Vol. II, No. 2—3 VERTEBRATA PALASIATICA Sep., 1958

周口店腫骨鹿顎骨的腫厚現象

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中國的腫骨鹿化石最早由司坦斯基研究，他將這類鹿的化石分入許多不同的屬內，而並未放入 *Megaceros* 屬。顎骨腫厚的性質是步林首先注意到的。後來楊鍾健對周口店第一地點的腫骨鹿 *Cervus* (*Euryceros*) *pachyosteus-Megaceros* (*Sinomegaceros*) *pachysteus* (Youug) 進行了全面的詳細研究，討論到下顎骨和角的腫厚度的變異範圍。此後，德日進和裴文中認爲周口店 13 地點標本的腫厚程度較差等性質定了一個新種扁角腫骨鹿 *M. flabellatus*.

不久以前在本文作者與胡長康發表的關於大角鹿類在中國的分佈一文中，認爲第一地點和十三地點的大角鹿屬於同一種，扁角鹿是腫骨鹿的同義語，本文主要是進一步論述我們對這個看法的根據。

賈蘭坡在 1951 年從事周口店第一地點發掘時已發現到堆積底部的腫骨鹿顎骨的腫厚情形與扁角鹿的相近。

大角鹿類顎骨腫厚的情形，在歐洲的正角鹿 (*Orthogonoceros*) 和美國森林層及德國中更新統下部的大角鹿中，也有同樣情形存在。

周口店十三地點的顎骨和第一地點底部的顎骨同樣表現有中等程度的腫厚現象，而後者上部地層標本的腫厚現象更强。在第一地點全部剖面中表現出顎骨腫大的情形逐步隨時間發展的情形。

大角鹿類角的形態變異性很大，有時甚至因個體的變異而被定爲新種。

第一地點的鹿角一般比較呈闊大的掌狀，十三地點標本同樣也成闊扁的掌狀，但在程度上比第一地點的標本稍差。

(周明鎮節譯)

ON THE EVOLUTION OF PACHYOSTOSIS IN JAW-BONES OF CHOUKOUTIEN GIANT-DEER *Megaceros pachyosteus* (YOUNG)

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As far back as in 1925 pachyostosed jaws of cervids have been described from China (cf. Zdansky, 1925, 1927). But all have been referred by this author to different genera of cervids, not to *Megaceros*. Three years later Bohlin recognized the real

nature of these thick jaw-bones (cf. Young, 1932, p. 38). He did not publish his view, but only discussed the matter with Young*. In 1932 the excellent work by YOUNG on the Artiodactyla of Choukoutien was published and with this book the proof and the whole abundance of *Magaceros* of Choukoutien, Locality 1, was given. Young, though discussing the wide range of variation of lower jaws and antlers, referred all remains of this locality to one species: *Cervus* (*Euryceros*) *pachyosteus*= *Megaceros* (*Sinomegaceros*) *pachyosteus* (Young). Four years later, Teilhard de Chardin, giving a paper on the mammalian fossils of Locality 9 (Choukoutien), observed that the pachyostosis of the *Megaceros*-jaws of this locality does not reach on the average the extreme degree of those of Locality 1. Based on this fact—and with knowledge of the better preserved materials of Locality 13 (Choukoutien)—he founded a

Explanation of Fig. 1a

Graphic presentation of cross-sections of lower jaws, using the available materials with definite record of horizon in the following institutes and collections: Institute of Vertebrate Paleontology, Academia Sinica, Peking; Choukoutien-Museum; Meseum of Geology, Peking; Museum of Geology, Nanking.—

The series shows that the osteological anomaly of lower jaws, which is "moderate" in the lower levels reaches a more and more extreme degréé in the upper layers. As far as we known, it is the first sample demonstrating the development of pachyostosis in *Megaceros*-jawbones within a relative long time (section of Locality 1, O-33 meters), an interesting example to this problem of palaeobiology.

(Young individuals with milk-dentition not counted

Index of lower jaw: $I=\frac{\text{Breadth of ramus under } M_3}{\text{Internal depth under } M_3}$. 100, cf. Teilhard and Pei, 1941, p. 86).

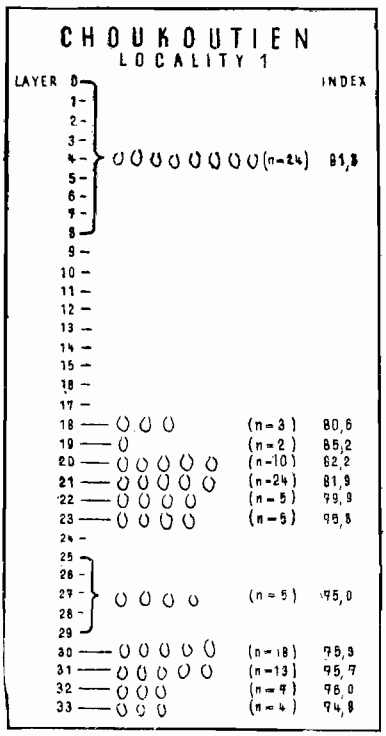

Figure 1a (Choukoutien, Locality 1)

new species *Eurycêros flabellatus*=*Megaceros* (*Sinomegaceros*) *flabellatus* (Teilhard de Chardin), [cf. Teilhard, 1936, p. 42]. In 1941, Teilhard and Pei referred all *Megaceros*-remains of Choukoutien, Locality 13, to this species. Finally the *Megaceros*-jaws of Chihcheng, Hopei, showing a "moderate" hyperostosis, have been referred to *Megaceros flabelatus* (Teilhard de Chardin), [Chia and Chai, 1957, p. 54].

*Personal communication by Dr. Young Chung-cheng, Peking.

After having studied the *Megaceros*-remains of Choukoutien* as already mentioned [Kahlke and Hu, 1958, p. 1], especially the newly discovered materials of 1951 (Locality 1, lower layers), we propose to drop the name *Megaceros flabellatus* (Teilhard de Chardin) as to be synonym with *Megaceros pachyosteus* (Young). In this paper we will finally state our opinion on this question.

The excavations of Locality 1 have fortunately been carried on in 1951 by Mr. Chia to reach the lower levels of this important fossil locality. By these works a series of about 40 more or less well preserved lower jaw-bones of *Megaceros* have been discovered. The materials of these excavations are yet unpublished. By the kindness of Mr. Chia it was possible to examine the new series (level 30—33m, Locality 1). Mr. Chia already noticed the relative "moderate" hyperostosis of the new jaw-bones and referred the *Megaceros*-remains of the lower levels of Locality 1 to *Megaceros flabellatus*, the giant-deer of Locality 13**.

The species *Megaceros (Sinomegaceros) flabellatus* (Teilhard de Chardin) 1936 (a) Mandible

The species was founded on the materials of Locality 9 (Choukoutien): some broken antlers, one upper maxilary, parts of a skull and some lower jaws, "distinctly thickened, and the cross-section of the horizontal ramus (under the molars) subcircular." It was shown that the pachyostosis of lower jaws (Loc. 9) on the whole does not reach the extreme degree observed in most specimens of Locality 1. Indeed, owing to lack of well preserved antlers, in this paper most attention was paid on the lower jaws. But in reality, we may assume that the materials of Locality 13 (Choukoutien) led Teilhard to found the new species. The materials of this place was published by Teilhard and Pei in 1941 as alreatly mentioned. By numerous specimens it was clearly shown that the hyperostosis of lower jaws (*Megaceros*) on the average does not reach the above cited extreme degree of Locality 1. It was stated too that the horizontal ramus (Loc. 13), though sub-circular in cross-section, looks elongated and slender as a whole, while the *pachyosteus*-mandibles show in this part-level of the last molars-an exaggerated hypertrophy of bony substance.

Until 1951 this difference between both localities in general could be accepted—without seeing a reason to found on it a new species—even though we could find few *flabellatus*-types in the upper layers as well as some *pachyosteus-types* already in the lower layers of Locality 1. But the whole series of the new discovered jaw-bones of the lowest horizons (layer 30—33 m, Locality 1) shows the *flabellatus*-type, and in between we have—accepting two species in the Choukoutien-area—*Megaceros flabel-*

*We are greatly indebted to Dr. Young Chung-cheng, Dr. Pei Wen-chung, Dr. Chow Minchen, Mr. Chia Lan-po and Miss Hu Chang-kang of the Institute of Vertebrate Paleontology, Academia Sinica, Peking, for giving their kind assistance. Furthermore we have to thank Mr. Kao Chensi and Mr. Hu Chengchi (Museum of Geology, Peking) and Mr. Chao Kingkoo (Institute if Paleontology, Academia Sinica, Nanking) for their valuable help.

**Personal communication by Mr. Chia, Institute of Vertebrate Paleontology, Academia Sinica, Peking.

Explanation of Figure 1b

Choukoutien, Locality 1

Cross-sections of lower jaws (0—22 m), 1/2 nat. size.

1 = C / C 119 9:17:5

2 = C / C 5523 LT—61:23

3 = C / C 87 Loc. 1

4 = C / C 92

5 = C / C 92 Loc. 1

6 = C / C 206 1928:72:88:57

7 = Loc. 1 1928:78:14:10

8 = C / C 93

9 = Loc. 1 36 : 13 : L-4

10 = Loc. 1 36 : 13 : J-4

11 = Loc. 1 36 : 6 : J-1

12 = Loc. 1 36 : 43 : N-2

13 = Loc. 1 36 : 21 : M-4

14 = Loc. 1 36 : 51 : J-4

15 = Loc. 1 36 : 52 : L-4

16 = Loc. 1 36 : 43 : P-3

17 = Loc. 1 36 : 49 : J-4

18 = Loc. 1 36 : 66 : K-3

19 = Loc. 1 36 : 54 : A-4

20 = Loc. 1 36 : 53 : J-4

21 = Loc. 1 36 : 55 : N-3

22 = Loc. 1 36 : 60 : J-3

23 = Loc. 1 36 : 83 : J-3

24 = Loc, 1 36 : 84 : K-2

25 = Loc. 1 36 : 87 : M-2

26 = Loc. 1 36 : 82 : P-1

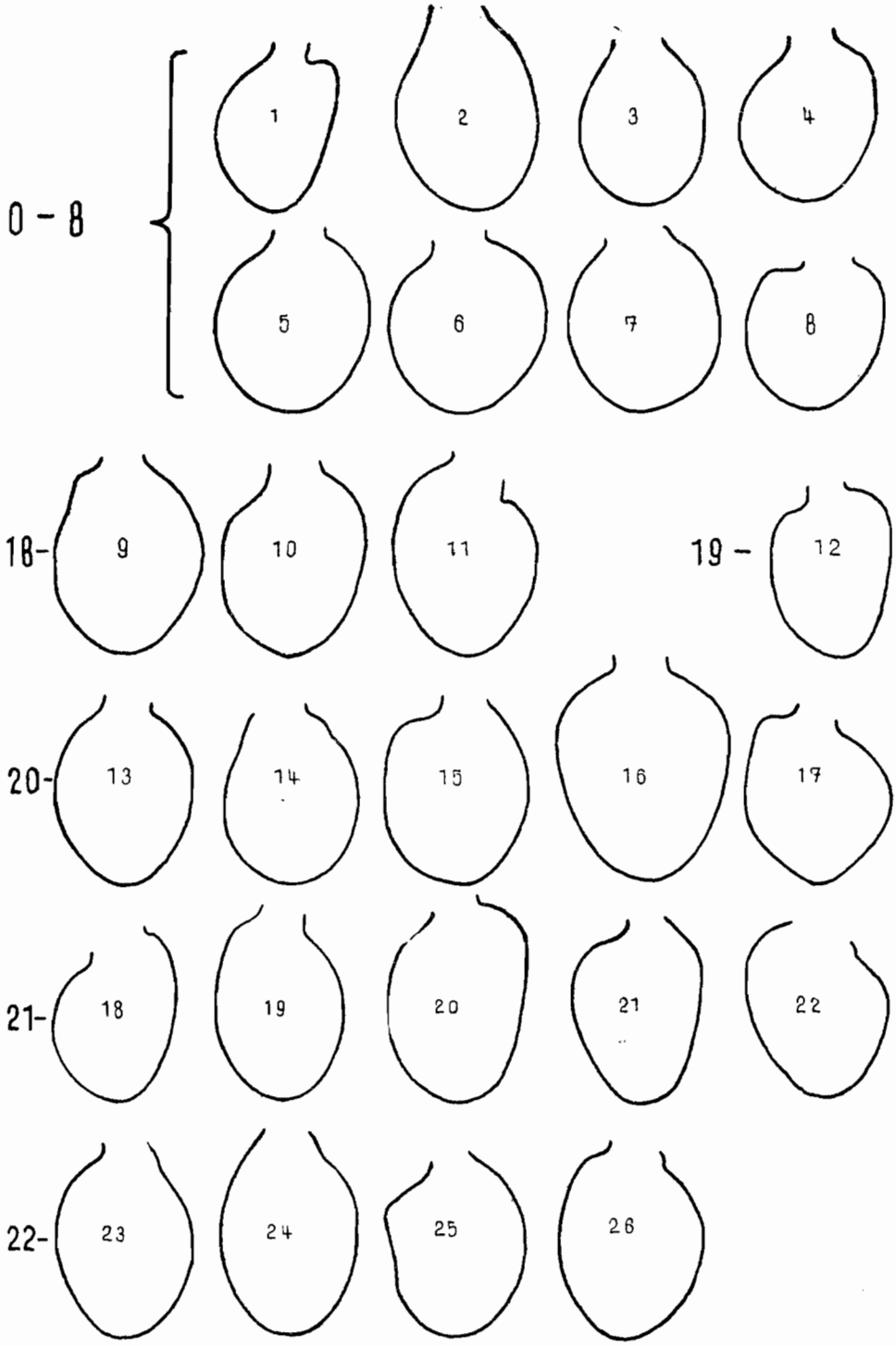
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Figure 1b

Explanation of Figure 1c

Choukoutien, Locality 1

Cross-sections of lower jaws (23—33 m), 1/2 nat. size.

27 = Loc. 1 36 : 99 : L-3	28 = Loc. 1 36 : 124 : B-0
29 = Loc. 1 36 : 126 : I-4	30 = Loc. 1 36 : 105 : C-3
31 = Loc. 1 36 : 166 : G-2	32 = Loc. 1 37 : 108 : I-3
33 = Loc. 1 37 : 165 : F-1	34 = Loc. 1 37 : 153 : E-0
35 = Loc. 1 L 30 : H 1 : 51 : 7	36 = Loc. 1 30 : D-5 : 51 : 33
37 = Loc. 1 L 30 : 8-5 : 51 : 34	38 = Loc. 1 51 : 7
39 = Loc. 1 L 30 : D-6 : 51 : 35	40 = Loc. 1 L 31 : J 2 : 51 : 39
41 = Loc. 1 L 31 : J 2 : 51 : 39	42 = Loc. 1 L 31 : G 2 : 51 : 48
43 = Loc. 1 L 31 : E 4 : 51 : 69	44 = Loc. 1 L 31 : 42 : 51 : 77
45 = Loc. 1 L 32 : K 0 : 51 : 153	46 = Loc. 1 L 32 : K 2 : 51 : 154
47 = Loc. 1 L 32 : K 0 : 51 : 153	48 = Loc. 1 L 33 : J 2 : 51 : 182
49 = Loc. 1 L 33 : K 2 : 51 : 182	50 = Loc. 1 L 33 : K 2 : 51 : 182

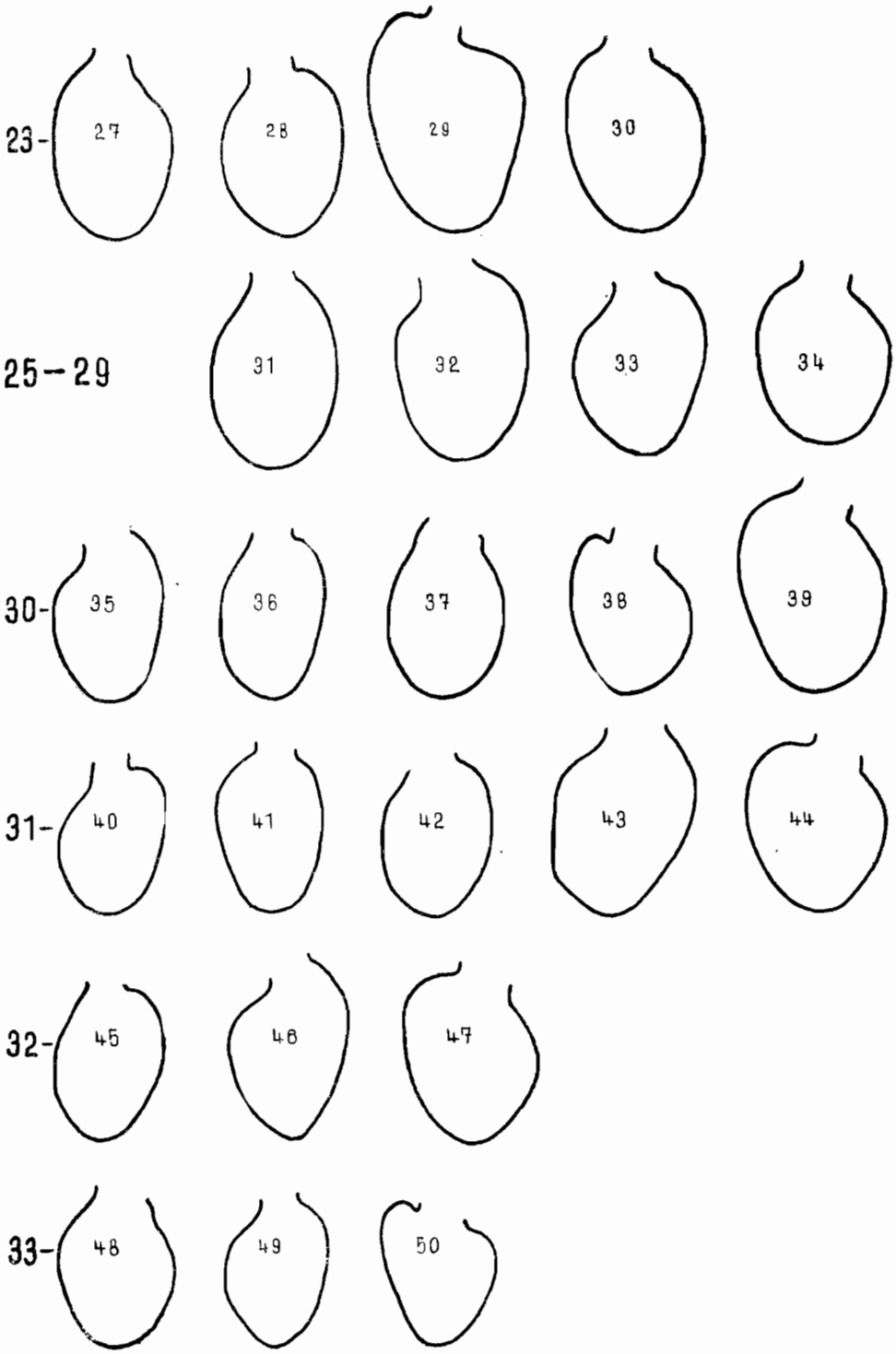
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Figure 1c

Explanation of Figure 2

Graphic presentation comparing range of variation (cross-sections of lower jaw-bones) of Localities 1 and 13 (n=251, well preserved specimens used only; Young individuals showing milk-dentition not considered), 1/2 nat. size.

Locality 1 (upper row)

1 = Loc. 1 37 : 173 : G 0 2 = Loc. 1 Q 2:12 : 54 : 1931

3 = Loc. 1 36 : 49 : L-4 4 = Loc. 1 7 : 24 : 17

5 = Loc. 1 $\frac{C}{C\ 93}$: yy : 1 6 = Loc. 1 : 136 : 46 : K-2

7 = Loc. 1 : 1929 : FF : 15 : $\frac{C}{C\ 182}$ 8 = Loc. 1 $\frac{C}{C\ 28}$ 33 : 9 : 21—2

Locality 13 (lower row)

1 = Loc. 13 : 34 : 251 2 = Loc. 13 : 34 : 257 3 = Loc. 13 : 34 : 251

4 = Loc. 13 : 34 : 298 5 = Loc. 13 : 33 : 155 6 = Loc. 13 : 34 : 291

7 = Loc. 13 : 34 : 174 8 = Loc. 13 : 34 : 194

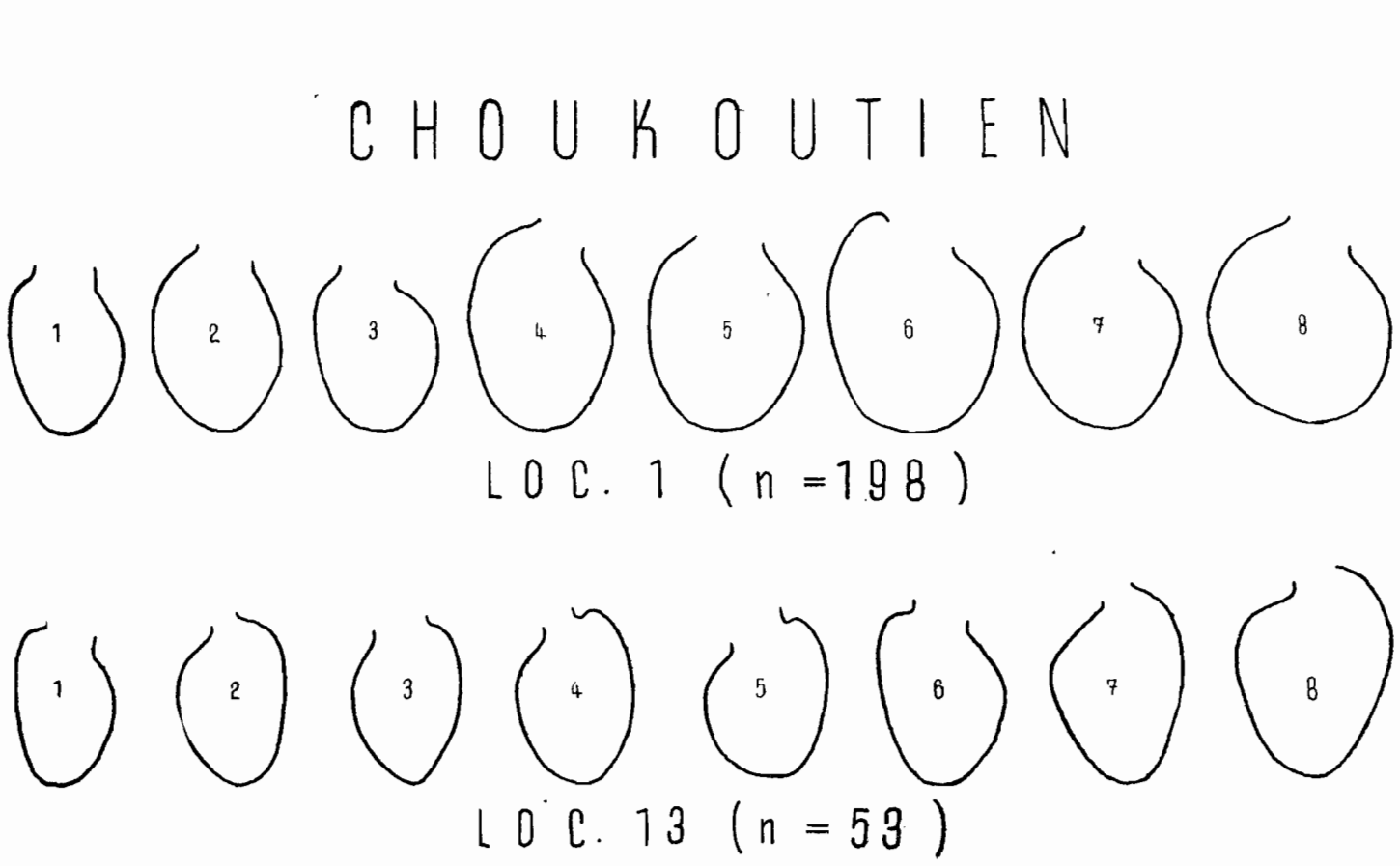

Figure 2

latus in the lower and *Megaceros pachyosteus* in the upper layers of Locality 1 (cf. Figure 1a—c). But this leads us to the question how to determine both species in jaw-bones, because there are transitions, even in the upper layers of Locality 1, as mentioned above (cf. Figure 2). We therefore, on the evidence of the discussed transitions of hyperostosis in lower jaws, propose to drop the name *Megaceros flabellatus* as to be synonym with *Megaceros pachyosteus*.

We may observe here that this osteological anomaly shown by the genus of *Megaceros* occurs in another group of large-antlered deer too, in the genus of *Orthogonoceros*. There is an agreement of all the authors [cf. Soergel, 1927, Azzaroli, 1953, Kahlke, 1956], that the pachyostosed jaw-bones of the Forest bed-series and different localities of Early Middle-Pleistocene (~Altpleistozän) of Germany are to be referred to the *verticornis*-group.

Recent excavations in Voigtstedt (Germany) [cf. Kahlke, 1956, p. 350] and investigations on materials of Mosbach near Wiesbaden (Germany) have brought some lower jaws of the *verticornis*-group that do not show any pachyostosis in this bone. It is generally accepted that the fauna of Mosbach has to be checked as earlier than the fauna of Süssenborn. The fauna of Voigtstedt, the recently discovered fossil locality of Middle-Germany, is of about the same geological age as Mosbach as shown by the study of elephant-remains* and other members of the fauna. In both localities we may see some early, not pachyostosed types of this genus, and so we have a preliminary time-unit of the development of pachyostosis in *Orthogonoceros* because in Süssenborn we find the remains of the latest type known today of this stock in Middle-Europe.

In Choukoutien, Locality 1, we have a similar time-unit with the exception that the very beginning is not represented by the materials of this area. The jaw-bones of Locality 13 and the lowest layers of Locality I already show a moderate pachyostosis in comparision with the advanced types of the upper levels. Nevertheless the geological section of Locality 1, Choukoutien, shows us a part of the development in this species step by step with numerous materials.

(b) Antlers

Unfortunately, for taxonomy of *Megaceros* we have to use the antlers because in teeth there are usually no distinctions between different species. The antlers on the other hand show a wide range of variation and may have led someone to found a new species on differences due to individual variation or due to progressive "degeneration" as in Choukoutien-deer. It is well known that we have had in Europe a similar development in antlers of *Orthogonoceros* of Early Middle-Pleistocene (~Altpleistozän) and a similar spliting into numerous species.

The antlers of Choukoutien, Locality 1, as described by Young in 1932, in general show an extreme palmation [cf. Young, 1932, pls. XII—XIII]. The antlers of Locality 13 of the same region, as described by Teilhard and Pei in 1941, show the high

*Personal communication by Prof. Dr. W. O. Dietrich, Berlin.

palmated antlers as well, but some specimens do not reach the extreme degree of those of Locality 1 [cf. Young, 1932, pl. XIII]. It is true that we have today only a few antlers of the Choukoutien-area which show enough details to be compared. But even comparing these few antlers we may notice that there are transitions in size and shape.

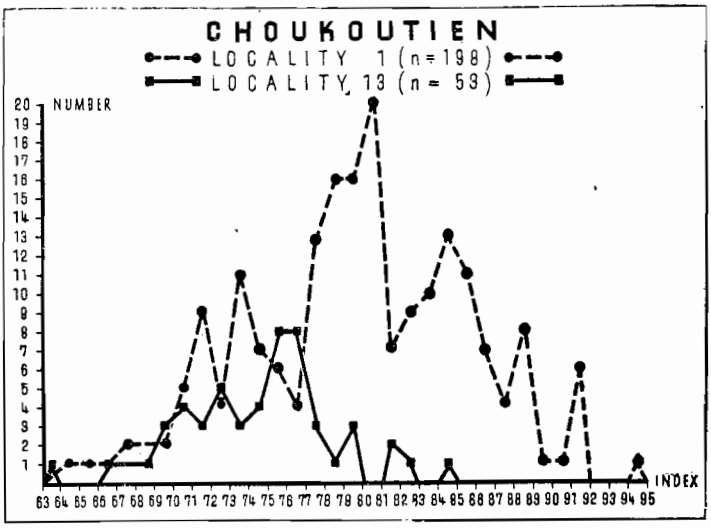

Figure 3 Ratio diagram comparing variation of cross-sections of lower jaw-bones of Localities 1 (n = 198) and 13 (n = 53). Well preserved specimens used only, Young individuals showing milk-dentition not considered.

The brow-tine (first tine) as a whole is not preserved in the specimens of Locality 1 (Choukoutien), but by an antler figured by Young [1932, pl. XIII] it can be deduced that it was reaching a similar expansion and palmation as in the specimens of Locality 13. Comparing the palmation of the distal parts of the antlers of both localities, we see that the specimens figured by Young [1932, pl. XII, fig. 1] and Teilhard and Pei [1941, pl. II, fig. 4; pl. III, figs. 1a—1b; pl. IV, fig. 1; pl. V, figs. 2a—2b] show a more or less palmated blade usually with long tines, while other specimens figured by Young [1932, pl. XII, figs. 2—3; pl. XIII, fig. 1] and Teilhard and Pei [1941, pl. IV, fig. 3; pl. VI, figs. 2a—2b] have an extreme broad palmation in this area and seem to have not developed real tines. That means that, seen as a whole, we have both variants in Locality 1 as well as in Locality 13. The extreme palmated antlers, quite remarkable, recall the type of some extremely palmated, "tine-less" antlers* of the genus of *Orthogonoceros* [cf. Harmer, 1899, Kahlke, 1956].

*The tines have been reduced to a few flat, edgeless lappets or have been vanished.

While comparing the antlers of the Choukoutien-area, we happen to notice two broken antlers not yet published (Locality 1), showing a lappet or bulb on the frontal part of the beam, between brow-tine and main-palmation of the distal antler, just at the same place, other species of *Megaceros* show the "middle-tine" (tine between brow-tine and distal palmation). We know, in general, that the Choukoutien Giant-deer and, quite remarkably the Steinheim-*Megaceros* show no middle-tine.

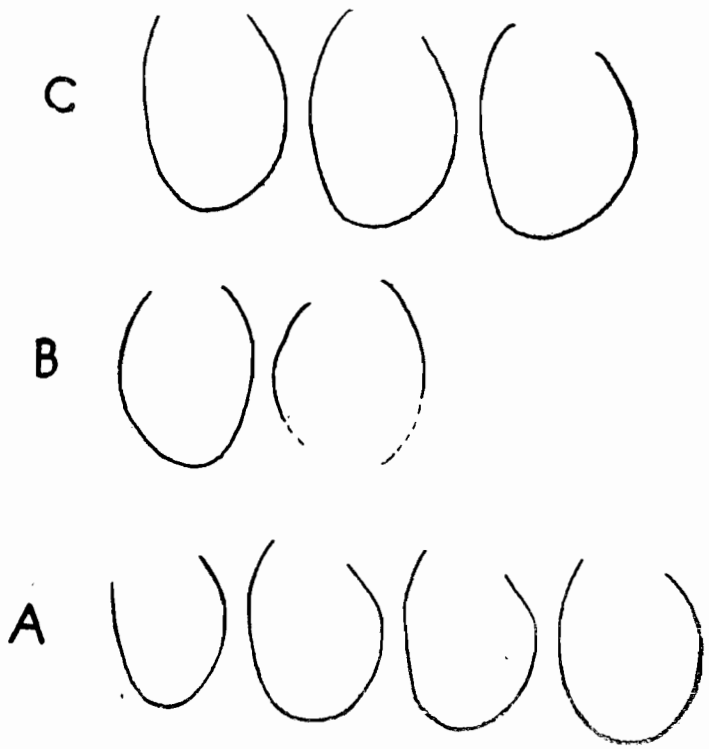

Figure 4 Graphic presentation of cross-sections of lower jaws of European *Megaceros* (1/2 nat. size).

C = Ireland (after Berckhemer, 1941)	Late-Pleistocene
B = Ehringsdorf near Weimar (Germany)	Late-Pleistocene (Riss-Würm-Interglacial)
A = Steinheim/Murr (Germany—after Berckhemer, 1941)	Middle-Pleistocene (Mindel-Riss-Interglacial)

It is not possible to state on the basis of these two antlers of Choukoutien that we can see in the lappet or bulb a rudiment of a former middle-tine that got lost. We would draw attention to the well known sample of reducing a lower tine in *Orthogonoceros* of Forest bed, Mosbach, Süssenborn and other localities, showing a secondary reduced, stout and extremely palmated antler of great variability. In Europe it was demonstrated by numerous materials that in this species the first tine (brow-tine) became

rudimentary and vanished finally in most antlers. But there are rudiments of this tine of different degrees in a few specimens. After accumulating further materials of the Middle-Pleistocene Giant-deer of China a detailed study on this object may be made again.

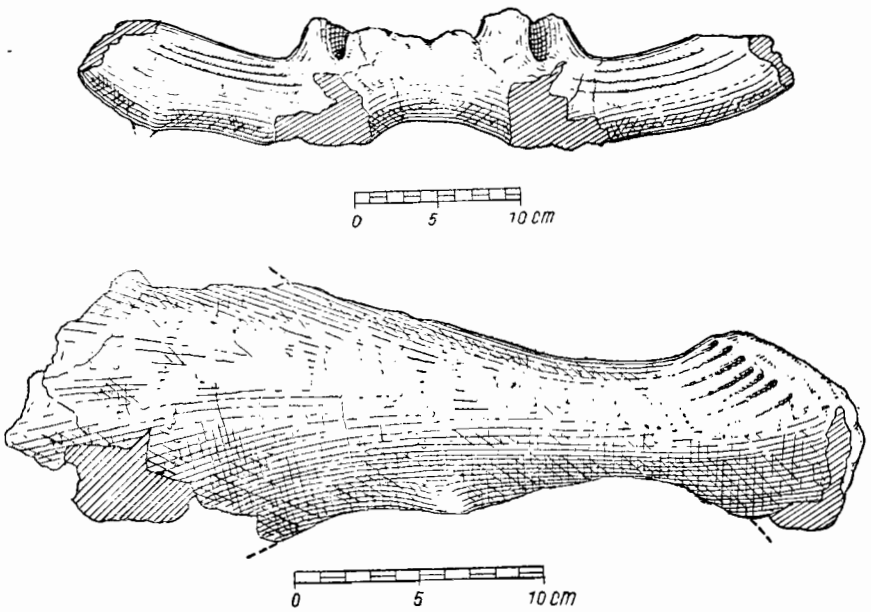

Figure 5 *Megaceros pachyosteus* (Young)
Antlers showing lappet or bulb between first tine (brow-tine) and distal palmation.

Here, the author should not discuss again the supposed causes of increasing of hypertrophy in bones and antlers of *Megaceros* and other cervids [cf. Joleaud, 1930, p. 195, Bachofen-Echt, 1938]. The author's opinion is that the main-facts of morphology are well known but we have to get new details, mainly observations on the time-unit of development. Some new facts, we think, are given by the recent excavations in China (Choukoutien, Locality 1, lower levels) and Germany (Voigtstedt).

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