

**THE GENUS *CHASMAPORTHETES* HAY, 1921 FROM
THE PLIOCENE OF RUSSIA, UKRAINE, MONGOLIA
AND TADZHIKISTAN**

by

Marina V. SOTNIKOVA

(Geological Institute, Russian Academy of Sciences, Moscow)

Published in

**Tatarinov L.P. (ed.), *Palaeotheriology*. Nauka, Moscow,
pp. 113–139 (1994). [In Russian]**

Translated by

Dmitry V. IVANOFF

*(National Museum of Natural History,
National Academy of Sciences of Ukraine, Kiev)*

2003

[INTRODUCTION]

The members of the family Hyaenidae were widely distributed over Palaeartic in Pliocene, but only the genus *Chasmaporthetes* Hay penetrated to Nearctic. This genus was first described in America, from the late-Pliocene deposits of Arizona (Hay, 1921). Subsequently, similar hyenas from North America, Europe, Asia and Africa were described under the different generic names.

Paucity and scatteration of the collections, and the long lack of finds of the associated lower and upper toothrows, resulted in much confusion and misconceptions in the diagnostics of these hyenas at the species- and even genus-levels. Only recently, nearly all the finds known to that date (Kurtén & Werdelin, 1988) from the Old and New Worlds have been revised to form a reasonably complete notion of the genus *Chasmaporthetes*.

The mentioned revision did not include, however, the fairly rich material from E. Licent's collection, collected in Nihewan and Yushe (China) in 1934–1937 and examined by Prof. Qiu Zhan-Xiang (1987). Some additional finds not received coverage are those from the localities Odessa Catacombs, Beregovaya, Kuruksay and Shamar, stored at the collections of Geological and Palaeontological Institutes, Russian Academy of Sciences, and of Odessa State University. They have not been previously described in detail, except for the material from Kuruksay (Sharapov, 1986; Sotnikova, 1989).

The genus *Euryboas* (= *Chasmaporthetes*) was first recorded in Asia by Sotnikova (1974, 1976) in the localities Shamar (Mongolia), Beregovaya (Russia, Transbaikalia) and Kuruksay (Tadzhikistan). In addition, when examining the carnivoran collection from Odessa Catacombs, two fragmentary mandibles, a cranial fragment and isolated teeth were identified by the author to belong to *Chasmaporthetes*. (The genus has not been formerly reported to be in the fauna of Odessa Catacombs.) These materials expand the current knowledge of geographical and stratigraphical distribution of the genus, and allow tracing some evolutionary alterations in this lineage of hyenas during Pliocene, as well as refining the diagnosis and solving several disputable points of specific and sub-specific taxonomy of the genus *Chasmaporthetes*.

Faunae from the cites Kuruksay, Beregovaya, Shamar and Odessa Catacombs are well known, some of their taxa have been detailed in literature. On the strength of geological, palaeomagnetic and palaeontological data the age of faunal assemblages of Shamar and Beregovaya was estimated as the late Pliocene (early Villafranchian, MN16), that of Kuruksay as late Pliocene (middle Villafranchian, MN17), and Odessa Catacombs as late Pliocene (the very beginning of Villafranchian, commencement of MN16a) (Sotnikova, 1980, 1989, Vislobokova *et al.*, 1993). The present paper is based on the *Chasmaporthetes* material from these four localities.

I am grateful to I.A. Odintzov and K.K. Pronin of Odessa State University for allowing me to study thehyaenid material from Odessa Catacombs. I thank J. Agustí and S. Moyà-Solà for their courtesy in organizing my visit to Instituto provincial de Paleontologia (Sabadell, Spain) to examine the collection from Layna. I am much obliged to Qiu Zhan-Xiang, Head of the Institute of Vertebrate Palaeontology and Palaeoanthropology (Beijing), for discussions of some questions concerning the *Chasmaporthetes* material from China. The figures were prepared by V.D. Kalganov and K.P. Firsova.

The study was supported by G. Soros Stipend and Russian Academy of Sciences.

The abbreviations used in the paper are as follows: PIN — Palaeontological Institute, Russian Academy of Sciences; GIN — Geological Institute, Russian Academy of Sciences; OGU — Metchnikoff State University (Odessa, Ukraine).

TAXONOMICAL HISTORY OF THE GENUS *CHASMAPORTHETES* HAY

The genus *Chasmaporthetes* was erected by Hay (1921) on the basis of a fragmentary edentulous mandible derived from the locality Cal Verde Mine (Arizona, North America). The second find, a toothed mandible, described from the locality Cita Canyon in Texas as belonging to a new genus *Ailuraena* Stirton *et* Christian, was subsequently synonymized with *Chasmaporthetes* by the same authors (Stirton & Christian, 1940, 1941).

Repenning (1967) was the first to suggest that the genus *Euryboas* Schaub, 1941 well known from the Pliocene of Eurasia and Africa is a junior synonym of the genus *Chasmaporthetes* Hay, 1921. This notion was supported by other workers (Savage & Curtis, 1970; Kurtén, 1971). However, a priority of the genus *Chasmaporthetes* was only established in 1977, when describing the material from Puebla de Valverde (Kurtén & Crusafont Pairó, 1977).

The genus *Euryboas* Schaub (type species is *E. bielawskyi* Schaub) was established on the basis of a mandible with teeth from the locality Roccaneyra in France (Schaub, 1941). Schaub also assigned to the same species a maxillary fragment with P3–4 from the locality Upper Valdarno in Italy and several postcranial remains from other Villafranchian sites in Western Europe. Schaub noted the similarity of the lower teeth of *Euryboas* to those of *Chasmaporthetes* from America. He did not, however, infer close relationships between these hyaenids because of lack of the cranial material in collections. He also compared the maxilla of *E. bielawskyi* from Valdarno with a skull from the locality Olivola (Italy), described previously by Del Campana (1914) as *Lycyaena lunensis*. Schaub noted that P4 in *L. lunensis* differs from that of *E. bielawskyi* in its larger parastyle and more shifted posteriorly protocone. He also reported of longer and more slender premolars in the species established by Del Campana.

Viret (1954) studied a series of hyaenid remains from several localities of European Villafranchian, similar to *L. lunensis* and *E. bielawskyi*, and arrived to a conclusion that they all comprise a fairly uniform group. Their differences stressed by earlier students were considered by Viret to be merely individual variation and sexual dimorphism within a single species. He convincingly demonstrated that all the dental characteristics of the type specimen of '*Lycyaena*' *lunensis* from Olivola and of the type species *Euryboas bielawskyi* from Roccaneyra are extreme morphotypes in the same species, and there is a series of remains from other localities, in which all the transitional (from '*L.*' *lunensis* to *E. bielawskyi*) characteristics in the upper dentition are expressed. Viret noted the absence of P1 on the skull of hyena from Saint-Vallier, while the specimens from Olivola and Senèze had distinct alveoli of P1. He did not consider this character as variable. Instead, he suggested that the P1 alveoli on the Saint-Vallier skull had been just obliterated during the animal's lifetime, which is not uncommon in carnivorans. From these considerations, Viret (1954) assigned the hyenas in question to a single genus and species, *Euryboas lunensis* (Del Campana).

The Viret's point of view was subsequently supported by Italian researchers. In revising old collections, a large carnivoran's mandible found by Forsyth Major in Olivola and initially determined as *Felis arvernensis* was later referred to *Euryboas lunensis* (Ficcarelli & Torre, 1967). It was Olivola that yielded a cranial specimen served as a holotype of *Euryboas lunensis* (= *Lycyaena lunensis* Del Campana). A suggestion was made that both this skull and the above-mentioned mandible belonged to the same individual. At the same time, it was found that this mandible does not differ from that of *E. bielawskyi* Schaub, a type species of *Euryboas*, from Roccaneyra. Hence the identity of *E. lunensis* and *E. bielawskyi*, the species whose original descriptions had been based on different fragments (a skull and a lower jaw), was deduced from the Olivola material.

Subsequent research considerably broadened the knowledge of geographical and stratigraphical distribution of this hyaenid group. *Hyaena borissiaki* Khomenko whose complete skeleton from the locality Dermedzhi (Moldova)¹ had been comprehensively described by Khomenko (1931) was assigned by Beaumont (1967) to the genus *Euryboas*.

The remains of these hyenas from Africa were first described by Ewer (1955) as *Lycyaena nitidula* from the locality Sterkfontein. Later, all the African finds from the Pliocene sites Sterkfontein, Swartkrans, Langebaanweg and from Omo River basin were attributed to the genus *Euryboas*.

A cranial fragment of *Euryboas lunensis* was described from the Middle East locality Gülyazi (Turkey) by Schütt (1971). The finds of similar hyenas from Mongolia, Tadzhikistan and Transbaikalia (Russia) were also assigned to the genus *Euryboas* (Sotnikova, 1974, 1976).

As already noted above, the synonymy of the genera *Chasmaporthetes* and *Euryboas* gained eventual acceptance. In 1977 a hyaenid from Puebla de Valverde (Spain) became the first European form described as *Chasmaporthetes lunensis* (Kurtén & Crusafont Pairó, 1977). In the same year, however, the American investigators Galiano and Frailey established a new species *Chasmaporthetes kani* Galiano et Frailey on the Frick Collection material presumably from the Villafranchian deposits of China. The authors undertook a cladistic analysis of all the finds of this hyaenid group and suggested considering both *Chasmaporthetes* and *Euryboas* as valid genera (Galiano & Frailey, 1977). The following composition of the genus *Chasmaporthetes* was proposed: *C. ossifragus* and *C. johnstoni* from America, *C. kani* from China, *C. nitidula* from Africa, *C. borissiaki* from Moldova, and *C. lunensis* to which a cranial fragment from Senèze and the holotype (a fragmentary maxilla from Olivola) were attributed. A mandible described from Olivola (Ficcarelli & Torre, 1967), which is most likely to be associated with a holotype, was not taken into account. The genus *Euryboas* (with the only species *E. bielawskyi*) was suggested to include, in addition to the type specimen from Roccaneyra and a cranial fragment from Valdarno, nearly all the remains from the localities Saint-Vallier and Etouaires.

When describing a new material of *Chasmaporthetes ossifragus* from the late-Blancan and early-Irvingtonian deposits of Florida (USA), Berta (1981) followed

¹ According to Khomenko, the remains of *C. borissiaki* derive from the deposits of 'Roussillon' age. In the modern view, however, there are only late-Ruscinian strata in the area of Dermedzhi Village, lying with erosion on Pontian sands. *C. borissiaki* is morphologically most primitive species among the hyenas of this group and differs considerably from both the Villafranchian and late-Ruscinian *Chasmaporthetes*. It cannot be ruled out, therefore, that the find described by Khomenko was probably yielded by lower horizons of the section, dated as late-Miocene (Pontian).

Galiano and Frailey in recognizing the validity of the genus and species *E. bielawskyi*.

The numerous material of the genus *Chasmaporthetes* from Yushe Province (China) of E. Licent's collection was described by Qiu (1987). He was the first to examine the occipital region of the skull in *Chasmaporthetes*. Qiu demonstrated the similarity of these hyenas with the genus *Thalassictis*, and included the cranial characters into the emended diagnosis of *Chasmaporthetes*. In addition, he found that the shape of the angular process of the mandible in *Chasmaporthetes* is a character taxonomically useful at the genus level. It is traceable in the type specimen from America (edentulous mandible from Arizona) and in other hyenas of this group from Asia, Europe and Africa (Qiu, 1987, fig. 5). On the basis of both his own and already known European material, Qiu demonstrated that the studied hyenas should not be separated into two genera. He stated that virtually all the characters used by Galiano and Frailey to distinguish between *Chasmaporthetes* and *Euryboas* are taxonomically not reliable at any rank, be it generic or specific. However, Qiu accepted as valid the species *C. kani* established by Galiano and Frailey, and assigned to it practically all the finds of *Chasmaporthetes* from the Pliocene to early-Pleistocene deposits of China.

In 1988 Kurtén and Werdelin generalized all the *Chasmaporthetes* material known to that date, except for the data published by Qiu and some materials of the collections being described in the present paper. Kurtén and Werdelin reviewed in detail, and revised in some cases, Eurasian and North American finds. They offered the most complete data on the *Chasmaporthetes* morphology and summarized the taxonomy of this poorly known hyaenid group (Kurtén & Werdelin, 1988).

Galiano and Frailey used the following six characters of the genus level to distinguish between *Euryboas* and *Chasmaporthetes*: (1) length of the facial region of the skull, (2) presence of P1, (3) shape of the dental rows, (4) size of the anterior cusps on p2–4, (5) size of P4 parastyle, (6) position of P4 protocone (Galiano & Frailey, 1977, p. 10).

Kurtén and Werdelin's thorough morphometric analysis showed that the P1 presence/absence in *Chasmaporthetes* is a character depending on the individual age. The muzzle length in the finds referred to the genera *Euryboas* and *Chasmaporthetes* is nearly the same, and the coefficient of variation for this variate is normal not only within the genus, but also within the species. According to Kurtén and Werdelin's data, the degree to which the dental rows are curved, as well as the relative position of p4 and m1 ('imbrication of teeth'), are rather varying in hyenas. The examination of the material from Kuruksay (Sotnikova, 1989) clearly demonstrated that this trait varies even within a single population of *Chasmaporthetes* (fig. 1). The fourth character, the size of the premolar anterior cusps, is also fairly variable. This was noted by Kurtén and Werdelin, and is clearly exhibited by the series of remains under description in the present paper. The parastyle size and the protocone position are not constant in hyaenids, as exemplified by *Thalassictis (Lycyaena) dubia*, *Ictitherium viverrinum* and some specimens assigned to *Euryboas* and *Chasmaporthetes* (Kurtén & Werdelin, 1988). Similarly, the variation in this character is evident in the examined material from Mongolia and Ukraine. Thus, the analysis of how the characters used by Galiano and Frailey are distributed across the material suggests that the separation of these hyenas into two genera is 'artificial' and cannot be adopted any longer.

In the present paper I follow Kurtén and Werdelin in considering the genus *Euryboas* Schaub as a synonym of the genus *Chasmaporthetes* Hay and recognize the content of the latter as follows: *C. borissiaki* (Khomenko), *C. lunensis* (Del Campana), *C. nitidula* (Ewer), *C. ossifragus* Hay and *C. exitelus* Kurtén et Werdelin.

SYSTEMATIC DESCRIPTION

FAMILY HYAENIAE GRAY, 1869

SUBFAMILY HYAENINAE MIVART, 1882

Genus *Chasmaporthetes* Hay, 1921

Chasmaporthetes: Hay, 1921

Ailuraena: Stirton & Christian, 1940

Euryboas: Schaub, 1941

Type species. *Chasmaporthetes ossifragus* Hay, 1921, late Pliocene (late Blancan), North America, Arizona.

Diagnosis. Medium-sized hyaenid. Limb bones are slender and gracile. Skull is basically constructed as that of *Thalassictis*. Basisphenoid lacks sagittal sulcus. Septum of auditory bulla is strongly shifted upwards, so that the upper chamber considerably decreases in size. Infraorbital foramen is under P4 anterior root. Nasal is broad, its posterior edge is blunt. Angular process of mandible is large, often forked. Mental foramen is invariably single. Dental rows are straightened and virtually lack any curvature at the level of carnassials. Dental formula is as follows: I3 i3, C1 c1, P1–4 p2–4, M1 m1. In most cases, p1 is lacking and P1 is present. Premolars are slender, with well-developed posterior accessory cusps and variable anterior ones. Protocone on P4 is strong, metastyle is elongated. Anterior and posterior accessory cusps on p4 are always well developed. The m1 lacks metaconid and has one large cusp (hypoconid) on its talonid. In early members of the genus, talonid possesses also entoconid and occasionally entoconulid. Hypoconid is centrally positioned on m1 talonid, being a laterally compressed blade-shaped cusp rounded in lateral view. Protoconid crest is coaxial with hypoconid blade. Deciduous dp4 bears no trace of metaconid and has two distinct cusps on its talonid. External cusp occupies the centre of talonid, its crest is connected with posterior crest of protoconid.

Included species. *Chasmaporthetes borissiaki* (Khomenko), presumably upper Miocene (Pontian), Moldova; *Chasmaporthetes exitelus* Kurtén et Werdelin, upper Miocene (Turolian), China; *Chasmaporthetes lunensis* (Del Campana), Pliocene – early Pleistocene (Ruscinian–Villafranchian), Eurasia; *Chasmaporthetes ossifragus* Hay, late Pliocene – early Pleistocene (late Blancan – early Irvingtonian), North America, *Chasmaporthetes nitidula* (Ewer), late Pliocene – Early Pleistocene, Africa.

Comparison. The genus differs from other hyaenids by its slender premolars with large, well-developed accessory cusps, and by the shape and position of the hypoconid on the m1 talonid.

Remarks. The revised diagnoses of the genus *Chasmaporthetes* have been given by Qiu (1987) and Kurtén and Werdelin (1988). These diagnoses complement each other, as the former is based on the examination of the cranial material and the latter stems from the sophisticated treatment of dental characteristics.

However, they are in marked disagreement when describing the lower carnassial, one of the pivotal points underlying the systematics of *Chasmaporthetes*:

<u>Qiu, 1987:</u>	<u>Kurtén & Werdelin, 1988:</u>
Metaconid on m1 is lacking or reduced	Metaconid is lacking
Talonid on m1 is uni- or bicuspid	Talonid is unicuspid

No described form of the genus *Chasmaporthetes* has been reported to have the metaconid on its m1, except for the holotype of *C. borissiaki* in which Khomenko (1931) pointed out the presence of a rudimentary metaconid cusp. However, when re-examining the *C. borissiaki* holotype, I found merely a small fold of enamel, presumably having nothing in common with the metaconid. A similar fold is also observed in the specimen IPLA-147 from the locality Layna and in one of three specimens of *Chasmaporthetes* from Shamar (PIN 3381-203). It is this fold that was evidently considered a rudimentary metaconid by Khomenko. Judging from the morphology of dp4 without any trace of a metaconid, however, it can be supposed that the metaconid was absent even at the earliest stages of *Chasmaporthetes* evolution.

Qiu (1987) was the first to pay attention to the presence of accessory cusps (entoconid and entoconulid) on the m1 talonid in *Chasmaporthetes* from China. By now, the similar talonid pattern was revealed in *Chasmaporthetes* from Layna, in all the specimens from Odessa Catacombs, and in *Chasmaporthetes* sp. from Africa (Langebaanweg). This obviously indicates to the constancy of this character.

For these reasons, the statement that a rudimentary metaconid is present on m1 should be excluded from the diagnosis. Instead, it must be emphasized that besides the hypoconid, the m1 talonid can bear additional elements, namely the entoconid and entoconulid.

Distribution. Late Miocene (Turolian), Pliocene – early Pleistocene (Ruscinian–Villafranchian) of Eurasia, late Pliocene – early Pleistocene (late Blancan – early Irvingtonian) of North America, late Miocene or early Pliocene (Langebaanweg) and late Pliocene – early Pleistocene of Africa.

***Chasmaporthetes lunensis* (Del Campana, 1914)**

Holotype. IGF 4377, skull from Olivola (Italy), late Villafranchian (early Pleistocene).

Diagnosis. Relatively large-sized species. Facial portion of skull is broad, p1 is lacking, anterior cusps on P2-3 and p2-3 are small or occasionally absent.

Included subspecies. It is possible to recognize three subspecies: *Chasmaporthetes lunensis lunensis* with a relatively long p4 and unicuspid m1 talonid; *Chasmaporthetes lunensis odessanus* ssp. nov. with a p4 being relatively long and m1 talonid having accessory cusps; *Chasmaporthetes lunensis kani* with a shorter p4 than in the nominotypical subspecies.

Comparison. Differs from *C. borissiaki* by its larger size, absence of p1 and proportionally broader P4 and m1. Differs from *C. nitidula* in its smaller anterior cusps on P2-3 and p2-3. Differs from *C. ossifragus* in its less massive cusps on P2-3 and p2-3.

Remarks. As already discussed above, the synonymy of the species *C. lunensis* and *C. bielawskyi* was established owing to the revision of old collections from the type locality Olivola (Ficarelli & Torre, 1967). Using the Frick Collection materials from China, Galiano and Frailey (1977) described a new species

C. kani. They proposed to consider both European species as valid and belonging to different genera: *Euryboas bielawskyi* and *Chasmaporthetes lunensis* (Galiano & Frailey, 1977). In his review of the Ruscinian and Villafranchian hyaenids, Qiu (1987) followed Galiano and Frailey in their recognition of all these three species, within a single genus *Chasmaporthetes* however. He assigned to *C. bielawskyi*, in addition to the holotype from Roccaneyra, the hyenas of this group from the localities Puebla de Valverde and Saint-Vallier (QSV-53), and to *C. lunensis* (besides the holotype from Olivola) the *Chasmaporthetes* remains from Schernfeld and Saint-Vallier (QSV-52). The distinction between these species was made on the following basis: *C. lunensis* is larger-sized, its P3 and p4 are relatively longer, P4 and m1 are not greatly enlarged, the nasal is narrower than in *C. bielawskyi*.

When revising the genus, Kurtén and Werdelin (1988) undertook a comprehensive morphometric analysis of the dentition in Eurasian *Chasmaporthetes*. It was shown on a series of bivariate diagrams that the dental characters in these hyenas have the coefficient of variation lying within the range given by G.G. Simpson for a single population. Hence the conclusion was drawn that there is no evidence for considering these Pliocene–Pleistocene hyenas to be a heterogeneous group. Apparently all the distinctions observed on the material are taxonomically of subspecific rank. It was proposed to regard the species *C. bielawskyi* and *C. kani* as junior synonyms for *C. lunensis* (Kurtén & Werdelin, 1988, pp. 53–55, figs 3–7).

Returning to the characters adduced by Qiu to differentiate between the European species, it may be only remarked that they all were inspected in the insufficiently sampled material, and so their use for these hyenas' diagnostics is difficult. What really catches one's attention is a large size of the *C. lunensis* holotype that was described from the late-Villafranchian deposits. As can be readily observed, all late members of *Chasmaporthetes* — both Chinese and American — are larger than the early ones, such as the Ruscinian forms of Eurasia. At the same time, how strong is a tendency of *Chasmaporthetes* to increase in size is yet to be demonstrated. For example, in the middle Villafranchian of Europe there were forms both very large (e.g. a specimen from Saint-Vallier) and perhaps the smallest among the whole sample of Villafranchian *Chasmaporthetes* (a specimen from Puebla de Valverde). Therefore, at the current stage of studying these hyenas it is probably worth relying rather upon the evidence from dental morphometrics, as proposed by Kurtén and Werdelin.

Distribution. Pliocene – early Pleistocene (Ruscinian–Villafranchian) of Eurasia.

***Chasmaporthetes lunensis lunensis* (Del Campana, 1914)**

Figs 2–5

- Lycyaena lunensis*: Del Campana, 1914, Pl. 1, fig. 2
Euryboas bielawskyi: Schaub, 1941, Pl. 18, figs 1–4, Pl. 19–20, figs 1–3
Hyaena marini: Villalta, 1952, Pl. 8, fig. 1, Pl. 10, figs 1–2
Euryboas lunensis: Viret, 1954, Pl. 8, figs 3–6, Pl. 9, fig. 1; Ficcarelli & Torre, 1967, p. 195; Schütt, 1971, S. 139, Taf. 19
Chasmaporthetes lunensis: Kurtén & Crusafont Pairó, 1977, p. 20
Chasmaporthetes lunensis lunensis: Kurtén & Werdelin, 1988, p. 48 (Part.)
Chasmaporthetes lunensis honanensis: Kurtén & Werdelin, 1988, p. 49 (Part.)
Chasmaporthetes kani progressus: Qiu, 1987, Taf. 3, Fig. 2–3, Tab. III–IV

Holotype. See the species description.

Diagnosis. The p4 is long relative to m1. Talonid of m1 has the only cusp, a large and blade-shaped hypoconid.

Material. Two cranial fragments with complete toothrows (PIN 3381-1, PIN 3381-324), two maxillary fragments with C–P3 (PIN 3381-204, PIN 3381-205), a fragmentary P4 (PIN 3381-206), three mandibular fragments (PIN 3381-2, PIN 3381-325, PIN 3381-203), a cranial fragment with deciduous dP2–4 (PIN 3381-202), a mandibular fragment with deciduous dp4 and permanent p4–m1 (PIN 3381-320), two upper canines (GIN 970-12, GIN 970-13), a fragmentary incisor with I1–3 (GIN 970-14), a p4 (GIN 970-15). Right and left mandibular rami without the angular and coronoid processes (PIN 2975-19).

Locality. Shamar (Mongolia): collections PIN 3381 and GIN 970. Beregovaya (Transbaikalia, Russia): collection PIN 2975.

Description. The facial portion of the skull is relatively broad. Width at canines is 59.5 mm (PIN 3381-1) and 56.0 mm (PIN 3381-324). Width of skull at the upper carnassial level is 90.0 mm (PIN 3381-1) and 88.5 mm (PIN 3381-324). There is a characteristic concavity situated between the roots of P4. The infraorbital foramen is very large and strongly shifted posteriorly to be positioned under the P4 anterior root. The row of incisors is slightly arched. The diastema between I3 and C is 4.2 to 4.5 mm. The incisors are middle-sized, sharp and trenchant. The I3 greatly exceeds in size the I1 and I2.

The upper canines are relatively slender, slightly compressed laterally, and have a smooth surface devoid of any crests, notches or rugosities. The cheek teeth are arranged in line, the anterior premolars are coaxial with P4. The diastema between the canine and P1 is virtually lacking.

P1 is a one-rooted, unicuspid, and relatively large tooth. It is present on all three specimens from Shamar. P2 and P3 are tall, relatively slender, with strong and clearly separated posterior cusps. The anterior portion of these teeth is narrow, their crown broadens distinctly at the level of the anteriormost part of the second (posterior) root. The anterior cusp on P2 is very weak or absent. The only unworn P3 from Shamar, PIN 3381-204, possesses very weak anterior cusp on the lingual side of the crown. P4 is long, its metastyle is low, well separated from the paracone and rather resembles in shape a posterior blade of the felid P4. The preparastyle is lacking, the anterior edge of the parastyle is delineated by two distinct crests ascending its tip from two sides. The protocone is large and massive. Its forward edge is either anterior to, or not reaching, the forward edge of the parastyle.

M1 is middle-sized and three-rooted (Tables 1,2).

The angular process of the mandible is massive and low-mounted, it goes only slightly beyond the level of the condyloid process. The mandibular depth at the coronoid process is 76.0 mm (PIN 3381-203). The mandibular length from the incisor row to the condyloid process is 189 mm (PIN 2975-19). The masseteric fossa is wide and deep, its anterior border extends to the level of the m1 posterior root. The mandible is deep at symphysis. The only mental foramen is large and situated under the anterior root of p3, closer to the ventral edge of the mandible than to the dorsal.

The incisors are tightly appressed to the canine. The latter is tall and relatively slender. The diastema between the canine and p2 is 7 to 11 mm. No specimen bears a trace of p1. The p2 is mostly tricuspid, but the degree to which the anterior cusp is developed varies between the specimens. The p3 is quite large, tri-

cuspid, its anterior cusp is small, the posterior one is well separated. The basal cingulum is well developed in the posterior part of the crown.

The p4 is large, with three distinct cusps. The anterior and posterior cusps are well separated from the principal one. The tooth somewhat resembles in appearance the p4 of large cats of the genus *Panthera*. The basal cingulum is strong. It is traceable even along the external edge of the crown in the specimens from Transbaikalia and Mongolia. In all the specimens, the basal cingulum creates an additional (the fourth) cusp near the posterior edge of the crown.

The m1 is relatively narrow, its paraconid and protoconid are well developed, and the metaconid is lacking. The posterior crest of the protoconid is connected and arranged in line with the talonid crest. The talonid bears the only large, sharp and blade-shaped cusp in all the specimens (Tab. 3).

Deciduous dentition. The dP2 is tricuspid, its anterior cusp is weak and poorly discernible, the posterior one is large and well separated. The tooth length is 13.2 mm, the width is 6.0 mm. The dP3 is relatively large, its preparastyle is bicuspid. The protocone is at the level of protocone, well separated and strongly shifted lingually from the anterior portion of the crown, the paracone and metastyle are subequal in size, the metastyle is positioned considerably lower than the paracone. The tooth length is 20.3 mm, the length at protocone is 16.7 mm, the width at protocone is 12.2 mm (PIN 3381-202). The dp4 lacks a metaconid, its talonid is large and bicuspid (see Tab. 4).

Comparison. Differs from other subspecies by its relatively larger p4 and in having the only large and blade-shaped cusp on the talonid.

Distribution. Late Pliocene – early Pleistocene (Villafranchian) of Eurasia.

Chasmaporthetes lunensis odessanus ssp. nov.

Figs 6, 7

Euryboas lunensis: Crusafont Pairó & Aguirre, 1971

Chasmaporthetes kani kani: Qiu, 1987 (Part.)

Etymology. In reference to the locality Odessa Catacombs.

Holotype. OGU 6, left mandibular ramus with c–m1, Odessa Catacombs, Ukraine, Pliocene (earliest Villafranchian, the lower part of MN16a zone).

Diagnosis. The p4 is long relative to m1. Talonid of m1 has one or two additional cusps (entoconid and entoconulid), besides hypoconid.

Material. In addition to the holotype, a maxillary fragment with P4 and alvioli of premolars (OGU 2903/50), fragments of two maxillae with P3–4 (OGU 33) and P2–3 (OGU 3236), isolated upper premolars P3 and P4 (OGU 3200, OGU 3224, OGU 3215), a mandible (OGU 3246/18), a deciduous dp4 (OGU 110).

Locality. Odessa Catacombs (Ukraine).

Description. The structure of the skull of *Chasmaporthetes* from Odessa Catacombs can only be inferred from the maxillary fragment and the dentition. The maxilla is noticeable for the strong concavity situated in the form of a well-marked fossa over P4 between the anterior and posterior roots of the tooth. The infraorbital foramen is large and wide, 10 mm in height and 7.2 mm in width (OGU 2903/50), and positioned between P3 and P4. P4 is relatively large, the protocone projection is well developed to form a strong protuberance. The anterior edge of the protocone may be either at the level of, or anterior to, the front edge of the parastyle. A peculiarity of P4 is the shape of the anterior edge of its crown: there

are two distinct crests running up to the tip of the parastyle on its lateral and lingual sides, and delineating in this way a flat triangular field at the front edge of P4. Any traces of a preparastyle are lacking in all the specimens. The parastyle is large, the paracone is tall and slender, and the metastyle is low. In lateral view, the basal line of the tooth crown forms a sinusoid that ascends against the paracone and deeply descends against the beginning of the metastyle.

P3 is tall and relatively slender, its crown broadens markedly at the level of the beginning of the tooth posterior root. The principal and posterior cusps are well developed, the anterior one varies in size: it is practically lacking in the specimen OGU 3236, weak in OGU 3200, strong and forming a distinct tip in OGU 3235.

Mandible. A single mental foramen is under p2, its length and height are 7.6 and 7.8 mm respectively (OGU 6). The masseteric fossa ends at the level of the posterior edge of m1 crown. The symphyseal portion of the mandible is of moderate massiveness, its greatest length at the upper part is 25 mm. The diastema between c and p2 is 7 mm. The canine is slender and smooth; a weak keel runs on its internal side. Any traces of p1 are lacking in all the specimens.

The anterior cusp of p2 is absent in both specimens. A distinct crest goes on the forward edge of the tooth crown; the basal cingulum rims the entire circumference of the crown. The posterior cusp is large and well separated. The structure of p3 and p4 is typical of the genus *Chasmaporthetes* in their anterior and posterior cusps being large and well separated from the principal one. The p3 and p4 strongly overlap each other in the toothrow of OGU 6, but this feature is worse expressed in another specimen (OGU 3246/18).

The m1 has a strong cingulum traceable along the whole perimeter of the tooth. The metaconid is lacking. As compared to other subspecies of *Chasmaporthetes*, the structure of the talonid is more complicated: it bears not only a large cusp (hypoconid) positioned in line with the para- and protoconid, but also a smaller one (entoconid) (OGU 6) or two (both entoconid and entoconulid) (OGU 3246/18) occupying the lingual side of the crown.

Comparison. Differs from other subspecies by the structure of its m1 talonid having one to two small accessory cusps besides the hypoconid.

Distribution. Pliocene (Ruscinian – earliest Villafranchian) of Eurasia.

***Chasmaporthetes lunensis kani* Galiano et Frailey, 1977**

Fig. 8

Chasmaporthetes kani: Galiano & Frailey, 1977, pp. 5–6, figs 1, 2

Euryboas aff. *bielawskyi*: Sharapov, 1986, p. 60, fig. 19

Chasmaporthetes kani kani: Qiu, 1987 (Part.)

Chasmaporthetes cf. *ossifragus*: Qiu, 1987, Taf. 3, fig. 4, Taf. 4, figs 2, 3, Taf. 5

Chasmaporthetes lunensis honanensis: Kurtén & Werdelin, 1988, pp. 49–50 (Part.)

Chasmaporthetes lunensis: Sotnikova, 1989, Pl. V, fig. 3, Pl. VII, figs 1, 2

Holotype. F:AM 99789, palatal portion of skull with complete toothrow, China, Shanxi Province, the locality Hsia-Chuang, deposits of Shouyang Formation, the Nihewanian age (terminal late Pliocene – early Pleistocene).

Diagnosis. The p4 is shorter than m1. Talonid of m1 bears the only large and blade-shaped cusp (hypoconid).

Material. Three incomplete mandibles with teeth (PIN 3120-352, PIN 3120-349, PIN 3120-26).

Locality. Kuruksay (Navrukho), Tadzhikistan.

Description. The material has been described in detail and illustrated by Sotnikova (1989, pp. 33–35, Pl. V, fig. 3, Pl. VII, figs 1, 2). The measurements are given in Tab. 3.

Distribution. Late Pliocene – early Pleistocene (probably the latter half of the Villafranchian), Asia.

PROBLEMS OF SUBSPECIFIC TAXONOMY OF THE GENUS *CHASMAPORTHETES*

Several authors attempted nearly simultaneously to classify into subspecies the Pliocene–early-Pleistocene *Chasmaporthetes* of Eurasia (Qiu, 1987; Kurtén & Werdelin, 1988).

The analysis of current data indicates that the basic characters useful for the subspecific diagnostics of *Chasmaporthetes* are the ratio of p4 length to m1 length and the presence/absence of additional elements (entoconid and entoconulid) on the m1 talonid. As a rule, these characters are stable within a population of hyenas (e.g., in *Chasmaporthetes* from one locality).

To divide *Chasmaporthetes* into subspecies, the former character was used by Kurtén and Werdelin, and the latter by Qiu. Respectively, these approaches resulted in two different divisions, geographical and stratigraphical.

Kurtén and Werdelin split the Pliocene to early-Pleistocene *Chasmaporthetes lunensis* of Eurasia into two subspecies. All the European finds were assigned to *C. l. lunensis*, except for the Perpignan hyena determined as *Chasmaporthetes borissiaki*.² All the Asian forms were referred to *C. l. honanensis* (Zdansky). The statistical treatment of the material available to that date showed that the p4 in the European forms is, on the average, longer than in the Asian (Kurtén & Werdelin, 1988, Tab. 10). At the same time, it was noted that the variation in the Asian sample is higher than in the European. This fact was explained by a much larger area from which the Asian specimens had been collected. Because of insufficient data on Europe, Kurtén and Werdelin compared in their scheme the average values of p4 length in the European and Asian forms, and not the length ratio of p4 to m1. Using the absolute values instead of the relative resulted in some degree of 'artificiality' of the proposed subspecific arrangement.

When the analysis of all the data — including those not incorporated into the Kurtén and Werdelin's revision — was undertaken with the use of the relative values, it became evident that the early representatives of *C. lunensis* of Asia and Europe had the same proportions of p4 and m1. In other words, the long p4 dominated in the Ruscinian and early-Villafranchian *C. lunensis* of Asia (fig. 9). For instance, the length ratios of p4 to m1 in the European forms are 96.8% (Roccaneyra, the end of MN16 zone) and 96.8–98.7% (Odessa Catacombs, the beginning of MN16 zone), and in the Asian forms are 94.6–97.5% (Shamar and Beregovaya, MN16) and 94.4% (Malancun, MN15).

Starting from the middle Villafranchian, however, the short p4 morphotype seems to become characteristic of Asia. The length ratio of p4 to m1 is within

² Judging from the proportions of its P4, a maxillary fragment from the locality Perpignan belongs rather to the group of Ruscinian-Villafranchian hyenas and should be assigned to *C. lunensis*. The species *C. borissiaki* is distinct from other *Chasmaporthetes* species in its proportionally narrower premolars. The width to length ratio of P4 in *C. borissiaki* is 45.4–46.7%, whereas in *C. lunensis* it is within 51.3–57.3% (the average value is 53.5%). In the hyena from Perpignan, this ratio is 52.5%, i.e., falls within the *C. lunensis* variation range.

88.3–89.3% in the *Chasmaporthetes* population from Kuruksay (MN17). The similar values are found in a series of remains described by Galiano and Frailey (1977) from the Shouyang Formation, Shanxi Province, China. The ratios of p4 length to m1 length in three mandibles from the type locality Hsia-Chuang (that produced a skull chosen as a holotype for *C. kani*) are 85.0, 86.0 and 86.2% respectively. Galiano and Frailey regarded these finds Nihewanian (early-Pleistocene) in age, *i.e.*, probably not older than mid-to-late Villafranchian. The short p4 is also characteristic of the hyenas described by Qiu as *Chasmaporthetes* cf. *osifragus* from the locality Mianchi (Loc. D) and from an unknown locality in Nihe-wan region. These remains are dated from the middle to upper Villafranchian — Loc. D is placed into MQ18 zone (Qiu, 1987, Tab. 15).

Thus, Kurtén and Werdelin are right in considering the short p4 to be a morphotype most typical for the Asian forms. However, as evidenced by the analysis performed, this morphotype became dominant only from the middle Villafranchian, whereas the Ruscinian and early-Villafranchian forms of both Europe and Asia had the long p4.

The Asian forms were assigned by Kurtén and Werdelin to the subspecies *C. lunensis honanensis*. The species *Hyaena honanensis* was originally described by Zdansky (1924, Pl. 23) on the material belonging to at least two different genera. Subsequently, Zdansky referred to this species the only specimen of that collection, a maxillary fragment with P4 and M1 (#2). In neither case, however, was designated a holotype for the species. The specimen #2 (whose current accession number is M1975, the collection of University of Uppsala Palaeontological Institute, Sweden) was considered by Kurtén and Werdelin (1988) to belong to *Chasmaporthetes* and chosen as a lectotype for the Asian subspecies *C. lunensis honanensis*. The authors did not take into account the work of Qiu (1987) where this same specimen had been proposed as a holotype for the species *honanensis*, but assigned to the genus *Crocuta*. According to Qiu, *Crocuta honanensis* is the most primitive member of the genus.

Regrettably, I did not have a chance to directly examine the fragmentary maxilla with P4 and M1, referred by Kurtén and Werdelin to *Chasmaporthetes*, and by Qiu to *Crocuta*. Judging from Zdansky's illustration and measurements, however, the P4 in the specimen #2 is proportionally broader than it is normally observed in *Chasmaporthetes*, and the P4 protocone is very strongly developed. All these characters indicate that the maxilla M1975 can be assigned rather to the genus *Crocuta* than to *Chasmaporthetes*. In addition, the name *Crocuta honanensis* was not formally reduced to synonymy with *C. lunensis honanensis*. Hence the name *honanensis* can be considered invalid for the genus *Chasmaporthetes*.

The Kurtén and Werdelin's diagnosis for the subspecies *C. l. honanensis* — 'p4, and possibly anterior premolars, shorter than in nominate subspecies' — by and large corresponds to the diagnosis for *C. kani*, given by Galiano and Frailey (1977, p. 2). The p4 is invariably short and m1 has a unicuspid talonid in the type series of *C. kani* from Hsia-Chuang. Therefore, all the Asian forms with a short p4 and a simplified talonid structure on m1 are considered in the present paper within the subspecies *C. lunensis kani* Galiano et Frailey.

There is, however, somewhat different view of the subspecies *kani*. Qiu (1987) revised and updated the diagnosis proposed by Galiano and Frailey for *C. kani*, and divided this species into two subspecies, *C. k. kani* and *C. k. progressus* Qiu. The division was made on the basis of the following characters: the size of the metastyle on P4 and the presence of accessory elements on the m1 talonid. The

forms with a short metastyle and, in most cases, with a complicated talonid of m1 were assigned to *C. k. kani*. In addition to the specimens of the *C. kani* type series, Qiu (1987) referred to the nominotypical subspecies all the finds described from Yushe Formation in China, and also the European forms from the localities Perpignan (Serrat d'en Vacquer), Layna and, with some doubt, Villaroya.

As mentioned above, the taxonomical appraisal of the material was mainly made using the P4 metastyle size and the m1 talonid structure. According to Qiu, in *C. k. kani* the ratio of P4 metastyle length to P4 length falls within 36.4–40.5%, and in later members of the genus, from Saint-Vallier and Puebla de Valverde, it equals to 43.1 and 42.0% respectively. However, the comparison of different data provided by several authors suggests that this character must be used with great caution, as there seems to be different criteria for measuring the P4 metastyle. For example, in Kurtén and Werdelin's and Qiu's publications these indices frequently differ from each other, though obtained from the measurements of the same material (Tab. 5).

Thus, of the characters presented in the diagnosis of *C. k. kani*, only the structure of m1 talonid appears to have a taxonomical significance.

A complicated talonid of m1 is observed in the Chinese specimen V 7275 having both the entoconid and entoconulid. The find derives from the lower horizons of Yushe Formation in Shanxi Province; these deposits are correlated with the late Ruscinian of Europe (Qiu, personal communication). A large entoconid is also present on the m1 talonid in the specimen IPSLA 147 from the Spanish locality Layna. On evidence from several investigators, the age of Layna ranges from the end of MN15 to the beginning of MN16. The fauna of Odessa Catacombs (Ukraine) is correlated with that of Layna. The m1 talonid is also complicated in *Chasmaporthetes* from Odessa Catacombs (with the entoconid in OGU 6, and both the entoconid and entoconulid in OGU 3246/18).

As can be readily noticed, the complicated structure of the m1 talonid is recorded in the forms of Ruscinian faunae and also of the earliest Villafranchian ones containing many Ruscinian survivors. In the later representatives of the genus *Chasmaporthetes*, the m1 talonid is invariably unicuspid.

However, among the Chinese material referred to *C. k. kani*, there are specimens either having or lacking the accessory cusps on the talonid. This material is a numerous series of remains collected from various localities, mostly in the deposits of Yushe and Shouyang Formations. At the present time, a sample from Yushe (Licent's collection) is more or less arranged across five stratigraphical levels within the Ruscinian and Villafranchian (Qiu, 1987). In the opinion of Galiano and Frailey, the fauna of Shouyang Formation (Frick Collection) is Nihewanian (early-Pleistocene) in age, *i.e.*, late-Villafranchian. Qiu dates this fauna as presumably early-Villafranchian, whereas Kurtén and Werdelin judge the Nihewanian within a wider temporal limits (late Pliocene or early Pleistocene) (Galiano & Frailey, 1977; Qiu, 1987; Kurtén & Werdelin, 1988). Such an approximate stratification probably led Qiu to assign to *C. k. kani* the heterochronous material not providing a clear idea of the evolutionary changes in *Chasmaporthetes* during the Ruscinian and Villafranchian.

Account must be taken of the fact that the species *C. kani*, as originally described, is a synonym of *C. lunensis* (Kurtén & Werdelin, 1988). Hence a subspecies established by Qiu (1987) within the species *C. kani* can only be a subspecies of *C. lunensis*. As concerns the taxon described as *C. kani kani*, it was based on a heterogeneous type series containing the material of two different taxa:

Chasmaporthetes lunensis with a short p4 and unicuspid talonid of m1 and *C. lunensis* with a long p4 and complex-structured talonid of m1. The former taxon corresponds to *C. kani* by diagnosis and must be classified as *C. lunensis kani*. In this case, the latter deserves its own subspecific name and, therefore, is described in the present paper as a new subspecies *C. lunensis odessanus*.

The subspecies *C. kani progressus* (= *C. lunensis progressus*) was established on the material from the upper horizons of Yushe Formation (Qiu, 1987). This find is considered late-Villafranchian in age. According to the diagnosis, *C. l. progressus* was larger-sized than the Ruscinian-Villafranchian forms and had a unicuspid talonid of m1³ and elongated metastyle on P4. In addition, it possessed a large and elongated p4. All these features unite *C. l. progressus* with the later forms of *C. l. lunensis* of the middle- and late-Villafranchian faunas of Europe (from Saint-Vallier and Olivola), so in the present paper we consider the taxon *C. lunensis progressus* as a junior synonym of *C. l. lunensis*.

[CONCLUSIONS]

The genus *Chasmaporthetes* differs markedly from other members of the family Hyaenidae, with the Miocene genera *Thalassictis*, *Lycyaena* and *Hyaenictis* being most similar to it morphologically. Kurtén and Werdelin believe that *Hyaenictis* is too specialized to be an ancestor of *Chasmaporthetes*. In their view, the latter may be derived from the most advanced representatives of the genus *Thalassictis*, such as *T. hyaenoides* with its relatively broad premolars or *Thalassictis* sp. with its m2 lost (Kurtén & Werdelin, 1988).

The earliest finds of *Chasmaporthetes* in Eurasia are known from China and Moldova. A new species *C. exitelus* Kurtén et Werdelin was described on the basis of a cranial fragment from the late-Miocene (Turolian) deposits of China. A skull and postcranial skeleton of *Chasmaporthetes borissiaki* (= *Hyaena borissiaki*) is known from presumably Pontian deposits in the Moldovian locality Dermedzhi (Khomeiko, 1931; Kurtén & Werdelin, 1988). The late-Miocene *Chasmaporthetes* were medium-sized and had the whole set of primitive features. Unfortunately, the material of the earliest Eurasian *Chasmaporthetes* is poorly arranged stratigraphically and too scanty to conclusively clarify the origin and early evolution of the genus.

At present, the Pliocene members of *Chasmaporthetes* are much better studied. They appeared in Eurasia in the terminal Ruscinian and became widely distributed. Their remains are found from Spain to China, being everywhere represented by *C. lunensis*. Within this species, however, some evolutionary trends are discernible, allowing one to distinguish several stages in the Ruscinian-Villafranchian history of *C. lunensis*.

The most marked changes observed in *Chasmaporthetes* occur in the relative lengths of p4 and m1 and in the lower molar structure. The earliest forms of the Pliocene *C. lunensis* had a relatively long p4 and complex-structured talonid of m1 (bearing the entoconid and entoconulid in addition to the main cusp, a hypoconid).

³ The illustration of *C. kani progressus* specimen V 7279 (Qiu, 1987, S. 31, Abb. 6A) depicts the m1 with a complicated talonid having two accessory cusps in addition to a hypoconid. When examining the collection of Institute of Vertebrate Palaeontology and Palaeoanthropology (Beijing), I checked this specimen, and V 7279 proved to have the only cusp, a hypoconid, on its talonid. According to Prof. Qiu Zhan-Xiang (personal communication), the figures on page 31 of his monograph were misarranged in print.

These hyenas were distributed over Eurasia at the end of Ruscinian and the beginning of Villafranchian. They are recognized here as members of a separate subspecies *C. lunensis odessanus*.

Starting from the middle of the early Villafranchian, the m1 talonid having one large cusp became a morphotype characteristic of *C. lunensis*. In hyaenids, the decrease in number of talonid cusps is interpreted as an advanced character. A similar decrease from two or three cusps to the only one is observed in the genus *Pachycrocuta* during the Pliocene and early Pleistocene. An analogous pattern is traceable in *Chasmaporthetes*. The occurrence of forms with a unicuspid talonid marks the next stage of *C. lunensis* evolution, succeeding *C. l. odessanus*. These *Chasmaporthetes*, with their relatively long p4 and unicuspid talonid of m1, are assigned here to the nominotypical subspecies *C. lunensis lunensis*.

Chasmaporthetes lunensis lunensis was widely distributed in the early Villafranchian of Eurasia. It persisted up to the end of Villafranchian in Europe. The latest European forms were noteworthy for large size and, probably, had a proportionally longer metastyle on their P4.

Beginning in about the middle Villafranchian, a relatively shorter p4 (than in the nominotypical subspecies) became a dominant morphotype in Asia. Such forms — referred here to the subspecies *C. lunensis kani* — were distributed from Tadzhikistan to China and existed up to the end of the Villafranchian.

It should be noted that there is a find from China, collected from approximately mid-to-late Villafranchian deposits, which has a long p4, *i.e.*, corresponding to the European morphotype. It was described as *C. kani progressus* Qiu, 1987 (= *C. lunensis lunensis*). The presence of such a form in China could be explained by the early-Pleistocene penetration of European subspecies into Asia. Another possibility is that this find actually derives from the older deposits.

The genus *Chasmaporthetes* made its appearance in North America later than in Eurasia and Africa, evidently as a result of invasion. The finds of *Chasmaporthetes ossifragus* (= *C. johnstoni*) are known from the terminal late Pliocene (late Blancan) of America. Two subspecies are distinguishable within the species *C. ossifragus*: *C. ossifragus ossifragus* with a long p4 and unicuspid talonid of m1, and *C. ossifragus* ssp.⁴ with a short p4 (relative to m1) and a unicuspid talonid. The former subspecies is known from the late-Blancan deposits, and the latter from the deposits of the latest Blancan and early Irvingtonian (Kurtén & Werdelin, 1988). As can be readily noticed from their diagnoses, *C. o. ossifragus* is close to *C. l. lunensis*, and *C. ossifragus* ssp. is close to *C. l. kani*. Hence it may be suggested that the appearance of *C. ossifragus* in North America was caused by the dispersal of *Chasmaporthetes* at the stage of *C. l. lunensis*. As regards the occurrence of *C. ossifragus* ssp. and the coexistence of two subspecies in America, this might result from the second, later, immigration of *Chasmaporthetes*, at the stage of *C. l. kani*.

At the end of the Villafranchian, the genus *Chasmaporthetes* became extinct across its entire range in Eurasia. It seems reasonable to link this event with the appearance and wide dispersal over Eurasia of large-sized members of the family Canidae. These canids, namely the medium-sized wolf and large-sized *Xenocyon*,

⁴ This form from Florida was described by Berta (1981) as *C. ossifragus*, and assigned to a separate subspecies *C. ossifragus* ssp. by Kurtén and Werdelin (1988). The proposed subspecies was not named however.

were more advanced in the mode of hunting and, presumably, occupied the ecological niche of *Chasmaporthetes*.

REFERENCES

[The Russian titles only]

- Khomenko I.P., 1931. *Hyaena borissiaki* n. sp. from the Roussillon fauna of Bes-sarabia. *Trudy Paleozoologicheskogo Instituta Akademii Nauk SSSR*, 1: 81–136. [In Russian]
- Sharapov S.S., 1986. *The Kuruksay Assemblage of the Late-Pliocene Mammals of the Afghan-Tadzhik Depression*. Donish, Dushanbe, 272 pp. [in Russian]
- Sotnikova M.V., 1974. Carnivorans of the Eopleistocene of Southern Tadzikistan. *Bulleten Moskovskogo Obshchestva Ispytateley Prirody, Otdel Geologicheskii*, 49 (5): 143–144. [in Russian]
- Sotnikova M.V., 1976. The upper-Pliocene Carnivora of Central Asia. *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya*, 11: 133–137. [in Russian]
- Sotnikova M.V., 1980. The late-Pliocene Mustelidae from the locality Shamar (Mongolian People's Republic). *Bulleten Komissii po Izucheniyu Chetvertichnogo Perioda*, 50: 138–145. [in Russian]
- Sotnikova M.V., 1989. The carnivorans of the Pliocene – Early Pleistocene: Stratigraphical significance. *Trudy Geologicheskogo Instituta Akademii Nauk SSSR*, 440: 1–125. [in Russian]
- Vislobokova I.A., Erbaeva M.V. & Sotnikova M.V., 1993. Early-Villafranchian stage in the history of the mammalian fauna of Northern Eurasia. *Stratigraphia i Geologicheskaya Korreliatsia*, 1993 (5): 87–96. [in Russian]

[Figure captions]

Figure 1. Variation in the arrangement of lower premolars in *Chasmaporthetes lunensis* from the locality Kuruksay

Figure 2. Cranial fragment of *Chasmaporthetes l. lunensis* PIN 3381-1, Shamar, Mongolia

Figure 3. Mandible of *Chasmaporthetes l. lunensis* PIN 2975-19, Beregovaya, Transbaikalia, Russia

Figure 4. Fragmentary mandible of *Chasmaporthetes l. lunensis* PIN 3381-2, Shamar, Mongolia

Figure 5. Mandible of *Chasmaporthetes l. lunensis* PIN 3381-203, Shamar, Mongolia

Figure 6. Cranial fragment with P3 and P4 of *Chasmaporthetes l. odessanus* OGU 2903-50, Odessa Catacombs, Ukraine

Figure 7. Mandible of *Chasmaporthetes l. odessanus* OGU 6, Odessa Catacombs, Ukraine

Figure 8. Mandible of *Chasmaporthetes l. kani* PIN 3120-325, Kuruksay (Navrukho), Tadzhikistan

Figure 9. Relationship between p4 length and m1 length in *C. lunensis*. 1 – Roccaneyra; 2 – Odessa Catacombs; 3 – Shamar; 4 – Beregovaya; 5 – Kuruksay; 6 – Yushe (Qiu, 1987); 7 – Shouyang (Galiano & Frailey, 1977); 8 – China, *C. cf. ossifragus* (Qiu, 1987); 9 – China, *C. kani progressus* (Qiu, 1987).

[Russian text in the Tables]

Table 1. Measurements of upper teeth of *Chasmaporthetes lunensis* from Shamar (in mm)

Measurements (in mm)									
	Right	Left	Right	Left					
I1 Length									
I1 Width									
I2 Length									
I2 Width									
I3 Length									
I3 Width									
C Length									
C Width									
P1 Length									
P1 Width									
P2 Length									
P2 Width									
P3 Length									
P3 Width									
P4 Length									
P4 Width									
M1 Length									
M1 Width									
* Alveolus									
** Worn tooth									

Table 2. Measurements of P4 in *Chasmaporthetes lunensis*

Characteristics	Shamar		Shamar		Odessa Catacombs			
	Right	Left	Right	Left	OGU-	OGU-	OGU-	OGU-
Length (in mm)								
Length along protocone (in mm)								
Metastyle length (in mm)								
Paracone length of metastyle (in mm)								
Width at paracone (in mm)								
Width at metastyle (in mm)								
Ratio of length along protocone to length (in %)								
Ratio of width at paracone to length (in %)								
Ratio of metastyle length to length (in %)								

Table 3. Measurements of lower jaws of *Chasmaporthetes lunensis*

Measurements (in mm)	Shamar			Beregovaya		Kuruksay			Odessa Catacombs	
				Right	Left				OGU-	OGU-
Length of c-m1 row										
Length of p2-m1 row										
Depth of mandible behind p2										
Depth of mandible behind m1 protoconid										
c Length										
Width										
p2 Length										
Width										
p3 Length										
Width										
p4 Length										
Width										
m1 Length										
Talonid length										
Width										

Table 4. Measurements of lower deciduous dp4 of *Chasmaporthetes lunensis*

Measurements (in mm) and characteristics	Shamar	Odessa Catacombs OGU-
Length		
Paraconid length		
Protoconid-talonid length		
Width		
Metaconid	absent	present

Table 5. Ratio of P4 metastyle length to P4 length in *Chasmaporthetes*

Perpignan		
Villaroya		
Saint-Vallier		
Shanxi (<i>C. kani</i> holotype)		