Russian Journal of Herpetology Vol. 11, No. 2, 2004, pp. 91 – 98

IDENTIFICATION OF SOME EURASIAN SPECIES OF *Elaphe* (COLUBRIDAE, SERPENTES) ON THE BASIS OF VERTEBRAE

Viatcheslav Yu. Ratnikov[1]

Submitted May 15, 2003.

The description of trunk vertebrae of eight species of the genus *Elaphe* is given. These are: *Elaphe climacophora*, *Elaphe dione*, *Elaphe longissima*, *Elaphe quatuorlineata*, *Elaphe rufodorsata*, *Elaphe schrencki*, *Elaphe situla*, *Elaphe taeniura*.

Keywords: Snakes (Colubrinae, *Elaphe*), Eurasia (former USSR), osteology, trunk vertebrae.

INTRODUCTION

Vertebrae are most frequently, if not the only parts of snake skeletons found in Late Cenozoic localities. This results from their high number in each individual and considerably more strength in comparison with skull bones. The complex structure of vertebrae, assuming numerous variants in morphology, allows identification of different taxa up to species level inclusively. The trunk vertebrae are most suitable for this purpose.

Despite of the rather large number of publications devoted to fossil snakes, the identification of fossil material may cause big difficulties. This is connected to difficulties in acquisition of the modern comparative material by paleontologists. As a result, this part of fossil remains may be identified incorrectly or not precisely enough. It being understood that geographical ranges of species in the past could strongly differ (and differed indeed) from the present ones, it is clear that the paleontologist should have an extensive information about skeletons of modern species. In such conditions a special study of osteology of modern forms with publication of obtained results is important.

Most publications, including descriptions of vertebrae of the genus *Elaphe*, are devoted to fossil remains and deals only with some modern species. Even monographic works contain descriptions of bones of only a few modern species found in the Late Cenozoic deposits (Auffenberg, 1963; Holman, 1998; Ratnikov, 2002; Szyndlar, 1984, 1991).

A large osteological collection, including 110 skeletons of 28 ratsnake species was studied by Helfenberger (2001). He compared the shape of some vertebral elements and some vertebral ratios in different species of ratsnakes, and presented results in tables. These results, along with data on topography of organs and biochemical researches, formed the basis for a new taxonomical scheme. Although such form of presentation of the material is acceptable for studying phylogeny, it cannot help determination of fossil remains. Beside absence of descriptions and illustrations of the material, this work did not embrace all aspects of vertebral morphology important for paleontologists (for example, shape of centrum). The table of indices contains only average values, while they vary not only between specimens, but also within a vertebral column.

The present paper deals with morphological features of trunk vertebrae of some *Elaphe* species from the territory of former USSR (Ananjeva et al., 1998). Unfortunately, the author has been confronted with the problem of acquisition of modern species (like other paleontologists), and the collection is not complete. Nevertheless, the results of the morphological study of this collection fill a gap at least partially in our knowledge.

The material used in this study is kept in the Institute of Geology of Voronezh State University and includes the following *Elaphe* species:

Elaphe climacophora (Boie, 1826) — 2 specimens;
Elaphe dione (Pallas, 1773) — 7 specimens;
Elaphe longissima (Laurenti, 1768) — 2 specimens;
Elaphe quatuorlineata (Lacepede, 1789) — 1 specimen;
Elaphe rufodorsata (Cantor, 1842) — 2 specimens;
*Elaphe schrencki*i (Strauch, 1873) — 3 specimens;
Elaphe situla (Linnaeus, 1758) — 1 specimen;
Elaphe taeniura Cope, 1860 — 1 specimen.

Snake vertebral terminology and numerical indices were used after Auffenberg (1963) and Szyndlar (1984). In this paper, “trunk vertebrae” designate presacrals that, in colubrines, lack hypapophyses.

[1] Geological Faculty, Voronezh State University, Universitetskaya pl. 1, Voronezh 394006, Russia. E-mail: Ratnik4@yandex.ru.

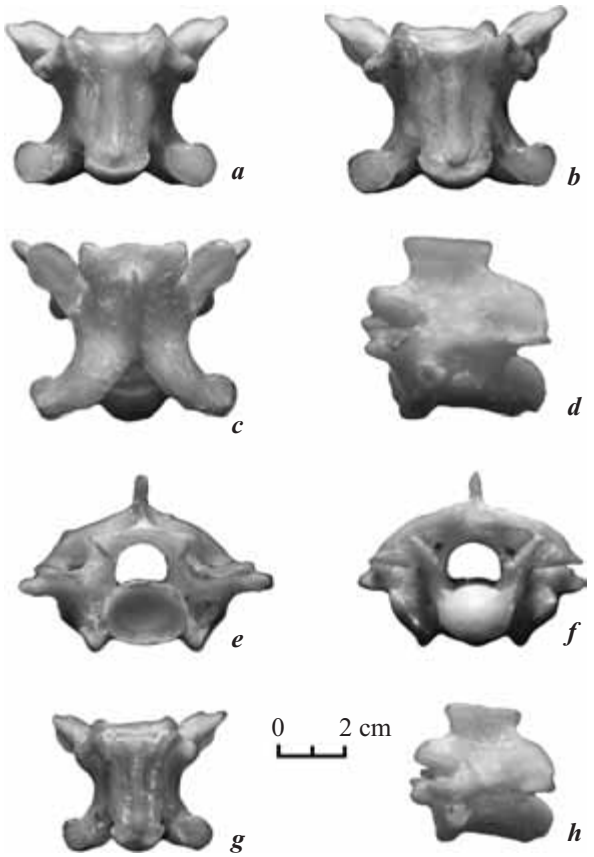

Fig. 1. Trunk vertebrae of *Elaphe climacophora*: *a*, anterior-trunk vertebra, ventral view; *b* – *f*, middle-trunk vertebra: ventral (*b*), dorsal (*c*), lateral (*d*), anterior (*e*), and posterior (*f*) views; *g* – *h*, posterior-trunk vertebra: ventral (*g*) and lateral (*h*) views.

DESCRIPTIONS

Elaphe climacophora (Boie, 1826)

(Fig. 1)

The centrum is short, with a flat ventral surface. The haemal keel is oblong, of moderate width, convex from below, with a pointed tip. Subcentral ridges are not developed; very weakly developed ridges and shallow subcentral grooves are present only on posterior trunk vertebrae. Subcentral foramina are usually absent or very small. The cotyle is slightly depressed dorsoventrally. Paracotylar foramina are very small or are absent. Subcotylar tubercles are absent. The zygosphene is convex in anterior view; its lateral lobes are usually more developed than the central one; the latter is generally absent, and in this case the anterior edge of the zygosphene is straight between the lateral lobes. Two weakly expressed lobes are sometimes observed instead of one central lobe. The neurapophysis is high and it overhangs posteriorly and rarely anteriorly. The prezygapophyseal articular surfaces are isometric or reniform. Short, spherically pointed prezygapophyseal processes are directed anterolaterally. The postzygapophyseal articular surfaces are reniform and directed laterally or are isometric. The interzygapophyseal ridges are rather marked and almost parallel to the axis of the centrum. Lateral foramina are clearly visible. Separation between para- and diapophyseal articular surfaces is not visible. Parapophyses of subquadrangular form slightly project anteriorly beyond the convex diapophyses.

Measurements and ratios: PR-PO = 3.3 – 5.2; CL = 2.5 – 4 – 1; PO-PO = 4.1 – 6.5; NAW = 2.6 – 3.7; ZW = 2.5 – 3.4; CTH = 1.3 – 2.0; CTW = 1.5 – 2.3; PR-PR = 4.1 – 6.6; CL/NAW = 0.89 – 1.39; PO-PO/NAW = 1.21 – 1.62; CTW/CTH = 1.0 – 1.22; ZW/NAW = 0.92 – 0.98; PR-PR/PR-PO = 1.16 – 1.32; CL/ZW = 0.96 – 1.23; PR-PR/NAW = 1.58 – 1.85.

Elaphe dione (Pallas, 1773)

(Fig. 2)

The centrum is long, rounded in ventral aspect. The haemal keel is comparatively wide, rather deep, rounded or flat in ventral view, spatulate; its edges slightly diverge in anterior part of the vertebra and merge with the cotylar rim; the posterior end of the haemal keel is smoothly rounded. The subcentral ridges can be absent on anterior trunk vertebrae, but they occur on more posterior ones and they reach their maximal development on posterior trunk vertebrae where they become rather high and extend from parapophyses up to posterior edges of pedicles. The subcentral grooves run between the haemal keel and subcentral ridges. Subcentral foramina are small and are frequently not visible. The cotyle is usually round, it is less often slightly depressed dorsoventrally; its ventral edge on posterior-trunk vertebrae can be straight. The paracotylar foramina are small. Subcotylar tubercles are absent. The zygosphene is straight or weakly convex in anterior view it shows equally developed lateral and central lobes in dorsal view. The low neurapophysis may overhang both posteriorly and anteriorly. The prezygapophyseal articular surfaces approach an oval form. The prezygapophyseal processes are long or of moderate length, roundly pointed and directed more laterally than anteriorly. The postzygapophyseal articular surfaces are round, subquadrangular or reniform, and are oriented laterally. The interzygapophyseal ridges are well developed and almost parallel to the axis of the centrum. Lateral foramina are clearly visible. There is no perceivable separation between para- and diapophyseal articular surfaces. Parapophyses of subtriangular or subquadrangular form, slightly project anteriorly beyond the convex diapophyses.

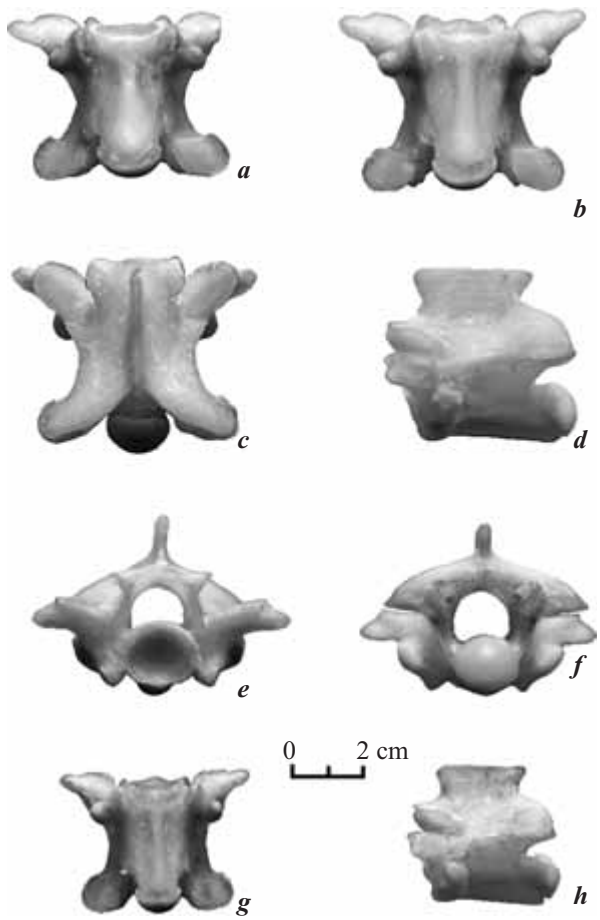

Fig. 2. Trunk vertebrae of *Elaphe dione*: *a*, anterior-trunk vertebra, ventral view; *b* – *f*, middle-trunk vertebra: ventral (*b*), dorsal (*c*), lateral (*d*), anterior (*e*), and posterior (*f*) views; *g* – *h*, posterior-trunk vertebra: ventral (*g*) and lateral (*h*) views.

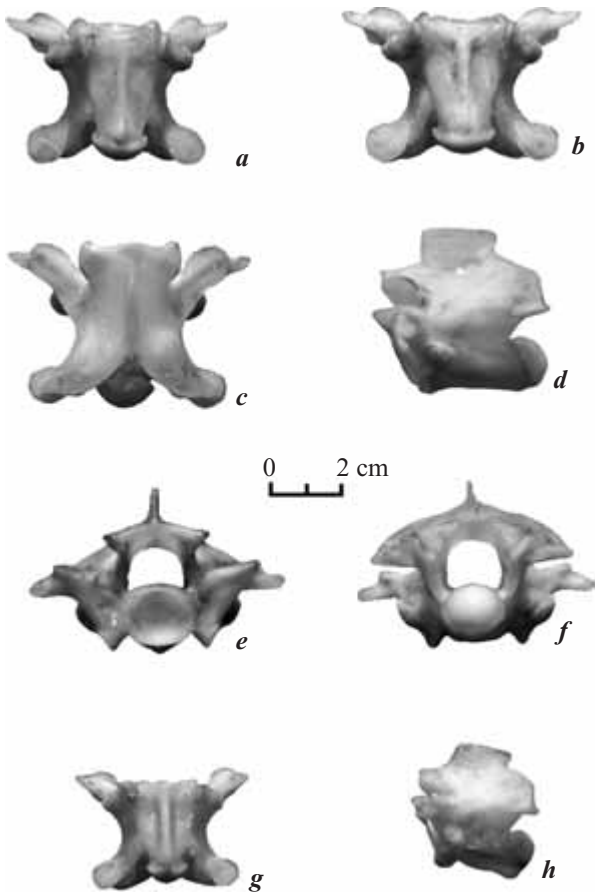

Fig. 3. Trunk vertebrae of *Elaphe longissima*: *a*, anterior-trunk vertebra, ventral view; *b* – *f*, middle-trunk vertebra: ventral (*b*), dorsal (*c*), lateral (*d*), anterior (*e*), and posterior (*f*) views; *g* – *h*, posterior-trunk vertebra: ventral (*g*) and lateral (*h*) views.

The parapophyses are equal or slightly larger than the diapophyses.

Measurements and ratios: PR-PO = 2.95 – 5.9; CL = 2.3 – 4.5; PO-PO = 3.35 – 6.5; NAW = 2.1 – 3.6; ZW = 1.9 – 2.8; CTH = 1.0 – 2.0; CTW = 1.0 – 2.5; PR-PR = 3.4 – 6.7; CL/NAW = 1.0 – 1.67; PO-PO/NAW = 1.48 – 1.96; CTW/CTH = 1.0 – 1.38; ZW/NAW = 0.78 – 1.0; PR-PR/PR-PO = 1.0 – 1.49; CL/ZW = 1.05 – 1.73; PR-PR/NAW = 1.52 – 1.97.

Elaphe longissima (Laurenti, 1768)

(Fig. 3)

The centrum is of subtriangular form. The haemal keel is thin and acute or rather wide and round in ventral view; it ends as a pointed tip; its posterior part is widened and its lateral limits became indistinct. The haemal keel of posterior trunk vertebrae is deeper and does not extend posteriorly. The subcentral ridges are blunt, but they precisely outline the lateral limits of the centrum, though they do not extend up to its posterior end. Shallow subcentral grooves may be present between the haemal keel and subcentral ridges, especially in posterior trunk vertebrae. Small subcentral foramina are usually placed symmetrically on each side of the haemal keel, in the first third of the centrum, but they can be absent. The cotyle is slightly depressed dorsoventrally. Small paracotylar foramina open on external walls of the cotylar rim and are not visible in anterior view. Subcotylar tubercles are not developed. The zygosphene is clearly convex in anterior aspect. Its anterior edge forms three lobes, the central lobe is not more strongly developed than the lateral ones and it may be even less developed. A high neurapophysis overhangs posteriorly and rarely anteriorly. The prezygapophyseal articular surfaces are reniform. The prezygapophyseal processes are rather long, usually pointed and directed more laterally than anteriorly. The postzygapophyseal articular

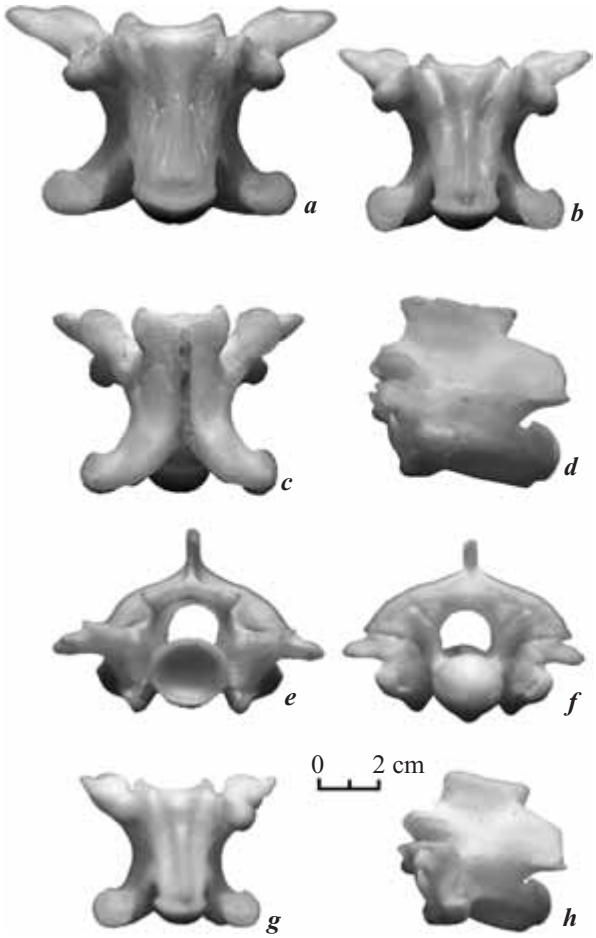

Fig. 4. Trunk vertebrae of *Elaphe quatuorlineata*: *a*, anterior-trunk vertebra, ventral view; *b* – *f*, middle-trunk vertebra: ventral (*b*), dorsal (*c*), lateral (*d*), anterior (*e*), and posterior (*f*) views; *g* – *h*, posterior-trunk vertebra: ventral (*g*) and lateral (*h*) views.

surfaces are reniform and oriented laterally. The interzygapophyseal ridges are fairly developed and almost parallel to the axis of the centrum. Lateral foramina are clearly visible. Paradiapophyses are well developed; the parapophyses are subquadrangular and they project little anteriorly from the convex diapophyses and are usually appreciably longer than the latter (but the contrary occurs in some cases). Szyndlar (1984) noted the following variation of vertebrae in this species: the haemal keel is often not well defined anteriorly; the epizygapophysis is sometimes present as a small tubercle; the anterior edge of zygosphene may be practically straight or concave with a median tubercle in dorsal view; the prezygapophyseal processes of large vertebrae are obtuse, often with widened ends.

Measurements and ratios: PR-PO = 2.1 – 4.3; CL = 1.7 – 3.5; PO-PO = 2.7 – 5.2; NAW = 1.7 – 2.9; ZW = 1.7 – 2.75; CTH = 0.9 – 1.6; CTW = 1.0 – 1.9; PR-PR = 2.9 – 5.4; CL/NAW = 1.0 – 1.29; PO-PO/NAW = 1.59 – 1.86; CTW/CTH = 1.0 – 1.33; ZW/NAW = 0.95 – 1.06; PR-PR/PR-PO = 1.16 – 1.38; CL/ZW = 0.94 – 1.29; PR-PR/NAW = 1.71 – 1.90.

***Elaphe quatuorlineata* (Lacepede, 1789)**
(Fig. 4)

The centrum is of subtriangular form and rather long. The haemal keel is well developed, usually rounded in ventral view. It extends anteriorly, joining the cotylar rim, and its posterior end is clearly distant from the condyle. The haemal keel of anterior trunk vertebrae gradually extends backward, where it is limited by a straight or round posterior edge and it is sometimes flattened ventrally. On mid- and posterior trunk vertebrae it does not extend backward, but it is deeper in posterior 2/3 of the length (in this connection, its ventral border becomes sigmoid in lateral view) and sometimes it is sharp ventrally. The subcentral ridges originate from the parapophyses and clearly outline the lateral edges of the centrum, reaching approximately up to its mid-length. Shallow subcentral grooves run between the haemal keel and subcentral ridges. They are better developed on posterior trunk vertebrae. Subcentral foramina are very small and are not always visible. The cotyle is slightly compressed dorsoventrally. Small or large paracotylar foramina open in fossae on each side of the cotyle. Because of the presence of subcotylar tubercles, the ventral part of the cotylar rim looks as a straight line. The zygosphene is clearly convex in anterior view; its anterior edge is concave, or is concave with a small median tubercle in dorsal view. The high neurapophysis overhangs backward; on anterior and mid-trunk vertebrae it overhangs forward too. The prezygapophyseal articular surfaces are of subquadrangular, reniform or oval form. Prezygapophyseal processes are rather long, usually pointed, and are directed more laterally than anteriorly. The postzygapophyseal articular surfaces are subquadrangular or reniform, and are oriented laterally. The interzygapophyseal ridges are well developed and almost parallel to the axis of the centrum. The lateral foramina are large. The paradiapophyses are well developed; diapophyses are convex and they strongly project laterally.

Measurements and ratios: PR-PO = 5.5 – 7.4; CL = 4.4 – 6.2; PO-PO = 6.0 – 9.2; NAW = 3.25 – 4.9; ZW = 3.1 – 4.3; CTH = 2.0 – 3.0; CTW = 2.1 – 3.3; PR-PR = 6.2 – 9.4; CL/NAW = 1.23 – 1.5; PO-PO/NAW = 1.85 – 1.95; CTW/CTH = 1.05 – 1.12; ZW/NAW = 0.88 – 0.96; PR-PR/PR-PO = 1.02 – 1.06; CL/ZW = 1.42 – 1.56; PR-PR/NAW = 1.91 – 2.0.

***Elaphe rufodorsata* (Cantor, 1842)**
(Fig. 5)

The centrum is elongate, rounded in ventral aspect. The haemal keel is comparatively wide, spatulate or oblanceolate on the majority of vertebrae, its ventral border is rounded or flattened. Its edges slightly diverge in the anterior part and they merge with the cotylar rim. The posterior end of the haemal keel is usually smoothly rounded and distant from the condyle; on posterior trunk vertebrae the haemal keel is deeper and its lateral edges are parallel. The subcentral ridges are absent on anterior trunk vertebrae, but they occur on more posterior ones and reach maximal length on posterior trunk vertebrae where they extend from the parapophyses up to a level posterior to mid-centrum. The subcentral grooves occur between the haemal keel, parapophyses and subcentral ridges (when they are present). The subcentral foramina are very small and are frequently not visible. The epizygapophyseal spines are weakly expressed or absent. The cotyle is round or slightly depressed dorsoventrally. The paracotylar foramina are from very small up to rather large. Subcotylar tubercles are usually absent. The zygosphene is straight or even concave in anterior view and three-lobed in dorsal view; its lobes are either developed equally or the central lobe may be weaker. The neurapophysis is low and can overhang backward and forward. The prezygapophyseal articular surfaces are oval. The prezygapophyseal processes are short, pointed, and are directed anterolaterally. The postzygapophyseal articular surfaces are subquadrangular or isometric. The interzygapophyseal ridges are marked and almost parallel to the axis of the centrum. The lateral foramina are usually visible. The separation between para- and diapophyseal articular surfaces is not discernible. The diapophyses are convex and project laterally; the parapophyses are usually of subtriangular form, where one of the tops being directed anteriorly and projecting beyond the diapophysis.

Measurements and ratios: PR-PO = 3.4 – 4.6; CL = 2.7 – 4.1; PO-PO = 3.25 – 4.4; NAW = 1.8 – 2.25; ZW = 1.8 – 2.25; CTH = 1.0 – 1.3; CTW = 1.0 – 1.7; PR-PR = 3.3 – 4.5; CL/NAW = 1.31 – 1.95; PO-PO/NAW = 1.74 – 2.05; CTW/CTH = 1.0 – 1.31; ZW/NAW = 0.93 – 1.0; PR-PR/PR-PO = 0.96 – 1.13; CL/ZW = 1.40 – 2.05; PR-PR/NAW = 1.83 – 2.14.

***Elaphe schrenckii* (Strauch, 1873)**
(Fig. 6)

The centrum is short, with a flat or weakly convex ventral surface. The haemal keel shows variation: wide or narrow, flattened or rounded in ventral view, with a pointed end almost reaching the condyle. It can be oblanceolate; in this case its most narrow part occurs at

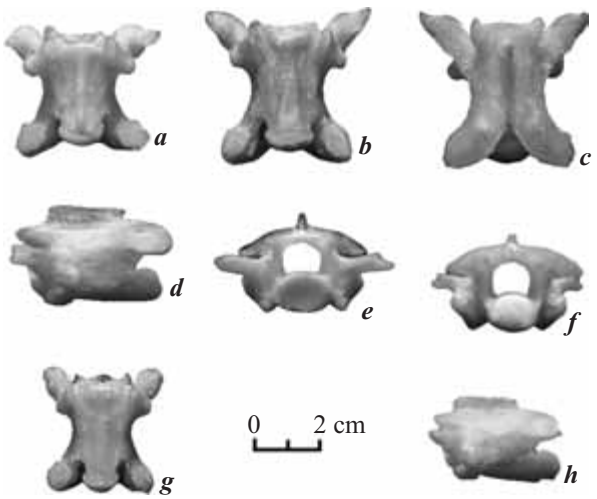

Fig. 5. Trunk vertebrae of *Elaphe rufodorsata*: *a*, anterior-trunk vertebra, ventral view; *b* – *f*, middle-trunk vertebra: ventral (*b*), dorsal (*c*), lateral (*d*), anterior (*e*), and posterior (*f*) views; *g* – *h*, posterior-trunk vertebra: ventral (*g*) and lateral (*h*) views.

the first third of the centrum length; its anterior part merges with the ventral part of the rim of the cotyle. It can be also gladiate; in this case its lateral sides are parallel, and its anterior part covers the ventral part of the rim of the cotyle. The haemal keel of last trunk vertebrae becomes very deep and assumes a sigmoid form in lateral view. Subcentral ridges are not visible on anterior trunk vertebrae. More posteriorly these structures gradually become apparent; they reach their maximal development on posterior trunk vertebrae, where they originate from parapophyses and almost reach the condyle. The subcentral grooves, which are not discernable on anterior trunk vertebrae, become deep and long on more posterior trunk ones. The subcentral foramina are small, but visible on each side of the haemal keel and its anterior half. The cotyle is round or slightly depressed dorsoventrally. The paracotylar foramina range from small to large. Subcotylar tubercles are absent. The zygosphene is convex in anterior view; in dorsal aspect, its lateral lobes are more strongly developed than the central one. Generally, the latter is absent, in this case the anterior edge of the zygosphene between the lateral lobes is straight. The high neurapophyses overhang posteriorly and rarely anteriorly. The prezygapophyseal articular surfaces are subquadrangular or reniform. Thin, pointed prezygapophyseal processes of moderate length are directed more laterally than anteriorly. The postzygapophyseal articular surfaces are isometric or reniform and are oriented laterally. The interzygapophyseal ridges are conspicuous and almost parallel to the axis of the centrum. The lateral foramina are usually visible. The separation between para- and diapophyseal articular sur-

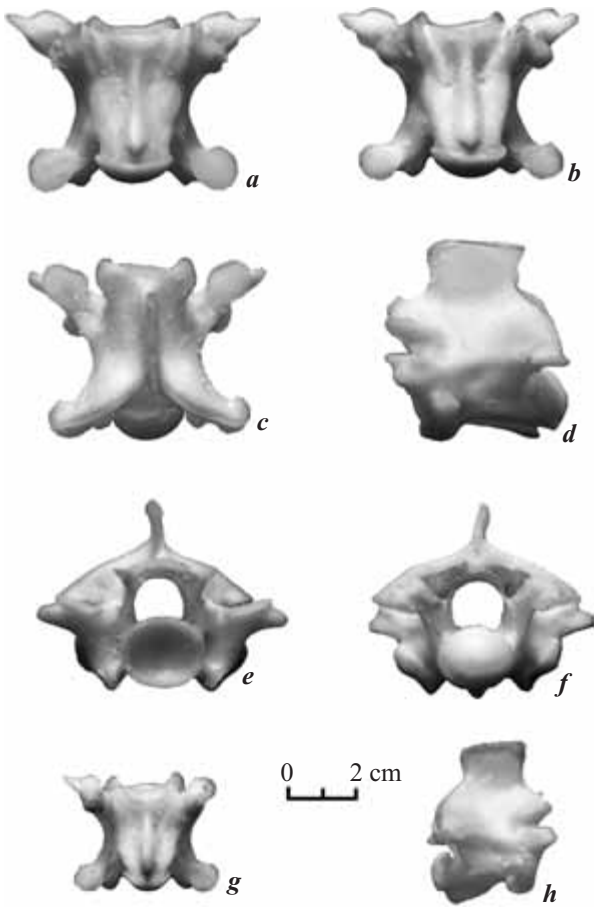

Fig. 6. Trunk vertebrae of *Elaphe schrencki*: *a*, anterior-trunk vertebra, ventral view; *b* – *f*, middle-trunk vertebra: ventral (*b*), dorsal (*c*), lateral (*d*), anterior (*e*), and posterior (*f*) views; *g* – *h*, posterior-trunk vertebra: ventral (*g*) and lateral (*h*) views.

faces is not discernible. The parapophyses are of subquadrangular form; they slightly project anteriorly beyond the level of the convex diapophyses.

Measurements and ratios: PR-PO = 3.1 – 5.4; CL = 2.2 – 4.35; PO-PO = 3.7 – 6.4; NAW = 2.1 – 3.45; ZW = 2.0 – 3.2; CTH = 1.2 – 2.2; CTW = 1.3 – 2.8; PR-PR = 3.7 – 6.6; CL/NAW = 1.02 – 1.41; PO-PO/NAW = 1.43 – 1.96; CTW/CTH = 1.06 – 1.27; ZW/NAW = 0.8 – 0.96; PR-PR/PR-PO = 1.11 – 1.23; CL/ZW = 1.1 – 1.49; PR-PR/NAW = 1.5 – 2.0.

***Elaphe situla* (Linnaeus, 1758)**
(Fig. 7)

The centrum is long; rounded in ventral aspect. The haemal keel is wide, deep, spatulate or oblanceolate; its edges in the anterior part of the vertebra diverge and merge with the cotylar rim; its posterior end forms a pointed tip. Subcentral ridges are absent on anterior

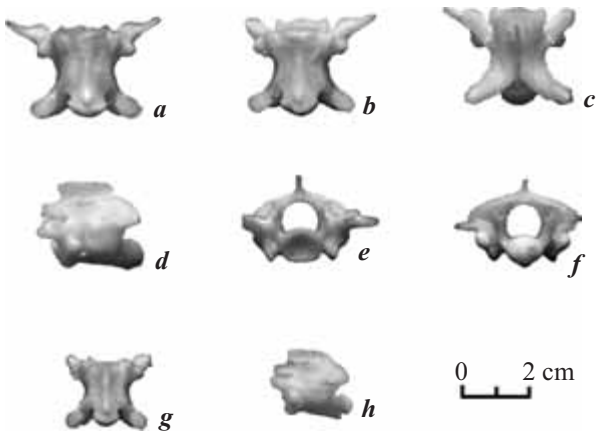

Fig. 7. Trunk vertebrae of *Elaphe situla*: *a*, anterior-trunk vertebra, ventral view; *b* – *f*, middle-trunk vertebra: ventral (*b*), dorsal (*c*), lateral (*d*), anterior (*e*), and posterior (*f*) views; *g* – *h*, posterior-trunk vertebra: ventral (*g*) and lateral (*h*) views.

trunk vertebrae, but they occur on more posterior ones and reach their maximal length on posterior trunk vertebrae, where they extend from the parapophyses to the posterior edges of the pedicles. Shallow subcentral grooves running between the haemal keel and the subcentral ridges are perceivable only on posterior trunk vertebrae. Subcentral foramina are usually not discernable. The cotyle is slightly depressed dorsoventrally. The paracotylar foramina are usually small. Subcotylar tubercles are absent. The zygosphene is convex in anterior aspect and three-lobed with equally developed lateral and central lobes in dorsal view. The low neurapophysis does almost not overhang both backward and forward. The prezygapophyseal and postzygapophyseal articular surfaces are obovate. The prezygapophyseal processes are long, acute, directed laterally and slightly anteriorly (the first of these observations does not coincide with the diagnosis of this species given by Szyndlar, 1991). The interzygapophyseal ridges are poorly developed. The lateral foramina are usually discernible. There is no visible separation between para- and diapophyseal articular surfaces. The parapophyses, of subquadrangular form, slightly project anteriorly beyond the convex diapophyses.

Measurements and ratios: PR-PO = 2.3 – 2.9; CL = 1.95 – 2.4; PO-PO = 2.45 – 3.4; NAW = 1.35 – 1.7; ZW = 1.3 – 1.75; CTH = 0.8 – 1.1; CTW = 0.9 – 1.3; PR-PR = 2.6 – 3.5; CL/NAW = 1.41 – 1.5; PO-PO/NAW = 1.81 –2.03; CTW/CTH = 1.09–1.18; ZW/NAW = 0.96–1.09; PR-PR/PR-PO = 1.13 – 1.21; CL/ZW = 1.37 – 1.5; PR-PR/NAW = 1.93 – 2.13.

***Elaphe taeniura* Cope, 1860**
(Fig. 8)

The centrum is rather short, with a flat ventral surface and with weakly concave lateral edges. The haemal keel is rather deep, slightly widened in its posterior part (in the anterior half of vertebral column) or of approximately identical width throughout its length (in posterior half of vertebral column); its posterior end is usually rounded. Low subcentral ridges originate from the paradiapophyses and extend up to posterior edges of the pedicles. Subcentral grooves occurring between the haemal keel and the subcentral ridges are perceivable on posterior trunk vertebrae. Subcentral foramina open on each side of the haemal keel in the first half of the centrum. The cotyle is slightly depressed dorsoventrally. The paracotylar foramina are small. Subcotylar tubercles are absent. The zygosphene is convex in anterior view and straight, four-lobed or concave in dorsal view. The high neurapophysis overhangs both posteriorly and anteriorly. The prezygapophyseal articular surfaces are approximately oval or rarely isometric. The prezygapophyseal processes are of moderate length, with a rounded tip, directed laterally and slightly anteriorly. The postzygapophyseal articular surfaces are round. The interzygapophyseal ridges are well developed and almost parallel to the axis of the centrum. The lateral foramina are clearly visible. No separation between para- and diapophyseal articular surfaces is discernible. The parapophyses are of close to subtriangular form, one of tops being directed anteriorly and projecting anteriorly to the convex diapophysis.

Measurements and ratios: PR-PO = 5.5 – 8.4; CL = 4.2 – 6.6; PO-PO = 7.1 – 10.6; NAW = 4.7 – 6.1; ZW = 4.2 – 5.0; CTH = 2.3 – 3.3; CTW = 2.3 – 3.9; PR-PR = 7.3 – 10.7; CL/NAW = 0.89 – 1.10; PO-PO/NAW = 1.51 – 1.78; CTW/CTH = 1.0 – 1.22; ZW/NAW = 0.82 – 0.89; PR-PR/PR-PO = 1.21 – 1.33; CL/ZW = 1.0 – 1.32; PR-PR/NAW = 1.55 – 1.80.

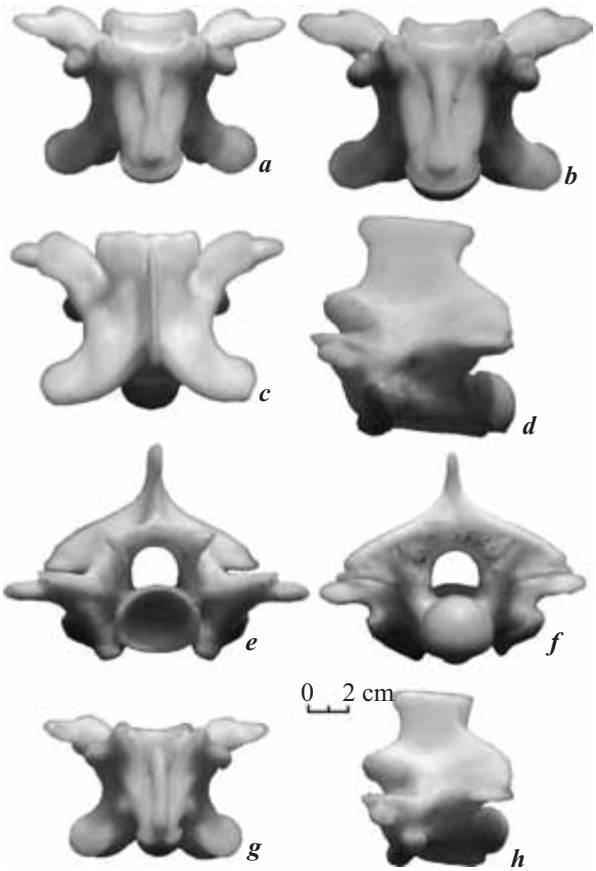

Fig. 8. Trunk vertebrae of *Elaphe taeniura*: *a*, anterior-trunk vertebra, ventral view; *b* – *f*, middle-trunk vertebra: ventral (*b*), dorsal (*c*), lateral (*d*), anterior (*e*), and posterior (*f*) views; *g* – *h*, posterior-trunk vertebra: ventral (*g*) and lateral (*h*) views.

CONCLUSION

Many characters given in the descriptions are similar in different species of the genus *Elaphe*. Probably, these characters may determine differences at levels higher than species. However, this cannot be confirmed, until comparison with other forms of the Colubrinae is carried out.

The most variable characters, the combination of which can be used for specific diagnoses within the genus *Elaphe* are the following: shape of haemal keel, shape of zygosphene, presence and degree of development of subcentral ridges, shape of centrum. They are summarized in Table 1. These characters allow to distinguish the eight species of *Elaphe* described above.

However, identification of fossil remains requires all, or nearly all details of the vertebral structure. But, it is worth mentioning, that snake vertebrae have several fragile elements which are often broken during fossilization process. Therefore characters connected to these elements, can be used only in rare cases. These elements are the: neurapophysis, prezygapophyseal processes, zygosphene, and articular zygapophyseal surfaces.

Most of the extreme values of indices have been obtained from the last (posteriormost) trunk vertebrae. This is connected to the sharp change of proportions of these vertebrae. Changes in the shape of other vertebrae are more gradual, and their ratio-indices remain within indicated limits.

Acknowledgments. The author thanks V. Orlova, S. Kudriavtsev, and L. Ioganssen for the possibility to prepare osteological material, Dr. J. C. Rage for his profound review of

TABLE 1. Comparison of Some Characters of Trunk Vertebrae in Some *Elaphe* Species

Species	Form of centrum	Form of haemal keel	Subcentral ridges	Zygosphene from the front	Zygosphene from above	Prezygapophyseal processes
E. climacophora	short, with flat ventral surface	oblong, of moderate width, convex from below, with a pointed posterior end	ridges present only on posterior trunk vertebrae, where they are weak	convex	crenate; lateral lobes usually more strongly developed than the central one	short, tip rounded
E. dione	long, convex from below	spatulate, comparatively wide, rather deep, rounded or flat from below	can be absent on anterior trunk vertebrae, but occur on subsequent ones	straight or weakly convex	crenate, with equally developed lateral and central lobes	long or of moderate length, tips rounded
E. longissima	subtriangular	thin and acute or rather wide and round from below, with a pointed posterior end	blunt; can not extend up to end of centrum	convex	crenate; lateral lobes usually more strongly developed than the central one	rather long, usually pointed
E. quatuorlineata	subtriangular, rather long	well developed, usually round from below, its posterior end distant from the condyle; posterior edge straight or rounded	reach approximately mid-length of centrum	convex	concave or concave with a small median tubercle	rather long, usually pointed
E. rufodorsata	long, convex from below	comparatively wide, rounded or flat, spatulate or oblanceolate on most vertebrae; posterior end usually smoothly rounded and distant from the condyle	absent on anterior-trunk vertebrae, but occur on subsequent ones; extend from parapophyses to posterior of mid-length of centrum on posterior trunk vertebrae	straight or concave	crenate; lobes developed equally or central lobe weaker	short, pointed
E. schrenckii	short, flattened or weakly convex from below	wide or narrow, flattened or rounded from below, with a pointed end almost reaching the condyle	absent on anterior trunk vertebrae, but occur on subsequent ones; extend from parapophyses almost up to mid-length of centrum on posterior trunk vertebrae	convex	crenate; lateral lobes more strongly developed than the central one, the latter can be absent	thin, pointed, of moderate length
E. situla	long, convex from below	wide, deep, spatulate or oblanceolate	absent on anterior trunk vertebrae, but occur on subsequent ones; extend from parapophyses up to posterior edges of pedicles	convex	crenate	long, acute
E. taeniura	rather short, flattened from below, with slightly concave lateral edges	rather deep, slightly widened in posterior part or of approximately identical width through its length; posterior end usually rounded	ridges are low; extend from parapophyses up to posterior edges of pedicles	convex	straight, four-lobed or concave	of moderate length, tips rounded

this paper and corrections the English. This work was fulfilled using financial support of the program "Universities of Russia" (grant UR.07.01.046).

REFERENCES

Ananjeva N. B., Borkin L. Y., Darevsky I. S, Orlov N. L. (1998). *Amphibians and Reptiles. Encyclopaedia of the Russian Nature* (*Zemnovodnye i Presmykayushchiesya. Éntsiklopediya Prirody Rossii*), Moscow [in Russian].

Auffenberg W. (1963), "The fossil Snakes of Florida," *Tulane Studies Zool.*, **10**(3), 131 – 216.

Helfenberger N. (2001), "Phylogenetic relationships of Old World ratsnakes based on visceral organ topography, osteology, and allozyme variation," *Russ. J. Herpetol.*, **8**(Suppl.).

Holman J. A. (1998), Pleistocene Amphibians and Reptiles in Britain and Europe, Oxford Univ. Press, New York – Oxford.

Ratnikov V. Yu. (2002), "Late Cenozoic amphibians and reptiles of the East-European plain," *Trudy NII Geol. VGU*, **10**, 138 [in Russian].

Szyndlar Z. (1984), "Fossil snakes from Poland" *Acta Zool. Cracov*, **28**(1), 1 – 156.

Szyndlar Z. (1991), "A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae," *Estudios Geol.*, **47**, 103 – 126.