopted in the present paper may not be the correct one, it seems to me, however, as if it were at least as reasonable as any other which has been suggested.

The upper canines.

Regarding the structure of the upper canines the following facts seem to me to be of importance: 1) Of the edges the one in front extends only half as far upwards from the point of the tooth as the back one, and is only close to the point equally pronounced as this latter. This condition reminds, except for the strong curvature of the canine, of a hunters knife which has an edge also on the back extending for a short distance above the point, and which is used for disembowelling the game. The double-edged part of the blade cuts in both directions when the knife is thrust in and the opening thus obtained is then the starting-point for the long cut. 2) The curvature of the tooth is equal and fairly strong. I have attempted to determine the centre of the circle of which the back edge forms a part and found it lying about 5 centimetres below the postglenoid process (fig. 1: *p*). For the front curve of the canine the centre lies a couple of centimetres below and well in front of the preglenoid edge (fig. 1: *a*). Roughly, the centre is the glenoid fossa and this means that the enlargement of the upper canines has taken place along lines, which were determined at a time when the teeth were still under the influence of the lower jaw (vide infra).

In a presentation of a cast of a skull of »*Felis smylodon*» WARREN (1854, pp. 257—258) gives a description of the upper canines of which the following is an extract: »The anterior edge is thicker than the posterior, which gives to the prehensile and cutting part a much greater power of division than that of the anterior edge.... The extremity is sharp pointed, so as to penetrate readily the flesh of its victim.... Now, if we consider the length of this tooth, its curved form, its narrowness, (like

that of a sword), its pointed extremity, its serrated edges, its deep implantation in the socket, we shall see in it one of the most formidable weapons of attack, which nature has invented. The Lower Jaw is remarkable . . .: 1st, the smallness of the coronoid process and of the angle wich it makes with the horizontal branch; an arrangement which would diminish the power of the temporal muscle, and thus weaken the operation of the lower jaw in the act of incising the food. The loss of this power is compensated by the movement of the head and upper jaw, which enables it to transfix its prey by the great canines, and then cut and tear it by a movement of the head backwards — an action which would not require the coöperation of the lower jaw. So we may believe, that while the upper jaw has a power much greater than that of other carnivorous animals, the lower jaw has actually less». Some parts of this quotation concern also other parts than the canines, but I have preferred not to dismember it.

In 1862[1] GAUDRY writes about *Machaerodus* (p. 114) that it »taillait, au moyen de ses canines en forme de lames de poignard, des lanières dans le cuir si épais des pachydermes de la Grèce antique».

Evidently around 1900 the »stabbing hypotheses» makes its appearance in the discussion. BRANDES suggests (1900, p. 106) that *Smilodon* attacked the armoured glyptodonts and used the upper canines »als Meissel . . ., die durch die Halsmuskulatur sehr energisch in den Panzer gestossen wurden[2]. Vielleicht wurde dann durch Rückwärtszerren ein Stück des Panzers herausgerissen und so das Innere, besonders das Blut der Thiere, zugänglich gemacht»[3]. The length of the canines and the thickness of the plates of the armour BRANDES considers to have developed parallely »wie der Wettbewerb zwischen Panzerplatten einerseits und Geschützen, Pulver und Geschossen andererseits». The armour of a *Glyptodon* is heavy and the idea that the fairly delicate point of a *Smilodon* canine would be able to penetrate it must, as far as I can see, be rejected.[4]

After MATTHEW's study of the muscular attachments on the skull and neck the stabbing hypothesis has been dominating to a degree that has

[1] See PILGRIM Pontian Bovidae of Europe, Brit. Mus. (N. H.) 1928, p. 97.

[2] Compare WEISSMAN 1902, p. 403: »vom unbewehrten Hals her» und ABEL 1908, p. 209 »den ungepanzerten Hals der grossen gepanzerten Glyptodonten».

[3] In a note BRANDES developes this further: »Es ist bei dem Bau des Gebisses sehr wahrscheinlich, dass die Räuber sich hauptsächlich von dem Blute der erschlagenen Thiere ernährten; vielleicht wurden von den Körpertheilen nur die blutreichen Organe, wie Herz, Lunge, Leber, Milz verzehrt».

[4] I find, however, in a Swedish edition of BREHM's »Tierleben» a statement that broken canines are commonly found in the jaguar (more than 5 % of a great material investigated) and it is suggested that this damage resulted from attacks on tortoises and alligators; it is of course not excluded that also *Smilodon* sometimes took a similar risk with a *Glyptodon*.

not been only of advantage. I can only quote a few expressions from the rich literature favouring this theory: »Tremendously powerful, quick downward blow» (MATTHEW 1910, p. 296). »The principal purpose» (regards the construction of the skull)... »is to obtain greater leverage and so render more effective the downward stabbing stroke of the tusks» (LULL 1917, p. 567). »The upper canines were exceedingly long stabbing and slicing structures» ... »operated by stabbing and slicing with the mouth open, causing the animal» (i. e. »thickskinned animals such as mastodonts and elephants») »to bleed to death» (ROMER 1933, p. 294). »... mit einem gewaltigen Hieb die Caninen an geeigneter Stelle einzuschlagen. Durch einen ebenso kraftvollen Ruck befreite sich Machaerodus von seinem Opfer und erweiterte mittels der messerscharfen Hinterkante der Caninen die Stiche zu langen Schnittwunden» (SCHAUB 1925, p. 262). SCOTT & JEPSEN (1936, p. 112) mean that »the machairodonts used their great sabres to strike a stabbing blow, as does a snake».

It has struck me that most of the treatises on the subject deal with the killing of the prey, and very little attention is paid to the at least equally important question how *Smilodon* and other machaerodonts fed upon the dead body. MARINELLI's paper of 1938 forms one exception. In 1924 (p. 32) he uses the word »Enterhaken» when he discusses the function of the large canines; in 1938 the possibility of a stabbing action is discussed at some length (p. 258, conclusion: »Es ist aus dieser Überlegung mit Sicherheit abzuleiten, dass die riesigen Eckzähne niemals durch wirklichen Biss, sondern jedesmal nur durch die Mitarbeit des ganzen Körpers, insbesondere der Muskulatur des Nackens und der vorderen Extremität, unterstützt durch die Wucht des im Ansprung an das Beutetier geworfenen Körpergewichtes in dessen Leib eingeschlagen werden konnten»). However, on p. 268 he discusses another alternative, namely that »dieser Räuber seine Eckzähne wie ein Eber als Hauer verwendete und etwa einer gefällten Beute mit einem einzigen Hiebe den Bauch aufzuschlitzen imstande war». On the following page this idea is somewhat further developed when MARINELLI suggests that the weak lower jaw and the muscles operating it should indicate »dass sich dieser Räuber hauptsächlich über die weicheren Eingeweide seiner Beute hermachte».

Personally, I do not think that the stabbing hypothesis is the only possible explanation, I even would go so far as to denounce it.[1] As already mentioned (p. 159) the centre for the arch formed by the upper canines lies about at the glenoid fossa. If the »stabbing blow» was struck with the whole head, the atlanto-occipital joint was the centre, and in that case the orientation of the canines is far from ideal (in fig. 1 *1* is an arch with its centre at *ao*). When raising the head to strike the whole

[1] MOORE 1933, p. 617:» ... it is very doubtful that the tusks were used in striking at prey, as a snake does with its fangs».

neck must, however, have been bent upwards at the same time, and the actual centre would then have been about at the joint between the first thoracal and the last cervical vertebrae. If the centre was situated so far back the strong curvature of the canines must decidedly have been to disadvantage (in fig. 1 the fine line above the arrow *3* is an arch with its centre at *tc;* the arrows *3* and *4* are parallel, the latter has in view to symbolize the effect on the canines if a blow is struck with the whole neck and head as leverage). MERRIAM & STOCK have observed this mechanical difficulty and suggest (l. c. p. 46) »that the downward stroke

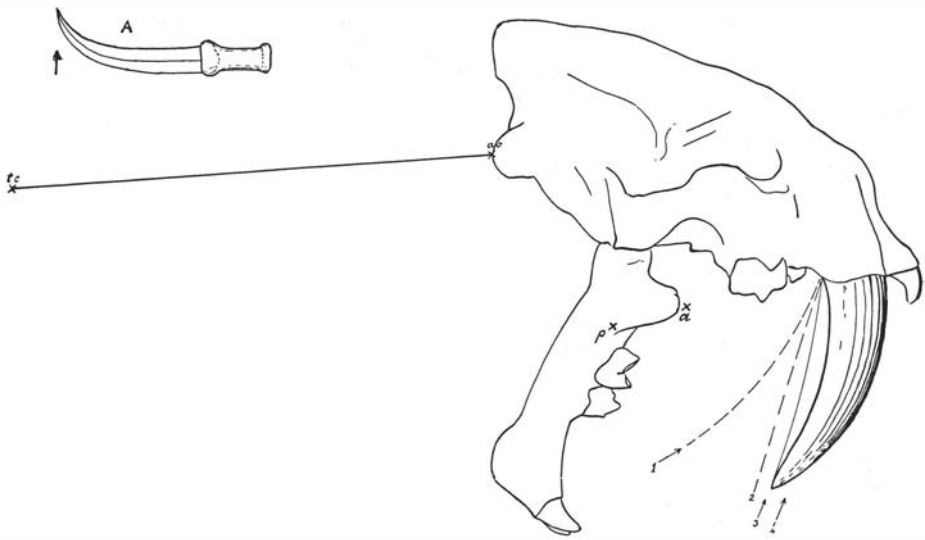

Fig. 1. *Smilodon californicus.* The skull copied from frontispiece in MERRIAM & STOCK 1932. Length of neck (*ao* — *tc*) measured on the mounted skeleton, l. c. Pl. 25. *2* is a line at right angles through *ao* and the base of the canine in front. For other indications see the text. > 1/6 nat. size. Fig. 1 *A*. Curved dagger used to strike with a movement as indicated by the arrow.

of the tooth must have been accompanied by a backward jerk in order to make it fully effective». We must remember that when the sabre-tooth was ready to »strike» it must in one way or another have attached itself to the victim[1]. This was of course panicstricken and it seems highly improbable that the assailant had full freedom to choose an ideal spot for the stab and to carry through the act of striking downwards and jerking backwards with its weapons, perhaps simple in itself but complicated also by the unfit shape of the teeth. The advocates of the stabbing hypothesis have of course had in mind that there is a pair of teeth, not only a single one. I only want to set down here that the pair of them must have increased the difficulties far beyond the extra force needed to drive

[1] I assume here for a while that *Smilodon* really killed for food; compare p. 170.

in two daggers instead of one; for instance one of the pair may hit on bone, the other not; or a bone may be wedged in between the teeth.

It seems to me that there must have been a fundamental difference between the attack of a sabre-tooth and that of the »normal» carnivora (fig. 2). I have my own bitter experience of the attack of a dog: it takes its aim and leaps straight towards the point thus selected. Its weapon of offence, the dentition, is under the influence of a set of muscles which can be used without in any way changing the momentum of the body during the attack. The jaws can be prepared for their work at any moment and, when the desired point is reached, they snap. A lion evidently

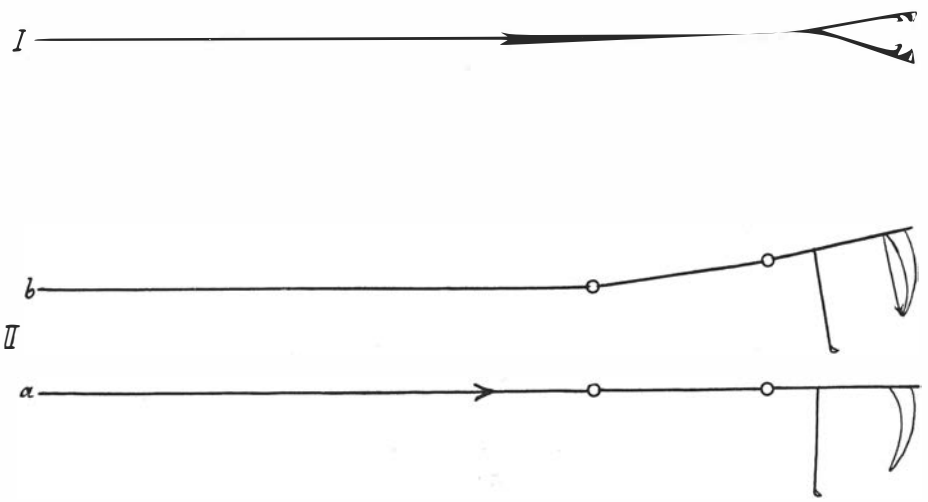

Fig. 2. Diagram of the modes of attack of *I* normal carnivors (e. g. dog); *II* machaerodonts (*a* and *b* = two phases). For explanation see the text.

does not attack like a dog, but in any case the movements of its body and head seeking a vulnerable point and the action of its teeth are entirely independent of each other. Obviously a dog can break the onward motion of its body in the moment when it bites. Otherwise with *Smilodon:* It hardly can have used its weapons after eyemark. Its body must have been brought to a stand with the paws after the leap, before the animal could think of striking, and the striking was performed with the fore part of the body with a movement at about right angles to the original direction of the attack. When the head was raised the eyes must have lost the control of the movements of the victim for a fraction of second and it does not seem possible that the »downward stroke» can have been well-aimed, as the animal hardly ever could have observed with its eyes the point where it was going to hit. To this comes that the imperfect control was apt to endanger the lower jaw, which hanged as far down as the tips of the tusks — it is not difficult to imagine what would have hap-

pened if the chin had received the blow. A stroke with the mouth closed would of course largely eliminate this danger (see below). We must, however, not omit the possibility that *Smilodon* was able to hold the head of its prey and thus fix the point which it wanted to hit.

As stated above the shape of the tusks does not go quite too well with the stabbing hypothesis. The question is now if it might possibly suggest some other use. I have had the opportunity to discuss various types of daggers with Dr MONTELL of the Ethnographical Museum, Stockholm, and learned that daggers used for stabbing have a straigt blade (as for instance the stiletto), whereas the oriental daggers with a more or less curved blade are exclusively used to rip up the belly of a foe (fig. 1 *A*). The tusks of *Smilodon* certainly look most like one of these curved daggers. A »slicing», »ripping» or »tearing» function must also be suspected from the structure of the teeth, which are curved in a direction opposite to the pressure to which they must have been subject when used for these purposes (see MARINELLI 1924, p. 33). It seems strange that the tusks, which were independent of their former antagonists in the lower jaw, were not straightened out — so easily as parts of the skeleton usually adapt themselves for a function — if stabbing has played any rôle worth mentioning or at least has been the main function. Also if the tusks were used, exclusively or mainly, for slicing, or the like, they must of course have been operated by the muscles attached to the occiput and the mastoid and these muscles must needs have been strong to be able to press the points through the skin and fix the head in a position favourable for the act of slicing — end even stronger than what would be required for stabbing, in which case the momentum of the fore part of the body would have increased the force of the stroke.

The gape.

A gape wide enough to free the points of the canines has been postulated long before the careful analysis of the muscle attachments was made. Already in 1842 A. POMEL has noticed most of the anatomical details which have been used in favour of the theory (p. 33): »La tête osseuse rappelle aussi dans ses proportions le type des Chats .... mais on doit s'attendre à trouver des modifications dans les détails anatomiques; en effet, pour que l'animal ait put se servir de ses énormes canines, et saisir sa proie avec facilité, il fallait dans l'articulation de sa mâchoire inférieure, une étendue de mouvements plus considérable: aussi la charnière, ou cavité glénoïde, dans laquelle se meut le condyle de cette mâchoire, était plus ouverte, et son apophyse postérieure moins saillante; la proéminence du temporal qui la forme (apophyse zygomatique) était aussi plus

saillante en dessous.» LYDEKKER (1884, p. 163) and FABRINI (1890, p. 125) make similar statements.

The range of motion is for the lower jaw of *Smilodon* 150° (MATTHEW 1910). For *Drepanodon oharrai* SCOTT & JEPSEN state (1936, p. 137): »Of particular interest is the series of modifications, which enabled the animal in life to open its jaws to the almost unbelievable angle of 165°—170°. The shape of the occipital condyles indicates that the head could be thrown back to an unusual degree, thus widening the gape.» *Eusmilus sicarius* could according to SINCLAIR & JEPSEN (1927, p. 405) swing its jaw »backward a full 180°». It is true that there might have been an enormous difference between what can be stated on a skull and what the animal has been able to accomplish when in life. It is, however, striking that as soon as the upper canines increase in size, the glenoid fossa follows suit and is lowered. This seems to have been the only way which nature has commanded to compensate the overgrowth of the tusks, as we find exactly the same combination in *Thylacosmilus*. And what else could it be than a device with the purpose to give the lower jaw a greater freedom of motion? ABEL denies this, at least as far as *Smilodon* is concerned, and states (1927, p. 137) »dass der Unterkiefer .... nicht so weit nach hinten gezogen werden konnte, wenn das Tier angriff, sondern der Einhieb in das Beutetier geschah mit den Eckzähnen allein. Auch bei der Nahrungsaufnahme brauchten die Kiefer nicht so weit geöffnet zu werden, wie es MATTHEW ... und OSBORN ... annahmen, da die lebenden Grosskatzen gleichfalls die Gewohnheit haben, den Brechscherenapparat seitlich an das Beutetier heranzubringen». There is, however, at least one difference between *Smilodon* and these cats in this regard. Even if the latter bring a piece of food into the mouth from the side, a maximum size of the piece is by no means set by the space between the canines and the corner of the mouth, whereas in the case of *Smilodon* the tusks must have stopped all pieces which were not »gauged» for the space strictly confined in front by the hind edge of the tusks.

Regarding *Eusmilus* SCOTT & JEPSEN state (1936, p. 141): »No other known sabre-tooth, except the great Pleistocene *Smilodon*, has such canines as those of *Eusmilus* ...» This latter can impossibly have used its canines for any purpose whatever, if the gape has not been wide enough to free the points of the upper canines. If this was necessary in one form, we must admit that it was at least possible in another. And even if the lower jaw of *Eusmilus* is exceptionally movable on the skull, the 150° in *Smilodon* are more than sufficient for the possibility in question.

MARINELLI means (1938, p. 263) that there results »für den Temporalis aus der Überhöhung des Schädelprofils keine Faserverlängerung wegen der gleichzeitigen Verkürzung des Schädels, wenn man die Längen der vom Proc. coronoideus zur äussersten Hinterhauptsecke ziehenden Faser ver-

gleicht». He admits, it is true, the importance of the short processus coronoideus, and states that it brings »die Insertionsstelle näher an die Gelenksachse heran und verringert dadurch bei gleichweiter Exkursion des Unterkiefers die tatsächlich im Muskel auftretende Dehnung». But he is inclined to look for the true explanation elsewhere (see p. 158). It is, however, in my opinion evident that a muscle attached to the extremity of the long backwards curved proc. coronoideus in, for instance, *Felis atrox* requires an attachment situated farther back on the skull than if the process is short and directed upwards as in *Smilodon*, i. e. the muscle has in both cases adapted itself in a way most favourable for its main func-

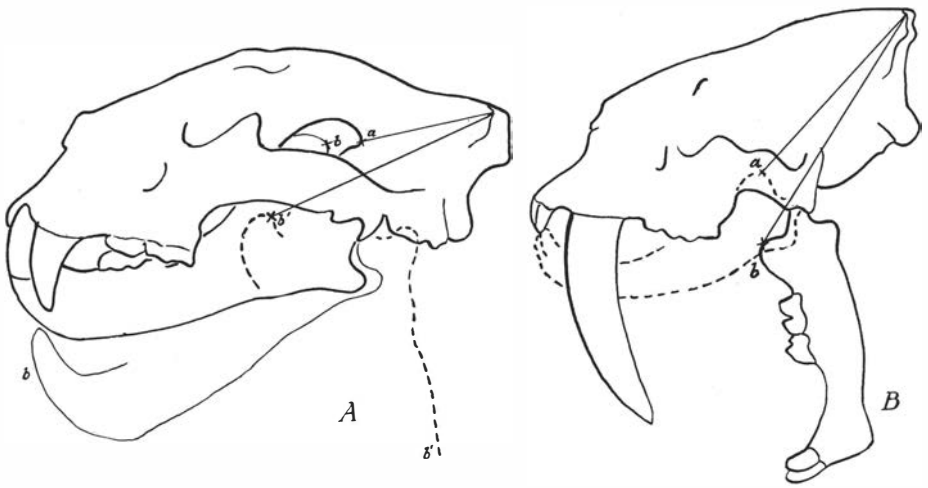

Fig. 3. *A Felis atrox* (after MERRIAM & STOCK, Pl. 26, fig. 1). *B Smilodon californicus* (after MERRIAM & STOCK, Pl. 1, fig. 1 and Pl. 2, fig. 5). The line to *b* indicating part of the temporalis muscle is for the sake of simplicity drawn straight. For further explanation see the text. — Both figures in about 1/6 nat. size.

tion: to close the jaws. What the difference in the shape of the proc. coronoideus actually means is illustrated by fig. 3. If the jaw of *Smilodon* is swung backwards from *a* to *b* the stretching of the temporalis muscle involved is about 27.5 % of the muscular length at *a* (actually somewhat more). The same amount of stretching in *Felix atrox* permits an opening of the jaws to *b* (fig. 3 A). If the jaw could be swung back as far as in *Smilodon* (= *b'*) this would involve a stretching amounting to about 82 %.

Perhaps the case could be put so: *Smilodon* has not given up the use of its front teeth, but the strain on the lower jaw must have been less than in *Felis atrox* as the lower canines are much smaller. The decrease in size of the lower canines was evidently correlated with the growth of the upper ones, the temporalis muscle thus could adapt itself freely in the sense proposed by MATTHEW without exposing the animal to the danger that the lower jaw would be pulled out of joint when the animal was

tearing with its front teeth. MARINELLI's statement is important, I only want to hold forth that the change in the relation between the front teeth and the temporalis muscle must have followed automatically in consequence of the primary changes which had the purpose to allow a wider gape.

If we see the problem historically we evidently must assume that the ancestors of the machaerodonts — perhaps not yet at all cat like — had about equal upper and lower canines and bit normally. In the *Dinictis* stage[1] normal biting was still possible, but it seems to be fairly reasonable to assume that the upper canines, beside their biting function, also were used for ripping the flesh of a prey[2]. During the following evolution the ripping more and more took the lead and finally displaced the biting entirely. As already mentioned (p. 164) the forceful neckmuscles can be satisfactorily explained, if such a function is assumed, and do not necessarily indicate that the tusks were used for stabbing a prey. On the other hand stabbing can not be precluded through this historical argument as it seems quite natural to assume that the points of the tusks were run through the skin with a jerk of the head as a prelude to the slicing; and of course this habit might then have taken such forms as could be properly described as »a tremendously powerful, quick downward blow» struck in order to kill a prey (compare, however, p. 162).

The gape must necessarily have widened by and by at least as long as the upper canines were not enough enlarged to reach below the chin and it is very difficult to conceive the stage when the animal gave up, closed its mouth, and tried to cut or strike with the small nubbins projecting below the chin. In *Smilodon* the projecting portion is fairly long and perhaps sufficient to produce a satisfactory effect, but the supposed change would necessarily have taken place long before this stage was reached. Even if we do not want to assume a stage when the upper canines were of no use whatever, i. e. that the change took place when the tips of the tusks still were covered by the lower jaw when the mouth was closed, it must have meant a very strong reduction in the effectiveness of the weapons when suddenly a half or so of the length of the upper canines was sacrificed — it must have meant a sudden down period in the ability of the animal to provide for itself. This same argument has been set forth by MATTHEW already in 1901 (p. 385).

Finally — and this is dictated purely by my own feelings in face of

[1] Even if the genus *Dinictis* was ancestral to the true cats, a similar stage must have been passed by the machaerodonts.

[2] Compare MARINELLI (1938, p. 249): »Doch kommt für die Katzen auch eine etwas andere Verwendung der Eckzähne in Betracht, wenn sie nämlich ihre Beute nicht durch den eigentlichen Biss, sondern im Ansprung überwältigen, wobei vor allem die oberen Canini wie Enterhaken in das Beutetier eingeschlagen werden...»

the subject — the carnivore temperament is so to say symbolized by the open mouth, the desire for the taste of the bloody flesh — and a carnivore pecking at the prey or even at carrion with its mouth closed seems to make a very strange picture.

The limbs.

It was early recognized that the fore limbs of certain machaerodonts were exceptionally strong and the attachments for the muscles on the olecranon are especially large (for instance GAUDRY 1862, p. 114[1]; see also MERRIAM & STOCK 1932, p. 115). On the other hand the flexors of the forearm, at least the biceps, seem to be comparatively week (MERRIAM & STOCK, Plates 22 and 37; p. 116). Among the authors who have studied the skeleton I want to hold forth SCHAUB, who points out that the attachments for the ligaments connecting the olecranon pit of the humerus and the ulna are large and that the forelimb thus must have had »besondere Zug- und Ruckfestigkeit» (1925, p. 259). »Der massive Bau der Vorderextremität, ihre mächtigen Muskelansätze, unter denen besonders die der Extensoren des Humerus und der Flexoren der Hand auffallen, die Verstärkung der Bänder und die hohe Spezialisierung des Carpus beweisen, dass der Arm von Machaerodus cultridens viel mehr zum Festhalten der Beute eingerichtet war als derjenige der rezenten Katzen. Er war geradezu Verankerungsorgan» (p. 260—261). In my opinion, a function as »Verankerungsorgan» would sooner call for well developed flexors also in the arm, I only think of what muscles we use ourselves when we want to hang on to something. MARINELLI seems here to be nearer to the truth in his description of the attack with the great tusks (1938, p. 262) where he suggests that »die Vorderextremitäten durch Wegstemmen des Körpers unterstützend mitgewirkt haben».

SCHAUB has shown that the arrangement of the carpal elements represents »einen für Raubtiere ganz eigenartigen Anpassungstypus» and means that the purpose of this is »dass der von den fünf Fingern proximalwärts ausgeübte Druck möglichst vollkommen auf das Scapholunare und damit auf den Radius konzentriert wird» (pp. 259—260). I have no material of any species at my disposal, but from a comparison between SCHAUB's fig. 4 and Plate 22, fig. 6 in MERRIAM & STOCK 1938 it seems as if there was a rather great difference between *Machaerodus cultridens* and *Smilodon californicus*. But also in the latter form the carpus seems to be better adapted to transmit a pressure from the hand to the forearm than, for instance, in *Felis atrox* (l. c. Plate 37, fig. 6), even if the lateral digiti are not so well linked up with the scapholunare through the unciforme as

[1] Compare SCHAUB 1925, p. 263.

in *M. cultridens*. This feature seems also to go well with the »Wegstemmen» which of course involves an increase of the pressure on the carpal bones.

The hind legs are weaker than the fore-legs. SCHAUB states (1925, p. 262): »Wirbelsäule und Hinterextremität sowie das vermehrte Gewicht der vordern Körperhälfte, das durch keine Verstärkungen der hintern Hälfte ausgeglichen ist, zeigen, dass Machaerodus cultridens nicht zu grossen Sprüngen befähigt war», and suggests that *Machaerodus* did not spring on to the back of its prey but hung on to the side with its forceful fore paws. SCOTT (1937) is well aware of the disproportion between fore and hind limbs, but he means that an immense leap opened the attack (p. 607).

The prey.

Most authors seem to assume that the prey has been large, thick-skinned animals such as elephants and the like. BRANDES' theory that *Smilodon* chiefly preyed on the contemporaneous armoured edentates can be accepted only with the modification given by WEISSMAN and ABEL (see p. 160). MATTHEW suggests (1916, p. 470) that *Mylodon* was the favourite prey. These animals were protected against the attacks of other carnivors by their »heavy hair and thick bone-studded skin» but these could not withstand the »tremendous hammer blows of his great dagger teeth». A few authors, among them POMEL (1843) and HERNANDEZ-PACHECO (1930) mention antelopes, deers and hipparions as the prey of *Machaerodus*, and ABEL (1922, p. 113) suggests that *Machaerodus* was the most dangerous enemy of *Hipparion*. It is probable that the more slow-moving animals must be given preference. One thing seems to be certain, namely that the prey must have been large of body, as it seems to be very unlikely that the large tusks, operated with so much muscular strength could have been used on, for instance, tiny antelopes, a prey which required a more delicate instrument and a higher precision; any large biting cat would in all regards be better fit for such prey even if this might be too small to satisfy its appetite.

Regarding the parts of the prey which *Smilodon* preferred there are different bids. BRANDES' opinion has already been referred to (p. 160). In the discussion following BRANDES' lecture Dr. MUCH (Vienna) pointed out that the European *Machaerodus* must have preyed on mammoths, rhinoceroses, aurochsen, and so on. After the prey was killed *Machaerodus* could »das Fleisch zerreissen oder sich auch nur an ihrem Blut sättigen». Blood-drinking was mentioned by MATTHEW in 1901 (p. 385). Blood sucking habits have been assumed by MERRIAM & STOCK, who mean to have found support for this theory in the structure of the palate of *Smilodon*.

All extreme carnivors are of course fond of blood, but to be able to live on blood chiefly or exclusively they must be able to drink it directly from the veins, i. e. to bite a wound and close their lips tightly around it, which latter seems to be a necessary condition for an effective sucking. In *Smilodon* this must have been at least very difficult if the mouth was closed, as the large tusks must have caused a leak in the vacuum. Otherwise sucking can not have been possible if not the whole length of the tusks was sunk into the flesh of the prey and in this case the lower jaw could perhaps have been applied tightly to the skin. But the sucking must have taken place with wide open mouth — which must have been an uncomfortable and ineffective method, especially as all muscles of the mouth must have been stretched. Blood sucking on an armoured beast like *Glyptodon* must have been impossible if, as BRANDES suggests, the wound was chiselled through the armour.

The other extreme is represented by those authors, who hold that *Smilodon* was a carrion-feeder. WEBER in 1904 means (p. 541) that the excessive development of the upper canines »lässt es fraglich erscheinen wie die Tiere sich ernähren und die Canini gebrauchen konnten». MATTHEW's hypothesis, which was then quite new, did not satisfy WEBER and he suggests: »Vielleicht waren es Aasfresser, die nur durch Verwesung erweichte Teile zerrissen und verschlangen». Lately MARINELLI proposes the same but for quite other reasons (1938, p. 268): »Auf einen grossen Pflanzenfresser kommen im Rancho la Brea zehn Räuber! Sammelten sich diese wie ein Rudel Hyänen um das Aas?»

Just this numerical anomally and further the disharmony in the development of the fore and hind legs, which reminds of the hyaena[1], led me to the same thought. As far as I can see there is nothing in the structure of *Smilodon* that speaks more in favour of a ferocious killer than of a carrion feeder. *Smilodon* is supposed to have had a low intelligence[2], and it is interesting to look at the reconstruction of the head of *Smilodon* at the side of *Felis atrox* in MERRIAM & STOCK (1932, figs. 3 A and B). The dull and sulky appearance of the former as compared with the keen looks of the latter goes extremely well with my opinion of the animals.

The hyaenas are far from innocent creatures. They often kill — but they prefer not to have this trouble when carrion is available. The same reservation must of course be made regarding *Smilodon:* it was most probably not harmless. But nothing seems to better hold forth its base

[1] The hyaenas have a few times appeared in the literature in connection with the machaerodonts, for example: *Smilodon neogaeus* was first named *Hyaena neogaea* by LUND. BOSE states (1880, p. 126) that the small facial portion as compared with the cranium is a Hyaenoid characteristic.

[2] There is, however, nothing in MOODIE's paper of 1922 that necessarily supports this.

inclinations than its occurence at Rancho la Brea. That packs of sabre-tooths haunted the region around the asphalt pools is evident. The animals were perhaps accustomed to find an easy meal every now and then at the pools. That thousands of them have drowned does not necessarily imply that all or even most of their attempts to reach entrapped herbivores were unsuccessful and led to a catastrophy for themselves. It is also possible that the smell from the pits attracted them. »The odors emanating from these pits where freshly excavated are, to human nostrils, strongly suggestive of carrion. Gases exhaled by animal bodies submerged

Fig. 4. *Smilodon californicus* feeding on the carcass of a young elephant. *Smilodon* is drawn according to the reconstruction given by MERRIAM & STOCK fig. 5 A.

in the plastic mass would accentuate this olfactory effect to such a degree as probably to attract carrion feeders» (MILLER 1912, p. 77).

In fig. 4 I have presented *Smilodon* feeding on the body of a young elephant—carrion or else light gotten prey. The drawing was made to illustrate what I think was the normal use of the tusks: slicing supported by the strong muscles of the neck and the extensors of the heavy fore-limbs. The scene around the carcass was probably livelier, with a number of sabre-tooth cats, and perhaps some dogs *(Aenocyon)* awaiting their chance at a respectful distance. Objections may also be made as to the place where *Smilodon* has applied its first cut — it would more likely have been the groin. I mean, however, that the tusks were not only used to rip up

the abdomen, but also to slice the meat into strips which then could be pinched between the front teeth and torn out.[1] The imperfection of the shearing part of the dentition (see for instance MARINELLI 1938, p. 269) would thus have been partly compensated by the action of the tusks. The tusks were also possibly used to shovel masses of sliced meat into the mouth.

It has been stated that the tusks very often have been broken during the life of the animal. The chances for such accidents would of course have been great if the tusks were used for stabbing. But also if they were used in the way which I have suggested here there were certain risks, for instance, if they were jammed between the ribs of the carcass. In neither case they would have been of much use when broken. Attempts to stab with them would have been futile, and they would in their broken condition hardly have been able to pierce the skin of a dead elephant. But there would always have been chances for the »invalids» to attack the soft meat which their fellow-creatures had exposed. The number of individuals with mutilated tusks at Rancho la Brea might of course be abnormally high just because the »non-stabbers» have more frequently sought their meals at the asphalt pits.

With its weak lower jaw *Smilodon* must have had very little success with the bones of the carcass[2] and I may be allowed to relate an observation made by Professor A. FREDGA in a discussion following a lecture by me. The idea that *Smilodon* has been a carrion feeder appealed to him and he meant that it might to some extent have taken the part of the vultures, and that it left to other beasts to take care of the bones and the parts of the meat which were more difficult to get at.

The statements above chiefly regard *Smilodon,* but possibly also forms as for instance *Machaerodus cultridens*. As put forth by SCHAUB (1925, p. 264) there were other machaerodonts of a more slender type »mit schlanken, luchs- oder gepardartigen Gliedmassen». These must have been more agile and probably more able to lead a life of a predacious carnivore.

[1] When my manuscript was ready Professor WIMAN and I compared notes and it turned out that Professor WIMAN for a long time past has been inclined to assume that *Smilodon* when feeding on a slain animal used its incisors and upper canines in the way which I have here accepted as the most probable.

[2] Compare, however, ABEL (1912, p. 500): »die wenigen noch übrigen Backenzähne .... als Brechwerkzeuge zu Zermalmen der grossen Röhrenknochen».

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Dr T. BORGH of the Zoological Institute, Uppsala, has kindly drawn my attention to this paper where the attack of a walrus on a seal is described. The walrus was harpooned by an Eskimo and PEDERSEN states »dass es mit seinen kräftigen Vorderextremitäten eine Fjordrobbe umklammert hielt und seine Hauer tief in den Bauch der Robbe gestossen hatte. Beide Tiere wurden dann von ihm an die Strand bugsiert und eine gleich von mir vorgenommene Untersuchung der Robbe zeigte, dass das Walross sie durch die blosse Umarmung, wodurch die Rückgrat und die Rippen zerbrochen waren, getötet hatte. Erst dann hatte es seine Hauer in den Bauch der Robbe gestossen und sie der Länge nach aufgerissen». The parallel between a machaerodont and a walrus is not perfect, the latter being an animal adapted to a life in water and rather different also in the structure of its canines. All information about the walrus, even if not directly applicable must, however, have its interest in connection with the machaerodonts.

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