Acta zool. cracov. **41**: 1-22, Kraków, 18 Dec.1998

Late Miocene snakes (Reptilia: Serpentes) from Polgárdi (Hungary): a second contribution

Márton VENCZEL

Received: 22 Oct.,
Accepted for publication: 5 May, 1998

VENCZEL M. 1998. Late Miocene snakes (Reptilia: Serpentes) from Polgárdi (Hungary): a second contribution. Acta zool. cracov. **41**: 1-22.

Abstract. New fossil ophidian materials from the Late Miocene (MN 13) localities of Polgárdi 2, Polgárdi 4 "Lower", Polgárdi 4 "Upper" and Polgárdi 5 (Hungary) are described. The ophidian assemblages contained at least ten different taxa: *Coluber hungaricus*, *Coluber* sp., *Coronella miocaenica* sp.n., *Elaphe kormosi*, *E. praelongissima*, *E. szyndlari* sp. n., *Telescopus* sp., *Natrix* cf. *N. longivertebrata* (Colubridae), *Macrovipera gedulyi* and *Vipera* sp. (Viperidae). All the taxa described in this paper belonged to extant genera, which widely replaced those of older faunas prior to the Messinian crisis. The Polgárdi localities produce the oldest fossil records of the genera *Coronella* and *Telescopus*, and, at the same time show the last occurrence of the genus *Macrovipera* in Central Europe. The composition of the snake assemblages of the Polgárdi localities, slightly differing in age, may evidence the fluctuating climatic conditions, which favoured a rapid spread of small sized modern colubrine snakes of Asiatic origin in Europe.

Key words: Serpentes, late Miocene, Hungary, osteology.

Márton VENCZEL, Muzeul Tarii Crisurilor, B-dul Dacia Nr. 1-3, R 3700 Oradea, Romania.

I. INTRODUCTION

The Polgárdi localities, bearing abundant vertebrate remains are well known in paleontological literature. Until now, five different fossil carst deposits have been distinguished in the carboniferous limestone quarries of Somló-Hill and Kőszár-Hill, near the village of Polgárdi (W-Hungary) (FREUDENTHAL & KORDOS 1989). The age of the vertebrate assemblages obtained from them may be defined as Pontian or Upper Turolian (mammalian biozone MN 13).

SZYNDLAR (1991a, 1991b), having re-examined of the type material of *Coluber hungaricus*, *Elaphe kormosi* and *Vipera gedulyi* coming from Polgárdi 2, taxa previously studied by BOLKAY (1913) and SZUNYOGHY (1932), recognized only *E. kormosi* and *V. gedulyi* as valid species. *Coluber hungaricus*, based on a single quadrate, was considered by this author a to be nomen dubium. It should be added that the above authors never used vertebrae in their studies.

In my previous paper (VENCZEL 1994) I have redescribed the snake remains of Polgárdi 2, considered as the classical locality, as well as remains coming from Polgárdi 4 "Lower" and Polgárdi 4 "Upper", the latters corresponding to fossil assemblages coming from two different fissure fillings (FREUDENTHAL & KORDOS 1989), in which I have found abundant additional material (cranial bones and vertebrae) of *Coluber hungaricus*, *Vipera gedulyi* ('Oriental vipers' group) and few remains refferable to *Vipera* sp. ('European vipers' group). A part of the type material of *E. kormosi* from Polgárdi 2 has been assigned to another extinct member of the genus: *E. praelongissima*, recorded from the other Polgárdi localities also. The remains of *Coronella* from Polgárdi 4 has been considered as closely related to those of the living *C. austriaca*. The remains from Polgárdi assigned to the genus *Natrix*, in spite of the opinions of BOLKAY (1913) and SZUNYOGHY (1932), very probably belonged to a single species, namely to *Natrix* cf. *N. longivertebrata.*

In this paper I intend to give an analysis of the snake remains coming from Polgárdi 5, as well as those from Polgárdi 4, which remained undescribed in my previous paper. All the remains belong to the paleontological collection of the Geological Museum of Hungary in Budapest.

A c k n o w l e d g e m e n t s.The author is grateful to Professor László KORDOS, for the loan of the fossil snake material and his kind help during this study.

II. SYSTEMATIC PART

Order *Serpentes* LINNAEUS, 1758

Family *Colubridae* OPPEL, 1811

Genus *Coluber* LINNAEUS, 1758

Coluber hungaricus (BOLKAY, 1913)

M a t e r i a l. Polgárdi 4 "Lower": one prefrontal (No. V.20598), 5 frontals (No. V.20599/1-5), 7 dentaries (No. V.20600/1-7), one fragmentary supraoccipital (No. V.20601), one axis (No. V.20602), 80 vertebrae (No. V.20603/1-80). Polgárdi 4 "Upper": one frontal (No. V.20604), one axis (No. V.20605), 120 vertebrae (No. V.20606/1-120). Polgárdi 5: three fragmentary basiparasphenoids (No. V.20607/1-3), 3 frontals (No. V.20608/1-3), 4 prootics (No. V.20609/1-4), 2 quadrates (No. V.20610/1-2), one ectopterygoid (No. V.20611), 8 compound bones (No. V.20612/1-8), 2750 vertebrae (No. V.20613/1-2750).

The prefrontal from Polgárdi 4 "Lower" is a small ring-shaped bone, with its lateral surface smooth. In posterolateral view the lacrimal foramen is small.

The frontals (Fig. 1 a-f) belonged to specimens varying in size. The shape of the bones are consistent with that of the bones from Polgárdi 4 "Lower" (VENCZEL 1994: fig. 2 m,n,o). The orientation and degree of development of the inner prefrontal process show some variation. In big specimens this structure projects laterally and slightly anteriorly. The septomaxillary process is relatively long and oriented anterolaterally, with its distal end slightly widened. The trabecular crest is well marked in all specimens.

The basiparasphenoids (Fig. 1 g,h and Fig. 2 a-c) from Polgárdi 5 closely resemble that from Polgárdi 4 "Lower" (VENCZEL 1994: fig. 1 d,e,f) and to a lesser degree those from Polgárdi 2 (VENCZEL 1994: fig. 1 a,b,c). In all three specimens the anterior portion of parasphenoid process is broken off. In the largest specimen (Fig. 2 a-c) the posterior portion of a relatively thin and high frontal crest is preserved. The foramina of the Vidian canal are positioned similarly to those in other specimens, while those of the abducens and cid nerves show some intraspecific variation. In the smaller specimens from Polgárdi 5 (Fig. 1 g,h) these structures are situated close to each other, while in the larger ones at some distance.

Four prootics (Fig. 1 i-k) from Polgárdi 5, assigned to this species, differ from each other and from those from Polgárdi 4 "Lower" (VENCZEL 1994: fig. 1 g) in the shape of the foramen for the

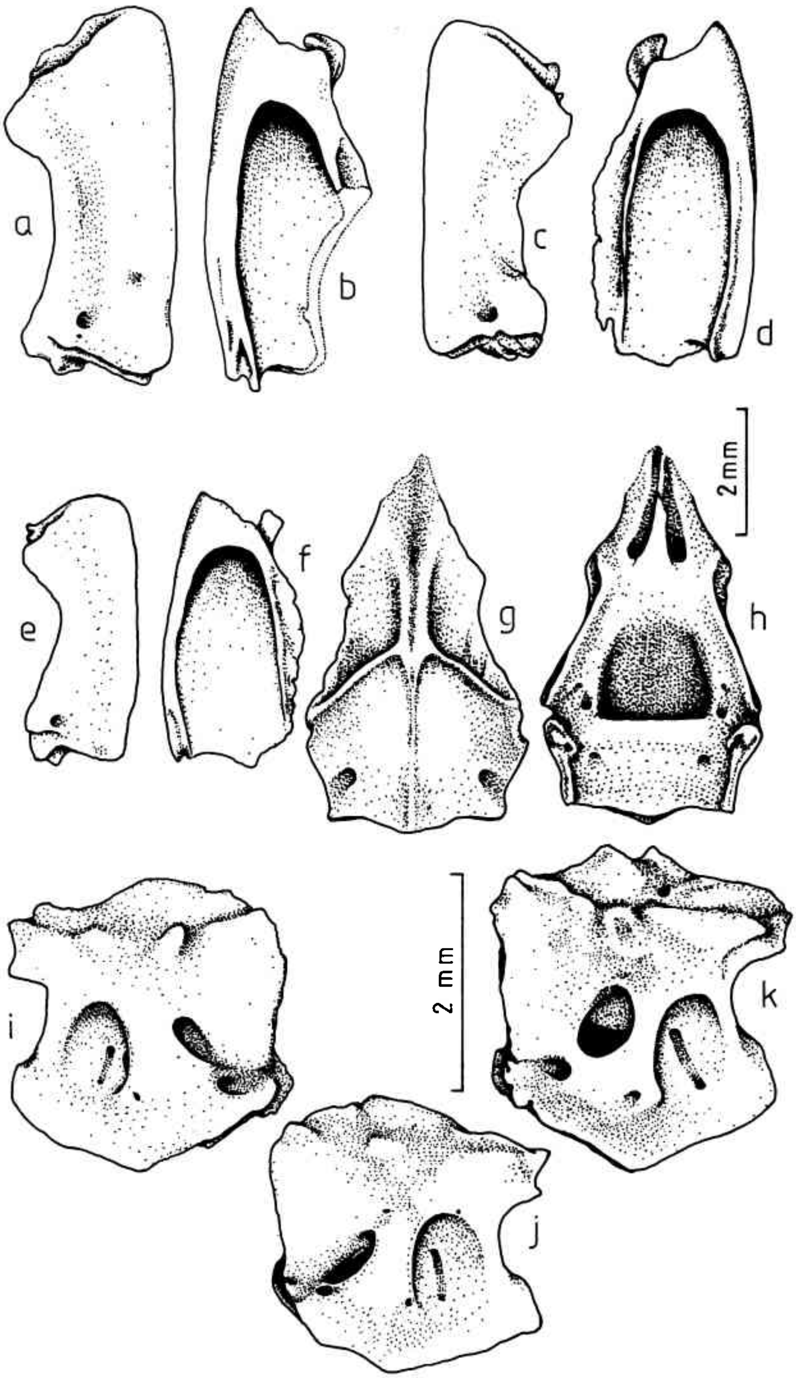

Fig. 1. *Coluber hungaricus*. a,b, c,d, and e,f – three frontals (Polgárdi 5, No. V.20608/1-3), g,h – basiparasphenoid (Polgárdi 5, No. V.20607/2), i-k – three prootics (Polgárdi 5, No. V.20609/1-3). a,c,e,h – dorsal views; b,d,f – medial views; g – ventral view; i-k – lateral views.

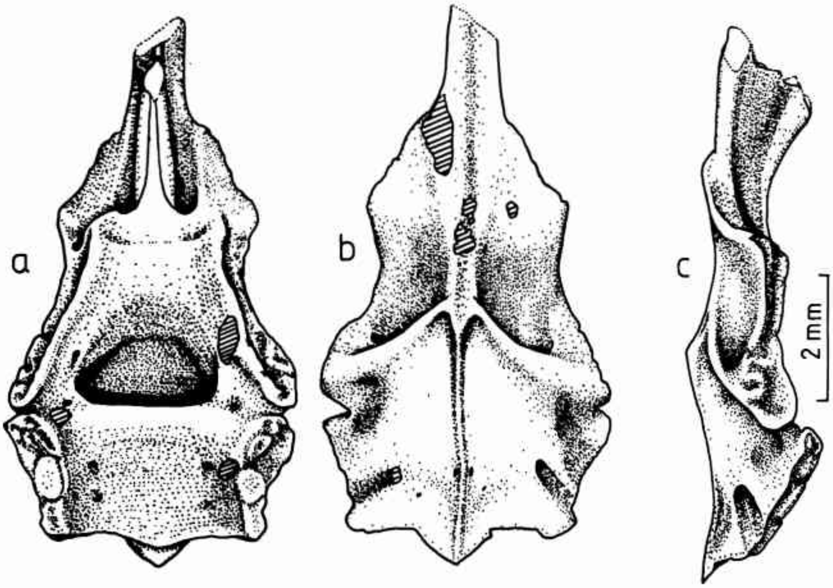

Fig. 2. *Coluber hungaricus.* a-c – basiparasphenoid (Polgárdi 5, No. 20607/1). a – dorsal view; b – ventral view; c – lateral view.

maxillary branch of the trigeminal nerve (V_2) and in the width of the laterosphenoid bar. A left prootic, belonging to a relatively large specimen, had an extremely thin laterosphenoid bar and its assignement to the above species is taken with some reserves. The supraoccipital crest is not well developed or even lacking in smaller specimens. The otic recess is relatively large in all the prootics.

The ectopterygoid (Fig. 3a) from Polgárdi 5, resembles those from Polgárdi 4 "Lower", but it is provided with somewhat longer ectopterygoid rami, and the stem near its distal end is not widened to the degree observed in the specimens from Polgárdi 4 "Lower" (VENCZEL 1994: fig. 2 k,l).

The trochlea quadrati of the quadrates (Fig. 3 b-e) from Polgárdi 5 is strongly built. The stem of the bone is relatively thin, with its proximal end widened in posterolateral view; the posterolateral margin is bent. The quadrate crest is sharp, becoming higher in the proximal portion. Consequently, in posterior view, the stem of the bone is thinner between the trochlea quadrati and the stapedial process. The latter structure is relatively small.

The dentary is provided with 15 teeth of proterodont type. Seven dentaries from Polgárdi 4 "Lower", with the posterior portion of the tooth row lacking, may have belonged to this species, too.

The compound bones (Fig. 3 f-i) from Polgárdi 5 show a wide range of intraspecific variation. Specimens of variable size differ from each other in the degree of development of the supraangular crest and in the height of the coronoid process as well as in the shape of the lateral flange. Usually, in large specimens the mandibular fossa becomes wider and the upper margin of the lateral flange bends laterally, producing its increased concavity. In some specimens layers of different density, interpreted here as growth layers, can be observed. Accordingly, 5-6 layers are preserved in the smaller specimen (Fig. 3 i) and 17-18 in the fairly big specimen (Fig. 3 g), which fact suggests that the former animal died after 5-6 seasons of growth and the latter after 17-18 seasons (the groth layers are probably equivalent to age in years).

The centrum of the axis (Fig. 3 j) equals in length that of the hypapophysis. The latter structure projects posteroventrally and is obtused-shape distally. The low neural spine projects anteriorly and posteriorly. The anterior overhang is smaller than the posterior one.

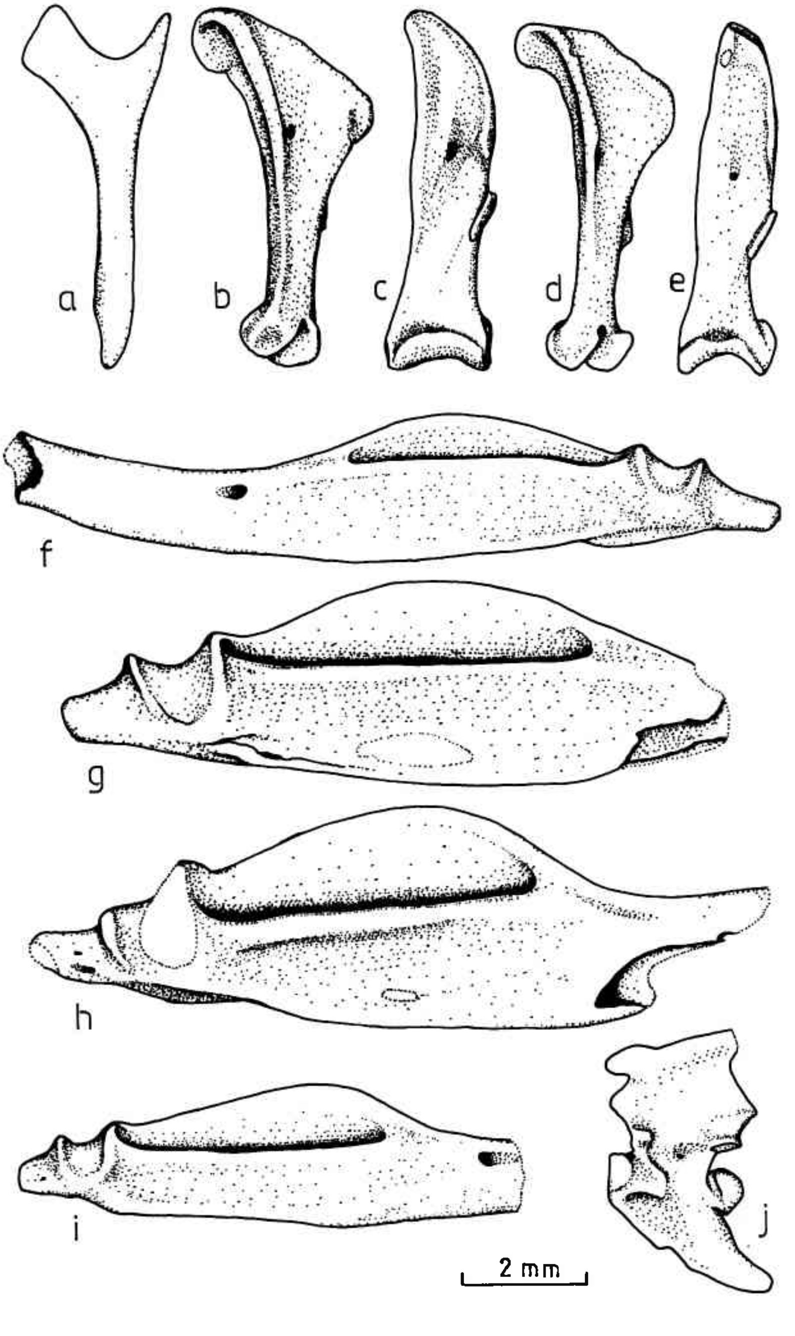

Fig. 3. *Coluber hungaricus*. a – left ectopterygoid (Polgárdi 5, No. V.20611), b,c, d,e – left quadrates (Polgárdi 5, No. V.20610/1-2), f-i – compound bones (Polgárdi 5, No. V.20612/1-4), j – axis (Polgárdi 5, No. V.20613/1). a – dorsal view; b,d – posterolateral views; c,e – posterior views; f-j – lateral views.

In their morphology the trunk vertebrae (Fig. 4) from Polgárdi 5 generally agree with those described from Polgárdi 4. Some minor differences observed may be considered as intraspecific variation. The dorsal edge of the neural spine, especially in larger specimens, is thickened (Fig. 4a-e). The anterior margin of the zygosphene is usually straight, but sometimes it is provided with a small central lobe or, rarely, is concave. The haemal keel is usually flattened and spatulate, but sometimes it is prominent and thin, provided with paired subcotylar tubercles (Fig. 4f). In the posteriormost trunk vertebrae (Fig. 4 g-i) the haemal keel is always prominent, with well developed subcentral ridges. Sometimes the parapophyses are longer than the diapophyses. In 100 trunk vertebrae measured from Polgárdi 5, the centrum length ranges from 3.28 to 4.63 mm and the centrum width from 2.30 to 3.34 mm. The centrum length / centrum width ratio ranges between 1.21-1.61 (mean = 1.37).

Comments. Considering all the above-described elements, *C. hungaricus* resembles the larger members of the genus in a number of features, e.g. the disposition of foramina in the basiparasphenoid is like that in *C. viridiflavus*, in shape the quadrate and compound bones approach those observed in both *C. viridiflavus* and *C. gemonensis*. The number of dentary teeth approaches that in *C. caspius*. Regarding morphology, the vertebrae, especially the largest ones from Polgárdi 5, show a great resemblence to those of *C. caspioides* (e.g. the shape of the zygosphene and of haemal keel, the length of the prezygapophyseal process, the height of the neural spine, the reduced interzygapophyseal ridges, etc.), known from the Lower Miocene (MN 4) locality of Petersbuch 2, Germany (SZYNDLAR 1993: fig. 6). The centrum length / centrum width ratio in *C. hungaricus* is nearly as high as in *C. caspioides*. However the former, as suggested by available remains, never reached the size of the latter. Some resemblence to *Elaphe kohfidischi* is also visible (e.g. the morphology of the basiparasphenoid and of the trunk vertabrae). The trunk vertebrae of a colubrine snake, described by SZYNDLAR (1995) from the Turolian/Ruscinian boundary (MN 13/14) of Maramena (Macedonia, Greece) may have been closely related those of *C. hungaricus* in morphology but somewhat larger in size.

Genus *Coronella* LAURENTI, 1768

Coluber sp.

M a t e r i a l. Polgárdi 5: one compound bone (No. V.20614), 1 axis (No. V.20615), 100 vertebrae (No. V.20616/1-100).

All the remains belonged to a small sized colubrine snake. The coronoid process of the compound bone is not prominent, and the supraangular crest weakly developed. The hypapophysis of the axis is relatively short (shorter than the centrum) and pointed distally. The vertebrae are of small size, resembling in some respect those of *C. ravergieri – nummifer* group (e.g. weakly developed haemal keel, wide zygosphene with well-developed central lobe, relatively long, thin and distally pointed prezygapohyseal processes, low centrum length / centrum width ratio).

Coronella miocaenica sp. n.

1994 *Coronella* cf. *C. austriaca* LAURENTI, 1768: VENCZEL, pp. 7-9, fig. 3.

H o l o t y p e. A mid-trunk vertebra (No. V.20617) (Fig. 6 a-e) .

T y p e l o c a l i t y. Polgárdi 4 "Lower".

T y p e h o r i z o n. Uppermost Miocene; Pontian or Upper Turolian (MN 13).

N a m e d e r i v a t i o n. From the Latin word for Miocene.

R e f e r r e d m a t e r i a l. Polgárdi 4 "Lower": one left frontal (No. V.20618), one fragmentary parietal (No. V.18970/a), one basioccipital (No. V.18970/e), two prootics (No. V.18970/b), two maxillae (No. V.18970/c and V.20619), one quadrate (No. V.18970/d), 2 compound bones (No.

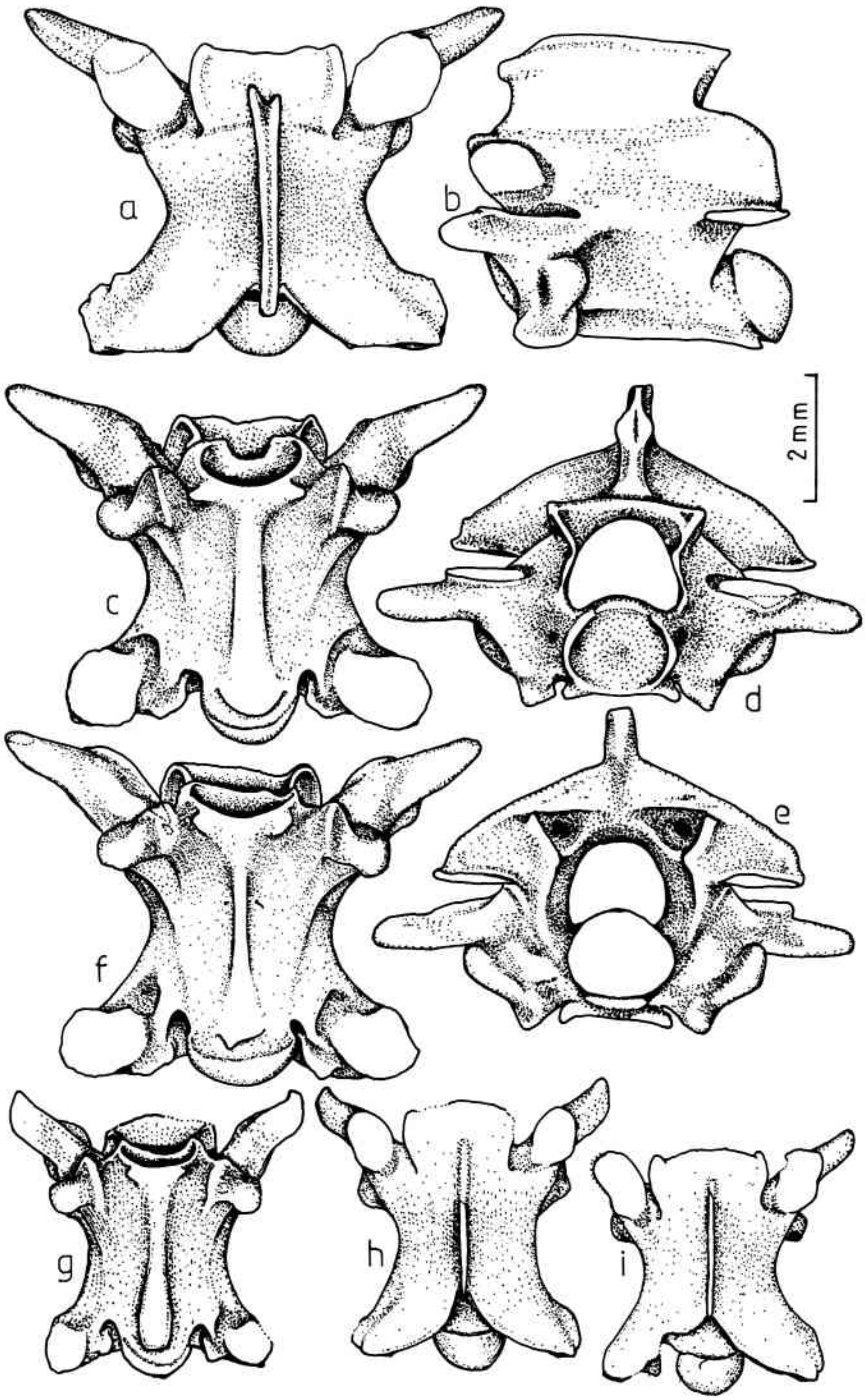

Fig. 4. *Coluber hungaricus*. a-e – midtrunk vertebra (Polgárdi 5, No. 20613/2), f – mid-trunk vertebra (Polgárdi 5, No. V.20613/3), g,h – posterior trunk vertebra (Polgárdi 5, No. V.20613/4), i – posterior trunk vertebra (Polgárdi 5, No. V.20613/5). a,h,i – dorsal views; c,e,g – ventral view; b – lateral view; d – anterior view; f – posterior view.

V.20620/1-2) and 350 vertebrae (No. V.18971/1-80 and V.20621/1-270). Polgárdi 4 "Upper": 1 right frontal (No. V.20622), 2 compound bones (No. V.20623/1-2), 130 vertebrae (No. V.18972/1-30 and V.20624/1-100). Polgárdi 5: 1 vertebra (No. V.20625).

D i a g n o s i s. A small colubrid snake, resembling *Coronella austriaca*, but with wider and longer prefrontal processes of the frontal; medially oriented prefrontal process of the maxilla; higher neural spine, less depressed neural arch and distinctly lower centrum length/centrum width ratio of the mid-trunk vertebae.

D e s c r i p t i o n o f h o l o t y p e. A mid-trunk vertebra preserved completely except for small portions of the pre- and postzygapophyses on the right lateral aspect of the bone, which are broken off.

In lateral view, the neural arch is depressed, with the neural spine distinctly longer than high, overhanging only posteriorly. The posterior margin of the neural laminae ("aliform process") is well developed, while the epizygapophyseal spine is absent. The paradiapophyses are incompletely differentiated into para- and diapophyseal portions; the parapophyses are longer than diapophyses The interzygapophyseal ridge is not prominent. The large lateral foramen is preserved.

In dorsal view, owing to the lateral extension of the pre- and postzygapophyses and lack of well-developed interzygapophyseal ridges, the vertebra is somewhat X-shaped. The roof of the zygosphene is straight with an indistinct median and two lateral lobes. The prezygapophyseal articular facets, oval in shape, are oriented anterolaterally. The prezygapophyseal processes are extremely short, cylindrical and obtuse distally. The dorsal margin of the neural spine is not thickened.

In ventral view, the centrum is moderately long and somewhat cylindrical in shape. The haemal keel is prominent, thin and spatulate. The subcentral ridges are present only close to the parapophyses. The postzygapophyseal articular facets, oval in shape, extend laterally. The subcentral foramina are present.

In anterior view the neural arch is depressed. The posterior margin of the neural laminae and the roof of the zygosphene are slightly convex. The paracotylar foramina are rather large and the cotyle is rounde.

In posterior view the zygantrum is somewhat wider than the condyle. The latter structure and the neural canal are rounded in shape.

The centrum length in the holotype vertebra is 3.51 mm, the centrum width 2.75 mm; the centrum is 1.27 times longer than wide. The length between the pre- and postzygapophyses is 4.29 mm, the width between the postzygapophyses is 5.19 mm, and between the prezygapophyses 5.29 mm. The width of the zygosphene is 2.35 mm, the height of the cotyle 1.41 mm and its width 1.43 mm.

D e s c r i p t i o n o f r e f e r r e d m a t e r i a l. The parietal, prootics, basioccipital, fragmentary maxilla, quadrate and a number of vertebrae have been described in my previous paper (VENCZEL 1994).

In dorsal view, the medial margin of the frontal is straight (Fig. 5 a-d), while the lateral margin is distictly concave and provided with a prominent lateral crest. The width of the bone near its posterior margin is as great as it is at the level of the external prefrontal process. Both prefrontal processes are prominent and of same length. The external prefrontal process projects laterally, while the internal one anterolaterally. The anteromedial margin is slightly convex. A distinct trabecular ridge is present in either frontal.

The maxilla from Polgárdi 4 "Lower", preserved whole, bears 15 tooth sockets. The prefrontal process is situated at the level of the 7th to 8th teeth, and the ectopterygoid process at the level of the 12th to 14th teeth. Both processes project medially being of the same width all over their length. The posterior teeth are somewhat enlarged.

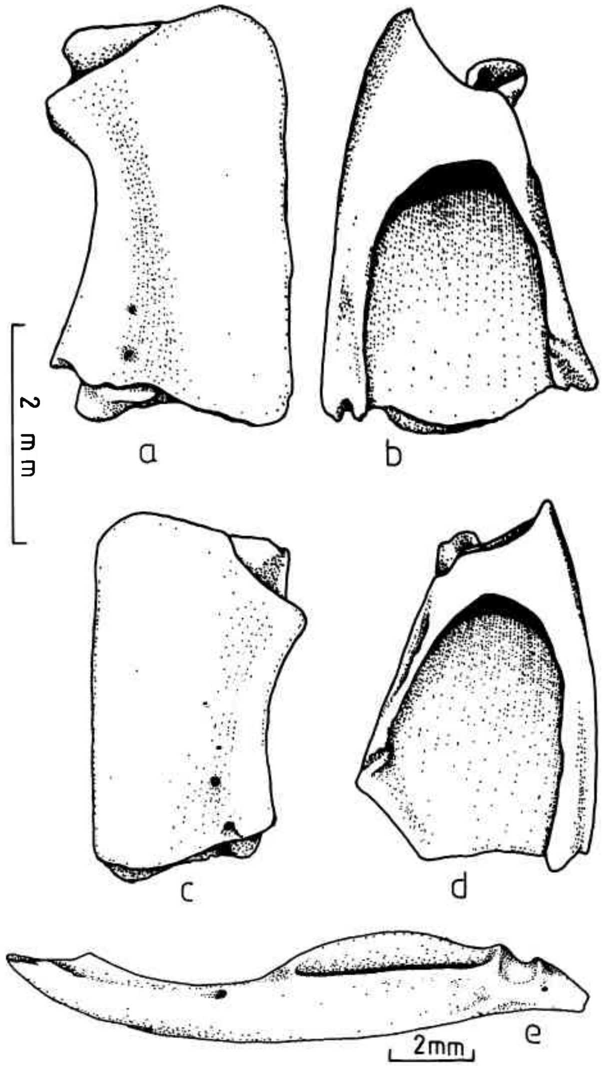

Fig. 5. *Coronella miocaenica* n. sp. a,b – left frontal (Polgárdi 4 "Lower", No. V.20618), c,d – right frontal (Polgárdi 4 "Upper", No. V.20622), e – left compound bone (Polgárdi 4 "Lower", No. V.20620/1). a,c – dorsal views; b,d – medial views; e – lateral view.

The compound bones (Fig. 5 e) agree in size and morphology (but are not identical) with the homologous elements of *Coronella austriaca.*

The trunk vertebrae show a wide intraspecific variation. The neural arch usually is depressed or moderately vaulted, provided with a neural spine longer than high and having its anterior margin straight or slightly overhanging anteriorly. The hypapophyses are sometimes very thin and prominent, which character is also observed in recent *C. austriaca*. The paradiapophyses are usually not differentiated completely into parapophyses and diapophyses. The posterior trunk vertebrae (Fig. 6 f-h) are provided with a very prominent haemal keel. In ventral view, the centrum is triangular in shape and the paradiapophyses expand strongly laterally. In thirty midtrunk vertebrae from Polgárdi 4

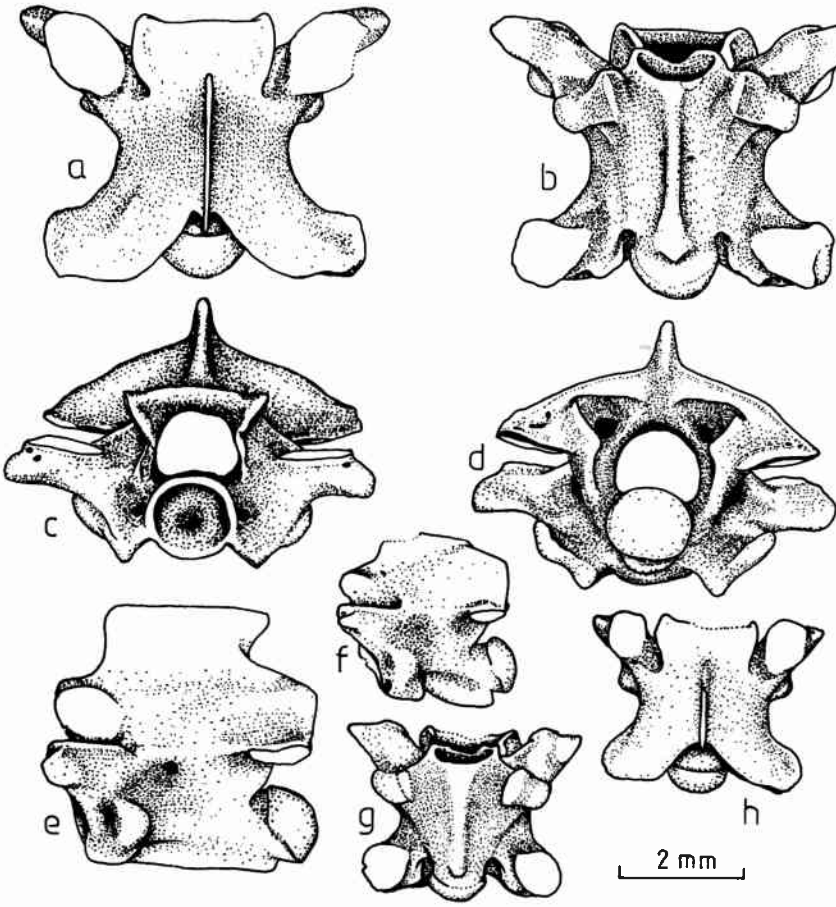

Fig. 6. *Coronella miocaenica* n. sp. a-e – holotype trunk vertebra (Polgárdi 4 "Upper", No. V.20617), f-h – posterior trunk vertebra (Polgárdi 4 "Upper"). a,h – dorsal views; b,g – ventral views; c – anterior view; d – posterior view; e,f – lateral views

"Lower" the centrum length ranges from 2.73 to 3.29 mm, and the centrum width from 2.11 to 2.97 mm. The centrum length/width ratio ranges between 1.07-1.34 (mean= 1.19). In thirty midtrunk vertebrae from Polgárdi 4 "Upper" the centrum length ranges from 2.53 to 3.41 mm, and the centrum width from 2.20 to 2.82 mm. The centrum length/centrum width ratio is between 1.02-1.42 (mean = 1.17).

D i s c u s s i o n. The prefrontal processes of the frontal in *Coronella miocaenica* n. sp. are distinctly wider and longer than in *C. austriaca* and *C. girondica*. The maxilla and the number of maxillary teeth of *C. miocaenica* n. sp. differ to some extent from those of both *C. austriaca* and *C. girondica*. The former possesses 15 maxilary teeth, with the prefrontal process situated at the level of the 6th to 7th teeth, and the ectopterygoid process at the level of the 12th to 13th teeth; the latter possesses 12 maxillary teeth, with the prefrontal process situated at the level of the 5th tooth, and the ectopterygoid process at the level of the 10th tooth. The prefrontal process in *C. miocaenica* n. sp. is the same width all over length and it is oriented medially, while in recent *C. austriaca* it tapers and projects posteromedially. The centrum length of trunk vertebrae in large specimens of *Coronella miocaenica* n. sp. reaches 3.5 mm, while the centrum length/centrum width ratio is distinctly lower than in the other members of the genus. On the contrary, the neural spine of mid-trunk vertebrae in *Coronella miocaenica* n. sp. is always higher than in *C. austriaca* and *C. girondica*. The base of the prezygapophyses of *Coronella miocaenica* n. sp. resembles in shape that in *C. austriaca*. The parapophyses in the former little exceed the length of the diapophyses, while in the latter the parapophyses are much longer than diapophyses. In *C. girondica* the proximal portions of the prezygapohyses are lightly built, while the parapophyses equal in length the diapophyses (SZYNDLAR 1984).

Based on the available fossil record, the genus *Coronella* may be considered an Asiatic immigrant, reaching Central Europe in the Late Miocene (MN 13), and the western part of the continent during Pliocene times (BAILON 1991).

Genus *Elaphe* (FITZINGER, 1833)

Elaphe praelongissima VENCZEL, 1994

M a t e r i a l: Polgárdi 4 "Lower": one fragmentary basiparasphenoid (No. V.20626/a), one intranasal (No. V.20626/b). Polgárdi 5: 2 vertebrae (No. V.20627/1-2).

The shape of the basiparasphenoid fragment is similar to that of the holotype, known from the same locality. All the foramina are situated similarly as in the latter, except those for the left anterior abducens and cid nerves, which are situated far from each other. The cid nerve turns ventrally at the level of the anterior Vidian foramen and exits in the ventral side of the basiparasphenoid in a common recess with the Vidian foramen.

The intranasal (Fig. 7a) is provided with a rather thick frontal process. The slightly bent ascending nasal process is relatively long and pointed distally. The dorsal groove is well marked. The ascending nasal process and the posterior margin of the bone approaches in shape to that observed in recent *Elaphe dione* (pers. obs.).

The vertebrae despite of their fragmentary state, agree in morphology with those described from Polgárdi 2 and Polgárdi 4 (VENCZEL,1994). The vertebral centrum is short and moderately vaulted,

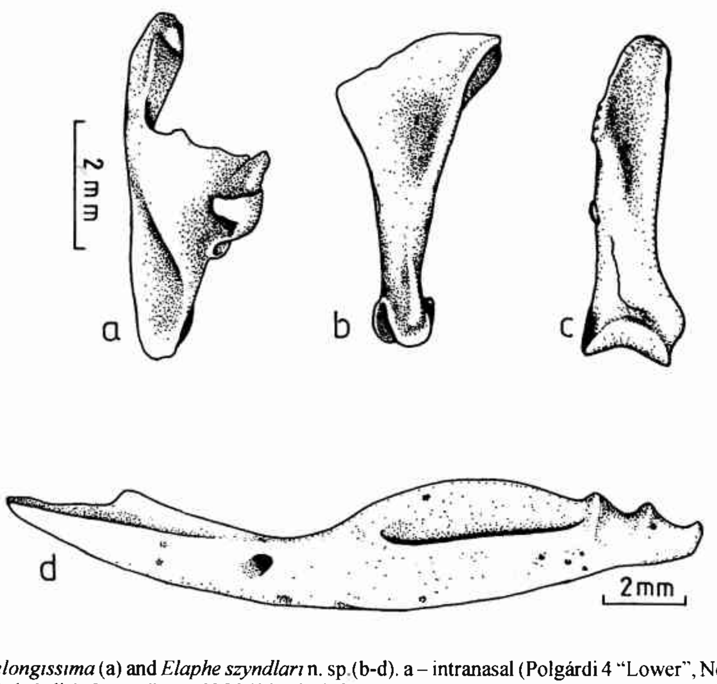

Fig. 7. *Elaphe praelongissima* (a) and *Elaphe szyndlari* n. sp.(b-d). a – intranasal (Polgárdi 4 "Lower", No. V 20626/b), b,c – right quadrate (Polgárdi 4 "Lower", No. V.20630), d – left compound bone (Polgárdi 4 "Upper", No V. 20634). a – dorsal view, b – posterolateral view, c – posterior view, d – lateral view.

the haemal keel is flattened and spatulate shaped, provided with small and paired tubercle below the cotyle lip. The margin of the zygosphene is concave, while the paradiapophyses are well differentiated into para-and diapophyseal portions. The parapophyses are longer than diapophyses.

Elaphe szyndlari sp. n.

Holotype. A fragmentary basiparasphenoid (No.V.20628) (Fig. 8 a-c).

Paratype. A basiparasphenoid (No. V.20629) (Fig. 8 d-f).

Type locality. Polgárdi 4 "Lower", W-Hungary.

Age. Late Miocene (MN 13).

Name derivation. In honour of Professor Zbigniew SZYNDLAR of the Polish Academy of Sciences in Kraków, Poland.

Referred material. Polgárdi 4 "Lower": 1 quadrate (No. V.20630), 2 compound bones (No. V.20631/1-2), 45 vertebrae (No. V.20632/1-45). Polgárdi 4 "Upper": 1 ectopterygoid (No. V.20633), 1 compound bone (No. V.20634), 7 vertebrae (No. V.20635/1-7).

Diagnosis. A medium-sized colubrid snake, with relatively long Vidian canals; small and turned upward suborbital flanges and an extremely low frontal step of the parasphenoid; the trunk vertebrae with a short centrum and a longer than high neural spine, straight zygosphene, short and distally pointed prezygapophyseal processes, indistinctly differentiated paradiapophyses and a flattened haemal keel.

Description of holotype. The holotype basiparasphenoid, with its parasphenoid process broken off, belonged to an adult individual.

In ventral view, a relatively deep groove starting in the central area runs anteriorly. The anterior Vidian foramina are covered by the pterygoid crests. The latter structures are wide apart and, running posterolaterally, they reach the lateral margin of the bone. The cid nerves exit separately through small foramina (situated in a depression), anterolateral to the Vidian openings (well seen on the left ventral side).

In dorsal view the anterior foramina of the abducens nerves, situated in the vicinity of the posterolateral corners of the pituitary fossa, open close to those for the cid nerves. The course of the latter nerves through the parasphenoid is variable on the right side the anterior portion extends in a furrow and where this branch exits on the ventral side of the bone, the margin of the parasphenoid forms an incisure. On the left side two foramina are visible anterior to the abducens nerve foramen. The posterior one is the entrance for the cid nerve to the parasphenoid, while the anterior foramen is the point where it turns downward and exits on the ventral side of the bone. The posterior margin is provided with a small central lobe. The suborbital flange is small, but somewhat wider than in the paratype specimen and the base of the frontal ridge of the parasphenoid shows a similar structure to that in the paratype (see below).

Description of paratype. The basiparasphenoid preserved complete belonged to a relatively small specimen.

In ventral view the parasphenoid tapers to two points. A shallow groove beginning in the central area extends over the parasphenoid. The suborbital flanges are very small. The basisphenoid crest is absent. The pterygoid crest, surmounting the distinct basipterygoid processes is high and laterally reaches the margin of the basisphenoid. The Vidian canal is relatively long. The anterior foramina open well inside the basisphenoid border and are not covered by pterygoid crests; the posterior foramina are situated at some distance from the posterolateral margin of the bone. Two small foramina are present anteromedially to the anterior Vidian foramina. The posterior margin is provided with a small central lobe.

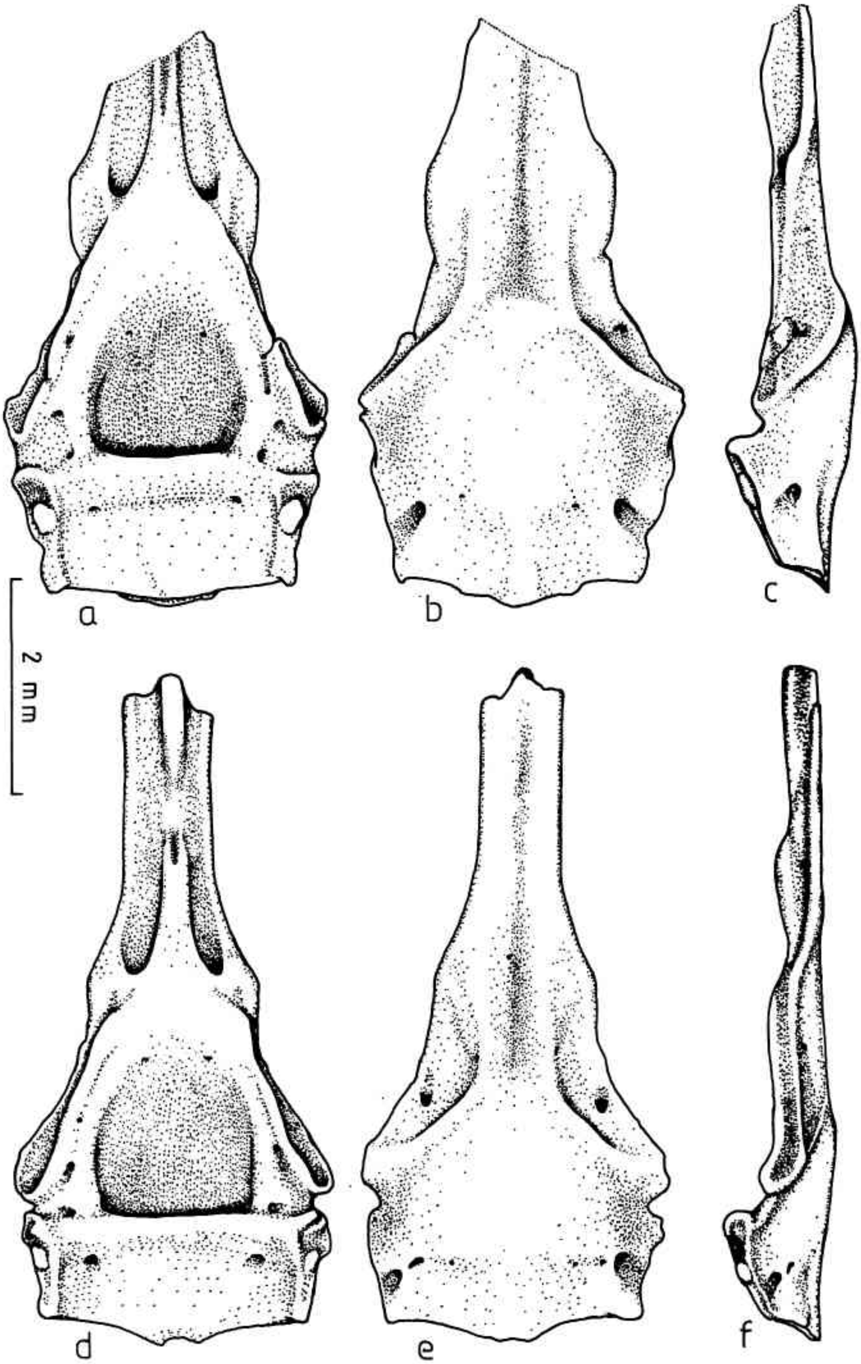

Fig. 8. *Elaphe szyndlari* n. sp. a-c – holotype basiparasphenoid (Polgárdi 4 "Lower", No. V.20628), d-f – paratype basiparasphenoid (Polgárdi 4 "Lower", No. V.20629). a,d – dorsal views, b,e – ventral views, c,f – lateral views.

In dorsal view, the frontal step is of low height and a simple structure. At this point a shallow groove opens anteriorly. The frontal ridge is better defined in the anterior portion of the parasphenoid. The pituitary fossa is large, delimited posteriorly by a noticeable bony lamella. The latter structure is penetrated on both sides by the paired abducens nerve. The course of the constrictor internus dorsalis branch of the trigeminal nerve (= cid nerve) is somewhat asymmetric, the foramen for its reentrance on the right side is situated anteriorly further to the front than its counterpart on the left side. In front of the latter there is another foramen and perhaps it is there that the cid nerve turns ventrally and exits through the anterior opening of the Vidian canal.

In lateral view the frontal step is of low height. The frontal ridge is slightly raised anteriorly.The suborbital flange is somewhat curved dorsally.

Description of referred material. The dorsal portion of the quadrate (Fig. 7 b-c) is widened. The trochlea quadrati is strongly built. The quadrate crest is low and inclined anterolaterally. It is produced in a prominences above the trochlea quadrati. The stapedial process is small.

The stem of the ectopterygoid tapers near the posterior tip. The external ramus forms a right angle with the internal ramus, the distal end of the latter being broken off.

The medial flange of the compound bone (Fig. 7 d) is aproximately twice as high as the lateral flange. The supraangular crest is present and the retroarticular process curved strongly medially.

The trunk vertebrae (Figs 9 and 10) of larger specimens are strongly built. In lateral view they are as high as long, with the neural arch moderately vaulted. The neural spine is distinctly longer than high, slightly overhanging anteriorly and posteriorly, the anterodorsal margin is not thickened. The interzygapophyseal ridge is weakly developed. The lateral foramina are situated in a shallow fossa. The paradiapophyses are indistinctly differentiated, the parapophyses are slightly longer than diapophyses. The subcentral ridges are undeveloped. In dorsal view the posterior notch of the neural arch is relatively deep. The epizygapophyseal spine is absent. The neural spine is thin and of similar width throughout its length. The zygosphenal roof is straight, delimited laterally by two small lobes. The prezygapophyseal articular facets are oval and directed anterolaterally. The prezygapophyseal processes are strongly built, pointed distally and approximately one-third the length of the prezygapophyseal diameter. In ventral view the centrum is slightly longer than wide, triangular in shape. The haemal keel is extremely low, thin-edged and indistinctly delimited laterally by very shallow subcentral grooves. The caudal portion of the haemal keel is slightly widened. The subcotylar tubercles are missing. The subcentral foramina are present. The postzygapophyses are oval and directed posterolaterally. In anterior view the neural arch is moderately vaulted. The zygosphenal roof is slightly convex. The neural canal is rounded and the cotyle flattened dorsoventrally. The paracotylar foramina are distinct. The parapophyses are triangular, not very prominent. In posterior view the neural arch is moderately vaulted. The zygantrum is wider than the condyle, which is slightly depressed dorsoventrally.

Basic measurements of the largest trunk vertebra: centrum length – 4.7 mm; centrum width – 4.32 mm; the length between the outer edges of the prezygapophyses – 7.14 mm; the length between the outer edges of the postzygapophyses – 6.91 mm; the length between the anterior margins of the prezygapophyses and posterior margin of the postzygapophyses – 6.05 mm; zygosphene width – 3.36 mm; cotyle height – 2.08 mm; cotyle width – 2.52 mm.

In morphology the other vertebrae generally agree in morphology with those figured, but some specimens shows a number of differences. In some cases the hypapophysis is more flattened and not widened in front of the condyle; the parapophysis is distinctly longer than the diapophysis; in small specimens the zygosphene is usually crenate and the prezygapophyseal processes are very short and thin.

D i s c u s s i o n. *Elaphe szyndlari* n. sp. differs in its relatively small size from all the fossil and living European members of the genus except the extinct *E. praelongissima* and the living *E. scalaris* and *E. situla.* The shape of the basiparasphenoid and quadrate approaches that observed in *E. situla*, but in the latter the suborbital flange is better developed and the frontal ridge of the parasphenoid differs in morphology. It differs from *E. praelongissima* by having distinctly longer Vidian canals. Moreover, in the above species the course of the cid nerves in the dorsal side of the bone is completely different. The suborbital flanges of the basiparasphenoid in *E. praelongissima* are slightly bent ventrally, while in *E. szyndlari* n. sp. they bend dorsally. The latter form, contrary to *E.*

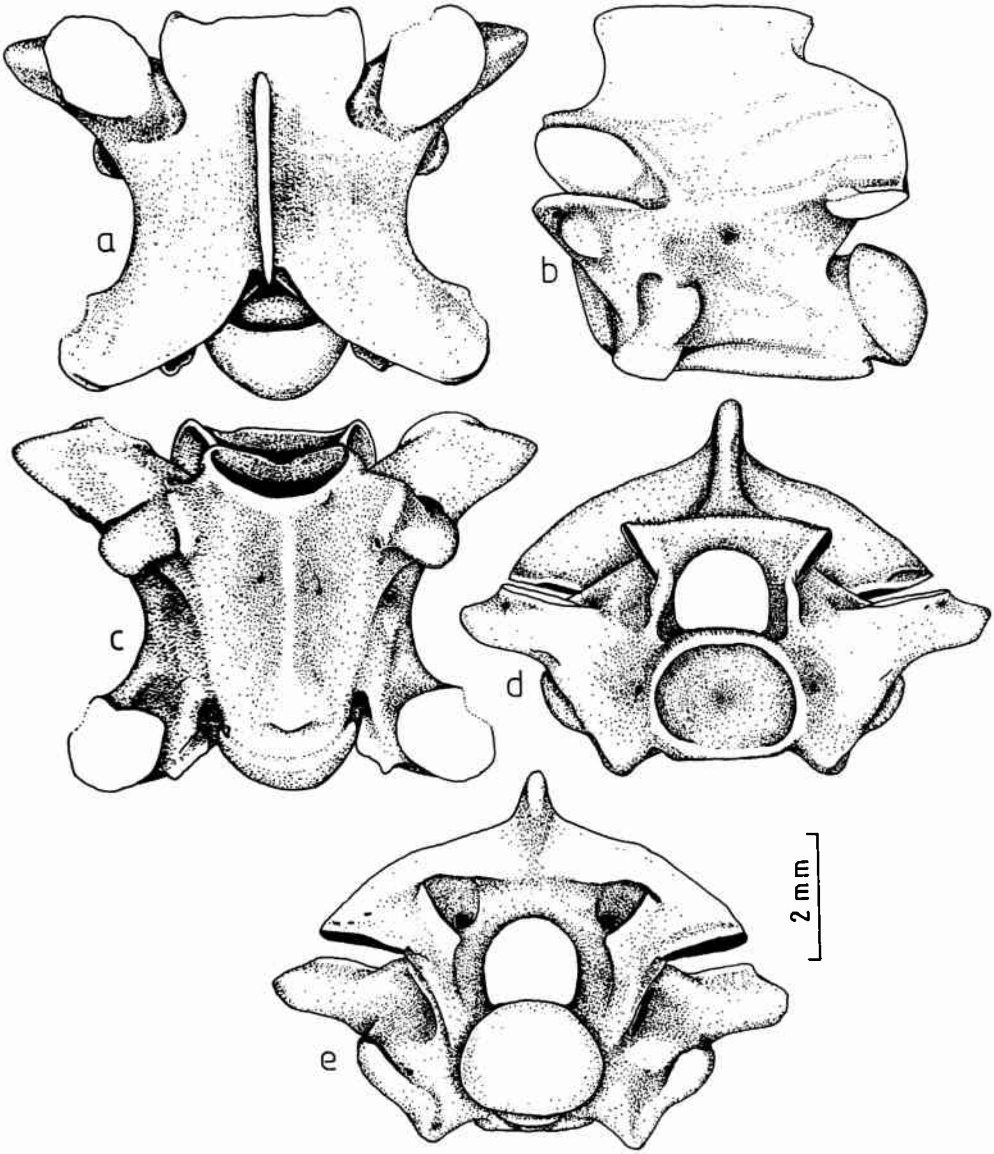

Fig. 9. *Elaphe szyndlari* n. sp. a-e – mid-trunk vertebra (Polgárdi 4 "Upper", No. V.20635/1). a – dorsal view; b – lateral view; c – ventral view; d – anterior view; e – posterior view.

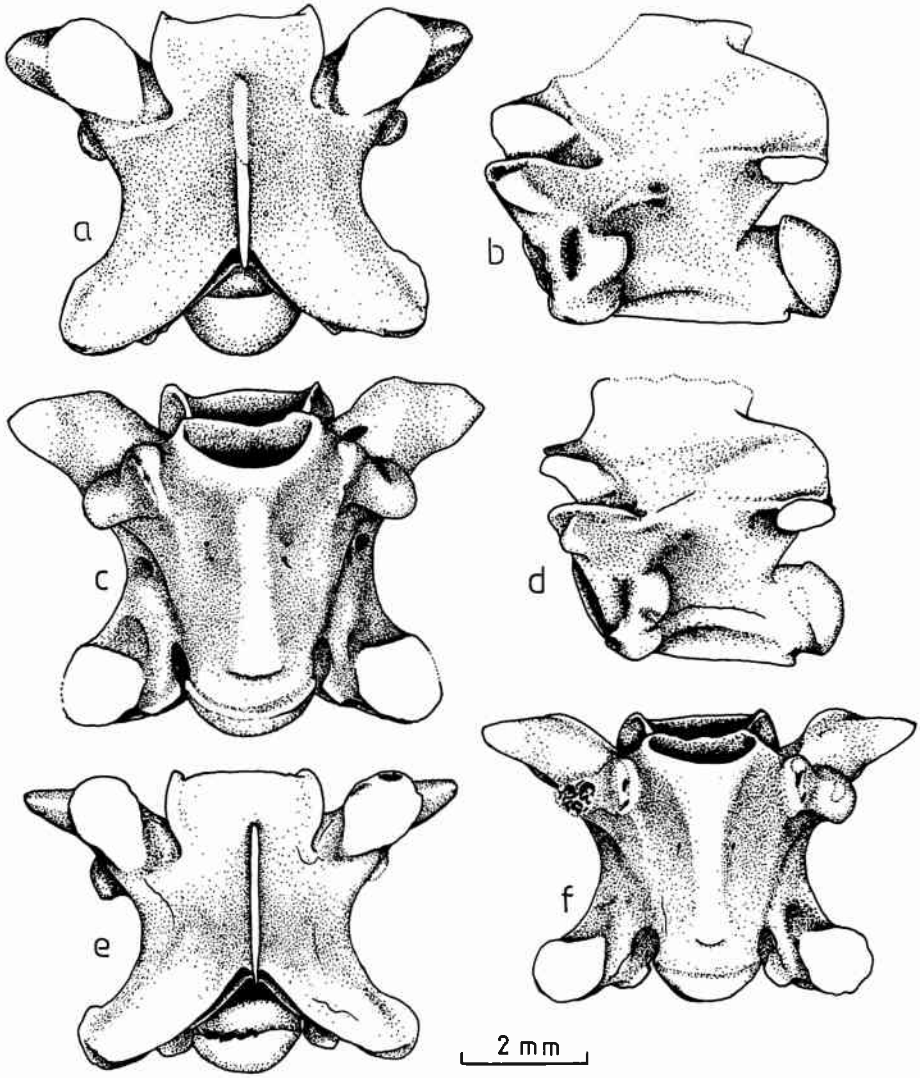

Fig. 10. *Elaphe szyndlari* n.sp. a-c – trunk vertebra (Polgárdi 4 "Upper", No. V.20635/2), d-f – trunk vertebra (Polgárdi 4 "Lower", No. V.20632/1). a,e – dorsal views; b,d – lateral views; c,f – ventral views.

praelongissima, is provided with a distinctly higher coronoid process, concave lateral flange and with a better defined supraangular crest of the compound bone. The trunk vertebrae of *E. szyndlari* n. sp. differ from those of *E. praelongissima* in having a distinctly lower neural spine, straight anterior margin of the zygosphene, strongly built, short and distally pointed prezygapophyseal process, less prominent haemal keel and lastly in having no paired tubercles below the cotyle lip. The trunk vertebrae of *E. szyndlari* n. sp. somewhat resemble those of recent *E. scalaris* (e.g. extremely low centrum length / centrum width ratio, straight or convex anterior margin of the zygosphene and distally pointed prezygapophyseal processes), but in the latter the neural spine is comparatively higher, the parapophyseal portion of the paradiapophyses is distinctly longer than the diapophyseal portion and the haemal keel is more prominent and spatulate.

Up to now, three different extinct species of *Elaphe* have been described from the Polgárdi localities: *E. kormosi*, found in Polgárdi 2 only, shows clear affinities with the larger members of the genus *Elaphe* (e.g. *E. quatuorlineata*, *E. kohfidischi*, *E. longissima*) and *Coluber* (e.g. *C. viridiflavus* and *C. caspius*) (BACHMAYER & SZYNDLAR 1985, 1987; SZYNDLAR 1991a, 1991b; VENCZEL 1994). On the other hand, *E. praelongissima* (recorded from the localities Polgárdi 2, Polgárdi 4 "Lower", Polgárdi 4 "Upper" and Polgárdi 5) and *E. szyndlari* n. sp. (found in Polgárdi 4 "Lower" and Polgárdi 4 "Upper") show a number of similarities to smaller members of the genus (*E. dione, E. scalaris* and *E. situla)*. At the same time it should be mentioned that a complete differentiation diagnosis between *E. praelongissima* and *E. szyndlari* n. sp. is impossible, because it is hardly demonstrable in the case of some cranial bones (e.g. intranasal, ectopterygoid, dentary, compound bone) and vertebrae (e. g. sacral and caudal vertebrae) to which of these two forms they may have be-.onged.

Genus *Telescopus* WAGEER, 1830

Telescopus sp.

M a t e r i a l. Polgárdi 4 "Lower": 3 vertebrae (No. V.20636/1-3); Polgárdi 4 "Upper": 7 vertebrae (No. V.20637/1-7).

The trunk vertebrae (Fig. 11) are of medium size and somewhat resemble those of living *Telescopus fallax.*

In lateral view the neural arch is depressed and provided with a neural spine distinctly longer than high, overhanging anteriorly and posteriorly. The interzygapophyseal ridge is poorly developed. The haemal keel is prominent. The parapophyseal and diapopyseal portions of the paradiapohyses are well diferentiated and equal in length. In dorsal view the anterior margin of the zygosphene is straight with an indistinct central lobe. The prezygapophyseal articular facets are oval in shape.The prezygapophyseal processes are 1/2-1/3 the length of the prezygapophyseal articular facets. They are flattened dorsoventrally and obtused distally. The dorsal margin of the neural spine is not thickened. The diapophyses are well developed and project laterally. In ventral view the centrum is short, with the subcentral ridge developed only in the vicinity of the parapophyses. The haemal keel is prominent and flattened and the same width over its whole length. Below the cotyle lip are present small sized subcotylar tubercles. The postzygapophyses are oval in shape. In ınterior view the neural arch is depressed, with a low neural spine. The zygosphene is straight and the neural canal of subquadrate shape. The cotyle is flattened dorsoventrally. Paracotylar foramina is well visible. In posterior view the neural arch is moderately vaulted. The condyle is depressed dorsoventrally.

The haemal keel of the posterior trunk vertebrae (Fig. 11 f,g) is prominent and forms a distinct step below the cotyle lip. The vertebral centrum is elongated and provided with an extremely low neural spine.

Fossils of the genus *Telescopus* have hitherto been recorded from the Bulgarian Middle Pleistocene of Varbeshnitsa only (SZYNDLAR 1991a).

Genus *Natrix* LAURENTI, 1768

Natrix cf. *N. longivertebrata* SZYNDLAR, 1984

M a t e r i a l. Polgárdi 4 "Lower": 42 vertebrae (No. V.20638/1-42). Polgárdi 4 "Upper": 7 vertebrae (No. V.20639/1-7). Polgárdi 5: 10 vertebrae (No. V.20640/1-10).

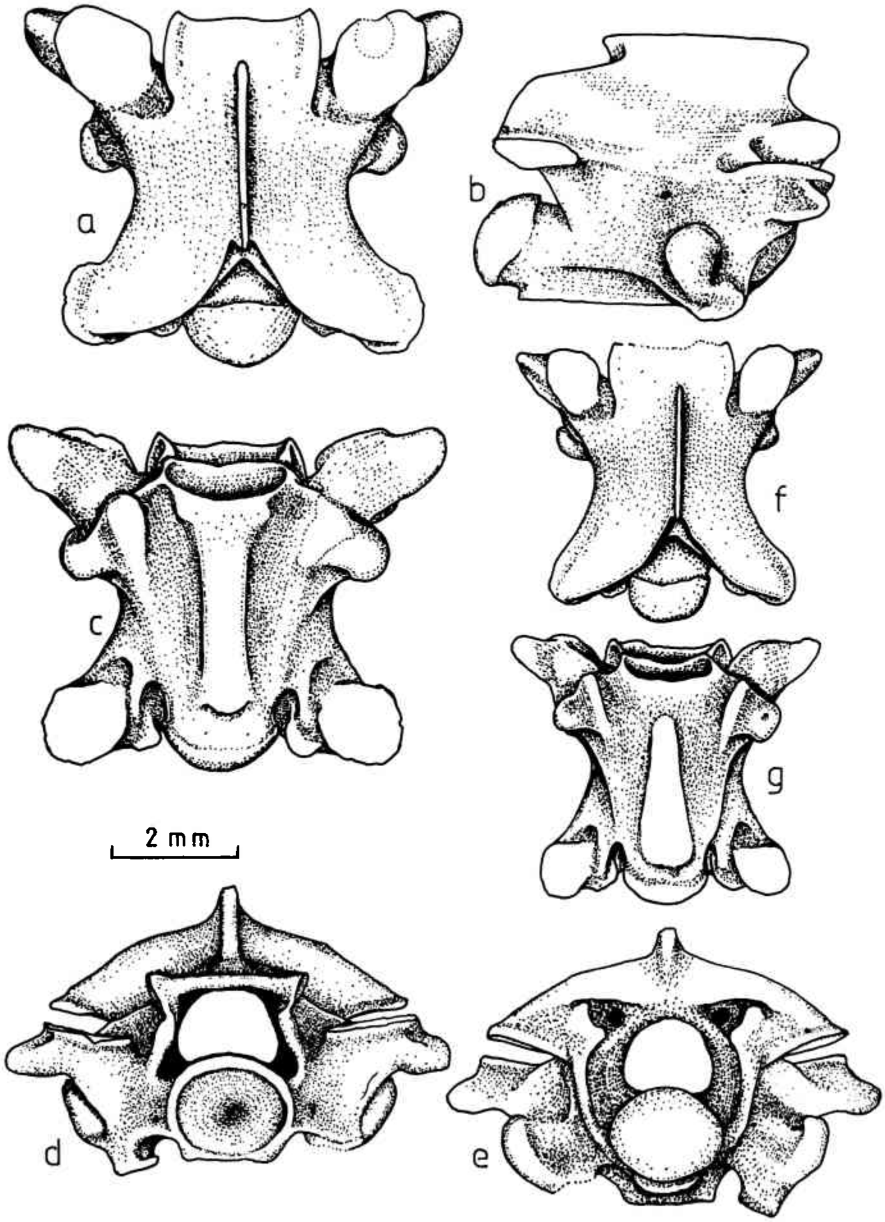

Fig. 11. *Telescopus* sp. a-e – mid-trunk vertebra (Polgárdi 4 "Upper", No. V.20636/1), f,g – posterior trunk vertebra (Polgárdi 4 "Lower", No. V.20637/1). a,f – dorsal views; b – lateral view; c,g – ventral views; d – anterior view; e – posterior view.

All the vertebrae are consistent with those described in my previous paper (VENCZEL 1994). In nine vertebrae from Polgárdi 5 the centrum length ranges between 3.38 and 4.8 mm, while the centrum width between 2.18 and 3.22 mm. The centrum length / centrum width ratio is between 1.43 and 1.72 (mean = 1.58). As it has been mentioned in my previous paper the morphology of the cranial bones, as well as the age of the remains were the reason for their assignment to the above taxon. Contrary to the opinions of BOLKAY (1913) and SZUNYOGHY (1932), there are no cranial bones or vertebrae that indicate the presence of another member of this genus, namely *N. tesselata*.

Family *Viperidae* OPPEL, 1811

Genus *Macrovipera* REUSS, 1927

In the last fifteen years several tentatives concerning the subdivision of the genus *Vipera* have been made (OBST 1983; GROOMBRIDGE 1986; ZEROVA in SZYNDLAR & ZEROVA 1992). They are supported by different morphological characters and immunological distances observed within the genus *Vipera* s.l..

The genus *Macrovipera* has been revalidated by HERMANN et al. (1992) for the 'lebetina' group of 'Oriental vipers' of GROOMBRIDGE (1986), consisting of four living species: *M. mauritanica, M.scweizeri, M. lebetina* and *M. deserti* and of four extinct species known from the Late Miocene (*M. burgenlandica, M. gedulyi, M. sarmatica*) and Early Pliocene of Europe (*M. kuchurganica*) (RAGE & SCHÄTTI 1993). The genus name *Daboia* is restricted to the living *D. russeli* of the 'Oriental vipers' group of GROOMBRIDGE (1986) and the extinct *D. maxima* from the Pliocene (MN 15) of Laina, Spain, described by SZYNDLAR (1988).

Macrovipera gedulyi (BOLKAY, 1913)

1913 *Vipera gedulyi* BOLKAY, pp. 225-226, fig. 4, pl. XII: 9-12;

1991b *Vipera gedulyi* BOLKAY: SZYNDLAR, pp. 246-247;

1993 *Macrovipera? gedulyi†* (BOLKAY, 1913): GOLAY et al., p.274;

1994 *Vipera gedulyi* BOLKAY, 1913: VENCZEL, pp. 19-27, figs.9 - 13 a-d.

M a t e r i a l. Polgárdi 4 "Lower": one left prefrontal (No. V.20641), one left exoccipital (No. V.20642), one left maxilla (No. V.20643), 40 vertebrae (No. V.20644/1-40). Polgárdi 4 "Upper": 25 vertebrae (No. V.20645/1-25). Polgárdi 5: one compound bone (No. V.20646), 35 vertebrae (No. V.20647/1-35).

The prefrontal (Fig. 12 a) somewhat resembles that of *Macrovipera lebetina*, its medial wall being convex, partially hiding the lacrimal foramen.

The exoccipital (Fig. 12 b) is somewhat similar to that described from Polgárdi 4 "Lower" (VENCZEL 1994: fig. 9 m). The circumfenestral crest is more prominent anterodorsally to the recess of the vagus-hypoglossal nerve foramina. The latter structure consists of three small foramina. Dorsally to them there are situated three foramina which traverse the lateral wall of the exoccipital.

The maxilla (Fig. 12 c,d) is provided with a single foramen of the dental canal, situated on the medial side of the base of the ascending process. The process is high, curved medially and provided with a sharp keel on its anteromedial side.

D i s c u s s i o n. All the remains are referrable to *M. gedulyi*. The morphology of different skeletal elements (including the cranial bones and vertebrae) having a wide range of intraspecific variation, indicates close relationships with the extinct *M. burgenlandica*, known from the Late Miocene (MN 11) of Kohfidisch, Austria (BACHMAYER & SZYNDLAR 1985, 1987; SZYNDLAR 1991b). The same is true when these bones are compared with the homologous bones of recent

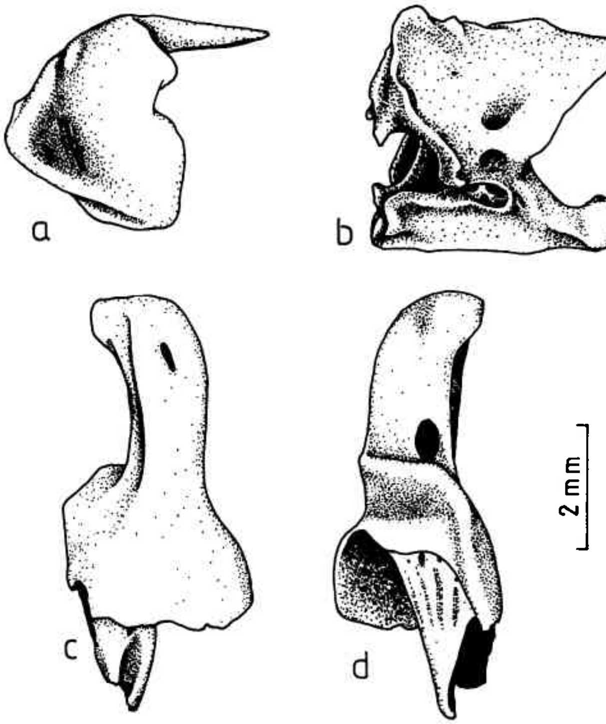

Fig. 12. *Macrovipera gedulyi* a – left prefrontal (Polgárdi 4 "Lower", No. V.20641), b – left exoccipital (Polgárdi 4 "Lower", No. V.20642), c,d – left maxilla (Polgárdi 4 "Lower", No. V.20643). a – posteroventrolateral view; b – lateral view; c – anterior view; d – posteromedial view.

M. lebetina. In the latter a number of morphological characters observed in the cranial bones, show a wide intraspecific variation too (ZEROVA & CHIKIN 1992).

The large vipers of 'Oriental vipers' group (sensu GROOMBRIDGE 1986) appeared in Europe during the Lower Miocene (SZYNDLAR 1987, 1988, 1991b; SZYNDLAR & SCHLEICH 1993; SZYNDLAR & BÖHME 1993) and belonged to the commonest snakes until the Late Miocene.

CONCLUDING REMARKS

The strongly fluctuating climatic conditions around Messinian times (MÜLLER 1983) may be evidenced even by the different compositions of the vertebrate faunas (including snakes (Fig. 13)) from the Polgárdi localities, which are situated within the same biostratigraphic unit (MN 13), but differing slightly in age (FREUDENTHAL & KORDOS 1989).

The most important feature of Polgárdi snake assemblages is being composed of extant genera only and the lack of some major ophidian groups (with members of Scolecophidia, Boidae and Elapidae) rather common in older faunas of the European Miocene. The first record of fossil members of the genera *Coronella*, *Telescopus*, as well as those of some smaller members of the genus *Elaphe* may be significant, too.

Comparing these data with the available fossil record from some older localities of the area, e.g. Rudabánya (MN 9) (SZYNDLAR, in prep.) and Kohfidisch (MN 11) (BACHMAYER & SZYNDLAR

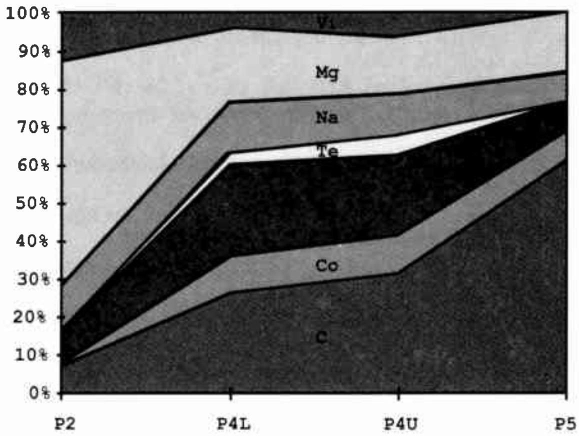

Fig. 13. Relative frequency of snakes in the Polgárdi localities. P2 – Polgárdi 2, P4L – Polgárdi 4 "Lower", P4U – Polgárdi 4 "Upper", P5 – Polgárdi 5; C – *Coluber*, Co – *Coronella*, E – *Elaphe*, Na – *Natrix*, Te – *Telescopus*, Mg – *Macrovipera*, Vi – *Vipera*.

1985, 1987; SZYNDLAR 1991a, 1991b), one may conclude that gradual changes in the older faunas with members of modern colubrids now inhabiting Central Europe must have been taken place well before the Late Miocene (MN 13 biostratigraphic unit). On the other hand, during Late Miocene/Early Pliocene (MN 13/14) times the southestern part of our continent, as indicated by the fossil record from Maramena, Greece, was still inhabited by elapids (*Naja* sp.), together with large vipers and small colubrine snakes (SZYNDLAR, 1995).

REFERENCES

BACHMAYER F., SZYNDLAR Z. 1985. Ophidians (Reptilia: Serpentes) from the Kohfidisch fissures of Burgenland, Austria. Ann. Naturhist. Mus. Wien, **87A**: 79-100.

BACHMAYER F., SZYNDLAR Z. 1987. A second contribution to the ophidian fauna (Reptilia: Serpentes) of Kohfidisch, Austria. Ann. Naturhist. Mus. Wien, **88A**: 25-39.

BAILON S. 1991. Amphibiens et reptiles du Pliocene et du Quaternaire de France et d'Espagne: Mise en place et évolution des faunes. Unpubl.Ph.D.thesis, Univ. Paris VI.

BOLKAY St. J. 1913. Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial periode. Mitt.Jb.König. ungar. Geol.Reichsanst., **21**(7): 217-230.

FREUDENTHAL M., KORDOS L. 1989. *Cricetus polgardiensis* sp.nov. and *Cricetus kormosi* SCHAUB, 1930 from the Late Miocene Polgárdi localities (Hungary). Scripta Geol., **89**: 71-100.

GROOMBRIDGE B. 1986. Phyletic relationships among viperine snakes. [In:] Z. ROCEK (Ed.) – Studies in Herpetology. Charles Univ., Prague. Pp:497-500.

HERRMANN H. W., JOGER U., NILSON G. 1992. Phylogeny and systematics of viperine snakes. III: Resurrection of the genus *Macrovipera* (REUSS 1927) (Reptilia, Serpentes, Viperidae) as suggested by biochemical evidence. Amphibia-Reptilia, **13**: 375-392.

OBST F. J. 1983. Zur Kenntnis der Schlangengattung *Vipera* (Reptilia, Serpentes, Viperidae). Zool. Abh. st. Mus. Tierk. Dresden, **38**(13): 229-235.

RAGE J. C., SCHÄTTI B. 1993. *Macrovipera*. Pp. 273-276 [In:] GOLAY et al. (Ed. Cultural Foundation Elapsoidea): Endoglyps and other major venomous snakes of the world. A checklist., Azemiops S.A., Geneva.

REDKOZUBOV O. I. 1987. (New data on snakes of the Pliocene of Moldavia). Izv. Akad. Nauk. Moldav. SSR, Ser.biol. khim. nauk, **1987**: 71.

RÖGL F., STEININGER F. F. 1983. Vom Zerfall der Tethys zu Mediterran und Paratethys. Ann. Naturhist. Mus. Wien, **85A**: 135-163.

SZUNYOGHY J. VON. 1932. Beiträge zur vergleichenden Formenlehre des Colubridenschädels, nebst einer kraniologischen Synopsis der fossilen Schlangen ungarns mit nomenklatorischen, systematischen und phyletischen Bemerkungen. Acta Zool., **13**: 1-56.

SZYNDLAR Z. 1984. Fossil snakes from Poland. Acta zool. cracov., **28**(1): 1-156.

SZYNDLAR Z. 1985. Ophidian fauna (Reptilia: Serpentes) from the Uppermost Miocene of Algora (Spain). Estud. Geol., **41**(5-6): 447-465.

SZYNDLAR Z. 1987. Snakes from the Lower Miocene locality of Dolnice (Czechoslovakia). J. Vertebr. Paleont., **7**(1): 55-71.

SZYNDLAR Z. 1988. Two new extinct species of the genera *Malpolon* and *Vipera* (Reptilia: Serpentes) from the Pliocene of Layna (Spain). Acta zool. cracov., **31**(27): 687-706.

SZYNDLAR Z. 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I. Scolecophidia, Boidae, Colubrinae. Estud. Geol., **47**(1-2): 103-126.

SZYNDLAR Z. 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II. Natricinae, Elapidae, Viperidae. Estud. Geol., **47**(3-4): 237-266.

SZYNDLAR Z. 1991c. Ancestry of Grass Snake (*Natrix natrix*): Paleontological evidence. J. Herpet., **25**(4): 412-418.

SZYNDLAR Z., ZEROVA G. A. 1992. Miocene snake fauna from Cherevichnoie (Ukraine, USSR), with description of a new species of *Vipera*. N. Jb. Geol. Paläon.,Abh., **184**(1): 87-99.

SZYNDLAR Z. 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). 4. Serpentes (Squamata, Reptilia). Münchner Geowiss.Abh.,(A), **28**: 39-42.

VENCZEL M. 1994. Late Miocene snakes from Polgárdi (Hungary). Acta zool. cracov., **37**(1): 1-29.

ZEROVA G. A. 1992. *Vipera (Daboia) ukrainica* - a new viper (Serpentes; Viperidae) from the Middle Sarmatian (Upper Miocene) of the Ukraine. N. Jb. Geol. Paläon.,Abh.,**184**(2): 235-249.

ZEROVA G. A., CHIKIN YU. A. 1992. Polymorphism of the structure of the separate skull-bones in *Vipera (Daboia) lebetina*. [In:] Z. KORSOS, I. KISS (Eds.) – Proc. 6th Ord. Gen. Meet. S.E.H., Budapest 1991. Hung. Nat. Hist. Mus., Budapest. Pp:497-500.