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Address of the Editor: Institute of Systematics and Evolution of Animals,
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Subscription rate: 55 USD (including postage by surface mail). There is also a possibility to order vertebrate or invertebrate issues only at half price. Supplements (special issues) if any, are extra paid. Single issues will be available at 17.50 USD (including postage).

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ISSN 0065-1710

Cover Design
Jerzy ŚWIECIMSKI

The rhinoceros on the cover presents a nearly complete specimen of the Pleistocene *Coelodonta antiquitatis*, excavated in the layers of ozocerite in Starunia (Eastern Carpathians), 1929. This unique exhibit is shown in the Natural History Museum (Institute of Systematics and Evolution of Animals), Cracow.

Druk i oprawa: Drukarnia Kolejowa Kraków sp. z o.o.
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Osteology of Russian toads and frogs for paleontological researches

Viatcheslav Yu. RATNIKOV

Received: 24 May, 2000

Accepted for publication: 28 Dec., 2000

RATNIKOV V. Yu. 2001. Osteology of Russian toads and frogs for paleontological researches. *Acta zoologica cracoviensia*, 44(1): 1-23.

Abstract. Osteological diagnosis of modern genera *Bufo* and *Rana* as well as species *Bufo bufo*, *B. gargarizans*, *B. verrucosissimus*, *B. viridis*, *B. raddei*, *B. calamita*, *Rana temporaria*, *R. chensinensis*, *R. arvalis*, *R. asiatica*, *R. amurensis*, *R. ridibunda*, *R. lessonae* and *R. nigromaculata* are given. The genera investigated are distinguished very easily, because practically all the skeletal elements, with the exception of distal elements of the limbs, have their specific generic features. Bufonids have 9-11 bones used for species identification. The most important of them are ilium, frontoparietale, maxillare, and parasphenoideum. Ranids have 6-7 such bones, the most important of which are ilium, frontoparietale, and scapula.

Key words: Osteology, *Bufo*, *Rana*, Modern species, Russia.

Viatcheslav Yu. RATNIKOV, Geological Faculty, Voronezh State University, University Sq. 1, Voronezh, 394693 Russia.

E-mail: gfkig304@main.vsu.ru

I. INTRODUCTION

The geological researches of anthropogenic deposits of the East-European platform conducted recently, have shown, that amphibian and reptile remains in them occur not so rarely as had been previously supposed. As a part of fossil fauna, they bear information concerning the geological past and can be used for the reconstruction of paleogeographical conditions and the determination of the geological age of bone-bearing deposits (RATNIKOV, 1995, 1996a). Most of the remains in quaternary sediments belong to modern species, requiring their careful study for comparison with fossil materials. Paleontologists should also take into consideration the change of systematic status of some forms in connection with the new ideas of the neoherpetologists and finding osteological distinctions in newly described species.

In the present paper the author brings criteria of identification of skeleton elements of some modern representatives of genera *Bufo* and *Rana*, which are often found in anthropogene deposits of Russia. He found these criteria when comparing the fossil remains with samples of osteological collection, which contains (sensu BORKIN, DAREVSKY, 1987) (the digits denote the number of specimens):

Bufo bufo (LINNAEUS) – 21,

Bufo verrucosissimus PALLAS – 8,

Bufo gargarizans CANTOR – 9,
Bufo viridis LAURENTI – 14,
Bufo raddei STRAUCH – 12,
Bufo calamita LAURENTI – 3,
Rana temporaria LINNAEUS – 10,
Rana chensinensis DAVID – 11,
Rana arvalis NILSSON – 37,
Rana asiatica BEDRIAGA – 6,
Rana amurensis BOULENGER – 6,
Rana ridibunda PALLAS – 19,
Rana lessonae CAMERANO – 8,
Rana nigromaculata HALLOWELL – 6.

The generic attributes of toad and frog bones are very rarely mentioned in articles describing fossil finds. Some information is contained in the works of BÖHME, 1977; HOLMAN, 1998; RAGE, 1974, but it is not complete. Therefore the present author gives a criterion of the generic identification he used, and where possible avoids mention data from those papers. He used the terminology of the above-mentioned authors and given by SANCHIZ (1998).

A c k n o w l e d g e m e n t s. The author thanks Prof. Z. ROČEK for examination of this paper and valuable remarks and he is also grateful to L. TITOVA for her help in translating the work in to English. This study was possible thanks to L. BORKIN, A. MASALYKIN, and V. ORLOVA who helped the author to complete the osteological collection.

II. FAMILY BUFONIDAE

Genus *Bufo* LAURENTI, 1768

Condylus occipitalis is wide, with parallel lateral margins; the borders of fossa condyloidea practically coincide with those of foramen jugulare (Fig. 1 A, B). Small and large openings of the very short anterior semicircular canal are very close to each other and have similar dimensions. Nasale are of subtriangular form or with a small S-shaped bend (Fig. 2 C-F). Pars lateralis ossis squamosi is at an acute angle to ramus zygomaticus (Fig. 4 C-H). Corpus parasphenoidei is wider than lateral processes, the length of the bone being less than the distance between the ends of lateral processes (Fig. 3 A-F). Two blades of the anterior pterygoid branch coincide in width along the greater part of its length, and there is an angle-shaped projection on the ventral blade (Fig. 4 A). Goniale is comparatively high, with low processus coronoideus considerably deviated laterally; dorsal margin of the bone proceeds as a crest, which ends under a coronoid process; posterior part of the bone is abruptly curved in S manner, the lateral margin forms a visible obtuse angle; the ventral part of the bone under the coronoid process is considerably compressed but does not form a crest; channel for Meckel's cartilage is in the middle part of the bone (Fig. 4 O). There is some space between two cotyles of atlas; neural arch in the upper part is very thick (Fig. 5 A-B). Vertebrae with large, often compressed bodies; the neural arch is massive in the upper part at breast vertebrae and is flattened dorsally at abdominal ones, being almost in the same plane with diapophyses; canalis neuralis of abdominal vertebrae is narrow especially at presacral vertebra (Fig. 5 D, E, H, I). Joint pits of urostyle are not separated; neural channel is low, having form of an equilateral triangle in anterior view; ventral bone surface is convex (Fig. 6 E). Clavicula widens medially, usually with considerable widening on the lateral end (Fig. 6 G-J). Cleithrum is of V-shape; the posterior margin of lamina marginalis cleithri, approaching margo scapularis, turns in caudal direction, forming subtriangular expansion of l. marginalis (Fig. 6 L). Pars acromialis and pars glenoidalis of scapula do not cover

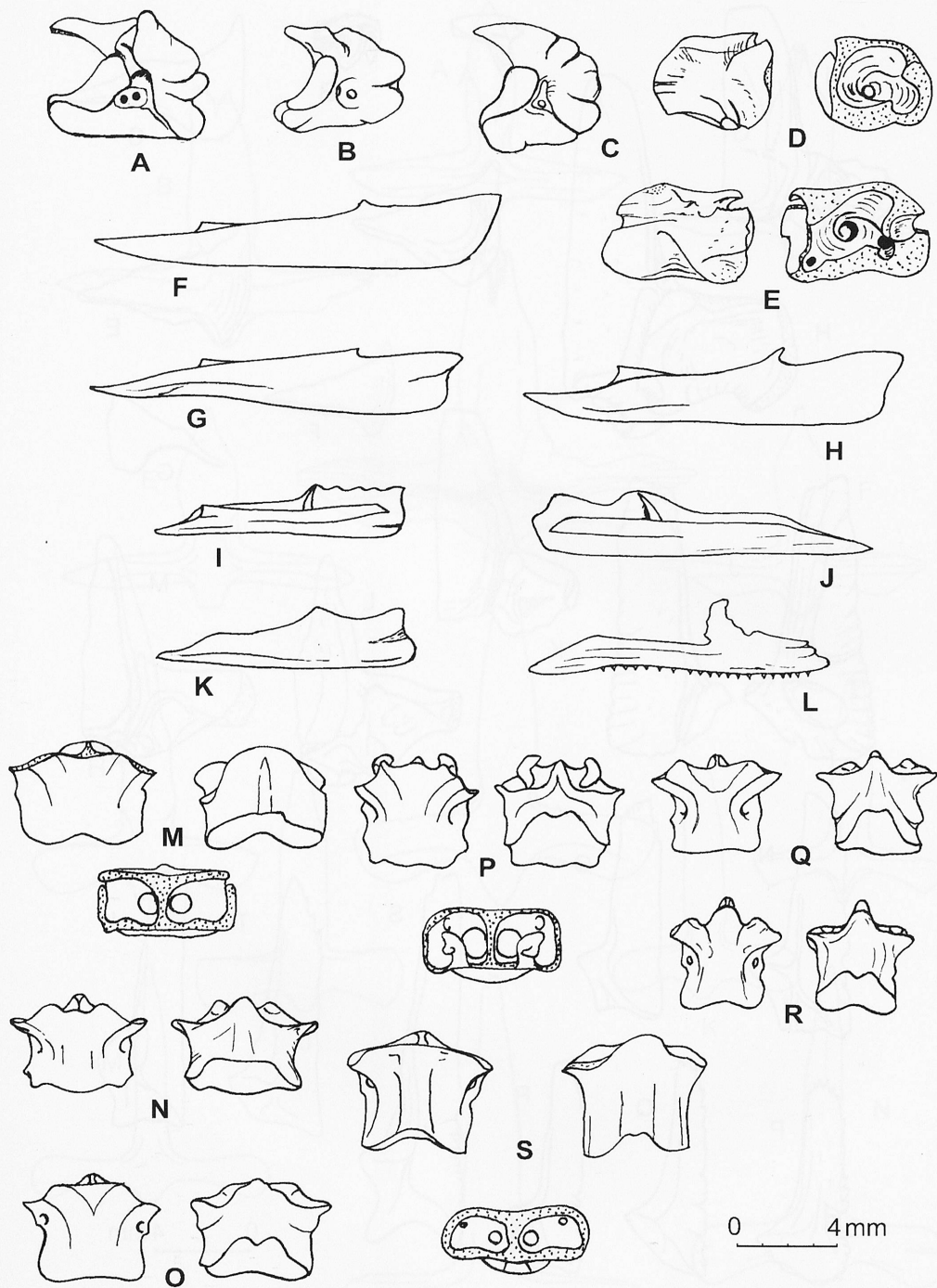


Fig. 1. Cranial bones. A-C – exoccipital, posterior view: A – *Bufo bufo*, B – *Bufo viridis*, C – *Rana temporaria*; D-E – prooticum, dorsal and ventral views: D – *Rana temporaria*, E – *Rana ridibunda*; F-L – maxillare, F-H, K, L – outer view, I-J – inner view: F – *Bufo bufo*, G – *Bufo gargarizans*, H – *Bufo verrucosissimus*, I – *Bufo viridis*, J – *Bufo raddei*, K – *Bufo calamita*, L – *Rana arvalis*; M-S – sphenethmoideum, dorsal, ventral (J, M, P- and anterior) views: M – *Bufo bufo*, N – *Bufo gargarizans*, O – *Bufo verrucosissimus*, P – *Bufo viridis*, Q – *Bufo raddei*, R – *Bufo calamita*, S – *Rana temporaria*.

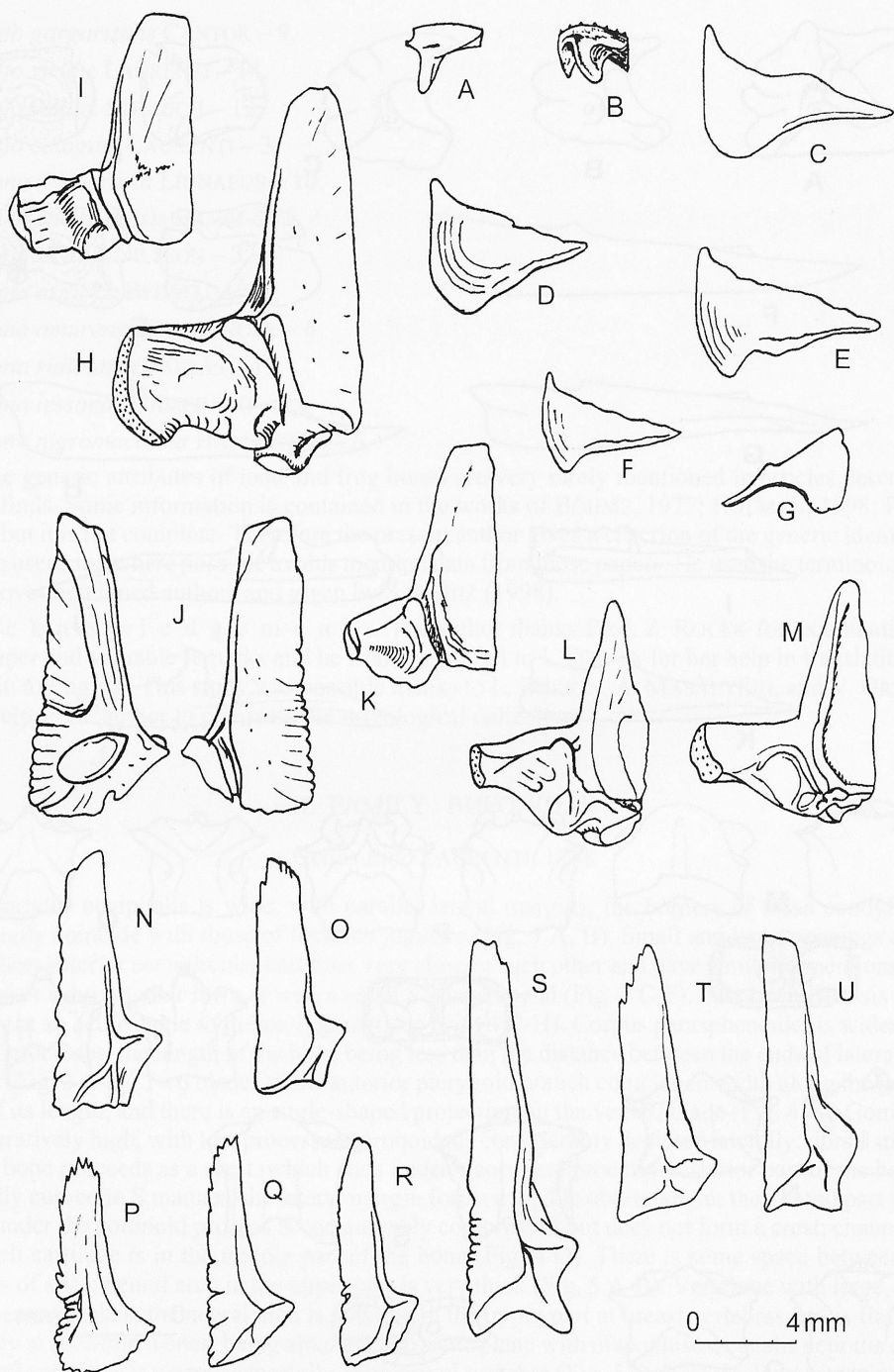


Fig. 2. Cranial bones. A-B – praemaxillare: A – *Bufo viridis*, anterior view; B – *Rana temporaria*, dorsal view; C-G – nasale, dorsal view: C – *Bufo bufo*, D – *Bufo viridis*, E – *Bufo raddei*, F – *Bufo calamita*, G – *Rana temporaria*; H-U – frontoparietale, dorsal view: H – *Bufo bufo* (fused with prooticum and exoccipitale), I – *Bufo gargarizans* (fused with prooticum), J – *Bufo verrucosissimus*, K – *Bufo viridis* (fused with prooticum), L – *Bufo raddei* (fused with prooticum and exoccipitale), M – *Bufo calamita* (fused with prooticum and exoccipitale), N – *Rana temporaria*, O – *Rana chensinensis*, P – *Rana arvalis*, Q – *Rana asiatica*, R – *Rana amurensis*, S – *Rana ridibunda*, T – *Rana lessonae*, U – *Rana nigromaculata*.

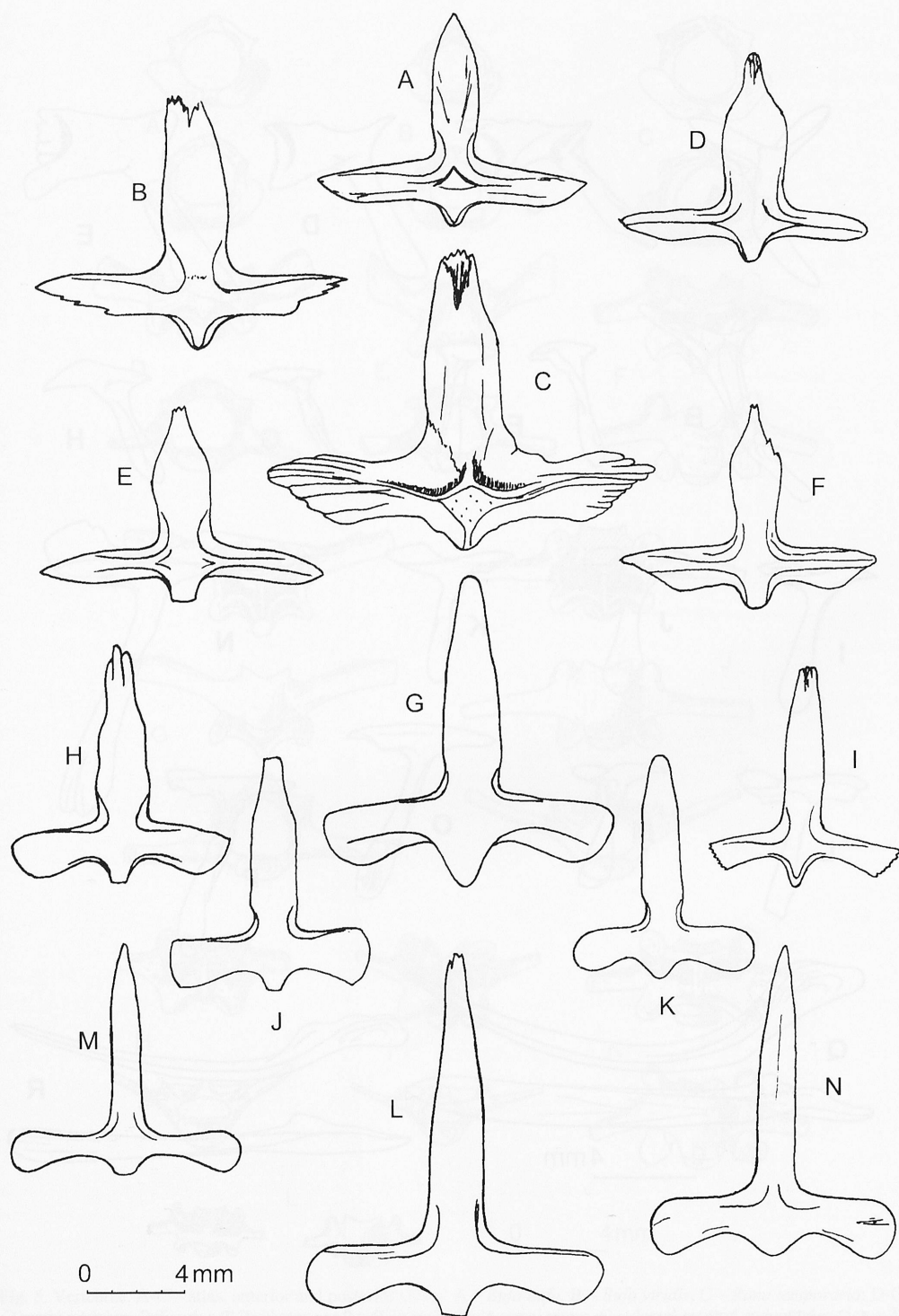


Fig. 3. Parasphenoideum, ventral view. A – *Bufo bufo*, B – *Bufo gargarizans*, C – *Bufo verrucosissimus*, D – *Bufo viridis*, E – *Bufo calamita*, F – *Bufo raddei*, G – *Rana temporaria*, H – *Rana chensinensis*, I – *Rana arvalis*, J – *Rana asiatica*, K – *Rana amurensis*, L – *Rana ridibunda*, M – *Rana lessonae*, N – *Rana nigromaculata*.

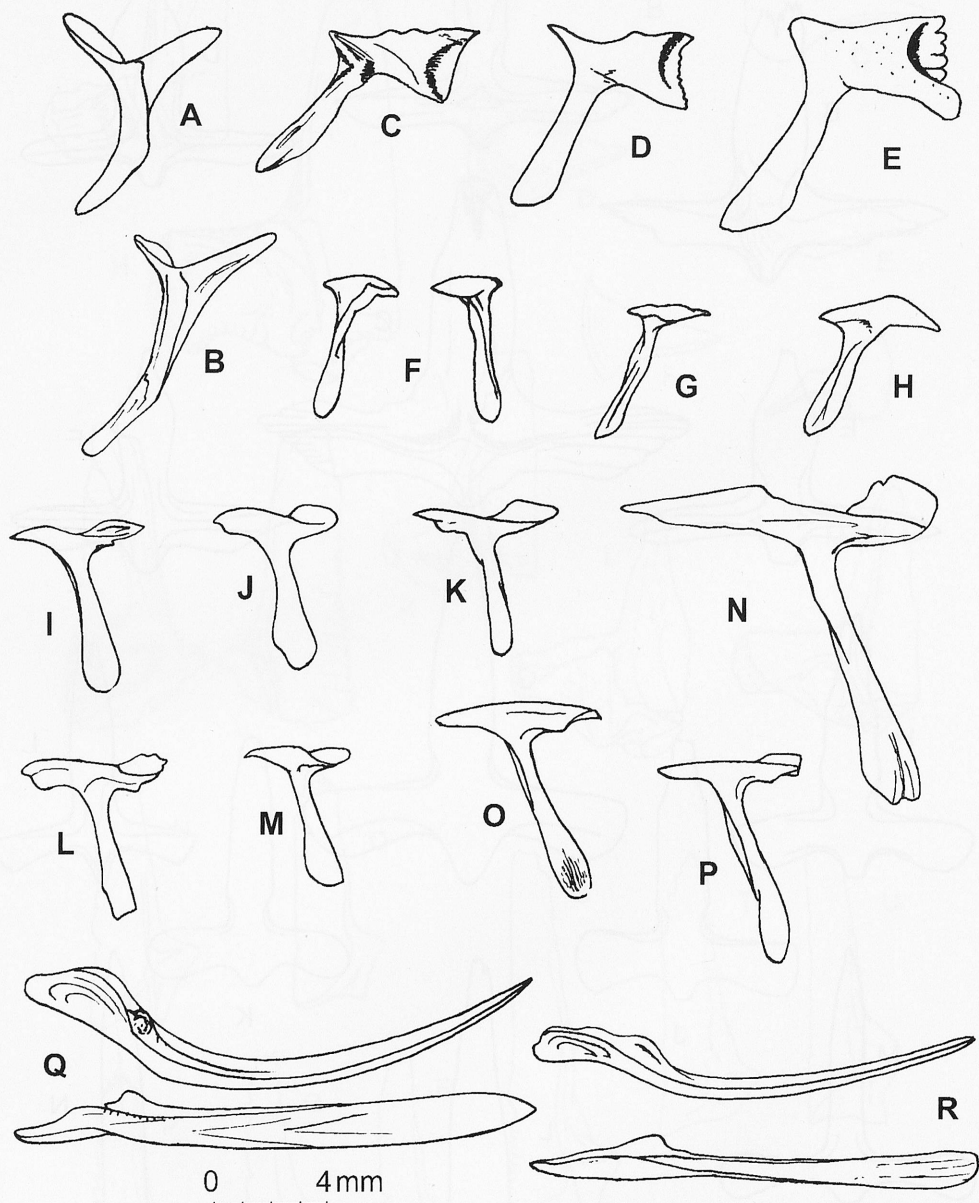


Fig. 4. Cranial bones. A-B- pterygoideum, outer view: A – *Bufo bufo*, B – *Rana arvalis*; C-P – squamosum, outer view: C – *Bufo bufo*, D – *Bufo gargarizans*, E – *Bufo verrucosissimus*, F – *Bufo viridis*, G – *Bufo raddei*, H – *Bufo calamita*, I – *Rana arvalis*, J – *Rana temporaria*, K – *Rana chensinensis*, L – *Rana asiatica*, M – *Rana amurensis*, N – *Rana ridibunda*, O – *Rana lessonae*, P – *Rana nigromaculata*; Q-R – goniale, dorsal and internal views: Q – *Bufo bufo*, R – *Rana arvalis*.

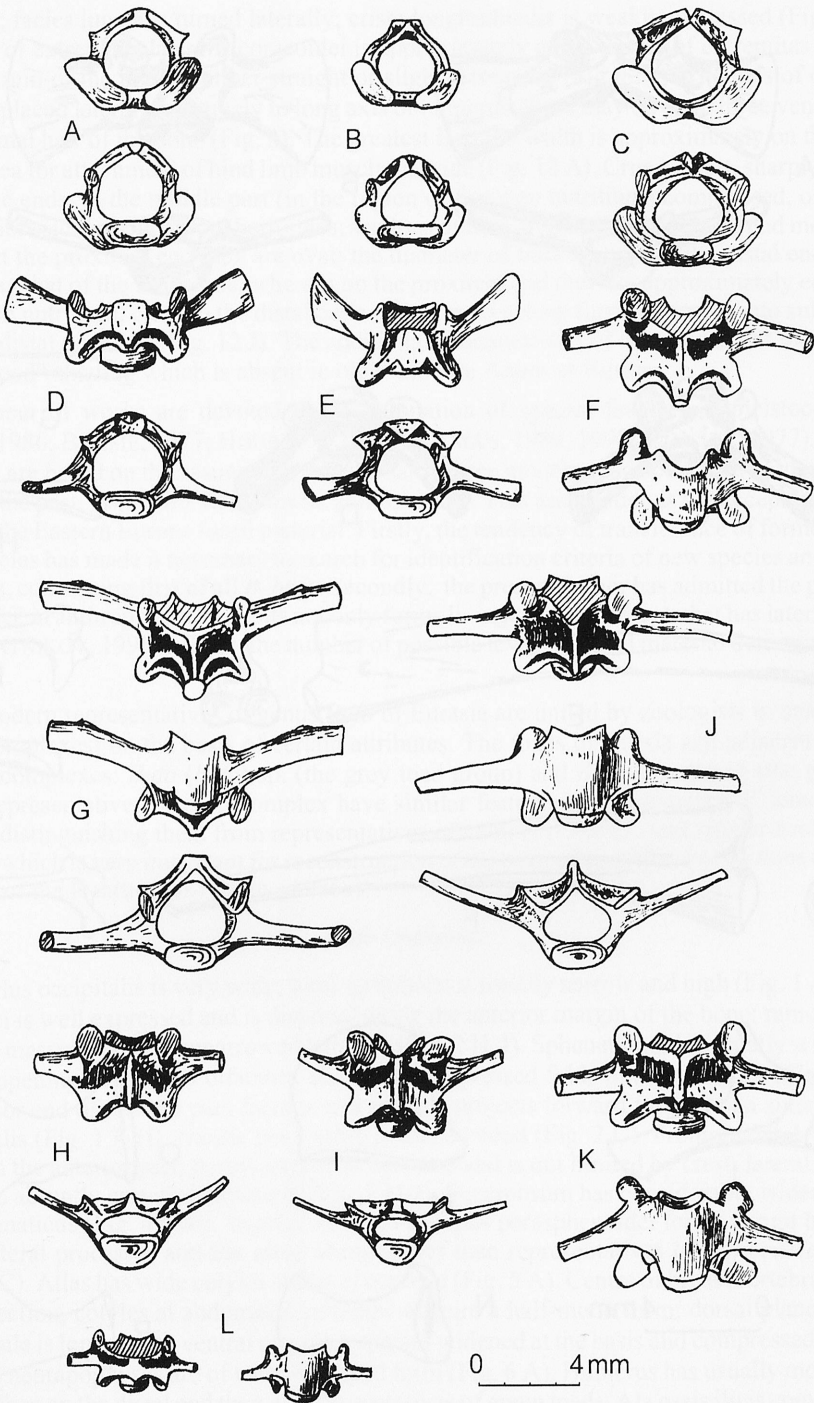


Fig. 5. Vertebrae. A-C – atlas, anterior and posterior views: A – *Bufo bufo*, B – *Bufo viridis*, C – *Rana temporaria*; D-G – breast vertebra, D-E – dorsal and anterior views, F- dorsal and ventral views, G – dorsal, ventral and anterior views: D – *Bufo bufo*, E – *Bufo viridis*, F – *Rana temporaria*, G – *Rana ridibunda*; H-L – abdominal vertebra, H-I – dorsal and anterior views, J – dorsal, ventral and anterior views, K-L – dorsal and ventral views: H – *Bufo bufo*, I – *Bufo viridis*, J – *Rana ridibunda*, K – *Rana temporaria*, L – *Rana arvalis*.

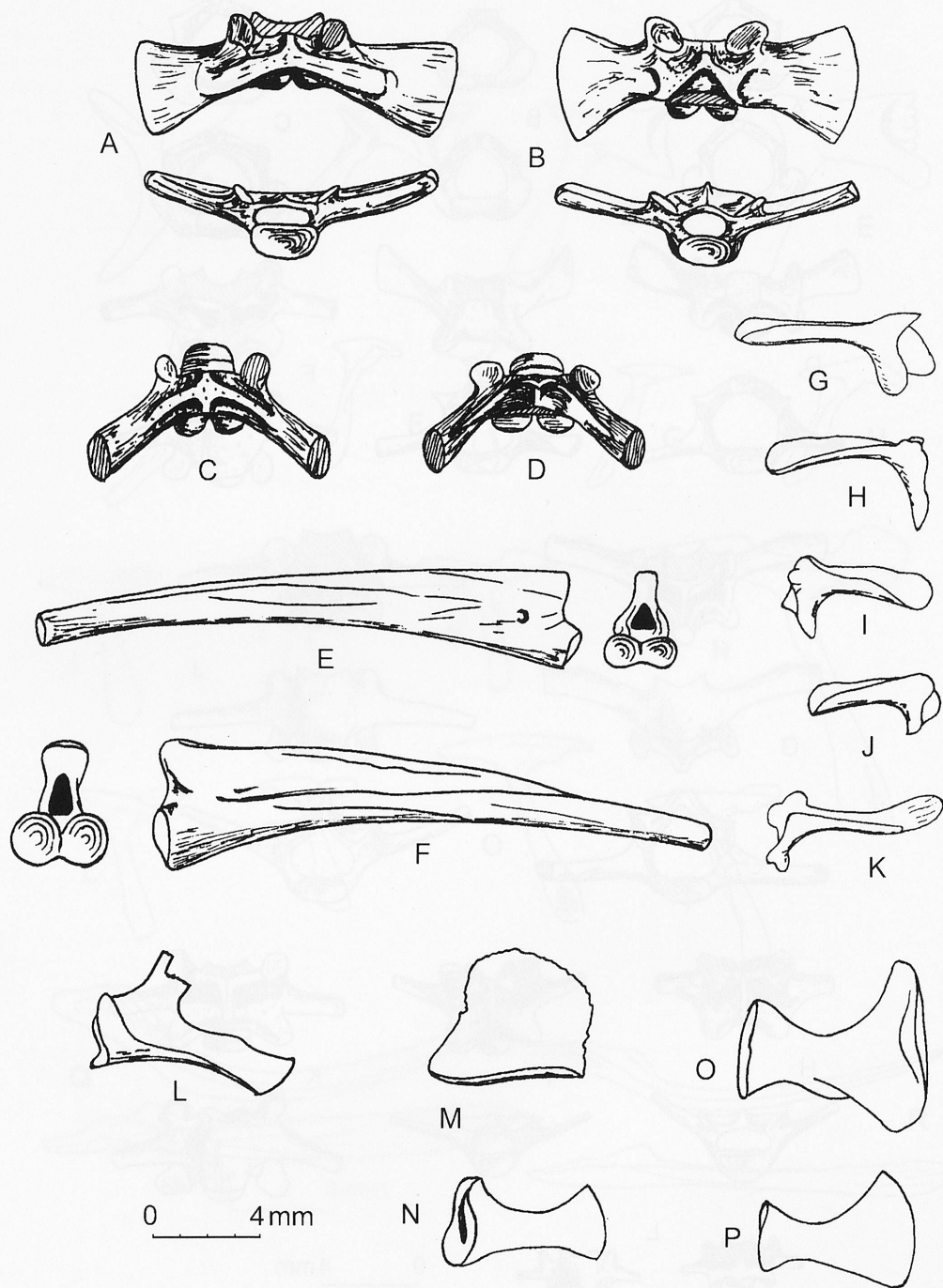


Fig. 6. A-D – sacrum, A-B – dorsal and anterior views, C-D – dorsal view: A- *Bufo bufo*, B- *Bufo viridis*, C- *Rana temporaria*, D- *Rana ridibunda*; E-F – urostyl, anterior and lateral views: E- *Bufo bufo*, F- *Rana temporaria*; G-K – clavícula, internal view: G- *Bufo gargarizans*, H- *Bufo viridis*, I- *Bufo raddei*, J- *Bufo calamita*, K- *Rana arvalis*; L-M – cleithrum, inner view: L- *Bufo viridis*, M- *Rana arvalis*; N-P – coracoideum, inner view: N- *Bufo gargarizans*, O-P- *Rana temporaria*: O – male, P – female.

each other; facies lunata is turned laterally; crista longitudinalis is weakly expressed (Fig. 7 A-F). The width of extremitas lateralis coracoidei is approximately equal to that of extremitas medialis; medial margin of the bone is either straight or slightly rounded (Fig. 6 N). The axis of olecranon trace is displaced laterally relatively to long axis of humerus; there may be up to three ventral crests on a proximal half of the bone (Fig. 8). The greatest ischium width is approximately on the middle line; the area for attachment of hind limb muscles is wide (Fig. 12 A). Crus is short, sharply widened towards the ends, in the middle part (in the region of foramen nutritium) compressed, often has a kiel from tibia side, rarely – from both sides; sections of tibia and fibula at the distal end more or less rounded, at the proximal end they are oval; the diameter of tibia section on the distal end is much smaller than that of the fibula one, whereas on the proximal end they are approximately equal; near the foramen nutritium, close to the distal bone end, there is a deep furrow, turning into sulcus intermedius in distal direction (Fig. 12 J). The additional characteristics of the majority of toad bones is specific “toad” shading which is absent in other modern Anura of Russia.

A number of works are devoted to the estimation of species features of pleistocene toads (BAILON, 1986; BÖHME, 1977; HODROVA, 1980; HOLMAN, 1989, 1998; SANCHIZ, 1977). All these researches are based on the assumption that the same three modern toad species existed in Western Europe in the past: *Bufo bufo*, *B. calamita*, and *B. viridis*. This assumption is not acceptable in diagnostics of the Eastern Europe fossil material. Firstly, the tendency of transference of former subspecies to species has made it necessary to search for identification criteria of new species and revision of old ones, concerning first of all *B. bufo*. Secondly, the present author has admitted the possibility of occurrence in anthropogene deposits not only forms living these at present, that has later proved to be true (RATNIKOV, 1996b). Thus, the number of possible levels of fossil material determination has increased.

The modern representatives of genus *Bufo* of Eurasia are united by zoologists in unsystematic groups (complexes) on the basis of certain attributes. The toads of Russia and adjacent countries form two complexes: *Bufo (bufo)* sp. (the grey toad group) and *Bufo (viridis)* sp. (the green toad group). Representatives of each complex have similar features in the structure of some skeleton elements, distinguishing them from representatives of another complex, and similar ecological attachment, which is very important for reconstruction of the paleogeographical conditions during the formation of the locality (RATNIKOV, 1996a).

Bufo (bufo) sp.

Condylus occipitalis is very wide; torus terminalis is usually narrow and high (Fig. 1 A). Elevatio prootici is well expressed and is disposed along the anterior margin of the bone; ramus lateralis prootici is massive, almost unnarrowed laterally (Fig. 2 H, I). Sphenethmoid is usually with narrow posterior openings of canalis olfactorii and weakly expressed folds in their cavities (Fig. 1 M-O). The anterior end of maxilla pars facialis as a process projects forward further than anterior end of pars dentalis (Fig. 1 F-H). Nasale has visible S-shaped bend (Fig. 2 C). Frontoparietale gradually narrows in the anterior part; dorsal surface is flattened and is not limited by crest; lateral margin of the bone is abruptly curved downwards (Fig. 2 H-J). Squamosum has considerably widened ramus retrozygomaticus (Fig. 4 C-E). Ventral surface of corpus parasphenoidei forms abrupt bend in region of lateral processes and has more abrupt relief than representatives of *Bufo (viridis)* sp. do (Fig. 3 A-C). Atlas has wide cotyles and oval condyle (Fig. 5 A). Centra of breast vertebrae are oval in cross section; cotyles at abdominal vertebrae acquire a half-moon form; dorsal plane of neural arch as a rule is longer than ventral one; diapophyses widened at the basis and compressed (Fig. 5 D, H). Sacral neurapophyses are of wide ^-shaped form (Fig. 6 A). Humerus has usually more convex dorsal surface on the distal end than do representatives of green toads. Ala ossis ilii is comparatively thick without pre-acetabular pit; subtriangular form is characteristic for the bone body (Fig. 10 A-C). Femur with comparatively short crista femoris (Fig. 12 C-E).

It was considered that only one species from the group of grey toads – *Bufo bufo* (L.) with several subspecies – existed on the territory of the former USSR (BANNIKOV et al., 1977). Not long ago

herpetologists acknowledged the independence of a Far Eastern subspecies, which is now included into the structure of *Bufo (bufo)* sp. under the species name *Bufo gargarizans* CANTOR (BORKIN, DAREVSKY 1987). The question of systematic position of the Caucasian subspecies has not yet been finally solved. Some herpetologists consider it an independent species (ORLOVA, TUNIEV 1989), whereas others (GÜNTHER 1985) are of the opinion that only one species exist in Europe. V. M. ČKHIKVADZE (1984) pointed to the existence of differences in osteology and independence of the Caucasian toad. The materials investigated by the present author show that the level of differences between *B. bufo* and *B. gargarizans* is the same as that between *B. bufo* and *B. bufo verrucosissimus*. He has therefore identified some fossil bones as *B. verrucosissimus* or *B. cf. verrucosissimus* (RATNIKOV 1992). In the last list of the former USSR herpetofauna (ANANJEVA et al. 1998) *Bufo verrucosissimus* is given as a species. In that work the description of osteological features of three grey toad species – *Bufo bufo* (L.), *Bufo gargarizans* CANTOR and *Bufo verrucosissimus* (PALL.) – is adduced.

Bufo bufo (LINNAEUS, 1758)

Lateral processes of sphenethmoideum are short, ventral crests on them being weakly expressed (Fig. 1 M). External surface of maxillare without folds; posterior process of pars palatina is underdeveloped, not projecting over the upper margin of pars facialis (Fig. 1 F). Frontoparietale gently narrowed toward the anterior end; facies cerebialis posterior are of elliptic form with a long axis almost perpendicular to margo sagittalis of the bone (Fig. 2 H). Ramus zygomaticus ossis squamosi is usually short; margins of ramus retrozygomaticus are parallel or slightly divergent, the upper margin often with wavy bend (Fig. 4 C). Lateral processes and corpus parasphenoidei are of equal width; on an axial line of the bone in region of lateral processes there is a well-defined crest recalling a “tick” in its outlines; straight lateral margins of the bone body that one abruptly bent turn into anterior margins of lateral processes; posterior process is usually narrow (Fig. 3 A). Scapula with comparatively wide head and narrow neck; the anterior margin of pars acromialis may be stretched in tenuitas acromialis (Fig. 7 A). Medial crest of humerus usually does not reach the middle of the bone, it is wide, with rounded margin, slightly deviated dorsally; spina medialis dorsalis can be observed, whereas spina medialis ventralis is barely noticable (Fig. 8 A). Ilium has often low but sometimes high tuber superior on which as a rule there is one large tubercle often displaced forward (Fig. 10 A). Femur has a single crista femoris; there is sometimes an additional obtuse crest in large specimens, which begins not far from the distal end of crista femoris (Fig. 12 C).

Bufo gargarizans CANTOR, 1842

The posterior part of ventral sphenethmoid area is wide; lateral processes are rather long with abrupt ventral crests (Fig. 1 N). Smooth fold is visible on external surface of maxillare from the anterior end; posterior process of pars palatina almost does not project over the upper margin of pars facialis (Fig. 1 G). Lateral margin of frontoparietale is as a rule weakly bent in an arch-like manner; facies cerebialis posterior is practically round (Fig. 2 I). Ramus zygomaticus ossis squamosi is usually comparatively long and thin, and the margins of ramus retrozygomaticus appreciably diverge (Fig. 4 D). Corpus parasphenoidei is wider than the lateral process; convex lateral margins of corpus, being gently bent, turn into anterior margins of lateral processes; “tick” in region of lateral processes is absent, there is a fairly wide ventral area in its place; the crest passing from one lateral process toward another is sometimes visible; the posterior process is usually wide (Fig. 3 B). Scapula with a comparatively wide head and narrow neck; anterior margin of pars acromialis may be stretched in tenuitas acromialis (Fig. 7 B). Medial crest of humerus usually reaches the middle of the bone, with rounded margin, greatly deviated dorsally; spina medialis dorsalis may be appreciably developed, whereas spina medialis ventralis is usually not visible (Fig. 8 B). Ilium has high tuber superior either with no small tubercles, or with one tubercle on its lateral surface (Fig. 10 B). Femur with the only crista femoris; sometimes there is an additional slightly visible obtuse crest in large specimens, which begins from the middle of crista femoris (Fig. 12 D).

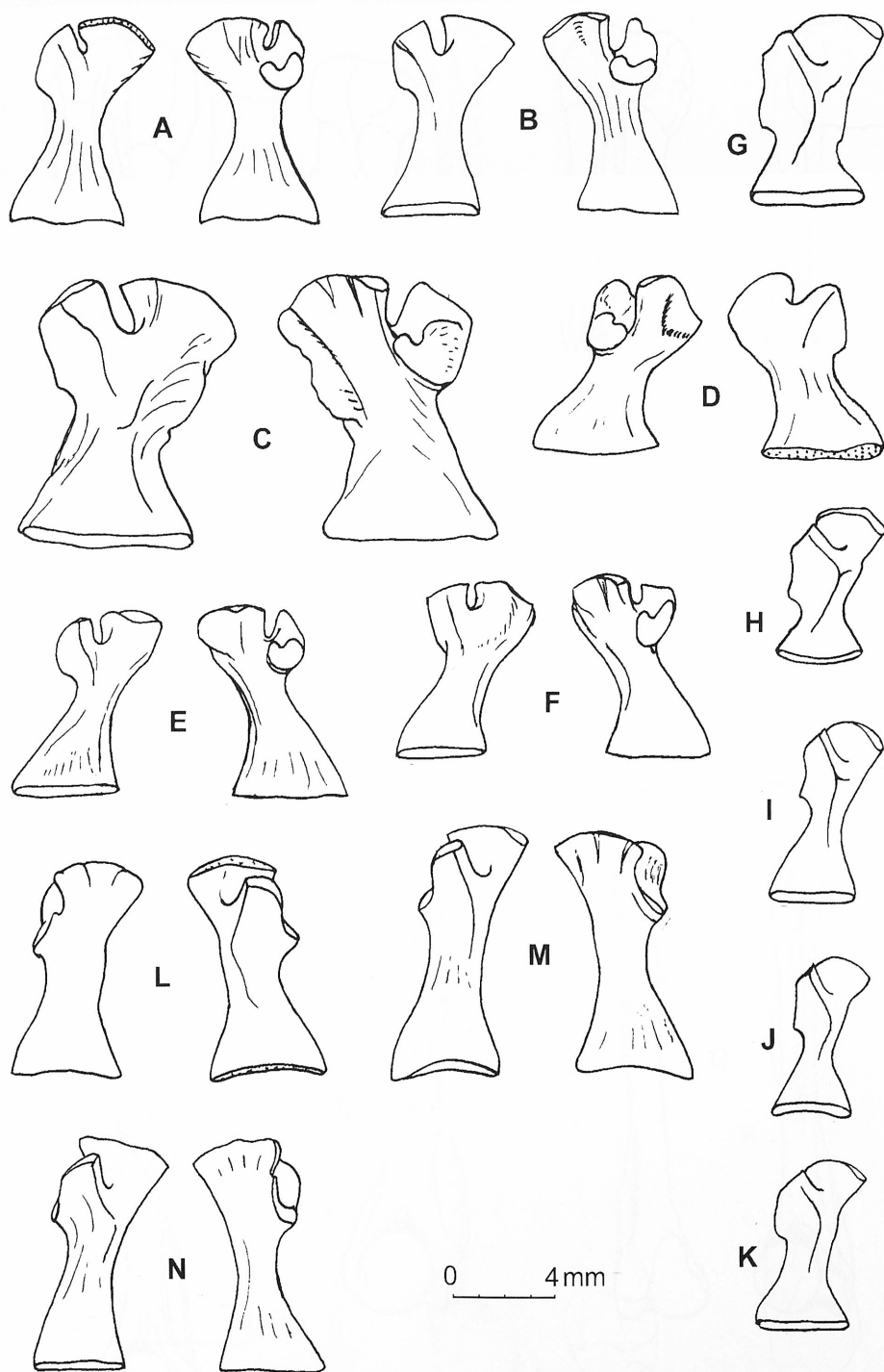


Fig. 7. Scapula. A-F, L-N – internal and outer views, G-K – internal view: A – *Bufo bufo*, B – *Bufo gargarizans*, C – *Bufo verrucosissimus*, D – *Bufo viridis*, E – *Bufo raddei*, F – *Bufo calamita*, G – *Rana temporaria*, H – *Rana chensinensis*, I – *Rana arvalis*, J – *Rana amurensis*, K – *Rana asiatica*, L – *Rana ridibunda*, M – *Rana lessonae*, N – *Rana nigromaculata*.

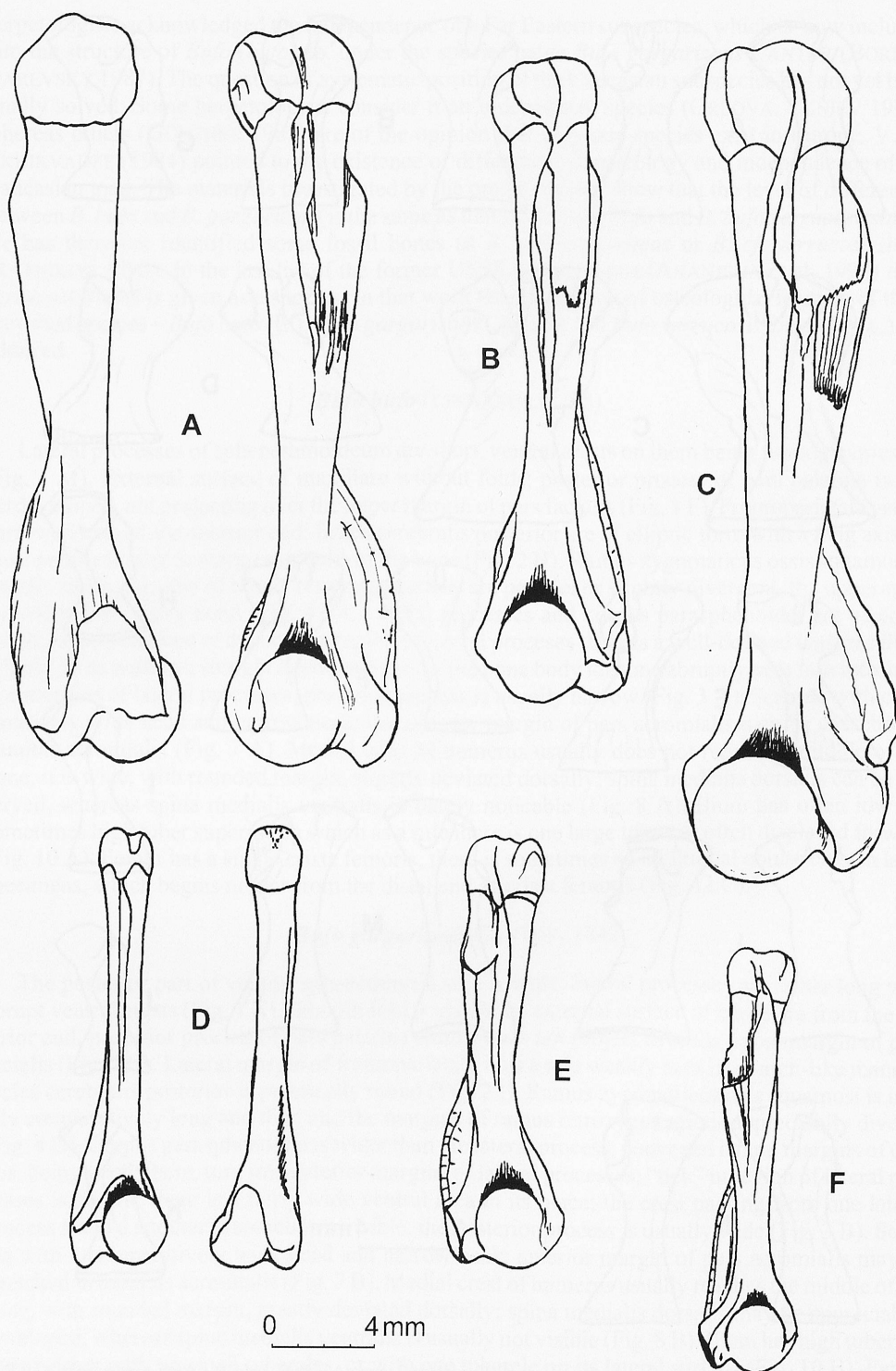


Fig. 8. Humerus (male). A, D – ventral and dorsal views, B-C, E-F – ventral view: A- *Bufo bufo*, B – *Bufo gargarizans*, C – *Bufo verrucosissimus*, D – *Bufo viridis*, E – *Bufo raddei*, F – *Bufo calamita*.

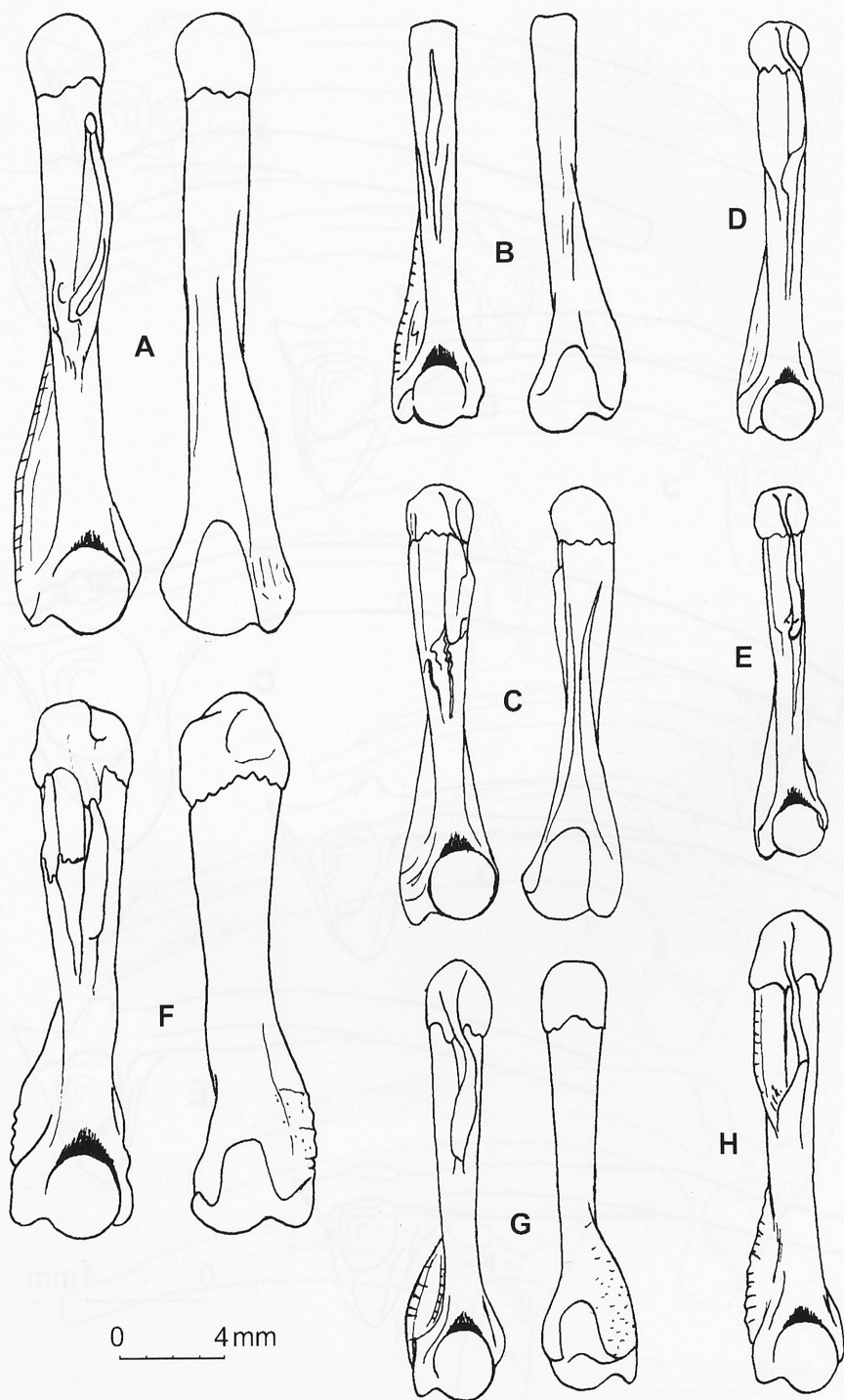


Fig. 9. Humerus (male). A-C, F-G – ventral and dorsal views, D, E, H- ventral view: A- *Rana temporaria*, B – *Rana chensinensis*, C – *Rana arvalis*, D – *Rana asiatica*, E – *Rana amurensis*, F – *Rana ridibunda*, G – *Rana lessonae*, H – *Rana nigromaculata*.

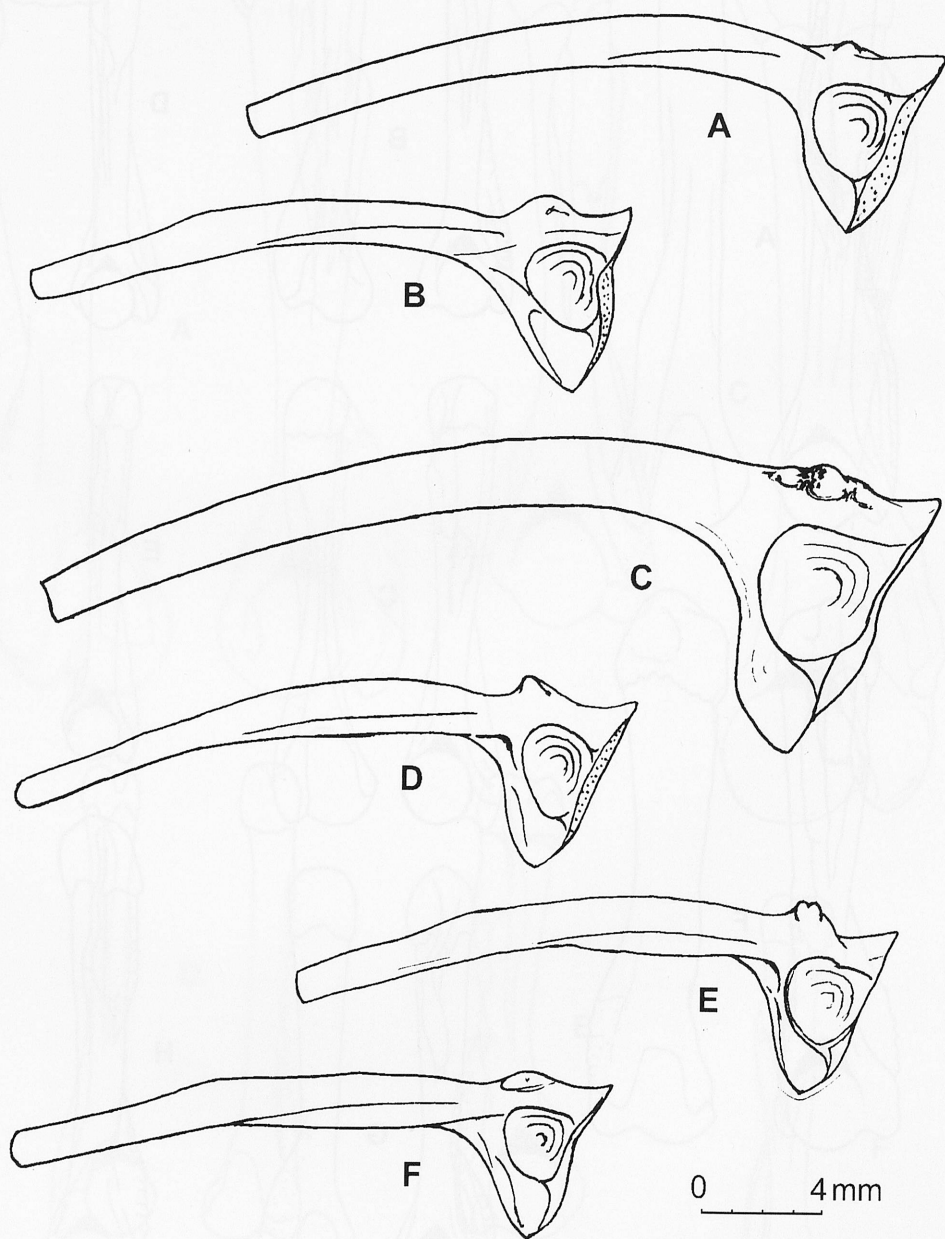


Fig. 10. Ilium, lateral view. A – *Bufo bufo*, B – *Bufo gargarizans*, C – *Bufo verrucosissimus*, D – *Bufo viridis*, E – *Bufo raddei*, F – *Bufo calamita*.

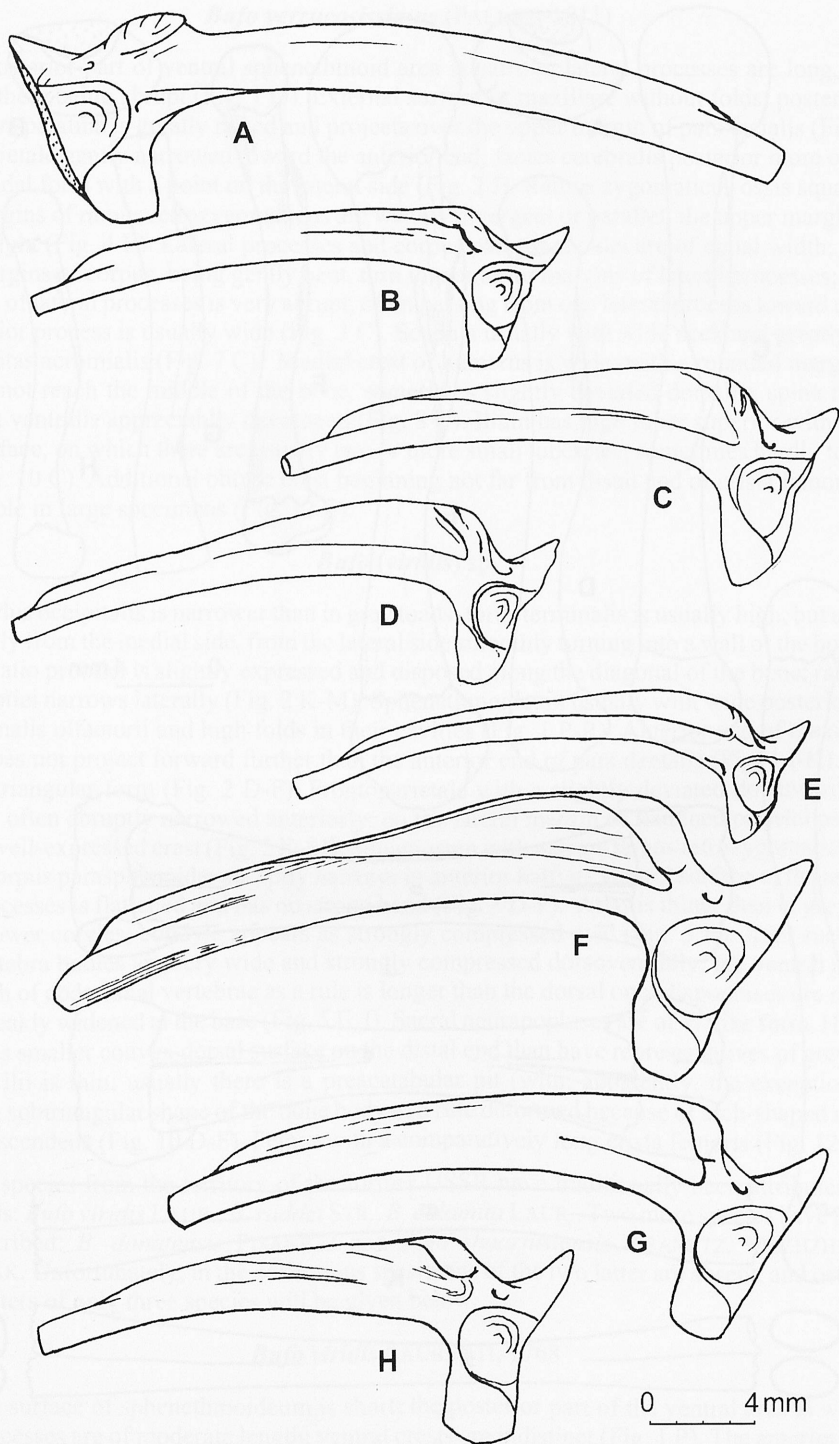


Fig. 11. Ilium, lateral view. A – *Rana temporaria*, B – *Rana chensinensis*, C – *Rana arvalis*, D – *Rana asiatica*, E – *Rana amurensis*, F – *Rana ridibunda*, G – *Rana lessonae*, H – *Rana nigromaculata*

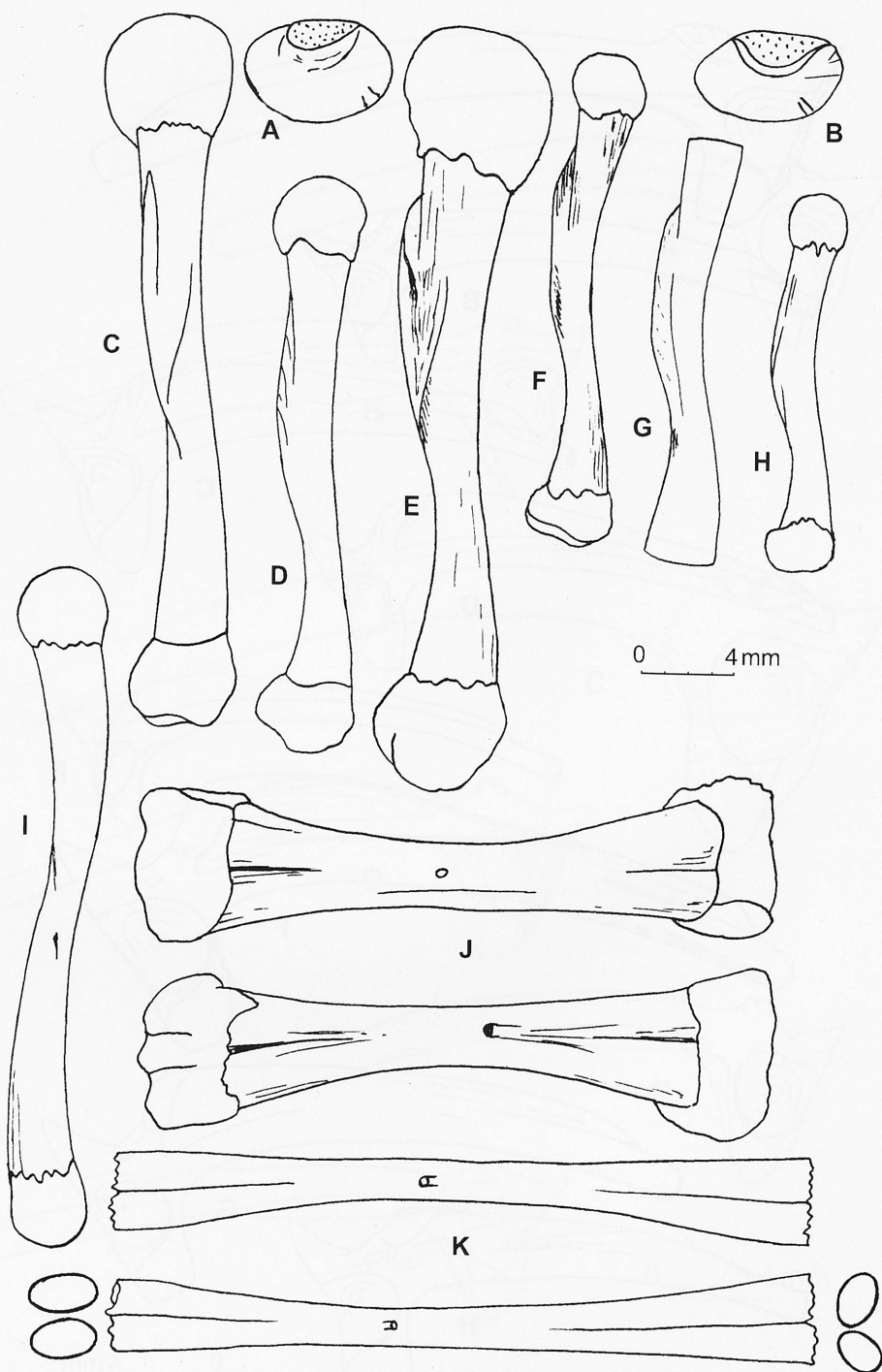


Fig. 12. A-B – ischium, lateral view: A – *Bufo viridis*, B – *Rana temporaria*; C-I – femur, ventral view: C – *Bufo bufo*, D – *Bufo gargarizans*, E – *Bufo verrucosissimus*, F – *Bufo viridis*, G – *Bufo raddei*, H – *Bufo calamita*, I – *Rana temporaria*; J-K – crus: J – *Bufo bufo*, ventral and dorsal views, K – *Rana temporaria*, dorsal, ventral views, and cross section of epiphyses.

Bufo verrucosissimus (PALLAS, 1811)

The posterior part of ventral sphenethmoid area is narrow; lateral processes are long, ventral crests on them being abrupt (Fig. 1 O). External surface of maxillare without folds; posterior process of pars palatina is greatly raised and projects over the upper margin of pars facialis (Fig. 1 H). Frontoparietale gently narrowed toward the anterior end; facies cerebralis posterior more often are of ellipsoidal form with a point on the lateral side (Fig. 2 J). Ramus zygomaticus ossis squamosi is short; margins of ramus retrozygomaticus are weakly divergent or parallel, the upper margin being fairly straight (Fig. 4 E). Lateral processes and corpus parasphenoidei are of equal width; straight lateral margins of corpus, being gently bent, turn into anterior margins of lateral processes; crest in the region of lateral processes is very abrupt, often passing from one lateral process toward another; the posterior process is usually wide (Fig. 3 C). Scapula usually with wide neck and greatly developed tenuitas acromialis (Fig. 7 C). Medial crest of humerus is wide, with a rounded margin, usually does not reach the middle of the bone, sometimes slightly deviated dorsally; spina medialis dorsalis et ventralis appreciably developed (Fig. 8 C). Ilium has high tuber superior with a rough lateral surface, on which there are usually two or more small tubercles, sometimes hardly to distinguish (Fig. 10 C). Additional obtuse crest beginning not far from distal end of crista femoris is always visible in large specimens (Fig. 12 E).

Bufo (viridis) sp.

Condylus occipitalis is narrower than in grey toads; torus terminalis is usually high, but abruptly limited only from the medial side, from the lateral side smoothly turning into a wall of the bone (Fig. 1 B). Elevatio prootici is slightly expressed and disposed along the diagonal of the bone; ramus lateralis prootici narrows laterally (Fig. 2 K-M). Sphenethmoideum usually with wide posterior openings of canalis olfactorii and high folds in their cavities (Fig. 1 P-R). Anterior end of maxilla pars facialis does not project forward further than the anterior end of pars dentalis (Fig. 1 I-K). Nasale has a subtriangular form (Fig. 2 D-F). Frontoparietale with a slightly deviated downward lateral margin, is often abruptly narrowed anteriorly; on the lateral margin of flattened parietal part there may be a well-expressed crest (Fig. 2 K-M). Squamosum with narrow ramus retrozygomaticus (Fig. 4 F-H). Corpus parasphenoidei abruptly narrows in anterior half; its ventral surface in the region of lateral processes is flattened and has no strong bend (Fig. 3 D-F). Atlas is thinner than in grey toads, with narrower cotyles; condyle appears as strongly compressed oval (Fig. 5 B). Joint surfaces of breast vertebra bodies are very wide and strongly compressed dorsoventrally; the ventral plane of neural arch of abdominal vertebrae as a rule is longer than the dorsal one; diapophyses are not widened or weakly widened at the base (Fig. 5 E, I). Sacral neurapophyses are of W-like form. Humerus usually has smaller convex dorsal surface on the distal end than have representatives of grey toads. Ala ossis ilii is thin; usually there is a preacetabular pit (with, apparently, the exception of *B. calamita*); subtriangular shape of the bone body as a rule deformed because of arch-shaped margins of pars descendens (Fig. 10 D-F). Femur with a comparatively long crista femoris (Fig. 12 F-H).

Three species from the territory of the former USSR have traditionally been attributed to the green toads: *Bufo viridis* LAUR., *B. raddei* STR., *B. calamita* LAUR.. Two more species have recently been described: *B. danatensis* PISANETZ and *Bufo shaartusiensis* PISANETZ, MEZHHERIN et SZCZERBAK. Unfortunately, in the collections specimens of the two latter are absent, and osteological characters of only three species will be given below.

Bufo viridis LAURENTI, 1768

Dorsal surface of sphenethmoideum is short; the posterior part of the ventral area is wide, the lateral processes are of moderate length; ventral crests are indistinct (Fig. 1 P). The anterior margin of maxilla pars facialis reaches the level of anterior margin of pars dentalis; on the posterior end of pars palatina there is a visible process; the external surface of the bone without folds (Fig. 1 I). Nasale is wide (Fig. 2 D). Frontoparietale gradually narrows toward the anterior end; low crest is

sometimes present on the lateral margin of flattened parietal part (Fig. 2 K). Pars horizontalis ossis squamosi is mostly widened in the middle part (Fig. 4 F). Corpus parasphenoidei is much wider than the lateral processes; the flattened part of the bone body is wide (Fig. 3 D). Clavicula is comparatively narrow and long (Fig. 6 H). Scapula is fairly short, with very wide collum scapulae and wide pars acromialis, whose anterior margin is stretched in tenuitas acromialis (Fig. 7 D). Humerus is long; crista medialis is narrow, with a straight margin, slightly deviated dorsally; spinae medialis dorsalis et ventralis are absent (Fig. 8 D). Ilium with high, long, asymmetrical tuber superior (the anterior end steeper than the posterior one), bearing variable amounts of tubercles (Fig. 10 D). Femur is comparatively thin, having the shortest crista femoris among the green toads (which is, however, longer than in the representatives of *Bufo (bufo)* sp. (Fig. 12 F).

Bufo raddei STRAUCH, 1876

Dorsal sphenethmoid surface is short; the posterior part of ventral area is narrow; the lateral processes long; ventral crests abrupt (Fig. 1 Q). The anterior margin of maxilla pars facialis does not reach the level of that of pars dentalis; processes on posterior end of pars palatina are weakly developed; the external surface of the bone without folds (Fig. 1 J). Nasale is of moderate width (Fig. 2 E). Frontoparietale considerably narrows in the anterior part; on the lateral margin of parietal part in adult specimens there may be a low crest (Fig. 2 L). Pars horizontalis ossis squamosi is not widened in the middle part; ramus retrozygomaticus has an arch-shaped upper margin (Fig. 4 G). The flattened part of corpus parasphenoidei is narrow; the lateral processes are mostly widened at about one-third of their length from the distal end where they are as wide as the bone body (Fig. 3 E). Clavicula is short and wide (Fig. 6 I). Scapula is long, with narrow collum scapulae; the anterior margin of pars acromialis may be stretched in tenuitas acromialis (Fig. 7 E). (Investigated material shows variations in the form of this bone: the scapulas of the toads from the Far East have comparatively wider collum scapulae than Mongolian specimens and are very similar to scapulas of *B. calamita*). Humerus (Fig. 8 E) is short and curved; the crista medialis is wide, with rounded margin, deviated dorsally; spinae medialis dorsalis et ventralis are well expressed. Ilium has a very high, symmetrically or almost symmetrically rising, tuber superior with large tubercle in the central part, in most cases split into two peaks or with a pit above (Fig. 10 E). Crista femoris is long, high, and thin (Fig. 12 G).

Bufo calamita LAURENTI, 1768

Dorsal sphenethmoid surface is long; the ventral crests abrupt; posterior part of ventral area of moderate width; lateral processes are long (Fig. 1 R). The anterior margin of maxilla pars facialis does not reach the level of the anterior margin of pars dentalis; process on posterior end of pars palatina is weakly expressed; there is a visible fold in the anterior part of the bone (Fig. 1 K). Nasale is narrow (Fig. 2 F). Frontoparietale is strongly narrowed in the anterior part; there is a clearly expressed crest along the lateral margin of the parietal part of the bone, extending on the frontal part in larger specimens (Fig. 2 M). Pars horizontalis of squamosum is widened in the middle part; ramus retrozygomaticus has somewhat abrupt bend of the upper margin at an obtuse angle (Fig. 4 H). Flattened part of corpus parasphenoidei is narrow; the width of the lateral processes is approximately the same almost along their extent and is appreciably less than corpus width (Fig. 3 E). Clavicula is short, of moderate width (Fig. 6 J). Scapula is long, its neck being wider than that of *B. raddei*; the anterior margin of pars acromialis can be stretched in tenuitas acromialis (Fig. 7 F). Crista medialis ossis humeri is of moderate width, with straight margin on the greater part of its length, slightly deviated dorsally; spina medialis dorsalis et ventralis are well expressed (Fig. 8 F). Ilium without preacetabular pit; tuber superior is high, short, narrow, sometimes with a single weakly developed tubercle in central part (Fig. 10 F). Crista femoris is long and thick (Fig. 12 H).

IV. FAMILY RANIDAE

Genus *Rana* LINNAEUS, 1758

Condylus occipitalis is narrow, gradually narrowing ventromedially; the borders of fossa condyloidea are visible, there is a narrow zone of bone between them and foramen jugulare (Fig. 1 C). Small and large openings of long anterior semicircular canal differ greatly in size and are quite far from each other (Fig. 1 D, E). Nasale is thin, elongated, weakly convex (Fig. 2 G). Pars lateralis of squamosum is located at an acute angle to ramus retrozygomaticus (Fig. 4 I-P). Parasphenoideum is thin; corpus parasphenoidei approximately corresponds to or is slightly wider than lateral processes; the distance between the ends of lateral processes shorter than or equal to the length of the bone (Fig. 3 G-N). Two blades of anterior pterygoid branch differ in width along their length (Fig. 4 B). Goniale relatively low with high processus coronoideus directed upwards and inside; the upper margin of the bone proceeds as a crest, extending along the length of coronoid process; the posterior part of the bone is slightly bent in an S-shaped manner, lateral margin without angle; channel for Meckel's cartilage is in the upper part of the bone under the coronoid process and widens anteriorly along its height; the lower part of the bone under coronoid process is strongly compressed with formation of a crest (Fig. 4 R). There is no space between the two cotyles of atlas; its neural arch is thin, in the upper part it is not ossified, hence its right and left branches are separated along the medial line (Fig. 5 C). Centra of vertebrae are small; neural arch in all vertebrae is approximately of the same thickness, towers above diapophyses; the diameter of neural channel decreases in caudal direction more gradually than in toads (Fig. 5 F, G, J-L). Join pits of urostyle are usually not separated, but sometimes can be; neural channel is high, from the anterior end of the bone it looks like an isosceles triangle; ventral bone surface is flattened in anterior part (Fig. 6 F). Clavicula is comparatively thin, and practically does not widen medially, having comparatively small expansion on the lateral end (Fig. 6 K). Cleithrum thin, quadrangular; small lamina marginalis cleithri extends along the anterior margin of the bone (Fig. 6 M). Scapula pars acromialis and pars glenoidalis cover each other; facies lunata is not turned outside; crista longitudinalis well developed (Fig. 7 G-N). Coracoideum is abruptly widened medially, so that extremitas medialis is considerably wider than e.lateralis; the medial margin of the bone smoothly rounded and in males is much more massive than in females (Fig. 6 O-P). Long axis of olecranon trace coincides with long axis of humerus; one, sometimes two ventral crests present on the proximal half of the bone (Fig. 9). Maximum width of ischium is observed in the field of the upper end of acetabular ledge; area for attachment of hind limb muscles is not wide (Fig. 12 B). Crus is long, gradually widening to epiphyses; in the middle part (in the area of foramen nutritium) it has more or less rounded section, occasionally with weak kiel; on the proximal end the diameters of cross sections tibia and fibula are practically equal, and their long axes are almost parallel; on the distal end these axes are at an acute angle, and diameter of the tibia section is less than that of the fibula; at foramen nutritium there may be a short furrow (Fig. 12 K).

Articles by BÖHME (1977), BÖHME, GÜNTHER (1979), ROČEK (1980) are devoted to the investigation of osteological features of the European species of frogs. However, they deal with only two bones: frontoparietale and ilium. The research presented here covers many more skeleton elements.

Modern frogs are divided into two groups: brown frogs – *Rana (temporaria)* sp., and green frogs – *Rana (esculenta)* sp.. Some skeleton elements demonstrate distinctions between them.

***Rana (temporaria)* sp.**

The crest may be present at outer margin of ramus retrozygomaticus ossis squamosi, only in its anterior half (Fig. 4 I-M). Corpus parasphenoidei comparatively wider than in green frogs (Fig. 3 G-K). Horizontal plates of vertebral neural arch abruptly (by ledge) thicken in the middle part, forming the well developed elevated platform (Fig. 5 F, K, L). Sacral neurapophis is inclined anteriorly or strongly extended without inclination; in the central part it is not bent backwards (Fig. 6 C). Crista medialis and c.lateralis in male humerus deviate dorsally (Fig. 9 A-E). Tuber superior on ilium is convex and usually complicated by small tubercles (Fig. 11 A-E).

The following species of Russia (BORKIN, DAREVSKY 1987) enter the structure of *Rana (temporaria)* sp.: *Rana temporaria* L., *R. chensinensis* DAVID, *R. arvalis* NILSSON, *R. asiatica* BEDRIAGA, *R. amurensis* BOULENGER, *R. dalmatina* BONAPARTE, *R. macrocnemis* BOULENGER. Osteological characteristics of the latter two will not be considered owing to the absence of reliable samples.

Rana temporaria LINNAEUS, 1758

Flat dorsal surface of frontoparietale is limited by linea transversalis and l.medialis located over margo orbitalis; l.prooticalis and l.occipitalis are as a rule present; channel between processus prooticalis and well-expressed p.occipitalis is present; sagittal margin is straight or sometimes serrated, usually deviates laterally at the anterior end of the bone (Fig. 2 N). Ramus zygomaticus of squamosum is comparatively wide, its lower margin is curved; the crest gradually disappearing caudally, is present in the anterior part of ramus retrozygomaticus at the outside margin; pars lateralis is considerably widened at the end (Fig. 4 J). Parasphenoid lateral processes are slightly narrower or equal to the width of corpus parasphenoidei, having straight or sometimes wavy margins; processus posterior is narrow (Fig. 3 G). Vertebrae usually have wide vertical and long horizontal plates of neural arch (Fig. 5 F, K). Caput scapulae accounts for 2/3 or sometimes 1/2-2/3 of the bone length; collum scapulae is wide or, rarely, of moderate width (Fig. 9 A). Iliac dorsal crest is usually lower than ala ossis ilii or occasionally equal to it in height; tuber superior with one or several tubercles, appreciably towers above the dorsal crest and even hangs above it or, rarely, is on the same level; pars descendens is usually wide (Fig. 11 A).

Rana chensinensis DAVID, 1875

Flat dorsal surface of frontoparietale is limited by linea transversalis and l. medialis located more often near margo orbitalis but sometimes moved medially; channel between processus prooticalis and well expressed p.occipitalis is present; sagittal margin is serrated or straight, it deviates laterally at anterior end of the bone, small sinus sagittalis is present or absent (Fig. 2 O). Ramus zygomaticus ossis squamosi is comparatively wide, its lower margin is curved; well expressed crest at the outer margin of ramus retrozygomaticus is absent; pars lateralis is weakly widened on the end (Fig. 4 K). Lateral processes are somewhat narrower than corpus parasphenoidei, which has wavy, straight or less often convex lateral margins; processus posterior is usually narrow but sometimes wide (Fig. 3 H). Vertebrae have wide neural arch vertical plates as well as long sometimes moderate, horizontal plates. Caput scapulae account for more than half but less than 2/3 of the bone length; collum scapulae is of moderate width or sometimes wide (Fig. 7 H). Dorsal crest is not higher than ala ossis ilii; tuber superior with small tubercles or without them, its height is at the level of crista dorsalis or lower; pars descendens is wide or, rarely, of moderate width (Fig. 11 B).

Rana arvalis NILSSON, 1842

Dorsal surface of frontoparietale is convex; relief is not stable; linea medialis is simple, approaching to sagittal margin, branchy or thickened posteriorly but it may be absent; small tubercles and channels may be present on parietal part; sagittal margin is considerably serrated and deviates laterally in anterior one third; large sinus sagittalis is present; processus occipitalis is weakly expressed; p.prooticalis is considerably displaced posteriorly (Fig. 2 P). Ramus zygomaticus ossis squamosi is relatively narrow, its lower margin even; crest on outer margin of ramus retrozygomaticus is absent; pars lateralis is considerably widened at the end (Fig. 4 I). Lateral processes are much narrower than corpus parasphenoidei which usually has wavy or straight lateral margins (př. 3 I). Vertebrae have narrow neural arch vertical plates as well as short, sometimes moderate, horizontal plates (Fig. 5 L). Caput scapulae accounts for about half the bone length; collum scapulae is narrow; anterior margin is concave, with most caudal point slightly distal from the middle of the bone (Fig. 7 I). Crista medialis and c.lateralis are well developed, the former being better developed than the latter; distal ends of these crests are very close to each other (Fig. 9 C). (Crista medialis in all other brown frogs is well developed, c.lateralis underdeveloped, distal ends of the crests are farther from

each other (Fig. 9 A, B, D, E). Usually dorsal crest is much higher than ala ossis ilii, its highest point being over tuber superior; pars descendens is narrow; tuber superior with small tubercles sometimes smooth (Fig. 11 N).

Rana asiatica BEDRIAGA, 1898

Flat dorsal surface of frontoparietale is limited by linea transversalis and l.medialis, the latter being located more medially from margo orbitalis; channel between processus occipitalis and p.prooticalis and underdeveloped l.prooticalis may be present; sagittal margin is serrated and deviates laterally in the anterior one third of the bone; sinus sagittalis may be present; processus occipitalis is poorly developed; p.prooticalis is slightly displaced posteriorly (Fig. 2 O). Ramus zygomaticus ossis squamosi is comparatively wide, its lower margin bent; acute crest is present on outer margin of the anterior part of ramus retrozygomaticus; pars lateralis is slightly widened at the end (Fig. 4 L). Parasphenoid lateral processes and corpus parasphenoidei are of equal width, the latter has straight lateral margins; posterior process is wide, sometimes narrow (Fig. 3 J). Vertebrae have narrow vertical and usually short horizontal plates of neural arch. Caput scapulae accounts for about half the bone length; margo anterior is twice abruptly bent; collum scapulae of moderate width (Fig. 7 K). Dorsal crest is higher than ala ossis ilii; its height is constant or decreases anteriorly; tuber superior usually slightly deviates laterally, without complicating tubercles sometimes with tubercles; pars descendens is wide (Fig. 11 D).

Rana amurensis BOULENGER, 1886

Flat dorsal surface of frontoparietale is limited by linea transversalis and l.medialis, located close to margo orbitalis; weakly expressed l.prooticalis may be present; processus occipitalis is poorly developed; sagittal margin of the bone serrated and deviates laterally in the anterior quarter; sinus sagittalis is absent or is small if any (Fig. 2 R). Ramus zygomaticus ossis squamosi is relatively narrow, its lower margin is even; crest is present on outer margin of anterior part of ramus retrozygomaticus; pars lateralis is widened at the end (Fig. 4 M). Width of lateral processes is greater or equal to the width of corpus parasphenoidei, which has straight, sometimes wavy, lateral margins; posterior process is usually wide and may be bifurcated (Fig. 3 K). Vertebrae have narrow neural arch vertical plates as well as short, sometimes moderate, horizontal plates. Caput scapulae accounts for about half the bone length; margo anterior is twice abruptly bent; collum scapulae is moderate to narrow (Fig. 7 J). Dorsal crest and ala ossis ilii are of equal height; the height of the former is constant to considerable extent; tuber superior is usually weakly convex, without complicating tubercles; pars descendens is short and narrow; relative length of junctura ilioischiadica is shorter, than that in other brown frogs, and the bone seems to be longer (Fig. 11 E).

R e m a r k s. A close morphological similarity of skeleton bones of *R. temporaria* and *R. chensinensis* should be noted. Moreover they have close ecological features. In many cases it is impossible to determine fossil remains of brown frogs to species level, but it is obvious that they belong to one of these two forms. For emphasis they have been determined as *Rana ex gr. temporaria* L. (RATNIKOV 1992, 1996b).

Rana (esculenta) sp.

Squamosum has a crest extending along the outer margin of ramus retrozygomaticus as a continuation of the upper margin of ramus zygomaticus (Fig. 4 N-P). Corpus parasphenoidei is relatively narrower than in brown frogs (Fig. 3 L-N). Horizontal plates of vertebral neural arch gradually thicken without forming the well-developed elevated platform or it is very narrow (Fig. 5 G, J). Sacral neurapophysis is inclined anteriorly, its right and left branches being bend backward before fusing in the centre of neural arch (Fig. 6 D). Crista medialis and c.lateralis in male humeri are not deviated dorsally (Fig. 9 F-H). Tuber superior on ilium is flattened laterally (Fig. 11 F-H).

The group of green frogs now includes the following species: *Rana ridibunda* PALL., *R. lessonae* CAMERANO and *R. nigromaculata* HALL.. So far the systematic situation of *R. esculenta* L. is not

clear. Some experts consider it as a hybrid form (BANNIKOV et al. 1977; BÖHME, GÜNTHER 1979), others as independent species (BORKIN, DAREVSKY 1987). Osteological characters of three species will be given below, in view of the absence of reliable specimens of *R. esculenta*.

***Rana ridibunda* PALLAS, 1771**

Relief on frontoparietale is well developed: as a rule, all four lines are present; processus occipitalis is well developed; processus prooticalis is displaced posteriorly; sagittal margin is fairly straight and deviates laterally at anterior end of the bone; lateral margin of frontal part abruptly turns and passes into anterior margin of processus prooticalis (Fig. 2 S). Ramus zygomaticus ossis squamosi is longer than ramus retrozygomaticus, which bears a wide spade-shaped process at the end; low obtuse-angle process is present in central part of pars horizontalis (Fig. 4 N). Width of lateral parasphenoid processes gradually increases towards the end where it reaches the value of maximal width of corpus parasphenoidei; processus posterior is narrow (Fig. 3 L). Caput scapulae accounts for about half the bone length; margo anterior is twice abruptly bent; collum scapulae is wide (Fig. 7 L). Crista medialis of humerus is comparatively long, its margin being abruptly bent at an obtuse angle; c.lateralis is long and narrow; crista ventralis secundaria may be present in large specimens (Fig. 9 F). Crista dorsalis of ilium is very high; tuber superior wide, the flat platform on it long and begins at low level (Fig. 11 F).

***Rana lessonae* CAMERANO, 1882**

Relief of frontoparietale is smoothed: very few lines are not distinguished; processus occipitalis is poorly expressed; p.prooticalis considerably displaced posteriorly; sagittal margin is serrated in parietal part and deviates laterally in anterior one third of the bone; lateral margin of frontal part turns smoothly and passes into anterior margin of processus prooticalis (Fig. 2 T). Pars horizontalis ossis squamosi is short, mostly widened in the middle part; ramus zygomaticus gradually narrows towards the anterior end (Fig. 4 O). Width of lateral parasphenoid processes abruptly increases towards the ends where it exceeds the value of the maximal width of corpus parasphenoidei; processus posterior is narrow (Fig. 3 M). Scapula is long; caput scapulae accounts for less than half the bone length; margo anterior is twice bent; collum scapulae narrow (Fig. 7 M). Cristae medialis et lateralis of humerus are usually comparatively short and wide, with round margins, hence the distal head of the bone seems to be wide; crista ventralis secundaria is absent or weakly expressed (Fig. 9 G). Crista dorsalis of ilium is high; tuber superior narrow, and the flat platform on it is long and begins at high level (Fig. 11 G).

***Rana nigromaculata* HALLOWELL., 1861**

Only linea transversalis and parietal piece of l. medialis are well developed on frontoparietal surface, two another lines are not expressed; the degree of processus occipitalis development differs; sagittal margin is rather straight and deviates laterally at anterior end of the bone; lateral margin of frontal part turns smoothly and passes into anterior margin of processus prooticalis (Fig. 2 U). Pars horizontalis ossis squamosi is very short; ramus zygomaticus is considerably thinner than ramus retrozygomaticus and narrows near anterior end (Fig. 4 P). Width of lateral parasphenoid processes gradually increases towards the ends where it exceeds the value of the maximal width of corpus parasphenoidei; processus posterior is wide (Fig. 3 N). Caput scapulae accounts for less than half the bone length; margo anterior is concave, with most caudal point near the middle of the bone; collum scapulae is narrower, than in *R. lessonae* (Fig. 7 N). Cristae medialis et lateralis of humerus are comparatively long and narrow, hence the distal head of the bone does not look wide; crista ventralis secundaria is present (Fig. 9 H). Crista dorsalis is somewhat higher than ala ossis ilii; tuber superior is wide, and the flat platform on it short and begins at low level (Fig. 11 H).

IV. CONCLUSION

Bone shape of toads and frogs permit their identification up to the level of species, complex, and genus. It is hardly possible to consider the above diagnostic criteria exhaustive. Further researches of fossil materials will probably make it possible to find additional features of the bone morphology of various anuran groups. Some observations carried out on a small number of specimens undoubtedly need control and more accurate definition.

In the skeletons of toads are to be found the greatest number of elements (9-11) which make it possible to define species. The most important of them are ilia, frontoparietalia, maxillaria, parasphenoidea, and male humeri.

Only 6-7 bones are used for specific identification of frogs. Most diagnostic elements are ilia, frontoparietalia, and scapulae. Other bones do not always give an unequivocal definition.

Genera are distinguished very easily: almost all skeletal elements, with the exception of distal elements of limbs, have their generic signs.

REFERENCES

- ANANJEVA N. B., BORKIN L. Y., DAREVSKY I. S., ORLOV N. L. 1998. Zemnovodnye i presmykayushchiesya. Encyklopedia prirody Rossii. 576 pp. ABF, Moscow. [In Russian].
- BAILON S. 1986. Los anfibios y los reptiles del yacimiento de Cueva Hora (Darro, Granada). *Antropología y Paleontología Humana*, **4**: 131-155.
- BANNIKOV A. G., DAREVSKY I. S., ISCHENKO V. G., RUSTAMOV A. K., SZCZERBAK N. N. 1977. Opredelitel' zemnovodnykh i presmykayushchikhsya fauny SSSR. 415 pp. Prosveschenie, Moscow. [In Russian].
- BORKIN L. J., DAREVSKY I. S. 1987. List of amphibian and reptiles of USSR fauna. [In:] I. S. DAREVSKY (ed.) – Amphibii i reptylii zapovednykh territory. 128-141. Moscow. [In Russian].
- BÖHME G. 1977. Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu, Mathematisch-Naturwissenschaftliche Reihe*, **26**(3): 283-300.
- BÖHME G., GÜNTHER R. 1979. Osteological studies in the European Water frogs *Rana ridibunda*, *R. lessonae* and *R. "esculenta"* (Anura, Ranidae). *Mitteilungen aus dem Zoologischen Museum in Berlin*, **55**(1): 203-215.
- ČIKHIKVAÐZE V. M. 1984. Survey of fossil tail and tailless amphibians of the USSR. *Izvestiya Akademii Nauk GSSR*, **10**(1): 5-13. [In Russian].
- ENGELMANN W.-E., FRITZSCHE J., GÜNTHER R., OBST F. J. 1985. Lurche und Kriechtiere Europas. 420 ss. Neumann Verlag, Leipzig.
- HODROVA M. 1980. A toad from the Middle Miocene at Devínska Nova Ves near Bratislava. *Věstník Ústředního ústavu geologického*, **55**(5): 311-316.
- HOLMAN J. A. 1989. Identification of *Bufo calamita* and *Bufo bufo* on the basis of skeletal elements. *British Herpetological Society Bulletin*, **29**: 54-55.
- HOLMAN J. A. 1998. Pleistocene Amphibians and Reptiles in Britain and Europe. 254 pp. Oxford University Press, New York-Oxford.
- ORLOVA V. F., TUNIEV B. S. 1989. To systematic of Caucasian grey toads of *Bufo bufo verrucosissimus* (PALLAS) group (Amphibia, Anura, Bufonidae) – *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii*, **94**(3): 13-24. [In Russian].
- RAGE J. 1974. Les batraciens des gisements des quaternaires europeens; Determination osteologique. *Bulletin mensuel de la Société Linnéenne de Lyon*, **43**(8): 276-289.
- RATNIKOV V. Yu. 1992. Eopleistocene and Pleistocene anuran faunas of the East European Platform. *Paleontological Journal*, **26**(1): 112-126. [In Russian]
- RATNIKOV V. Yu. 1995. Late Cenozoic evolution of batrachofauna of the East-European Platform. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Geologicheskii*, **70**(5): 98-103. [In Russian].
- RATNIKOV V. Yu. 1996a. Methods of paleogeographic reconstructions based upon fossil remains of amphibians and reptiles of the Late Cenozoic of the East European Platform. *Palaeontological Journal*, **30**(1): 77-83.
- RATNIKOV V. Yu. 1996b. On the finds of Green Toads (*Bufo viridis* complex) in the late Cenozoic of the East European Platform. *Palaeontological Journal*, **30**(2): 225-231.
- ROČEK Z. 1980. A contribution to the systematics of European ranid frogs (Amphibia, Ranidae) on the basis of the incrassatio frontoparietalis. *Věstník československé společnosti zoologické*, **44**(3): 219-229.
- SANCHIZ B. 1977. La familia Bufonidae (Amphibia, Anura) en el Terciario europeo. *Trabajos sobre Neogeno-Cuaternario CSIC*, **8**: 75-111.
- SANCHIZ B. 1998. Salientia. Encyclopedia of Paleoherpertology. Part 4. 276 pp. Verlag Dr. Friedrich Pfeil, München.

