

Late Miocene snakes from Polgárdi (Hungary)

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Abstract. Snake remains from the Late Miocene (MN 13) localities of Polgárdi 2 and Polgárdi 4 (Hungary) belong to at least eight different taxa: *Coluber hungaricus*, *Coronella* cf. *C. austriaca*, *Elaphe kormosi*, *Elaphe praelongissima* sp.n., *Natrix* cf. *N. longivertebrata* (Colubridae), *Vipera gedulyi*, *Vipera* sp. 1 («Oriental viper» group), and *Vipera* sp. 2 («European viper» group) (Viperidae). The ophidian assemblage from Polgárdi 4 was dominated by small colubrids, while that from Polgárdi 2 by *Vipera gedulyi*. The composition of the snake fauna indicates rapid faunistic and paleoecological changes at the end of the Miocene.

Key words: *Serpentes*, Late Miocene, Hungary, osteology.

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I. INTRODUCTION

In the Upper Carboniferous limestone quarry of the Somló-Hill and Kőszár-Hill, located near the village of Polgárdi in western Hungary, several Late Miocene localities bearing vertebrate remains were unearthed: Polgárdi 1, discovered in 1909; Polgárdi 2, discovered in 1910 (known in the literature as the classical Polgárdi locality); Polgárdi 3, discovered in 1971; Polgárdi 4, discovered in 1984 (named Polgárdi 4 "Lower" and Polgárdi 4 "Upper" in order to distinguish remains coming from two different fissure fillings in the southern wall of the quarry); and Polgárdi 5, discovered in 1988 (FREUDENTHAL and KORDOS 1989; JÁNOSSY 1991). On the basis of mammalian remains (FREUDENTHAL and KORDOS 1989) the age of these fossil deposits can be defined as Pontian or Upper Turolian (mammalian biozone MN 13).

The first report on the fossil vertebrate assemblage from Polgárdi 2 was given by KORMOS (1911). The herpetofauna of this site was described by BOLKAY (1913) and then by FEJÉRVÁRY-LÁNGH (1923), SZUNYOGHY (1932), SZALAI (1934), MŁYNARSKI (1966), and SZYNDLAR (1991a, 1991b). Based on skull bones, BOLKAY (1913) recognized 5 snake species (*Coluber hungaricus*, *Elaphe kormosi*, *Natrix natrix*, *Natrix tessellata*, and *Vipera gedulyi*). SZUNYOGHY (1932) allocated all these taxa (except for *Vipera gedulyi*) to living species, but these changes were not accepted by subsequent authors (e.g. MŁYNARSKI

1961; RAGE 1984, 1987; SZYNDLAR 1985, 1991a, 1991b). SZYNDLAR (1991b), after re-examination of the type material from Polgárdi 2, recognized *Elaphe kormosi* and *Vipera gedulyi* as valid taxa, while *Coluber hungaricus* (the description of which was originally based on a single quadrate only) was considered by this author to be a nomen dubium.

The present paper redescibes the classical ophidian collection from Polgárdi 2 as well as describes the snake remains recently discovered at Polgárdi 4. On the basis of the entire available ophidian material (including also vertebrae, reported here for the first time), the taxonomic position of the taxa described by BOLKAY (1913) and SZUNYOGHY (1932) is reevaluated.

The fossil material described below belongs entirely to the paleontological collection of the Museum of the Hungarian Geological Institute in Budapest.

A c k n o w l e d g m e n t s . I am grateful to Dr. László KORDOS (Budapest) for loaning me the fossil snake material for study and giving valuable information on the fossil deposits from Polgárdi. Dr. Jean-Claude RAGE (Paris) and Dr. Zbigniew SZYNDLAR (Kraków) critically commented on the manuscript; besides, Dr. SZYNDLAR imparted some unpublished data to me and allowed me to examine a comparative osteological collection under his care.

II. SYSTEMATIC PART

Order *Serpentes* LINNAEUS, 1758

Family *Colubridae* OPPEL, 1811

Genus *Coluber* LINNAEUS, 1758

Coluber hungaricus (BOLKAY, 1913)

(Figs 1 and 2)

1913 *Zamenis hungaricus* BOLKAY, pp. 223-224, pl. XII: 3;

1932 *Zamenis* cfr. *Dahli* SAV.: SZUNYOGHY, pp. 10 and 49;

1939 *Zamenis hungaricus* BOLKAY: KUHN, p. 28;

1961 *Coluber* cf. *najadum* (EICHWALD): MŁYNARSKI, p. 23;

1963 *Coluber hungaricus* BOLKAY: KUHN, p. 20;

1984 *Coluber hungaricus* (BOLKAY): RAGE, p. 44;

1991a *Coluber hungaricus* (BOLKAY): SZYNDLAR, p. 115.

Type material of BOLKAY (1913). – Polgárdi 2: one right quadrate (holotype, No. Ob-4464/Vt.76).

Referred material. – Polgárdi 2: one fragmentary basiparasphenoid (No. Ob-4463/1), 3 fragmentary compound bones (No. Ob-4463/2), 2 fragmentary maxillae (No. Ob-4465/2), 5 vertebrae (No. V.19002). Polgárdi 4 "Lower": one frontal (No. V.19663), one fragmentary basiparasphenoid (No. V.18988), 3 prootics (No. V.18989), one exoccipital (No. V.18990), 2 ectopterygoids (No. V.18991), 2 quadrates (No.

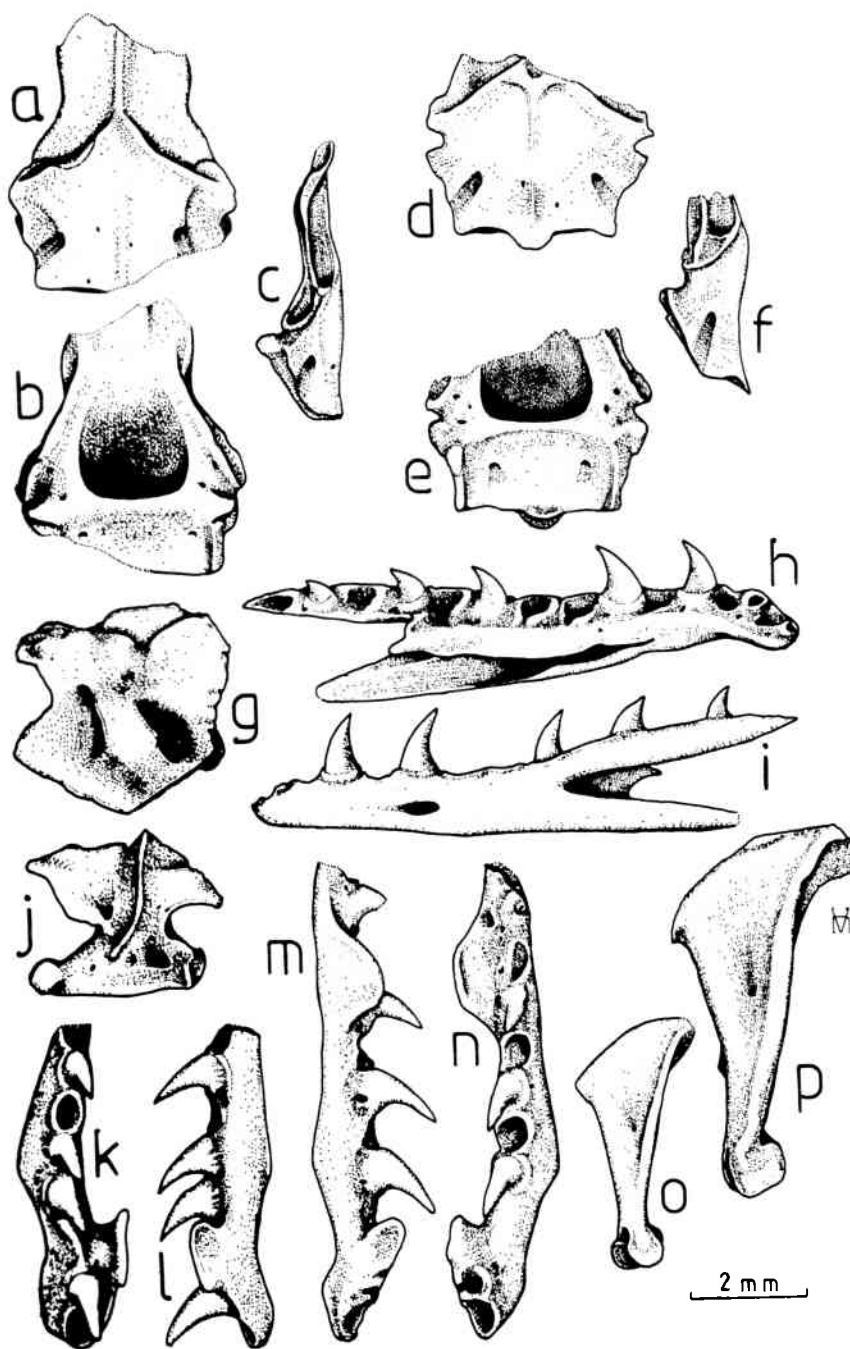


Fig. 1. *Coluber hungaricus*. a-c – basiparasphenoid (Polgárdi 2, No. Ob-4463/a), d-f – basiparasphenoid (Polgárdi 4 "Lower", No. V.18988), g – right prootic (Polgárdi 4 "Lower", No. V.18989/a), h,i – left dentary (Polgárdi 4 "Upper", No. V.18998/a), j – right exoccipital (Polgárdi 4 "Lower", No. V.18990), k,l – right maxilla (Polgárdi 4 "Upper", No. V.18997/a), m,n – left maxilla (Polgárdi 4 "Upper", No. V.18997/b), o – right quadrate (holotype; Polgárdi 2, No. Ob-4464/Vt.76), p – right quadrate (Polgárdi 4 "Lower", No. V.189992/a). a,d,k,n – ventral views; b,e – dorsal views; c,f,g,i,j – lateral views; h,l,m – medial views.

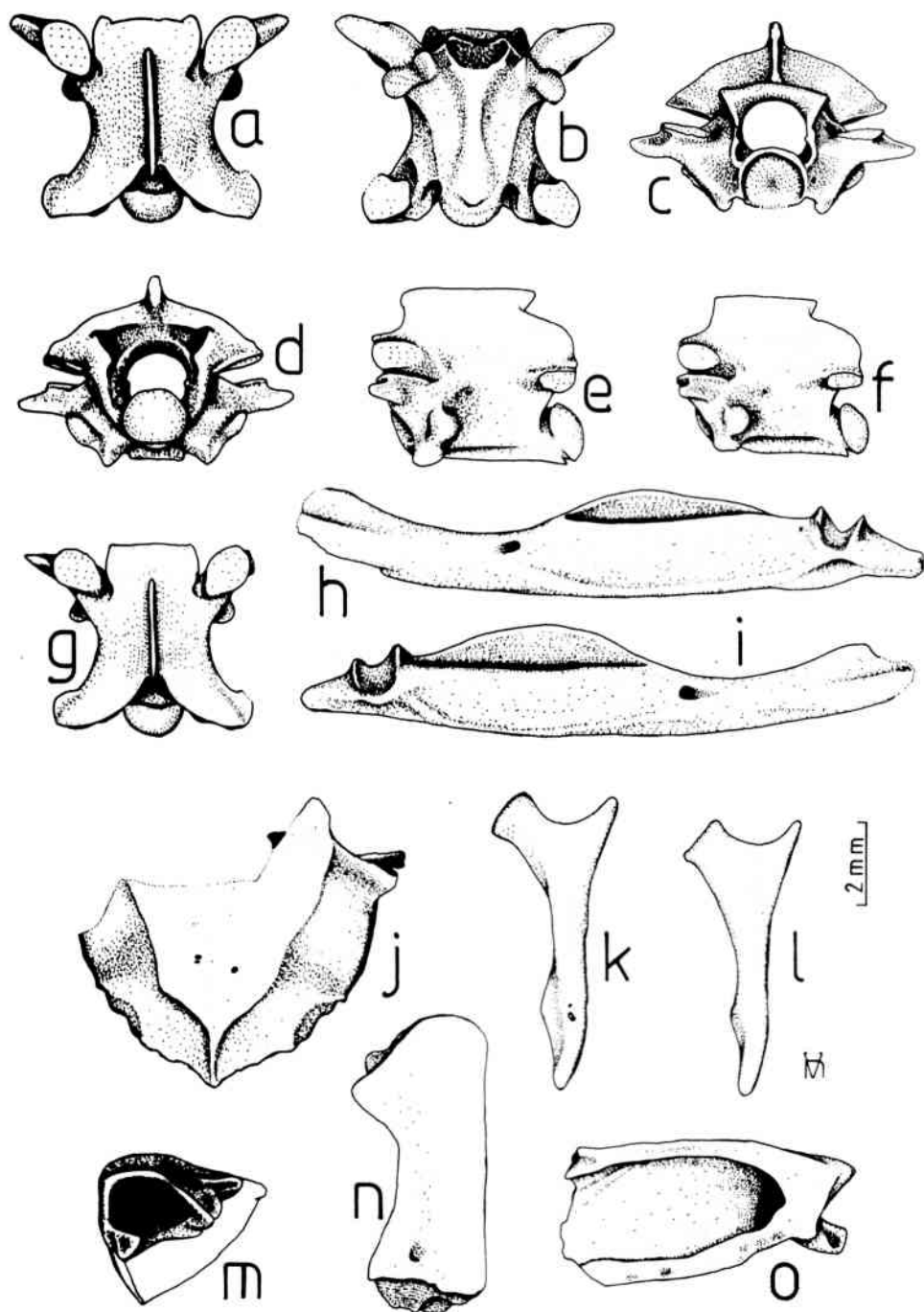


Fig. 2. *Coluber hungaricus*. a-e – trunk vertebra (Polgárdi 4 "Upper", No. V.19000/a); f,g – trunk vertebra (Polgárdi 4 "Upper", No. V.19000/b), h – left compound bone (Polgárdi 4 "Upper", No. V.18999/a), i – right compound bone (Polgárdi 4 "Lower", No. V.18994), j – parietal (Polgárdi 4 "Upper", No. V.18996), k – left ectopterygoid (Polgárdi 4 "Lower", No. V.18991/a), l – left ectopterygoid (Polgárdi 4 "Lower", No. V.18991/b), m-o – left frontal (Polgárdi 4 "Lower", No. V.19663). a,g,j,k,l,n – dorsal views; b – ventral view; c,m – anterior views; d – posterior view; e,f,h,i – lateral views; o – medial view.

V.18992), 3 fragmentary maxillae (No. V.18993), one fragmentary compound bone (No. V.18994), 230 vertebrae (No. V.18995). Polgárdi 4 "Upper": one fragmentary parietal (No. V.18996), 2 fragmentary maxillae (No. V.18997), 3 dentaries and dentary fragments (No. V.18998), 4 fragmentary compound bones (No. V.18999), 320 vertebrae (No. V.19000).

Emended diagnosis. – A small colubrid snake, most resembling the recent *Coluber gemonensis* but differing from it in having longer Vidian canals of the basiparasphenoid, shorter rami of the ectopterygoid, a smaller number of dentary teeth, and relatively shorter prezygapophyseal processes of the middle trunk vertebrae (the processes are shorter than or equal to the prezygapophyseal articular facets).

Description. – Frontal (Fig. 2 m-o): The anterior margin of the bone is slightly convex. The anterior and external prefrontal processes project slightly laterally. The septomaxillary process is long, rectangular in medial view, and anterolaterally oriented. The frontal aperture is ovate in shape. The trabecular crest is well marked.

Parietal (Fig. 2 j): The descending part of the bone is convex. The dorsal surface is slightly depressed; the parietal crests converge near the posterior border of the bone. A distinct postfrontal process is preserved on the right side of the bone.

Basiparasphenoid (Fig. 1 a-f): Two fragmentary bones, both with parasphenoid portions missing, do not differ substantially from each other. The common foramina are situated far from the posterior margin of the bone; the anterior openings of Vidian canals are hidden under the pterygoid crests, the latter inclined anterolaterally. The anterior foramina of the abducens nerve and those for the constrictor internus dorsalis branch of the trigeminal nerve (cid nerve) are located close to each other on either side of the pituitary fossa. According to the information given on the accompanying label, specimen No. Ob-4463/1 from Polgárdi 2 was referred by BOLKAY (1913: 199) and SZUNYOGHIY (1932: 9) to the recent *Natrix tessellata*.

Exoccipital (Fig. 1 j): The occipital and circumfenestral crests are well developed. The postoccipital foramen is large; the postoccipital crest is well marked. The vagus-hypoglossal nerve foramen is accompanied posteriorly by a small additional foramen.

Prootic (Fig. 1 g): The lateral wall of the bone is pierced by two large foramina of equal size, separated from each other by the laterosphenoid. The anterior foramen serves as a passage for the maxillary branch of the trigeminal nerve (V_2), while the posterior one is for the mandibular branch of the trigeminal nerve (V_3); the latter is accompanied posteriorly by a small foramen for the facial nerve. The roof of the bone is moderately crested. The otic recess in the posterior wall of the bone is relatively deep.

Maxilla (Fig. 1 k,l): Only posterior maxillary fragments are present in the material. The teeth are isodont; two terminal teeth are preceded by a diastema. The posterior end of the bone is slightly bent medially and distinctly constricted dorsally. The ectopterygoid process, situated medially to the diastema, projects anteroventrally. Two maxillary fragments, belonging to somewhat larger specimens (Fig. 1 m,n), possess shorter ectopterygoid processes and broader diastemas; they are also provided with prefrontal processes, slightly longer than wide; these bony fragments are tentatively referred to *Coluber hungaricus*.

Ectopterygoid (Fig. 2 k,l): The stem of the bone is straight, widening near the posterior tip. The external ramus is either slightly constricted (Fig. 2 k) or not (Fig. 2 l). The internal ramus is slender and tapering; it is shorter than or equal to the external ramus.

Quadrate (Fig. 1 o,p): The holotype quadrate (BOLKAY 1913, pl. XII: 3; Fig. 1 o of this paper) belonged to a small specimen. The upper ends of the bones are widened in posterolateral view and they are slightly tapering in medial view. The posteromedial margin is bent, especially in the larger specimen (Fig. 1 p). The quadrate crest is better defined above the level of the stapedial process; its anterodorsal portion is produced into a distinct lobe projecting medially. The stapedial process is rather small in the holotype, being better defined in the larger specimen.

Compound bone (Fig. 2 h,i): The medial flange is higher than the lateral flange, the external surface of the latter being slightly concave. The supraangular crest is well defined. The retroarticular process is tapering posteriorly and slightly curved medially.

Dentary (Fig. 1 h,i): The dentaries have 15 teeth or tooth sockets each. The teeth are of proterodontic type. The Meckel's groove closes completely at the level of the 6th tooth. The mental foramen lies at the level of the 7th tooth, while the compound notch approaches the level of the 10th tooth.

Vertebrae (Fig. 2 a-g): The neural spine of the cervical vertebrae is longer than high; the hypapophysis (shorter than the centrum length) is directed posteroventrally and sometimes widened distally. The centrum of the trunk vertebrae is moderately long and subtriangular from below. The centrum length is 3.72–4.27 mm (N=23). The centrum length/centrum width ratio is 1.23–1.49 (mean 1.36). The haemal keel is flattened and spatulate or rounded. In younger specimens (with relatively larger neural canals) the keel is weakly defined. The neural arch is moderately vaulted. The neural spine is distinctly longer than high, overhanging slightly anteriorly and posteriorly; the anterior overhang is rarely absent (Fig. 2 f). The zygosphenes are straight or convex, with two lateral lobes and an indistinct median lobe. The prezygapophyseal articular facets are oval, while the postzygapophyseal articular facets are round or obovate. The prezygapophyseal processes are usually equal to the articular facets in length and pointed distally. The paradiapophyses are prominent, divided into dia- and parapophyseal portions, which are of equal length. The cotyle and condyle are rounded. The lateral, subcentral and paracotylar foramina are distinct.

Remarks. – The above-described skeletal elements resemble those of small members of the genus *Coluber*, especially the recent *C. gemonensis*; similarities between the holotype quadrate of *C. hungaricus* and that of *C. gemonensis* were observed by SZYNDLAR (1991b). Earlier, SZUNYOGHY (1932) allocated this element to the living *C. najadum*, while MŁYNARSKI (1961) noticed its similarity to the quadrates of the genus *Natrix*. Two other quadrates, distinctly larger than the holotype, display a somewhat different morphology.

The frontals, parietal and prootic closely resemble homologous elements of the recent *Coluber gemonensis*.

Some minor morphological differences between two basiparasphenoid fragments (e.g. shorter Vidian canals in the specimen from Polgárdi 2) may be related to intraspecific variation in *Coluber hungaricus*. The Vidian canals of this snake are longer than the canals

of *C. gemonensis*, but they are significantly shorter than those observed in *C. najadum* – *C. rubriceps* group and in the related extinct *C. planicarinatus* from the Late Miocene (MN 11) of Kohfidisch, Austria (BACHMAYER and SZYNDLAR 1987). The anterior abducens nerve foramina and cid nerve foramina of the latter group (including *C. planicarinatus*) are widely separated, while in *C. hungaricus* they are situated close to each other.

The anteriorly projecting ectopterygoid process of the maxilla is a characteristic feature of larger members of the genus *Coluber* (e.g. *C. viridiflavus* and *C. caspius*); it was however found in the fossil *Elaphe algorensis*, the latter being characterized by a mixture of features of both *Coluber* and *Elaphe* (SZYNDLAR 1985).

On account of some morphological similarities observed between compound bones of *C. hungaricus* and the living *C. caspius*, SZYNDLAR (1932) referred two compound bones (No. Ob-4463/2) to the latter species. However the possible presence of *C. caspius* in the fossil beds of the Polgárdi localities has not been confirmed by vertebrae.

The number of dentary teeth of *Coluber hungaricus* (15) approaches that observed in *C. caspius* (usually 16-17 teeth); in the remaining living members of the genus the number of dentary teeth is higher.

The middle trunk vertebrae of *C. hungaricus* most resemble those of the living *C. gemonensis*, but differ from them in having longer and distally pointed prezygapophyseal processes.

Genus *Coronella* LAURENTI, 1768

Coronella cf. *C. austriaca* LAURENTI, 1768

(Fig. 3)

Material. – Polgárdi 4 "Lower": one fragmentary parietal (No. V.18970/a), 2 prootics (No. V.18970/b and V.19664), one fragmentary maxilla (No. V.18970/c), one quadrate (No. V.18970/d), one basioccipital (No. V.18970/e), 80 vertebrae (No. V.18971). Polgárdi 4 "Upper": 30 vertebrae (No. V.18972).

Description. – Parietal (Fig. 3 l): Only a small posterior fragment is preserved. The allocation to *Coronella austriaca* is based on the shape of the parietal crests, which do not converge on each other before reaching the posterior margin of the bone.

Prootic (Fig. 3 k): The bone closely resembles that of the living *Coronella austriaca*. The anterior prootic foramen (for V₂ nerve) is accompanied anteroventrally by a smaller foramen. The posterior prootic foramen (for V₃ nerve) is distinctly larger than the anterior one. The otic recess in the posterior wall of the bone is shallow. The supraoccipital crest is weakly developed.

Basioccipital (Fig. 3 m): The left posterolateral part of the bone is missing. The median and basioccipital crests are weakly developed; the basioccipital process is absent. The basioccipital tubercle is underdeveloped.

Maxilla (Fig. 3 i,j): Only a posterior fragment is preserved. The posterior maxillary tooth is somewhat enlarged. The ectopterygoid process slightly projects anteriorly, while the prefrontal process is directed medially.

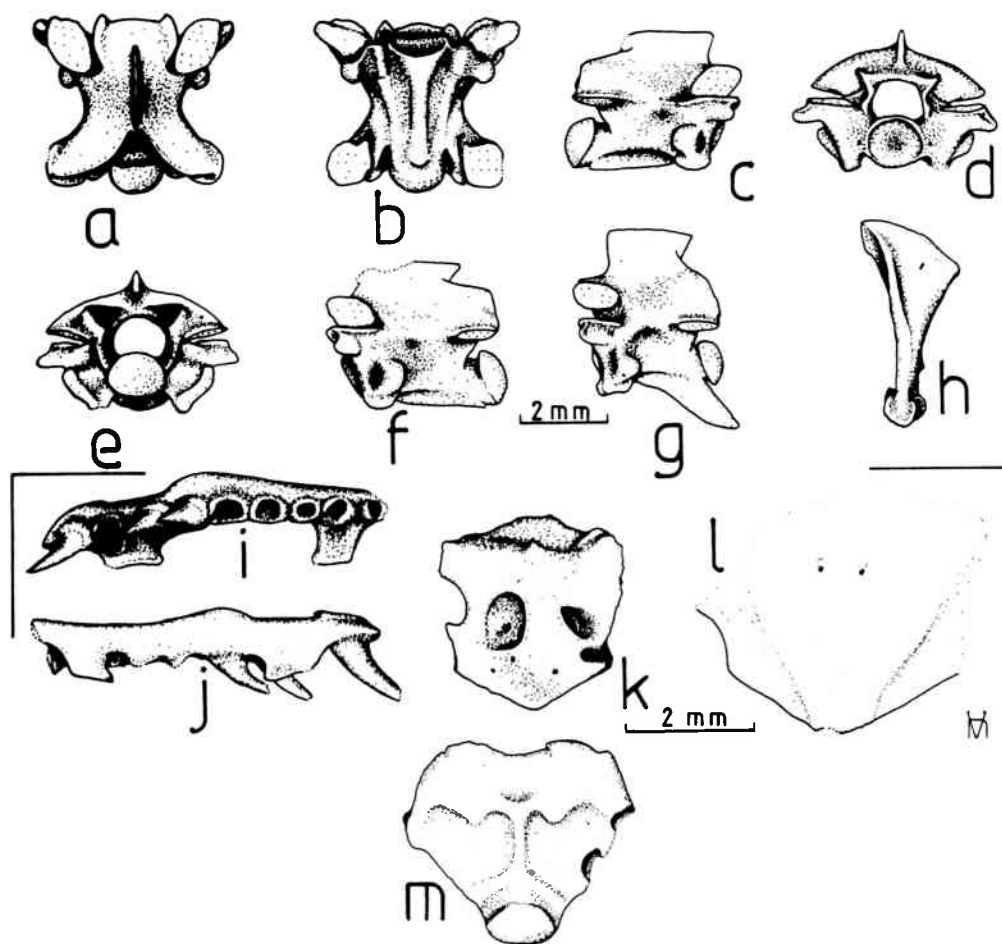


Fig. 3. *Coronella* cf. *C. austriaca*. a-e – trunk vertebra (Polgárdi 4 "Upper", No. V.18972/a), f – trunk vertebra (Polgárdi 4 "Upper", No. V.18972/b), g – cervical vertebra (Polgárdi 4 "Upper", No. V.18972/c), h – left quadrate (Polgárdi 4 "Upper", No. V.18970/d), i, j – right maxilla (Polgárdi 4 "Lower", No. V.18970/c), k – right prootic (Polgárdi 4 "Lower", No. V.18970/b), l – parietal (Polgárdi 4 "Lower", No. V.18970/a), m – basioccipital (Polgárdi 4 "Upper", No. V.19665). a, l – dorsal views; b, i, m – ventral views; c, f, g, k – lateral views; d – anterior view; e – posterior view; h – posterolateral view; j – medial view.

Quadrate (Fig. 3 h): The bone is relatively short and widened dorsally. The quadrate crest is well defined and it begins above the level of the trochlea quadrati. The latter structure is strongly built and wide in lateral or posterior view. In lateral view the bone is distinctly bent medially.

Vertebrae (Fig. 3 a-g): The neural spine of the cervical vertebrae is slightly longer than high; the hypapophysis is shorter than the centrum length, with a tapering tip (Fig. 3 g). The middle trunk vertebrae have relatively long centra. The centrum length of eleven trunk vertebrae from Polgárdi 4 "Lower" ranges between 2.52 and 3.10 mm, while the centrum

length / centrum width ratio is 1.18-1.34 (mean 1.24). In ten specimens from Polgárdi 4 "Upper" the centrum length is 2.60-3.41 mm, while the centrum length / centrum width ratio is 1.16-1.42 (mean 1.25). The haemal keel is prominent and rounded. The neural arch is depressed; the neural spine is distinctly longer than high. The zygosphenes are straight, sometimes with an indistinct median lobe and always with two well-developed lateral lobes. The prezygapophyseal processes are two to three times shorter than the prezygapophyseal articular facets. The paradiapophyses are divided into dia- and parapophyseal portions, the latter being expanded laterally. The cotyle and condyle are slightly depressed dorsoventrally.

The vertebrae of the living *Coronella austriaca* are usually more depressed, provided with lower neural spines as well as with haemal keels and subcentral ridges developed to a lesser degree than in vertebrae from Polgárdi. The centrum length / centrum width ratio in the fossil vertebrae is distinctly lower than in the examined recent *C. austriaca*. However all these differences are of minor taxonomic importance and cannot be a basis for establishing a new fossil species.

Remarks. – The above-described cranial bones and vertebrae are the oldest record of the genus *Coronella*. REDKOZUBOV (1987) reported *C. austriaca* from the Late Pliocene (MN 16) of Chishmikiy, Moldavia, but the fossil record of this form is mostly restricted to the Quaternary (SZYNDLAR 1984, 1991a, 1991b). Another member of the genus (*Coronella* cf. *C. girondica*) was described from the Late Pliocene (MN 16) of Seynes in France and les Medas in Spain as well as from several Quaternary localities of France (Lower Pleistocene of Balaruc VII, Middle Pleistocene/Holocene of Grotte du Lazaret) and Spain (Late Pleistocene of Solana del Zamborino) by BAILON (1991).

Vertebrae of the extinct *Hispanophis coronelloideus* from the Late Miocene (MN 13) of Algora, Spain, are very similar to those of *Coronella austriaca*; however, its basiparaspheoid differs strongly from that of the genus *Coronella* (SZYNDLAR 1985).

Genus *Elaphe* FITZINGER, 1833

Elaphe kormosi (BOLKAY, 1913)

(Figs 4 and 5)

1913 [pars] *Coluber Kormosi* BOLKAY, p. 224, pl. XII: 5,7,8;

1932 *Elaphe longissima* LAUR. (= *Coluber Kormosi* BY.): SZUNYOGHY, pp. 10 and 49-50;

1939 *Coluber kormosi* BOLKAY: KUHN, p. 18;

1961 *Elaphe longissima* (LAURENTI): MŁYNARSKI, pp. 25-26;

1963 ?"*Coluber*" *kormosi*: KUHN, p. 21;

1984 *Elaphe kormosi* (BOLKAY): RAGE, p. 46;

1991a *Elaphe kormosi* (BOLKAY): SZYNDLAR, pp. 118 and 120.

Type material of BOLKAY (1913). – Polgárdi 2: one basioccipital (No. Ob-4465/a), one ectopterygoid (No. Ob-4465/c), one fragmentary basiparaspheoid (No. Ob-4465/d), one fragmentary palatine (No. Ob-4465/e) (syntypes).

Referred material. – 15 vertebrae (No. V.19001).

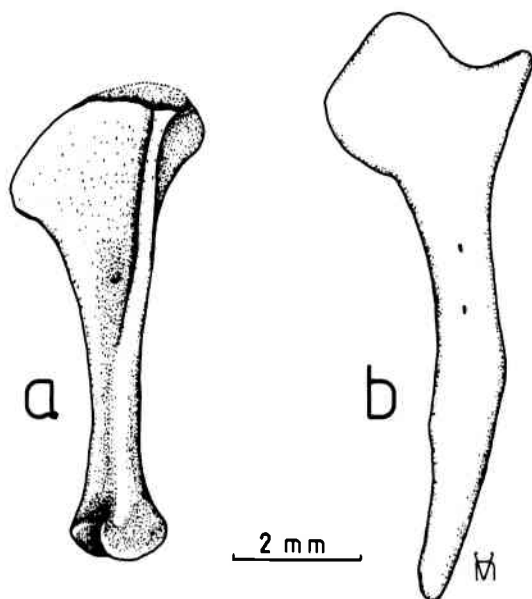


Fig. 4. *Elaphe kormosi*. a – right quadrate (Polgárdi s, No. Ob-4465/h), b – left ectopterygoid (Polgárdi 2, No. Ob-4465/c). a – posterolateral view; b – dorsal view.

Emended diagnosis. – A large-sized colubrid snake, having a broad dorsal portion and posteromedially curved margin of the quadrate, short internal ramus and laterally bent stem of the ectopterygoid, centrum length of middle trunk vertebrae exceeding 6 mm, flattened haemal keel, neural spine longer than high, straight zygosphene, and short and obtuse prezygapophyseal processes.

Description. – Ectopterygoid (Fig. 4 b): The stem of the bone is long, bent laterally, and tapering distally. The external ramus is broad and square, while the internal ramus is very short and tapering.

Quadrate (Fig. 4 a): The bone was figured also by BOLKAY (1913, pl. XII: 7). The stem is relatively thin; the quadrate crest is better defined in the dorsal portion of the bone. The posteromedial margin is curved. The trochlea quadrati is strongly built. The dorsal end of the bone is distinctly widened.

Basioccipital (cf. BOLKAY 1913, pl. XII: 8): The bone is distinctly wider than long, pentagonal. The basioccipital crest lacks a basioccipital process, but it is provided with well-defined lateral lobes. The median crest branches off before the occipito-condylar tubercle, being separated from the latter structure by a deep furrow.

Basiparasphenoid: Only a rostral part of the parasphenoid process has been preserved. **Palatine** (cf. BOLKAY 1913, pl. XII: 5): Only a posterior portion of the bone has been preserved.

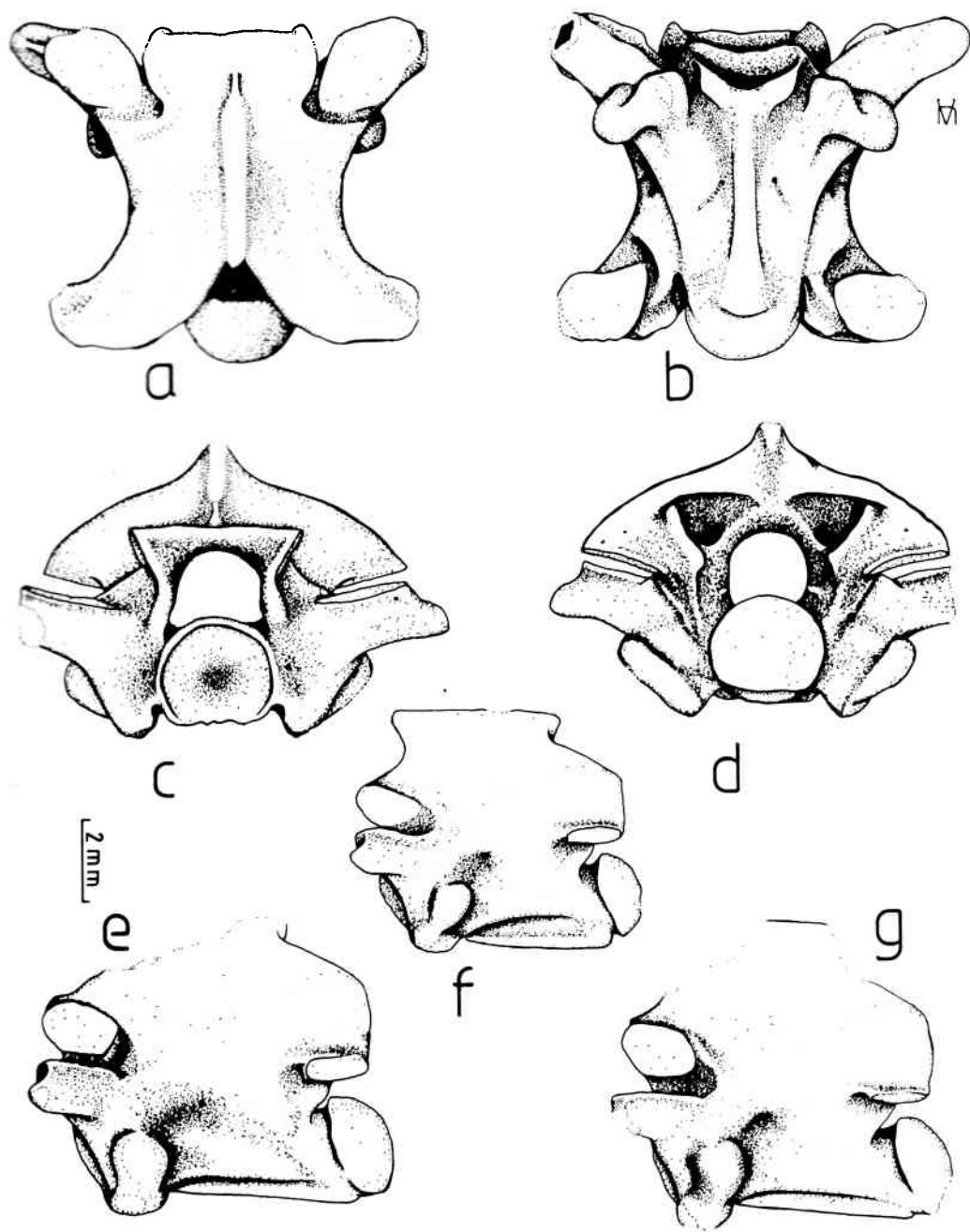


Fig. 5. *Elaphe kormosi*. a-e – trunk vertebra (Polgárdi 2, No. V.19001/a), f – posterior trunk vertebra (Polgárdi 2, No. V.19001/c), g – trunk vertebra (Polgárdi 2, No. V.19001/b). a – dorsal view; b – ventral view; c – anterior view; d – posterior view; e, f, g – lateral views.

Vertebrae (Fig. 5): The centrum is moderately long, subtriangular from below. The centrum length in six vertebrae ranges between 5.52 and 6.82 mm, while the centrum length / centrum width ratio is 1.22-1.32 (mean 1.29). The neural arch is moderately vaulted, without epizygapophyseal spines. The neural spine is somewhat longer than high, thickened dorsally, overhanging anteriorly and posteriorly. The haemal keel is flattened, slightly widening posteriorly. In a smaller specimen (coming from the posterior trunk portion of the column), the keel is prominent (Fig. 5 f). The subcentral ridges are better defined in the vicinity of the paradiapophyses. The zygosphene is straight, with small lateral lobes. The pre- and postzygapophyseal articular facets are oval. The prezygapophyseal processes are slightly flattened dorsoventrally, obtuse, and shorter than the prezygapophyseal articular facets. The paradiapophyses are prominent, weakly separated into dia- and parapophyseal portions. The cotyle and condyle are rounded. The lateral, subcentral, and paracotylar foramina are well seen.

Remarks. – The above-described cranial bones and vertebrae resemble those of larger members of the genus *Elaphe* and *Coluber*. Of the cranial bones, the basioccipital is comparable to homologous bones of *Elaphe quatuorlineata* and *E. longissima*. The ectopterygoid and quadrate mostly resemble those of *E. quatuorlineata* (as it was pointed out by SZYNDLAR 1991b). The trunk vertebrae are comparable to those of *Coluber viridiflavus* and *C. caspius* as well as to vertebrae of the fossil *Elaphe kohfidischi* from the Late Miocene (MN 11) of Kohfidisch, Austria. The vertebrae of *C. viridiflavus* are provided with longer prezygapophyseal processes, while their centra are distinctly shorter (lower centrum length / centrum width ratio) than in *Elaphe kormosi*. The haemal keel of *E. kohfidischi* and *Coluber caspius* is thin, high and spatulate, but their centrum length / centrum width ratio approaches that of *Elaphe kormosi*. A snake somewhat similar to *E. kohfidischi* (as *E. cf. E. kohfidischi*) was reported from the Late Miocene (MN 12) of Cherevichnoie, Ukraine, by SZYNDLAR and ZEROVA (1992).

Elaphe praelongissima sp.n.

(Figs 6 and 7)

Holotype. – One basiparasphenoid (No. V.19004/Vt.149) (Fig. 6 a-c).

Type locality. – Polgárdi 4 "Lower".

Type horizon. – Uppermost Miocene; Pontian or Upper Turolian (MN 13).

Name derivation. – From latin *prae*-, before, and *longissima*.

Referred material. – Polgárdi 2: one quadrate (No. Ob-4465/f), one ectopterygoid (No. Ob-4465/g), one premaxilla (No. Ob-4465/h), 75 vertebrae (No. V.19003). Polgárdi 4 "Lower": one prootic (No. V.19005), one exoccipital (No. V.19666), 4 quadrates (No. V.19006), one vomer (No. V.19667), one fragmentary dentary (No. V.19007), 40 vertebrae (No. V.19008). Polgárdi 4 "Upper": 2 compound bones (No. V.19009), 40 vertebrae (No. V.19010).

Diagnosis. – A typical medium-sized colubrid snake, with reduced suborbital flanges, small frontal step of the basiparasphenoid, and relatively short Vidian canals. Trunk vertebrae characterized by their short centrum, vaulted neural arch, concave or notched zygosphene, and obtuse prezygapophyseal processes.

Description of holotype. – Well-preserved basiparasphenoid (Fig. 6 a-c). In ventral view, a broad groove extends anteriorly through the parasphenoid. The suborbital flanges are weakly defined. The sagittal basisphenoid crests are present and extend from the central area close to the posterior border of the bone, this last being provided with three distinct lobes. The pterygoid crests (surmounting weakly developed basipterygoid processes) are inclined anteriorly, covering partially the anterior foramina of the Vidian canals. The common foramina, situated far from the posterolateral corners of the bone, are accompanied by grooves directed posterolaterally. The posterolateral portions of the bone are slightly convex. Additional paired foramina are visible, medial to the common foramina. In lateral view, the suborbital flanges are not bent upward. The frontal step is reduced. In dorsal view, the trabecular processes and trabecular grooves are well defined. The anterior foramina of the abducens and cid nerves are situated close to each other.

Description of referred material. – Prootic (Fig. 6 h): The occipital crest is weakly developed. The anterior prootic foramen (V₂) is oval and accompanied anteroventrally by a smaller foramen. The posterior prootic foramen (V₃) is somewhat larger. A small orifice for the facial nerve (VII) is situated posteriorly and the laterosphenoid foramen anteroventrally to the V₃ foramen. The otic recess is rather shallow.

Exoccipital (Fig. 6 j): The circumfenestral crest surrounding posteriorly the otic recess is well marked. The occipital crest is well developed and the parotic process is relatively large. The vagus-hypoglossal nerve foramina are situated in a deep concavity. The exoccipital tubercle is relatively short.

Ectopterygoid (cf. BOLKAY 1913, pl. XII: 6): This element was originally allocated by BOLKAY to *Elaphe kormosi*. The stem of the bone is slightly bent with a tapering tip. The square external ramus is situated at a right angle to the internal ramus, the latter being thin and pointed distally.

Quadrate (Fig. 6 f,g): In medial view the trunk of the bone is of equal thickness throughout its length. In posterolateral view the stem and the posteromedial margin are straight. The quadrate crest is sharp and prominent above the level of the stapedia process. The dorsal portion of the quadrate crest is produced as a rectangular lobe, slightly projecting medially.

Compound bone (Fig. 6 k): The lateral flange is lower than the medial; the lateral surface of the former is slightly concave. The retroarticular process is bent ventromedially.

Dentary (Fig. 6 d,e): The posterior portion of the bone is missing. The anterior end is slightly curved medially. The teeth are proterodontic. Meckel's groove closes completely at the level of the 6th tooth. The mental foramen lies at the level of the 8-9th teeth, while the compound notch approaches the level of the 11th tooth.

Vomer (Fig. 6 i): The posterosuperior process is missing. The premaxillary process is relatively long and tapering. The nasal process is slightly widened distally.

Vertebrae (Fig. 7): The neural spine of the cervical vertebrae is higher than long; it overhangs either both anteriorly and posteriorly or posteriorly only (Fig. 7 f). The zygosphenes are concave; the hypapophysis is straight, shorter than the centrum length and directed posteroventrally, with tapering or blunt tip (Fig. 7 l). In the middle trunk vertebrae the neural arch is vaulted and without epizygapophyseal spines. The neural spine is as

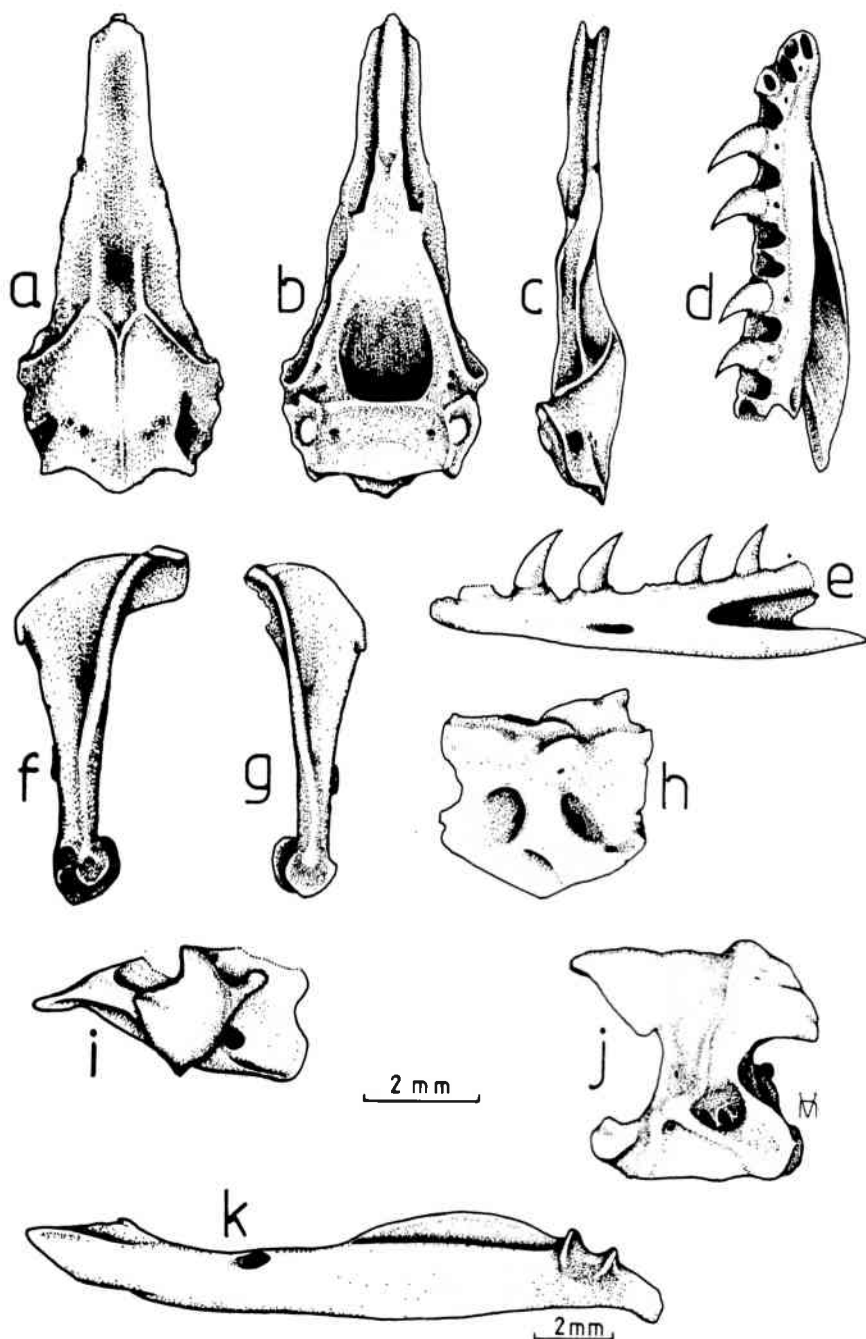


Fig. 6. *Elaphe praelongissima* n.sp. a-c - basiparasphenoid (holotype; Polgárdi 4 "Lower", No. V.19004/Vt.149), d,e - left dentary (Polgárdi 4 "Lower", No. V.19007), f - right quadrate (Polgárdi 4 "Lower", No. V.19006/a), g - left quadrate (Polgárdi 2, No. Ob-4465/f), h - right prootic (Polgárdi 4 "Lower", No. V.19005), i - left vomer (Polgárdi 4 "Lower", No. V.19667), j - right exoccipital (Polgárdi 4 "Lower", No. V.19666), k - left compound bone (Polgárdi 4 "Upper", No. V.19009/a). a - ventral view; b - dorsal view; c,e,h,i,j,k - lateral views; d - medial view; f,g - posterolateral views.

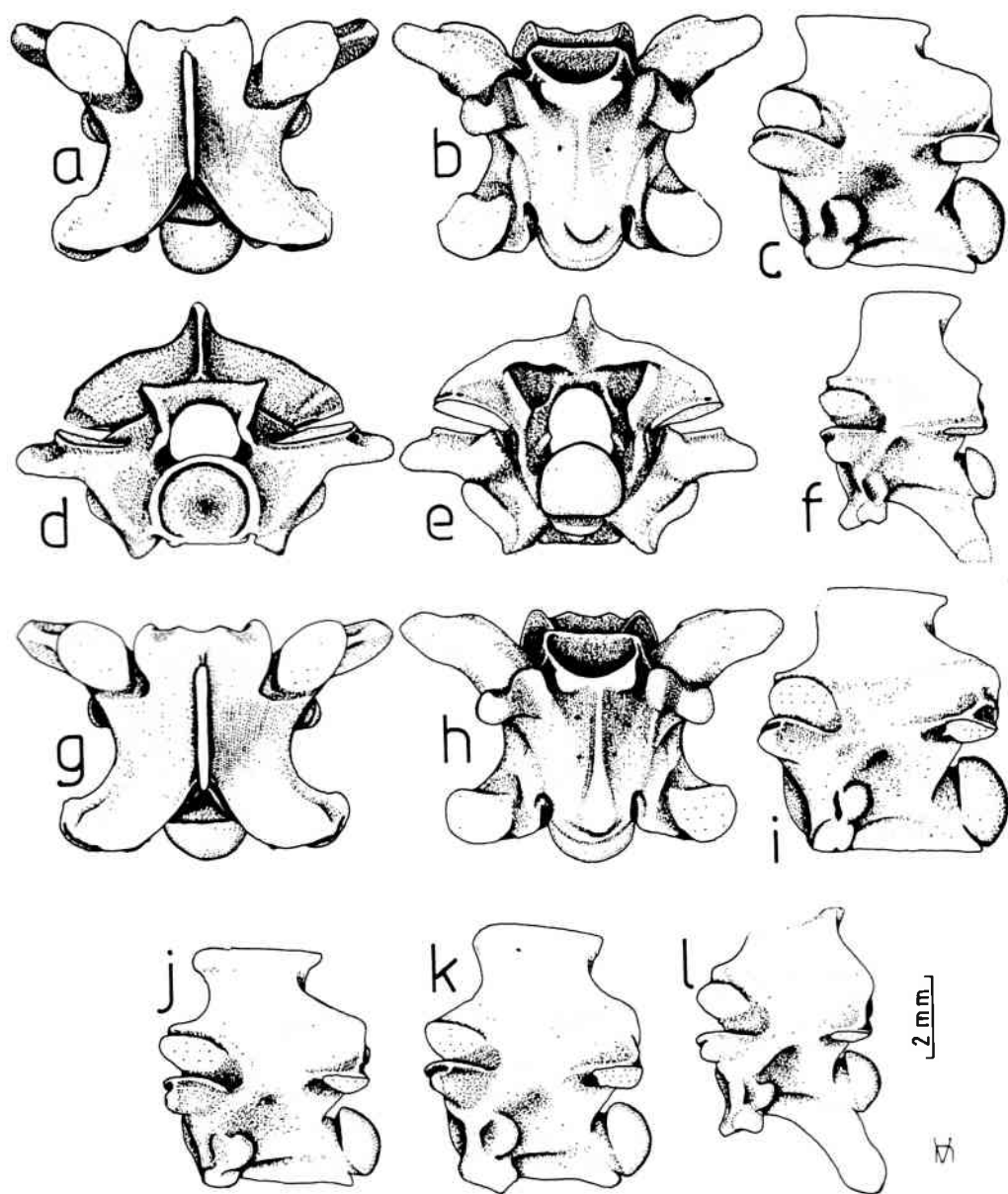


Fig. 7. *Elaphe praelongissima* n.sp. a-e – trunk vertebra (Polgárdi 4 "Upper", No. V.19010/a), f – cervical vertebra (Polgárdi 4 "Lower", No. V.19008/b), g,h – trunk vertebra (Polgárdi 4 "Upper", No. V.19010/b), i – trunk vertebra (Polgárdi 4 "Upper", No. V.19010/c), j – trunk vertebra (Polgárdi 4 "Upper", No. V.199010/d), k – trunk vertebra (Polgárdi 4 "Lower", No. V.199008/a), l – cervical vertebra (Polgárdi 4 "Lower", No. V.199008/c). a,g – dorsal views; b,h – ventral views; c,f,i,j,k,l – lateral views; d – anterior view; e – posterior view.

high as long and it overhangs both anteriorly and posteriorly (the posterior overhang is usually better defined); the dorsal edge of the spine is thickened. The paradiapophyses are distinctly divided into dia- and parapophyseal portions. The parapophysis is longer than diapophysis; sometimes the former is provided with a posteroventral extension (Fig. 7 k). In ventral view the centrum is triangular, slightly longer than wide. In twelve vertebrae from Polgárdi 2 the observed range of the centrum length is 3.97-4.98 mm (mean 4.59), while the centrum length / centrum width ratio is 1.02-1.16 (mean 1.09). In twelve vertebrae from Polgárdi 4 "Upper" the centrum length is 4.10-5.16 mm (mean 4.53), while the centrum length / centrum width ratio 1.00-1.19 (mean 1.11). The prominent haemal keel is spatulate; it is thin below the cotyle rim, whereas its posterior portion is widened and flattened. The subcentral ridges are better defined in the vicinity of the parapophyses. The subcentral foramina are distinct; sometimes they are doubled (Fig. 7 h). The anterior margin of the zygosphenes is concave, usually with a small median notch or it is notched crenate; in anterior view this structure is straight or slightly convex. The prezygapophyseal articular facets are oval, while the postzygapophyseal articular facets are of various shapes, although usually obovate. The prezygapophyseal processes are distinctly obtuse and slightly curved anteriorly; they are as long as the prezygapophyseal articular facets or somewhat shorter. The interzygapophyseal ridges are strongly developed, especially in the postzygapophyseal area. The cotyle and condyle are rounded; the ventral margin of the cotyle is usually accompanied with two small tubercles.

Comparisons and comments. – The basiparasphenoid of *Elaphe praelongissima* differs from living members of the genus in having its common foramina situated far from the posterolateral borders of the bone. It approaches the condition observed in the living *E. dione*. It differs from the fossil *E. kohfidischi* and *E. algorensis* in having a much smaller frontal step and in absence of a frontal crest. It differs from *E. kormosi* in its smaller dimensions and different morphology of the ectopterygoid, quadrate and vertebrae. In its shape the quadrate of *E. praelongissima* somewhat resembles that of *E. situla*, but in the latter the anterodorsal lobe is much smaller. The compound bone and premaxilla of *E. praelongissima* resemble those of the living *E. longissima*; this is also the case as regards the vomer, but the vomerine foramen is significantly larger in the latter snake. The vertebrae resemble those of *E. longissima* and the fossil *E. paralongissima* from the Late Pliocene of Poland (SZYNDLAR 1984). The paradiapophyses are similarly built in *E. praelongissima* and *E. paralongissima*, but the haemal keel is more flattened in the latter. A sharp posteroventral extension of the parapophyses occurs also in some other members of the genus *Elaphe*, e.g. in the living *E. guttata* (personal observation). The vertebrae of *E. praelongissima* are much smaller than those of the aforementioned forms.

E. kormosi and *E. praelongissima* undoubtedly represented two distinct lineages; the former was related to *E. kohfidischi*, while the latter belonged to a hypothetical lineage leading to the extant *E. longissima*.

Genus *Natrix* LAURENTI, 1768

Natrix cf. *N. longivertebrata* SZYNDLAR, 1984

(Fig. 8)

M a t e r i a l. – Polgárdi 2: one fragmentary basiparasphenoid (No. Ob-4466/a), 2 basioccipitals (No. Ob-4466/b and c), 3 fragmentary parietals (No. Ob-4466/d,e,f), 2 fragmen-

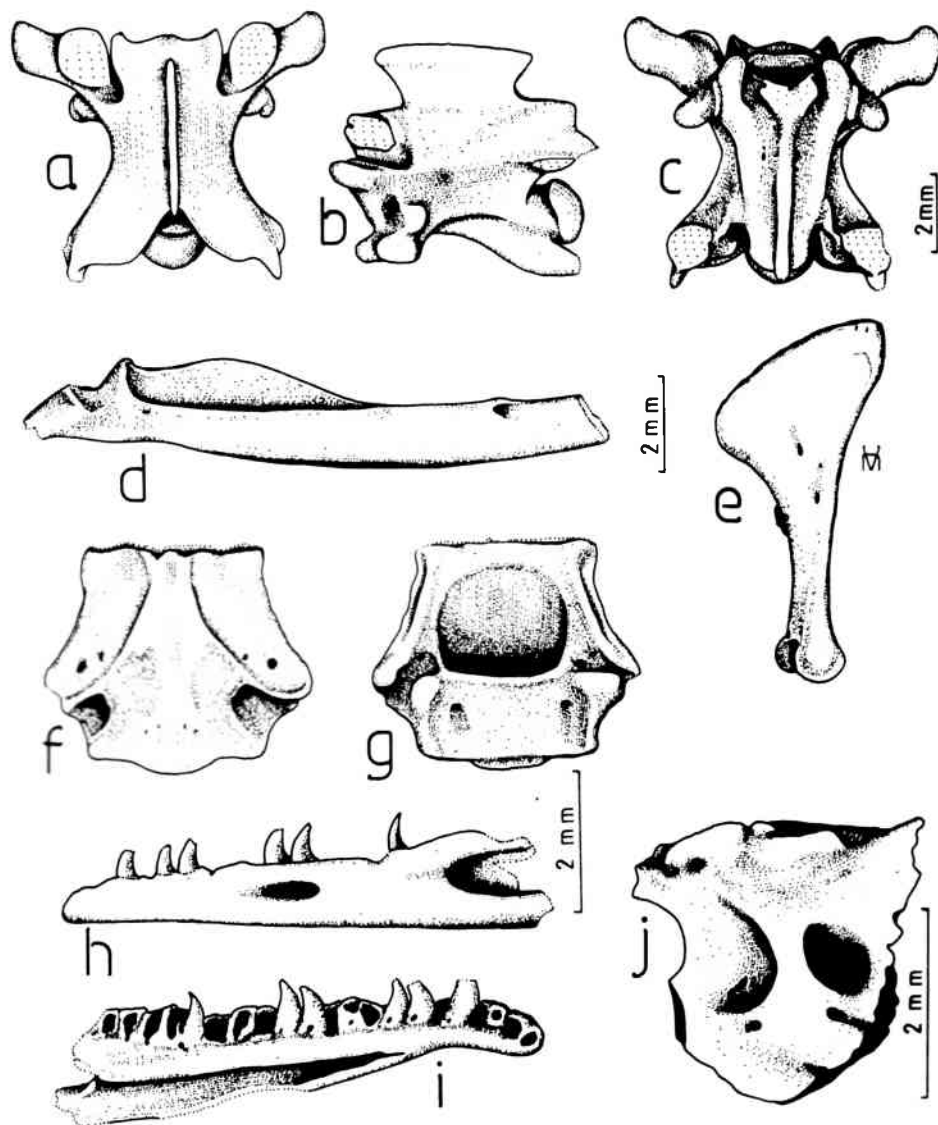


Fig. 8. *Natrix* cf. *N. longivertebrata*. a-c – trunk vertebra (Polgárdi 4 "Lower", No. V.18997/a), d – right compound bone (Polgárdi 4 "Lower", No. V.18974/d), e – right quadrate (Polgárdi 4 "Lower", No. V.18974/a), f, g – basiparasphenoid (Polgárdi 2, No. Ob-4466/d), h, i – left dentary (Polgárdi 4 "Upper", No. V.18976/a), j – right prootic (Polgárdi 4 "Lower", No. V.19670). a, g – dorsal views; b, d, h, j – lateral views; c, f – ventral views; e – posterolateral view; i – medial view.

tary compound bones (No. Ob-4463/b,c), 60 vertebrae (No. V.18973). Polgárdi 4 "Lower": one prootic (No. V.19670), 3 quadrates (No. V.18974/a,b,c), 3 compound bones (No. V.18974/d,e,f), 185 vertebrae (No. V.18975). Polgárdi 4 "Upper": 2 fragmentary dentaries (No. V.18976/a,b), one compound bone (No. V.18976/c), 100 vertebrae (No. V.18977).

Description. – Parietal: The best-preserved fragment is very similar to that described by BACHMAYER and SZYNDLAR (1987) from the Late Miocene of Kohfidisch, Austria, as well as to the parietals of the living *Natrix natrix*. The parietal crests do not contact before reaching the posterior margin of the bone.

Basioccipital: This element is also very similar to the basioccipitals of the living *Natrix natrix*. It has a basioccipital crest similarly oriented as in *N. natrix* (basioccipital process is lacking), well developed basioccipital tubercles, and strongly built occipitocondylar tubercles; the median crest is lacking.

Prootic (Fig. 8 j): The roof of the bone is strongly crested. The relatively thin laterosphenoid partitions off the anterior (V₂) and posterior (V₃) prootic foramina. An orifice for the cid nerve (V₄) pierces the bone below the V₂ foramen; a small opening for the facial nerve (VII) is situated behind the V₃ foramen. The otic recess is shallow.

Basiparasphenoid (Fig. 8 f,g): The basiparasphenoid fragment was originally labelled as *Natrix tessellata* (BOLKAY 1913; SZUNYOGHY 1932). In ventral view the sagittal basisphenoid crest is lacking. The Vidian canals are short, with posterior orifices covered by the pterygoid processes. The cid nerve foramina are visible on both sides of the bone. In dorsal view the foramina for the abducens and cid nerves are distinct; the anterior foramina for the abducens nerves are situated close to those for the cid nerves.

Quadrate (Fig. 8 e): The stem of the bone is slender, while its dorsal portion is strongly widened. The anterolateral margin is slightly concave. The quadrate crest is weakly developed.

Dentary (Fig. 8 h,i): The bone is relatively slender, with the anterior end curved medially. The mental foramen lies at the level of the 12-13th teeth. The Meckel's groove closes completely at the level of the 8th tooth, while the compound notch approaches the level of the 19th tooth.

Compound bone (Fig. 8 d): The bone is slender. The mandibular fossa is relatively large; the medial flange is twice as high as the lateral flange. The supraangular foramen is situated far from the mandibular fossa. The retroarticular process is curved ventrally.

Vertebrae (Fig. 8 a-c): The vertebrae are most similar to those of the living *Natrix natrix*; the centrum length / centrum width ratio in the vertebrae from Polgárdi is distinctly lower than in the type material of *N. longivertebrata* (SZYNDLAR 1984).

Remarks. – In the morphology of its basiparasphenoid and prootic *Natrix* from Polgárdi holds an intermediate position between the "ancient" and "modern" patterns of the *Natrix longivertebrata* – *N. natrix* lineage (SZYNDLAR 1991c). On that account as well as regarding the age of the fossils, the above described remains are here compared with *N. longivertebrata*. The presence of another member of the genus, the living *N. tessellata*, in the Polgárdi deposits cannot be confirmed. It should be added that the remains of *N. tessellata* reported previously by SZUNYOGHY (1932) from geologically younger Hungarian localities (e.g. Uppermost Pliocene (MN 17) of Villány-3) belonged actually to this species (personal observations).

Family *Viperidae* OPPEL, 1811

Genus *Vipera* LAURENTI, 1768

Vipera gedulyi BOLKAY, 1913

(Figs 9-12, 13 a-d)

1911 *Vipera* sp.: KORMOS, p. 63;

1911 ? *Bitis*: KORMOS, p. 63;

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

1932 † *Vipera Gedulyi* BY.: SZUNYOGHY, pp. 10 and 50-52, fig. 116;

1939 *Vipera gedulyi* BOLKAY: KUHN, p. 23;

1963 *Vipera gedulyi* BOLKAY: KUHN, p. 32;

1984 *Vipera gedulyi* BOLKAY: RAGE, p. 56, fig. 33 C,D;

1988 *Vipera gedulyi* BOLKAY: SZYNDLAR, pp. 702, 704;

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

Type material of BOLKAY (1913). – Polgárdi 2: 15 fragmentary basiparasphenoids, 2 frontals, 6 prefrontals, 2 fragmentary parietals, one prootic, one exoccipital, 8 basioccipitals, 19 fragmentary maxillae, 206 isolated venom fangs, 25 fragmentary compound bones, 30 fragmentary ectopterygoids (syntypes, No. Ob-4467/Vt.74).

Referred material. – Polgárdi 2: 2 fragmentary dentaries (No. V.13102/a), one fragmentary palatine (No. V.13102/b), 1000 vertebrae (No. V.13103). Polgárdi 4 "Lower": one fragmentary basiparasphenoid (No. V.18978/a), one basioccipital (No. V.18978/b), one exoccipital (No. V.18978/c), one prootic (No. V.18978/d), 2 fragmentary pterygoids (No. V.18978/e), one fragmentary ectopterygoid (No. V.18978/f), 4 fragmentary compound bones (No. V.18978/g,h,i,j), 200 vertebrae (No. V.18979). Polgárdi 4 "Upper": one frontal (No. V.18980/1), one fragmentary dentary (No. V.18980/2), one fragmentary compound bone (No. V.18980/3), 130 vertebrae (No. V.18981).

Emended diagnosis. – A large viperine snake most resembling the living *Vipera lebetina*. It is characterized by a long and broad basioccipital process of the basioccipital; high and sharp (on the anteromedial edge) ascending process of the maxilla; middle trunk vertebrae with crenate zygosphenes; neural spines lower than long and overhanging both anteriorly and posteriorly, and acute parapophyseal processes.

Description. – Prefrontal (Fig. 9 e-g): The posterodorsal process of the prefrontal (for the articulation with the frontal) is variable in length. The lacrimal foramen, situated in a large fossa, is visible in posterolateral view. The former structure is variable in shape and size and it is accompanied dorsally by a smaller foramen. In a few examined specimens of the recent *Vipera lebetina* the medial wall of the prefrontal is convex; in consequence, in posterolateral view the lacrimal foramen is hidden.

Frontal (Fig. 9 a-d): The anterodorsal ridge of the frontal (for the reception of the prefrontal) is continuous or interrupted by a shallow groove running toward the inner prefrontal process. The premaxillary process is relatively small; in anterior view it is subtriangular. The frontal aperture is of variable shape.

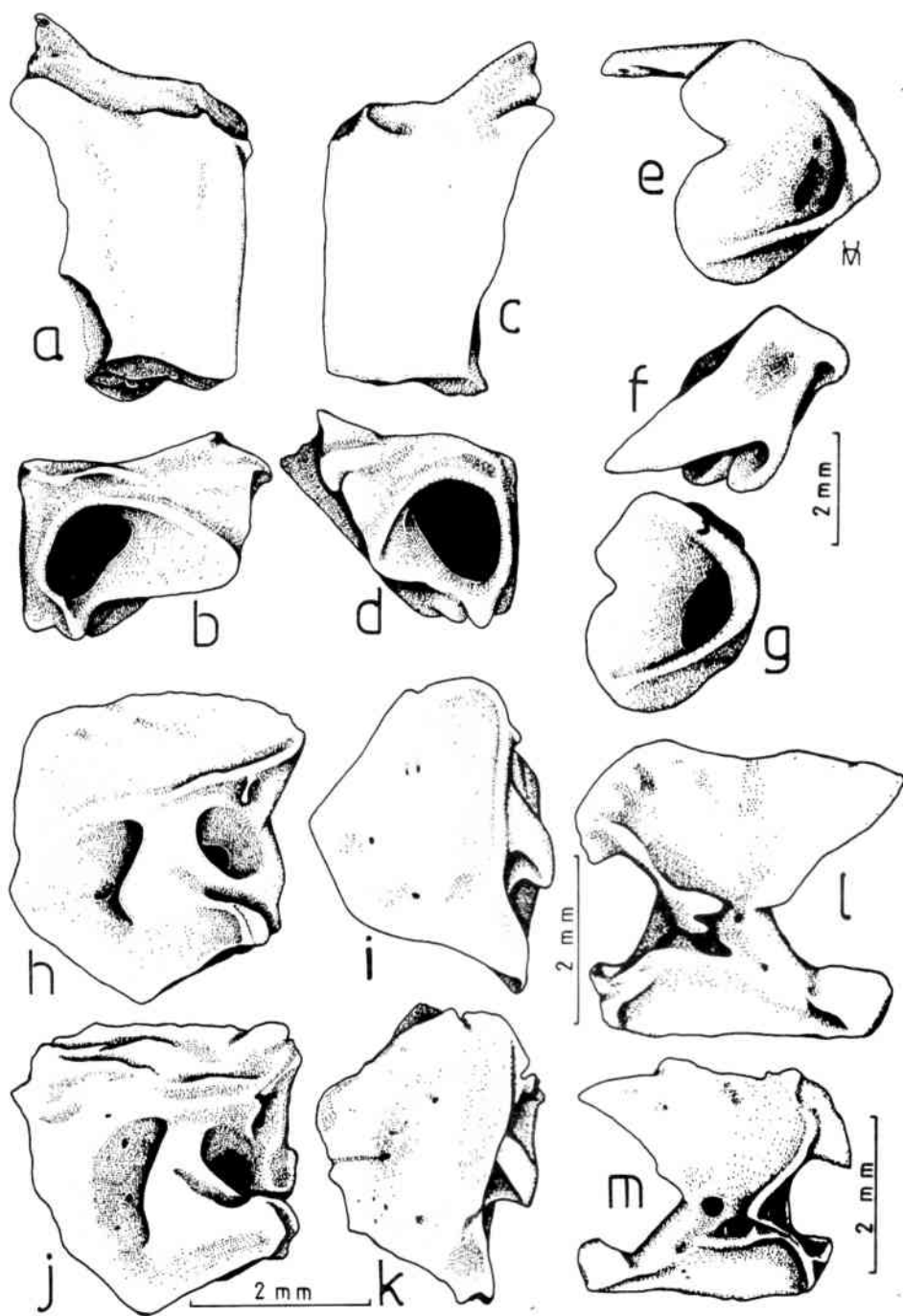


Fig. 9. *Vipera gedulyi*. a,b – left frontal, c,d – right frontal, e,f, and g two right prefrontals, h,i – right prootic (syntypes; Polgárdi 2, No. Ob-4467/Vt.74), j,k – right prootic (Polgárdi 4 "Lower", No. V.19671), l – left exoccipital (syntype; Polgárdi 2, No. Ob-4467/Vt.74), m – right exoccipital (Polgárdi 4 "Lower", No. V.18978/c). a,c,f,i,k – dorsal views; b,d – anterior views; e,g – posteroventrolateral views,

Parietal (cf. SZUNYOGHY 1932: fig. 116): The morphology of the bone does not differ from the homologous bones of the recent *Vipera lebetina*, in shape resembling those figured by ZEROVA and CHIKIN (1991: figs 5/II, 6/II, 7/II).

Basioccipital (Fig. 10 a-f): In ventral view the bones are subtriangular, with weakly developed basioccipital tubercles. The median crest is absent. The basioccipital process is elongate and variable in shape. The biggest specimen (Fig. 10 a,b) is provided with a very long and broad basioccipital process, while the remaining ones (Fig. 10 c,d and e,f) have comparatively shorter and thinner processes. The basioccipital shown in Fig. 10 e,f in shape resembles that of *Vipera burgenlandica*, but in the latter the basioccipital process is distinctly shorter.

Exoccipital (Fig. 9 l,m): The exoccipital crest is situated near the anterodorsal margin of the bone. It runs toward the posterior margin of the vestibular window and fuses into the circumfenestral crest. In the specimen from Polgárdi 4 the circumfenestral crest is continuous; in the exoccipital from Polgárdi 2 (Fig. 9 l) a deep furrow, extending from the posterior margin of the otic recess to the vagus-hypoglossal nerve foramina, divides the crest into dorsal and ventral parts. The vagus-hypoglossal nerve foramina are located in the slightly elongated common recess. The paroccipital process is relatively large.

Basiparasphenoid (Fig. 10 g-i): In all specimens distal ends of the parasphenoid portion are missing. The suborbital flanges are prominent. In ventral view the basisphenoid crest is usually well defined, reaching the posterior border of the bone, it produces a distinct spur (cf. BOLKAY 1913, pl. XII: 11). In the specimen No. V.18978/a the crest is bifurcated posteriorly. The posterior orifice of the Vidian canal and the cerebral foramen are distinctly separated from each other; sometimes they are covered by a bony crest. The anterior opening of the Vidian canal lies on the lateral margin of the bone, near the anterolateral corner of the pituitary fossa. In dorsal view the lateral sides of the crista sellaris are pierced by paired canals for the abducens nerves. The anterior foramina for the abducens nerves and the foramina for re-entry of the cid nerves are located in deep common furrows on both sides of the pituitary fossa. The nerves continue anteriorly in the common canals or furrows; in some specimens the furrows are rather shallow or the canals are not ossified completely from above. These variations are concordant with those observed in the recent *Vipera lebetina* by ZEROVA and CHIKIN (1991).

Prootic (Fig. 9 h-k): The roof of the bone is crested. In the specimen from Polgárdi 2 the foramen for the V₂ nerve is round and completely surrounded by the lateral wall of the prootic (Fig. 9 h), while in the bone from Polgárdi 4 "Lower" (Fig. 9 j) the V₂ opening is continued in a deep fissure to the anteroventral corner of the bone. The V₃ foramen is hidden below the laterosphenoid bar; the latter structure is pierced by the cid nerve foramen, continued anteroventrally in a deep and narrow furrow.

Maxilla (Fig. 10 j): In anterior view the trunk of the bone is convex. The distal part of the ascending process is curved medially. A strong ridge occurs on the anteromedial side of the bone, although in some specimens it is weakly defined. Near the top of the ascending process (usually on its anterolateral side) a small foramen is situated; in one specimen it opens on the posteromedial side, while in another one it is present on both sides. Two foramina of the dental canal are situated in an oval or rounded fossa on the medial side of

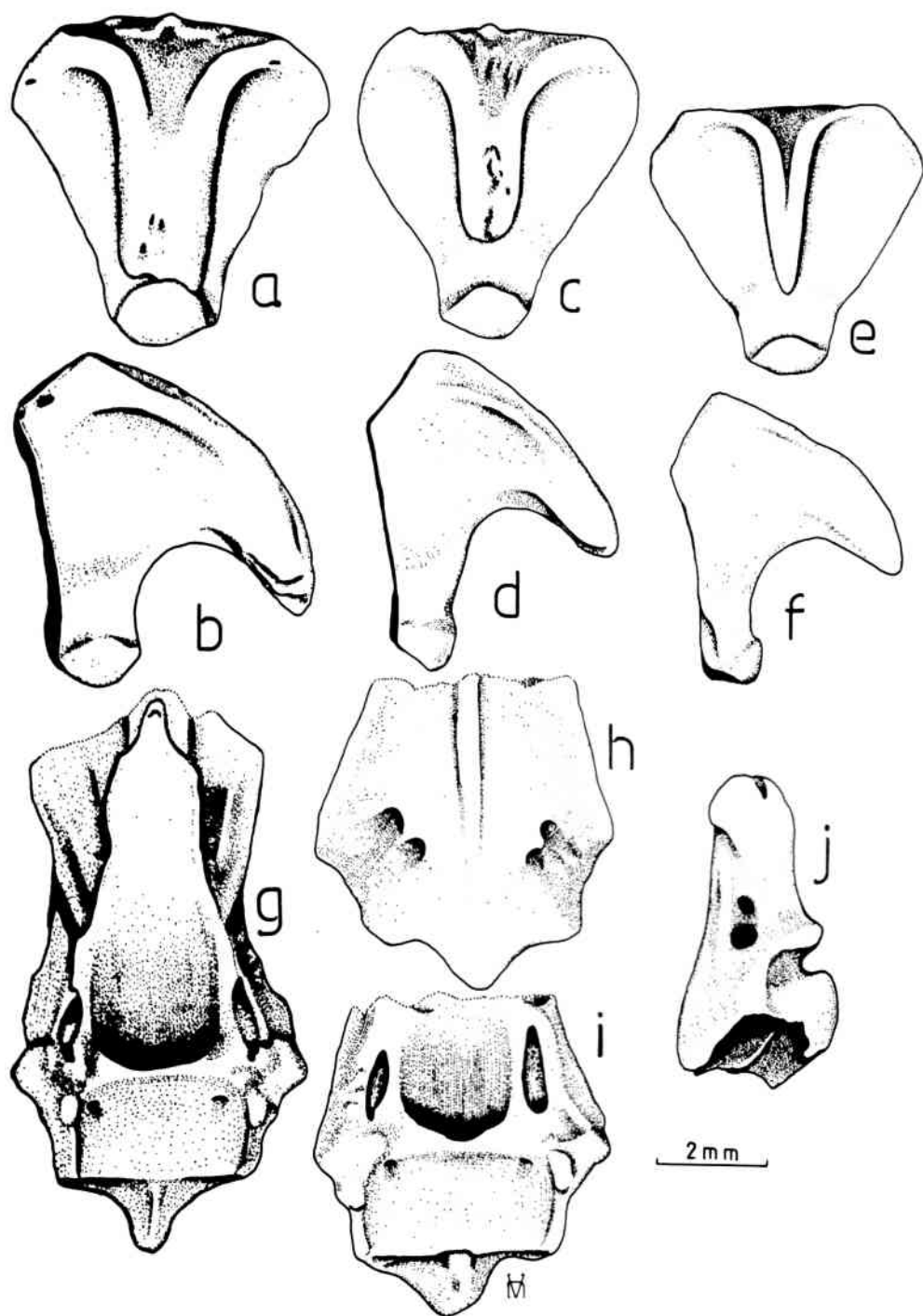


Fig. 10. *Vipera gedulyi*. a, b, c, d, and e, f – three basioccipitals, g, h, and i – two basiparasphenoids, j – right maxilla (syntypes; Polgárdi 2, No. Ob-4467/Vt.74). a, c, e, h – ventral views; b, d, f – lateral views; g, i – dorsal views; j – posteromedial view.

the bone. The ectopterygoid-maxillary articulation is formed by a relatively deep fossa, delimited dorsally by a well-developed transverse ridge.

Palatine: It is short and laterally compressed. It possesses four tooth sockets. Pterygoids are preserved in small fragments only.

Ectopterygoid (Figs 11 a-d; 13 d): In all specimens the posterior portions are broken off. The lateral side of the anterior portion (i.e., the external ramus) is bent downward. A small projection extending from this last structure is oriented anteriorly or anteromedially. The internal ramus is variable in shape and size. Its anterior margin is convex or straight (cf. Fig. 11 c). The medial margin of the stem of the bone is slightly bent ventrally.

Dentary (Fig. 11 e,f): The bone is strongly built; the anterior end is curved medially. Meckel's groove reaches the level of the first tooth. The mental foramen is located at the level of the 6-7th teeth, while the compound notch approaches the level of the 8th (9th) tooth.

Compound bone (Fig. 11 g,h): In all specimens the anterior part is broken off. The medial flange is approximately three times as high as the lateral flange. The mandibular fossa is variable in shape. The retroarticular process is relatively large, bent medially or ventromedially.

Axis (Fig. 11 i): The centrum is relatively short and equal in length to the hypapophysis. The neural spine is oriented posteriorly; the pleurapophyses are broken off.

Anterior trunk vertebrae: The neural spine of the anteriormost cervical vertebrae is relatively high and inclined posteriorly. The zygosphenes are convex from above and concave in anterior view. The hypapophysis is broken off (Fig. 11 j). The neural spine of the anterior trunk vertebrae is usually higher than long or as high as long. The hypapophysis is long (but shorter than the centrum length) and sometimes it tapers caudally.

Middle trunk vertebrae (Fig. 12): The centrum is moderately elongate; the neural arch is depressed. The neural spine overhangs anteriorly and posteriorly; it is usually as high as long but its height diminishes in more posterior trunk vertebrae. The paradiapophyses are differentiated into dia- and parapophyseal portions. The parapophyseal processes are strongly built, acute and directed anteroventrally. The hypapophysis is relatively short, straight and directed posteroventrally (Fig. 12 e). In dorsal view the zygosphenes are crenate, with the lateral lobes usually sharp and protruding anteriorly (Fig. 13 b). The prezygapophyseal articular facets are subsquare-shaped. The prezygapophyseal process is short and acute. In ventral view the centrum is longer than wide; the subcentral ridges are better defined in the vicinity of the parapophyses. The postzygapophyseal articular facets are usually rectangular. In anterior view the zygosphenes are usually straight. The paracotylar foramina are well marked, sometimes doubled (Fig. 12 c). The cotyle and condyle are rounded; the latter is provided with a short neck. In sixteen middle trunk vertebrae from Polgárdi 2 the centrum length ranges between 6.50 and 8.47 mm, while the centrum length / centrum width ratio is 1.30-1.62 (mean 1.43). In twelve vertebrae from Polgárdi 4 "Lower" the centrum length is 5.42-7.31 mm; the centrum length / centrum width ratio 1.24-1.41 (mean 1.32). In seven vertebrae from Polgárdi 4 "Upper" the centrum length is 5.79-6.27 mm; the centrum length / centrum width ratio 1.36-1.39 (mean 1.37).

In the posteriormost trunk vertebrae the subcentral ridges and the keels below the cotyle rim are prominent; the hypapophysis is short and somewhat sigmoid (Fig. 12 f).

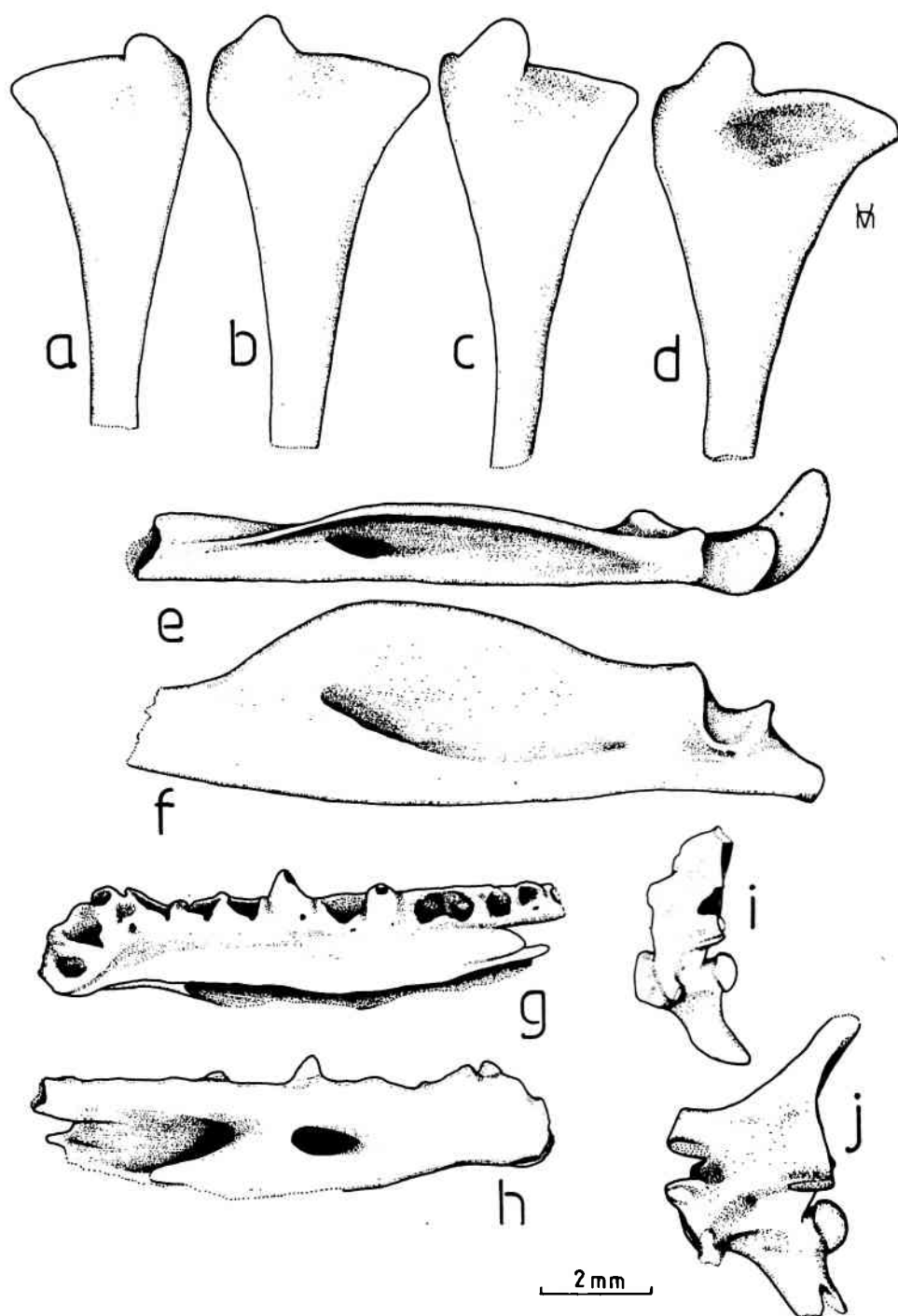


Fig. 11. *Vipera gedulyi*. a-d – four ectopterygoids (syntypes; Polgárdi 2, No. Ob-4467/Vt.74), e,f – left compound bone, g,h – right dentary (Polgárdi 2, No. V.13102/b), i – axis (Polgárdi 4 "Lower", No. V.19668), j – anterior cervical vertebra (Polgárdi 4 "Lower", No. V.19669). a-e – dorsal views; f,h,i,j – lateral views; g – medial view.

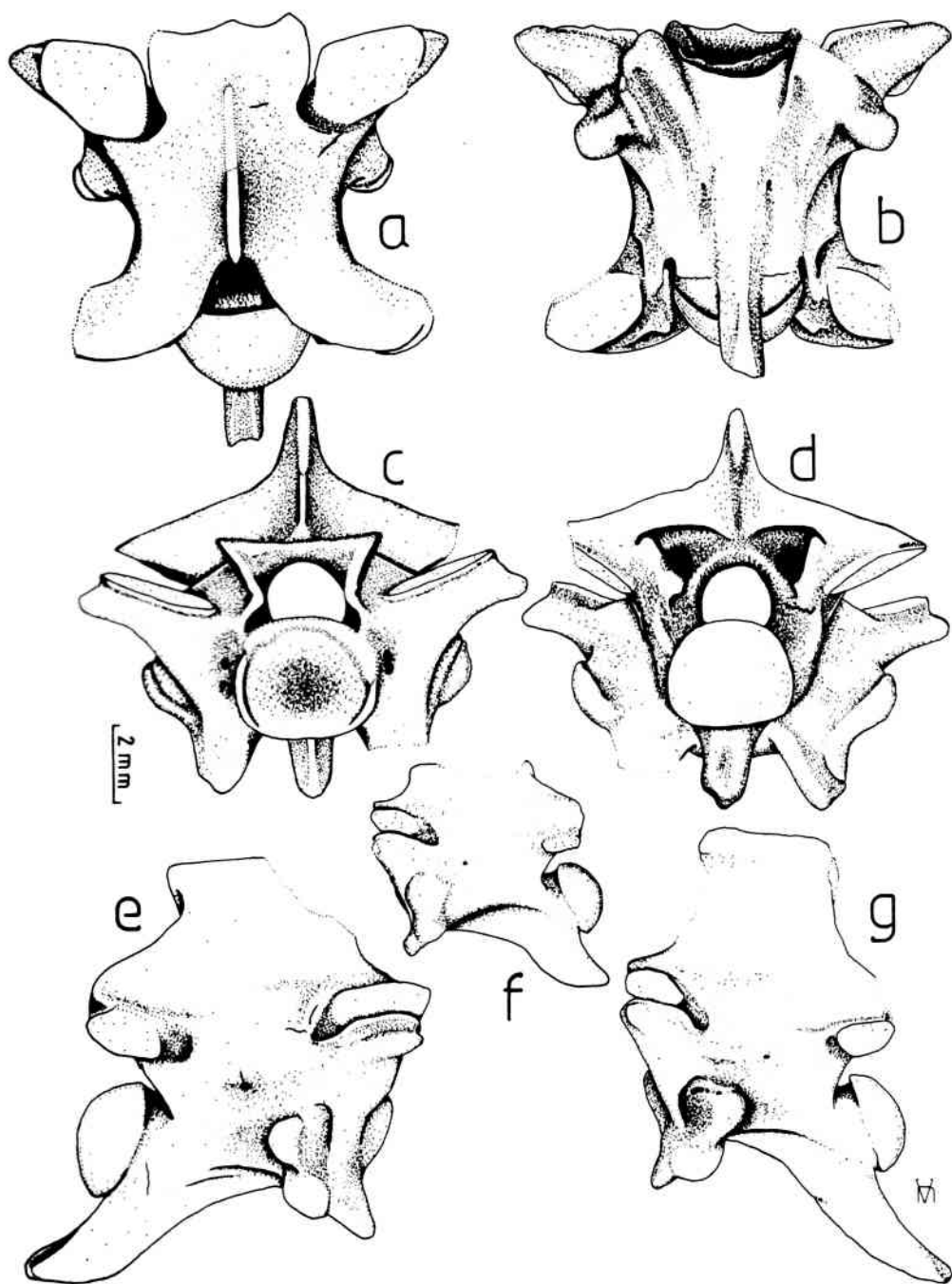


Fig. 12. *Vipera gedulyi*. a-e – trunk vertebra (Polgárdi 4 "Lower", No. V.18979/a), f – posterior trunk vertebra (Polgárdi 2, No. 13103/c), g – cervical vertebra (Polgárdi 2, No. V.13103/b). a – dorsal view; b – ventral view; c – anterior view; d – posterior view; e, f, g – lateral views.

Remarks. – *Vipera gedulyi* is clearly referable to the »Oriental viper« group of the genus *Vipera* (sensu GROOMBRIDGE 1986). The cranial bones and vertebrae closely resemble those of the living *V. lebetina* as well as some fossil members of the »lebetina« complex, namely *V. burgenlandica*, *V. kuchurganica*, *V. ukrainica* and *V. sarmatica*. It differs from *V. burgenlandica* from the Late Miocene of Kohfidisch, Austria (BACHMAYER and SZYNDLAR 1987), in the morphology of its basioccipital process (distinctly shorter and thinner in *V. burgenlandica*) and dentary (with the mental foramen lying at the level of the 8th tooth and the compound notch reaching the level of the 9th tooth in *V. burgenlandica*). The vertebrae of *V. burgenlandica* are provided with higher neural spines in the middle trunk region of the column; their parapophyseal processes are obtuse and the hypapophyses in the posterior trunk vertebrae are straight. Despite these differences, the geologically older *V. burgenlandica* seems to be the closest extinct relative of *V. gedulyi*. Relationships between *V. gedulyi* and, on the other hand, *V. sarmatica* from the Late Miocene (MN 9) of Kalfa, Moldavia, and *V. kuchurganica* from the Lower Pliocene (MN 14) of Kuchurgan, Ukraine (ZEROVA et al. 1987), both described exclusively on the basis of vertebrae, are less clear. *V. ukrainica*, described recently from the Late Miocene (MN 9) of Gritsev, Ukraine (ZEROVA 1992), lacks a ridge on the anteromedial wall of the ascending process of the maxilla; the ventral (bearing fangs) portion of the bone is lower than in *V. gedulyi*. Its ectopterygoid, dentary, compound bone and vertebrae differ in some details from the homologous elements of *V. gedulyi*. A basioccipital referred by ZEROVA (1992: fig. 4) to *V. ukrainica*, with strongly defined basioccipital tubercles and small bulges on both sides of the base of the basioccipital process, most probable belonged to another snake, namely the elapid *Naja romani*, previously reported from the same locality (SZYNDLAR and ZEROVA 1990).

Vipera sp. 1

(Fig. 13 e)

Material. – Polgárdi 2: 2 vertebrae (No. V.18982). Polgárdi 4 "Lower": 8 vertebrae (No. V.18983).

Description and remarks. – The material belonged to the »Oriental viper« group. The vertebrae differ from those of *Vipera gedulyi* in having elongated prezygapophyseal articular facets, longer prezygapophyseal processes and longer neural spines, beginning above the anterior portion of the zygosphen. The parapophyseal process is longer and thinner than in *V. gedulyi*; it is depressed dorsoventrally and directed anteriorly. In this aspect the remains are somewhat similar to those from the Pliocene of Vallée de la Canterrane (BAILON 1991) and to *Vipera* sp. from the Late Pliocene (MN 16) of Balaruc II (BAILON 1989, 1991). At the same time, considering the broad intraspecific variation range of *V. gedulyi*, as evidenced above, we cannot exclude the possibility that the remains belonged to this last species.

Vipera sp. 2

(Fig. 13 f,g)

Material. – Polgárdi 2: 3 fragmentary parietals, 12 vertebrae (No. V.18984). Polgárdi 4 "Lower": 6 vertebrae (No. V.18985). Polgárdi 4 "Upper": one fragmentary ectopterygoid (No. V.18986), 7 vertebrae (No. V.18987).

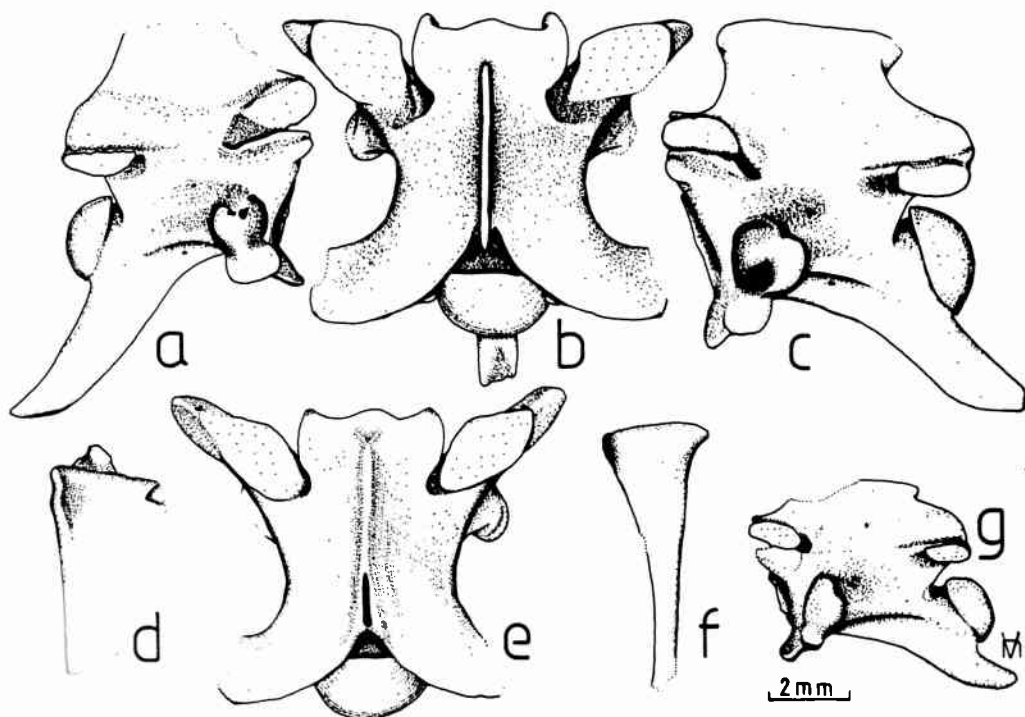


Fig. 13. a-d – *Vipera gedulyi*: a – cervical vertebra (Polgárdi 2, No. V.13103/a), b,c – trunk vertebra (Polgárdi 4 "Lower", No. V.18979/b), d – right ectopterygoid (Polgárdi 4 "Lower", No. V.18978/f. e – *Vipera* sp. 1: trunk vertebra (Polgárdi 4 "Lower", No. V.18983/a). f,g – *Vipera* sp. 2: f – left ectopterygoid (Polgárdi 4 "Upper", No. V.18986), g – trunk vertebra (Polgárdi 2, No. V.18987/a). a,c,g – lateral views; b,e,f – dorsal views; d – ventral view.

Description. – Parietal: SZUNYOGHY (1932) allocated two parietal fragments to *Vipera* cf. *aspis* and one to *V.* cf. *ammodytes*. Regarding their size and morphology, the above remains belonged indeed to the »European viper« group (sensu GROOMBRIDGE 1986).

Ectopterygoid (Fig. 13 f): The stem of the bone is slender; the anterior margin is slightly convex; the lateral side is bent downward and it lacks an anterior projection, this last feature being characteristic of *Vipera gedulyi*.

Vertebrae (Fig. 13 g): The centrum is long; the neural arch is depressed and without epizygapophyseal spines. The centrum length in four vertebrae from Polgárdi 2 ranges between 4.92 and 4.99 mm, while the centrum length / centrum width ratio is 1.47-1.73. The neural spine is low and long. The lateral foramen is well defined. The parapophyseal process is depressed dorsoventrally and obtuse. The hypapophysis is directed backward and tapering caudally. The zygosphenes are crenate, with a small central lobe. The prezygapophyseal processes are short. The prezygapophyseal articular facets are oval (sometimes

elongate or subquadrate); the postzygapophyseal articular facets are square. The haemal keel is prominent below the cotyle rim. The hypapophysis of the anterior precaudal vertebrae is nearly as long as the centrum.

Remarks. – The remains above are clearly referable to the »European viper« group, but no more precise identification of this material is possible.

III. CONCLUDING REMARKS

During the Upper Turolian times the climate was characterized by strong fluctuations between short warm and cooler phases (MÜLLER 1983), culminating in the well known Messinian event (RÖGL and STEININGER 1983). The vertebrate fauna from Polgárdi 4 lived in diversified environments as indicated by the composition of the faunas of birds (numerous marsh birds together with those inhabiting drier areas; JÁNOSSY 1991), mammals (numerous steppe elements, but also woodland dwellers), amphibians (anurans and salamanders), and reptiles (turtles, lizards, and snakes; personal observations).

As indicated by the available material, the snake fauna from Polgárdi 4 was dominated by small colubrids. Polgárdi 2, although belonging to the same biostratigraphical unit, is somewhat younger in age (FREUDENTHAL and KORDOS 1989). According to KRETZOI (1952), the landscape of Polgárdi 2 was characterized by scrubby, partially forested steppe vegetation. Contrary to Polgárdi 4, the commonest snake in the ophidian assemblage of Polgárdi 2 was *Vipera gedulyi*. This fact may have been connected with a rapid change in the paleoecological conditions at the end of the Miocene.

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