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HYSTRIX PRIMIGENIA (WAGNER) IN THE PLIOCENE FAUNA
FROM WĘŻEStudy on the Tertiary bone breccia fauna
from Węże near Działoszyn in Poland

PART XIV*

Abstract. — A description is here given of the bone remains of a Pliocene porcupine, identified as *Hystrix primigenia* (Wagner), found at Węże near Działoszyn and heretofore recorded from Pikermi (Greece) and Roussillon (France). An analysis of the lower molars shows certain similarities in the enamel structure with *H. sivalensis* Lydekker, described from the Pliocene of India (Siwalik Hills) and that of the living *H. cristata* L. Differences in structure of outer enamel loops, particularly those of the upper molars, the presence of accessory elements in the crowns of these molars (in the posterior parts of teeth) might possibly be suggestive of a new species. Nevertheless, in spite of incomplete material, a number of features identical with those in *H. primigenia* postulate the assignment of the Działoszyn form to that species.

INTRODUCTION

The porcupine remains were discovered, together with a varied fauna of insectivores, other rodents and large hoofed and carnivorous mammals, within an old karst doline in the Zelce hill near the village Węże (Samsonowicz, 1934). A fragment of skull was etched out from the previously exploited calcareous breccia. The other here considered remains were discovered in 1955 in the same deposits by members of the staff of the Palaeozoological Laboratory at the Wrocław University. All the specimens belong to the collections of the Muzeum Ziemi (Museum of the Earth) in Warsaw.

* Parts I-V — see *Acta Geol. Pol.*, vol. II-V/1952-55; parts VI-XIII — *Acta Palaeont. Pol.*, vol. I-V/1956-60.

The first mention of the probable presence of genus *Hystrix* sp., based on some fragments of incisors, is found in a paper by Samsonowicz (1934, p. 158). The remains of that animal have not, thus far, been described from Tertiary or Quaternary faunas of Poland. Hence its occurrence at Weże constitutes the first in Poland, and the third in Europe, Pliocene site with representatives of Hystricinae.

The present paper has been prepared at the Palaeozoological Laboratory of the Polish Academy of Sciences in Warsaw, with Professor R. Kozłowski as its Director. Through the courtesy of Mrs T. Czyżewska of Wrocław the writer had the opportunity of comparing his material from the Weże breccia with materials of the living *Hystrix cristata* L., kindly loaned by the Zoological Museum of Wrocław. Acknowledgements are due to Mr W. Siciński, a laboratory assistant of our Institute, for the excellent preparation of the here described remains, to Miss M. Czarnecka for doing the photography, and to Mrs J. Humnicka for the English translation of this paper. Text- and plate-figures are prepared by the writer.

DESCRIPTION

Order **Rodentia** Bowdich, 1821

Family **Hystricidae** Burnett, 1830

Subfamily **Hystricinae** Lyon, 1907

Genus *Hystrix* Linnaeus, 1766

Hystrix primigenia (Wagner)

(pl. I, fig. 1-3; pl. II, fig. 1-5; text-fig. 1-4)

1848. *Lamprodon primigenius* Wagner; A. Wagner, *Urweltliche Säugethiere...*, p. 374, pl. 4 (12), fig. 7,8 (*vide* M. Schlosser, 1884, and Ch. Depéret, 1890).
1360. *Lamprodon primigenius* Wagner; A. Wagner, *Neue Beiträge...*, p. 129, pl. 5, fig. 12 (*vide* M. Schlosser, 1884, and Ch. Depéret, 1890).
1884. *Hystrix primigenia* Wagner; M. Schlosser, *Die Nager...*, p. 45-46 (27-28). (non *Hystrix major?* Gervais).
1890. *Hystrix primigenia* Gaudry (sp. Wagner); Ch. Depéret, *Les animaux pliocènes...*, p. 43-47, pl. 4 (7), fig. 12-16 (non *Hystrix refossa* Gervais).

Material. — Specimen No Rod. 1, a fragmentary palate with the right P⁴-M³ and the left M¹-M³; specimen No Rod. 2, fragment of mandible lacking the incisor, the ramus ascendens of the coronoid process and the remaining articular processes, with preserved P₄-M₂; specimen No Rod. 3, lower milk premolar; specimen No Rod. 4-6, two lower and one upper incisors, incomplete. The just mentioned specimens belong to three or four individuals of different age.

Dimensions (in mm):

Length of palate	approx.	55.0
Average width of palate measured between lingual borders of molars	approx.	15.0
Length of P ⁴ -M ³		45.5
Length and width of: P ⁴		13.2/11.8
M ¹		11.0/10.0
M ²		11.0/10.0
M ³		10.0/ 9.0
Antero-posterior width of upper incisor		8.5
Lingual-labial width of same		6.5
Width and height of choanae internae		20.0/25.0
Length of P ₄ -M ₂		36.0
Supposed length of P ₄ -M ₃ (M ₃ being measured along the alveoles)	approx.	47.0
Length and width of: P ₄		12.4/ 9.7
M ₁		11.7/11.2
M ₂		11.7/11.2
M ₃	approx.	10.0/ 9.7
Antero-posterior width of lower incisor		8.8
Lingual-labial width of same		7.0

Description. — *Skull and upper teeth.* The closed sagittal suture of palate and slightly worn teeth suggest that the skull belongs to a young

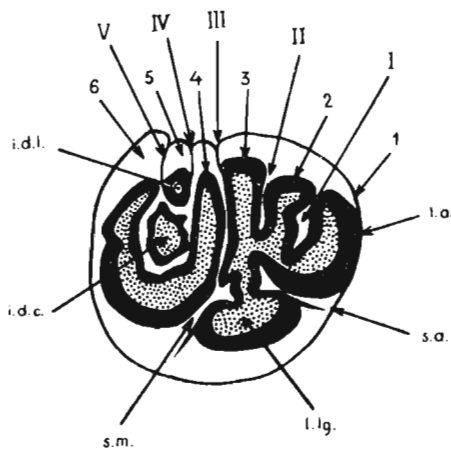


Fig. 1. — Structure plan in P⁴, from top: I-V re-entrant folds, 1-6 lobes, s. a. anterior sulcus, l. a. anterior lobe, s. med. median sulcus, i. d. c. central dentine islet, i. d. l. labial dentine islet.

adult¹ individuals. Tooth-rows mutually parallel. Teeth strongly differentiated (P⁴ being the largest and M³ the smallest), highly hypsodont, labially hooked.

¹ The terminology in respect to individual age after Jackson (1928).

In P^4 (fig. 1) the crown is composed of two parts: the anterior consists of four lobes, of which one is on the lingual side, the other three on the labial; the posterior consists of an arched field of dentine and two dentine islets — the central (i. d. c.) and the labial (i. d. l.). Labially the tooth with five re-entrant folds. The labial re-entrant fold III is connected with re-entrant fold on the lingual side of tooth and formed a medial

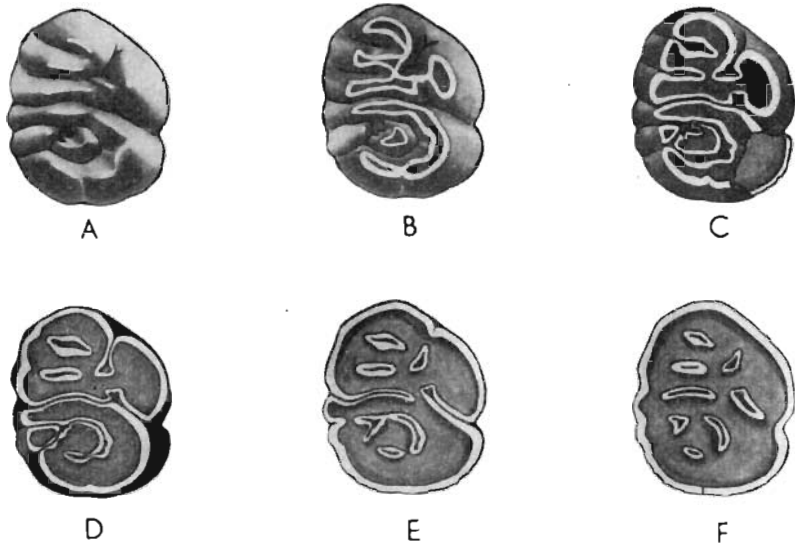


Fig. 2. — Hypothetical stages of the wearing down in P^4 : A "immature-young" stage, B "young", C "young-adult", D "adult", E "adult-old", F "old"; approx. $\times 2$.

sulcus (m. s.). The anterior lobe (l. a.) between re-entrant fold I and the anterior re-entrant fold is strongly developed and turned towards the front. The lingual lobe of the anterior portion of tooth (l. lg.) of the same size as the anterior.

A hypothetical development line (fig. 2), not based on serial thin sections, but on a series of reconstructions representing the supposed six successive stages of the wearing down of P^4 , shows changes affecting the pattern of enamel loops and dentine fields, also those in the mutual relations of the anterior and posterior portions of the tooth and of the various enamel folds, depending on the extent of wear.

M^1 and M^2 — each composed of two parts: the anterior consists of two re-entrant folds, of which the labial is perpendicular to the long axis of teeth, while the lingual is oblique and turned to the front; the posterior displays a structure resembling that of the posterior part of P^4 . Within the dentine field on the anterior portion of the crown there is an elongate enamel islet, either uniform or bifurcating.

M³ with smallest dimensions, oval-shaped, with the greatest antero-labial — postero-lingual diameter. In spite of the slight degree of wearing in the posterior portion of the crown this tooth shows some similarities in the structure of its anterior portion with M¹ and M². The posterior

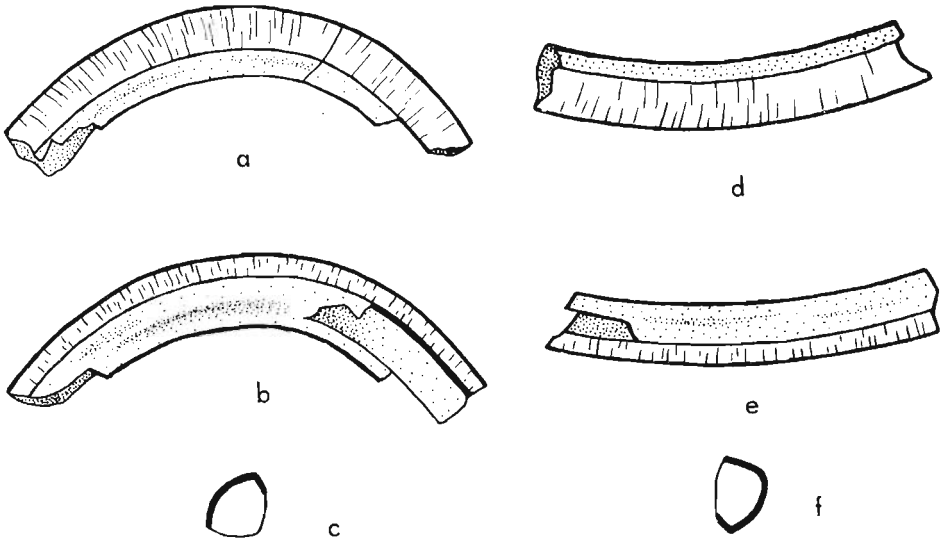


Fig. 3. — Structure of incisors: a upper incisor on labial side, b the same on lingual side, c cross section of upper incisor, d lower incisor on labial side, e the same, on lingual side, f cross section of lower incisor; nat. size (specimen Rod. 4-6).

portion of the crown, however, provided with numerous and unworn cusps, resembles that of M³ in *Hystrix cristata* L.

The lingual re-entrant folds of all teeth are obliquely turned towards the front and terminally slightly bifurcated, while the labial re-entrant folds are subparallel to the long axis of teeth. The lingual parts of re-entrant folds III and IV are distinctly turned backwards (fig. 1).

The upper incisors are stout, strongly curved. Pigmentation of enamel faint yellow, frequently grey or somewhat pinkish. The band of enamel on the labial side involves slightly more than two thirds of the lateral surface of tooth, that on the lingual side slightly less than one third. In cross section the incisor ovaly triangular (the enamel side semicircular). The enamel surface with extremely delicate, elongate grooves, discernible in oblique light. The enamel itself compact, secondarily cracked (fig. 3 a-c).

Choanae internae broad on the palatal side, and posteriorly in the shape of a high, rounded and even-sided triangle. Greatest diameter runs dorso-ventrally. Two cavities observable in the maxillar bone above the

right tooth-row (pl. I, fig. 1 *a-b*): the anterior one is large (*a*), obliquely placed above the contact of M^1 and M^2 (foramen sphenopalatinum); the posterior one is small (*b*), situated above M^3 (foramen alveolare M^3). A vestigial jugal arch (processus jugalis ossis maxillaris) (pl. I, fig. 1c) occurs above P^4 , turned slightly towards the front and the labial side of the upper jaw. A wide, gently descending depression stretches above this process forming the antero-lateral part of the maxilla.



Fig. 4. — Alveole pattern in mandible, schematically; nat. size.

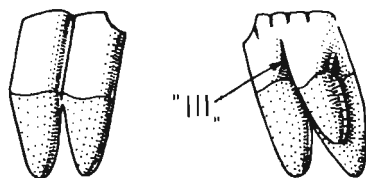


Fig. 5. — Structure of P_4 , schematically: *a* on labial side, *b* on lingual side, "III" lower (accessory) groove; approx. $\times 2$.

Mandible (pl. II, fig. 1-5). Fragment of mandible lacking M_3 , but with its alveoles preserved: two anterior ones (small) and one posterior (large and round). A similar pattern in the arrangement of alveoles occurs in the place of P_4 , but the other way about. Each of the remaining teeth has 4 alveoles², the anterior-lingual and the posterior-labial roots being stronger than the anterior-labial and posterior-lingual ones (fig. 4). The molars, P_4 excepted, are quadrate with low crowns (the degree of wearing down being considerably stronger than that in upper teeth).

The occlusal surface of molars is coated by an outer band of enamel of more or less uniform thickness and enamel islets occur within the field of dentine. In M_1 there are from 5 to 6 islets, in M_2 there are 6. Some of the islets, particularly so the anterior ones, have a tendency to bifurcate. In teeth which are more worn, the number of enamel islets may possibly increase to 6-7 on M_1 and 7-8 on M_2 .

P_4 is with the crown twice as high, nearly right-angled. The labial re-entrant fold, directed obliquely backwards, reaches the base of the crown. Lingually two others (II and III) occur still opened up. About 1 mm lower down, between them, we may observe the lower groove on the lingual side of the crown surface (fig. 5 „III”). Posterior portion of tooth, with internal enamel islet of re-entrant fold IV, delimited from the anterior part of crown by a labial re-entrant fold turned backwards

² The alveole pattern on the mandible could be examined, since during treatment in acetic acid the teeth were separated from the mandibular bone.

and by the lingual re-entrant fold III, which is parallel to the long axis of tooth. An arcuately curved enamel islet occurs within the field of dentine in this tooth. A vestigial loop of enamel (pl. II, fig 5x) suggests the presence of a small anterior islet or a vestigial anterior re-entrant fold I.

The lower incisor (fig. 3 d-f) less strongly bent, with similar structure of the band of enamel and analogous transverse section as in the upper incisors.

In a detached premolar (pl. II, fig. 1, 2) with slightly smaller dimensions, structure of the band of enamel resembles that in the mandibular P₄. A vestigial islet of enamel on the lingual side possibly suggests an upper molar. The high crown and the poorly differentiated roots — to judge from the outline of the broken off rooted part — indicate that this is a milk tooth.

The long bones of this animal are thus far unknown.

COMPARISON OF FOSSIL REMAINS OF *HYSTRIX PRIMIGENIA* (WAGNER) FROM WEŻE WITH LIVING REPRESENTATIVES OF HYSTRICIDAE BURNETT

On the size of the collected fragments, and the *Theridomys*-pattern of the tooth structure, they are referable to the genus *Hystrix* Linnaeus of the subfamily Hystricinae Lyon. Hence, the present writer does not discuss here any of the forms belonging to the family Erethizontidae Thomas. These differ in smaller dimensions and a different pattern of dentition. Neither can any members of the subfamily Atherurinae Lyon be here taken into account, since the total length of the upper and lower tooth-rows in these forms does not, as a rule, exceed 30 mm, while the tooth-pattern, displaying a varying degree of brachyodontism, differs distinctly from the plan of tooth structure found in Hystricinae. A comparison has, therefore, been made of the fossil remains from Weże with *Hystrix cristata* L., *H. africae-australis* Peters and *H. subcristata* Swinhoe. These three recent species differ fundamentally from one another in tooth structure, slightly different appearance of the nasal region and differences of outer morphology. The length of tooth-rows agrees on the whole (see tbl. 1). They differ distinctly from the fossil Weże porcupine not in dimensions only, but likewise in specific pattern of the enamel loops of molars. Since the recent material of *H. africae-australis* and *H. subcristata* was not accessible to the writer, he was unable to carry out a closer analysis of their dentition or to compare them with the fossil representative of the Weże species.

The Weże specimens resemble the recent *Hystrix cristata* in the

general structure of the first and second upper and lower molars. The structure of P^4 — size excepted — is essentially different. The lingual lobe (l. lg.) of the anterior portion of that tooth in the recent porcupine is considerably larger, this being most likely connected with the complete reduction of the anterior lobe (l. a.) in the recent form. Distinct differences are also observable in the posterior portions of molars in *H. cristata* where the central islet of dentine (in an unworn tooth) is connected into one whole with the dentine islets of the labial and lingual lobes of enamel, and at a later stage of the wearing down produces one or two islets of enamel. In the fossil Weże form, on the other side, the field of dentine of the analogous tooth region is strongly arched and involves the central and the labial islets. In an unworn tooth this produces two re-entrant folds IV and V, while in an older tooth — two or three islets of enamel. The last upper molars of both species are similar, except that in the fossil form the long axis of this tooth is directed somewhat antero-labially — postero-lingually. The lower dentition in *H. cristata* is considerably more delicate. Moreover its P_4 is not only smaller (though in an old individual it nearly attains the size of that in *H. primigenia*), but more distinctly triangular too and its roots, particularly the posterior ones, differ so markedly from the molar and premolar roots of *H. primigenia* from Weże that there is no difficulty at all to distinguish a recent porcupine tooth from that of Weże. Further comparisons of the lower teeth do not show any fundamental differences, except that the number of enamel islets on molars of the living form is never more than 6, while in the fossil teeth from Weże, Pikermi and Roussillon there may be as many as 8 of them.

COMPARISON OF FOSSIL REMAINS OF *H. PRIMIGENIA* (WAGNER) FROM WEŻE WITH OTHER FOSSIL REPRESENTATIVES OF HYSTRICIDAE BURNETT

Two main groups may be differentiated among the whole family of Hystricidae, practically from the very beginning of the Neogene. They differ in the length of tooth-rows, modifications of the Theridomys-pattern and in the brachyodontism or hypsodontism of crown. To the first group belong all the forms included into the subfamily Hystricinae Lyon. In addition to size, these are characterized in the first place by the hypsodontism of molars. They are represented by large Pliocene porcupines such as *Hystrix primigenia* (Wagner) from Pikermi, Roussillon and Weże, *H. refossa* Gervais from Perrier and Montpellier (though some authors believe this species to be early Pleistocene in age), *H. etrusca* Bosco from the upper strata of Val d'Arno (early Pleistocene), *H. leucura*

Sykes, likewise from the Lower Pleistocene (the Pinjor beds in the Siwalik Hills of India), the Pliocene *H. sivalensis* Lydekker (Dhok Pathan also in the Siwalik Hills), two forms described from South Africa: *H. major* Greenwood and *Xenohystrix crassidens* Greenwood (Makapan Valley, the *Australopithecus prometheus* horizon, equivalent of Villafranchian). Moreover, to this group are likewise referred small forms of the genus *Hystrix* L. present in the Oligocene: the doubtful „*H.*” *lamandini* Filhol (Phosphorites du Quercy) and the Miocene *H. suevica* Schlosser (Häder near Dinkelscherben, Salmendingen and Dinotheriensände), as well as the smaller-sized *H. bessarabica* Rjabinin from the Pliocene of Bessarabia (Taraklia beds) and *H. hirsutirostris* Brandt from the early Pleistocene of Bavaria. The last named species as well as a number of other specifically indeterminate forms constitute a kind of transition to the recent Hystricinae Lyon. All the above mentioned species of the genus *Hystrix* L. are characteristic by the more or less conspicuous hypsodontism of molar crowns, and on the whole, by the strong development of their roots.

To the other group belong all the forms included into the subfamily Atherurinae Lyon. In addition to smaller dimensions, they are distinguishable by the varying brachyodontism of the molar crowns. Besides recent genera of this subfamily forms such as *Sivacanthion complicatus* Colbert and *Hystrix lagrelli* Lönnberg, are also referable to this group (see tbl. 1). The former has been discovered in the lower Siwalik beds at Chinji, the latter in Pontian beds (Honan, North China). These two species, as has been correctly pointed out by Landry (1957), differ very distinctly from Hystricinae Lyon, not only in smaller dimensions of the tooth-rows, but in the first place in different tooth structure and the brachyodontism of molars.

When comparing the Weże remains with the typical form *Hystrix primigenia* (Wagner) from Pikermi and Roussillon, the only observable differences are those in the occlusal pattern of both — the lower and the upper jaw. This is particularly stressed by the accessory islets of dentine in the Weże forms, as well as by the slightly different number of enamel islets and by the specific pattern of structure in the upper premolar. Thus the outline of teeth, though different in every one of the three representatives of this species, is of no great significance here. This feature may safely be regarded as a highly variable character (varying degree of the wearing down of teeth). Four grooves (re-entrant folds) are observable on the labial side of the upper molars of *H. primigenia* — P⁴ included — while in the Weże specimen there are 5 grooves in P⁴ as well as in the remaining teeth. On the basis of the preserved unworn

loops in the Pikermi porcupine, it may be supposed that there are as many as 7 (though 6 are more common), sometimes even 8 islets of enamel. *Hystrix primigenia* (Wagner) from Roussillon is characterized by better differentiation of the size of teeth, in that M_3 is the smallest one and growing narrower towards the back. The number of the islets of enamel on the molars of that form never exceeds 7. Perhaps, when the teeth are more strongly worn down, the number of the enamel islets may be up to 8, but the writer has failed to ascertain this in the figures of Depéret (1890). P_4 differs from the Weże premolar in more distinct narrowing folds of its anterior portion. The posterior portion of that tooth has not been distinctly figured by Depéret (*l. c.*, pl. 4-7, fig. 12); apparently it strongly resembles analogous parts in the Weże and Pikermi specimens. The number of roots in M_3 and the alveole pattern are identical in both forms.

In what the structure of the skull is concerned, *Hystrix primigenia* comes, according to Schlosser (1884), nearest to *H. cristata* L. These two forms, however, differ distinctly in the position of the sphenopalate foramen. Owing to the fragmentary state of preservation of the Weże skull, it has not, unfortunately, been possible to make closer comparisons in this respect.

In spite of somewhat smaller dimensions, *Hystrix sivalensis* Lydekker resembles the Weże form, particularly so in the pattern of the enamel loops on M_1 and M_2 . This similarity is well discernible on the premolar of the Weże specimen as this tooth is relatively little worn. It is interesting to note that a detached milk tooth (specimen No Rod. 3) is very nearly identical with the molars of the porcupine from the Siwalik Hills in respect to the size and the pattern of the enamel loops. The lack of figures of the occlusal surface of the maxillary teeth in a young individual from the Siwalik Hills (Lydekker, 1884, fig. 5) renders closer comparisons impossible.

Hystrix cf. subcristata Swinhoe, described from the early Pleistocene of Northern China (Choukoutien, Shansi and elsewhere) by Pei (1936), Teilhard de Chardin (1936, 1941) and Young (1934), does not differ to any great extent from the living *H. cristata* L. Hence, also its comparison with the fossil porcupine from Weże bears the same character as that of *H. primigenia* (Wagner) with *H. cristata* L. generally speaking.

A primitive character, common to practically all the Mio-Pliocene species of *Hystrix* L. is the distinct differentiation of roots in all the maxillary and mandibular teeth. In the recent *H. cristata* the lower premolar e. g. has one deep and slightly bifurcated alveole (of a mature individual), the posterior roots being intimately fused. Together with the

Table 1

Measurements of upper and lower dentition in recent and fossil Hystricinae, including two representatives of Atherurinae

Teeth	H Y S T R I C I N A E																A T H E R U R I N A E					
	<i>Hystrix primigenia</i> (Wagner) Weże near Działoszyn Lower-Middle Pliocene		<i>Hystrix primigenia</i> (Wagner) Roussillon Middle Pliocene		<i>Hystrix primigenia</i> (Wagner) Pikermi Lower Pliocene		<i>Hystrix major</i> (?) Greenwood Makapan Valley Villafranchian		<i>Xenohystrix crassidens</i> Greenwood Makapan Valley Villafranchian		<i>Hystrix sivalensis</i> Lydekker Siwalik Middle Pliocene		<i>Hystrix cristata</i> Linnaeus NW-Africa Recent		<i>Hystrix africae-australis</i> Peters S-Africa Recent		<i>Hystrix cf. subcristata</i> Swinhoe N-China Plio-Pleistocene		<i>Hystrix lagrelli</i> Lönnerberg N-China, Honan Pliocene, Pontian		<i>Sivacanthion complicatus</i> Colbert Siwalik (Chinji) Upper Miocene-Lower Pliocene	
	L	B	L	B	L	B	L	B	L	B	L	B	L	B	L	B	L	B	L	B	L	B
P ⁴ - M ³	45.5		—		41.0		—		—		—		29.8 - 36.0		30.0 - 38.5		28.0 - 32.0		20.5 - 22.0		—	
M ¹ - M ³	31.2		—		29.4 ^x		—		—		—		21.2 - 26.0		21.8 - 27.5		20.5 - 22.0		14.4 - 15.6		—	
I	8.5	6.5	—	—	8.0 ^x	—	—	—	11.5 - 12.0	10.5 - 11.0	—	—	7.3 - 8.0	7.0 - 7.1	6.3 - 8.5	6.0 - 7.4	—	—	—	—	—	—
P ⁴	13.2	11.8	—	—	12.0 ^x	11.6 ^x	—	—	12.0	12.0	—	—	8.5 - 10.5	8.0 - 9.0	8.2 - 11.0	7.3 - 10.5	6.0 - 10.0	5.5 - 7.5	5.1 - 6.0	4.5 - 5.5	—	—
M ¹	11.0	10.0	11.2 ^x	11.0 ^x	10.0 ^x	10.5 ^x	—	—	10.5 - 12.5	12.0	—	—	7.2 - 8.0	7.0 - 9.0	7.3 - 9.5	7.0 - 9.0	7.0 - 7.4	6.5 - 7.3	5.1 - 5.3	4.5 - 5.4	—	—
M ²	11.0	10.0	11.0 ^x	10.0 ^x	9.7 ^x	10.5 ^x	—	—	11.5 - 13.0	12.0	—	—	7.4 - 9.0	7.0 - 9.0	6.5 - 9.0	7.0 - 8.5	7.0 - 7.4	6.5 - 7.2	5.1 - 5.3	4.1 - 5.2	—	—
M ³	10.0	9.0	—	—	9.7 ^x	9.7 ^x	—	—	—	—	—	—	6.6 - 8.5	6.0 - 8.0	8.0 - 9.0	6.5 - 7.5	6.0 - 7.0	5.5 - 6.5	4.1 - 4.8	3.5 - 4.3	—	—
P ₄ - M ₃	47.0 ^x		45.0		42.0 ^x		—		56.0 ^x		—		32.5 - 38.5		32.6 - 40.0		32.5 - 37.0		22.0		22.0 ^x	
M ₁ - M ₃	33.5 ^x		32.5 ^x		31.1 ^x		—		42.0 ^x		—		24.8 - 28.2		24.5 - 30.0		25.0 - 27.0		16.0		—	
M ₁ - M ₂	23.5		22.5 ^x		20.0 ^x		—		28.5 ^x		19.0		16.5 - 18.5		15.8 - 20.0		16.0 - 18.0		10.0		11.0	
I	8.8	7.0	—	—	8.5 ^x	—	—	8.0	—	—	—	—	6.5 - 7.5	6.5	6.2 - 8.0	5.0 - 7.0	—	—	—	—	—	—
P ₄	12.4	9.7	11.5	10.8 ^x	12.0	9.8 ^x	13.0	9.5	14.0 - 17.0	12.0 - 13.5	—	—	7.8 - 10.5	7.0 - 8.0	8.2 - 10.0	6.0 - 8.0	7.5 - 10.0	6.0 - 8.2	5.0 - 6.0	5.0 - 5.2	6.1	—
M ₁	11.7	11.2	11.5	10.0 ^x	11.0	10.0 ^x	—	9.5	14.0	11.0	10.0 ^x	9.5 ^x	7.8 - 8.5	7.0 - 8.0	7.5 - 9.5	7.2 - 8.0	7.4 - 9.0	6.0 - 8.0	5.0 - 6.0	4.0 - 4.5	5.3 ^x	4.4 ^x
M ₂	11.7	11.2	11.0	10.0 ^x	11.0	10.0 ^x	—	—	14.5	11.5	9.0 ^x	9.0 ^x	8.7 - 10.0	7.8 - 9.5	8.3 - 10.5	7.0 - 8.2	9.5 - 9.0	7.0 - 8.0	5.0 - 5.7	5.0 - 5.5	5.2 ^x	4.4 ^x
M ₃	10.0 ^x	9.7 ^x	9.0	8.2 ^x	9.0	8.8 ^x	—	—	—	10.5	—	—	8.2 - 9.5	7.5 - 9.0	8.5 - 10.0	6.0 - 7.7	9.0	7.2	4.2 - 5.0	4.0 - 4.5	—	—

L = Largest anterior-posterior diameter.

B = Largest lingual-labial diameter.

^x = Approximate measurements from figures of other authors

faintly marked anterior roots they form the so-called papilliform roots. The weak differentiation of roots in this species is still better discernible on the remaining molars, particularly so in those of the maxilla. Well developed alveoles are observable in nearly all the more primitive and older forms, similarly as in all forms of the subfamily Atherurinae Lyon. In the Oligocene form „H”. *lamandini* Filhol, P₄ and M₃ are provided with three alveoles, while the remaining teeth have each four alveoles. An analogous pattern of alveoles also occurs in specimens from Węże, Pikermi and Roussillon, as well as in species such as *H. sivalensis*, *H. refossa* Gervais, *H. major*(?) Greenwood and *Xenohystrix*(?) *crassidens* Greenwood³ (Lydekker, 1884; Greenwood, 1955; Landry, 1957).

Sivacanthion complicatus Colbert, already mentioned hereabove, displaying a most intricate structural pattern of re-entrant folds and loops, resembles *H. primigenia* (Wagner) from Węże in the general outline of the surface of wear on the molars only. In the posterior portions of crowns of M₁ and M₂, the band of enamel between re-entrant folds I and II may perhaps be considered as bearing some analogy to the accessory central and labial cusp on the upper molars of the fossil form from Węże. Hence the structure of these teeth displays closer alliance with the subfamily Hystricinae Lyon. The brachyodontism of the molars of *Sivacanthion* Colbert is of course an important difference in these forms.

The comparison of the Węże remains with *Hystrix refossa* Gervais is made difficult by the unsatisfactory state of preservation of this last species, its incomplete description and differences in the degree of the wearing down of teeth. *H. refossa* has been, on the one hand, regarded as the only late Pliocene species (Schlosser, 1884), on the other hand as identical with *H. major* Gervais which approaches *H. primigenia* (Wagner), (Depéret, 1890). At present, together with *H. etrusca* Bosco, it is referred to the Villafranchian horizon (Bosco, 1898; Landry, 1957; Zeuner, 1959). In the opinion of some authors *H. refossa*, *H. etrusca* and *H. leucrura* represent the transition evolutionary stages to the recent porcupine species of *H. cristata* L., and perhaps *H. hirsutirostris* Brandt (Depéret, 1890; Landry, 1957).

Hystrix etrusca Bosco, already by Major (1878) identified as *Hystrix* sp., does not, in the size and morphology of dentition, differ much from *H. refossa* Gervais. The other species from Euro-Asia, such as *H. leucrura* Sykes (Matthew, 1929) and *H. bessarabica* Rjabinin (1929, p. 112-115, pl. 10, fig. 1, 1a), differ from *H. primigenia* (Wagner) in smaller dimen-

³ An interpretation of the uncertain systematic position of the two just named species is given here later.

sions. A more detailed analysis of the upper dentition in *H. bessarabica*⁴ and a comparison with the specimens from Weże, as well as with the drawings of *H. primigenia* (Wagner) from Pikermi, show that there are great similarities in the tooth structure and in the general morphology of the skulls. In spite of differences in the wearing down of teeth in Taraklia and Pikermi specimens, the structure of P⁴ is identical. The same concerns the pattern structure of the molars, especially M¹ and M² in the specimens from Pikermi and Weże. The latter differs only in the structure of P⁴, chiefly by the presence of the anterior sulcus (a. s.).

Observations of some specimens of living *Hystrix cristata* L. in the different growth stages show that the number of islets and of enamel folds on the premolars and molars in this species is inconstant, fitting into individual variation. This concerns the enamel folds, too.

It seems that a Pikermi form, of smaller size, however, also occurs in the Taraklia fauna.

The South-African species *Hystrix major* and *Xenohystrix crassidens* (see tbl. 1), referred to hereabove, constitute supplementary material toward the knowledge of the thus far described Hystricinae faunas from the Old World. The first named of them, represented by a fragmentary mandible with preserved premolar and vestigial first molar, is apparently similar with *H. primigenia* (Wagner). This resemblance is suggested not by dimensions of teeth only, but by their enamel pattern too, particularly so on the premolar. This tooth likewise resembles the premolars of the form from Pikermi and Roussillon, and even those of the species *H. sivalensis* Lydekker. *Xenohystrix crassidens* could reasonably be considered as a new species if it were not for the upper dentition, which displays similarities of structure with that of *H. primigenia*. The large mandible, however, (the premolar attaining a length of up to 17 mm) and robust incisors (with diameter of 11 mm), do not supply adequate evidence for the establishment of a new genus. Hence the writer thinks the assignment of this form to *Hystrix crassidens* (Greenwood) as more justifiable. The lack of figures of the surface of wear on molars of this species does not allow a closer comparison with the remains from Weże and from other localities of *H. primigenia* (Wagner).

The description of *Hystrix astasobe*, the first fossil porcupine from North Africa, given by Bate (1951), was based on a very badly preserved fragment of skull. Hence the systematic position of that form is quite uncertain. Most likely the skull belonged to a late Pleistocene porcupine.

⁴ Based on photocopy of Rjabinin's paper (1929), kindly sent by Dr L. I. Alekseeva from Moscow.

PALAEOGEOGRAPHIC AND PALAEOECOLOGIC CONCLUSIONS

On evidence of the present distribution and mode of life of the whole Old World subfamily Hystricinae, it may be postulated that *H. primigenia* (Wagner), and all the related fossil porcupines of Europe and Asia, had lived during the Pliocene in very similar life environment. The northern range of their distribution may simultaneously be shifted 10—12 degrees farther north, to the 50 or 52° North latitude in Europe, in Asia 40° or even more. The climate of that time must have been much warmer too than that now prevailing there, the mean annual temperature probably attaining 20°C above zero, possibly even more.

Hystrix primigenia, similarly as the living Africo-Asiatic porcupines, must have lived in a mountainous steppe-desert environment (the Bush, the Savannahs), whose common haunts were the abandoned hiding places of small carnivores or natural crevices and caves. Since these animals lead a „solitary” life, it is not surprising that their fossil remains are rare and meagre.

PHYLOGENETIC CONCLUSIONS

The ancestry of *Hystrix primigenia* (Wagner) and of its allied forms is still an open question. The very few reported finds of fossil porcupines and still more so the incompleteness and unsatisfactory state of preservation of their remains render impossible any wider approach to that problem. The descent of typical porcupines of the genus *Hystrix* L. directly from Miocene European forms seems very improbable. It is possible that *H. primigenia* (Wagner) is a link in the evolution of the highly specialized lineage (with high hypsodontic crowns), originating probably in Central Africa. This would be suggested by the remains of a closely allied species *H. major* (?) Greenwood and *H. crassidens* (Greenwood), reported from the *Australopithecus prometheus* beds. Some evidence is available indicating close genetic connections with the subfamily Atherurinae Lyon (*Sivacanthion complicatus* Colbert). Probably in the early Miocene or even earlier the evolutionary line of Hystricinae Lyon separated from the structurally primitive subfamily Atherurinae and was specialized under different environmental conditions.

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Warszawa, March 1960

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ANDRZEJ SULIMSKI

HYSTRIX PRIMIGENIA (WAGNER) W PLIOCENSKIEJ FAUNIE Z WĘŻÓW KOŁO DZIAŁOSZYNA

Streszczenie

Autor opisuje szczątki kostne rzadko spotykanego, lecz stosunkowo szeroko rozprzestrzenionego w pliocenie Europy jeżozwierza, oznaczonego tu jako *Hystrix primigenia* (Wagner). Gatunek ten znany był dotychczas z dwóch stanowisk: dolnego pliocenu Grecji (Pikermi) i środkowego pliocenu Francji (Roussillon). Znaleździisko w Wężach k. Działoszyna jest trzecim punktem występowania tego gatunku, i to najdalej wysuniętym ku północy (51° szer. geogr. płn.).

Znalezione szczątki tego zwierzęcia należą do kilku osobników różnego wieku: fragment czaszki — do osobnika dojrzałego (zęby stosunkowo słabo jeszcze starte), fragment żuchwy — do starczego, a luźny ząb przedtrzonowy (mleczny) — do młodego. Szczegółowa analiza dolnego i górnego uzębienia wykazuje podobieństwo z *Hystrix sivalensis* Lydekker (środkowe warstwy Siwałik), zapewne też z późnopliocenijskim *H. refossa* Gervais (z Perrier i Montpellier), z wczesno-plejstocenijskim *H. etrusca* Bosco (górne warstwy Val d'Arno), z afrykańskim *H. major* (?) Greenwood (warstwy Makapan z poziomu *Australopithecus prometheus*) i ze współczesnym *H. cristata* Linnaeus. Różnice w budowie zewnętrznych pętli szkliwa, szczególnie w tylnych częściach zębów górnej szczęki (obecność dodatkowych wysepek dentyne) mogłyby sugerować nowy gatunek. Zgodne wymiary fragmentów czaszki i żuchwy z typowymi przedstawicielami z Pikermi i Roussillon, ogólny charakter budowy obu szczęk i ich zębów z jednej strony i skąpy jeszcze materiał z drugiej, pozwala jedynie na zaliczenie szczątków z Wężów do *H. primigenia* (Wagner).

Sądząc z rozmieszczenia stanowisk tego gatunku i innych kopalnych jeżozwierzy szczególnie na terenie Europy i Azji, ich północną granicę rozprzestrzenienia w plio-

cenie można przeprowadzić wzdłuż 51° (lub wyżej) szerokości geograficznej. Można również przyjąć, że klimat i warunki życia tego zwierzęcia nie wiele odbiegały od warunków w jakich żyją dzisiejsze tropikalne i subtropikalne jeżozwierze Afryki i południowej Azji.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 321)

Schemat budowy P⁴, od góry: I-V bruzdy, 1-6 płyty, s. a. sulcus anterior, l. a. lobus anterior, s. med. sulcus medialis, i. d. c. insula dentinae centralis, i. d. l. insula dentinae labialis.

Fig. 2 (p. 322)

Hipotetyczne stadia starcia P⁴: A stadium „immature-young”, B „young”, C „young-adult”, D „adult”, E „adult-old”, F „old”; ca × 2.

Fig. 3 (p. 323)

Budowa siecznych: a górny sieczny od strony labialnej, b to samo od strony lingwalnej, c przekrój poprzeczny górnego siecznego, d dolny sieczny od strony labialnej, e to samo od strony lingwalnej, f przekrój poprzeczny dolnego siecznego; wielk. nat. (okazy Rod. 4-6).

Fig. 4 (p. 324)

Układ alweol w dolnej szczęce, schematycznie; wielk. nat.

Fig. 5 (p. 324)

Budowa P₄, schematycznie: a od strony labialnej, b od strony lingwalnej, „III” dolna (dodatkowa) bruzda; ca × 2.

Pl. I

Fig. 1. Fragment czaszki: a foramen sphenopalatinum, b foramen alveolare M³, c processus jugalis ossis maxillaris; wielk. nat. (okaz Rod. 1).

Fig. 2. To samo od dołu: d choanae internae.

Fig. 3. Prawy szereg zębów P⁴-M³: s. a. sulcus anterior, l. a. lobus anterior; × 2.

Pl. II

Fig. 1. Luźny mleczny przedtrzonowy, od góry: a szczątkowy guzek labialny (?); × 2 (okaz Rod. 3).

Fig. 2. To samo, schematycznie: I-IV bruzdy, 1-5 płyty.

Fig. 3. Fragment prawej żuchwy z P₄-M₂, od strony labialnej; wielk. nat. (okaz Rod. 2).

Fig. 4. To samo, od góry.

Fig. 5. Szereg zębów dolnych, od góry: I-IV bruzdy, 1-5 płyty, x szczątek bruzdy; × 2.

Tab. 1 (p. 328/329)

Zestawienie pomiarów górnego i dolnego uzębienia u współczesnych i kopalnych Hystericinae, z uwzględnieniem dwóch przedstawicieli Atherurinae.

АНДРЖЕЙ СУЛИМСКИ

HYSTRIX PRIMIGENIA (WAGNER) В ПЛИОЦЕНОВОЙ ФАУНЕ
ИЗ ВЕНЖЕ БЛИЗЬ ДЗЯЛОШИНА

Резюме

Автор описывает костные остатки дикобраза редко встречаемого, но сравнительно широко распространенного в плиоцене Европы, определенного тут как *Hystrix primigenia* (Wagner). Вид этот известен был до сих пор из двух мест: нижнего плиоцена Греции (Pikermi), и среднего плиоцена Франции (Roussillon). Местонахождение в Венже около Дзялошина в Польше является третьим местом нахождения этого вида, притом наидалее выдвинутым к северу (51° геогр. сев. широты).

Найденные остатки этого животного относятся к нескольким особям разного возраста: фрагмент черепа принадлежит особи зрелого возраста (зубы сравнительно мало истертые), фрагмент челюсти — к старческой, а отдельный предкоренной зуб — к молодой особи (зуб этот является молочным). Тщательный анализ верхних и нижних зубов указывает на подобие с *Hystrix sivalensis* Lydekker (средние слои Сивалик), с поздне-плиоценовым *H. refossa* Gervais (Perrier, Montpellier), с ранне-плейстоценовым *H. etrusca* Bosco (верхние слои Val d'Arno), с поздне-плиоценовым *H. major*? Greenwood (слои Makapan Valley, горизонт *Australopithecus prometheus*) и с современным *H. cristata* Linnaeus. Некоторые незначительные отличия в строении наружных петель, особенно в задних частях зубов верхней челюсти (наличие добавочных островков дентина), могли бы внушать мысль о новом виде *Hystrix* L. Однако слишком скудный материал не позволяет различить остатков из Венже от *Hystrix primigenia* (Wagner).

Судя по размещению местонахождений этого вида и иных третичных и четвертичных дикобразов Европы, Азии и Африки, можно провести северную границу их распространения вдоль 51° или даже 52° географической широты. Точно также на основании современных климатических и экологических условий, господствующих в области обитания Hystricidae Burnett, можно признать подобные же условия бытия для ископаемого дикобраза из Венже.

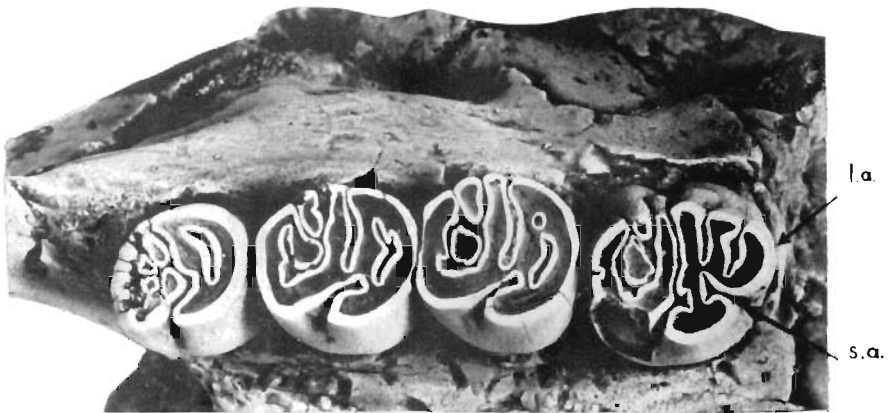
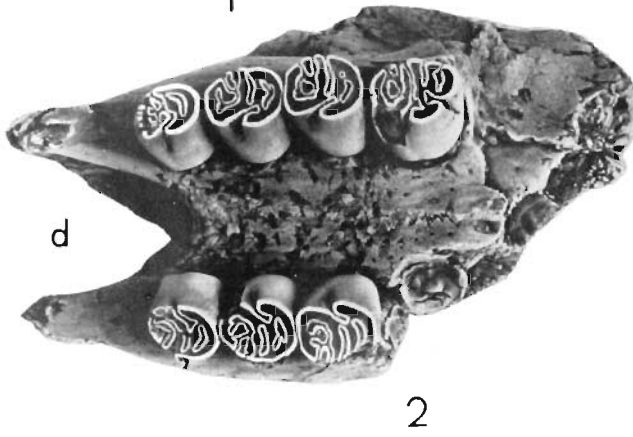
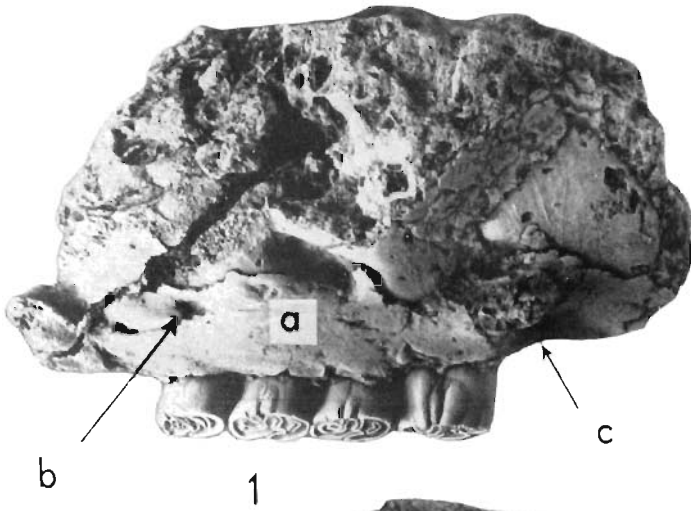
EXPLANATIONS OF PLATES

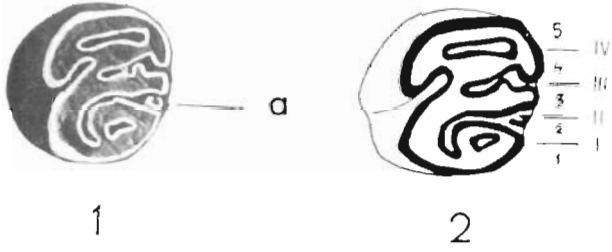
Pl. I

- Fig. 1. Fragment of skull: *a* sphenopalatine foramen, *b* alveolar foramen M^3 , *c* jugale process of maxilla; nat. size (specimen Rod. 1).
Fig. 2. The same, from below: *d* internal choanae.
Fig. 3. Right tooth-row P^4-M^3 : *s. a.* anterior sulcus, *l. a.* anterior lobe; $\times 2$.

Pl. II

- Fig. 1. Detached milk premolar, from top: *a* vestigial labial (?) cusp.; $\times 2$ (specimen Rod. 3).
Fig. 2. The same, schematically: *I-IV* re-entrant folds, *1-5* lobes.
Fig. 3. Fragment of right mandible with P_4-M_2 , on the labial side; nat. size (specimen Rod. 2).
Fig. 4. The same, from above.
Fig. 5. Lower tooth-row, from above: *I-IV* re-entrant folds, *1-5* lobes, *x* vestigial re-entrant fold; $\times 2$.

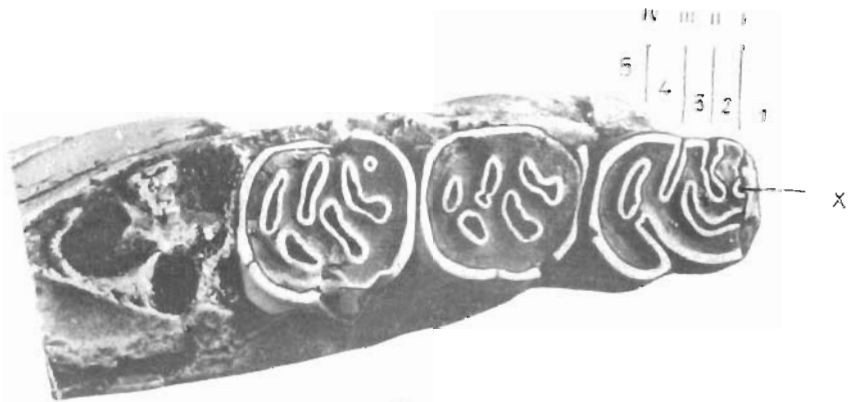




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