

## ICTITHERIUM VIVERRINUM (CARNIVORA, HYAENIDAE) FROM UPPER MIOCENE OF WESTERN SLOVAKIA

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**Abstract:** This paper addresses the first find of the primitive hyaenid species *Ictitherium viverrinum* from the territory of Slovakia. It is another find of the rare Upper Miocene member of the *Carnivora*. The fragment of the lower jaw with premolars  $P_3$ ,  $P_4$  and molar  $M_1$ ,  $M_2$  - alveole and nearly whole posterior part of the mandible is described. The ictithere evolution, phylogenetical status and comparison with related species is briefly focused in this article.

**Key words:** Miocene, taxonomy, evolution, *Hyaenidae*, *Ictitherium*.

### Introduction

*Ictitherium viverrinum* (Roth & Wagner 1854) is a civet-like hyenid and belongs to the genus range of *Ictitherium*. There are at present no indications that the former subfamily *Ictitheriinae* represents a natural grouping taxa. Rather it seems to be simply an accumulation of forms that share a number of primitive traits that set them apart from other *Aeluroidea* but lack characteristics of more derived hyaenids such as *Crocota* and *Hyaena* (Werdelin in litt.). It is probable, that this genus range and all hyenas evolved in the Lower Miocene from herpestids or another closely related branch of the *Aeluroidea*. This is shown not only by the paleontological material but can also be proved by karyological and serological analyses of recent hyenas. Until the Upper Miocene civets (*Viverridae*) were occasionally present in the fossil record. This family which contains 35 recent species (Corbett & Hill 1991) is related to the so called civet-like hyenas. In the older literature this group was considered a member of the *Viverridae* (Kurtén 1954).

On the contrary, current analyses indicate that the hyenas (also the ictitheres) are closest to either felids or herpestids, but not to viverrids. Again, primitive hyaenids and viverrids just happen to share some primitive characters inherited from earlier ancestors. In the so called "Hipparione faunas" they entirely disappeared in fossil record. It is possible that the major accent of hyenid evolution occurred just after that. Ictitheres - the most primitive hyaenids are the direct descendants of Miocene herpestids. The majority of the researchers considered the genus *Protictitherium* as ancestral for *Hyaenidae*. It is well known that the hyaenids are only a specialized evolutionary lineage - branch of the herpestids (Kretzoi 1938). The evolution was not realized in one line only but was very wide and mosaical with plenty of parallels and blind phylogenetic courses. The first primitive hyenas are found from the Vallesian. In the Turolian the great variety of hyaenid like forms is presented. It seems that just in this period of time the hyenas reach maximum of diversification. Comparing the situation with the more recent periods (Pleistocene, Recent) we can see that their family-phylogeny is more or less in the stage of stagnation. The possible

reason for their departure from Eurasia was the great canid invasion at the beginning of the Pleistocene epoch.

The primitive hyaenids or ictitheres evolved into three major evolutionary lineages. They are grouped as the *Ictitherium*, *Thalassictis* and *Plioviverrops* genus ranges. Only the thalassictine branch has evolutionary descendants. The others probably became extinct without successors. It is possible that the recently separated subfamily *Protelinae* has its origin in the *Plioviverrops* group (Thenius 1966). The true or classical ictitheres were probably small forms like *Protictitherium*. Werdelin (1991) recently recognized six valid species of the genus *Ictitherium*. They are: *I. viverrinum*, *I. pannonicum*, *I. tauricum*, *I. intuberculatum*, *I. ibericum* and *I. kurteni*. At the beginning of the Pliocene they spread with a maximum of radiation, to live in all Eurasia and North Africa. In our opinion, they could have been more widely distributed in Africa, for example the youngest hyaenid species *Hyaenictitherium namaquensis* Stromer 1931 from Langebaanweg in South Africa (Turner 1986). The question arises if this species can to be considered as a member of the thalassictine group or if its advanced evolutionary descendants that is the true hyaenids.

*Ictitherium viverrinum* is known from many fossil sites from Eurasia, but up to now this genus was not known in fossil evidence from the territory of Slovakia. In this work the occurrence of a fragment of the lower jaw with three teeth is presented from the locality Borský Jur, which lies in Western Slovakia Fig. 1.



Fig. 1. Geographical position of the locality Borský Jur (Lower Turolian).

This place corresponds to the north-east prominence of the Vienna Basin.

### Systematic paleontology

|             |                                   |
|-------------|-----------------------------------|
| Class       | <i>Mammalia</i> Linnaeus 1758     |
| Order       | <i>Carnivora</i> Bowdich 1821     |
| Suborder    | <i>Fissipedia</i> Burmeister 1791 |
| Superfamily | <i>Aeluroidea</i> Flower 1869     |
| Family      | <i>Hyaenidae</i> Gray 1821        |
| Genus       | <i>Ictitherium</i> Wagner 1848    |

*Ictitherium Viverrinum* Roth & Wagner 1854

#### Synonymy :

*Galeotherium* gen. nov. Wagner 1840 (genus caelebs)  
*Ictitherium* gen. nov. Wagner 1848 (nomen nudum)  
*Ictitherium viverrinum* sp. nov. Roth & Wagner 1854  
*Ictitherium robustum* (Nordmann) Gaudry 1862-67  
*Thalassictis gracilis* sp. nov. Hensel 1862  
*Thalassictis viverrina* (Roth & Wagner) Hensel (1862)  
*Ictitherium gaudryi* sp. nov. Zdansky 1924  
*Ictitherium sinense* sp. nov. Zdansky 1924  
*Ictitherium robustum* Gaudry-Arambourg & Piveteau 1929  
*Ictitherium viverrinum* Roth & Wagner - Kretzoi 1938  
*Palhyaena ?gaudryi* Zdansky-Kretzoi 1938  
*Sinictitherium sinense* gen. nov. Kretzoi 1938  
*Ictitherium robustum* (Nordmann) Gaudry - Zapfe 1948  
*Ictitherium viverrinum* Roth & Wagner - Solounias 1981  
*Ictitherium viverrinum* Roth & Wagner - Kurtén 1982  
*Ictitherium viverrinum* Roth & Wagner - Werdelin 1988  
*Ictitherium viverrinum* Roth & Wagner - De Beaumont 1988  
*Ictitherium viverrinum* Roth & Wagner - Werdelin & Solounias 1991

**Type (lectotype):** Bayerische Staatsammlung, München: 56, mandible (Kretzoi 1938)

**Type locality:** Pikermi, Greece

**Type level:** Turolian (MN Zone 11-13), Upper Miocene

**Localities:** Montredon (France); Vösendorf (Austria); Borský Jur (Slovakia); Pikermi, Samos, Vathylakkos, Ravin de Zouaves (Greece); Titov Veles (Macedonia); Belka, Chobruchi, Grebenniki, Novaja Elisavetovka (Ukraine); Loc. 12, Loc. 31, Chen Chia Mao Kou, Chen Kou, Chin Kou, Chou Chia Kou, Huan Lou Kou, Liao Wan Kou, Nan Ho, Ta Tung Kou, Yan Mu Kou (China).

### Material

A fragment of the lower jaw (MH-001 - Dr. Hornáček's collection, Tmava) with the premolars  $P_3$ ,  $P_4$  and molar  $M_1$  and the posterior part of the mandible well preserved (see Figs. 2, 3). The front part of the fragment from  $P_3$  and angular processus are broken. The fossil is little destructed, the teeth are with any abrasions. The bone has a light-brown color, while the teeth are dark brown and black. The jaw was disintegrated and composed from several tiny fragments.

### Geological background

The locality Borský Jur is situated 3 km west from the village Sekule (75 km NW from Bratislava) in the former brickmine

(see Fig. 1). The basic sediments are Pannonian clays, probably from Upper Pannonian age (Lower Turolian). The site belongs paleogeographically to the Central Paratethys (Vienna Basin). The development of the Neogene in this region is very miscellaneous which influenced with lateral and vertical facial changes. The province of the Vienna Basin was greatly modified from Oligocene to Middle Miocene in paleoenvironmental point of view. Marine communities were typical with the coming of continental tectonic activity in the Paratethys, continual regression of the sea began. The last junction with the Central Paratethys was in the Middle Miocene - Badenian. The brackish water communities (lacustrine and fluvatile) development is typical (Buday et al. 1962). The associations of gastropods have great significance for litho-stratigraphy in the Pannonian age. These gastropods form so called "Congeria beds" - an alphabetical zonation scheme. The presence of these species - *Melanopsis vindobonensis* and *Congeria subglobosa* in Borský Jur indicates the zone E (Upper Pannonian) (Bernor et al. 1988). In the middle part of the exposure there is a sandy horizon with thickness 3-10 cm which consists of river sand and gravel layers. These layers are occasionally weathered to a grayish or yellowish brown. Therefore, the color of fossil bones characteristically ranges from black to brown or reddish-brown. The fragments of fossils of the vertebrates are abundant in fine gravel grains. These fragments are the isolated bones, teeth, parts of horns, turtle armours, etc. This faunistic assemblage belongs to the Upper Miocene "Hipparione faunas". Specifically it is the second wave of the vertebrate communities which are coming into the Vienna Basin. From the site of Borský Jur these following groups of vertebrates are found; pisces - occurrence of conical teeth and fragments of the fin thorns; fragments of the plastrons and carapace of the turtles; crocodile abdomen shield; and from mammals - rodents (*Steneofiber* cf. *jaegeri*), perissodactyls (*Hipparion primigenium*, *Dicerorhinus* cf. *schleiermacheri*); artiodactyls (*Procapreolus dichotomus*) and carnivores (*Ictitherium viverrinum*, *Perunium ursogulo*).

### Systematic part

#### Mandible

The major part of the right mandible of an adult specimen is preserved with alveoles  $M_2$  dex., molar  $M_1$  and premolars  $P_3$  and  $P_4$  (see Fig. 2). The front part of the mandible is not present which means that  $P_2$ , canine and all the incisors are lacking. The other parts of the mandible are well preserved, with the exception of a little cracking in the anterior part. This fracture makes it possible to see the mandibular canal by which the nerves and veins reach the teeth. The alveole of the  $P_2$  root system is preserved. The corpus of the mandible is gracile, morphologically corresponding to the primitive ictithere type. In the posterior part there is a broken point of the angular prominence of the bend of the jaw and a tiny gap has been broken into the masseteric pit. The coronoidal processus is very well preserved. This processus has typical variable features. It has an extreme height and relatively small width in the superior part. The mandible gap (incisura mandibularis) is slightly rounded in the dorso-medial course. On the back side this mandibular gap continues towards the flat of the coronoid prominence. This gap formed on the lingual side with the inner flat of this prominence which has a relatively sharp edge. The condyl (processus condylaris) is undisturbed, with a well preserved caput mandibulae,

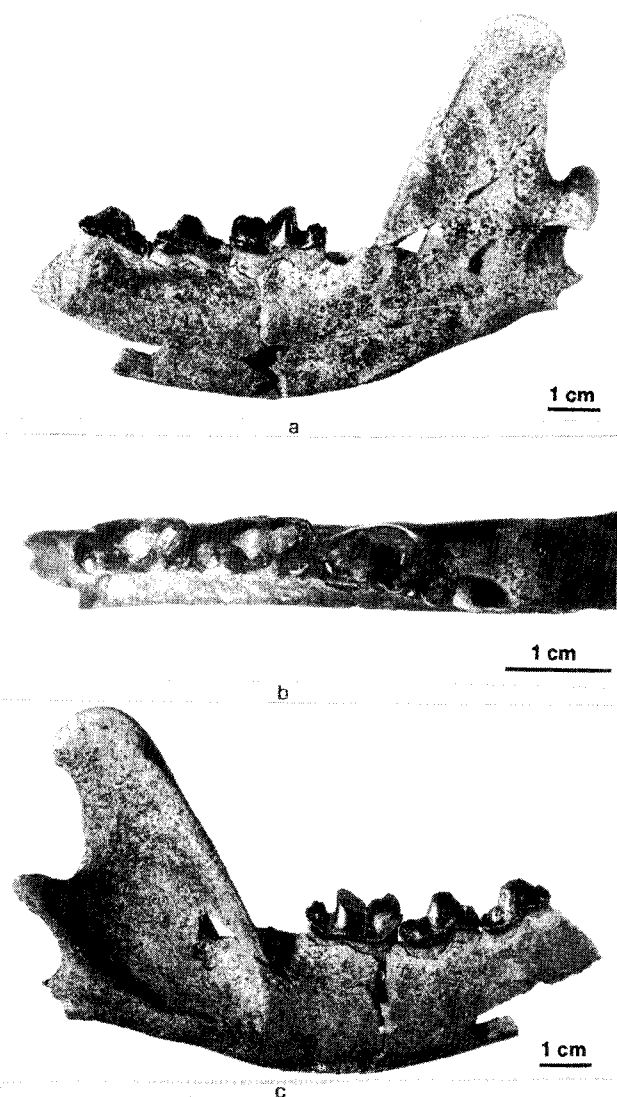


Fig. 2. *Ictitherium viverrinum* Roth & Wagner 1854 - fragment of the lower jaw with preserved  $M_1$ ,  $P_3$  and  $P_4$  from Borský Jur (Western Slovakia): a - lingual, b - occlusal, c - buccal.

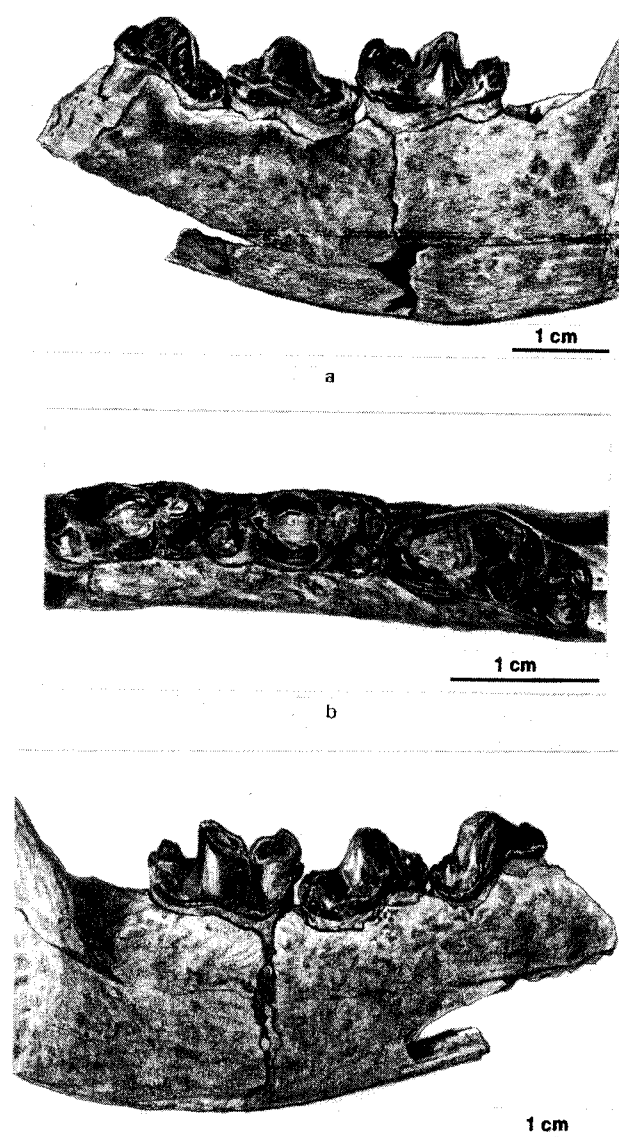


Fig. 3. *Ictitherium viverrinum* Roth & Wagner 1854 - detailed sketches of the dentition: a - lingual, b - occlusal, c - buccal.

which has great importance in the functional system of the jaw junction. The external part of the caput is strong abraded, and there is possibility to see the inner structure of the bone. The caput basis is much stronger and thicker on the ventral side. The axis of the ellipsoid shaped junctional caput runs from the ventro-lateral side in dorso-medial direction. In this place the caput narrows into the so called "neck". On the frontal side there is a little wing cavity (fossa pterygoidea) into which the lateral wing muscle (musculus pterygoideus lateralis) was inserted. Although, the angular prominence in the dorso-caudal part is broken, we can see from the triangle base that this prominence was relatively long.

On the ventral part the foramen mandibularis which is surrounded by bony prominences (lingulae mandibularis) can be observed well. This pit is an entry for the canalis mandibularis. On the buccal side, the prominence of the jaw lies in the dorso-lateral part. A large ellipsoid cavity, narrowed in its

lower part, (the so called masseteric cavity (fossa masseterica)) can be seen.

On the mandible two different bent structures are clearly formed. They are linea mylohyoidea (on the lingual and buccal side) and linea obliqua.

### Dentition

#### $M_1$

The first lower molar, the centre of carnassial function, is transversally elongated, and the outline of the crown basis is irregular in form. In the anterior part, central longitudinal axis runs parallel with the alveolar curve. The talonid part is strongly returned into the medial course. The anterior and posterior walls have a concave character. The lingual wall of the molar is slightly concave, differently formed than the buccal wall, which is much more concave. The angle between the lingual

and buccal side of the anterior part of  $M_1$  (in the dorsal view) is remarkably strong. All components of the talonid and trigonid are undisturbed.

The trigonid has a strongly developed metaconid and the protoconid is much lower than the paraconid. The protoconid is the highest of all the cusps of the crown. These elongated two-top formed paraconid cusps form the most important structure of the molar. These two marginal cusps (same sized) are situated more towards the buccal side. The both structures have concave buccal walls and are separated by a small triangular cut, which is further narrowed and continually lead to the buccal cingulum. The metaconid is roughly triangular in shape with surrounded culmination. The position of this cusp is lower than the protoconid but higher than the paraconid. The talonid is surrounded by a slight groove which ends in the cingulum. In the anterior part this groove runs continually in the rostral part. The lower basic part of the metaconid is strongly whetted, without the cingular wall. Between the protoconid and metaconid, there is a deep cavity which formed a thin notch which is falling into the central groove. The protoconid and paraconid lingual walls are surrounded by a narrow and continual cingulum. The cingulum in the trigonid side is much more pronounced than in the talonid side. The central trigonid area consist of two flats approximately the same in size converging towards the base. The cingulum on the buccal side is more abraded than the lingual cingulum. The shearing blade is biggest on the lingual side of the tooth.

The small flats of the hypoconid on the buccal side are the lowest lying parts of whole molar. Both are elongated and rounded. The marginal, posterior flat created the caudal edge, which has a half of the entoconid height. The entoconid cusp is separated from hypoconid by a groove, which surrounded the anterior talonid flat and leads to the lingual cingulum. The whole distal part (talonid) has about one third length of the crown metaconid and lies in the same level with the protoconid, which is a typical viverrid feature. Both shearing flats of the protoconid and paraconid are slightly bent and formed about half of the whole  $M_1$ - crown height. The trigonid cusp created a bigger central field, which is not straight but slightly convex. Metaconid reached about three quarters of the protoconid height (other dental paramaters see in Tab. 1 and Tab. 2). A relatively big trigonid is the next important viverrid feature. The talonid is still relatively big, which indicates a primitive hyaenid stage. There is no ridge going from the hypoconid aslant to the front of the protoconid (viverrid mark).

**Table 1:** Dental measurements of the *Ictitherium viverrinum* from Borský Jur (Slovakia).

| Measurements in mm | P <sub>4</sub> | P <sub>3</sub> | M <sub>1</sub> | M <sub>2</sub> |
|--------------------|----------------|----------------|----------------|----------------|
| Length (max.)      | 13.6           | 12.5           | 15.6           | 5.5            |
| Width (max.)       | 6.5            | 6.2            | 7.2            | 4.1            |
| Height (buk.)      | 8.1            | 8.0            | 11.1           | -              |
| Height (ling.)     | 9.8            | 7.1            | 5.5            | -              |

The robusticity of the  $M_1$  in comparison with other teeth is mainly due to its important "carnassial" function. The length of the talonid compared to the trigonid is 5.2 to 10.5, index 0.5 (in mm). The carnassial is broader between metaconid and protoconid, narrow part lies on the border of the trigonid and talonid. The single  $M_2$  originally had one root. The alveole has a longitudinal round shape. This tooth was the smallest in the whole dentition, which corresponds to the evolutionary trend of the reduction of the post- $M_1$  areas. This is an advanced and typical feature in the *Hyaenidae*. The alveole has a remarkable feature situated on the lingual side.

#### P<sub>4</sub>

This tooth has an elongated crown base shape in outline. However, the anterior part is more sharpened than the oval posterior part. The anterior side of the crown has a strongly developed convex wall. The angle between the lingual side of the anterior and mesial part of the tooth is clearly evolved. Premolar  $P_4$  has a bigger length and width than  $P_3$ . The typical feature of this premolar is that it has not developed the metaconid. This means that only the protoconid is strongly formed and the paraconid is relatively weak. On the paraconid surface which has a clear tooth flat, which is curved aslant up to the protoconid. The cingulum of the paraconid is less prominent on the lingual side. In the protoconid, a relatively high front ridge is well observed. The major occlusal surface of the premolar is in the part of the protoconid, which is fully open and broadly running into the talonid. Here on this place on the end, it is strongly abraded.

The talonid is relatively strong and bigger than the  $M_1$ -talonid. The external hypoconidal buccal wall is remarkably whetted. The talonid occlusal surface is not recognizable. The entoconid is more remarkable especially its occlusal flat.

The position of the tooth in the jaw is more or less symmet-

**Table 2:** Dentition parameters of the *Ictitherium* from miscellaneous localities after various authors.

|             |                | <i>Ictitherium viverrinum</i><br>Pikermi | <i>Ictitherium pannonicum</i><br>Polgardi | <i>Ictitherium pannonicum</i><br>Novaja Emet. | <i>Ictitherium spelaum</i><br>Black Sea | <i>Thalassictis robusta</i><br>Mixed Sample | <i>Thalassictis robusta</i><br>Kishinev | <i>Ictitherium viverrinum</i><br>Borský Jur |
|-------------|----------------|--|---|---|---|---|---|---|
| Length      | P <sub>3</sub> | 12.97                                    | 15.60                                     | 16.60   | 13.68                                   | 13.50                                       | 13.90                                   | 12.50                                       |
| Width       | P <sub>3</sub> | 6.36                                     | 7.50                                      | 7.72  | 6.59                                    | 6.80  | 6.65                                    | 6.20  |
| Height      | P <sub>3</sub> | 8.20                                     | -   | -   | -                                       | -   | -                                       | 8.00  |
| Length      | P <sub>4</sub> | 14.47                                    | 16.67                                     | 16.95   | 15.10                                   | 14.60                                       | 15.10                                   | 13.60                                       |
| Width       | P <sub>4</sub> | 7.32                                     | 8.40                                      | 9.05  | 7.72                                    | 7.30  | 7.36                                    | 6.50  |
| Height      | P <sub>4</sub> | 9.48                                     | -   | -   | -                                       | -   | -                                       | 9.80  |
| Length      | M <sub>1</sub> | 17.20                                    | 19.58                                     | 20.18   | 16.80                                   | 17.30                                       | 17.50                                   | 15.60                                       |
| Width       | M <sub>1</sub> | 7.60                                     | 9.70                                      | 9.16  | 8.34                                    | 7.86  | 7.85                                    | 7.20  |
| Tal. Length | M <sub>1</sub> | 11.40                                    | 6.00                                      | 5.52  | 4.20                                    | -   | -                                       | 4.20  |

rical, however in some places it shows an asymmetrical pattern. The paraconid has half height of the protoconid and lies more lingual from the central longitudinal axis of the tooth. All the dorsal occlusal surfaces are remarkably flattened. Entoconid is the lowest part of the premolar. It is interesting that  $P_4$  has a broader pattern in the talonid region. The distal part of the tooth formed approximately two fifths of the whole premolar length.

### $P_3$

The third lower premolar is rather similar to the  $P_4$  but some differences exist. First of all this third premolar is shorter, narrower and the smallest. The cingulum has an analogical structure on the lingual side. The paraconid is weaker and without occlusal surface. The protoconid is about one third broader than in  $P_4$ . Its occlusal surface is not so strongly opened. This surface runs into the hypoconid in the narrowed, sharpened small ridge which is compressed. The central flat is not as large as in the  $P_4$ . The caudal edge is weaker with little curving. The buccal walls are more concave and little flattened. The groove between the hypoconid and protoconid is weaker. The outline of the crown base is more oblong.

All the teeth are relatively little abraded which indicates, that they are fresh forecut with sharp edges on the crown cusps. Molar  $M_1$  has strong viverrid features. Premolars have a minimum of differences, between teeth there are intraalveolar shelves - septa.

### Comparison

In the framework of the *Ictitherium* genus range, several species have been recognized by several authors. Semenov (1985) recognized the validity of five species; *I. viverrinum*, *I. ibericum*, *I. pannonicum*, *I. sinense*, *I. gaudryi*. In 1988 he described a new icthere species from Middle Sarmatian of Ukraine - *Ictitherium spelaeum*. It seems that this is the member of the close related genus "*Thalassictis*". Werdelin (1991) has the same opinion. Werdelin (1991) considered valid taxa: *I. viverrinum*, *I. pannonicum*, *I. tauricum*, *I. ibericum*, *I. intuberculatum* and new species *I. kurteni*. Most members of the subfamily are similar in their dental morphology, but there are often differences in size (for example *I. viverrinum* and *I. pannonicum*). Others are considered as conspecific species (*I. intuberculatum* and *I. viverrinum*).

First of all I focused on the important species *Thalassictis robusta*, Gervais 1850 ex Von Nordmann which is often confused with *I. viverrinum*. We can find significant differences not only in biometrical features but also in the morphology of individual teeth. Intervals of the biometrical parameters are nearly the same with *I. viverrinum*.

The lower premolars  $P_2$ - $P_4$  of the *I. viverrinum* are stronger and most rounded with blunter cusps, whereas in *T. robusta* they are more compressed with sharpened cusps (Kurtén 1954). The lower first molar  $M_1$  in *T. robusta* has a shearing blade represented by the paraconid and protoconid much more highly placed over the talonid than *I. viverrinum*. Carnassial formed somewhat more than two thirds of the crown length. This last feature is not so reliable, because *I. viverrinum* has commonly trigonid, which reached two thirds of the  $M_1$  crown length. Semenov wrote about the proportion of the talonid in the  $M_1$  of *I. viverrinum* is 28-32% - which means that the trigonid has even

more than two thirds of the length. *T. robusta* has a carnassial blade more compressed and sharpened.

The basic distinction between *I. viverrinum* and *T. robusta* is in the metaconid height. In this work the described dentition has a higher, slightly sharpened metaconid which corresponds to the three quarters of the adjacent protoconid height.

The next species is very close to *I. pannonicum* Kretzoi 1952. It was found in the territory of Hungary at Polgardi (Early Pliocene) for the first time. Formerly this taxon was not absolutely recognized, as the characteristics of the new species given by Kretzoi were doubtful for a long time. First of all because he separated the holotype from the specimen Ob/2653, which was not documented in the original article with any photos and paintings. For this reason doubts about the identification of the new species are justified. A description of the specimen without figures was published and the major feature of  $M_2$  is not represented. Only specimens lacking  $M_2$  are documented. In the last decade discussion about the named species *I. pannonicum* (Semenov 1985) was started by Semenov (1985), using new material from the northern parts of Black Sea region (Grivec, Ukraine), with a large  $M_2$  - a characteristic of *I. pannonicum*. This species has very little reduced post-molars. All the teeth are slightly bigger in biometrical parameters (see Tab. 2). The important fact is that the masseteric cavity reached the talonid level, which is a decisive distinction from *I. viverrinum*, where this cavity spread only to the posterior margin of the  $M_2$ . However the major difference which distinguish this species from *I. viverrinum* is its larger size. It is not possible to say that the talonid of  $M_1$  could be reduced (30 % of the length) as stated for the species mentioned by Kretzoi (1952). It can be seen that the two species are closely related, and they could be conspecific. Nevertheless, up to now we have no other marked features besides the size of the post-molars.

*Ictitherium ibericum* Meladze 1967, is a relatively badly known member of the *Ictitherium* genus range. Its size and shape is close to *I. viverrinum*, but it has shorter and broader premolars.

*Ictitherium intuberculatum* Ozansoy 1965, has a similar size and other metrical parameters close to *I. pannonicum* from Polgardi. It is stated that some proportional differences in the  $M_2$  and  $M_1$  exist and both these species could be conspecific (Werdelin 1991).

*Ictitherium tauricum* Borissiak 1915, is only slightly different from *I. viverrinum*, but also has significantly broader premolars. The major feature is the  $P_4$  - a change of place in its anterior part. It can't be certified remarkable enlarged  $P_3$  - the typical mark of the *I. kurteni*, which determined this taxon from all related species of the "*Ictitherium*" group.

*Protictitherium crassum* Depéret 1892, is another closely related species from Vallesian. The trigonid has a clearly wide based outline. The metaconid is stronger and much lower than the paraconid groove. In the talonid part the entoconid is dominant. The hypoconid is slightly smaller than the ectoconid. The acessorial frontal tubercle of the  $P_4$  is more strongly developed than in the  $P_3$ . In the  $P_2$  this part is completely lacking. Premolar  $P_4$  is slightly wider than  $M_1$ . Premolar  $P_3$  has a more stronger lingual cingulum than *I. viverrinum*. The external crown edge in the back side of the  $M_1$  is strongly evolved. This is a distinctive feature of the  $M_1$  of *Ictitherium viverrinum*. *I. viverrinum* has this structure poorly formed. The protoconid of *P. crassum* is relatively higher and has a sharpened form. The assumed greater age of the *P. crassum* may also argue against ascribing the Boriský Jur material to this species.

The other structures of the remaining jaw fragment are very hard to evaluate. The coronoidal prominence is very variable in shape. The gracility of jaw is unambiguously different from most of the other robust species (*Hyaenictitherium hyaenoides*, *H. wongii* and *T. robusta*). It is not possible to classify some other important features, such as the upper molars, pattern and other craniometrical parameters (the palatinum width, condylo-basal length, the difference among ectotympanal chambers of the otical capsules, etc.).

### Paleogeography

The *Ictitherium* genus range which is chronologically defined from Upper Astaracian to Upper Pliocene had created a great geographical distribution. Ictitheres have lived in the whole of Eurasia and in the Pliocene they reached as far as northern Africa (Thenius 1966). The centre of their origin was probably the western part of their areal distribution, and from there they quickly spread up to the far East. We would divide their distribution into three major bioprovinces according to their fossil records:

1. Western province - including the areas with finds from Spain, France, Germany, Austria, Slovakia, Poland, Hungary, Macedonia and Tunisia (probably also from Czech Republic, one unpublished specimen, Fejfar in verb.).
2. Middle-Eastern province - Greece, Moldavia, Turkey, Georgia, Iran and India.
3. Eastern province - many localities from China.

### Discussion of evolutionary aspects

On the basis of their dental structure, the ictitheres considered as a transitional group in the evolution from *Viverridae* to *Hyaenidae*. According to authors from last century they are still viverrids of the primitive hyaenoid stage (Roth & Wagner 1854), Von Nordmann (1858), Gaudry (1862-67). Today after collecting a great amount of study material (mainly from China) most authors suggest that the ictitheres are members of the *Hyaenidae*, although a very primitive stage with abundant viverrid features (Thenius 1969; Müller 1970). If we look closely at the members of this subfamily of the hyenas, all in addition to the basic *I. viverrinum* have a predominance of the advanced so called hyaenid markers. Strongly reduced talonid on the  $M_1$ , reduced  $M_2$ , most robust building of the mandible, single teeth and other characteristics are typical.

Various opinions on the origin of these species and of the whole group have been suggested. Crusafont & Petter (1969) derived the genus *Ictitherium* from genus *Progenetta* (syn. *Miohyaena*). We can hardly suggest the existence of some direct forebears. It is most probable that the ictitheres like the hyenas have a polyphyletic origin and that their evolutionary steps have been played in mosaic manner. After Kurtén (1954) it is possible to divide the ictithere evolution into the three major lineages:

- 1 - *Protictitherium* - *Ictitherium*.
- 2 - *Thalassictis* - with abundant evolutionary descendants (*Lycyaena*, *Chasmaporthetes*, *Hyaenictis*).
- 3 - *Plioviverrops* - separated branch.

In the framework of the family *Hyaenidae* Thenius (1969) distinguish three subfamilies: *Ictitheriinae*, *Hyaeninae* and *Protelinae*. We can consider the circuit of the genus *Protictitherium* as ancestral for ictitheres. From this branch two genera *Ictith-*

*erium* and *Thalassictis* (Kurtén 1982) are dichotomically segregated. It is very complicated to discuss the origin of the *Protelinae* branch, the subfamily which is often separated. It is very little known and obscure group. We have no knowledge of fossil representatives (besides *Proteles amplidenta* from the Pleistocene) and we can not exactly state the phyletical status. The *Plioviverrops* branch manifests some affinity to the the recent species *Proteles cristatus* (Thenius 1966). A single recent monophyletic member could have evolved from this branch. The "*Protictitherium*" genus circuit is unfortunately known only from dental material. They were mostly small forms, geologically the oldest hyaenids of all. It is not clear if *Protictitherium* is a natural monophyletic group or not and if their trend "to be smaller" is a specific feature of the genus or a general trend in hyaenid evolution (Werdelin 1991). *Ictitherium viverrinum* is the most documented species from the whole family in the fossil record. Others are rarely found and often identified according to variable characteristics. The general distinct mark of the genus *Ictitherium* from the genus *Protictitherium* are relatively broader premolars, relative lowering of the  $M_1$ -trigonid. In the genus *Thalassictis* we already find advanced features. The talonid of the  $M_1$  is more reduced than in the *I. viverrinum*, while  $M_2$  and  $P_4$  are elongated. The lower paraconid and high protoconid are surviving primitive features. The following stages of the phylogeny are bigger, typical hyaenid forms (*Hyaenotherium*, *Miohyaenotherium*, *Hyaenictitherium*). All are the members of the "thalassictine" group and are derived from genus *Thalassictis*. The species of this group are more abundant in the fossil record than "true" ictitheres. The next development was focused into the two basic branches. One of them was the group of the hypercarnivorous hyenas with major genus *Lycyaena*, *Hyaenictis* and *Chasmaporthetes*. The second branch starting with *Palinhyaena reperta* and leads directly to the recent representatives *Hyaena* and *Crocuta*. They are both characterized by a trend towards body enlargement and the development of carnassial and crushing structures in the dentition. The oldest known member of the *Ictitheriinae* is "*Thalassictis*" *spelaeum* (originally *Ictitherium spelaeum*) from the Astaracian (Lower Pannonian) of Ukraine MN 9 (Semenov 1988). This species belongs to the earliest Hipparione faunas in Eastern Europe. Until now the oldest finds were dated to the Upper Astaracian. The find from Gritsev is from half of the Vallesian.

In the Turolian the radiation and diversification of the hyaenid carnivores into different species reached its maximum. The ictitheres also reached their greatest radiation (mainly *Ictitherium* and *Thalassictis*). Today we recognize six valid species. The identification of *I. pannonicum* Kretzoi 1938 and *I. intuberculatum* Ozansoy 1965 is uncertain, while *Ictitherium pannonicum* is different from *I. viverrinum* only in size dimensions. It could be jointed with altogether greater body dimensions. It could be only a slightly deviation in the framework of sexual dimorphism in the *I. viverrinum*, or geographical race.

Although usually hyenas and civets have developed only minimal differences between the sexes, the situation with ictitheres could have been different. From analyses of their body structure and their paleoecology we can suggest, that they performed the function of the canid-types.

Is it undoubtful that the main line of the phylogeny began from the "thalassictine" group. *Ictitherium* became extinct without leaving descendants, so it was a blind evolutionary branch. It was one from the amount of species, which we know from the period of the greatest expansion of the hyaenid forms - the Turolian.

## Paleoecology

In most literature *Ictitherium viverrinum* is regarded as a "civet-like hyaenid". According to some authors several features such as a long, narrow skull and rostrum, generalized premolars, relatively big  $M_1$  talonid and relatively little reduced  $M_2$  made it comparable to the smaller or medium sized canids, for example recent jackals. It is very probable, that they had a similar life style to recent forms of canid carnivores. The distinction was only in some shorter extremities of "viverrid" type.

They inhabited the areas, which were covered with forests or forested steppes. In the some places (e.g. Pikermi) the ecological conditions resembled the open landscape of the African savannas. The various habitats in which they lived prove their wide ecological tolerance. At the end of the Miocene most parts of Eurasia were in the warm, subtropical climatic zone. The great Pannonian and Vienna Basins also provided ideal conditions for the progress of the mammal associations. The region had vast forested formations, closely related in flora to the recent Mediterranean and Subboreal species. There were great river systems, lagoons and lakes, resulting from the multiple regression of the Tethys.

Ictitheres shows two ecological and morphogenetic courses of specialization. One of them is based on the long-headed, short legged probably exclusive sylvicol forms (*Thalassictis*), the second on the short-headed, long legged steppe forms (*Hyaenotherium*, *Hyaenictitherium*). Intermediate, conservative forms - *Ictitherium* sp. (Kretzoi 1938) remain between these two specialized branches.

The ictithere group also included forms, which did not live in forested areas and therefore the name "forest" or "Wald" (German) hyenas (mainly in the older literature) for ictitheres is not accurate.

Abel (1922) classified the ictitheres as scavengers, possible Pontian vicars of the recent jackals. Orlov (1941) after detailed study of the Eastern European forms suggest that for example *Hyaenotherium wongii* (formerly *Ictitherium hipparionum*) was a very fast runner and he believed it to have been highly predaceous. Today we know that all the members of the so called "thalassictine" group were basically very similar to canids or canid like form, and that they hunted in groups. Thalassictines were more ecologically preadapted. For this reason they are more abundant in the fossil record than other ictitheres. They represented the function of the wolves or wild dogs among the hyenas. The skull of the *Hyaenictitherium hyaenoides* has strong phenetical similarities with the skull of the African wild dog (*Lycaon pictus*) or with the skull of the big Pleistocene wolf (*Canis dirus*). The last representant of the so called "wolf-hyenas" was *H. namaquensis* from the Ruscinian of South Africa (Turner 1988). It is not excluded that the hunting abilities of the recent hyenas (*Crocota crocuta*), which have often been shown by many experts, although only in certain specific ecological conditions, are hereditary residues from their ancestors. Various authors speculated on the functional status of these animals in former ecosystems. Because they were small or medium sized forms, they certainly do not belong to the major predators. The available analogical example from the recent carnivores for small ictitheres could be the African civet (*Civettictis civetta*) or Indian civet (*Viverra zibetha*). Certainly they were more specialized flesh-eaters than these recent civets. Their food probably consisted of a varied range of the evertbrates, small vertebrates and also plants. For the big

forms we suggest the active predation, mainly for miscellaneous ungulates which were very abundant in the period (Semenov 1985).

The fossil record from various places shows several species of ictitheres and other hyaenid carnivores often coexisted. This fact was possible only because they had a wide adaptive radiation, and differentiation of the food resources, comparable to that of recent coexisting large species of hyenas *Crocota crocuta* (spotted hyena) and *Hyaena brunnea* (brown hyena) in the southern Kalahari (Mills 1989). The brown hyena is more a scavenger, eating tiny food, but the spotted hyena has been preadapted to hunting medium sized or big prey (72 %). Kurtén (1954) has found out from the study of various species that the majority of the teeth are relatively little worn. The Kishinev specimens represented individuals that died at an age of less than 2 years. Only one pathological specimen appears to have been a little bit older, more than 3 years. It seems that the correlation between size and the average frequency of young versus old or senile specimens in the collection is striking. The rates of mortality are higher in small forms (Kurtén 1953), so that the majority of individuals die young, with unworn or slightly worn teeth.

## Conclusions

The finds of Tertiary members of the hyaenid carnivores from the territory of Slovakia are not abundant. The situation is similar in the viverrids, their finds are also rare and often only fragmentary. These species are documented from our area: *Megaviverra carpathorum* (Kretzoi & Fejfar 1982) and *Lophocyon carpathicus* (Fejfar & Schmidt-Kittler 1987). The transitional *Ictitherium* group from Slovakia was not added. The rarity of similar fossils is explained by scarcity of localities in Slovakia with this age (Upper Miocene, Turolian). True and advanced hyenas are not so rare and are common in the Pleistocene. For example: *Pachycrocota perrieri* (Villafranchian - Hajnáčka, Strekov), *Pachycrocota robusta* (Gombasek Cave), *Crocota crocuta spelaea* (Gombasek and Prepoštská Caves).

*Ictitherium viverrinum*, described in this paper, represents a phylogenetically very important member, because it stands at the beginning of the whole hyaenid evolution. The major emphasis was focused on the description of the morphology of the fragment, and determination and statement of its phylogeny. The majority of the morphological, odontological and biometrical parameters indicated that the find belongs to widely distributed Turolian species *I. viverrinum*. During the fossil collection, the gastropods were also collected from the same place which is very important and gives the probable age of the fossils as well as of the river sediment. The accompanying vertebrate fauna has an Upper Pannonian (Lower Turolian, MN 11) age. A similar find of an *Ictitherium viverrinum* mandible fragment originated from the nearby locality of Vösendorf in Austria which is a little bit older (Early Vallesian, MN 9) (Zapfe 1948).

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