Nyctereutes sinensis Schlosser (Canidae, Mammalia) from the Pliocene Breccia in Węże (Poland)

Abstract: A skull, mandible, and dentition of Nyctereutes sinensis (Schlosser) from the Pliocene bone breccia at Węże near Działoszyn are described.

INTRODUCTION

Several fragments of bones of Nyctereutes have been found in the bony breccia from Węże near Działoszyn in addition to very many other remains of mammals which have been discussed in numerous papers. Stach (1954) wrote about a fragmentary skull of Nyctereutes, but he failed to determine the species represented by it because of its bad state of preservation. Further preparation of the breccia provided a few more specimens, which have added to our knowledge of Nyctereutes from Węże. It is these remains that constitute the material for the present study.

The Nyctereutes specimens from Węże are in the possession of the Muzeum Ziemi, Polish Academy of Sciences, in Warsaw (collection MZ VIII-Vm-355). For comparison I used 10 skulls of adult N. procyonoides (Gray) from the Białowieża Forest (gathered in 1960—1965). Skulls of the fox and dog were also used for this purpose. In adjusting the measurements and indices to my material I based myself on the paper by Wyrost (1967).
I wish to express my hearty thanks to Prof. Zbigniew Rzyzewicz, of the Palaeozoological Department, University of Wroclaw, for his kind concern in my work and frequent discussions, to Prof. Kazimierz Kowalski, of the Institute of Systematic Zoology, Polish Academy of Sciences, in Kraków for the loan of the skull of *Nyctereutes* described by Stach (1954), and to Docent Zdzisław Pucek, of the Mammals Research Institute, P. A. Sc. at Białowieża for the loan of the skulls of recent *N. procyonoides* (Gray). I am also indebted to Miss L. Łuszczeńska for the care she has taken in preparing the photographs.

**DESCRIPTION OF MATERIAL**

Family *Canidae* Gray, 1821  
Subfamily *Caninae* Gill, 1872  
Genus *Nyctereutes* Temminck, 1839

*Nyctereutes sinensis* (Schlosser)  
(Pl. XXV—XXVIII)

1903 *Vulpes sinensis* Schlosser; M. Schlosser, Die fossilen Säugethiere...  
p. 24, Pl. I, Fig. 6.
1924 *Vulpes sinensis* Schlosser; O. Zdansky, Jungtertiäre Carnivoren...  
p. 15, Pl. II, Figs. 3 and 4.
1927 *Vulpes sinensis* Schlosser; O. Zdansky, Weitere Bemerkungen über fossile Carnivoren aus China, p. 8, Pl. 1, Fig. 8.
1931 *C. (Nyctereutes) sinensis* Schlosser; P. Teilhard de Chardin and C. C. Young, Fossil Mammals from... p. 56.
1934 *Nyctereutes sinensis* (Schlosser); W. G. Pei, Carnivora from... p. 39.
1941 *Nyctereutes sinensis* (Schlosser); Teilhard de Chardin & Pei W. C.,  
The Fossil Mammals..., p. 12.
1942 *Nyctereutes sinensis* (Schlosser); P. Teilhard de Chardin and P. Leroy,  
Chinese Fossil Mammals, p. 41.

Material. Three fragments of skulls and one of mandible; all specimens heavily damaged, the skull MZ VIII-Vm 355/1 of a young animal, with P^4 newly grown and still without molars, showing the best state of preservation.  
The skull (Plates I and II) shows the characters mentioned by Teilhard & Piveteau (1930) as common to *Canis megamastoides* Pomel from the Auvergne Mts., *Vulpes sinensis* Schlosser from China and *C. (Nyctereutes) procyonoides* Temm. from eastern Asia. Therefore, its preorbital region is slightly sunken, the frontal and nasal regions convex (Fig. 1), the sagittal crest is high, the tympanic
bulla large and strongly convex, and the pterygoid process broad and sturdy. 

Viret (1954) draws attention also to the broad palatine of *N. megamastoides* (Pomel), its large postorbital processes and occipital condyles, and small frontal sinus not extending beyond the postorbital processes. These characters can also be demonstrated on the specimens from Węże. Viret thinks that the frontal process of the maxilla of this species does not rise so far to the rear as in foxes. My observations show that modern *N. procyonoides* (Gray) and *V. vulpes* L. do not differ from each other in this respect and the specimens

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**Fig. 1. Outlines of skull profile.**

2. *C. (Nycterutes) sinensis* Schlosser; Teilhard & Piveteau, 1930, Pl. XVII, Fig. 1b.
3. *Nycterutes sinensis* (Schlosser); MZ VIII-Vm 355/1

**Table I**

<table>
<thead>
<tr>
<th>Measurement</th>
<th><em>N. sinensis</em> (Schlosser) MZ VIII-Vm 355/1</th>
<th><em>N. procyonoides</em> (Gray) variation range</th>
<th><em>V. vulpes</em> L. MZUW No. 50</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Basal basion-prostion length</td>
<td>125.6</td>
<td>102.5—118.5</td>
<td>137</td>
</tr>
<tr>
<td>2. Morphological opistion-nasion axis of neurocranium</td>
<td>84.4</td>
<td>69.3—76.5</td>
<td>79.4</td>
</tr>
<tr>
<td>3. Morphological nasion-prostion axis of visceral skull</td>
<td>59.7</td>
<td>49.5—61.8</td>
<td>74</td>
</tr>
<tr>
<td>4. Anatomical opistion-segkorbion axis of neurocranium</td>
<td>70.1</td>
<td>60.3—66.6</td>
<td>65.8</td>
</tr>
<tr>
<td>5. Anatomical segkorbion-prostion axis of visceral skull</td>
<td>75.9</td>
<td>62.5—72.3</td>
<td>87.5</td>
</tr>
<tr>
<td>6. Width at temporal constriction behind postorbital processes</td>
<td>33.7</td>
<td>19—22</td>
<td>21.4</td>
</tr>
<tr>
<td>7. Greatest frontal width between postorbital processes</td>
<td>40.4</td>
<td>29.8—37</td>
<td>35.7</td>
</tr>
</tbody>
</table>

1
from Weże also resemble them (the posterior margin of the frontal process of the maxilla lies above the posterior part of the crown of P⁴). The situation of the maxillary process in these skulls is connected with the size of the facial portion of the lacrimal, which forms only a small part of the edge of the orbit.

The skull of Nycterastes from Weże is larger than that of recent N. procyonoides (GRAY) and somewhat smaller than the skull of the fox (Table I, 1). The skulls of dogs of the same length are regarded as short (Wyrost, 1967). The neurocranium of the specimen discussed is long as compared with the basal length (Tables I, 1 and 2, and II, 1) and broad, the temporal constriction behind the postorbital processes being smaller than that in N. procyonoides (GRAY) and V. vulpes L. (Table I, 6). The length ratio of the neurocranium to the visceral skull in the specimen from Weże resembles that for the skulls of N. procyonoides (GRAY) (Tables I, 2—5 and II, 4 and 5). According to the classification used for dog skulls by Wyrost (1967), the skull of N. sinensis (Schlosser) from Weże is short-faced like hat of N. procyonoides (GRAY), whereas the skull of the fox is long-faced. The upper carnassial, P⁴, in relation to the basal length of the skull, is larger than in N. procyonoides (GRAY) and V. vulpes L. (Table II, 3).

The orifices in the skull of N. sinensis (Schlosser) from Weże are disposed as follows: the foramen palatinit major lies at the level of the posterior part of the crown of the carnassial, the foramen alare anterior close to the posterior margin of the pterygoid, and the orbital fissure further orally, beside it. The foramen tubae auditivae is situated near the postglenoidal process and the foramina lacerum posterior and stylomastoideum behind and at the side of the tympanic bulla. The arrangement of the foramina is similar to that in the fox skull. The large external auditory meatus is sited at the side of the tympanic bulla so that it is not seen from behind the skull.

Mandible (Fig. 2). The only specimen of the mandible from Weże (MZ VIII-Vm 355/3), in which the front part, up to P⁴, and the coronoid process

<table>
<thead>
<tr>
<th>Index</th>
<th>N. sinensis (Schlosser) MZ VIII-Vm 355/1</th>
<th>N. procyonoides (Gray) variation range</th>
<th>V. vulpes L. MZUW No. 50</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Basal length: morphological axis of neurocranium</td>
<td>67</td>
<td>62-3—67</td>
<td>58</td>
</tr>
<tr>
<td>2. Basal length: temporal constriction</td>
<td>26-8</td>
<td>16-2—20-6</td>
<td>15-6</td>
</tr>
<tr>
<td>3. Basal length: P⁴ length</td>
<td>11-1</td>
<td>8-8—10-3</td>
<td>9-8</td>
</tr>
<tr>
<td>4. Morphological axis of neurocranium: morphological axis of visceral skull</td>
<td>70-7</td>
<td>70—84-7</td>
<td>93-2</td>
</tr>
<tr>
<td>5. Anatomical axis of neurocranium: anatomical axis of visceral skull</td>
<td>108-3</td>
<td>100-5—110</td>
<td>133</td>
</tr>
</tbody>
</table>
are broken away, belonged to an adult animal. The horizontal ramus is high and thick (height behind \( P_4 \) — 15 m., width — 9 mm., height behind \( M_3 \) — 21 mm., width — 7 mm.). The ascending ramus, slightly inclined towards the rear, forms an angle of more than 65° with the lower edge of the mandible. The same angle is about 75° in \( N. procyonoides \) (Gray) and 71° in \( V. vulpes \) L. A groove runs along the anterior edge of this ramus and ends near \( M_3 \). The subangular lobe is present but evidently smaller than in \( N. procyonoides \) (Gray),

![Fig. 2. Nyctereutes sinensis (Schlosser); fragment of left mandibular half, MZ VIII-Vm 355/3. × about 1. The broken line is used for the parts which are lacking in the specimen](image)

whereas the angular process is just above the row of cheek teeth and less massive than in \( N. procyonoides \) (Gray). The masseteric fossa is large and deep and situated high above the lower edge of the mandible. The mandibular foramen is displaced farther from the lower edge of the mandible than in the fox, but not so far as in \( N. procyonoides \) (Gray); this foramen is large, like that in the fox.

Dentition (Table III). The teeth of the upper jaw of \( Nyctereutes \) from Węże have been described by Stach (1954). \( P^4 \) of the skull MZ VIII-Vm 355/1 is distinguished by its deuterocone, smaller than in the specimen described by Stach. The upper molars are large and trapezoid in shape; the hypocone occurs even on \( M^2 \). The length index of \( P^4 \) to \( M^1+M^2 \) is 68·5 for the specimen MZ VIII-Vm 335/4, 67·6—85·3 (very variable) for \( N. procyonoides \) (Gray), and 84 for \( V. vulpes \) L. In \( N. megamastoides \) (Pom.) this index also shows great variation (Viret, 1954).

The teeth \( P_4-M_2 \) are preserved on the mandible MZ VIII-Vm 355/3. The protoconid of \( P_4 \) is high and pointed, the hypoconid is lower by half, with a rounded top, and it is displaced near to the protoconid (Fig. 3). The posterior cingulum is pronounced. \( P_4 \) of \( N. procyonoides \) (Gray) is shorter and its cusps are small and low. The lower carnassial, \( M_1 \), has large and stout cusps of the
Table III

Measurements of Lower Teeth of *M. sinensis* (Schlosser)

<table>
<thead>
<tr>
<th>Measurements</th>
<th>Węże MZ VIII-Vm 335/3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length</td>
</tr>
<tr>
<td>P₄</td>
<td>10</td>
</tr>
<tr>
<td>M₁</td>
<td>16</td>
</tr>
<tr>
<td>M₂</td>
<td>9.6</td>
</tr>
<tr>
<td>M₃</td>
<td>6</td>
</tr>
<tr>
<td>M₁—M₃</td>
<td>33</td>
</tr>
</tbody>
</table>

trygonid, but its hypo- and endoconid are small and low (Fig. 4). M₁ of *N. procyonoides* (Gray) is shorter, narrower and lower, but its protoconid is equally massive as in Nyctereutes from Węże (index of M₁ length to height: MZ VIII-Vm

![Fig. 3. Nyctereutes sinensis (Schlosser) MZ VIII-Vm 335/3; lower premolar P₄. × about 3 Labial aspect on the left-hand side, wearing surface on the right](image)

355/3 — 57.5, *N. procyonoides* (Gray) — 49.9 — 62.1, *V. vulpes* L. — 64.9 — 71.4). The posterior portion of the crown of M₂ is damaged, it has three pointed, broad and low cusps preserved. In comparison with M₁ this tooth is large, in height it resembles M₂ in the fox and *N. procyonoides* (Gray), in which it

![Fig. 4. Nyctereutes sinensis (Schlosser), MZ VIII-Vm 335/3; lower carnassial M₁ seen from the labial side. × about 3](image)

is however shorter and narrower. The length ratio of M₁ to M₂ in *Nyctereutes* from Węże is high (60), being lower for the fox and *N. procyonoides* (Gray) (40.6—58.6). The length ratio of M₁—M₃ to M₁ is lower than that in the fox and *N. procyonoides* (Gray), it is, respectively, 48.5 and 54.8 — 67. Both these indices indicate the large size of the molars situated behind the carnassial; in the fox and *N. procyonoides* (Gray) these teeth are remarkably smaller.
REMARKS

Stach (1954) described the occurrence of a member of the genus Nyctereutes in the Pliocene breccia from Węże and substantiated this generic membership by the characters of the cranial fragment with the upper dentition that he used for study (‘the profile of the skull mildly sloping from the frons, its slight concavity in the preorbital region, but, above all, the generally quadrangular shape of the molars and the relation of their size to that of the fourth premolar’ l. c., p. 201). The specimens found later in the breccia from Węże confirm this determination.

Nyctereutes from Węże differs from V. vulpes L. particularly in its long and broad neurocranium, the short facial portion of the skull, the presence of the subangular lobe of the mandible, and the large size of the molars situated behind the carnassials.

It much resembles recent N. procyonoides (Gray) especially in the structure of the skull, but it was larger than this last species, had the subangular lobe of the mandible considerably less pronounced, whereas its molars were relatively larger and more quadrangular.

N. megamastoides (Pomel), occurring in the Pliocene of Western Europe (Viret, 1954), was larger than Nyctereutes from Węże. Moreover, the snout part of the skull MZ VIII-Vm 355/1 is more narrowed (young specimen?), the angle of inclination of the tympanic bulla to the mid-line of the skull is larger (about 55°), the frontal sinus extends beyond the postorbital processes and therefore farther than in the skulls of N. megamastoides (Pomel), the subangular lobe of the mandible is less pronounced and the angular process is situated lower. The length index of P4 to M1+M2 is 68.5 for Nyctereutes from Węże and 74—81 for N. megamastoides (Pomel) from Saint-Vallier.

N. sinensis (Schlosser) from the Pliocene (Teilhard & Young, 1931), Villafranchian (Zdanisky, 1924, 1927; Teilhard & Piveteau, 1930) and Lower Pleistocene (Pei, 1934; Teilhard & Pei, 1941) of China is similar to Nyctereutes from Węże in size (basion-prosthion length of skull: MZ VIII-Vm 355/1 from Węże — 126 mm., N. sinensis (Schlosser) from Nihowan — 128 and 130 mm.; width between postorbital processes, respectively, 40.4 and 44 mm.). Nyctereutes from Węże shows also far-reaching similarities to N. sinensis (Schlosser) in the structure of the skull and teeth, whereas the differences concern the shape of the ascending ramus of the mandible, whose anterior edge is evidently slanting in the specimen MZ VIII-Vm 355/3 from Węże, in which it is also higher and has a less pronounced subangular lobe; its M1 lacks a small enamel ridge between the hypoconid and the postero-external edge of the crown. The great variation in the characters of N. sinensis (Schlosser) allows the supposition that the above-mentioned differences do not go beyond the range of variation of this species.

Bate (1937) described the remains of Vulpes vinetorum from Tabun Cave in Palestine. They were jaws with teeth. Kurten (1965) referred these remains
to the genus *Nycteretes*. I have some doubts whether his arguments are fully convincing. Both the species of *Nycteretes* and those of *Vulpes* show great variation in the structure of their teeth and mandible and, therefore, the arguments given by Kurten (size, structure of M') are not sufficient to justify the change of the genus. In addition, the remains of *V. vinetorum* Bate were found in Layer C of Tabun Cave, beside a large number of bones of hoofed animals (e.g., *Bos*, 28%; *Gazella* was also present), which indicate conditions corresponding to dry grassland. In such areas one may rather come across a fox, such as modern *V. v. flavescens* Gray, *V. v. palestina* Thomas, or any others. Besides, both the modern and fossil *Nycteretes* species belong to the forest mammals and so we should not expect to find their remains in the above-mentioned association (*Gazella*); it is for this reason that Bate's (1937) determination should be maintained.

According to Stroganov (1962), today *N. procyonoides* (Gray) inhabits mixed or deciduous forests or brushwoods near rivers, brooks, stagnant waters or lakes. Rocky debris is its characteristic habitat. It lives on small hills, slopes, in rock crevices, among stones, etc. Its diet includes aquatic and semi-aquatic animals, such as fish, mollusks and frogs, all the year round, and it is particularly diversified in summer. The occurrence of *Nycteretes* in the Upper Pliocene breccia from Weże permits some conclusions concerning the landscape surrounding the cave. It must have been a stony area covered by a mixed forest with the predominance of deciduous trees. There was certainly some water (river?) in the neighbourhood and wood clearings or flood meadows were common. These remarks agree with the description of the environment presented in my papers on the deers from Weże (Czyżewska, 1959, 1960, 1968).

On the basis of the dentition the individual age of the specimen represented by the skull MZ VIII-Vm 355/1 was determined to be 5—6 months of life. In *N. procyonoides* (Gray) the specimens of this age occur late in the summer or early in the autumn. Young raccoon-dogs keep together near the nest and form a group, which suggests that *Nycteretes* nested somewhere near the cave at Weże. The bones of *Nycteretes* found in the breccia examined belonged presumably to specimens that got into the cave incidentally.

The Pliocene species of *Nycteretes* differ from modern *N. procyonoides* (Gray) in the fact that their molars are larger than the carnassials. *N. procyonoides* (Gray) is an omnivorous animal, though animal food predominates in its diet (especially in summer), and its molars are relatively small. The Pliocene species, with remarkably larger molars, were probably more phytotrophous. A distinctive character of *Nycteretes* is the strong development of the digastric muscle, which is connected with the occurrence of the subangular lobe. This is an adaptation for the wide gape of the jaws, which is to assist in the work of the carnassials while biting food into pieces, particularly useful on account of the relatively short facial portion of the skull. A very pronounced subangular lobe occurs in *N. procyonoides* (Gray) and *N. megamastoides* (Pomel), and it is smaller in *N. sinensis* (Schlosser). Judging
by the strong and large teeth and the high and thick mandible, the food of the Pliocene Nyctereutes may have been much harder than that of the modern species, whose teeth are small and the mandible thin and delicate.

The locality of Węże lies in the western part of the range of Nyctereutes in Eurasia. Keeping in mind the characters of the structure of the skull, mandible and dentition, I think that such forms of the genus Nyctereutes as have been found at Węże (small subangular lobe and other characters) may have given rise to big and more phytophagous N. megamastoides (Pomel) from the end of the West European Pliocene, on the one hand, and, on the other hand, to N. sinensis (Schlosser) from East Asia. Contemporary N. procyonoides (Gray) has, in all probability, evolved from the Early Pliocene members of this very species.

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REFERENCES


STRESZCZENIE

Autorka opracowała szczątki jenota pochodzące z plioceńskiej brekcji kostnej z Wężów koło Działoszyna zaliczając go do gatunku *Nyctereutes sinensis* (Schlosser), znanego z pliocenu i dolnego pleistocenu Azji Wschodniej. Autorka nie zgadza się z poglądem Kurtena (1965), który do rodzaju *Nyctereutes* włącza gatunek *Vulpes vinetorum* Bate z jaskini Tabun w Palestynie. W pracy tej zamieszczono również uwagi paleoekologiczne i filogenetyczne.

РЕЗЮМЕ

Автор обработала остатки скелета енотовидной собаки из плиоценской костной брекции из деревни Венже в окрестности Дзиалошына. Этот экземпляр она квалифицировала к виду *Nyctereutes sinensis* (Schlosser), который известный из плиоцена и нижнего плейстоцена Восточной Азии. Автор пререкается взгляду Куртена (1965), который включает к роду *Nyctereutes* вид *Vulpes vinetorum* Bate из пещеры Табун в Палестыне. Работа содержит тоже палеоэкологические и филогенетические замечания.
PLATES
Plate XXV

_Nyctereutes sinensis_ (Schlosser), MZ VIII-Vm 355/1; skull seen from above. × 1
T. Czyżewska
Plate XXVI

*Nycterereutes sinensis* (Schlosser), MZ VIII-Vm 355/1; a ventral view of the skull. × 1
Plate XXVII

*Nyctereutes sinensis* (Schlosser), MZ VIII-Vm 355/1; skull seen from the left side. × 1
Plate XXVIII

*Nyctereutes sinensis* (Schlosser)
1. MZ VIII-Vm 355/1; skull seen from the side of the occiput. × 1.
2. MZ VIII-Vm 355/3; teeth P₄—M₂. × 2.
3. MZ VIII-Vm 355/3; fragment of left mandibular half seen from the labial side. × 1.
4. MZ VIII-Vm 355/3; fragment of left mandibular half seen from the lingual side. × 1.
Redaktor zeszytu: Prof. dr Kazimierz Kowalski