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**A CONTRIBUTION TO THE SYSTEMATICS OF EUROPEAN RANID
FROGS (AMPHIBIA, RANIDAE) ON THE BASIS OF THE INCRASSATIO
FRONTOPARIETALIS**

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Abstract: On the basis of the *incrassatio frontoparietalis*, which is a thickened, well limited part of the frontoparietal bone, covering in ranids three openings in the dorsal wall of the endocranium, and thus substituting missing parts of the wall, it is possible to hypothesize phylogenetic relationship of the European green and brown ranids. It is shown that the *incrassatio frontoparietalis* can be satisfactorily used on the taxonomical level of species.

INTRODUCTION

European ranids were classically divided into two main groups on the basis of external characters, but the evolutionary relationships of species in each of these groups is still poorly understood. Classical taxonomic methods restricted to the description of external body features (e. g. coloration and proportion) and ecology, behaviour, etc. are not always sufficient for hypothesizing the phylogeny of the species. When taking into account only the above attributes, sufficient attention is not given to the selection of examined characters, so that characters influenced by the adaptability of animals are judged equivalently to characters reflecting phylogenetic relations. Modern systematics bases taxonomic classification on true phylogenetic relations, and attempts to minimize the utilization of adaptive characters because they may more often reflect parallel or convergent evolution. Moreover, the evaluation and choice of characters suitable for taxonomic study is complicated by the more conspicuous nature of adaptive characters over phylogenetic characters.

Externally, frogs are conspicuously uniform because of adaptive characters. When searching for phylogenetic characters, the most conservative structures, i.e. these which remain relatively stable during the course of evolution are preferred. Therefore, many papers have been recently published which hypothesize frog systematics from genetical data (karyotype analysis, electrophoresis of blood proteins, DNA hybridization, immunological reaction). Osteological characters are considered among the most conservative and are thus excellent predictors of phylogeny. As the majority of the fossil record are bones, using osteological material of different ages, changes of the skeleton at different stages of evolution can be followed. The chosen osteological character can then be evaluated as one of phylogenetic or only adaptive value.

The *incrassatio frontoparietalis* is a suitable character. It is defined by a thickened part of the frontoparietale projecting from its ventral surface and covering the openings in the dorsal wall of the endocranium. This character

fortunately indicates the size and extent of the dorsal openings of the endocranium, as the latter are not always preserved and are of different size in higher frog taxa. In the course of vertebrate evolution the endocranium underwent various changes (e.g. its dorsal wall was being gradually reduced, so that in advanced mammals it is limited only to the base of the skull). The reason for these changes is not clear, it is evident, however, that they cannot be caused by adaptive answer of an organism. Therefore, the *incrassatio frontoparietalis* can be considered a valuable phylogenetic character, i.e. it can be used for ascertainment of vertebrate phylogenetic relationships.

The question arises, to which taxonomical level (familial, generic, specific) this character is useful. Špinar (1975, 1976) drew attention to considerable morphologic differences between frontoparietal *incrassations* of various frog families and of species within the family Pelobatidae. The aim of this paper is to decide: (i) to which taxonomical level the *incrassatio frontoparietalis* can be used, (ii) whether *incrassatio frontoparietalis* enables us to satisfactorily hypothesize the phylogenetic relationship of European representatives of the family Ranidae.

NOMENCLATURE AND DESCRIPTION OF THE INCRASSATIO FRONTOPARIETALIS IN THE RANIDAE*)

The frontoparietale of ranids is a paired dermal-cranial bone elongated in rostral-caudal direction and divided by a sagittal suture (*sutura sagittalis* Bolkay). It forms a substantial part of the dorsal wall of exocranium between orbits. Rostrally, it contacts the nasale forming the *sutura transversalis* Bolkay. Laterally, it forms a part of the orbit margin (*margo orbitalis* Bolkay), latero-caudally, it contacts the prootic bone (*margo prootica* Bolkay) and caudally the *occipitale laterale* (*margo occipitalis* Bolkay). At the level of the rostral two-thirds (approximately *margo orbitalis*), the lateral margin of the frontoparietale is bent slightly ventrally (*lamina perpendicularis* Bolkay), so that the *processus orbitalis* projecting from this margin is better visible when viewed laterally.

The *incrassatio frontoparietalis* is comprised of a *facies cerebralis anterior* and two *facies cerebrales posteriores*. The *facies cerebralis anterior* is divided by sagittal suture, and fills the opening in the endocranium (*fenestra frontalis*). *Facies cerebrales posteriores* are conspicuously inward projecting oval plates filling the *fenestrae parietales* of the endocranium. *Facies cerebralis anterior* either is projecting entirely or only rostrally, while the caudal part is an indentation. The third pattern is that the entire *facies* is a depression in the bone. For detailed nomenclature see Text Fig. 1.

Description of the *incrassatio frontoparietalis* in individual species

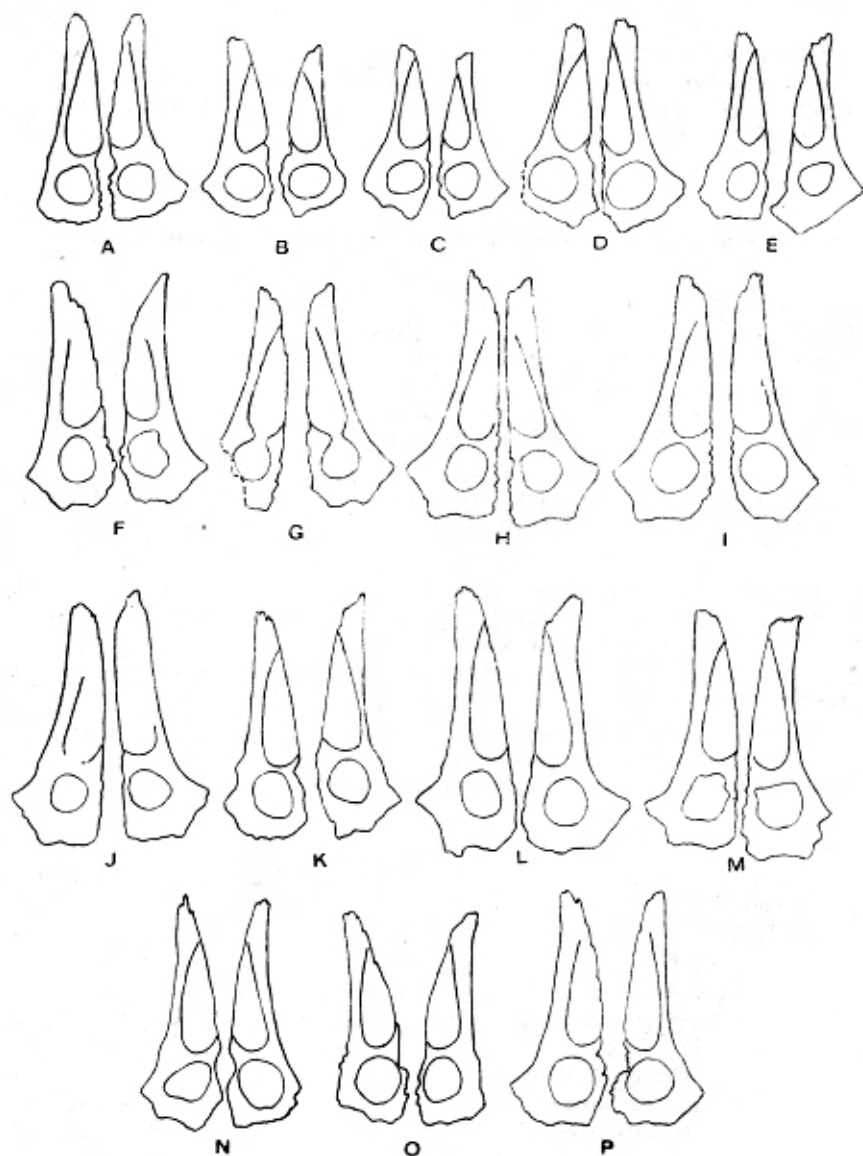
The basic configuration of the pattern is identical in all ranid species and is described above. The following text mentions only differing features between species. In all cases, both left and right frontoparietals were examined. The material is deposited in the collections of the Department of Paleontology, Faculty of Natural Science, Charles University, Prague.

*) When naming parts of the frontoparietale, I have mostly followed the terminology of Bolkay (1919), although not always anatomically correct. The adopted names are followed by the author's name.

Rana esculenta L. (Text Fig. 2, Pl. Fig. 1)

Sixteen specimens are examined (8 ♂♂, 8 ♀♀: loc. Malý Horusický Pond, leg. Roček, June 1972).

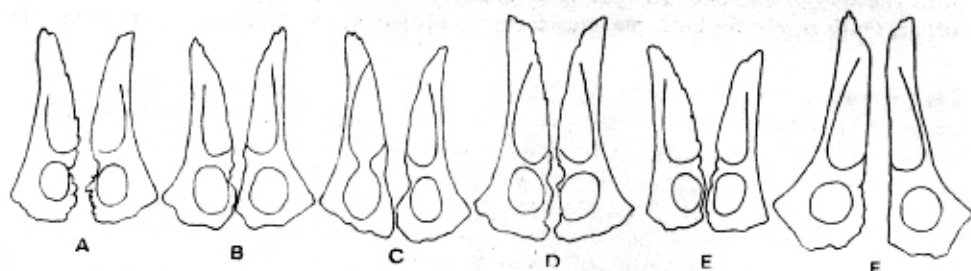
In most cases, the margo sagittalis of the frontoparietale transcends arch-like into the margo anterior, so that both margins are not sharply separated from each other. Only rarely do both margins form an obtuse angle. In all cases, however, the



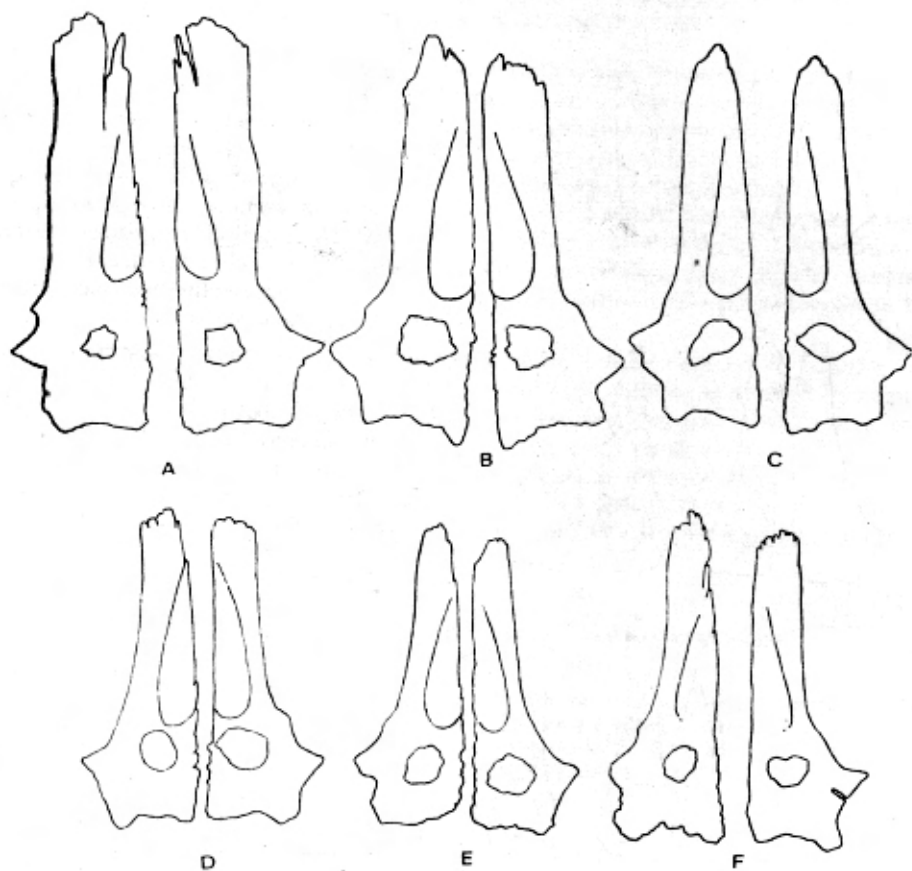
Text Fig. 2. Variability of the increassatio frontoparietalis in *Rana esculenta*.

lateral margin of the facies cerebri anterior is directed antero-medially, and terminates at the margo sagittalis.

The facies cerebrales posteriores are separated from the facies cerebri anterior by the gap spatium interfaciale, corresponding with the taenia tecti transversalis of the endocranium. However, anomalous cases do occur where the facies cerebri



Text Fig. 3. Variability of the incrassatio frontoparietalis in *Rana esculenta lessonae*.



Text Fig. 4. Variability of the incrassatio frontoparietalis in *Rana ridibunda*.

anterior is connected with the facies cerebrales posteriores by bridges (see Text Fig. 2 G), indicating that the taenia tecti transversalis is partly interrupted. Also between the facies cerebralis posterior and margo sagittalis lies a strip of unthickened bone, separating both facies cerebrales posteriores from each other (corresponding to the taenia tecti medialis of endocranium).

The facies cerebralis anterior is defined by a slight indentation of the ventral surface of the anterior portion of the frontoparietale. In contrast, the facies cerebrales posteriores are raised areas, projecting into the cranial cavity and thus filling fenestrae parietales in the endocranium.

The variability of shape, and proportional relation of both parts of the pattern and the space between them are shown in Text Fig. 2. No sexual differences of this character were observed. Sexual dimorphism was also not observed in the other species although insufficient numbers were examined for a statistical statement.

Rana esculenta lessonae Camerano (Text Fig. 3)

Six specimens were examined (3 ♂♂, 3 ♀♀: loc. Ruda near the town Veselí nad Lužnicí, leg. Roček, June 1972).

No marked character can be found in the configuration of the *incrassatio frontoparietalis* in *R. e. lessonae* that differs from any in *Rana esculenta*. Specimens with anomalously formed frontoparietal *incrassatio* do occur (see Text Fig. 3 C), some asymmetrically.

Rana ridibunda Pall. (Text Fig. 4, Pl. Fig. 2)

Six specimens were examined (1 ♂, 5 ♀♀: loc. Constanta, Roumania, leg. Roček, July 1971 — Text Fig. 4 A, B; loc. Navodari, Roumania, leg. Roček, July 1975 — Text Fig. 4C; loc. Lozencec, Bulgaria, leg. Roček, July 1975 — Text Fig. 4D; loc. Hostivice near Prague, leg. Špinar, May 1970 — Text Fig. 4E, F).

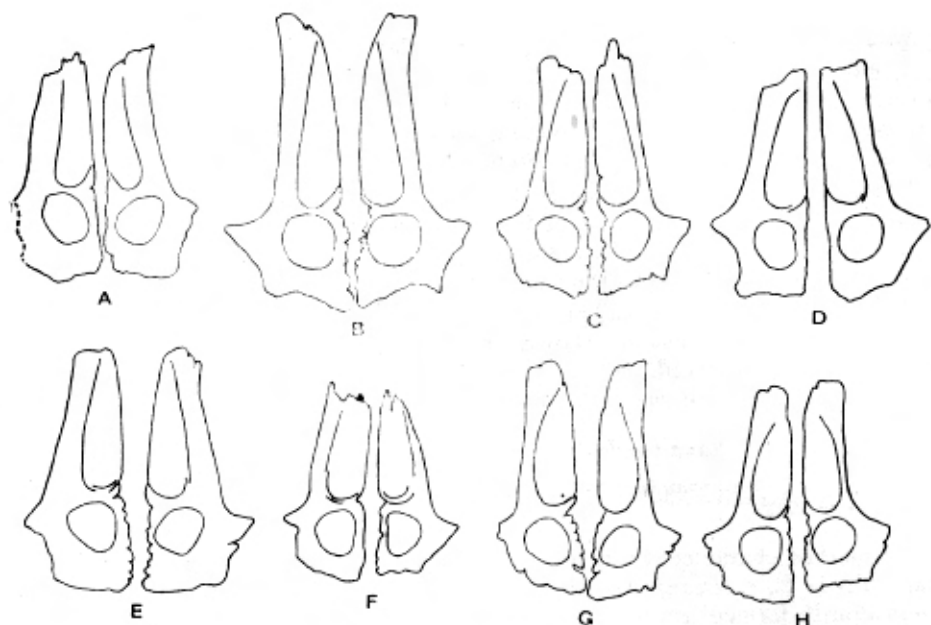
The lateral margin of facies cerebralis anterior is directed either towards the margo sagittalis or toward the point where the margo sagittalis and margo anterior intersect. Unlike the condition in *Rana esculenta*, the facies cerebralis anterior is convex, not an indentation into the bone. However, this projection is not very conspicuous rostrally.

The facies cerebrales posteriores are separated from the rostral part of the pattern by the wide spatium interfaciale. In most cases they are irregularly shaped, with sharp margins and projecting considerably into the openings of the endocranium.

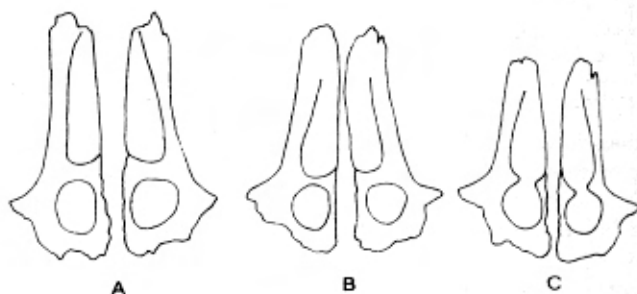
Rana temporaria L. (Text Fig. 5, Pl. Fig. 3)

Eight specimens were examined (1 ♂, 7 ♀♀: loc. Žofín, Novohradské Mts., leg. Anděra & Vohralík, May 1971 — Text Fig. 5A, B, C; loc. Miedzygórze, Poland, leg. Roček, August 1972 — Text Fig. 5D, E, F; loc. Horní Albeřice, Rýchory Mts., leg. Lipenský, June 1975 — Text Fig. 5G, H).

For this species the *incrassatio frontoparietalis* cannot be unambiguously defined. For example, for both specimens from Horní Albeřice the frontoparietale and the *incrassatio frontoparietalis* are identical but differ from all other examined *Rana temporaria* specimens. The margo sagittalis of their frontoparietals forms a right angle with the margo anterior, and the latter again forms an approximately right angle with the margo orbitalis. The lateral margin of the rostral part of the *incrassatio frontoparietalis* in the two above-mentioned specimens turns rostro-medially and terminates at the margo sagittalis. In all other specimens the lateral margin



Text Fig. 5. Variability of the increassatio frontoparietalis in *Rana temporaria*.



Text Fig. 6. Examples of the increassatio frontoparietalis in *Rana dalmatina*.

of facies cerebrales anterior is directed to or terminates at the margo anterior, or at the common intersection of margo anterior and margo sagittalis.

In the rostral part, the border of facies cerebrales anterior sharply projects internally, a feature typical of all examined specimens. Caudally the facies cerebrales anterior is depressed, and its projecting caudal margin is rounded, not sharp.

Unlike green ranids, a more or less conspicuous incisura medialis is formed in most but not all specimens. The facies cerebrales posteriores are similar to those of *Rana esculenta*. The spatium interfaciale is very narrow in some specimens.

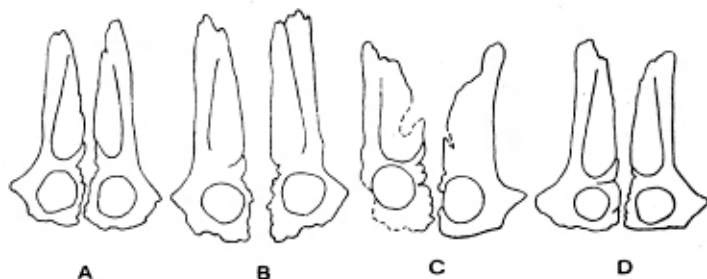
Rana dalmatina Bon. (Text Fig. 6)

Three specimens were examined (1 ♂, 2 ♀♀: loc. Lozencek, Bulgaria, leg. Roček, July 1975 — Text Fig. 6A, B; loc. Putnok, Hungary, leg. Roček, May 1971 — Text Fig. 6C).

The basic shape of the increassatio frontoparietalis is identical with *Rana temporaria*. In all three specimens, the lateral margin of the facies cerebrales anterior is

directed toward the margo anterior. The facies cerebralis anterior is also depressed in the caudal part and projecting in the rostral part.

Remarkably, the facies cerebralis anterior is connected with the facies cerebralis posterior in one specimen (see Text Fig. 6 C).

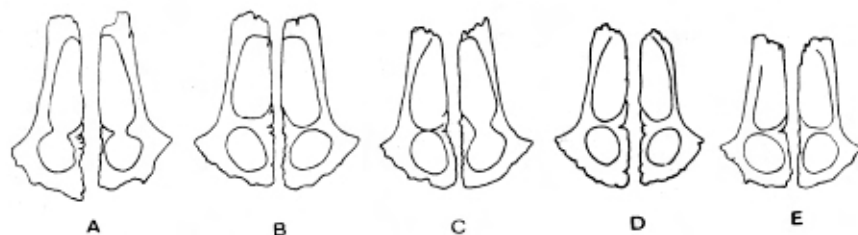


Text Fig. 7. Examples of the incassatio frontoparietalis in *Rana arvalis* and *Rana arvalis wolterstorffi*.

Rana arvalis Nills, *Rana arvalis wolterstorffi* Fejervary (Text Fig. 7)

Four specimens were examined (2 ♂♂, 2 ♀♀: loc. Bohemia (specific locality unknown. From Frič's collections of the National Museum, Prague) — Text Fig. 7A; loc. Soroksár, Hungary, leg. Kovács, 1957 — Text Fig. 7B, C; loc. Osa, Hungary, leg. Kovács, 1957 — Text Fig. 7D).

The frontoparietale and the incassatio frontoparietalis are similar to the previously described brown ranid species. In some cases (Text Fig. 7 B) the incassatio frontoparietalis can be very indistinct.



Text Fig. 8. Examples of the incassatio frontoparietalis in *Rana iberica*.

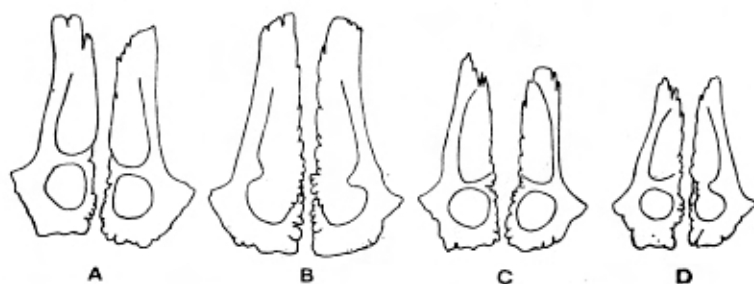
Rana iberica Boul. (Text Fig. 8)

Five specimens were examined (1 ♂, 4 ♀♀: loc. Arroyo de San Juan, Villa Franca del Biergo, provincia de León, Spain, leg. Knoepfler, September 1976).

The lateral margin of the facies cerebralis anterior is directed toward the margo anterior. In most cases, however, it does not reach the margo. Either this part of the incassatio frontoparietalis ends rostrally in a distinct arch-like border (a specific character of this taxon — see Text Fig. 8 A, B), or the lateral margin of facies cerebralis anterior becomes rostrally indistinct. The facies cerebralis anterior in the rostral part projects internally, the margin being very acute, but in the caudal part it is depressed and lacks a rounded projecting border, as in *Rana temporaria*, except on the medio-caudal margin of facies cerebralis anterior.

The facies cerebralis posterior is oval-shaped and surrounded by a rounded and projecting margin. The remainder is depressed to the level of the surrounding bone.

When compared with the entire *incrassatio frontoparietalis*, *spatium interfaciale* is relatively narrow. In some specimens the anterior and posterior parts of the pattern closely touch or are connected by a bridge. This phenomenon need not occur symmetrically (see Text Fig. 8 C).



Text Fig. 9. Examples of the *incrassatio frontoparietalis* in *Rana macrocnemis*.

Rana macrocnemis Boul. (Text Fig. 9)

Four specimens were examined (4 ♂♂: loc. Azau, Caucasus, leg. Lipenský, July 1974).

The caudal part of the facies cerebralis anterior is depressed and separated from the *spatium interfaciale* either by a rounded ridge (as is the case with brown ranids) or by a sharp ridge. The facies cerebralis posterior projects into the endocranium openings, and the margin is sharp. The lateral part of facies cerebralis posterior is concave, the medial part is flat.

In two of the four investigated specimens both parts of the *incrassatio frontoparietalis* would be probably connected either symmetrically or only on one side. This connection can be so extensive that the *taenia tecti transversalis* of the endocranium is developed only slightly laterally (see Text Fig. 9 B).

Rana graeca Boul. (Text Fig. 10)

Two specimens were examined (1 ♂, 1 ♀: loc. Pirin, Bulgaria; precise locality not available, collections of the National Museum, Prague).

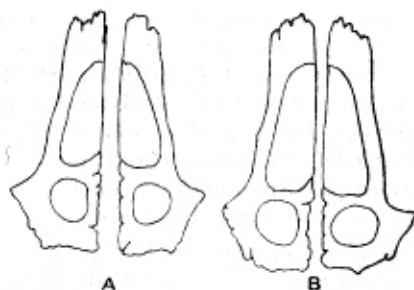
The facies cerebralis anterior is distinct rostrally and the margin terminates at the *margo sagittalis*. Caudally it is slightly depressed and can transcend without any border into the lateral part of the *spatium interfaciale* (Text Fig. 10 A).

The facies cerebralis posterior is projecting internally, and has a reticulation of grooves on its surface.

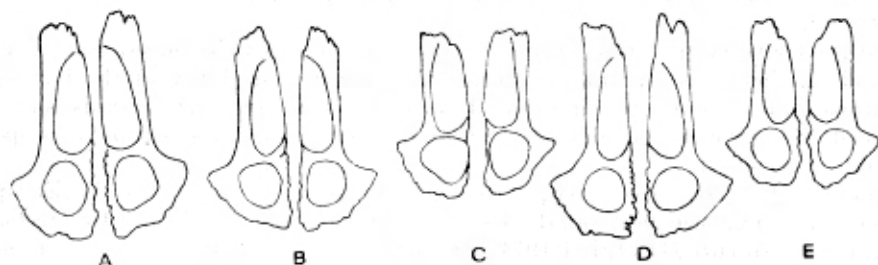
Rana latastei Boul. (Text Fig. 11)

Five specimens were examined (2 ♀♀; the other 3 were eviscerated: loc. Como, Italy, leg. Pozzi, 1977).

The *incrassation* is typical of other taxa of brown ranids. Specific features are: depression of the caudal part of facies cerebralis anterior is bordered laterally, caudally and medio-caudally by a sharp ridge, slanting inwards. A similar sharp ridge forms the margin of facies cerebralis posterior forming a cup-like concavity. These features, however, are not equally conspicuous in all specimens and cannot be used as diagnostic characters for the species of brown ranids.



Text Fig. 10. Examples of the incrassatio frontoparietalis in *Rana graeca*.



Text Fig. 11. Examples of the incrassatio frontoparietalis in *Rana latastei*.

DISCUSSION

The above observations reveal that the incrassatio frontoparietalis of green ranids markedly differs from that of brown ranids. Differences are: (i) The lateral margin of the facies cerebralis anterior is straight or slightly bent in green ranids, directed rostro-medially, and terminates at the margo sagittalis. In all species of brown ranids the lateral margin is directed toward the margo anterior where it either terminates or becomes indistinct. In several individuals of different species it is sharply bent (often at an angle less than 90° — see Text Fig. 8 A, B, C and Text Fig. 10). To generalize, the outline of the rostral part of the incrassatio frontoparietalis is approximately triangular in green ranids, while in brown ranids it is approximately oblongated. (ii) In all species of brown ranids, the facies cerebralis anterior projects internally and the margin is sharply defined. In the caudal part it is depressed, and separated from the spatium interfaciale by a rounded projecting ridge. In both species of green ranids this part of the incrassation is differently shaped, as is described in the following text.

Both species of green ranids are conspicuously different in frontoparietal incrassation. In *Rana esculenta* the facies cerebralis anterior is slightly indented into the frontoparietale, and has a rounded margin. The facies cerebrales posteriores are oval-shaped. The facies cerebralis anterior in *Rana ridibunda* is flat or even slightly convex, projecting away from the level of the surrounding bone. In some specimens this part becomes inconspicuous or lacking. The facies cerebrales posteriores are irregularly shaped with broken outlines. The incrassatio frontoparietalis in the *Rana esculenta lessonae* does not differ from that in the nominate form.

The differences between the different brown ranid species are not great, and the range of variation of frontoparietal incrassations is so wide that it is difficult to find

diagnostic characters. Therefore, *Rana temporaria*, *Rana dalmatina*, *Rana arvalis* (including *Rana arvalis wolterstorffi*) and *Rana macrocnemis* cannot be distinguished from each other. In some individuals of *Rana iberica* the facies cerebralis anterior is conspicuously bordered rostrally where the lateral margin sharply bends and terminates on margo sagittalis. The only diagnosable species is *Rana graeca* which has a reticulation on the surface of facies cerebralis posterior. Unfortunately, I had only two specimens at my disposal making this conclusion unreliable. *Rana latastei* had a distinct morphology for most but not all specimens.

When hypothesizing the phylogeny of the European ranids on the basis of the incrassatio frontoparietalis, we must argue that both species of green ranids had to speciate much sooner than the several geographical populations of brown ranids which are considered by some to be good species. It results from the considerable differences between the incrassatio frontoparietalis in *Rana esculenta* and *Rana ridibunda*.

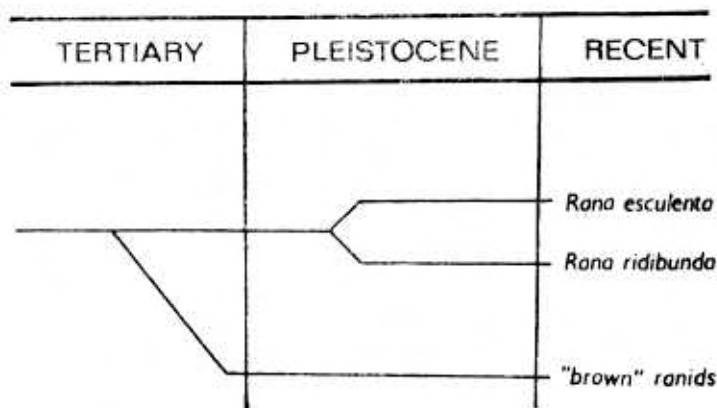
On the contrary the brown ranids, although forming a well defined group, cannot be well distinguished specifically owing to the wide variability of the incrassatio frontoparietalis. In my opinion the European species of brown ranids have not reached the sufficient genetic isolation, and their taxonomical status as a species should be reviewed.

These facts enable us to reconstruct the phylogenetic history of the European ranids. Although the first ranid fossils are known from the Upper Cretaceous of Africa (Vergnaud-Grazzini 1974), the first known European ranid is from the Lower Eocene, *Rana plicata* Filhol, 1876/7. The newly described *Rana trausisi* from the Upper Pliocene of Willershausen (German Federal Republic) (Špinar, in press) possesses characters of both green and brown ranids. Špinar (l. cit.) considers this fossil a representative of the common ancestor of the ranids from which developed the two species of green ranids and later all forms of brown ranids. However, according to Terentjev (1950), the Oligocene *Rana aquensis* Coq. is supposedly a typical representative of the green ranids. The ancestors of European ranids may have been morphologically more similar to green ranids and the divergence of green and brown ranids has resulted in greater morphological change in the brown ranid lineage (Text Fig. 12). Undoubtedly, two main groups evolved: green and brown ranids (in the literature they sometimes are named *Rana esculenta* species group and *Rana temporaria* species group). Fossils of brown ranids are younger, suggesting that the brown ranids split off the main green ranid lineage sometime between the Miocene and the end of the Tertiary. In the Recent, both groups are distinguished morphologically and ecologically, and their species are reproductively isolated.

Rana esculenta and *Rana ridibunda* are well-defined species on the basis of incrassatio frontoparietalis as well as by other morphological and osteological characters and to a certain extent also ecologically. The reproductive isolation, however, does not prevent mutual breeding. As for *Rana esculenta lessonae*, the incrassatio frontoparietalis, other morphological characters and its ecology suggest that this taxon is only an ecological variant and not a subspecies.

As for single forms of brown ranids, considered species in the literature, it can be stated that some of them are more ancient (e.g. *Rana graeca*), better defined morphologically and ecologically, and others are of younger age, and less genetically isolated. It was mentioned above that only one or two forms differ markedly from the basic incrassatio frontoparietalis. Therefore, it can be supposed that Recent forms of European brown ranids are much younger than the forms of green ranids.

The question arises, whether there is adequate ground for classifying these forms as species. Not only the results of study of the *incrassatio frontoparietalis*, but also the instability and wide variability of other morphological characters and insufficient degree of reproductive isolation contradict such classification.



Text Fig. 12. Hypothesized phylogeny for the ranids of Europe.

SUMMARY

1. Three basic types of the *incrassatio frontoparietalis* can be distinguished in European representatives of the family Ranidae: *Rana esculenta* type, *Rana ridibunda* type and a type common to all species of brown ranids (with the exception of *Rana graeca*, for which insufficient information was available).

2. The major differences are found in the rostral part of the *incrassatio*.

3. No sexual dimorphism was ascertained for this character.

4. Some specimens have an anomalously shaped *incrassatio* as the rostral and caudal parts are fused together in various degrees.

5. On the basis of the *incrassatio frontoparietalis* and other taxonomically important characters we hypothesize that the lineage of green ranids has been the main stem, from which the lineage of brown ranids diverged at the end of Tertiary. Both species of European green ranids are more ancestral than the species of brown ranids, whose taxonomic status should be reviewed.

Acknowledgement

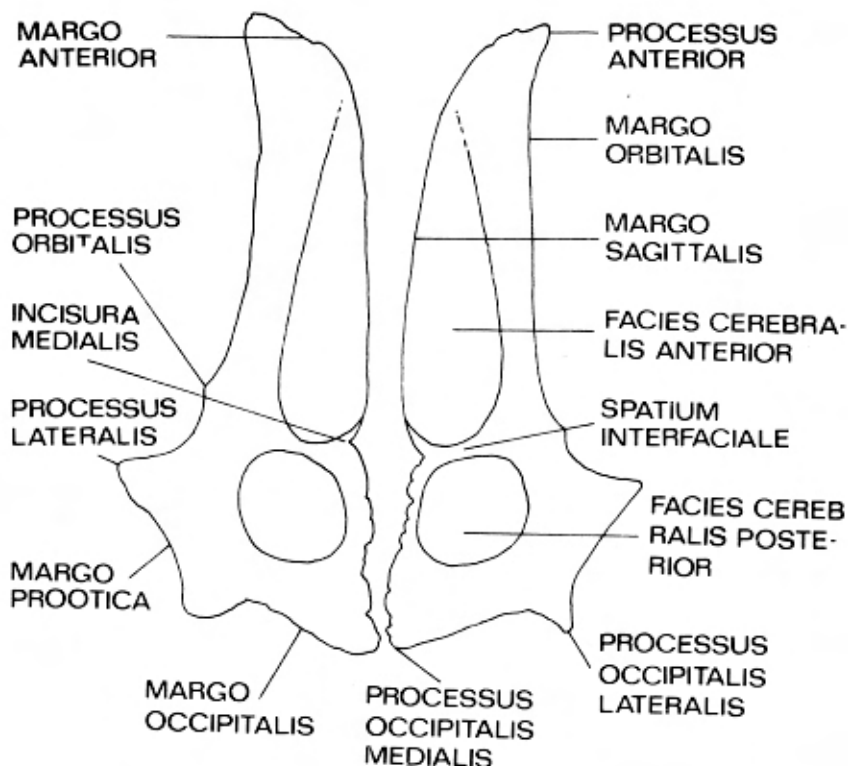
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LITERATURE CITED

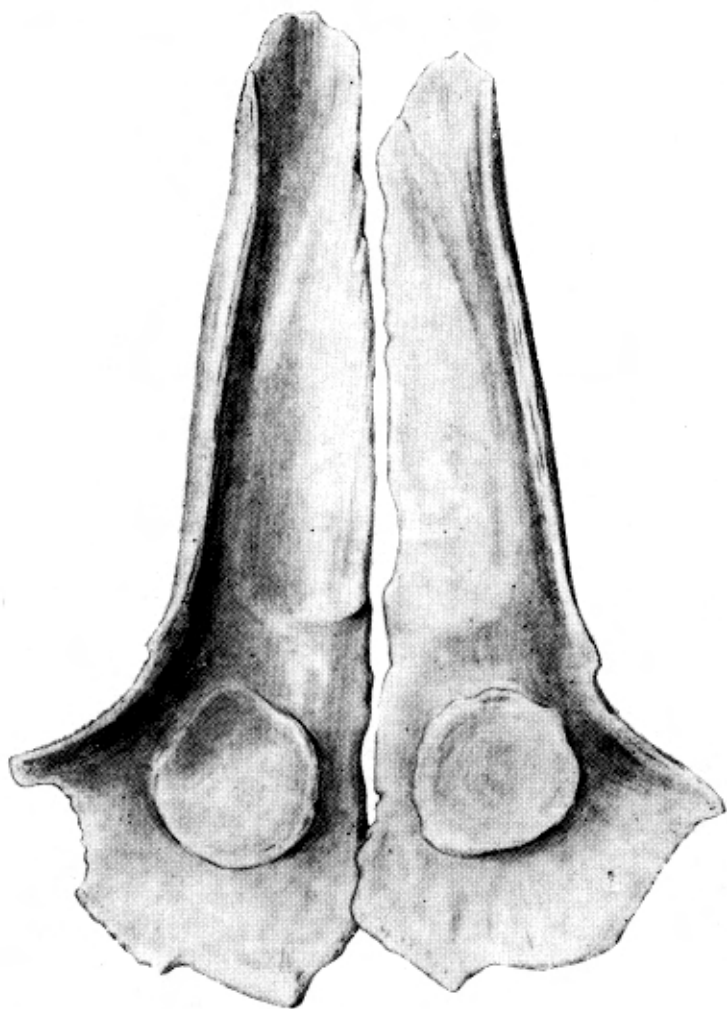
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The Text figure 1 and the Plate figures 1—3 will be found at the end of this issue.

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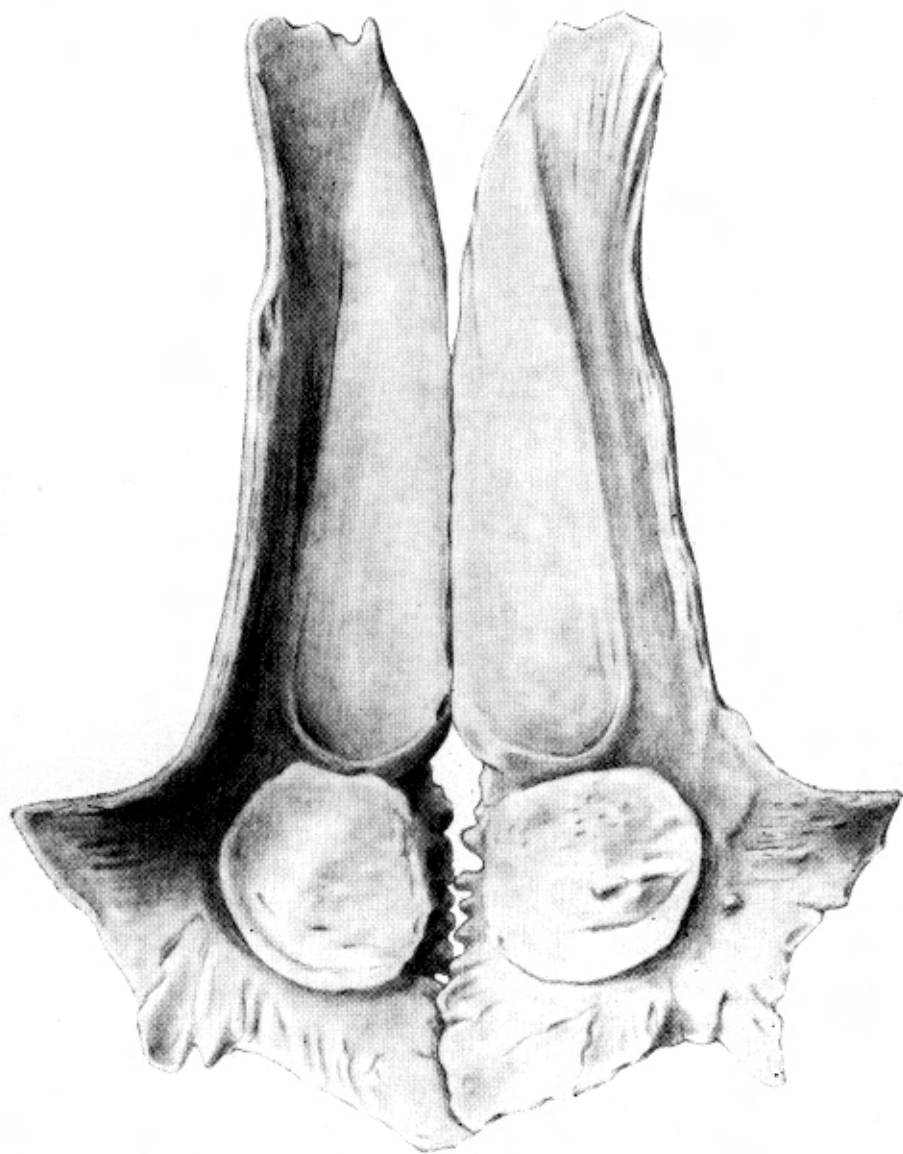
Text Fig. 1. Ventral surface of the frontoparietals of generalized ranid, together with a terminology for the increasatio frontoparietalis.



Pl. Fig. 1. The *incrassatio frontoparietalis* type of *Rana esculenta*.



Pl. Fig. 2. The *incrassatio frontoparietalis* type of *Rana ridibunda*.



Pl. Fig. 3. The *incrassatio frontoparietalis* type common to brown ranids.