2. The sabre-toothed[1] tigers once more.

By

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In 1940 I published a short paper in which I expressed the opinion that the machairodonts were not necessarily ferocious killers but more probably fed on carrion. In opposition to my view, SIMPSON (1941) defended the theory first advanced by WARREN (1853) and since embraced by »most authors». The writers who advocate opinions analogous to mine form a small minority (it might add a little to the strength of this minority to point out that we all reached the conclusion that the machairodonts were — or may have been — carrion-feeders independently). The fact that *Smilodon* occurs in far greater abundance than any of the other felines — it is outnumbered only by a canid, *Aenocyon dirus* (MERRIAM & STOCK 1932, pp.17-21; ABEL 1926 pp 235 *et seq.*) — I consider one of the strongest items of evidence favouring the view I hold (1940, p.170). It would deprive this remarkable frequency of much of its value as positive evidence if a similar accumulation of bones of true cats or some other really exclusive carnivore could be brought to light as a parallel. I do not know of any such case. On the contrary, I have myself seen how comparatively abundant among the carnivores at Chow-Kou-tien are the hyaenas. MERRIAM & STOCK (*op.cit.*pp.22 *et seq.*) try to explain the mass occurrence of *Smilodon* as a compensatory feature, offsetting certain racial and individual disadvantages. SCOTT (1937, p.607) wishes to explain the »great preponderance» as due to »inferior intelligence in failing to avoid the deadly traps». This »intellectual inferiority» was another factor which made me believe that *Smilodon* was mainly dependent on carrion for its food (1940, p.170). In a recent paper (1944) ABEL states (no doubt correctly) that animals entrapped in the asphalt pools would sink so rapidly that they thus were drowned, i.e. they were never within reach of possible carrion-feeders after putrefaction had set in. At the same time ABEL mentions that, in the absence of carrion, vultures keep a lookout for game that has become weakened through wounds or disease. According to BREHM the same is true of the hyaenas, and it may have been true of *Smilodon* as well.

[1] The late Professor C. WIMAN claimed that »knife-toothed» would be a better designation for these animals, as the teeth were not used in the way a sabre usually is.

SIMPSON gives an exhaustive analysis of the use of the upper canines. The comparison between the snakes and the machairodonts is carried out in detail, and it is suggested that if the latter were unable to use their teeth as stabbing weapons this must have been equally true of the former, a conclusion that would be contrary to observed facts. There are, however, important differences between the two types — so important that the parallel is probably of no real significance. To begin with we shall only consider the Solenoglypha. The fangs in these snakes are finely pointed, like needles, and therefore easily penetrate the skin of a prey even if they are applied at somewhat unfavourable angles. They can be folded backwards (and evidently are) when the snake has struck home. If they were not, the shock would probably break them (see below). Further »the bite which follows the strike is of great importance» (KLAUBER 1939, p.17). In the sabre-toothed tigers the musculature operating the lower jaw must have been too weak to be able to support the action of the upper canines to any worth-while degree (*cf.* MERRIAM & STOCK 1932, p.25; SIMPSON holds »that the activities here considered normal for saber-tooths were not impeded and may well have been assisted by the mandible», *loc. cit.* p. 9; the main function, according to SIMPSON, was stabbing; this motion was, however, performed with the mouth wide open *i. e.* with the lower jaw in a most unfavorable position for biting). KLAUBER gives a very interesting description of how a rattlesnake uses its fangs (pp. 17 *et seq.*):

»If, in the strike, a rattler's jaws are open so as to be exactly in opposition, that is, having an opening of 180 degrees, with the upper jaw held vertically, and if the fangs are erected perpendicularly so that the basal section points directly forward . . . . , then the point section vill be directed at an angle of about 25 degrees to any plane surface at which the blow be aimed, or 65 degrees from maximum effectiveness. Even allowing for a jaw opening greater than 180 degrees, and a tipping of the maxillary to permit the fangs to be erected more than 90 degrees . . . . there is still an oblique rather than a perpendicular approach of the point. But once the point has gained entrance, then both the curve in the fang and the folding action of the maxillary serve to accentuate the penetration produced by the squeezing pressure of the bite, particularly as the fang has a much smaller radius of curvature (about one-sixth) than the hinge distance of the upper jaw. It is true that the folding and the curve both sacrifice depth of penetration in favor of horizontal penetration, but they insure injection below the skin of the victim, which is the important point. This combined sliding with horizontal penetration is much less likely to be stopped by a bone than perpendicular penetration, and likewise the hook effect serves to hold to the prey or enemy momentarily. When the fang is folded, the emission aperture is directed inward toward the victim, which is a further advantage to the snake».

Cf. BREHM-EKMAN, V, p. 93 (translated from the Swedish text):

»When the snake has thrown its head towards the prey and thereby driven in its fangs, the maxillary that was originally lowered is rapidly pulled backwards.

In this vay the wound in front of the lower orifice of the (venom) canal is enlarged; the orifice will therefore no longer be choked up by the flesh or the hide of the attacked animal, but instead the venom will be sucked out of the canal».

It is true that the angle of application might cause the machairodonts the same difficulties, but otherwise the mechanism is quite different in the snake. In the rattlesnakes the curvature of the fangs is irregular and near the point the teeth are even slightly curved forwards. This undoubtedly allows a somewhat more favourable angle of application; further, the rather sharp bend in the middle of the tooth (we do not always find the regular curvature seen in the canines of *Smilodon*) must give the bite a jerkiness that may make it easier for the point of the fangs to penetrate the skin. Of the teeth shown in KLAUBER'S Fig. 45, only those of *Bothrops atrox* are ideally curved and these less curved fangs are more used for stabbing than for hooking and they may be »definitely of the stabbing type, as compared to the rattler's» KLAUBER, *op. cit.* p. 20).

The proteroglyphe snakes, *Naja*, *Micrurus (=Elaps)*, and others have immovable fangs; in this respect they form a parallel to the machairodonts, but the fangs are short, and when the snake attacks an enemy or a prey it bites. BREHM-EKMAN V, p. 118, translated from the Swedish text:

»When he *(Micrurus)* sometimes bites, he does not withdraw his head immediately after the strike as the species of the viper family are accustomed to do but holds on long and firmly with his jaws».

TOMES 1904, p. 321: »Thus the Cobra, the most destructive to human life, has upon the maxilla from one to three solid small teeth behind the poison fang, which is itself small»..... »The poison fang is not more than a quarter or a third of an inch long»..... »The Cobra bites like a dog whereas the viperine snakes, though sometimes biting also, often merely strike with their much longer fangs».

I do not think that it can be very profitable to couple the sabre tooth problem with problems connected with the fangs of snakes. SIMPSON also remarks that the analogy is imperfect. A closer analogy »is found among the harmless ruminants, *Moschus*, *Tragulus,* and their allies» SIMPSON has »not found a detailed description of the exact mode of use of the tusks in the living forms, although several authors speak of the males as hacking or striking downward with the head». BREHM (1920, Säugetiere IV, p. 82) :»Die Männchen bestehen heftige Kämpfe und gebrauchen ihre scharfen Eckzähne in gefährlicher Weise. Sie gehen aufeinander los, suchen sich mit den Hälsen zu umschlingen, um die Zähne einzusetzen, und reissen dann tiefe Wunden in Fell und Fleisch. Man findet, dass fast alle erwachsenen Männchen die Narben solcher Kämpfe an sich tragen». If this be true[1] there can be no question of stabbing. It would rather seem that the fighting males locked each other with their tusks, which were squeezed

[1] In BREHM-EKMAN we find added to the translation of the original text a statement that »this is said to be so».

into the antagonist's neck (not thrust with a stabbing movement), and the ripping was done later, when the fighters tried to disengage themselves. Thus, as far as the quotation from BREHM goes the musk deer cannot be adduced in support of the stabbing hypothesis. No information is given in BREHM as to how *Tragulus* uses its tusks.

Though I still do not see that the »classic» stabbing hypothesis is »the most useful treatment of this subject», I must of course examine it as a possibility, as I actually did in my first paper. SIMPSON (*op. cit.* Figs. 1 A-D) reconstructed four ways in which the stabbing might have taken place. Three of these were rejected, partly on the same grounds as they were rejected by me. In my opinion, however, MERRIAM & STOCK'S suggestion (*cf.* BOHLIN *op. cit.* p.162; SIMPSON *op. cit.* pp. 4 *et seq.*) shows a quite possible way out of the difficulties connected with the problem; the resulting wound would be such as that in SIMPSON'S alternative B, although inflicted, rather, by a movement such as that in C combined with a backward jerk (SIMPSON understands the same passage in MERRIAM & STOCK'S paper differently!). I consider stabbing in this way mechanically possible and the objections I nevertheless made (*op. cit.* pp. 162-164) apply to other difficulties. The most important of these is that the area round the point of incision could not possibly have lain within the tiger's field of vision while it was preparing to strike. Therefore it could not administer well aimed blows.[1] The more complicated the movements needed for effective stabbing, the less the chances for the tiger to find a spot where the tusks could be thrust in, as the prey was undoubtedly wild with fear trying to rid itself of the assailant. It seems to me especially difficult under such circumstances to find a spot where the two dagger-like canines standing approximately 10 cm apart could be plunged in so that both encountered the same or nearly the same resistance. If one of the tusks struck bone, or even if the surface against which the blow was aimed was oblique, so that the tusks did not hit it simultaneously, there would have been a great torsional strain on the tips of the tusks as well as on the neck. This objection ought to be understood by anybody who has tried to break up stony soil with a two-pronged hoe. It is not of much use to imagine »singletoothed» machairodonts and appreciate their advantages or disadvantages as compared with those having a pair of teeth, *i. e.* the type that once actually existed. But if it can be demonstrated that stabbing with a pair of teeth was a difficult or even risky enterprise this must be considered as an argument antagonistic to the stabbing hypothesis. If, on the other hand, the teeth were mainly used for slicing, the animal could carefully choose where to cut and it never ran the risk of striking with full force against bone.

[1] This is evidently true of the snakes as well. »The viper takes a bad aim and often misses, an imperfection which it has in common with all poisonous snakes». (BREHM-EKMAN, V, p. 97.)

SIMPSON'S alternative D is subject to the same objections — and this in a still higher degree, as the movements necessary for such a performance are still more complicated. This mode of stabbing is reconstructed so as to agree with the centre of curvature of the tusks etc. and thus it is theoretically possible One thing, however, I do not understand and that is how the «attacking momentum» could »be utilized in driving in the sabers.» The points of the canines could not be directed forwards at the moment of the attack unless the animal bent its head backwards so that its neck was at right angles to its back, a most uncomfortable attitude! SIMPSON certainly does not wish to imply that the stabbing was performed in this way. It is, however, the position that would profit most from the attacking momentum. According to SIMPSON the machairodonts thrust their tusks into the prey with a movement that, in its final phase, would have a direction almost opposite to that of the attacking momentum. It is easy to show with the aid of a parallelogram of forces that stabbing in this way would be impossible unless the attacking momentum were very small; further, it can be demonstrated that the strain on the delicate tips of the canines would be very great, The animal as a whole would, in spite of its ability to bend its head, neck and back at will when leaping, function as a curved javelin, and I have heard from athletes that a javelin that is curved ever so little near its point does not remain standing when it strikes the ground but turns over and slides along with the rear end forwards[1].

And so we find ourselves once again left with what I consider the most natural action *i. e.* that forward lunge and the stabbing motion must have been two distinct phases of the attack. My figure showing the attack of *Smilodon* on a young *Archidiskodon imperator* was drawn in order to emphasize the shortcomings of alternative D.

SIMPSON (*op. cit.* p. 6) mentions as »direct evidence of use of a canine saber» »a skull of *Nimravus* with a wound exactly such as would be produced by pure stabbing motion by the associated *Eusmilus*» *Cf.* SCOTT & JEPSEN 1936 p. 148: »Much the most likely explanation is that the wound was given by a stabbing blow from the sabre of *Eusmilus*». Pl. XXI Fig. 1 b in the same paper shows a wound about 2 cm long. If inflicted by *Eusmilus* by pure stabbing the canine would have penetrated to a point where its anteroposterior diameter was about that long, *i. e.* to about 6 cm. above the tip (*cf.* SCOTT 1937, Fig. 383 [p, 619].) The tooth would then have penetrated the frontal »piercing to the sinus», but it must then also have penetrated the inferior lamella of the frontal, the orbitosphenoid or other bones roofing the orbit, thus piercing into the orbit as well, and its tip would have reached approximately to the level of the upper

[1] This is in fact what the fangs in the vipers do. Their attachment to a movable maxillary may be an adaptation to the special way of striking met with among the solenoglyphe snakes, at the same time as it affords protection for the fragile pointed fangs when these are not in use.

toothrow. To judge from the drawings, enough of this region is preserved to show possible damage done to the bones mentioned and it would be of the greatest interest to get a detailed record of this unique case.[1]

Whether the sabre-toothed tigers killed for food or fed on carrion the cutting up of the dead body must have taken place in the same way, Here stabbing or various types of slicing as proposed by SIMPSON, with the exception of what is called straight slicing, would seem to be of small effect. The purpose was to cut loose pieces of the meat or the entrails in order to consume them, and this would require methodical work. SIMPSON insists that slicing must be preceded by stabbing and I have nothing to say to the contrary. The only question is: how great did this motion need to be. A few close-range thrusts as when a surgeon pierces the skin with a hypodermic needle may have sufficed. »The practical impossibility of cutting tender meat with a sharp knife without hacking or sawing motion» (SIMPSON *op. cit.* p. 6) has very little to do with our case as *Smilodon* undoubtedly tore the muscles to pieces in the easier way along the fibres, not across them. A piece of meat, even if it is not very tender can be torn to pieces with the tines of a fork if one end is properly fastened; no hacking or sawing are needed. In a carcass the muscles are attached to bone and the sabre tooth only had to rip them up to form »fringes», which could then be torn out with the incisors. Even so the meat may turn out to be rather tough. It is, however, a fact that raptorial birds are able to tear their prey to pieces with their hooked upper beak.

In my paper (1940, p. 164) I paid due attention to the strong head-depressors. A little reflection will make clear that very strong muscles are indeed necessary to prevent the head from being bent backwards when the tusks are used for slicing. We need only think of the strain on the wrist when we try to rip with the point of a long-bladed knife. It is true that unilateral pressure on the walls of the alveoli may have gradually changed the position of the tusks — everybody knows that children who suck their fingers run the risk of protruding incisors. The various types of slicing illustrated by SIMPSON must, however, have influenced the alveoli in a quite similar way.

It is not necessary to assume that *Smilodon*, at a single cut, ripped up a gash a metre long or so in the hide of its slain prey or in a piece of carrion. In my reconstruction (1940, Fig. 4) the folds formed behind the tusks were probably difficult to cut through and the tiger may have been forced to start a new cut close to the original incision. It could continue in this fashion until muscles or bowels were exposed to its satisfaction and the meal proper then begin.

[1] It seems rather unlikely that a tooth could be driven so deep through the hard bone of the skull roof without causing extensive splintering and fracturing of the bone surrounding the wound. An attempt to stab in the way suggested by SCOTT'S figure would most probably result in the point of the tooth slipping off against the top of the braincase.

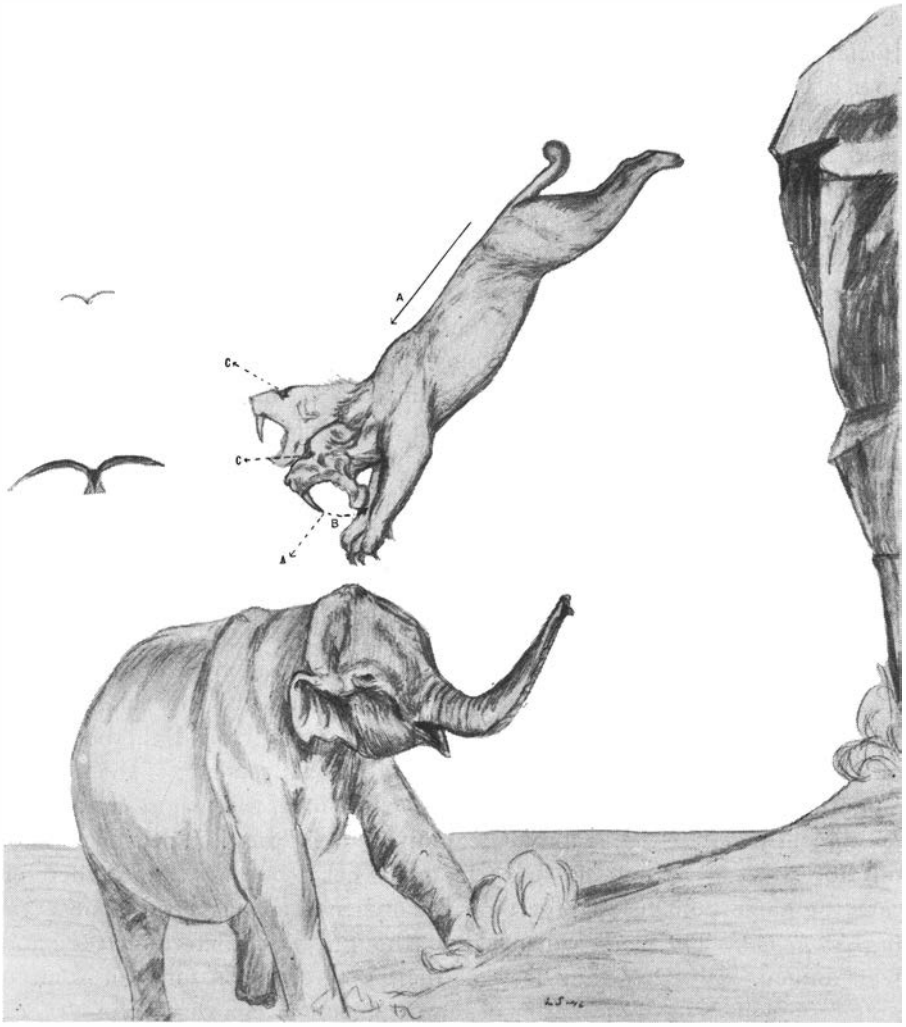

Fig. 1. *Smilodon* attacking a young elephant (after OSBORN'S 'Proboscidea' Part II; p. 947). Drawn by Miss LAJLA SVENSSON from directions given by the author. — A. Attack. B. Stabbing motion. C. Look.

Finally there is the question of how *Smilodon* used its limbs. Could it leap or not?

As always in palaeontology, we have to rely upon our experience of living animals; and the more aberrant a fossil form is the more difficult will be the reconstruction of its habits. That is why the »sabres» of the machairodonts are and will always be a matter of dispute. But when it comes to the structure of the body as a whole, it is easier to find parallels. We can tell that *Smilodon* can hardly have been »so fleet of foot as the lion or the tiger» (MERRIAM & STOCK 1932, p. 25). This is evident from the relatively massive fore part of the body, the relatively short hind limbs,

the short metapodials, etc. These are characters which we usually do not associate with leaping. The young lady who draw the figure in the present paper after the reconstruction by MERRIAM & STOCK and a sketch by the author protested energetically, insisting that an animal so proportioned would not have been able to jump. And she wanted to add a little to the length of the hind limbs to make the picture look more 'natural'.

There is no doubt that the hind limbs are relatively shorter than in the true cats and that they are also relatively weaker, as is evident from the table of indices below, as well as from MERRIAM & STOCK'S paper [p. 25]. »With a build particularly sturdy in front, the strong front extremities and the powerful muscles which operated them denote great striking and grasping strength. In the face of this development, the hind quarters appear to be relatively slender, although the major hind limb elements are comparable in size to those in the large living felines, differing from them most strikingly in some of their proportions.» As far as I can see what counts when we have to decide how an animal used to employ its extremities is the relative strength of fore and hind limb in the individual. That the hind limbs happen to be as well developed as in some leaping cats has very little to do with the matter. The strength of the hind limbs may well have been exactly the same, but the strong development of the fore body made *Smilodon* considerably heavier, and the muscular strength that will suffice for the propulsion of the comparatively light body of a lion or a tiger may, in the case of *Smilodon* have fallen short of the requisite amount. The hyaenas (which are also carnivores with short hind limbs) are evidently not in the habit of leaping at their prey. Their hind limbs are, however, as strong as those in many cats; but we cannot therefore draw the same conclusion regarding the hyaenas as has been done regarding *Smilodon*. There are other factors, though, which determine the habits of an animal. Whether they leap at their prey from an ambush or attack it after pursuit is partly a matter of temperament. Regarding *Smilodon*, our conclusions are strongly influenced by its great likeness to the cats, though seemingly they are based on measurements taken on the skeleton and other observations. The suggestion by MERRIAM & STOCK that individuals of *Smilodon* not seldom leapt so extensively that their backs finally became deformed — because *spondylitis deformans* is often observed in the skeletal material — is interesting but highly improbable. SIMPSON states (*op. cit.* p. 10): »MERRIAM and STOCK (1932, p. 25) point out that in *Smilodon* the hind limbs are comparable in size (and also in strength) to those of the large living felines and, far from supposing that leaping was unlikely, these best informed of authorities on smilodont anatomy conclude that these are special adaptations for leaping or lunging at prey». It is universally recognized that MERRIAM & STOCK are the greatest living authorities on the osteology of *Smilodon*; but yet I find it difficult to accept views respecting

Table of indices (all multiplied by 100):

	Smilodon	*Felis atrox*	*Hyaena brunnea*
Length: Humerus/Femur	93.75	87.65	93.45
» Radius/Tibia	97.12	95.30	119.89
» Metacarpus/Metatarsus	96.97	85.81	112.94
Hu+Ra+Mc/Fe+Ti+Mt (Fore limb/Hind limb)	95.41	90.33	106.60
Humerus: Width lower end/Length	(+) 32.47	(−) 27.97	21.03
Ulna: Depth olecranum/Length	(+) 13.12	(−) 9.35	11.99
Radius: Proximal width/Length	(+) 18.81	(−) 15.58	10.39
Femur: Width lower end/Length	(−) 22.11	(+) 22.39	15.28
Tibia: Proximal Width/Length	(−) 27.64	(+) 28.14	20.43

biological habits which are mere suggestions. A closer study might reveal that MERRIAM & STOCK are right, but such a study has not yet been made.

MERRIAM & STOCK disagree with me on another biological point. According to them *Smilodon* sucked the blood of its prey, whereas I have tried to show that this was impossible. SIMPSON does not dicuss this question.

ABEL (1944) deals partly with the same problems as I have done in the present paper. Of special interest is his anlysis of the food habits of *Thylacosmilus* (pp. 90 *et seq.*) which very closely reminds one of the suggestion made regarding *Smilodon* (see BOHLIN 1940, pp. 170—172).

Summary.

1. The numerous individuals (more than 3000 recovered) that perished in the tar pools at Rancho la Brea indicate that *Smilodon* had preferred light gotten prey and that it therefore might have had a taste for carrion. One may also call in question whether such hordes of carnivores could supply themselves with fresh meat, as big hunting carnivores are usually comparatively scarce *(cf. Felis atrox)*.

2. The analogy between the fangs of the snakes and the sabres of *Smilodon* is too incomplete to furnish a clue for interpreting the latter. In the Solenoglypha, which have long fangs, these are finely pointed and can be folded backwards when the animals attack. The Proteroglypha have short fangs and bite like dogs. *Moschus*, *Tragulus*, and others are more like *Smilodon*, but unfortunately the information available regarding the way in which these small ruminants use their canines is scarce and contradictory.

3. It is argued against the stabbing hypothesis that it is difficult to understand how the animal could take aim and how it could avoid stabbing in places where bones or other irregularities would endanger the sabres. Under all circumstances stabbing (combined with upward or downward

slicing) would be of little use in cutting up the prey. Straight slicing, preceded by a jerking motion to make the sabres penetrate through the hide or into the meat or the bowels, appears to admit of more methodical work. Very strong depressor muscles are needed for this operation.

4. Stabbing as the final phase of a lunging attack is impossible, in view of the way in which the points of the sabres are directed. The forward momentum cannot in a case like this be changed in one directed almost in the opposite direction. Instead there will be be a strain on the tips of the sabres equal to the resultant of the force of forward motion and that of the stabbing motion.

5. The direct evidence consisting of a *Nimravus* skull with a supposed stabbing wound needs closer investigation.

6. The arguments adduced to prove that *Smilodon* made leaping attacks are unsatisfactory. The heavy fore body reminds one of the hyaena and the short and comparatively weak hind paws suggest that the hind legs were even less fit for leaping than those of the hyaena. A long paw with a well-developed tuber calcanei, as in *Felis atrox*, is undoubtedly of importance for the elasticity of the leap.

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