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EDITORS:

V. K. TING AND W. H. WONG

Series C. Volume 1

Fascicle 3.

**ON A NEW FOSSIL PORCUPINE FROM
HONAN WITH SOME REMARKS ABOUT THE
DEVELOPMENT OF THE HYSTRICIDAE**

BY

EINAR LÖNNBERG
STOCKHOLM

WITH 1 PLATE



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Vol. I. Fascicle 3

PALÆONTOLOGIA SINICA.

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On A New Fossil Porcupine from
Honan with Some Remarks about the
Development of the Hystridæ

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With 1 Plate



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ON A NEW FOSSIL PORCUPINE FROM HONAN WITH SOME REMARKS ABOUT THE DEVELOPMENT OF THE HYSTRICIDAE.

BY

EINAR LÖNNBERG.

Hystrix (Acanthion) Lagrelli n. sp.

A fossil skull from Honan collected 10 li north of Mien-Chih-Hsien, about 65 km. W. of Honan-Fu with a slight inclination towards N., ^{20/4} 1921.

In several respects this skull (fig. 1 a, 2, 3 & 4 a) is in a rather good state of preservation, although it is somewhat crushed. The zygomatic arches are broken. On the right side (fig. 2) this arch is entirely missing. On the left (fig. 3) the most proximal parts remain, so that it can be seen, that the outer bar of the infraorbital foramen has been stout and triangular in section, while the inferior bar of the same has been flattened and slender. By this the fossil skull differs from the most primitive of the now living *Hystricidae* like *Trichys* and *Thecurus*. From the same, and also from *Atherurus* it differs still more by the development of its nasals, the length of which is more than one third of the upper length of the skull. At the same time the frontal region is shortened. The comparatively great size of the nasals can be well seen on the specimen (fig. 1 a), although the left nasal is missing, and the right probably mutilated at the anterior end. The teeth are all present (fig. 2, 3 & 4 a) and appear to be hypsidont.

On the whole this fossil skull represents the stage of development among the *Hystricidae*, which usually is named "*Acanthion*", that is the section containing the more primitive members of the genus *Hystrix*, because, as I have proved elsewhere,* the transition from the lower to the higher members of this genus is so gradual, that it is impossible to draw any sharp line of demarkation between a genus *Acanthion* and a genus *Hystrix*, although, of course, there is a wide difference between the highest of the latter, and the lowest of the former. The division is, however, with our present knowledge of intermediate forms wholly artificial and has been based on characters, that

* Ark. f. zool. Bd. 15 nr. 18. On the Chinese Porcupine, *Hystrix suberistata Swinhoe* with remarks on other members of the genus.

do not hold good through the series, and such characters which partly have proved to have been misunderstood, or even erroneous.

In fact the fossil skull reminds in its general appearance very strongly about *Hystrix (Acanthion) javanica*,* and it may be said to have reached on the whole the same stage of development as that one. A comparison with the same will therefore be made below, but first the following measurements may be recorded.

Total length of the fossil skull from gnathion to occipital surface is 100 mm.

Length of right nasal (probably a little too short as it may be broken in front)	35 mm.
" " mesial frontal suture	33 "
" " parieto-occipital region	30 "
Breadth of right nasal	10 "
Least postorbital width	34.0 "
Width across <i>meatus auditorius</i>	43.7 "
Length of bulla	14 "
Width " "	10 "
Hind surface of <i>proc. mast.</i> to front of bulla	17.7 "
Least distance between bullae	15 "
Width of skull between inner walls of <i>for. infraorbit.</i>	19.6 "
Diastema	28.5 "
Length of molar series (including p^4)	22 "
Length of palate inside incisors mesially	48 "
Width " " between p^4	6 "
" " " " m^3	8.5 "
" " each incisor	5 "
Length " p^4 : 6 mm.; breadth of the same 5.5 mm.	
" " m^1 : 5.3 " ; " " m^1 : 5.4 mm.	
" " m^2 : 5.3 " ; " " m^2 : 5.2 "	
" " m^3 : 4.8 " ; " " m^3 : 4.3	

With regard to the upper aspect of the fossil skull the nasals appear to be more rounded off at their posterior end than in *H. A. javanica*, so that the frontonasal suture has been more curved, not so straight transverse as in the recent animal with its posteriorly nearly square nasals. Unfortunately the anterior shape and extension of the nasals of the fossil skull cannot be ascertained, but it is probable, that they have

* A skull of this species has been reproduced at the side of the fossil one in figs 1 b, and 4 b, to facilitate a comparison.

been a little (perhaps 3 mm.) longer than is indicated in the table of measurements. The palatal extensions of the premaxillaries is approximately similar to the same in *H. ("A.") javanica*, although longer (cf. fig. 4 a. & b.) and narrower. The breadth of the frontal region of the skull is a little larger than in the recent animal, and there are no indications of any postorbital processes.

In consequence of the crushing and torsion of some parts of the fossil skull it is not quite easy to make out the complete shape of the posterior parts of the premaxillary, but on the right side the suture between the premaxillary and the frontal* can be made out (fig. 1 a.) The nasal process of the premaxillary appears to be about 6—7 mm. broad and nearly squarely truncate.

The remains of the roots of the upper or outer, and the lower bars of the *foramen infraorbitale* are very similar to the corresponding ones of *H. ("A.") javanica*. The vertical diameter of the flattened lower bar is about 2 mm. in both. The transverse diameter of the root of the outer bar (i. e. measured from the outer flat surface and to the inner edge, because it is triangular in section) is about 9 mm. in the fossil skull, or rather more than in the skull of *H. javanica* used for comparison.

The snout is in the fossil decidedly more slender than in *H. ("A.") javanica* (cf. fig. 4 a & b.) Probably this difference has at the middle of the premaxillary region amounted to about 15 %, and the distance between the inner walls of the foramina infraorbitalia, i. e. the transverse diameter of the skull at that place is about two mm. longer in the recent animal, which is equal to nearly 10 %. As the fossil specimen and the skull of *H. ("A.") javanica* used for comparison are very nearly of the same size, these relations have a certain value. Otherwise the dimensions are, of course, somewhat variable individually.

The width of the skull at the audital meatus is very similar in both. The bullae on the other hand are very much smaller in the fossil one (cf. fig. 4 a & b) The difference amounts to about 3 ½ mm. in length and 3 in breadth in favour of the recent specimen. As a result of this the interspace between the bullae is decidedly smaller in the recent than in the fossil form.

The molars of the fossil form are also decidedly smaller than those of *H. ("A.") javanica*, and, as the measurements and figures (fig. 4) prove, almost cylindrical, while in the latter the longitudinal diameter is conspicuously longer. In consequence of this the molar series of the recent species becomes longer than that of the fossil one.

In spite of the great general likeness between the fossil skull from Honan and the

* This suture must not be confounded with a transverse fracture of the frontal behind the same.

recent *H. ("A.") javanica* there are thus quite well conspicuous differences, but I consider these to be only of specific importance and apt to prove, that the former belongs to a species, which as yet has not received any name. It is therefore a great pleasure to me to dedicate it to Mr. AXEL LAGRELIUS, who with untiring energy has done so much to promote Professor J. G. ANDERSSONS scientific researches in China.

In the present time the most primitive members of *Hystricidae* as *Trichys*, *Thecurus* and the less specialised of the so called "*Acanthion*"-group are confined to Southeastern Asia, chiefly the Sunda Islands. The members of the "*Acanthion*"-group, which have reached the continent are already more highly developed in several respects. One genus of rather primitive *Hystricidae*, viz. *Atherurus* differs from the others from a geographical point of view, as its members are not only to be found in Southern Asia, but also in the West African forest region, where not less than four species have been described. A fossil species of *Atherurus* has also been described by LYDEKKER from the Karmul district, Madras. This proves that the early *Hystricidae* have had opportunities of spreading themselves very widely. Fossil members of this family appear, however, to be very rare. Leaving out such forms, that have been counted to *Hystrix* and found in India and Europe the following have been named.

Anchitheriomys from miocene layers in Germany is, as it seems, only known from teeth, and as it is said to be as large as a beaver, it is not probable, that it is a fore-runner of any now living form.

Oreomys is described from miocene layers of central France, but about this I have not been able to gain any information, as its description has not been available.

It is thus of the greater interest to have received the fossil remains of a rather primitive "*Acanthion*" from the main land of Asia and from a comparatively so northern locality as Honan a little south of 35° N. lat.* This is, of course, an undisputable proof, that primitive *Hystricidae* of a similar type once inhabited great parts of Southern Asia. There are also certain indications, that they once were common in Southern China, because the present collections contain fossil remains of this kind (chiefly incisors) from three other localities in Honan in addition to the one recorded above, viz. at Hsin-An-Hsien, outside the gates; Hsin-An-Hsien, 8 li SE., Shan-Pan-Kou-Fsun, 1/2 li. S.; and Hsin-An-Hsien, 15 li N. Shang-Yin-Kou.

Unfortunately it is for the present not possible to state, to which geological period these finds may be attributed, because there are no leading fossils found in connection with them.** It cannot, however, be subjected to any doubt, that the climatic con-

* Thus about the same latitude as the Mediterranean region.

** The rock matrix is red.

ditions of Central China at that time, when these Porcupines lived there, were rather different from the now prevailing ones. Such a conclusion can be arrived at, if it is considered, that in the present time all primitive *Hystricidae* live in a tropical climate, and it might without mistake be added, in moist countries with a rich forest vegetation. At least this is the case with the Sunda Islands, which constitute the home of *Trichys*, *Thecurus*, and some of the most primitive members of the "*Acanthion*"-group. The same may also hold good for the Malay Peninsula and adjoining countries, where some of the species of *Atherurus* are at home, and certainly it is true for the West African forest region, where the remaining lot of the species of *Atherurus* lives. There is no reason to presume that the primitive *Hystricidae* in former days have been able to live and thrive under conditions unlike those, which in the present time appear to be necessary to their welfare. The presence of species of *Atherurus* as well in the West African forest region as in Southeastern Asia, to some degree bridged by the find of *A. karnuliensis* in the Madras province of Southern India, has many wellknown analogies as f. i. the Pottos in West Africa and a species also lingering in a forest in East Africa on one hand, and the Lories of Southern Asia on the other. The distribution of the *Traguloidea* with *Hyemoschus* in West Africa and *Tragulus* in Southeastern Asia together with the fossil *T. sivalensis* in India shows much resemblance with that of *Atherurus*. These facts and many others of a similar character are generally, and as I think, with full right, interpreted as proofs for that a humid forest region of great expansion once connected Southern Asia and West Africa, although it is not necessary to assume, that this connection was direct and continuous, at least not all the time. During that epoch forest loving animals had, however, a great opportunity of spreading. When later the climate changed and became more dry, the forests disappeared in certain tracts with less humidity, and the forest animals succumbed to the altered and less suitable conditions of life offered to them, or they had to adapt themselves and get accustomed to other habits in different natural surroundings. In Africa these changes of climate have played important parts as well for the distribution of the elements of the faunas, as also for the development of not only different habits of certain animals, but also for the development of new forms altogether, as the present writer has pointed out in another connection.

Having thus shortly discussed the habits and requirements of life of the lower, or comparatively primitive *Hystricidae* in connection with the geographical distribution of the same, it is of interest to make a comparison with the corresponding features of the more specialised and most highly developed members of the same family. viz. *Hystrix* s. str. If this subject is taken up, it is seen at the first glance, that none of

these latter is a forest animal in the true sense of the word, on the contrary they live in treeless countries, or at least in tracts of land, where the forests are much broken up and of quite another character than the humid tropical forest, in which the more primitive members of the family feel at home. Often the countries inhabited by the large and specialised Porcupines have a rather dry climate as f. i. certain parts of northern India, Persia, Transcaspia, Transcaucasia, the Mediterranean countries, East and South Africa etc. They are often at home on rocky hills, in steppe country, sometimes even in almost desert-like districts. Secondly these Porcupines have in many places found themselves well at home in cultivated areas, where they also could enjoy the products of the plantations.

When, as we have seen, the primitive *Hystriidae* are, at least chiefly, bound to the tropical and humid forests, they may have originated under such conditions of life, that are offered in similar forests. On the other hand the biggest and most highly developed members of the family belong to the more open and more or less steppe-like countries with a drier climate. It may then be questioned whether the latter are not to be regarded as products of such natural surroundings and such a climate. I think this must be the case. It is no uncommon thing, that, if one of two related animals lives in the forest and the other in the open country, the latter is the more specialised and more highly developed.

It appears to me most probable, that the change of the climate from humid to more dry, which in its turn resulted in the gradual disappearance of the thick forests, just may have been a stimulus to further development to these animals.

If it now is discussed how the development and specialisation of the higher *Hystriidae* has taken place, it will be found, that this development makes itself known in increased bodily size (a product of the favourable adaptation), shortening of the tail, increase of the armature (increase in length of the quills etc.), but above all in the much altered structure of the skull. The latter makes itself chiefly known in the enlargement of the nasal cavity together with an inflation of the whole skull. The widening of the nasal cavity, perhaps necessary for the increased development of the olfactory organ,* could be effected simply by the enlargement of the bones constituting the walls of the same. The increase in size of the remaining portion of the skull necessary to counterbalance the great nasal cavity and also needed to afford a greater area for in-

* It may assumed, that a more effective organ of scent would be of great value in a dry climate, when the animals had to go in search of roots, bulbs and other under ground food stuff, when fresh vegetable green matter was not available all the year round.

sertion of muscles etc., could not be so easily realized, because the brain cavity did not need an enlargement by far in the same degree as the nasal cavity. In fact the brain case occupies in the primitive *Hystriidae*, f. i. *Trichys* or *Atherurus* etc., a comparatively much greater part of the whole skull, than it does in the highest members of *Hystrix*. In consequence of this the cerebral portion of the skull could not be enlarged so simply as has been the case with the nasal cavity by widening of its walls. The object has, however, been attained in an analogous manner as in the Elephants by the development of air-cavities in the diploë of the bones. These air cavities stand, of course, in connection with the nasal cavity and by them the bones are thickened and their surface increased without that their weight becomes too heavy.

It is the increase in size of the bones surrounding the nasal cavity and the general inflation of the skull by means of the air cavities mentioned, which have so completely transformed the skull of the most specialised Porcupines, that it has only little resemblance to that of the more primitive members of the family. Through the pneumatic inflation of the cranial bones and in consequence of the backward elongation of the nasal cavity the postorbital processes and the postorbital constriction have disappeared. By means of the great lengthening of the nasal bones and their extension backwards the frontal region has become comparatively much shortened and so to say pushed backwards. In consequence of the widening of the nasal cavity the rostral portion is no longer set off from the remainder of the skull, as is the case in the most primitive members of the family; and so on.

These changes have not been sudden, but have taken place gradually. Already in the the most primitive now living members of the "*Acanthion*"-group the first steps are taken in the direction, which leads to the most developed true *Hystrix*. It is then of great interest to see, that the same is the case with the fossil species from Honan. The nasals of the same have increased in size, so that they are longer than the mesial frontal suture, and they extend so far back, that their posterior end is on a level with the middle of the upper bar of the infraorbital foramen. The rostral portion is still rather narrow, but not set off, and the nasal processes of the premaxillaries are comparatively broad. There is no postorbital process and the postorbital constriction is reduced to a minimum, and so on.

From this incipient stage represented by the most primitive members of the "*Acanthion*"-group, such as f. i. the fossil one from Honan, or perhaps from some still somewhat earlier stage the development has according to my opinion gone in, to some degree, different directions, and the different recent species have so to say reached up to their present high standard along somewhat different ways.

I am thus unable to agree with LECHE,* who in a recent paper, in which he discusses the phylogenetic development of the *Hystricidae* expresses himself with the following words: "Die beiden — — — extremen Typen, *Trichys* und *Hystrix senegalica* sind nämlich durch eine Reihe Arten verbunden, welche, — — —, bei einem Vergleiche der östlichen Arten mit den westlichen in ihrer Gesamtorganisation eine Differenzierungsreihe, somit eine geographische Formenkette darstellen, welche also nicht nur als eine morphologische sondern als eine wirklich phylogenetische Reihe aufzufassen ist".

It would be very nice and quite made to pattern, if this was true, but I do not think that it is so simple in reality.

For the further development of the *Hystricidae* to their highest perfection from the early "*Acanthion*"-stage the widening of the nasal cavity appears to have been of essential and perhaps primary importance, and the other changes of the cranial structure may be more or less consequences in connection with the same. This widening has been effected by the enlargement of the bones encasing this cavity with the olfactory organ. Of greatest importance in this connection are the nasals, which form the roof of the nasal cavity, the premaxillaries, which constitute the anterior floor and part of the lateral walls, and also the maxillaries, which partake in forming the floor and posterior portion of the side walls. If all these bones had been enlarged in the same degree the nasal cavity would have had a similar structure in all the high Porcupines. This is, however, not the case. On the contrary, it may be said that these bones have become enlarged in several different ways, which may be shortly sketched below.

In *Hystrix subcristata* from China the nasals have been greatly lengthened, so that they measure considerably more than half the occipito-nasal length, or about 58 % of the same, and extend about 25 mm. beyond the ends of the nasal processes of the premaxillaries. On the other hand the nasals are not much broadened. They are of subequal breadth from their anterior to their posterior end, with the exception that they are rounded off posteriorly. Their greatest combined width is contained about twice in their mesial length, and it is about 31 % of the basal length of the skull. The premaxillaries are not enlarged. The nasal processes are truncate at their posterior end, but not especially widened, so that their breadth there is contained four times in the breadth of a single nasal. By this the nasal cavity has been considerably lengthened, which has been effected by means of the increase in length of the nasals (which in its turn has resulted in a shortening of the frontal region). The height of the nasal

* Morphologisch-geografische Formenreihen bei den Säugetieren. K. Fysiografiska Sällsk. Handl. N. F. Bd. 31. Nv. 10. Lund 1921.

cavity has also become increased, because the nasals are rather strongly vaulted, especially in front.

With this type "*Acanthion*" *klossi* and allies have a great general resemblance.

As the representative of quite another type I select *Hystrix hirsutirostris* from Persia. In this animal the nasals are rather short, so that their length is even less than half the occipito-nasal length (measured in a straight line). In an adult specimen chosen as an example it is about 47 %, but it looks even less in consequence of the arched skull. The nasals extend in fact very little beyond the hind end of the premaxillaries and are nearly squarely truncate behind. They are rather flat compared with those of f. i. *H. subcristata* but of uniform breadth in their whole extension like them. Their combined breadth is about the same as in the former type (exhibited by the just mentioned species), as well absolutely expressed in millimeters, as also compared with the basal length of the skull, of which measurement it is about 30 %. But as the nasals in *H. hirsutirostris* have not become lengthened, their combined breadth is more than half their length, approximately about $\frac{4}{7}$ of the same.

If thus the difference between the two types hitherto discussed with regard to the nasals chiefly consist in their comparatively lesser length and square ending in *H. hirsutirostris*, the premaxillaries of the same exhibit an extremely aberrant shape. These bones are namely so immensely expanded in their posterior parts, that they practically retain the same breadth from their palatal portion to the end of their nasal processes, which are broadly truncate. The breadth of each of these processes even exceeds that of a nasal with 4—6 mm. In consequence of this expansion posteriorly together with the extension backwards the premaxillary just reaches the lachrymal, or at least very nearly so, and by this it excludes or nearly excludes the frontal from any contact with the maxillary. As a result of this the latter bone partakes less than usual in forming the lateral wall of the nasal cavity. The enlargement of the latter is thus to greatest extent effected by the very strong expansion and also extension backwards of the premaxillaries.

In consequence of the fact that the nasals of *H. hirsutirostris* have not been extended backwards, they have not encroached upon the frontal region, which accordingly is not shortened, but occupies an area, which mesially has a length of about 34 % of the occipitonasal length. For *Hystrix subcristata* the corresponding percentage is only about 20 %, which thus proves the very different shape and proportions of the skulls of these two species.

Hystrix leucura belongs to the same type of development as *H. hirsutirostris*.

If we now turn our attention to *Hystrix africa-australis*, we will meet with still another type of development. In this species the nasals have a very different shape

compared with the foregoing ones. They are not broader in front than in the others, but very strongly expanded in their posterior portion and broadly rounded behind. The dimensions are somewhat variable, but in typical adult specimens from Cape the greatest breadth of a nasal is not far from twice its anterior breadth. The combined width of both nasals is about 80—81 % of their mesial length, and from 42 to nearly 45 % of the basal length of the skull in adult specimens. The nasals are also somewhat more extended longitudinally than in *H. hirsutirostris*, but somewhat less than in *H. subcristata*, so that their mesial length is about 50 to 56 % of the occipito-nasal length. The mesial length of the frontal region is thus not more reduced than that it constitutes 30—33 % of the occipito-nasal length.

The nasal processes of the premaxillaries on the other hand are not lengthened nor expanded. They are on the contrary attenuated and wedge-shaped in their posterior extremity, which just meets a similarly pointed nasal process of the frontal. In some specimens it may even happen, that the nasal processes of the premaxillaries and the frontals do not meet, but are separated from each other by the maxillary, which thus may come into contact with the nasal. (cf. below). In any case the premaxillary is always very widely separated from the lachrymal, which all means, that the maxillary is to a much greater extent than in *H. hirsutirostris* and allies forms the lateral wall of the nasal cavity. Most essential for the enlargement of the latter cavity in *H. africae-australis* is, however, the great transverse expansion of the nasals posteriorly, and their vaulted character adds to this.

From the description above is apparent, that the widening of the nasal cavity of *H. africae australis*, has taken place according to a different plan and has been effected in a different way than in the two types described before. A comparison with the other species of *Hystrix* as well as with the more primitive Porcupines makes it most probable, that the shape of the nasal process of the premaxillary with its attenuated and pointed posterior end (as described above) is a result of a reduction, which has been brought about by the pressure on this bone by the strong lateral expansion of the adjoining parts of the nasals, perhaps together with an upward growth of the maxillary.

In Central Africa lives another somewhat different species *H. stegmanni* MÜLL. With regard to the general shape of the nasals it resembles *H. africae-australis* very much, thus the combined greatest breadth of the nasals is about 76 % of their mesial length, and about 42 % of the basal length of the skull. The length of the nasals is about 55 % of the occipito-nasal length, and the mesial length of the frontal region about 30 % of the same. The only difference of somewhat striking nature is, that the nasal processes of the premaxillaries are not pointed behind, but comparatively broad

so that the end is truncate, and the suture with the frontal can amount to about 7 mm. in length. It is, however, in all ages shorter than the fronto-maxillary suture. The premaxillaries partake thus somewhat more in forming the lateral wall of the nasal cavity than in the next former type, and in connection with the somewhat greater height of the nasal processes of the premaxillaries the nasals are less vaulted in *H. stegmanni* than in *H. africæ-australis*. The stage of inflation appears to be somewhat variable in both. Compared with the fact that the nasal processes of the primitive Porcupines as a rule are truncate behind *H. stegmanni* appears in this respect less specialised than *H. africæ-australis*.

In East Africa lives the still more highly developed *Hystrix galeata* THOS., which distinguishes itself by having the nasals as well long as broad. They are, however, also broad in front, so that the anterior width of a nasal is fully two thirds or more, usually 69—76 % of its greatest breadth. The latter is nearly 45 % of the basal length of the skull, but only 68.5 % of the mesial length of the nasals, because these bones are much more extended backwards than in *H. africæ-australis*. A result of this latter fact is that the mesial length of the nasals amount to 63 % of the occipito-nasal length of the skull, but the frontal region, which has been encroached upon, has become reduced to a mesial length, which corresponds only to 21 % of the occipito-nasal length. This latter condition thus reminds about the same in *H. subcristata*, but it is somewhat variable in different specimens.

In addition to this great expansion of the nasals in all directions *H. galeata* also has very broad nasal processes to its premaxillaries, measuring from 17 to more than 20 mm. in width. The fronto-premaxillary suture is thus fully as broad as the fronto-maxillary suture. At the same time the nasal processes of the premaxillaries extend further backwards, than they do in *H. stegmanni*; usually to the vertical through the anterior margin of the lachrymal. The nasal cavity of this type has thus been enlarged as well by the expansion of the nasal bones in all directions as through the widening of the nasal processes of the premaxillaries.

The name *Hystrix cristata* LIN. is usually confined to the Porcupines of the Mediterranean countries. A certain variation makes itself known among these animals. A general characteristic appears, however, to be rather long nasals, the breadth of which is rather moderate and less than in *H. galeata*. The greatest combined width of the nasals corresponds to between 53 and 61 % of the mesial nasal length, and to between 32.5 and 40 % of the basal length of the skull. The frontal region is necessarily short, in consequence of the length of the nasals. The difference in breadth of the nasals in front and at the broadest place is by far not so great as in the South-African

Porcupines, but the relation is usually more similar to that found in *H. galeata*, although varying between 65 and 74 %, seldom as low as 61. The shape of the nasal processes of *H. cristata* appears to be rather variable, sometimes forming a comparatively broad suture with the frontal, sometimes more attenuated behind, in which case the maxillary extends higher up on the side of the skull.*

In some parts of Western Africa, Senegambia, a big, but as yet little known Porcupine occurs. A skull of such an origin in British Museum Nat. Hist. has very long nasals, but at the same time they are very broad. At their widest place they have a greater width than the corresponding bones not only of *H. cristata*, but also than *H. galeata*. The greatest combined breadth of the nasals of this specimen is 72 % of their length and not less than 49 % of the basal length of the skull, thus comparatively more than in *galeata*. They are, however, somewhat narrowed in front, so that the least breadth there is only about 55 % of the greatest breadth. By this latter feature it differs from *galeata*, which it otherwise resembles in its great height of skull and comparatively broad nasal processes to the premaxillaries. The skull of a Porcupine, which LECHÉ has received from the Zoological garden in Hamburg, and which he has described and figured, resembled in most cases the skull mentioned above, and the author just quoted uses for it the name *H. senegalica*. This may also be in accordance with GERVAIS, although CUVIER's type appears to have been rather too young to prove anything with certainty.

From this short description it may be apparent, that the highly specialised Porcupines, which in the present time inhabit certain countries from Eastern Asia to Western and Southern Africa have got their nasal cavities enlarged in different ways, if a generalised or primitive type like f. i. *A. javanica* is taken as starting point. The desirable enlargement can evidently be effected chiefly by the following methods: 1. by elongation backwards of the nasal bones. 2. by expansion of the nasal processes of the premaxillaries. 3. by expansion of the nasal bones, which can take place *a.* chiefly in the posterior portion of these bones, or *b.* along their entire length. Finally the enlargement of the nasal cavity may be effected by means of two or more of these methods. In all cases a certain enlargement of all bones forming the walls of the nasal cavity are to some degree necessary for the widening of the cavity itself, but this enlargement is nevertheless effected in such a varying degree for the different bones, that the above stated rules find application. It is also easy to point out the different species which represent these different phases of development. Thus *Hystrix subcristata* with

* The apparent variability in the skulls of *Hystrix cristata* may partly be due to the fact that many such are described and figured from material from menageries and zoological gardens, which is less satisfactory.

its elongated nasals is developed according to rule 1., and to the same group are to be counted some allied forms like f. i. *klossi*.

The *Hystrix hirsutirostris* and *leucura* group represents a development according to rule 2.

Hystrix africae-australis and *stegmanni* conform to rule 3 a. These three groups thus represent rather onesided phases of development, while the remaining most highly specialised like *H. cristata* and *H. galeata* have, especially the last, utilised all possibilities for the enlargement of the nasal cavity.

If the development has started in one direction and as in *H. subcristata* the nasal bones have become greatly elongated, there is no probability, that it will change in a directly opposite direction and again shorten them to a degree almost corresponding to the primitive starting point and produce a widening and enlargement of the nasal cavity only by expansion of the nasal processes of the premaxillaries as in *H. hirsutirostris*. There can thus not be any direct lineage between these two types. For a similar reason it is just as difficult to believe in such a reversion of the development that by reduction in length of the nasals a form like *H. africae-australis* was derived from one like *subcristata*, or by extreme reduction of the premaxillaries from one like *hirsutirostris*. Therefore I must decline to believe in any direct line of descent between any of these three types of development.

It is really difficult even to believe in the development of a form with such a structure of the skull as *H. galeata* from such a one as *H. africae-australis*, which latter has reached a rather high degree of specialisation by an immense expansion of the nasals only behind without any corresponding widening in front, nor any extension backwards, and in which the premaxillaries apparently have been subjected to reduction with regard to their nasal processes, while the former (*galeata*) has built up its enlarged nasal cavity by widening all bones forming its walls. It seems much more natural to assume, that the immediate ancestors of the *galeata* and *cristata* groups have resembled the so called "*Acanthion*" forms with rather long nasals and moderately developed premaxillaries. From such a stage of development the Porcupines mentioned could easily be derived only by a widening of the bones mentioned.

There is thus no such continuous gradual development from East to West as LECHÉ has expounded having taken place among the *Hystriidae*, nor is there any orthogenesis in the true sense of the word. On the contrary it appears most likely, that an independent development and specialisation from more primitive forms has arisen several times as a result of the changed conditions of life.

That the primitive *Hystriidae* have had an opportunity of spreading themselves

very widely in former days, when the for them necessary conditions of life existed over greater areas, is proved by the presence of *Atherurus* in Africa as mentioned above. The find in Central China of the above described primitive "*Acanthion*" gives also a very valuable hint, that animals on this stage of development have had a much greater distribution than in the present time, and this is highly interesting and of great importance for the understanding of the development of the recent higher members of the genus *Hystrix*, because from such a generalised starting-point as an animal with such a structure and shape of the skull and its bones as the fossil species from Honan any of the now existing types of Porcupines could take their origin. My theory is thus that at an early date, cotemporary with the spreading of *Atherurus* from Asia to Africa, in the then existing forest belt with a warm and humid climate also primitive Porcupines, similar to the one described above, extended their area of distribution to Western Asia and Africa. When later on the climate changed, as already discussed above, the Porcupines had to adapt themselves to the new conditions, and this they did *independently* of each other, some by means of elongating the nasals, some by widening the premaxillaries, some others again by expanding the nasals etc.

LECHE seems also to lay much stress upon, that the development and specialisation of the higher *Hystriidae* took place gradually as the animals extended their distribution from East to West,* so that from *Trichys* to *Hystrix senegalica* (which he regards as the most highly developed member of the family) should be at one time "eine geographische Formkette" and "eine wirklich phylogenetische Reihe". I am afraid that the geographical part of that statement as well must be contradicted, even if the opposite ends of the chain are regarded to be those mentioned. This is partly done already by the breaking up of the supposed direct lineage. Partly LECHE has also himself lessened the importance of the statement concerning the "geographical" form series, when he considers *H. africana-australis* as the third stage of development among the higher Porcupines, while he puts *galeata* as nr 6, *cristata* as nr 7, and *senegalica* as nr 8. The native country of *galeata* at least must be situated between the supposed oriental origin and that of the comparatively lower *africana-australis*.

It is not the geographical distance from the home of the ancestral forms, which is the chief factor producing the differentiation and specialisation of a certain organism, but it is the adaptation to the natural conditions in the country, where the animal has to live. It is thus no rule, that the geographically from the origin most distant animals

* — — — "dass die Differenzierung mit dem Vordringen der Vertreter dieser Familie von Osten nach Westen im Grossen und Ganzen Schritt hält". LECHE l. c. p. 10.

are the most specialised. On the contrary it is not uncommon, that the races living at the periphery of the area of distribution of a form series are the most primitive, because they may not have needed to become adapted to any strongly different conditions of life.

Finally with regard to the species of *Atherurus* as well LECHE has tried to maintain his theory about a higher development of the *Hystricidae* in the same degree as their habitat is situated further west. He points out for that purpose that *Atherurus africanus* is more specialised than the Malayan forms in having the frontal region of the skull more vaulted and more pneumatic than in the latter. This is very interesting, but it becomes still more so, if it is compared with THOMAS' descriptions of two other African species of *Atherurus*, which to judge from their origin must be typical forest animals. About one of these, *A. centralis* from Monbuttu, the author quoted writes: "differs från *A. africanus* by its flatter less inflated and narrower frontal region and better defined postorbital processes. Teeth small and delicate." About the other, *A. burrowsi* from Aruwimi, the same author says "cheekteeth small, rounded, and apparently less high-crowned than usual. — — — "frontal region not inflated at all". — — — "nasals very small short, narrow, parallelsided". These quotations appear to prove, that very primitive *Hystricidae* have found their way as far towards the West as into the West African forest region and that they in spite of their remoteness from their supposed ancestral home in Southeastern Asia have not been subjected to any specialisation or higher development. I think that the explanation of this fact is, that they have been able to remain under the same, or at least very similar, conditions of life as from the beginning, viz. in a humid tropical forest. It appears also that this fact speaks strongly for the theory set forth above about the development of the more specialised Porcupines just in connection with the changed climatic conditions, and that this has taken place independently in different regions and from a starting point similar to that stage, which is represented by the interesting fossil Porcupine from Honan.

Explanation of Figures.

Fig. 1. *a.* Upper view of the skull of *Hystrix (Acanthion) lagrellii* n. fossil from Mien-Chih-Hsien. Honan. Central China. *b.* The same view of the recent *H. (A.) javanica* F. CUV. from Java.

Fig. 2. Right lateral view of the same fossil skull.

Fig. 3. Left lateral view of the same.

Fig. 4. *a.* Palatal aspect of the same fossil skull. *b.* Palatal aspect of the same skull as is figured in fig. 1. *b.*

All figures a little less than nat. size.



1a



1b



2



4a



4b

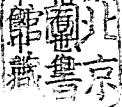


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河南澠池之豪豬科動物化石

倫貝原著
周贊衡節譯



此篇所研究之豪豬科動物，僅有一類，其地質時代尚未明瞭，蓋同地所採集之他種動物，均非標準化石。觀近今之中等豪豬科動物，均生長於熱帶森林中，或溫濕之地，如馬來半島及其附近，如是可推想中。當此類豪豬繁殖時代，其氣候必甚溫濕，故草木繁盛，迨後氣候漸變乾燥，草木漸衰，此類豪豬因之絕跡矣。

賴氏豪豬 (*Hystrix (Acanthion) Lagrelii* n. sp.) 頭骨一具，得於河南澠池縣北十里，化石大部，雖稍受擠壓，然保存尚屬完美，其顱骨之環已斷，在右邊 (Fig. 2) 此環完全遺失，其左邊 (Fig. 3) 則僅餘一部，下眼眶之外門甚粗，其剖面成三角形，但其次門則扁平而細長，此類化石與現今生活之豪豬科中之最下等者如 *Trichys* & *Theourus* 比較，頗不相似，其鼻部之發達，竟占頭骨上面長度三分之一而過之，此點已與上述二種及 *Atharurus* 大不相同矣。 (Fig. 1a.) 其牙齒均保存，圖中之 (Fig. 1b & Fig. 1c) 為現今之爪哇豪豬 (*Hystrix (Acanthion) javanica*) 之頭骨用以與化石比較者，其形態頗近似也。

河南澠池之豪豬科動物化石

借 閱 記 號

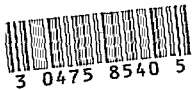
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第三冊

瑞典倫貝著

河南澠池豪豬動物化石

中華民國十三年十二月 農商部地質調查所印行



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瑞典倫貝著

第三冊

河南澠池豪豬動物化石

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