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Zoology. — *"Androgenic origin of Horns and Antlers."* By Prof. J. F. VAN BEMMELEN.

(Communicated in the meeting of September 29, 1918).

In his excellent work "die Saugetiere", MAX WEBER gives as his opinion about the origin of the cephalic armament of numerous Ungulates, that horns and antlers originally started in both sexes as defensive weapons against enemies, but later on more and more came to be used as instruments of offence by the males in their fights for the females, and so either have grown an exclusive attribute of the male sex, or at least have developed much more strongly than in the female sex.

In this instance therefore WEBER evidently shares the opinion pronounced by TANDLER and GROSS in their paper: Die biologischen Grundlagen der sekundaren Geschlechtscharaktere, where they say: "All secondary sexual features were originally specific features, properties therefore, characteristic of a certain species, even of a whole order of Vertebrates, without their primarily having any connection with the genital sphere."

In their commentary on this proposition they remark: "Hitherto in the morphology of the sexual characteristics too little attention has been paid to the question, how much of them is peculiar not for the sex, but for the species." As a special example they cite the case of the horns of Cavicornia, "which do not constitute a sexual characteristic in themselves, but only in their shape, which differs for males and females, whereas on the contrary it is identical in masculine and feminine castrates."

"The same is the case with the hairiness in man. We have been able to show that such an eminently secondary sexual feature of the male sex, as the beard, is also found in old castrates, but there in form and extension resembles that of old women."

According to TANDLER and GROSS the question should not be formulated "Is an organ a secondary sexual feature", but: "How much in the development of an organ is specific, how much sexual."

Though this assertion might be granted, yet I believe to be justified in opposing to it another view: viz. that the evolution has been just the reverse; the cephalic armament arising in males as a means of attack in their duels for the females, and afterwards passing to

the latter in a more or less reduced form and only in some of the species (according to the well-known rules of monosexual transgressional heredity), the result being that the horns now could be used in both sexes as means of defence.

As arguments in favour of this opinion may be cited:

1 In Deer the antlers are absent in all females except those of the Reindeer, and precisely in this species a useful application of the horns, not connected with any sexual function, and alike for both male and female may be conceived, viz. the digging up of food from under the snow, though some authorities (e.g. BREHM) deny this function.

2. Among Antilopes, besides genera in which both sexes are horned, others occur in which only the male possesses these attributes, and in the majority of cases the horns of the females are smaller than those of the males. The latter moreover show a tendency to hypertrophic growth, just as is the case with deer, leading to unwieldy size or to sundry strange shapes (e.g. screwlike contortions) which seem to stand in direct contradiction with the requirements of practical use.

3. The same is the case with Cattle, Sheep and Goats, as shown by the four-horned goat, or the excessive development of the horns in the carbon and other buffaloes.

4. Even in Giraffes, whose minute pedicles with their small os cornu may probably be considered as rudiments of formerly better differentiated antlers (compare Ocapia and Sivatherium) the males possess higher and stronger hornstumps than the females, and moreover the unpaired nasal knob. In Ocapia on the other hand the horns are primarily absent in the female, and the same was probably the case during their whole life in those of Siva-, Hellado- and Samotherium.

5. The more original kinds of Ruminants: the Tragulidae and Camelidae, are destitute of horns, and so were the oldest and primitive extinct Artiodactyla (Pantolestidae, Anoplotheridae) as well as all Nonruminantia amongst them. The oldest fossil deer likewise did not yet possess antlers, as the muskdeer does up to this day, though the miocene Palaeomeryx according to RÜTIMEYER and SCHLOSSER was already provided with them. Perhaps this might be considered as an indicatiou that the tendency to the formation of antlers arose independently in the tribe of the Cervidae, but also as the manifestation of a far older hereditary inclination to the production of bony frontal appendages of the male. This tendency then must have been in abeyance in the tribe of the Artiodactyla in general; in Deer

it probably reappeared, and from thence continually increased in potency and complication.

This conception according to my view is strengthened by the fact, that also among the Suidae a tendency to the formation of bony protuberances on the dorsal side of the skull undoubtedly occurs and appears in stronger manifestation in the male sex than in the female, as is shown by the monstrous skull of the male African wart-hog.

6. In Protoceratinae likewise the skull of the male only was provided at its upper side with a complete set of paired bony excrescences.

7. According to MARSH both sexes of the Dinoceratidae possessed these bony protuberances (and the large dagger-like tusks besides), yet in the male they grew unto a larger size than in the females. We might conclude from this that the tendency to the production of bony knobs on the skull is even older than the separation of Ungulates into Artio- and Perissodactyles.

8. The annual shedding of the antlers and their regeneration in Cervinae is apparently connected with the rut. The same appears to be the case in Antilocapra.

9. The abovementioned bony processes on the head of Giraffidae, (sensu latiori) Suidae, Protoceratinae and Dinoceratidae, cannot reasonably be considered as really practical weapons, as they are far too cumbrous and hypertrophic for that. Neither can this be the case with the antlers of most Deer or the horns of numerous Antilopes, Cattle, Sheep, and Goats.

On the other hand they wear to a very high degree the character of sexual attributes, in their exuberance, unpractical build, curious complication, obviousness and variability.

10. In the first (primitive) members of the Ruminantia antlers and horns apparently arose at a relatively late stage, though this may be further removed in the geological past than is generally supposed. In any case the appearance or return of this feature is younger than the remaining peculiarities of Artiodactyla.

As I consulted the literature on the subject, I found that in considering horns and antlers as sexual attributes, I had come to a similar conclusion as the well-known popular author on questions of evolution in Zoology, BÖLSCHE, has set forth in his Tierbuch IV, der Hirsch. Yet on the first cause of the origin of frontal appendages our opinions disagree, for BÖLSCHE sees in the excrescences on the roof of the skull of so many Ruminants nothing more than originally purely ornamental attributes, and ascribes their birth to a periodical exuberance of energy of growth, manifesting

itself in exostoses of the bones of the cranial roof, especially and at last exclusively of the frontal bones. In his opinion the periodicity of this surplus of growth-energy keeps time with the rut of the males, but its presence should be ascribed to the regression of another differential feature of the male sex, viz. the ensiform tusks, as they still occur in Suidae, Tragulidae and the unhorned muskdeer.

The strongest expression of this opinion is given by BÖLSCHE in the words (p. 88) "The pedicle is no weapon." On p. 89 he continues: "As we saw, the idea "weapon" cannot be applied without reserve to the beam, although it may occasionally be used as such. Far exceeding that application and evidently its real nature, this beam is an ornamental product, a somatical arabesk, abstract from all usefulness, rhythmic in structure, with an inherent connection with the erotic side of life. The pedicle, in principle a product of the skull like the beam, cannot by any means be considered as a weapon, at the same time however it does not want erotic connections."

Against these views I think objections may be raised in two respects. In the first place there is no plausible reason, why the origin of horns and antlers should not be connected with single combats between males belonging to the same species, in which the more primitive mode of fighting with tusks (as still found among hogs) was gradually replaced by knocking of the foreheads against each other.

The question, whether this new custom was the immediate or the indirect cause of the exostotic hypertrophic process (Lamarckism versus Darwinism) may be passed over in silence here as in all similar cases. Nor do I want to deny that exuberant growth, in cooperation with periodical sexual maturity, exerted an important influence on their development, as it still does, every time the antlers are shed and renewed: we need only remember how profoundly this renewal is disturbed by every injury to the male sexual glands.

In the same way, BÖLSCHE's verdict: "The pedicle is no weapon", seems to me to be liable to serious doubt. Already in itself, the comparison of the long pedicle in the Muntjac-deer with the shorter ones of the remaining Cervidae leads to the conception, that the pedicle should be considered as an organ in a state of regression. To the same consideration leads a survey of the extinct Deer: in the middle-miocene Palaeomeryx-species no separation exists between pedicle and beam, they only show a long bony outgrowth of their frontal bones, slightly forked at its top. This excrescence therefore might be considered as a pedicle of extraordinary length. In the

first fossil deer showing a separate pedicle, the latter is very long, like that of the existing Muntjac.

In accordance with this observation is the fact that in Sivatherinae no rose can be detected near the base of their gigantic and ramified antlers, which therefore as a whole might be considered as pedicles.

Starting from the fact that in recent Giraffes the small hornstumps permanently retain their covering of hairy skin, the same may have occurred in their extinct allies: the Sivatherinae, and perhaps likewise in the first antlered ancestors of Deer. The separation of the latter's antlers into pedicle and beam, combined with the phenomena of yearly shedding and regeneration, the "rubbing" of the "velvet", in short the entire process of the renovation of the antlers, so inconvenient and dangerous for the stag, might then have developed from a similar primitive condition as that in Sivatherinae, where the frontal bony outgrowths, clad with hairy skin, must gradually have increased in size and complication. If one applies to the latter the designation "pedicle", it follows that for them just the contrary might be true of what is implied in BÖLSCHE's assertion: viz. the pedicle would have originated as a weapon and only lost this function in the Giraffes proper.

In the second place I cannot see sufficient reason for accepting such an intimate and strict connection between the regression of the tusks in the upper jaw of the stag and the progression of their antlers, as necessarily follows from the supposition that a surplus of growing energy should pass from those tusks to the frontal bones.

Against this hypothesis it may be objected that the male Protoceratinae as well as the Dinoceratidae were provided with powerful tusks, largely protruding from their mouths, and yet had a whole range of paired and single bony knobs and projections on the roof of their skulls, somewhat like those still found in the (male) warthogs. Among deer the male Muntjac still possesses strong tusks projecting downward and outward out of the mouth from under its upper lip, and yet carries well-developed, though simple antlers.

There is moreover little reason for the assumption that in Cavicornia the same course of events should have taken place as in Cervicornia, viz. a regression of large tusks, going hand in hand with an increased growth and a higher complication of frontal appendages, and yet the origin of these excrescences may be attributed to similar causes in all Horn- and Antlerbearing Ungulates.

On the other hand there is nothing incomprehensible in the fact that the upper tusks of Deer should have been reduced, as soon as they were no longer used as weapons, because the male Deer got accus-

tomed to a new mode of fighting which made them acquire antlers.

This vicariating development can be understood, without taking refuge to such an intricate correlation between upper tusks and antlers, as BÖLSCHE does, where he speaks of a surplus of energy of growth, set free by retardation in the development of tusks, and manifesting itself in hypertrophic excrescences on the frontal bones.

When we proceed in this course of thought, the question unvoluntarily arises, if the far higher development of tusks in the male sex of so many species of mammals might not be considered as a support for the abovementioned hypothesis about the androgenic origin of frontal appendages. The difference between the two phenomena lies especially in the fact, that with canines modified to tusks or incisors prolonged into darts, only their stronger development and differentiation need be ascribed to influences of sexual, especially male nature, while for horns and antlers also their first appearance had to be traced to this same cause. But this does not exclude that the tusks of Elephants and Cetacea, the canines of so many Apes, Carnivores and Ungulates etc. find their most plausible explanation in the assumption, that in so far as they are larger than the other teeth and also differ in shape and position from the incisors and molars, they may be considered as an acquisition of the male sex, which afterwards passed to the female, but in reduced proportion, and so to a certain extent again lost its monosexual character. Especially the growth far over the limits of practical fitness may be adduced as an argument for this hypothesis; we should only remember the tusks of the Mammoth curled up in a complete circle, the gigantic canines of the male walrus or the usually unilateral dart of the male Narwhal.

In this connection I should like to move the question whether the uncouth tusks of the extinct Sabretoothed tiger (Machairodus), might not have formed a special attribute of the male sex, as beyond doubt they were far from practical in defence as well as offence. With certainty this is the case with the Walrus. Also the upper canines of the Babirussa, which perforate the upper lip, and are curled up dorsally and backwards, give us a good example of hypertrophic growth far beyond the limits of real usefulness.

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