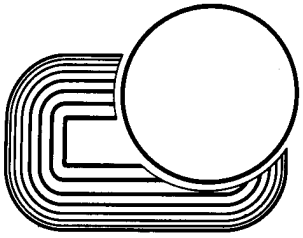

TAXONOMY AND DISTRIBUTION OF TERTIARY DISCOGLOSSIDS (ANURA) OF THE GENUS *LATONIA* V. MEYER, 1843

ZBYNĚK ROČEK

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ABSTRACT

Definition of the genus *Latonia* v. MEYER, 1843 (Anura, Discoglossidae) and description of all its known skeletal elements are given. Taxonomic revision based on both articulated skeletons and disarticulated bones from the Late Oligocene to Pliocene deposits of various European localities revealed that *Prodiscoglossus vertaizoni* FRIANT, 1944 is in fact the earliest known *Latonia* identical with that from the French locality Coderet, both of the Late Oligocene age. The Miocene representatives of the genus, namely *Latonia seyfriedi* v. MEYER, 1843, *L. gigantea* (LARTET, 1851), *L. ragei* HOSSINI, 1993, and *Latonia* sp. have been widely spread in western, central, and eastern Europe. General evolutionary trends that can be recognized in the Miocene and Pliocene material are appearance of the secondary dermal sculpture on the maxillae in some species, and gigantism. Summary of evolution within the genus *Latonia* and a revised description of the holotype of *L. seyfriedi* and all other known material from the type locality Öhningen (including a newly discovered specimen) are given. It was confirmed that *Discoglossus giganteus* WETTSTEIN-WESTERSHEIMB, 1955 and *Pelobates robustus* BOLKAY, 1913 are synonyms of *Latonia*, and the same holds (besides mentioned "*Prodiscoglossus*" *vertaizoni*) also for *Diplopelturus ruscinensis* DEPÉRET, 1890. *Latonia fejfari* (ŠPINAR, 1975) and *L. kolebabi* ŠPINAR, 1976 are synonyms of *L. gigantea*. Since *L. gigantea* and *L. ragei* were described on the basis of disarticulated bones (the principal diagnostic character being presence or absence of sculpture on the maxilla), whereas *L. seyfriedi* was based on articulated skeletons embedded by their dorsal side in matrix, the taxonomic relations among these three forms remain unsolved until chemical preparation of the latter holotype will be possible. Available data on the geographic and stratigraphic distribution are summarized and discussed (together with structural evolution within the genus) on the background of the palaeogeographic and palaeoclimatic situation in Europe during the Neogene.

KEY WORDS : AMPHIBIA, ANURA, TERTIARY, EUROPE, EVOLUTION, PALAEOGEOGRAPHY.

RÉSUMÉ

La définition du genre *Latonia* v. MEYER, 1843 (Anura, Discoglossidae) et une description de tous les éléments squelettiques connus sont données. Une révision taxonomique, basée sur les squelettes articulés et sur les os isolés provenant de divers gisements européens allant de l'Oligocène supérieur au Pliocène, montre que *Prodiscoglossus vertaizoni* FRIANT, 1944 de l'Oligocène supérieur est, en fait, le plus ancien *Latonia*; il est identique à celui de Coderet, autre gisement français de l'Oligocène supérieur. Au Miocène, les représentants du genre, c'est-à-dire *Latonia seyfriedi* v. MEYER, 1843, *L. gigantea* (LARTET, 1851), *L. ragei* HOSSINI, 1993, et *Latonia* sp. étaient largement répandus en Europe occidentale, centrale et orientale. Les tendances évolutives générales qui peuvent être reconnues sur le matériel du Miocène et du Pliocène sont l'apparition d'une sculpture secondaire dermique sur le maxillaire, chez certaines espèces, et le gigantisme. L'évolution au sein du genre *Latonia* est brièvement exposée. Une description révisée de l'holotype de *L. seyfriedi* et de tous les autres spécimens connus de Öhningen, la localité-type (qui inclut un fossile récemment découvert) est fournie. Il est confirmé que *Discoglossus giganteus* WETTSTEIN-WESTERSHEIMB, 1955 et *Pelobates robustus* BOLKAY, 1913 sont synonymes de *Latonia*, ce qui est vrai aussi, outre "*Prodiscoglossus*" *vertaizoni* déjà mentionné, pour *Diplopelturus ruscinensis* DEPÉRET, 1890. *Latonia fejfari* (ŠPINAR, 1975) et *L. kolebabi* ŠPINAR, 1976 sont synonymes de *L. gigantea*. Comme *L. gigantea* et *L. ragei* ont été décrits sur la base d'os isolés (le principal caractère diagnostique étant la présence ou l'absence de sculpture sur le maxillaire), alors que *L. seyfriedi* a été basé sur des squelettes articulés dont la face dorsale est

engagée dans le sédiment, les relations taxonomiques entre ces trois formes restent indéterminées en attendant qu'une préparation chimique de l'holotype de *L. seyfriedi* soit possible. Les données disponibles sur la distribution géographique et stratigraphique sont résumées et discutées (ainsi que l'évolution structurale dans le genre) en tenant compte de la situation paléogéographique et paléoclimatique en Europe pendant le Neogène.

MOTS-CLÉS : AMPHIBIA, ANURA, TERTIAIRE, EUROPE, ÉVOLUTION, PALÉOGÉOGRAPHIE.

INTRODUCTION

Since 1843 when H. von Meyer established the genus *Latonia* based on an articulated skeleton exposed by its ventral side (Fig. 1 ; v. Meyer 1845, tab. 4), a considerable number of large anurans was described (or their occurrence reported) under various names. Disregarding those which were erroneously assigned to *Rana* without any taxonomic analysis (*Rana gigantea* LARTET 1851), and to the Pelobatidae because of sculpture (*Miopelobates zapfei* WETTSTEIN-WESTERSHEIMB, 1955, *Miopelobates fejfari* ŠPINAR, 1975, and perhaps also *Archipelobates giganteus* K. TATARINOV, 1970), all were referred to the Discoglossidae. Except the first form (*Latonia seyfriedi* v. Meyer, 1843), all others were described on the basis of isolated bones. Disarticulated and incomplete material provided another sort of information than the holotype of *L. seyfriedi*, and this prevented their direct comparison. This is why some authors decided to describe their findings only as "large discoglossids", others (Sanchíz & Mlynarski 1979) referred all findings to *L. seyfriedi*. However, recent studies by Hossini (1992, 1993) and Rage & Hossini (in press) revealed that there were at least two large and distinct forms of *Latonia* occurring in the Tertiary of Europe. The question arose which are their relations to *Latonia seyfriedi*, as well as to other material of *Latonia* reported under various names from numerous European sites.

SYSTEMATIC PART

DISCOGLOSSIDAE Günther, 1854

Diagnosis based on skeletal characters - Praemaxilla, maxilla and vomer dentate, dentary edentate ; 8 praesacrals with opisthocoelous centra and imbricated neural arches ; atlas free ; sacral vertebra with transverse processes moderately dilated and inclined posteriorly ; sacro-urostylar articulation mono- (*Barbourula*) or bicondylar; urostyle with one pair of transverse processes that can be rarely accompanied by an additional, rudimentary pair ; free ribs on V2-V4 also in adults ; shoulder girdle arciferous ; scapula short, partly covered anteriorly with clavicle ; fossa cubitalis humeri shallow ; sternal complex triradiate ; proximal part of tibiofibula on cross-section consisting of 2 elliptic bones fused with one another, the long axes of both being parallel (mainly after Hossini 1992 ; Rage & Hossini in press).

Remarks - Since *Bombina* was ascertained to be a paedomorphic discoglossid (Smirnov 1989), separation of the family Bombinidae from the Discoglossidae seems to be unjustified. Similarly unjustified is the independent family Latoniidae Špinar, 1978 because the genus *Latonia* shares many characters with *Discoglossus*, more than with *Alytes* and *Bombina*.

LATONIA v. MEYER, 1843

1843 - *Latonix* (ex err.) - v. Meyer, p. 396.
1843 - *Latonia* - v. Meyer, p. 579.
1851 - *Rana* (partim) - Lartet, p. 41.
1890 - *Diplopelturus* - Depéret, p. 172.
1913 - *Pelobates* (partim) - Bolkay, p. 217.
?1941 - *Palaeopelobates* - Kuhn, p. 360.
?1941 - *Archaeopelobates* - Kuhn, p. 362.
1944 - *Prodiscoglossus* - Friant, p. 562.
1955 - *Discoglossus* (partim) - Wettstein-Westersheimb, p. 808.
1955 - *Miopelobates* - Wettstein-Westersheimb, p. 812.
?1970 - *Eopelobates* (partim) - Estes, p. 305.
1975 - *Miopelobate* (ex err.) - Špinar, pl. 1, figs 3,4.
1975 - *Neusibatrachus* (partim) - Špinar, p. 62, Fig. 5.

Species typica - *Latonia seyfriedi* v. Meyer, 1843, by monotypy.

Diagnosis (see also Hossini 1992 ; Rage & Hossini in press ; Špinar 1978) : snout-vent length up to about 200 mm ; skull moderately wider than long ; frontoparietal fused in both adults and youngs (trace of median suture being visible on inner surface of anterior part of bone), foramen parietale sometimes present, no foramina pro aa. occipitales, frontoparietal incrassation consisting of two parts (elongated anterior and circular posterior) ; teeth along posterior margin of vomer; 2 coronoid processes on praearticular, distinct recess on bottom of sulcus cart. Meckeli at

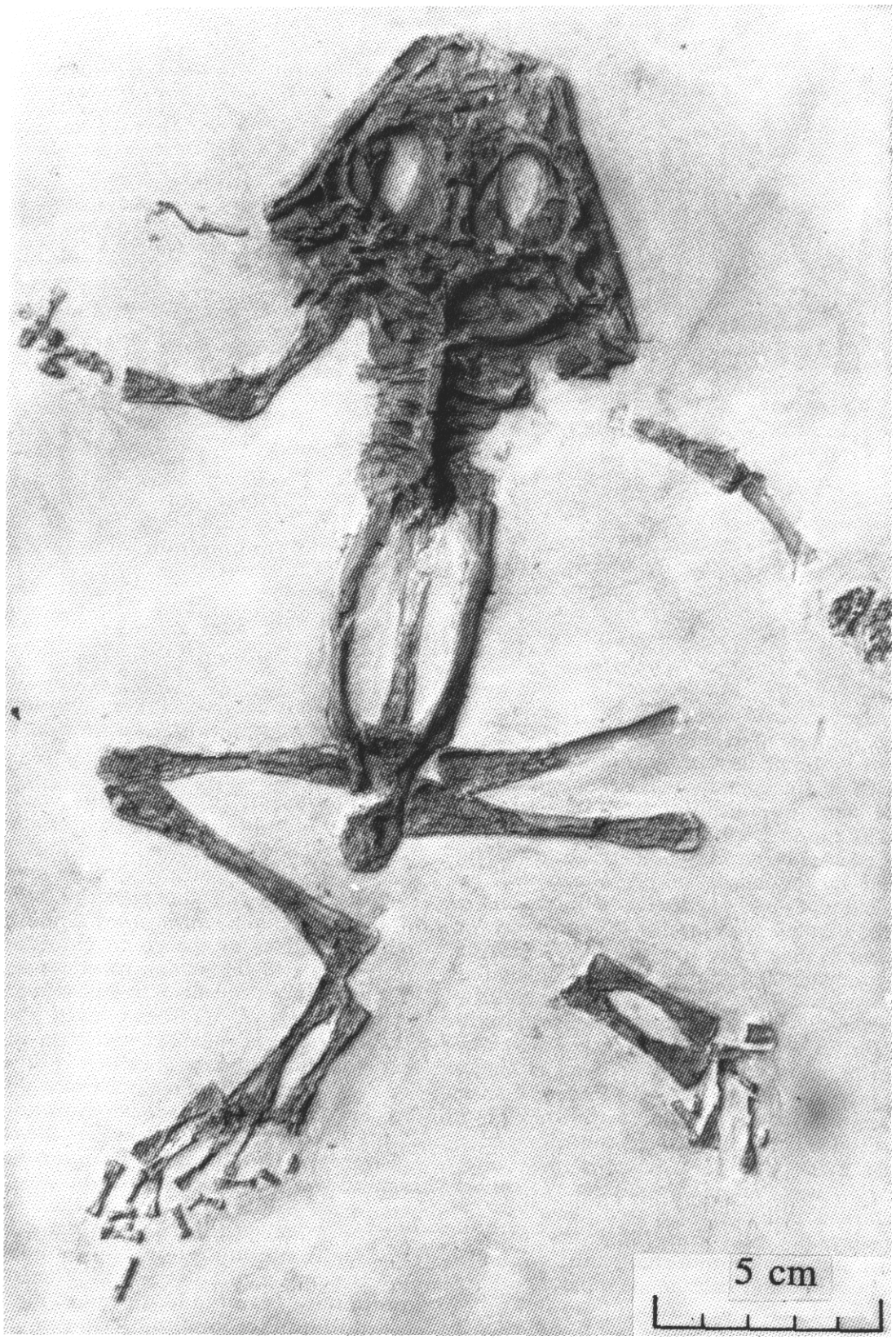


Figure 1 - ***Latonia seyfriedi*** v. MEYER, 1843, holotype. Middle Miocene (Astaracian), Öhningen. Staatliches Museum für Naturkunde Karlsruhe, uncatalogued. See also v. Meyer (1845, tab. 4). *Holotype, Miocène moyen (Astaracien), Öhningen, sans numéro de catalogue. Voir aussi v. Meyer (1845, planche 4).*

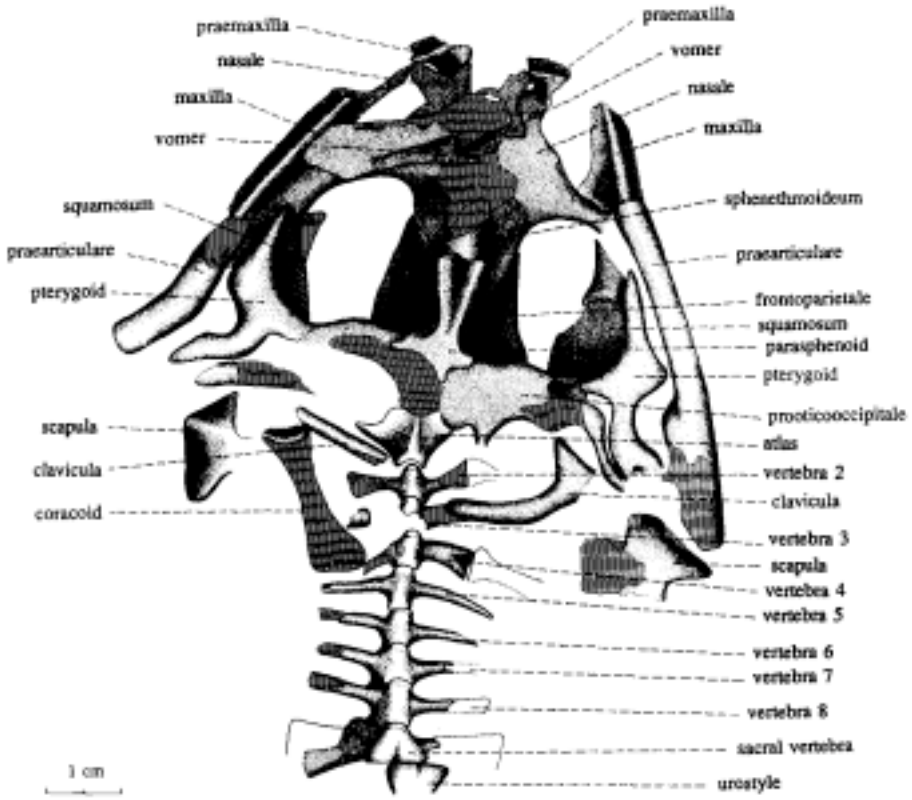


Figure 2 - ***Latonia seyfriedi*** v. MEYER, 1843, holotype. Skull and axial skeleton in ventral view. Middle Miocene (Astaracian), Öhningen. Staatliches Museum für Naturkunde Karlsruhe, uncatalogued. Hatched is broken bone, white areas are imprints in matrix. *Vue ventrale du crâne et du squelette axial. Miocène moyen (Astaracien), Öhningen. Sans numéro de catalogue. Hachuré : surface cassée, en blanc : empreinte des os.*

level of proc. coronoideus ; proc. pterygoideus maxillae slender and long, large depression on the inner posterior part of maxilla ; prooticooccipital with distinct supracondylar depression on occipital part, prominentia ducti semicircularis posterioris running out in prominent ridge ; surfaces of contact between frontoparietal, parasphenoid and sphenethmoid, and frontoparietal, parasphenoid and prooticooccipital distinctly and irregularly striated ; transverse processes on V2-V4 dilated at their ends and articulated (or fused in some individuals) with ribs ; atlas usually (but not always) with median keel on its ventral surface ; shape of lateral crista on humerus as in Fig. 17, crista ventralis prominent and not extending up to proximal end of bone, caput humeri shifted laterally ; crista ossis ilii thin with sharp edge declined dorsomedially, upper margin of pars ascendens ossis ilii makes an angle approximatively 120° with pars cylindriformis, upper margin of acetabulum terminates posteriorly with marked and nearly pointed elevation ; femur S-shaped, with short keel not reaching proximal end of bone, and shorter than tibiofibula ; astragalus and calcaneum different in size and not fused.

Description of general structural scheme : Prooticooccipital (Fig. 5 ; see also Špinar 1978, pl. 66) does not differ substantially from that in *Discoglossus*, however, typical features of both genera are better pronounced in *Latonia*. The dorsal part of the bone (called the ramus lateralis by Špinar 1978) is slender, moderately increasing in width towards the crista parotica. The crista is V-shaped, with its anterior branch (proc. prooticus rostralis brevis *sensu* Špinar 1978) shorter, and the posterior branch (proc. prooticus caudalis longus *sensu* Špinar 1978) longer. The shape of the crista parotica no doubt corresponds to the ramus paroticus squamosi ; however, the latter element still remains unsufficiently investigated. The contact area for the frontoparietal is indented and striated (compare corresponding contact area in the frontoparietal in Fig. 7G ; pl. 1-6), sometimes with thin but prominent partitions separating furrows and grooves, directed towards the tectum synoticum (see also Špinar 1978, pl. 66b). The prominentia ducti semicircularis posterioris (crista prootica posterior *sensu* Špinar 1978) is prominent as an extensive thin lamina (Fig. 5) terminated by a knob, and similar knob may be (but not necessarily is) on its dorsal end. There is a thin horizontal lamina running from the lower end of the lamina towards the crista parotica. On the anterior surface of the bone is rather prominent elevation devoid of periost. This is the contact area for the palato-

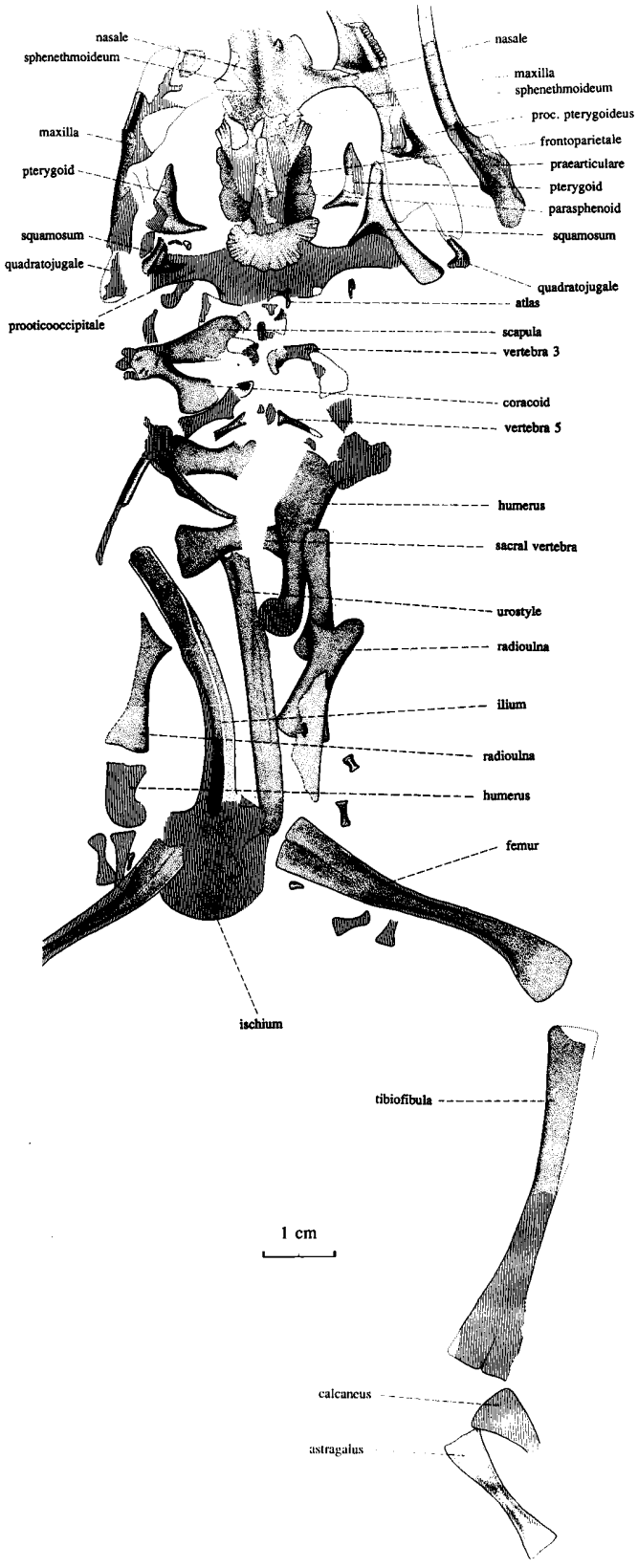


Figure 3 - ***Latonia seyfriedi*** v. MEYER, 1843. Whole specimen in ventral view. Middle Miocene (Astaracian), Öhningen. Paläontologisches Institut der Universität Zürich, coll. no. A II 28. Hatched is broken bone, white areas are imprints in matrix. *Spécimen complet en vue ventrale. Miocène moyen (Astaracien), Öhningen. Hachuré : surface cassée, en blanc : empreinte des os.*

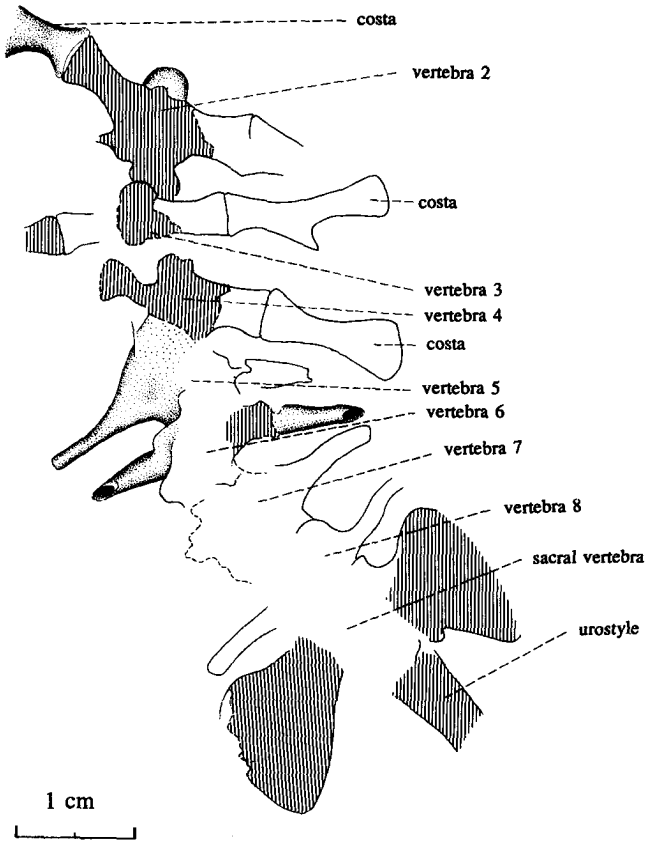


Figure 4 - ***Latonia seyfriedi*** v. MEYER, 1843. Vertebral column in ventral view. Middle Miocene (Astaracian), Öhningen. Paläontologisches Museum der Universität Zürich, coll.No. A II 27. Hatched is broken bone, white areas are imprints in matrix. See also v. Meyer (1845, tab. 6, Fig. 1). *Colonne vertébrale en vue ventrale. Miocène moyen (Astaracien), Öhningen. Hachuré : surface cassée, en blanc : empreinte des os. Voir aussi v. Meyer (1845, planche 6, fig. 1).*

quadrate (Špinar 1978 termed it the crista prootica anterior). Its ventral margin was adjoined by the ramus interior pterygoidei. Immediately dorsal to this elevation is a horizontal groove (sulcus venae jugularis), sometimes partly roofed. Its medial end may be even overbridged in some individuals (Fig. 5B) which results in formation of a short canal. Between the medial end of the sulcus and the foramen prooticum is a small foramen, most probably for the cranial nerve VI.

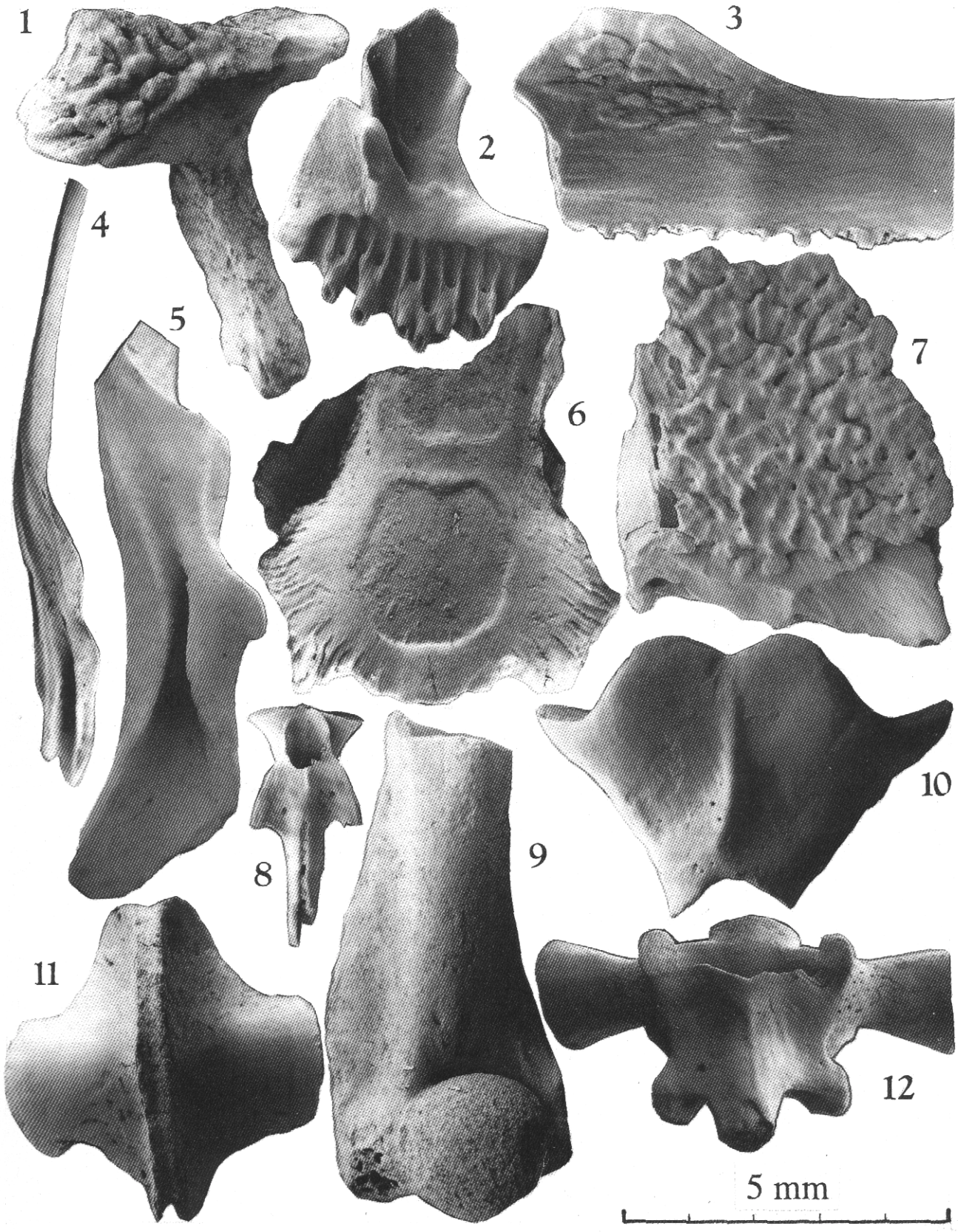
Sphenethmoid (Fig. 6A) - Its dorsal surface (tectum nasi and lamina supraorbitalis) is flat, with anterior-posterior striation corresponding to that on the adjoining contact surface of the frontoparietal (Fig. 7E). Similar striation is on the ventral surface of the bone, indicating the contact area for the pars medialis parasphenoidei. The lamina supraorbitalis seems to be extensive, and its anterolateral margin may vary in shape, in accordance with the extent of cartilage that completed the postnasal wall and the lamina in living animals. There was probably rather sharp transition between ventral and lateral surfaces of the bone. Parahyoid ossifications are preserved in the paratype of *L. vertaizoni* (see Fig. 19).

Praemaxilla (Fig. 8A-C, pl. 1-2 ; see also Bolkay 1913, pl. 11, Fig. 2 ; Mlynarski *et al.* 1982, Fig. 6) is smooth on its outer surface, with a deep recess on the inner side at the basis of the pars facialis (marked by an arrow in Fig. 8A). There is a low crista running on the inner surface of the pars facialis from its medial margin into this recess. The medial margin of the pars facialis is abruptly though not sharply bent, and correspondingly concave is its lateral margin. There is some variation in shape and extent of the pars palatina, and in presence or absence of the recessus marsupiatus on the outer surface lateral to the basis of the pars facialis. However, since the material available is limited one cannot say whether this is due to intra- or interspecific variation.

Maxilla (Figs 9-11, pl. 1-3 ; see also Bolkay 1913, pl. 11, Fig. 1 ; Špinar 1975a, Fig. 4a) - The processus posterior is always prominent though there seems to be certain variation in its posterior and medial extent. Characteristic is the posterior depression on the inner surface of the bone below the processus zygomaticomaxillaris, but the depression is delimited anteriorly by variously expressed ridge. Also the groove for the palatoquadrate bar may be either deep or shallow, and the same holds for the recess containing the processus maxillaris anterior palatoquadrati in living animals. The tooth row extends posteriorly beyond the lamina horizontalis. The long proces-

PLATE 1

Latonia gigantea (LARTET, 1851). Middle Miocene (Sarmatian), Gritsev. **1**, left squamosum (ZIK 3341). **2**, right praemaxilla in inner view (ZIK 3300). **3**, posterior section of right maxilla (ZIK 3308). **4**, left praearticular of young individual (ZIK 3317). **5**, left praearticular of medium-sized individual (ZIK 3332). **6**, frontoparietal in ventral view (ZIK 3339). **7**, frontoparietal in dorsal view (ZIK 3306). **8**, urostyle of young individual (ZIK 3315). **9**, left humerus (ZIK 3324). **10**, atlas in ventral view (ZIK 3301). **11**, ischia (ZIK 3318). **12**, V3 in dorsal view (ZIK 3305). *Miocène moyen (Sarmatien), Gritsev. **1**, squamosal gauche. **2**, prémaxillaire droit en vue interne. **3**, partie postérieure du maxillaire droit. **4**, préarticulaire gauche d'un individu jeune. **5**, préarticulaire gauche d'individu de taille moyenne. **6**, frontopariétal en vue ventrale. **7**, frontopariétal en vue dorsale. **8**, urostyle d'un individu jeune. **9**, humérus gauche. **10**, atlas en vue ventrale. **11**, ischia. **12**, en vue dorsale.*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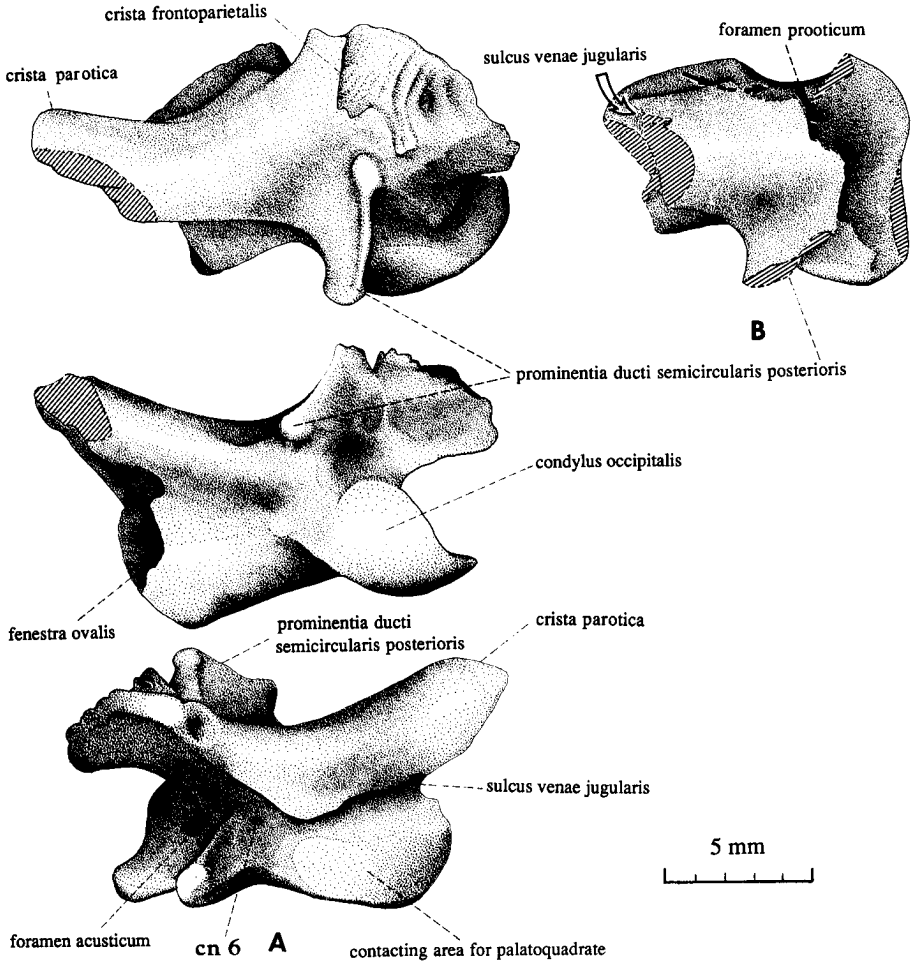


Figure 5 - **A, *Latonia gigantea*** (LARTET, 1851). Left prooticooccipital in dorsal (above), posterior (middle), and anterior (below) views. Middle Miocene (Astaracian), La Grive St. Alban (MNHN LGA 1193). **B, *Latonia ragei*** HOSSINI, 1993. Left prooticooccipital in dorsal view. Black broken arrow is canal on medial end of sulcus venae jugularis, cn 6 is orifice of canal for 6th cranial nerve. Lower Miocene (Agenian), Laugnac (Paris 6, LG 2011). See also Spinar (1978, pl. 64). *Prooticooccipital gauche en vue dorsale (en haut), postérieure (au centre), et antérieure (en bas). Miocène moyen (Astaracien), La Grive St. Alban. Prooticooccipital gauche en vue dorsale. La flèche noire en ligne interrompue représente un canal dans la partie médiane du sulcus venae jugularis, cn6 est un orifice du canal pour nerf crânien VI. Miocène inférieur (Agénien), Laugnac. Voir aussi Spinar (1978, pl. 64).*

sus posterior was present in living animals but it is nearly always broken off in isolated fossil maxillae. The processus zygomaticomaxillaris is low, with its upper margin horizontal and straight. The margo orbitalis is smooth, only within its anterior section close to the processus palatinus is a groove (sulcus nasolacrimalis). There is usually an edge running down from the processus palatinus on its medial surface, either joining the lamina horizontalis or separated from its margin by a wide groove. Anterior to the latter process is usually a depression called the fossa maxillaris. The lamina horizontalis continues anteriorly by a lowering edge running from its end towards the anterior margin of the bone. Dorsal to the edge is usually a triangular area (wide anteriorly and tapering posteriorly) ; this is the contact area for the praemaxilla. Hence, the lamina anterior maxillae adjoined this bone laterally in a considerable extent. This is also evidenced by the toothless portion of the lamina anterior. The outer surface of the maxilla is smooth or covered with sculpture, the latter being separated from the compact bone by a framework of irregularly perforated bone so that it can be easily broken off in some fossils. This, together with the fact that in young individuals the sculpture is rudimentary or the bone is nearly smooth (Fig. 11A) suggests that such sculpture is secondary, not primary as for instance in pelobatids. The presence or absence of sculpture on the maxilla indicates an evolutionary trend (see p. 33) and may be used as a taxonomic criterion.

Squamosal (Fig 2, 3, Pl. 1-1) is preserved in the specimens from Öhningen but it is only partially exposed or fragmentary. As can be judged by one isolated squamosal from Gritsev (Pl. 1-1), which was associated with *Latonia* on the basis of its sculpture, the lamella alaris was rather small. Long, horizontal and straight dorsal margin of the processus zygomaticomaxillaris maxillae suggests that morphology of the corresponding part of the lamella alaris squamosi was similar.

Quadratojugal (Fig. 3) was present and apparently fused with the quadrate in a hook-like element.

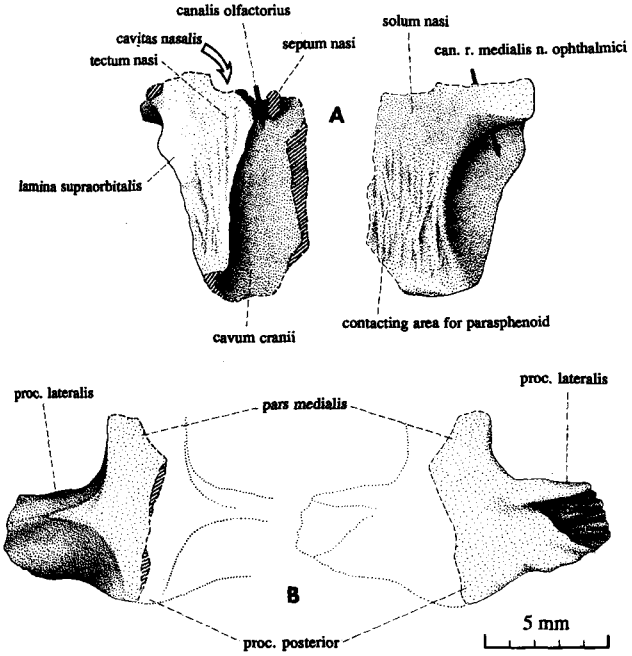


Figure 6 - ***Latonia gigantea*** (LARTET, 1851). **A**, sphenethmoid in dorsal (left) and ventral (right) views. Pliocene (Ruscinian), Ivanovce (DP FNSP 218a). **B**, parasphenoid in ventral (left) and dorsal (right) views. Pliocene (Ruscinian), Ivanovce (DP FNSP 219a). Dotted lines represent reconstructed parts. ***A**, sphénethmoïde en vues dorsale (à gauche), et ventrale (à droite). Pliocène (Ruscinien), Ivanovce. **B**, parasphenoïde en vues ventrale (à gauche) et dorsale (à droite). Pliocène (Ruscinien), Ivanovce. Les parties reconstituées soont indiquées par des lignes interrompues.*

Nasal (Figs 2, 3) - All preserved nasals are fragmentary and exposed by their ventral surface. Isolated nasals are extremely rare among the anuran fossil material, and difficult to assign taxonomically. This is why no precise information on this element in *Latonia* is available.

Frontoparietal (Fig. 7, Pl. 1-6,7 ; see also Špinar 1975a, Fig. 1a, pls I-II ; 1976a, Fig. 3 ; 1978, pls. 64, 65) - The pars contacta (which fixed the frontoparietal to the neural endocranium) is weakly expressed in the largest (hence the oldest) specimens (dotted line in Fig. 7F). In most individuals (not so large and thus younger) the pars contacta is thin and high. It continues anterolaterally in horns ("anterior horn" in Fig. 7) the dorsal surface of which is unsculptured. The anterior part of the frontoparietal incrassation is long and ovoid, deeper anteriorly than posteriorly. In large individuals (Fig. 7F) it is separated from the posterior part of the incrassation by an U-shaped ridge which is not confluent with the original margins of the pars contacta. This ridge is absent in young and medium-size individuals where anterior part of the frontoparietal incrassation is a simple depression, or this part of the incrassation is delimited by ridges only laterally (Fig. 7E). In some specimens (Fig. 7E) one may easily distinguish anterior part of the pars contacta (rough, with anteriorly directed furrows) which adjoined the sphenethmoid. The posterior part of the bone was high both in young and old individuals (Fig. 7C ; see also Špinar 1978, pl. 65c,d). There can be little foramina in the posterior surface of the bone, but they vary in number, position, and size and are thus of no diagnostic value (contrary to foramina for the aa.occipitales in *Pelobates*). For developmental changes see *Latonia gigantea*.

Vomer (Figs 2, 8D) - One vomer from Sansan may be associated with *Latonia* ; those on the holotype of *L. seyfriedi* are too crushed to be useful for description. Morphology of this tooth-bearing element may be seen in Fig. 8D.

Parasphenoid (Figs 2, 6B) - Its posterior margin runs out in a wide median convexity (processus posterior). Most of the ventral surface of the bone is flat or, as can be judged by condition in the holotype of *L. seyfriedi*, even depressed in the median part of the pars medialis. Posteriorly, this flat surface is clearly delimited by ridges coming from the lateral margin of the pars medialis and from the processus posterior. Both turn laterally and fuse with each other, but they do not reach the tip of the processus lateralis. On the inner surface of this lateral process, there is a triangular indented area with furrows directed laterally. This is the contact area for attachment to the ramus interior pterygoidei.

Pterygoid (Figs 2, 3, 8E ; see also v. Meyer 1845, tab. 6, Fig. 1) is best observable in Zürich specimen A II 27 but similar to other specimens it is embedded in matrix so its full shape cannot be ascertained. General proportions of the three rami can be seen in the illustrations. The ramus interior was probably slender and in contact with the lateral process of the parasphenoid. The ramus maxillaris was broader, and its morphology was in agreement with that of the posterior termination of the lamina horizontalis. The size and shape of the ramus posterior were in agreement with those of the processus posterolateralis squamosi that is, however, imperfectly preserved in few specimens available.

Praearticular (Fig. 12 ; Pl. 1-4, 5 ; see also Bolkay 1913, pl. 11, figs 3,4 ; Rage & Vergnaud-Grazzini 1972, pl. 1, Fig. 9 ; Špinar 1978, pl. 67) is characteristic by the diagnostic features of the genus (presence of two coronoid processes, distinct recess in the bottom of the sulcus for the Meckel's cartilage at the level of the coronoid pro-

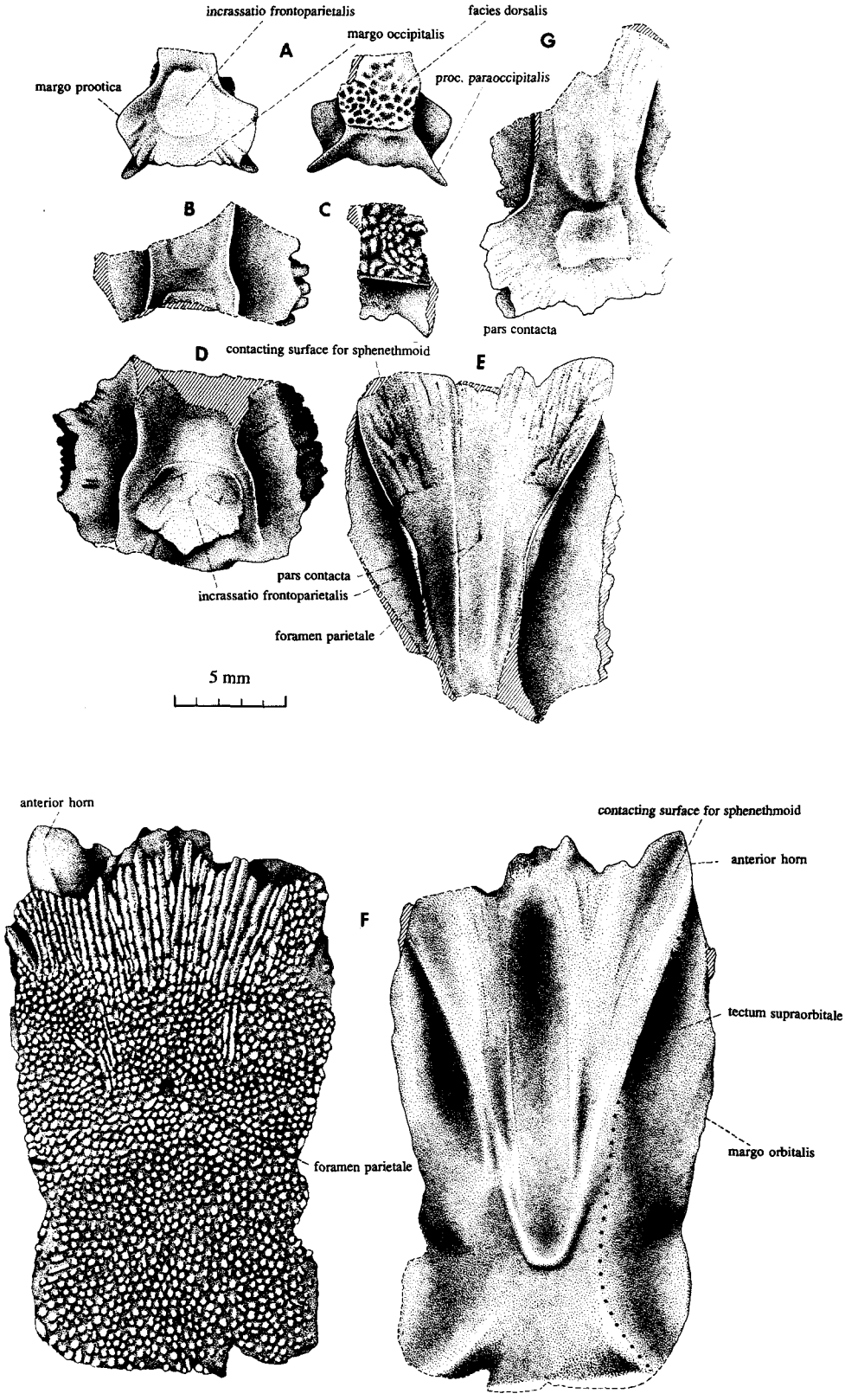


Figure 7 - **A-F**, development of frontoparietal in ***Latonia gigantea*** (LARTET, 1851) from Sansan (Middle Miocene, Astaracian). A, young individual, ventral (left) and dorsal (right) views (MNHN, Sa 13453). B, fragment of middle part of bone in ventral view (FSL 165.967). C, postero-dextral part of bone (FSL 165.976) corresponding in size to that in B. D, postero-medial part in ventral view (FSL 150.917). E, anterior part in ventral view (MNHN, Sa 13489). F, fully grown individual (neotypus ; MNHN, Sa 13448) in dorsal (left) and ventral (right) views. Heavy dotted line indicates margin of pars contacta. **G**, ***Latonia gigantea*** (LARTET, 1851), frontoparietal in ventral view. Middle Miocene (Astaracian), La Grive St. Alban (MNHN LGA 1194). Hatched is broken bone. See also Spinar (1978, pls 64, 65). ***A-F****, développement du frontopariétal de* ***Latonia gigantea*** *(LARTET, 1851) de Sansan, Miocène moyen, Astaracien).* ***A****, individu jeune, en vues ventrale (à gauche) et dorsale (à droite).* ***B****, fragment de la partie centrale d'un os en vue ventrale.* ***C****, partie droite postérieure d'un os de taille similaire à celui figuré en B.* ***D****, partie médiane postérieure en vue ventrale.* ***E****, partie antérieure en vue ventrale.* ***F****, individu adulte en vues dorsale (à gauche) et ventrale (à droite). La marge de la pars contacta est marquée par la ligne fortement pointillée.* ***G****,* ***Latonia gigantea*** *(LARTET, 1851), frontopariétal en vue ventrale. Miocène moyen (Astaracien). La Grive St. Alban. En hachuré : surface cassée. Voir aussi Spinar (1978, planches 64, 65).*

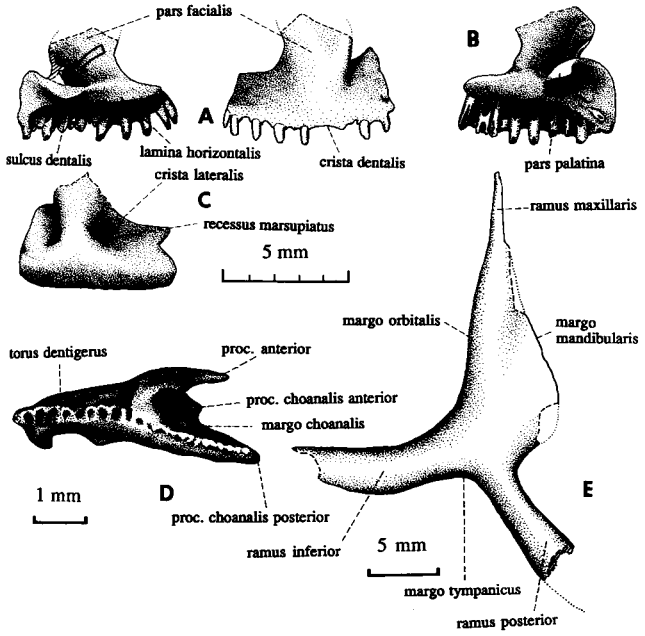


Figure 8 - **A, *Latonia gigantea*** (LARTET, 1851), right praemaxilla in inner (left) and outer (right) views. Middle Miocene, Astaracian), Sansan (FSL 165.801). **B, *Latonia gigantea*** (LARTET, 1851), left praemaxilla in inner view. (Middle Miocene, Astaracian), Sansan (MNHN, Sa 13467a). **C, *Latonia ragei*** HOSSINI, 1993, left praemaxilla in outer, slightly dorsal view. Lower Miocene (Agenian), Laugnac (Poitiers, Lg 2002). Arrow marks depression on the basis of the pars facialis. A-C in the same scale. **D, *Latonia gigantea*** (LARTET, 1851), left vomer in ventral view. Middle Miocene (Astaracian), Sansan (FSL 165.999). **E, *Latonia seyfriedi*** v. MEYER, 1843, left pterygoid in ventral view. Middle Miocene (Astracian), Öhningen (Pal. Inst. Zürich, A II 27). ***A, Latonia gigantea*** *(LARTET, 1851), prémaxillaire droit en vues interne (à gauche) et externe (à droite). Miocène moyen (Astaracien) Sansan.* ***B, Latonia gigantea*** *(LARTET, 1851), prémaxillaire gauche en vue interne. Miocène moyen (Astaracien), Sansan.* ***C, Latonia ragei*** *HOSSINI, 1993, prémaxillaire gauche en vue externe. Miocène inférieur (Agénien), Laugnac. La dépression sur la base de la pars facialis est marquée par une flèche. A-C à la même échelle.* ***D, Latonia gigantea*** *(LARTET, 1851), vomer gauche en vue ventrale. miocène moyen (Astaracien), Sansan. E, Latonia seyfiedi v. MEYER 1843., ptérygoïde gauche en vues ventrale. Miocène moyen (Astaracien), Öhningen.*

cess, distinct depression on the posterior part of the outer surface of the bone above the crista mandibulae externa). However, variation exists in mutual proportions of both coronoid processes, in the inclination and shape of the processus coronoideus, in presence or absence of the foramen located posterior to the basis of the latter process, in course and depth of the sulcus pro cartilago Meckeli, and in morphology of the bone between the sulcus and lateral depression (this is sometimes flat and clearly delimited ; see Fig. 12G). Although much of this variation is age-dependent and individual, some characters (for instance the last one) seem to prevail in some samples.

Dentary is known only in the articulated skull of *L. vertaizoni* holotype (Fig. 19) but except for the fact that its mentomandibular portion was thickened nothing can be said about its detail morphology.

Vertebrae - Vertebral column consists of eight opisthocoelous praesacrals, their neural arches are imbricate, with strong and long spinal processes (except for V8 ; see Fig. 13L) ; the centrum is cylindrical, rather compressed in its mid-length. The atlas (Fig. 13C, G ; 14B, G ; Pl. 1-10) either has its crista ventralis well developed or the ventral surface of the centrum is smooth. The neural canal may be oval or triangular (compare Fig. 14B, G). Both articular fossae for occipital condyles may be well separated or fused. None of these characters is of taxonomic importance. V2-V4 (Figs 2 ; 3 ; 13A, B, D, H ; 14D, F ; 19 ; Pl. 1-12) bear stout transverse processes that are wider distally than proximally, and are articulated with ribs. The rib on V3 bears rather long, slender and posterolaterally directed outgrowth (Figs 3 ; 14 C ; 19). All ribs are wider at their ends and constricted in the middle. V5-V8 (Figs 13F, I, L ; 14A, H ; 19) may be well distinguished from each other after inclination and length of their transverse processes. They do not differ from those in *Discoglossus*. The sacral vertebra (Fig. 13 E, J, K; see also Spinar 1978, fig. 2) has its transverse processes moderately dilated, inclined posterolaterally. Certain variation exists in course of their anterior margin which can be either perpendicular to the main body axis or even slightly turned anteriorly (in *L. seyfriedi* ; see Figs 2, 3, 4), or directed posteriorly. This character seems to indicate taxonomic differences (at least between *seyfriedi* and other species of *Latonia*).

Urostyle (Fig. 15 ; see also Rage & Vergnaud-Grazzini 1972, pl. 1, figs 1-6) does not differ basically from that in other discoglossids, and similar to *Discoglossus* it has a narrow dorsal fissure. Certain individual variation exists in the presence of horizontal lamina posterior to the transverse processes (Fig. 15B, C), which may produce in some cases an additional pair of processes (Fig. 15D). Similar variation was found in Cretaceous discoglossid-like anurans from central Asia (Roèek & Nessov 1993, text-fig. 16 C).

Clavicle (Figs 2, 19) is preserved only in articulated skeletons [i.e., holotypes of *L. seyfriedi* and *L.* ("*Prodiscoglossus*") *vertaizoni*]. It is curved, slender medially, and dilated and slightly bifurcated laterally for attachment with the pars acromialis scapulae.

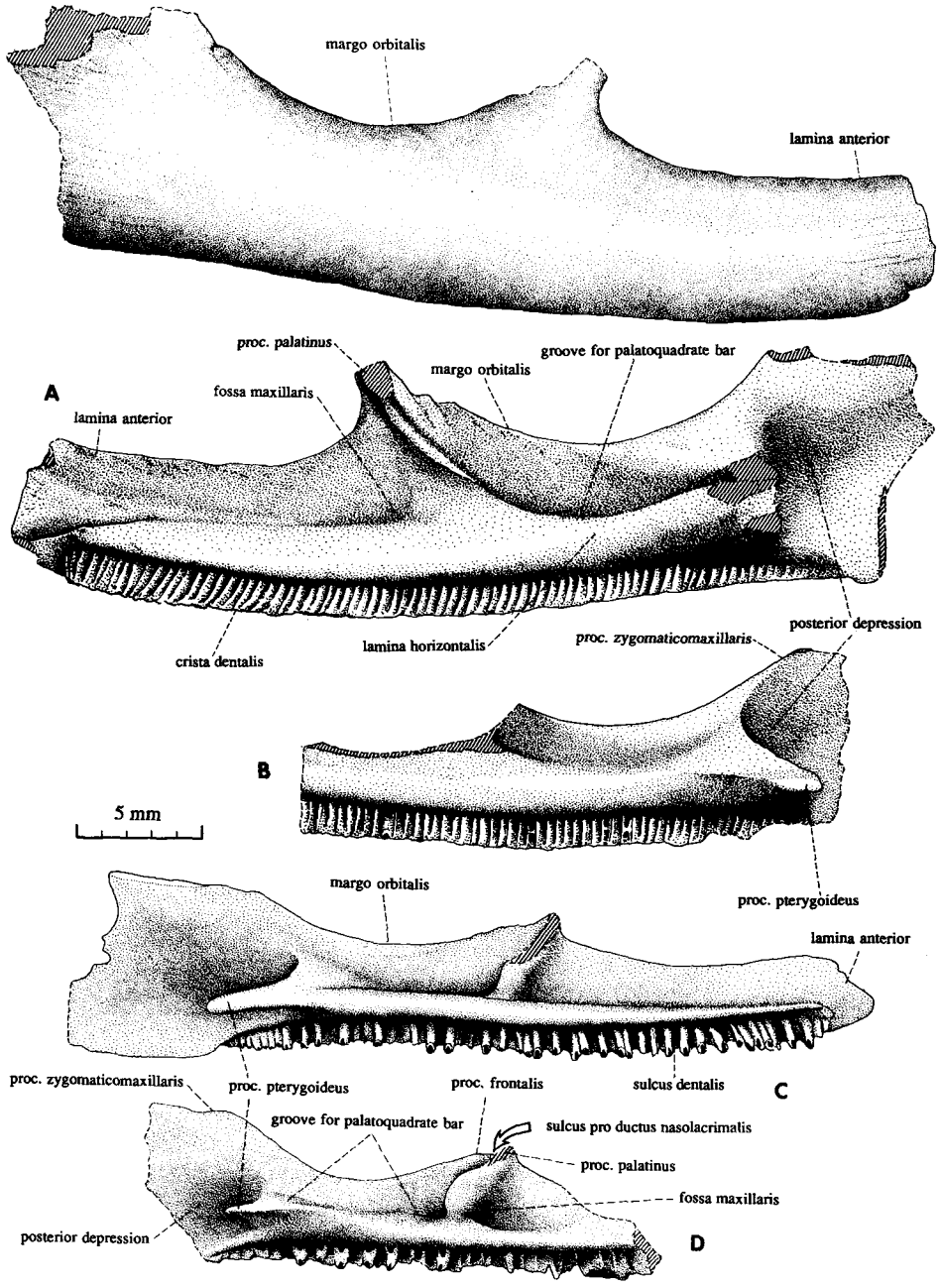


Figure 9 - **A, *Latonia ragei*** HOSSINI, 1993, holotype. Right maxilla in outer (above) and inner (below) views. Lower Miocene (Agenian), Laugnac (FSL 150.800). **B, *Latonia ragei*** HOSSINI, 1993, left maxilla in inner view, reversed for comparison with holotype. Lower Miocene (Ageanian), Laugnac (FSL 150.815). **C, *Latonia vertaizoni*** (FRIANT, 1944), left maxilla in inner view. Lower Miocene (Agenian), St. Gérand le Puy (MNHN, uncatalogued). **D, *Latonia gigantea*** (LARTET, 1851), left maxilla in inner view. Pliocene (Ruscinian), Ivanovce (DP FNSP 212/4). ***A, Latonia ragei*** *HOSSINI, 1993, holotype. Maxillaire droit en vue externe (en haut) et interne (en bas). Miocène inférieur (Agénien), Laugnac.* ***Latonia ragei*** *HOSSINI, 1993, maxillaire gauche en vue interne, inversée pour comparaison avec l'holotype. Miocène inférieur (Agénien), Laugnac.* ***C, Latonia vertaizoni*** *(FRIANT, 1944), maxillaire gauche en vue interne. Miocène inférieur (Agénien), St-Gérand-le-Puy. D,* ***Latonia gigantea*** *(LARTET 1851), maxillaire gauche en vue interne. Pliocène (Ruscinien), Ivanovce.*

Coracoid (Fig. 16C-H ; see also Rage & Vergnaud-Grazzini 1972, pl. 1, Fig. 8) seems to be highly variable in *Latonia*. Rage & Hossini (in press) even distinguish two types of them, one straight and another curved. As Rage (pers. comm.) suggested both may be found in a single species (straight in the holotype of *L. seyfriedi* and in Zürich specimen A II 28, see Figs 2, 3, and curved, or with a "bump", in Zürich specimen A II 27, see Fig. 16H). Hossini (1993) supposed that this difference may reflect sexual dimorphism. This variation seems not to be of taxonomic importance.

Scapula (Fig. 16A, B ; see also Špinar 1975b, pls. III, IV ; 1978, pl. 68 ; Sanchíz & Mlynarski 1979, Fig. 1-3) - Its suprascapular part is short and wide, on its anterior margin connected with the pars acromialis by a thin lamina called the tenuitas cranialis. This gives an impression that the bone is short and robust. The pars glenoidalis is originally of about the same height as the pars acromialis but it is broken off at the level of glenoid fossa in most specimens.

Humerus (Fig. 17, Pl. 1-9 ; see also Rage & Vergnaud-Grazzini 1972, pl. 1, Fig. 7 ; Špinar 1978,

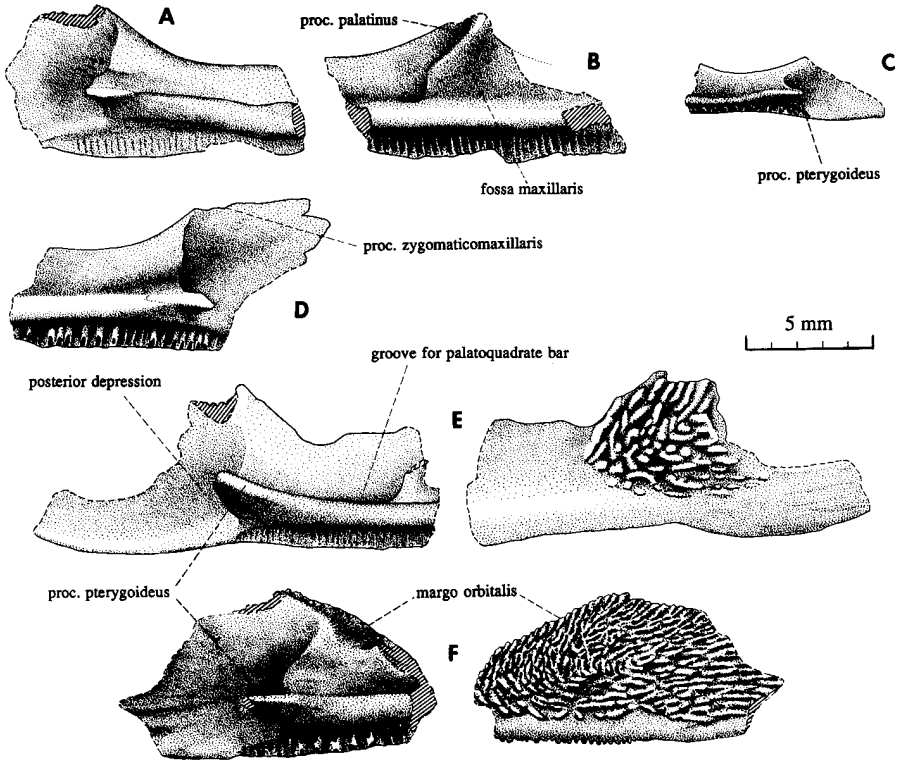


Figure 10 - **A, *Latonia vertaizoni*** (FRIANT, 1944), left maxilla in inner view. Upper Oligocene, Coderet (FSL 423.630). **B,** *Latonia vertaizoni* (FRIANT, 1944), left maxilla in inner view. Upper Oligocene, Coderet (FSL 423.540). **C, *Latonia vertaizoni*** juv., right maxilla in inner view. Upper Oligocene, Coderet (FSL 423.540). **D, *Latonia vertaizoni*** (FRIANT, 1944), right maxilla in inner view. Upper Oligocene, Coderet (FSL 423.542). **E, *Latonia gigantea*** (LARTET, 1851), left maxilla in inner (left) and outer (right) views. Middle Miocene (Astaracian), La Grive St. Alban (MNHN, LGA 1190). **F, *Latonia gigantea*** (LARTET, 1851), left maxilla in inner (left) and outer (right) views. Lower Miocene (Orleanian), Dolnice (DP FNSP 251). ***A, Latonia vertaizoni*** *(FRIANT, 1944), maxillaire gauche en vue interne.* ***B, Latonia vertaizoni*** *(FRIANT, 1944), maxillaire gauche en vue interne.* ***C, Latonian vertaizoni*** *juv., maxillaire droit en vue interne.* ***D, Latonia vertaizoni*** *(FRIANT, 1944), maxillaire droit en vue interne.* ***E, Latonia gigantea*** *(LARTET, 1851) maxillaire gauche en vues interne (à gauche) et externe (à droite).* ***F, Latonia gigantea*** *(LARTET, 1851), maxillaire gauche en vues interne (à gauche) et externe (à droite).*

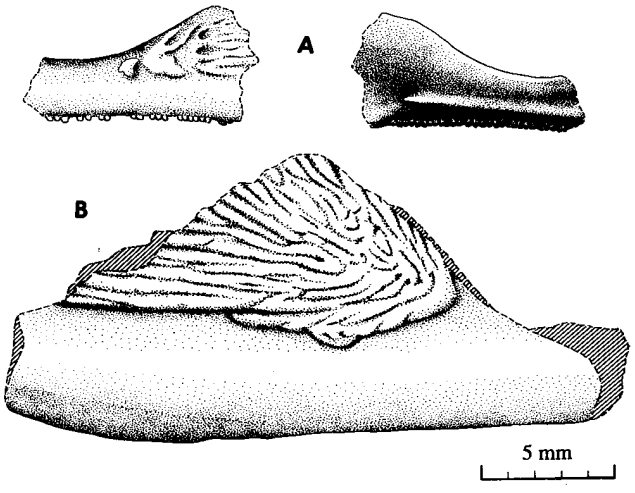


Figure 11 - Development of sculpture on maxilla in ***Latonia gigantea*** (LARTET, 1851) from Sansan (Middle Miocene, Astaracian). **A,** juvenile (MNHN, Sa 13452), left maxilla in outer (left) and inner (right) views. **B,** adult (MNHN, Sa 13450), right maxilla in outer view. *Développement de la sculpture sur le maxillaire (Miocène moyen, Astaracien).* ***A,*** *juvénile, maxillaire gauche en vue externe (à gauche) et interne (à droite).* ***B,*** *adulte, maxillaire droit en vue externe.*

pl. 69) - Typical for *Latonia* (but in lesser extent also for *Discoglossus*) is that the margin of the crista medialis is sharply bent in its upper part. This, together with concave margin of less extensive crista lateralis and laterally shifted caput humeri, gives an impression that the bone is broken in its distal section (Fig. 17G). Asymmetrical position of the caput is typical for *Latonia*. In *Discoglossus* the ball is moreless in the axis of the bone. The crista ventralis is well developed, and it is paralleled in its distal section by another one, less developed. The degree of development of all these cristae reflects sexual dimorphism rather than taxonomic differences because it is associated with muscles which are attached to them.

Radioulna does not bear taxonomic characters and cannot be morphologically distinguished from that in other related anurans.

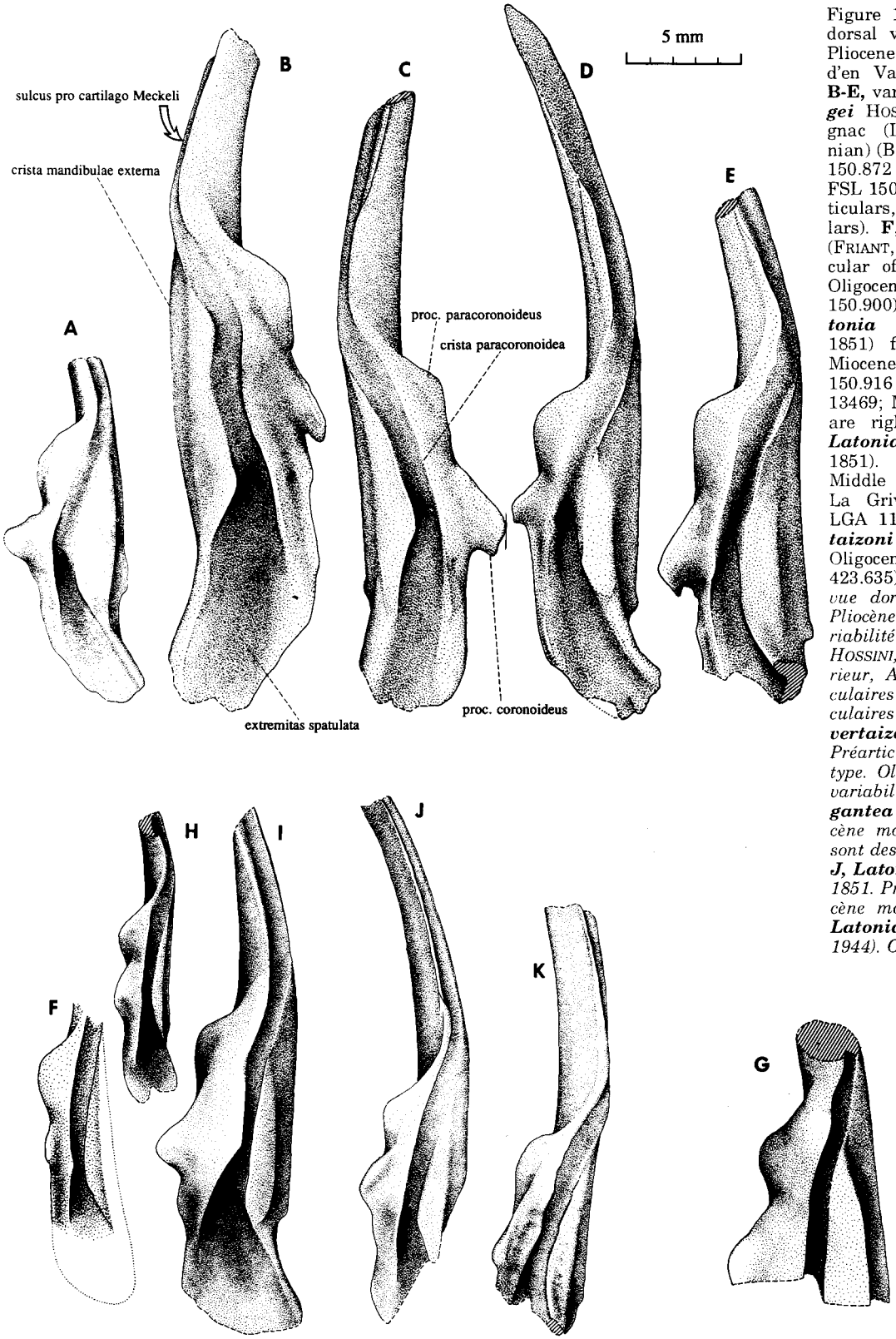


Figure 12 - Praearticulars in dorsal view. **A**, ***Latonia*** sp. Pliocene (Ruscinian), Serrat d'en Vacquer (FSL 150.169). **B-E,** variation in ***Latonia ragei*** HOSSINI, 1993 from Laugnac (Lower Miocene, Agenian) (B, FSL 150.869 ; C, FSL 150.872 ; D, FSL 150.865 ; E, FSL 150.866 ; B,C, left praearticulars, D,E right praearticulars). **F**, ***Latonia vertaizoni*** (FRIANT, 1944). Right praearticular of the holotype. Upper Oligocene, Vertaizon (FSL 150.900). **G-I**, variation in ***Latonia gigantea*** (LARTET, 1851) from Sansan (Middle Miocene, Astaracian) (G, FSL 150.916 ; H, MNHN, Sa 13469; MNHN, Sa 13451 ; all are right praearticulars). **J**, ***Latonia gigantea*** (LARTET, 1851). Right praearticular. Middle Miocene (Astaracian), La Grive St.Alban (MNHN, LGA 1189). **K**, ***Latonia vertaizoni*** (FRIANT, 1944). Upper Oligocene, Coderet (FSL 423.635). *Préarticulaires en vue dorsale.* **A**, ***Latonia*** *sp. Pliocène (Ruscinien).* **B-E**, ***variabilité chez Latonia ragei*** *HOSSINI, 1993 (Miocène inférieur, Agénien). (B,C, préarticulaires gauches, D, E, préarticulaires droits).* **F**, ***Latonia vertaizoni*** *(FRIANT, 1944). Préarticulaire droit de l'holotype. Oligocène supérieur.* **G-I**, *variabilité chez* ***Latonia gigantea*** *(LARTET, 1851) (Miocène moyen, Astaracien) (tous sont des préarticulaires droits).* **J**, ***Latonia gigantea*** *(LARTET, 1851. Préarticulaire droit. Miocène moyen (Astaracien).* **K**, ***Latonia vertaizoni*** *(FRIANT, 1944). Oligocène supérieur.*

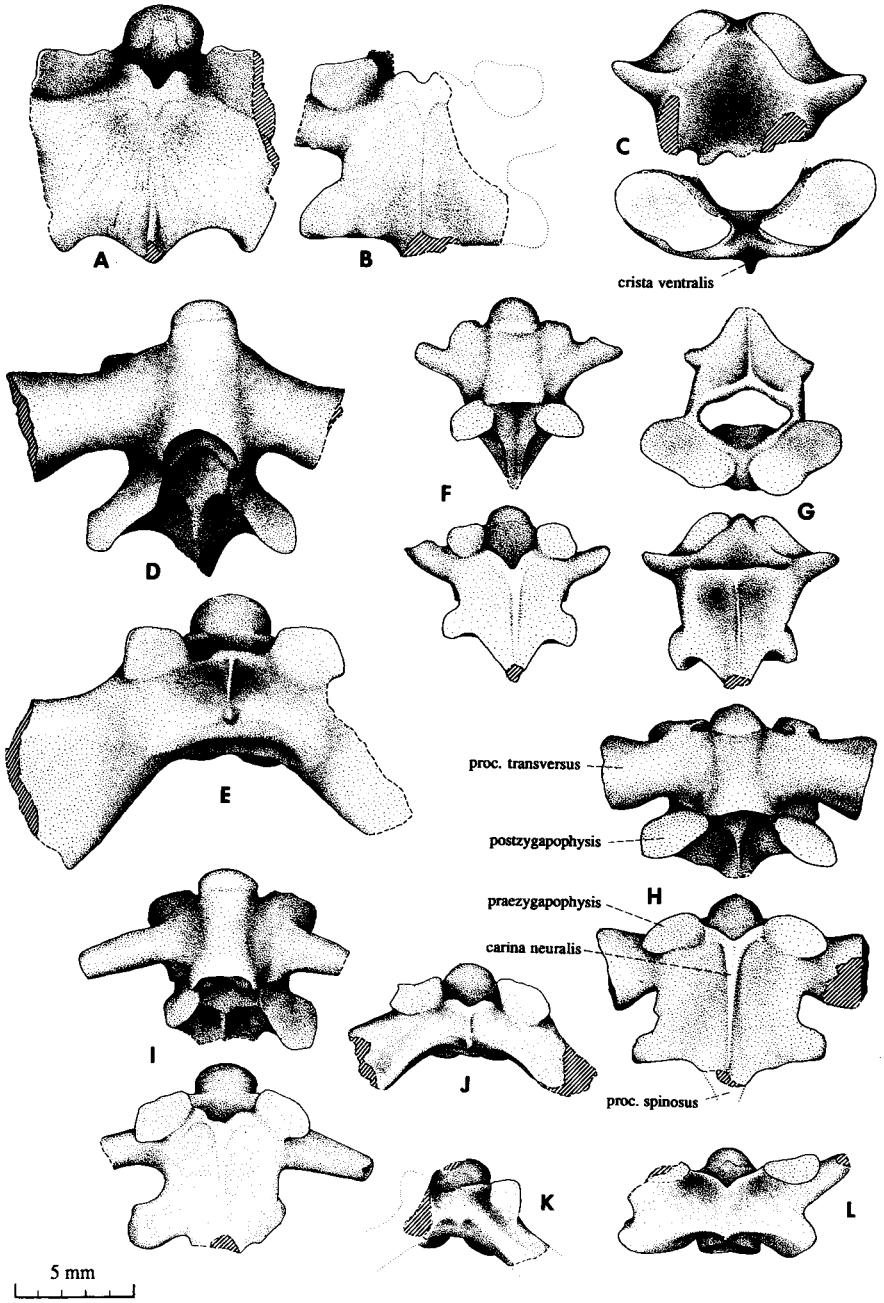


Figure 13 - Praesacral vertebrae (A, B, D), atlas (C), and sacral vertebra (E) of ***Latonia gigantea*** (LARTET, 1851). Sansan (Middle Miocene, Astaracian), (A, FSL 150.962, B, FSL 150.963, both in dorsal view ; C, FSL 150.964, centrum of atlas in dorsal and anterior views ; D, MNHN, Sa 13457, V3 in ventral view ; E, MNHN, Sa 13458, dorsal view). Praesacral vertebrae (F, H) and atlas (G) of ***Latonia gigantea*** (LARTET, 1851). Middle Miocene (Astaracian), La Grive St. Alban (F, FSL 165.800, ventral and dorsal views ; G, FSL 165.798, anterior and dorsal views ; H, FSL 165.799, ventral and dorsal views. Praesacral vertebra (I) and sacral (J, K) vertebrae of ***Latonia vertaizoni*** (FRIANT, 1944). Upper Oligocene, Coderet (I, FSL 423.633, ventral and dorsal views ; J, FSL 423.502, dorsal view ; K, FSL 423.592, dorsal view). Praesacral vertebra (L) of ***Latonia ragei*** HOSSINI, 1993. Lower Miocene (Agenian), Laugnac (Paris 6, Lg 2007, dorsal view). *Vertèbres présacrées (A, B, D), atlas (C) et vertèbre sacrée (E) de* ***Latonia gigantea*** *(LARTET, 1851) (Miocène moyen, Astaracien) (tous les deux en vue dorsale ; C, centrum d'un atlas en vues dorsale et antérieure ; D, V3 en vue ventrale ; E, vue dorsale). Vertèbres présacrées (F, H) et atlas (G) de* ***Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien) (F, vues ventrale et dorsale ; G, vues antérieure et dorsale ; H, vues ventrale et dorsale). Vertèbre présacrée (I) et vertèbres sacrées (J, K) de* ***Latonia vertaizoni*** *(FRIANT, 1944). Oligocène supérieur (I, vues ventrale et dorsale, J, vue dorsale ; K, vue dorsale). Vertèbre présacrée (L) de* ***Latonia ragei*** *HOSSINI, 1993. Miocène inférieur (Agénien) (vue dorsale.*

Carpals (Fig. 19) are best preserved in the holotype of *L.* (*"Prodiscoglossus"*) *vertaizoni*, however, their detail morphology cannot be studied.

Ilium (Fig. 18 ; see also Bolkay 1913, pl. 11, Fig. 6 ; Hodrová 1987a, text-fig. 1) is basically same as in *Discoglossus*. Its pars ascendens is well prominent and the same holds true for the tuber superius. Consequently, the dorsal margin of the bone between the both is deeply and widely concave. The tuber may be prominent from the outline of the bone (Fig. 18E) but in most cases it is an arch-like transition of the dorsal margin of the bone between its posterior section and the crista ilii (Fig. 18A). Variation in size of the tuber is most probably dependent on sexual dimorphism. Underneath the tuber is well developed depression (fossula tuberis superioris) which is

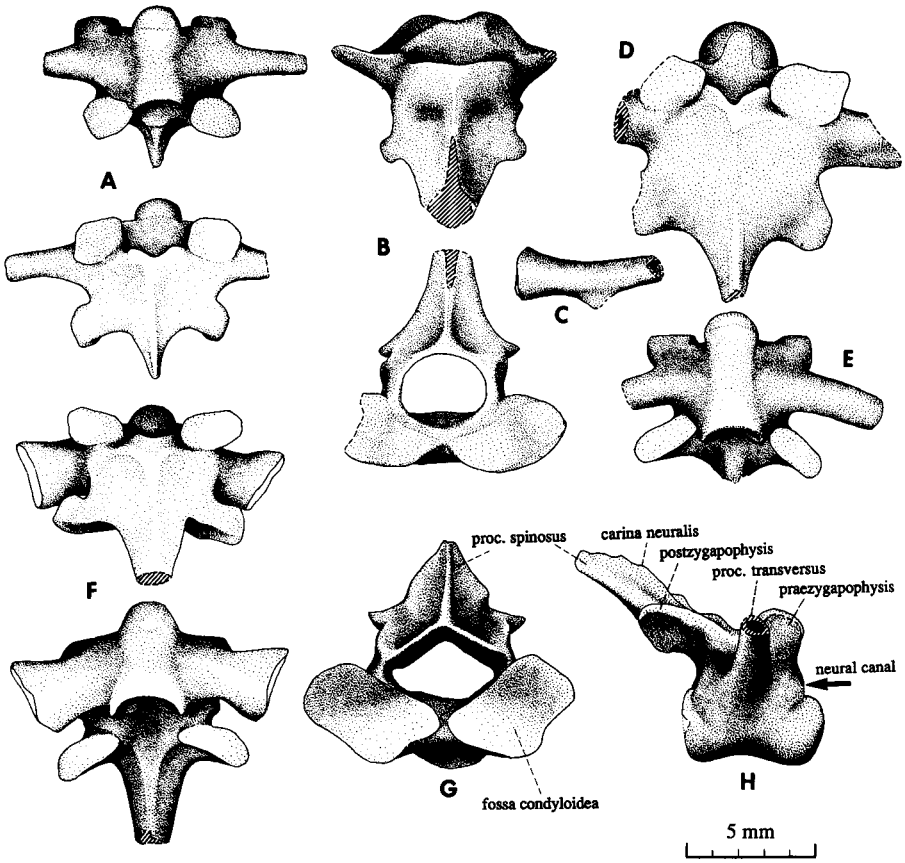


Figure 14 - **A, *Latonia vertaizoni*** (FRIANT, 1944). V7 in ventral (above) and dorsal (below) views. Upper Oligocene, Coderet (FSL 423.634). **B, *Latonia ragei*** HOSSINI, 1993. Atlas in dorsal (above) and anterior (below) views. Lower Miocene (Agenian), Laugnac (Paris 6, Lg 2004). **C, *Latonia ragei*** HOSSINI, 1993. Rib with posterior process broken off. Lower Miocene (Agenian), Laugnac (Paris 6, Lg 2008). **D, *Latonia ragei*** HOSSINI, 1993. V6 in dorsal view. Lower Miocene (Agenian), Laugnac. (Paris 6, Lg 2005). **E, *Latonia ragei*** HOSSINI, 1993. V5 in ventral view. Lower Miocene (Agenian), Laugnac. (Paris 6, Lg 2006). **F, *Latonia gigantea*** (LARTET, 1851). V4 in dorsal (above) and ventral (below) views. Middle Miocene (Astaracian), La Grive St. Alban (MNHN, LGA 1191). **G, *Latonia gigantea*** (LARTET, 1851). Atlas in anterior view. Middle Miocene (Astaracian), La Grive St. Alban (MNHN, LGA 1192). **H, *Latonia gigantea*** (LARTET, 1851). V7 in lateral view. Pliocene (Ruscinian), Ivanovce (DP FNSP 227a). ***A, latonia vertaizoni*** *(FRIANT, 1944). V7 en vues ventrale (en haut) et dorsale (en bas). Oligocène supérieur.* ***B, Latonia ragei*** *HOSSINI, 1993. Atlas en vue dorsale (en haut) et antérieure (en bas). Miocène inférieur (Agenien).* ***C, Latonia ragei*** *HOSSINI, 1993. Côte avec processus postérieur cassé. Miocène inférieur (Agénien).* ***D, Latonia ragei*** *HOSSINI, 1993. V6 en vue dorsale. Miocène inférieur (Agénien).* ***E, Latonia ragei*** *HOSSINI, 1993. V5 en vue ventrale. Miocène inférieur (Agenien).* ***F, Latonia gigantea*** *(LARTET, 1851). V4 en vue dorsale (en haut) et ventrale (en bas). Miocène moyen (Astaracien).* ***G, Latonia gigantea*** *(LARTET, 1851). Atlas en vue antérieure. Miocène moyen (Astaracien).* ***H, Latonia gigantea*** *(LARTET, 1851). V7 en vue latérale. Pliocène (Ruscinien).*

usually pierced by one or more small foramina in its bottom. Ilia are very common in material of isolated bones of *Latonia*, and they are among the elements that best indicate its occurrence.
Ischia (Pl. 1-11) - Similar to radioulnae these elements bear no diagnostic characters and are associated with other material of *Latonia* only on the basis of their size.

Femur (Figs 3, 19) is slightly S-shaped and shorter than tibiofibula (F/T ratio in *L. seyfriedi* holotype is 0.89, in Zürich specimen A II 28 is 0.9).
Tibiofibula is seemingly an element without much taxonomic importance but Hossini (1992) pointed out that in *Latonia* (and most probably also in all other discoglossids) both elliptical components on cross section have their long axes parallel with one another.

Astragalus - calcaneum (Figs 1, 19 ; see also v. MEYER 1845, tab. 4) are not fused and the former element is longer than the latter.

LATONIA GIGANTEA (LARTET, 1851)

1851- *Rana gigantea* - Lartet, p. 41.
1859 - *Rana sansaniensis* - Gervais, pl. 64, Fig. 23.
1865 - *Latonia rugosa* - Cope, p. 105
1890 - *Latonia gigantea* - Lydekker, p. 129.

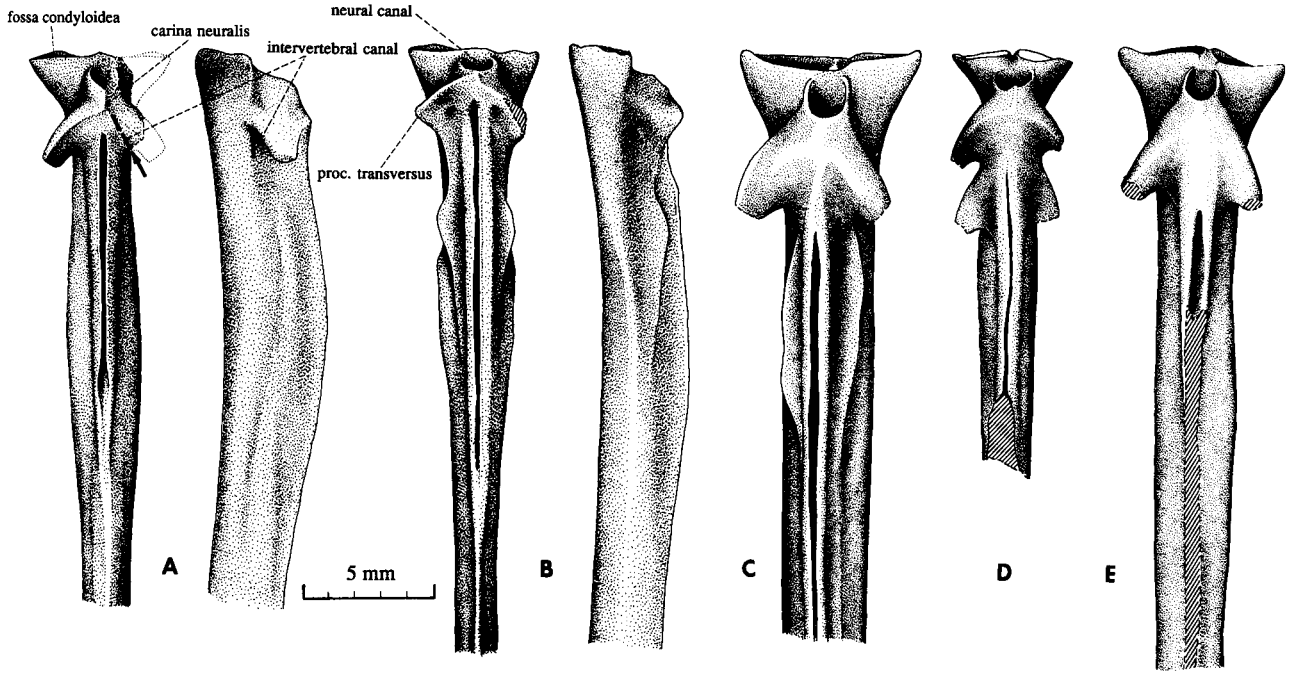


Figure 15 - Urostyles in dorsal and lateral views. **A, *Latonia ragei*** HOSSINI, 1993. Lower Miocene (Agenian), Laugnac (FSL 150.816). **B, *Latonia*** sp., holotype of "***Diplopelturus ruscinensis***" DEPÉRET, 1890. Pliocene (Ruscinian), Serrat d'en Vacquer, (FSL 38.903). See also Depéret (1890, pl. 19, fig. 15, and Rage & Vergnaud-Grazzini (1972, pl. 1, figs 1, 2). **C, *Latonia gigantea*** (LARTET, 1851). Middle Miocene (Astaracian), Sansan (MNHN, Sa 13449). **D, *Latonia ragei*** HOSSINI, 1993. Lower Miocene (Agenian), Laugnac (Paris 6, Lg 2012). **E, *Latonia gigantea*** (LARTET, 1851). Middle Miocene (Astaracian), La Grive St. Alban, (MNHN, LGA 1187). Dotted lines represent reconstructed parts. *Urostyles en vues dorsale et latérale.* ***A, Latonia ragei*** *HOSSINI, 1993. Miocène inférieur (Agénien).* ***B, Latonia*** *sp., holotype de* "***Diplopelturus ruscinensis***" *DEPERET, 1890. Pliocène (Ruscinien). Voir aussi Depéret (1890, pl. 19, fig. 15 et Rage & Vergnaud-Grazzini (1972, pl. 1, fig. 1, 2).* ***C, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien).* ***D, Latonia ragei*** *HOSSINI, 1993. Miocène inférieur (Agénien).* ***E, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien). Les parties reconstituées sont en lignes interrompues.*

1913 - *Pelobates robustus* - Bolkay, p. 219, pl. 11, figs 1-5.
1913 - *Rana batthyanyi* - Bolkay, p. 221, pl. 11, figs 6, 7.
1955 - *Discoglossus giganteus* - Wettstein-Westersheimb, p. 808, pl. 1, Fig. 1a.
1955 - *Miopelobates zapfei* - Wettstein-Westersheimb, p. 812, pl. 2, Fig. 3a.
1970 - *Discoglossus* cf. *D. giganteus* - Vergnaud-Grazzini, p. 48.
1970 - *Miopelobates robustus* - Estes, p. 328.
1975 - *Miopelobates fejfari* - Špinar, p. 41, Fig. 1a; pl. 1, figs 1, 2.
1975 - *Neusibatrachus estesi* - Špinar, p. 62, Fig. 5
1976 - *Latonia zapfei* - Špinar, p. 287, Fig. 3a.
1976 - *Latonia fejfari* - Špinar, p. 287, Fig. 3b.
1976 - *Latonia kolebabi* - Špinar, p. 287, Fig. 3c.
1981 - *Latonia seyfriedi* - Chkhikvadze, p. 152.
1984 - *Latonia sayfriedi* (ex err.) - Mlynarski, p. 140.
1992 - *Latonia* cf. *L. fejfari* - Hossini, p. 88.

Holotypus - Not stated.

Lectotypus - Frontoparietal ; Muséum National d'Histoire Naturelle Paris, coll. n° MNHN, Sa 13448, designated by Rage & Hossini (in press). Illustrated in Rage & Hossini (in press). See also Fig. 7F.

Stratum Typicum - Astaracian (MN 6), Middle Miocene.

Locus Typicus - Sansan (Gers, France).

Diagnosis (partly after Rage & Hossini in press): Sculpture on frontoparietal of adult consisting of small, irregularly and densely scattered tubercles on its posterior part, tubercles tend to fuse into irregular ridges diverging anteriorly in its anterior part ; in young individuals pit-and-ridge sculpture ; proc. zygomaticomaxillaris maxillae covered with sculpture, with ridges and tubercles arranged in parallel arches open posterodorsally ; transverse processes of sacral may be dilated to such a degree that its anterior margin is perpendicular to main body axis.

Description - Frontoparietal and maxilla in adults are described below. Other elements are conform with general description of the genus. The urostyle may bear an additional pair (or

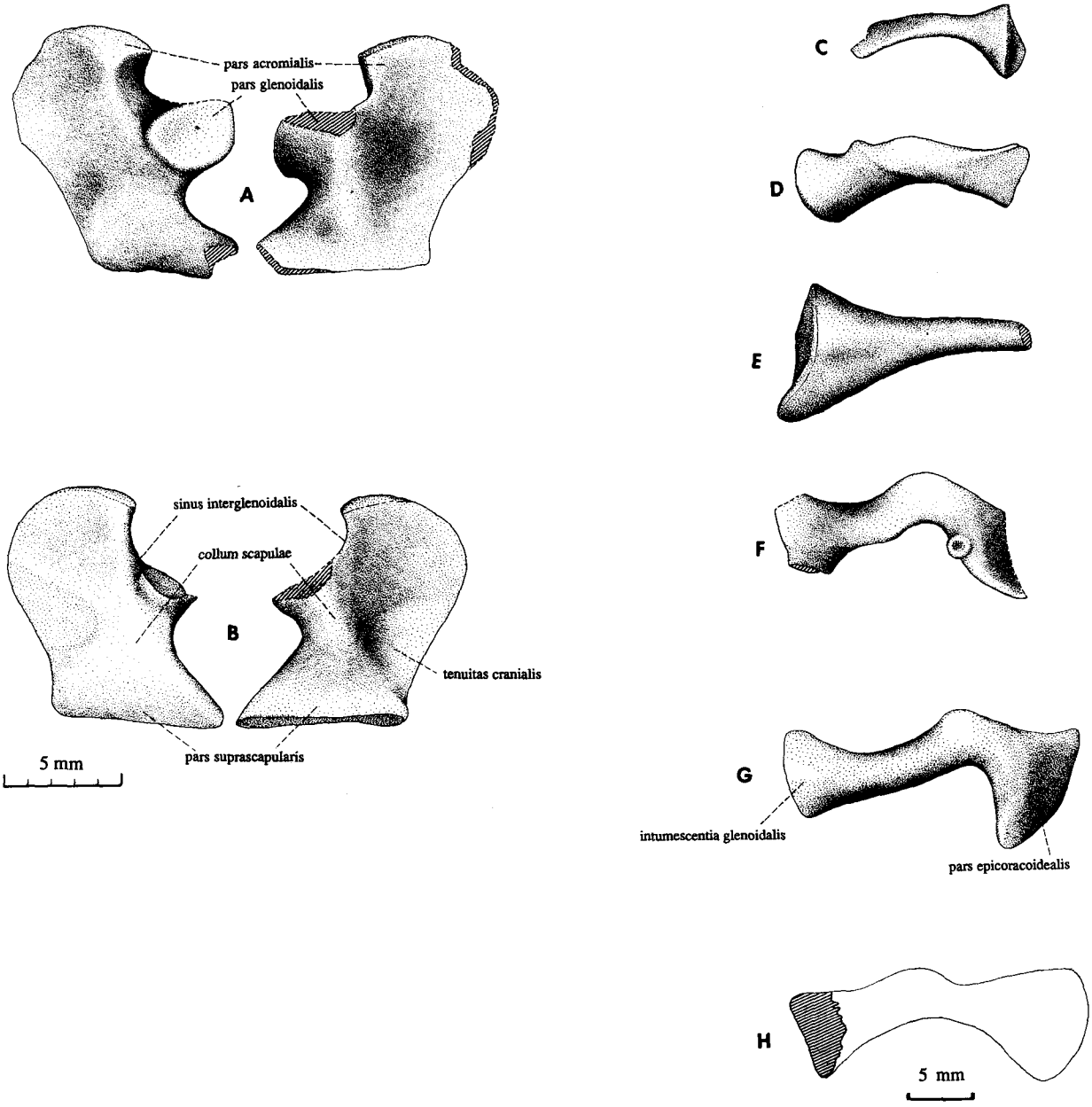


Figure 16 - Scapulae (A, B). **A, *Latonia gigantea*** (LARTET, 1851) in outer (left) and inner (right) views. Middle Miocene (Astaracian), Sansan (MNHN, Sa 13459). **B, *Latonia ragei*** HOSSINI, 1993, same aspects. Lower Miocene (Agenian), Laugnac (Paris 6, Lg 2009). Coracoids (C-H). **C, F, *Latonia gigantea*** (LARTET, 1851). Middle Miocene (Astaracian), Sansan (C, MNHN, Sa 13455 ; F, MNHN, Sa 13456). **D, *Latonia*** sp. Pliocene (Ruscinian), Serrat d'en Vacquer (FSL 150.171). **E, *Latonia ragei*** HOSSINI, 1993. Lower Miocene (Agenian), Laugnac (Paris 6, Lg 2010). **G, *Latonia gigantea*** (LARTET, 1851). Middle Miocene (Astaracian), La Grive St. Alban (MNHN, LGA 1195). **H, *Latonia seyfriedi*** v. MEYER, 1843. Middle Miocene (Astaracian), Öhningen (Pal. Inst. Zürich, A II 27). H in different scale. Scapulae (A, B). ***A, Latonia gigantea*** *(LARTET, 1851) en vues externe (à gauche) et interne (à droite). Miocène moyen (Astaracien).* ***B, Latonia ragei*** *HOSSINI, 1993, mêmes vues. Miocène inférieur (Agénien). Coracoïdes (C-H).* ***C, F, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien).* ***D, Latonia*** *sp. Pliocène (Ruscinien).* ***E, Latonia ragei*** *HOSSINI, 1993. Miocène inférieur (Agénien).* ***G, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien).* ***H, Latonia seyfriedi*** *v. MEYER, 1843. Miocène moyen (Astaracien). II est à une échelle différente.*

even pairs) of transverse processes (see also Vergnaud-Grazzini 1970, Fig. 2c).

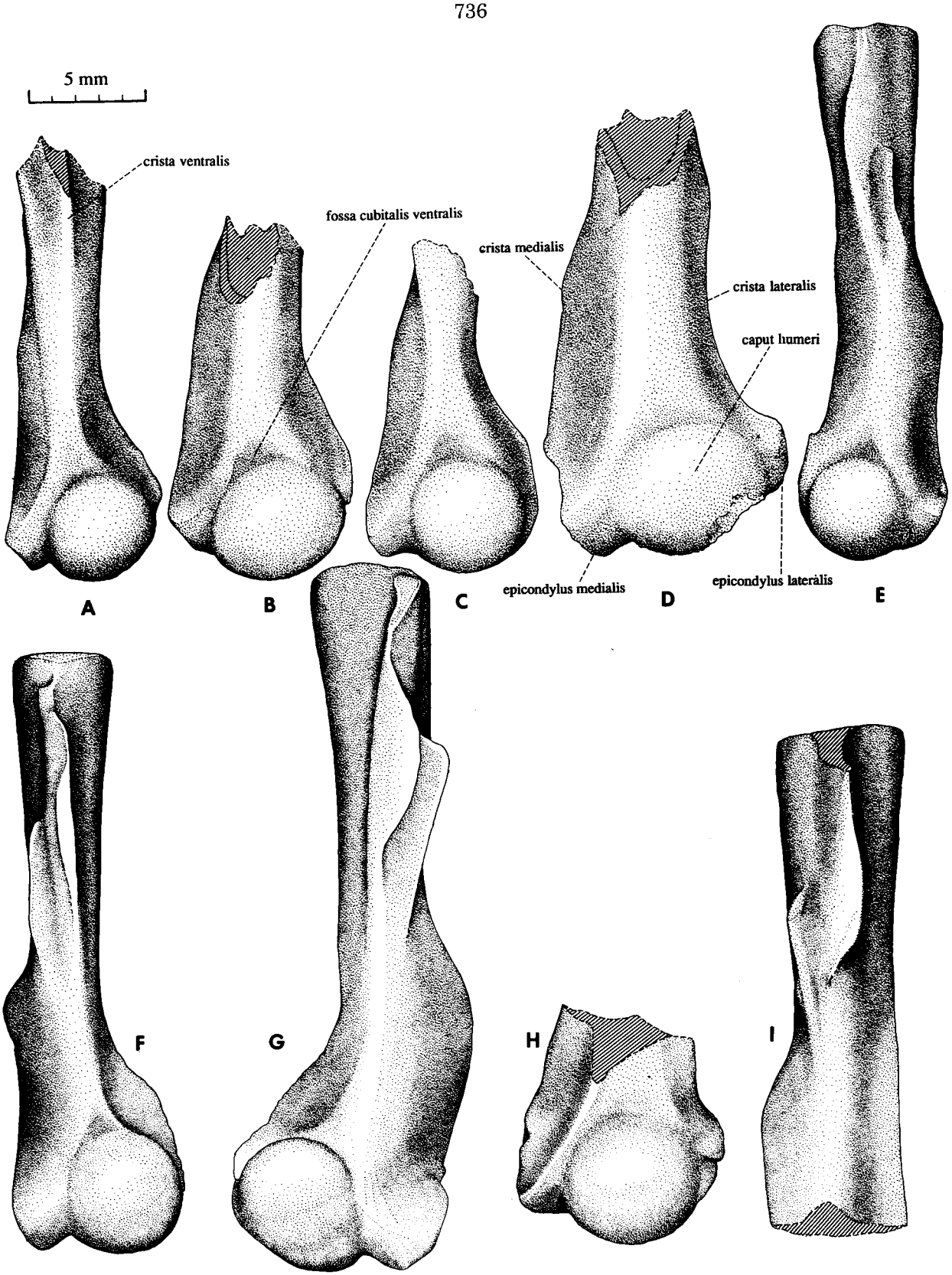
Development : Frontoparietal (Fig. 7) - In young individuals (Fig. 7A) the posterior part of the facies dorsalis seems to be narrower than the margins of the pars contacta at the corresponding level. This may be inferred from symmetrical, apparently not damaged margins of the facies dorsalis. Similar condition, however, may be found in some of much larger specimens. For instance in MNHN, Sa 13464a with estimated frontoparietal length about 15 mm and with the posterosinistral margin of the facies dorsalis intact, the extent of the facies dorsalis is smaller than that in the pars contacta, but sculpture (see below) consists already of tubercles. Hence, extent of the tectum supraorbitale was probably subject of individual variation. Since it was thin it is broken off in most isolated frontoparietals. However, its definitive extent in adult may be estimated from the condition in the holotype of *L. seyfriedi* (Figs 1, 2). The pars contacta in young individuals is extending ventrolaterally as a thin lamina. It is intact in the youngest known individual (Fig. 7A) but broken off in older ones. With increasing age it becomes thick and blunt. In young individuals, the posterior part of the incrassatio frontoparietalis is only slightly elevated above the level of the inner surface of the pars contacta, whereas it is well delimited, with projecting margins in some older ones (Fig. 7D, pl. 1-6). However, certain variation exists in degree of development of this part of the incrassation, and the same holds true for its anterior part which is a simple elongated depression in youngs, rimmed laterally by low but sharp ridges in individuals with estimated frontoparietal length about 20 mm (Fig. 7E), but low and rounded in the largest ones. The sculpture substantially changes in the course of development. Whereas in youngs it is in the form of irregular pits of various size and depth, in adults it consists of small tubercles in the posterior part and along the margo orbitalis, whereas in the medial anterior part of the facies dorsalis the tubercles tend to fuse into ridges. To summarize development of the frontoparietal one may say that developmental variation concerns extent of the tectum supraorbitale, height of the margins of the pars contacta in its anterior part, nature of sculpture and, perhaps, details of the incrassatio frontoparietalis. However, general pattern of the incrassation is stable throughout development.

Maxilla (Fig. 11) - In young individuals the shape of maxilla does not differ from that in *Discoglossus*. On its outer surface, at the level of the posterior part of the margo orbitalis, sculpture begins to develop as isolated elevations. Towards the posterior, these elevations tend to have shape of horizontal, parallel ridges. In adults, the sculptured area is well delimited, and sculpture consists of parallel ridges (Fig. 11B) or tubercles arranged in the same way (Fig. 10E, F). It also seems that in young individuals the posterior depression on the inner surface is not anteriorly delimited (Fig. 11A, right, but compare with Fig. 10C), whereas in adults it is always marked with more or less sharp edge.

Stratigraphic Distribution - Lower Miocene to Upper Pliocene.

Geographic Distribution - Sansan, France (Rage & Hossini in press) ; La Grive St.Alban, France (Hossini 1992) ; Opole, Poland (Mlynarski 1984 : 133 ; Mlynarski *et al.* 1982 : 109) ; Przeworno I and II, Poland (Mlynarski 1976 ; 1984 : 133 ; Sanchíz & Mlynarski 1979 : 154) ; Dolnice, Czech Republic (Špinar 1975a : 45) ; Devínska Nová Ves (Neudorf), Slovakia (Wettstein-Westersheimb 1955 : 808, 812) ; Ivanovce, Slovakia (Špinar 1978 : 292) ; Polgárdi, Hungary (Bolkay 1913 : 219, pl. 11, figs 1-7) ; Arondelli, Italy (Vergnaud-Grazzini 1970 : 48) ; Gritsev, Ukraine ; Kuchurgan, Ukraine (Chkhikvadze 1981 : 152) ; Belomechetskaya, Russia (Chkhikvadze 1988). Probably also Sète, France (Bailon 1991 : 58-59, Fig. 15B).

Remarks - The reason for including "*Pelobates robustus*" into the synonymy of *L. gigantea* is the type of sculpture on the maxilla and a peculiar groove separating the main sculptured area from the nearest anterior sculptured field and bifurcating ventrally (see Bolkay 1913 : 219, pl. XI, Fig. 1). As for its size, it fits well into the variation range of nearly 180 maxillae of *L. gigantea* from Sansan. Same holds for "*Rana batthyanyi*". *L."fejfari"* was placed into the synonymy of *L. gigantea* because of basically same type of sculpture on the maxilla. Only in some specimens from Dolnice (Fig. 10F) sculpture seems to be more delicate and tubercular than in specimens from other localities (*cf.* Fig. 10E, 11B, pl. 1-3). However, this slight difference seems not to be taxonomically significant. No other differences were found. *L. "kolebabi"* was based on the fragmentary frontoparietal the tectum supraorbitale of which was apparently broken off. Although Vergnaud-Grazzini (1970 : 49-50) did not mention whether fragments of the maxillae from the Upper Pliocene of Arondelli are sculptured or not, it seems probable (according to the age of locality and morphology of other elements) that this form belongs to *L. gi-*


5 mm
crista ventralis
fossa cubitalis ventralis
crista medialis
crista lateralis
caput humeri
epicondylus medialis
epicondylus lateralis
A
B
C
D
E
F
G
H
I

gantea too. However, this should be confirmed by further material. Mlynarski (1976 : 2, Fig. 1) referred material mentioned and illustrated in Spinar (1972 : 289, text-Fig. 95A, pl. 182-1, 2) as *Discoglossus giganteus* from the locality near Frantikovy Láznì. Hodrová (1987a : 98) mentioned it as *Latonia* sp. In fact, this material comes from Dolnice and according to large number of other elements it may be assigned to *L. gigantea*.

LATONIA RAGEI HOSSINI, 1993

1992 - *Latonia* n. sp. (non nommée) - Hossini, p. 106, figs 20-22.
1993 - *Latonia ragei* - Hossini, p. 239, Fig. 1.

Holotypus - Almost complete right maxilla with proc. posterior and tips of proc. pterygoideus and proc. palatinus broken off ; Centre des Sciences de la Terre, Université Claude-Bernard, Villeurbanne, FSL 150.800. See Fig. 9A.

Stratum Typicum - Agenian (=Aquitanian), MN 2, Lower Miocene.

Locus Typicus - Laugnac (Lot-et-Garonne, France).

Diagnosis - Maxilla without sculpture ; transverse processes of sacral vertebra only slightly dilated distally, declined posteriorly.

Description - All maxillae are considerably uniform ; slight differences may be ascribed to developmental variation (except, possibly, the nature of the posterior termination of the lamina horizontalis which is the contact area for the pterygoid). The maxilla may reach more than 40 mm in length. There are some faint imprints of vessels on its outer surface but no signs of sculpture in any developmental stage. The total number of tooth positions on the maxilla is about 65. There is a shallow groove crossing the margo orbitalis in its posterior moiety onto the outer surface of the bone (similar to that passing through sculptured area in *L. gigantea*). The largest praearticulars could be estimated to reach about 40 mm. The longitudinal vertical depression below the posterior surface of the processus coronoideus is present in considerable number of specimens, including a foramen in its bottom. It seems that location of the recess in the bottom of the sulcus for the Meckel's cartilage is more posteriorly in larger (i.e. older) individuals. Hossini (1993) included length of the scapula among the diagnostic characters of this species - in contrast to other species of *Latonia* it seems to be longer. However, this character can be age-dependent, and can reflect relations between ossified scapula and cartilaginous suprascapula. The angle between the pars ascendens and ala ossis ilii is about 120^0 (Hossini 1993). No differences between this and other species of *Latonia* could be found in other skeletal elements. The frontoparietal is not known.

Stratigraphic Distribution - Lower Miocene.

Geographic Distribution - Laugnac (France). Possibly also Ulm, Germany (see below).

Remarks - Taxonomic independence of this form can be confirmed only on the basis of comparison with *L. seyfriedi* from Öhningen that would reveal whether maxillae in the latter species are sculptured or smooth. This can be done only after further preparation of the holotype or Zürich specimen. Hossini (1992 : 123) assigned *Latonia* from Coderet to *L. ragei*, mainly on the basis of smooth maxillae and shape of scapula. Large disarticulated smooth maxilla and praearticular from the locality Ulm, Westtangente in S Germany (MN 2a), deposited in the Staatliches Museum für Naturkunde in Stuttgart, may be tentatively assigned to *L. ragei* too.

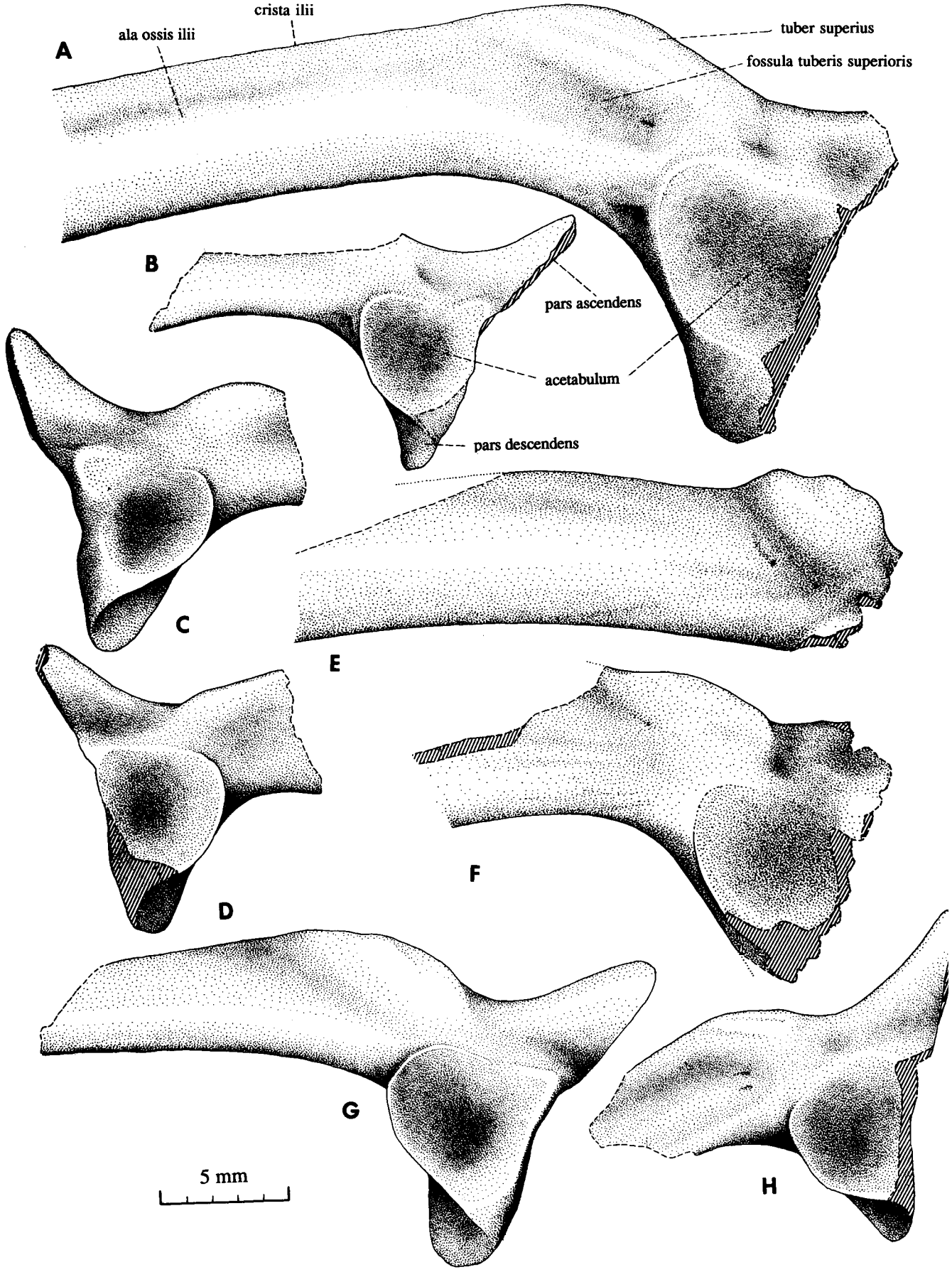
LATONIA SEYFRIEDI v. MEYER, 1843

1843 - *Latonix* (*Ceratophrys*) *Seyfriedii* (ex err.) - von Meyer, p. 396.
1843 - *Latonia* (*Ceratophrys*) *Seyfriedii* - von Meyer, p. 580.

Holotypus - Articulated skeleton exposed by its ventral side ; Staatliches Museum für Naturkunde Karlsruhe, uncatalogued. Illustrated in v. Meyer, 1845, tab. 4. See also Figs 1, 2.

Stratum Typicum - Middle Miocene ("im sogenannten Kesselstein").

Figure 17 - Left (A-D, F, H, I) and right (E, G) humeri. **A-D *Latonia ragei*** HOSSINI, 1993. Lower Miocene (Agenian), Laugnac (A, FSL 150.846 ; B, FSL 150.848 ; C, FSL 150.849 ; D, FSL 150.850, D originally right but reversed for comparison). E, ***Latonia*** sp. Pliocene (Ruscinian), Serrat d'en Vacquer, (FSL 38.903 ; see also Depéret 1890, pl. 19, fig. 17, and Rage & Vergnaud-Grazzini 1972, pl. 1, fig. 7). **F, G, *Latonia gigantea*** (LARTET, 1851). Middle Miocene (Astaracian), La Grive St.Alban (F- FSL 150.969 ; G, MNHN, LGA 1188). **H, I, *Latonia gigantea*** (LARTET, 1851). Middle Miocene (Astaracian), Sansan (H- FSL 150.903 ; I- FSL 150.901). *Humérus gauches (A-D, F, H, I) et droits (E, G).* ***A-D, Latonia ragei*** *HOSSINI, 1993. Miocène inférieur (Agénien). D, originellement droit mais inversé pour comparaison).* ***E, Latonia*** *sp. Pliocène (Ruscinien) ; voir aussi Depéret 1890, pl. 19, fig. 17, et Rage & Vergnaud-Grazzini 1972, pl. 1, fig. 7).* ***F, G, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien).* ***H, I, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien).*


A
ala ossis ilii
crista ilii
tuber superius
fossula tuberis superioris
B
pars ascendens
acetabulum
pars descendens
C
E
D
F
G
H
5 mm

Locus Typicus - Öhningen ("Oeninger Steinbruch"), S Germany.

Diagnosis - Frontoparietal with margins of both tecta supraorbitalia converging towards the anterior ; anterior margin of transverse processes of sacral vertebra perpendicular to main body axis ; ratio femur/tibiofibula about 0.9.

Other Material - Paläontol. Institut Zürich, catalogue numbers A II 27 and A II 28.

Redescription of Holotype (Figs 1, 2) - The specimen is exposed by its ventral side, its dorsal side being embedded in matrix. Chemical preparation is desired in order to ascertain whether the maxillae are covered with sculpture or not. After v. Meyer described the specimen in 1845 the matrix was smoothed, undoubtedly for purposes of public exhibition. It is not excluded that also some parts of the skeleton which seem to be present in v. Meyer's pl. 4 (op. cit.) were destroyed in this way.

In the frontoparietal, the margins of the tectum supraorbitale are well seen and obviously intact, as well as the anterior part of the pars contacta. The bone which forms the anterior margin of the left orbit is at the same level as the frontoparietal and may be thus determined as the nasal. The ventral surface of the anterior part of the frontoparietal is covered with crushed bone, except for a little intact piece that may be interpreted as the posterior ventral part of the sphenethmoid. It is overlain by the parasphenoid which is depressed along its mid-line and has a sharp ridge on its either side, at the transition between the pars medialis and lateral processes. Both praemaxillae are preserved at the anterior end of the skull, but disarticulated from one another and exposed by their inner side. Their precise shape cannot be restored. That of the right side (left in Figs 1, 2) is joined by a flat bone which may be interpreted as the inner surface of the right nasal. At the half-distance between the anterior end of the skull and the anterior end of the frontoparietal there are two little elements that seem to have posterior margins dentate. Most probably they are the vomers. The right part of the skull (left in Figs 1, 2) towards the maxilla is overlain by a flat, elongated, and crushed bone that is difficult to determine. Both maxillae are exposed by their inner sides, the left one is obscured by matrix, but it may be judged from the analogy with that of the right side that the process directed posteromedially into the orbit can be the processus zygomaticomaxillaris, with adjacent section of the margo orbitalis. In the posterolateral corner of each orbit is a flat smooth bone situated at the level of the processus zygomaticomaxillaris and the tectum supraorbitale. Although the extent of this bone (especially in the left orbit) is rather large, it can be interpreted as the lamella alaris squamosi. The left praearticular bears medially a sign of the processus coronoideus, whereas the processus paracoronoideus is well distinguishable. Both pterygoids are preserved almost in their original position, but since they are embedded in matrix their precise shape cannot be restored. The prooticooccipital is badly crushed but in the left one the prominentia ducti semicircularis posterioris is observable. An isolated element posterior to the right prooticooccipital is most probably its broken off distal part. The bone paralleling medially the ramus posterior of the left pterygoid is difficult to determine. It could be the processus posterolateralis squamosi.

The vertebral column consists of complete number of articulated opisthocoelous (8 praesacral and 1 sacral) vertebrae. The atlas is still articulated with the skull, and bears a distinct median keel on its ventral surface. V2-V4 have stout transverse processes, those of V2 and V4 (undoubtedly also that of V3, but this is overlain by the clavicle) are adjoined by imprints of ribs that were not ankylosed to them. The sacral vertebra is bicondylar posteriorly (the urostyle is slightly displaced) and its transverse processes (preserved for the most part as imprints) have their anterior margin perpendicular to the axis of the vertebral column.

The dorsal parts of the scapulae are preserved on both sides. On the left side, at the level of V3 is slightly curved and laterally bifurcated bone. This is the clavicle. It seems that only fragment

Figure 18 - Left (A, B, E, F, G, H) and right (C, D) ilia. **A, *Latonia gigantea*** (LARTET, 1851), Middle Miocene (Astaracian), Sansan (MNHN, Sa 13460). **B, *Latonia gigantea*** (LARTET, 1851), Middle Miocene (Astaracian), Sansan (MNHN, Sa 13461). **C, *Latonia gigantea*** (LARTET, 1851), Middle Miocene (Astaracian), La Grive St.Alban (FSL 150.977). **D, *Latonia vertaizoni*** (FRIANT, 1944), Upper Oligocene, Coderet (FSL 423.832). ***E, Latonia ragei*** HOSSINI, 1993, Lower Miocene (Agenian), Laugnac (FSL 150.830). **F, *Latonia ragei*** HOSSINI, 1993, Lower Miocene (Agenian), Laugnac (FSL 150.837). **G, *Latonia gigantea*** (LARTET, 1851), Middle Miocene (Astaracian), La Grive St. Alban (MNHN, LGA 1186). **H, *Latonia ragei*** HOSSINI, 1993, Lower Miocene (Agenian), Laugnac (Paris 6, Lg 2001). *Illions gauches (A, B, E, F, G, H) et droits (C, D).* ***A, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien).* ***B, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien).* ***C, Latonia gigantea*** *(LARTET, 1851). Miocène moyen (Astaracien).* ***D, Latonia vertaizoni*** *(FRIANT, 1944). oligocène supérieur.* ***E, Latonia ragei*** *HOSSINI, 1993. Miocène inférieur (Agénien).* ***F, Latonia ragei*** *HOSSINI, 1993. Miocène inférieur (Agénien).* ***G, Latonia gigantea*** *(LARTET, 1851). miocène moyen (Astaracien).* ***H, Latonia ragei*** *HOSSINI, 1993. Miocène inférieur.*

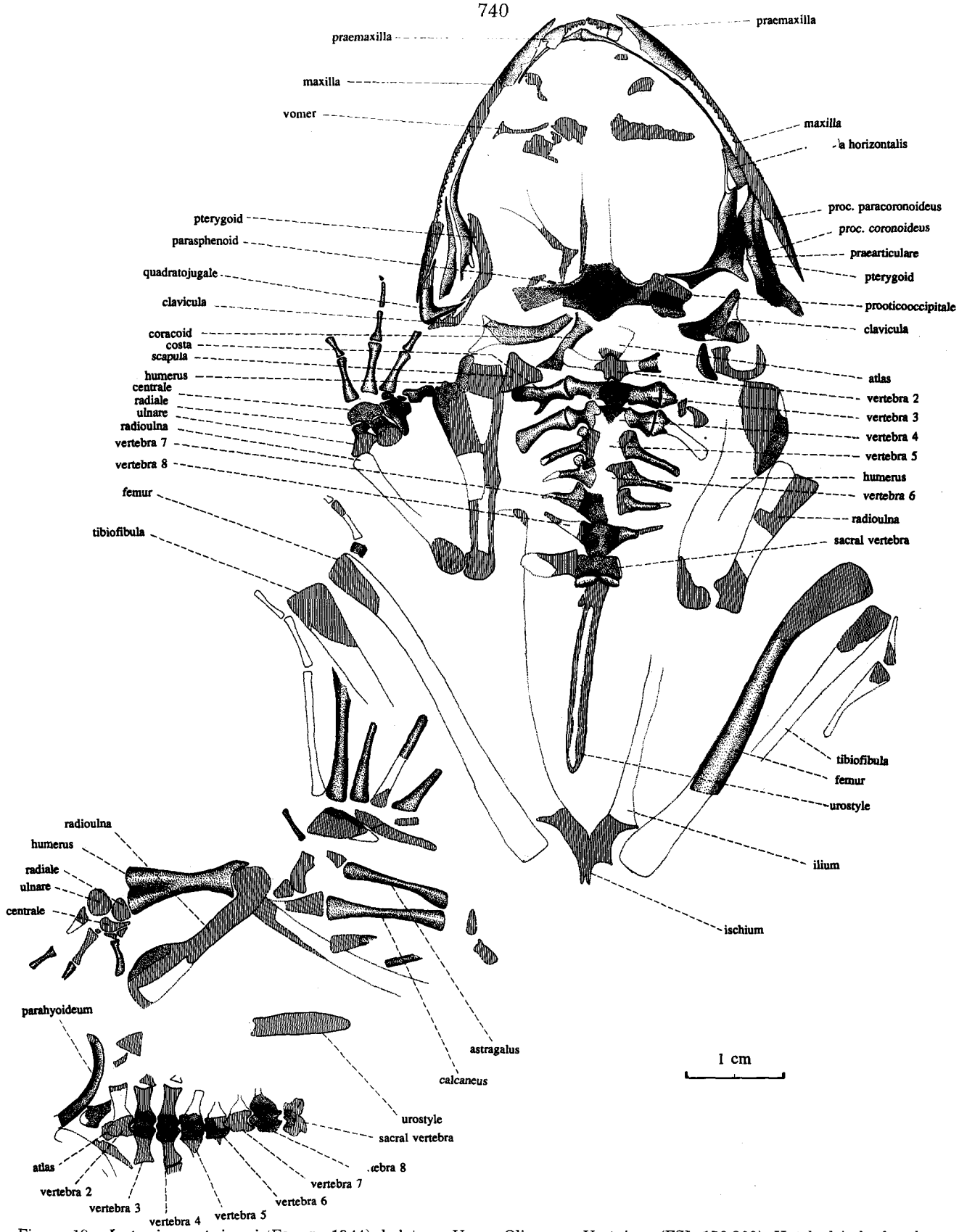


Figure 19 - ***Latonia vertaizoni*** (FRIANT, 1944), holotype. Upper Oligocene, Vertaizon (FSL 150.900). Hatched is broken bone, white areas are imprints in matrix. *Holotype. Oligocène supérieur. Vertaizon. Hachuré : surface cassée, en blanc : empreinte des os.*

of it is preserved on the right side. The right coracoid is preserved but it is badly crushed except for its intumescentia glenoidalis.

Other skeletal elements are as in v. Meyer (1845, pl. 4). See also Fig. 1.

Description of specimens from Paläont. Inst. Zürich - Similarly to the holotype, specimen A II 28 (Fig. 3) is a skeleton exposed by its ventral side and embedded in matrix by its dorsal side. The frontoparietal is preserved but its orbital margin seems to be damaged, especially in its posterior part. The pars contacta is well distinguishable (especially on the left side of the individual), including a striated area for the contact with the sphenethmoid. In contrast, the central part is crushed up to the level of sculpture. This crushed area is adjoined ventrally by remnants of the pars medialis parasphenoidei. The area of the posterior part of the frontoparietal is occupied by a flat broken bone which is characteristic by radially oriented furrows on its margins. Although the situation is rather obscure (and is schematized in Fig. 3), the mentioned furrows suggest that this is the posterior part of the frontoparietal. The anterior ventral surface of the frontoparietal is adjoined by small fragments of the porous bone, and similar fragments are located also more anteriorly. Most probably these are remnants of the sphenethmoid. Anterior to the frontoparietal are large flat bones separated in the mid-line by a suture. Their posteromedial parts are striated similarly to the contact areas of the frontoparietal with the sphenethmoid. Both bones may be thus interpreted as nasals exposed by their ventral surfaces. The praemaxillae disappeared but both maxillae are preserved, both as fragments and imprints. In that on the left side the processus pterygoideus can be discerned. Immediately dorsal to this process the inner surface of the bone is broken away and the area consisting of irregularly perforated bone is exposed, similar to that in the anterior middle part of the frontoparietal where it no doubt indicates the basal layer of sculpture. This might be also the case with the maxilla but further evidence for the presence of sculpture on the maxilla is desirable. Both quadratojugals are crushed but preserved approximately in their original position. The prooticooccipitals are compressed and broken into small pieces but their original shape is distinguishable. The left squamosal is nearly complete, including its processus posterolateralis. The fragment lying over the distal end of the right prooticooccipital may be interpreted as the squamosal only after its location. Both pterygoids are not complete, and their remnants are displaced into the orbits. The lower jaws are entirely displaced from their original position, and only right praearticular is preserved, with its posterior ventral part broken off. However, both coronoid processes are well distinguishable.

The vertebral column is disarticulated and fragmentary. On the posterior border of the prooticooccipital is an arch-like element that can be interpreted as remnant of the atlas. Only transverse processes of V3 and V5 are preserved. Those of the sacral vertebra are crushed but it can be supposed that outlines of the crushed transverse processes correspond moreless to their original shape, i.e., that their anterior margin is perpendicular to the axis of the vertebral column. The urostyle is preserved in whole its length but precise morphology of its proximal part cannot be discerned.

From the anterior appendicular skeleton only humeri and radioulnae may be identified with no doubts. Some other fragments along the vertebral column can be determined, though only tentatively. The element designated as the coracoid in Fig. 3 corresponds by its general shape to that in *Latonia*, but because of several small foramina accompanied by grooves, this interpretation must not be necessarily correct. The adjacent transverse element could be the scapula.

The (probably left) ilium is preserved and detached from the sacral process. The ischiadic part of the pelvis is broken into small pieces and only its posterior shape can be discerned. The proximal part of the right femur, and complete left femur, tibiofibula, and astragalus are preserved, besides some disarticulated phalanges. It is not excluded that large indeterminate fragments located along the vertebral column might belong to another individual.

Specimen A II 27 (v. Meyer 1845, tab. 6, Fig. 1) includes remnants of more than one individual. This is evidenced by three praearticulars (one in the upper part, adjacent to the pterygoid, another in central part, left to the atlas, and the third in the right part). Some elements (such as the pterygoid and praearticulars) are exposed by their ventral sides, but the vertebrae (judging by the condition in V2, with the typical course of the border between the periost of the centrum, and the periost-free surface of the condyle which is developed only on the dorsal side ; compare Figs 4, 14D) seem to be exposed by their dorsal sides.

The vertebral column is complete, including ribs. The atlas is displaced from its original position,

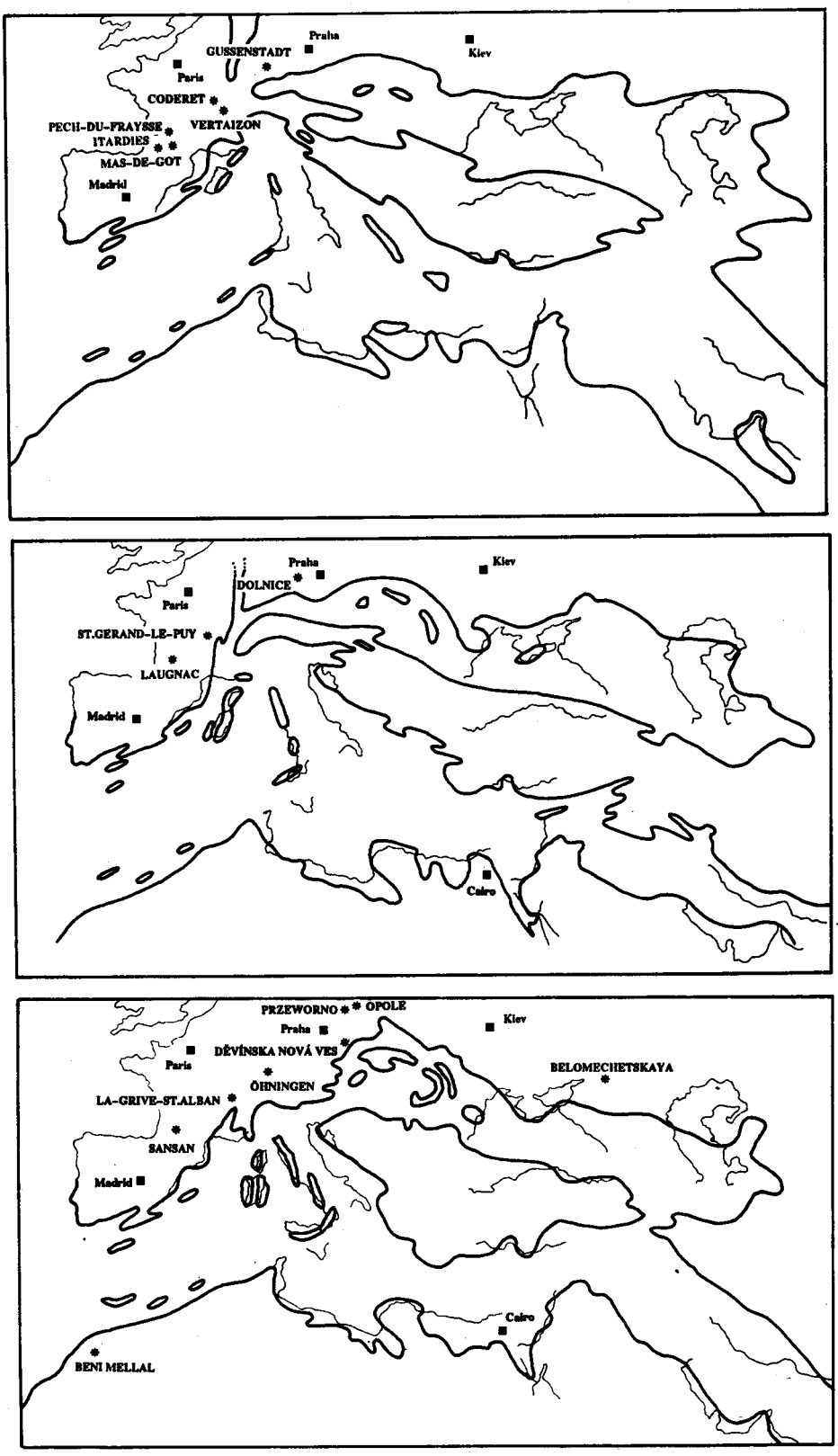
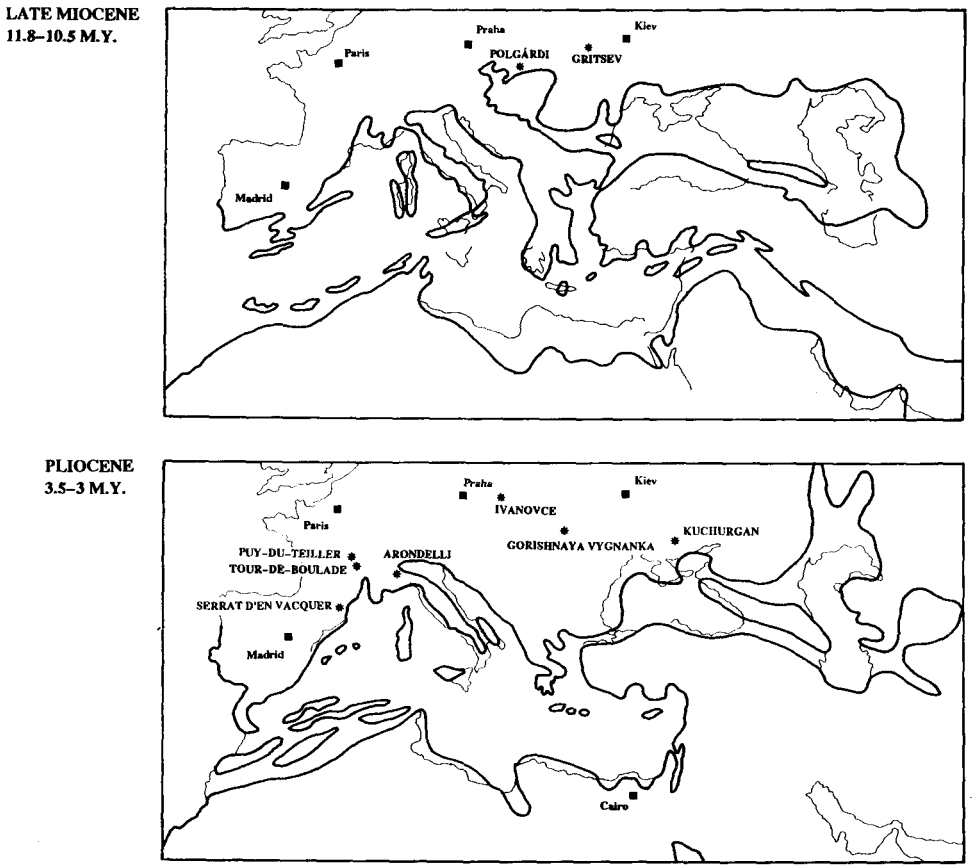


Figure 20 - Main stages of paleogeographic development in central and southern Europe, with approximate position of finding sites with ***Latonia*** (marked by asterisks). Thin lines represent contemporary continental outlines. Based on palinspastic maps by Rögl & Steininger (1983). *Stades principaux du développement paléogéographique en Europe centrale et du Sud, avec positions approximatives des gisements à Latonia (marquées par les astérisques). Contours des continents actuels en ligne fine. Basé sur les cartes palinspastiques de Rögl & Steininger (1983).*



but remained close to V2 and V3. It is exposed posteriorly. The centra of all praesacrals (Fig. 4) are crushed but transverse processes and ribs are either intact (at least proximally, see V2, V5, V6) or preserved as complete imprints. The rib on V3 bears typical posterior process. The sacral processes are crushed but they seem to be dilated and their anterior margin was originally about perpendicular to the axis of the vertebral column. Some time after von Meyer described the specimen in 1845 it was broken into two halves along the urostyle and later stuck together. Consequently, the urostyle was destroyed and is lacking now.

Besides the humeri, radioulnae, ilia, and one complete femur (distinctly S-shaped), also both clavicles are preserved (one close to the pterygoid, another one close to the right praearticular, both with bifurcated lateral end), as well as the pterygoid (in the upper left part of the specimen). In the latter bone, only the ramus posterior and tip of the ramus interior are broken off (Fig. 8E), however, because it is partly embedded in matrix its precise extent cannot be determined. Close to the proximal end of the left humerus there is an imprint of the bone that was interpreted by Rage & Hossini (in press) as the coracoid. This interpretation is correct (Fig. 16H). Other preserved elements are imprints of the suprascapulae and fragments of the prooticooccipitals.

Stratigraphic distribution - Middle Miocene.

Geographic distribution - Öhningen, S. Germany (v. Meyer 1843a ; 1843b ; 1845).

Remark - Both specimens with articulated skulls are embedded in sediment by their dorsal side. Consequently it is impossible to say whether maxilla is covered with sculpture. For this reason, further preparation is needed. Only after solution of this problem it will be possible to decide whether *L. seyfriedi* is conspecific with some of other species of *Latonia* recognized in this paper (in any case it would have the nomenclatoric priority), or if it is distinguishable from all of them.

LATONIA VERTAIZONI (FRIANT, 1944)

1944 - *Prodiscoglossus vertaizoni* - Friant, p. 561, Fig. on p. 562.
1992 - *Latonia* cf. *L.* n.sp. de Laugnac - Hossini, p. 113.

Holotypus - Complete skeleton exposed by its ventral surface, preserved on a single slab with part of the postcranial skeleton of another individual ; Centre des Sciences de la Terre, Université Claude-Bernard, Villeurbanne, FSL 150.900. Illustrated in Friant (1944 ; 1960, figs 7, 8). See also Fig. 19.

Stratum typicum - Stampien, Upper Oligocene.

Locus typicus - Vertaizon (Puy-de-Dôme, France).

Diagnosis - Maxilla smooth ; proc. coronoideus of praearticular less elevated if compared with other species of *Latonia* ; transverse processes of sacral vertebra narrow, only slightly dilated towards their ends, approximately perpendicular to main body axis.

Redescription of holotype (see Fig. 19) - The skeleton is exposed by its dorsal side but only ventral elements are preserved (cf. Friant 1944 : 561 ; 1960 : 125, 127). The individual was not fully matured because the cartilaginous epiphyses of the femurs and tibiofibulae were obviously large (ends of bones are flat) and not preserved as imprints (i.e., they were detached before fossilisation).

The sphenethmoid, frontoparietal, and nasals are not preserved. Only basal part of the right prooticooccipital with a short section of the semicircular canal is preserved. Similarly, only ventral parts of the praemaxillae are preserved, but they do not display any special features. Their outer surface is smooth. On both maxillae their anterior laminae are preserved, and the posterior half of the right maxilla is broken off above the lamina horizontalis. Removing of matrix along its outer surface up to the level of the teeth revealed that this surface is smooth. The quadratojugal is preserved on the left side, only slightly displaced from the original position. The right pterygoid is well preserved, with its ramus maxillaris and ramus interior nearly in the original position. The posterior part of the parasphenoid is preserved in dorsal (i.e. inner) view ; it is obvious that there was a distinct processus posterior, and that anterior and posterior margins of the lateral processes were raised, with rather deep depression between them. The processus coronoideus of the praearticular (especially on the right side ; see also Fig. 12F) is nearly vertical, but prominent in lesser degree than in other forms of *Latonia*. There is a vertical shallow groove running down on its posterior surface. The dentary is preserved as a thin, vertically compressed bone, with its mentomandibular part distinctly thickened. Among indeterminate fragments scattered inside skull outlines might be a remnant of the vomer.

The vertebral column consisted of eight praesacral opisthocoelous vertebrae. The atlas is preserved for the most part as an imprint of its ventral surface. V3 and V4 bear stout transverse processes, rather constricted in the middle, with articulated free ribs. The ribs belonging to V3 bear posterolaterally directed process, those on V4 lack such process. V5-V8 are provided with long and slender transverse processes ; those on V5 are directed posterolaterally, on V6 and V7 laterally, and on V8 anterolaterally. The sacral vertebra is preserved only as a short proximal section of the left transverse process ; this is, however, sufficient to indicate that the anterior margin of the process was perpendicular to the axis of the vertebral column. The urostyle is horizontally broken along the whole its length ; it is obvious that there was a longitudinal cavity at the level of the vertebral centra, and a pair of short posterolaterally directed processes. The clavicle is an arch-like element with two outgrowths on its lateral end, possibly with a groove along its posterior margin. The coracoid was recovered from matrix left to the atlas ; it is distinctly S-shaped, with its intumescentia glenoidalis rounded, and the pars epicoracoidealis dilated and dorsoventrally flattened. Only fragment of the flattened dorsal part of the left scapula is preserved. Both humeri are preserved in lateral view. It is obvious that their crista ventralis was conspicuously prominent. Both radioulnae are crushed and for the most part preserved as imprints in matrix. The distal part of the left anterior limb is comparatively well preserved. One may distinguish the centrale, radiale, and ulnare in the carpal region, and nearly complete fingers. The pelvic girdle is partly crushed, with the ilia preserved as imprints. It can be judged from the imprint of the left ilium that its anterior tip was horizontally compressed, slightly dilated, and it could reach the level of V8. The femur was distinctly S-shaped, the tibiofibulae are represented by crushed bone and incomplete imprints. The astragalus and calcaneum were free. The tarsal elements are too crushed to be determinable, and only proximal phalanges of toes are preserved.

There is still another individual preserved behind the left posterior limb of the individual just described. It can be considered as the paratype. Its size was about 3/4 of the former (judging by the length of the humeri and radioulnae), and is, similar to the former individual, also preserved in dorsal aspect. It is broken at the level of the floor of the neural canal ; consequently, only broken transverse processes or their imprints are preserved. Close to the cranial end of the column there is a pair of arch-like elements that are in touch medially, and tapering laterally. It may be inferred from the shape and position of these elements that they are parahyoid ossifications. Right hand is rather well preserved, with three broken carpal elements comparable to those in the holotype.

Stratigraphic distribution - Stampien (Upper Oligocene, MP 30) to Agenian (Lower Miocene, MN1 and MN2).

Geographic distribution - Vertaizon, Coderet, sites included under the name St-Gérand-le-Puy, France.

Remarks - "*Prodiscoglossus*" was transferred to *Latonia* because of presence of two coronoid processes on the praearticular, the nature of the costo-vertebral articulation, morphology of the rib on V3, and S-shaped femur. There are no diagnostic characters that would distinguish "*Prodiscoglossus*" from *Latonia*. Špinar (1976b : 54-55), on the basis of data published by Friant (1944 ; 1960), considered *Opisthocoelellus weigelti* KUHN, 1941 identical with *Prodiscoglossus vertaizoni* FRIANT, 1944. This suggests that taxonomic identity of this Geiseltal discoglossid should be re-studied (if its fragmentary nature allows), on the background of contemporary knowledge on *Latonia*. Isolated maxillae from St. Gérand le Puy (Fig. 9C) and Coderet (Fig. 10C, D) agree in absence of sculpture ; they are larger than those of *Discoglossus* and do not differ from those of *L. vertaizoni*. This, together with corresponding age was the main reason why this material is assigned to the latter species. Hossini (1992 : 113) considered material from Coderet even identical with *L. ragei* from Laugnac. This is not excluded (in such a case *L. ragei* would be a synonym of *L. vertaizoni*) because both taxa are separated only on the basis of gigantism of the form from Laugnac (perhaps also by the shape of sacral transverse processes but this should be confirmed by more numerous material). The Oligocene material from Mas de Got, Itardies, and Pech du Fraysse published by de Bonis *et al.* (1973 : 110) and Crochet (1971 : 316) should be re-investigated and compared with *L. vertaizoni*.

LATONIA sp.

1890 - *Diplopelturus ruscinensis* - Depéret, p. 172, pl. 18, figs 15-20.

Geographic distribution - Serrat d'en Vacquer, France.

Remarks - "*Diplopelturus*" is a synonym of *Latonia* because of (1) other skeletal elements of the corresponding size from Serrat d'en Vacquer (its locus typicus) belong to *Latonia* (Fig. 12A, 16D, 17D), and (2) that the principal diagnostic character of "*Diplopelturus*" (i.e., the lamina horizontalis of the urostyle is dilated posterior to the transverse processes which gives an impression of the second, additional pair of the transverse processes ; both pairs are connected with a section of moderately dilated lamina which causes that the proximal pair of the transverse processes is also dilated antero-posteriorly) occassionally occurs also in *L. ragei* (Fig. 15C, D ; see also Vergnaud-Grazzini 1970, Fig. 2C). Some possibility that *Diplopelturus* could be a synonym of *Latonia* was already suggested by Rage & Vergnaud-Grazzini (1972 : 86). Additional material is needed for a decision whether "*Diplopelturus*" is conspecific with some known forms of *Latonia* or if it might be considered a separate species.

LATONIA sp.

The discoglossid from the Middle Miocene (Astaracian, MN7) of Beni Mellal in Morocco is represented only by humeri, ilia and urostyles. According to Vergnaud-Grazzini (1966 : 54) this form recalls large discoglossids (i.e., *Latonia*) from La Grive St.Alban, and is different (though not too much) from contemporary *Discoglossus*. This suggests that it belongs to *Latonia* (see also Sanchíz & Alcover 1984) but further material is needed before a decision will be made whether it represents a separate form or it can be assigned to some of already existing. Because of some minor morphological differences and its geographic occurrence the former possibility is preferred for the time being.

LATONIA indet.

Sanchíz (1989) briefly mentioned *Latonia* from 18 sites of continental Greece. Age of these localities is Vallesian to Ruscinian. He referred all this material to "giant *Latonia seyfriedi*". Since other information was not yet published nothing precise can be said about taxonomic assignment of this material.

Hodrová (1987b : 348-352) mentioned unidentified material of *Latonia* from the Astaracian

(MN6-8 in her 1987a paper, but MN8-9 in 1987b) of the locality Suchomasty 3 (Czech Republic).

Hossini (1992 : 124) tentatively assigned to *Latonia* several fragmentary vertebrae from the locality Saint-Menoux (age not given).

MATERIAL POSSIBLY RELATED TO *LATONIA*

Several specimens from the Middle Eocene deposits of Geiseltal, deposited in the Geiseltalmuseum in Halle (Saale), display characters on the basis of which it would be possible to relate them to the genus *Latonia*. This concerns the holotype of *Archaeopelobates eusculptus* KUHN, 1941 (GM CeIII/6728 ; illustrated in Kuhn 1941, pl. 4, Fig. 1 and pl. 8, Fig. 3) and holotype of *Palaeopelobates geiseltalensis* KUHN, 1941 (GM 6692 ; illustrated in Kuhn 1942, pl. 1, Fig. 4 and Estes 1970, Fig. 10). Estes (1970 : 305) considered both specimens conspecific with *Eopelobates hinschei* (KUHN, 1941). However, their frontoparietal is remarkably similar to that of *Latonia*. For instance, the posterior margin of the facies dorsalis runs out in a short vertical ridge slanting down onto the facies posterior but tapering and disappearing before reaching the ventral margin of the bone. This is well seen in all adult *Latonia* (see e.g. Špinar 1978, pls. 64a, 65a,c) whereas in pelobatids there is a wide median convexity instead caused by a median element incorporated into the frontoparietal complex in the course of development (Roček 1981, figs 43, 50). There is no foramen pro a.occipitalis on the facies posterior of the frontoparietal ; its presence is characteristic for pelobatids. Further typical characters of these specimens are as follows : The facies dorsalis is much wider anteriorly than posteriorly, its lateral margins being moderately compressed close to its posterior end. The tectum supraorbitale is not developed. The frontoparietal, nasals and maxillae are covered with sculpture ranging from pits (nasal, posterior part of the frontoparietal, middle part of the maxilla) to straight grooves (anterior part of the frontoparietal, posterior part of the maxilla), both pits and grooves being separated by rather wide, rounded ridges. The anterior outer surface of the maxilla is smooth and sculpture reaches up to the level of the processus frontalis. There is no sharp border between smooth and sculptured surfaces.

Besides characters of the frontoparietal and maxilla that recall those of *Latonia*, in specimen GM 6692 the posterior part of the otic capsules are provided with long, discoglossid-like processes (called the prominentia ducti semicircularis posterioris in Fig. 5). Such long, compressed outgrowths were never found in pelobatids. On the same specimen (GM 6692) there seems to be disarticulated rib on the left side, belonging to V3, with a distinct, posterolaterally directed outgrowth.

Unfortunately, decisive characters on both specimens are not preserved. On the left side of GM 6728 is only part of the praearticular exposed from below the maxilla, and presence or absence of two coronoid processes can only be estimated (but not evidenced) on the basis of bone proportions.

These two specimens may be considered belonging to a single form because of the same type of sculpture and some other characters. Tentatively assigned to them may be GM 6689 in which only right part of the frontoparietal is preserved. On the other hand, discoglossid affinities of these specimens are contradicted by the trasverse processes of the posterior vertebrae which are strongly inclined anteriorly, and by presence of the parasagittal ridges on the neural arches. Both these features are typical for pelobatids. Kuhn's (op. cit. : 363) statement that praesacral vertebrae are procoelous cannot be unequivocally confirmed, and also unfused sacral and urostyle (in adult) may deserve some attention. Moreover, in GM 6755 are ilia that bear well pronounced tuber superius. This confused situation suggests that the taxonomic status of these specimens should be reinvestigated.

Archipelobates giganteus, considered to be a pelobatid by K.Tatarinov (1970), is a large fossil anuran from the Late Pliocene of the Ukrainian locality Gorishnaya Vygnanka. As it was never formally described it should be considered the nomen nudum (Chkhikvadze 1984 : 6). However, its large size and presence of sculpture may indicate that it could be *Latonia*.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The first record of the Discoglossidae in Europe is from the Middle Jurassic of England (*Eodiscoglossus oxoniensis* EVANS, MILNER & MUSSET, 1990). Another discoglossid, *Eodiscoglossus santonjae* MELENDEZ *in* VILLALTA, 1957 is from the Late Jurassic and early Cretaceous (Estes & Sanchíz 1982) of Spain. Hitherto undescribed anuran with supposedly discoglossid affinities is known from the Jurassic of Portugal (Krebs, pers. comm. 1981). *Wealdenbatrachus jucarensis* FEY, 1988 from the Early Cretaceous of Spain is most pro-

LOCALITY	AGE *)	ORIGINAL DETERMINATION	SOURCE
Mas de Got and Itardies, Quejcy (France)	Middle Oligocene	*Discoglossus* cf. *giganteus*	de Bonis et al.,1973: 110
Montalban (France)	Middle Oligocene	*Discoglossus* cf. *giganteus*	Rage, 1984, tab.1
Les Chapelins (France)	Middle Oligocene	*Discoglossus* cf. *giganteus*	Rage, 1984, tab.1
Antoingt (France)	Middle Oligocene	*Discoglossus* cf. *giganteus*	Rage, 1984, tab.1
Boningen (France)	Upper Oligocene	*Discoglossus* cf. *giganteus*	Rage, 1984, tab.1
Pech du Fraysse (France)	Upper Oligocene	*Discoglossus giganteus*	Crochet, 1971: 316
Vertaizon (France)	Upper Oligocene (Stampien)	*Prodiscoglossus vertaizoni*	Friant, 1944
Gussenstadt (Germany)	Upper Oligocene (Chattian)	tibiofibula "ähnlich schlank wie an dem rezenten Wasserfrosch aber über doppelt so lang"	Dehm, 1935: 53, pl.4, fig.16
Coderet (France)	Upper Oligocene (MP 30 and MN 0)	*Latonia* cf. *L. vertaizoni*	this paper
St. Gérand le Puy (France)	Agenian (MN 1 and MN 2)	*Latonia* cf. *L. vertaizoni*	this paper
Laugnac (France)	Agenian (MN 2b)	*Latonia ragei*	Hossini, 1993
Navarette del Rio (Spain)	Agenian (MN 2b)	*Latonia* sp. II	Sanchíz, 1977: 104
Dolnice (Czech Republic)	Orleanian (MN 4)	*Miopelobates fejfari*	Špinar, 1975a
La Grive St.Alban (France)	Astaracian (MN 5, MN 7 and MN 8)	*Latonia gigantea*	this paper
Belomechetskaya (Russia)	Tchokrakian (MN 5)	*Latonia* cf. *seyfriedi*	Chkhikvadze, 1988
Sansan (France)	Astaracian (MN 6)	*Latonia gigantea*	Rage & Hossini, 1993
Devínska Nová Ves (Slovakia)	Astaracian (MN 6)	*Discoglossus giganteus*	Wettstein–Westersheimb, 1955: 808
Devínska Nová Ves (Slovakia)	Astaracian (MN 6)	*Miopelobates zapfei*	Wettstein–Westersheimb, 1955: 812
Devínska Nová Ves (Slovakia)	Astaracian (MN 6)	*Neusibatrachus estesi*	Sanchíz & Mlynarski, 1979: 158
Beni Mellal (Morocco)	Astaracian (MN 7)	*Discoglossus* sp.	Vergnaud–Grazzini, 1966: 54
Opole (Poland)	Astaracian (MN 7)	*Latonia* cf. *seyfriedi*	Mlynarski et al., 1982: 109
Opole (Poland)	Astaracian (MN 7)	*Latonia seyfriedi*	Mlynarski, 1984: 133
Öhningen (Germany)	Astaracian (MN 7)	*Latonia seyfriedi*	von Meyer, 1843b: 580
Przeworno II (Poland)	Astaracian (MN 8)	*Discoglossus giganteus*	Mlynarski, 1976; 1979: 154–158
Przeworno II (Poland)	Astaracian (MN 8)	*Latonia seyfriedi*	Mlynarski, 1984: 133
Przeworno I (Poland)	Middle Miocene	*Latonia* cf. *seyfriedi*	Sanchíz & Mlynarski, 1979: 154
Suchomasty 3 (Czech Republic)	Astaracian (MN 6–8)	*Latonia* sp.	Hodrová, 1987b
Gritsev (Ukraine)	Vallesian (MN 9a)	*Latonia gigantea*	this paper
Can Llobaterez (Spain)	Vallesian (MN 9)	*Latonia* sp. I	Sanchíz, 1977: 104
Masía del Barbo II (Spain)	Vallesian (MN 10)	*Latonia* sp. I	Sanchíz, 1977: 104
Rudabánya (Hungary)	MN 11	*Latonia* sp.	Roček, pers. observ.
Tardosbánya (Hungary)	MN 12	*Latonia* sp.	Roček, pers. observ.
Polgárdi (Hungary)	Turolian (MN 13)	*Rana batthyanyi*	Bolkay, 1913: 221
Polgárdi (Hungary)	Turolian (MN 13)	*Pelobates robustus*	Bolkay, 1913: 219
continental Greece	Vallesian – Ruscinian	*Latonia seyfriedi*	Sanchíz, 1989: 89
Kuchurgan (Ukraine)	Ruscinian (MN 14)	*Latonia seyfriedi*	Chkhikvadze, 1981: 152
Ivanovce (Slovakia)	Ruscinian (MN 15)	*Latonia kolebabi*	Špinar 1978: 292
Serrat d'en Vacquer (France)	Ruscinian (MN 15)	*Diplopelturus ruscinensis*	Depéret, 1890: 172
Séte (France)	Ruscinian (MN 15)	*Latonia* sp.	Bailon, 1991: 58–59
Tour–de–Boulade and Puy–du–Teiller (France)	"Villanyian"	"*Pipa*? ou animal trés voisin"	Pomel, 1844: 593
Arondelli (Italy)	"Villanyian" (MN 16)	*Discoglossus* cf. *D. giganteus*	Vergnaud–Grazzini, 1970: 48–53
? Gorischnaya Vygnanka (Ukraine)	Late Pliocene	*Archipelobates giganteum*	Tatarinov, 1970; ex Chkhikvadze, 1981:152
Püspökfürdö (Hungary)	Early Biharian	*Pelobates robustus*	Fejérváry, 1917: 154

Table 1 - Geographic and stratigraphic distribution of the genus ***Latonia***. *) Mainly after Mein (1990) and Steininger *et al.* (1990). *Distribution géographique et stratigraphique du genre* ***Latonia***. **) Principalement d'après Mein (1990) et Steininger et al. (1990).*

bably another discoglossid. Although most of this material is fragmentary, its relations to the Discoglossidae seem to be beyond doubt. However, one should also take into consideration a peculiar group of Cretaceous anurans represented by the genus *Gobiates,* which display transitional morphology between the leiopelmatids and discoglossids (Rocek & Nessov 1993).

Paleogene discoglossids of Europe are known from the Middle Eocene of Geiseltal (*Opisthocoelellus weigelti* KUHN, 1941, *Germanobatrachus beurleni* KUHN, 1941, and *Rana carbicola* KUHN, 1941). Although Geiseltal anurans are considerably crushed and Kuhn's diagnoses insufficient, the discoglossid affinities of this material seem to be clear (see also Vergnaud-Grazzini & Wenz 1975 ; Špinar 1976b : 54). *Opisthocoelellus hessi* Špinar, 1976 from the Oligomiocene of Bechlejovice (Czech Republic), and *Discoglossus troscheli* (v. MEYER, 1852) from the Upper Oligocene of Rott near Hennef in Germany are other two discoglossids.

Among the Neogene European discoglossids belongs (besides *Latonia*) an undeterminated and probably lost discoglossid from the Lower Miocene of the vicinity of Mainz (Hochheim) mentioned by Zittel (1893 : 421). *Pelophilus agassizi* TSCHUDI, 1839 is a peculiar anuran from the Middle Miocene locality Öhningen that was considered by Mlynarski *et al.* (1982) to be closely related to *Bombina*. Isolated bones of *Bombina* of the same age were described from Opole, Poland by Mlynarski *et al.* (1982), and other Polish localities Waze I and Rebielice Królewskie I of Pliocene age (Sanchíz & Mlynarski 1982 : 159). Material determined as Discoglossidae was reported from several Miocene (Escobosa de Calatanazor, Venta del Moro, Alcoy) and possibly also Pliocene (El Arquillo II) localities of Spain (Sanchíz 1977 : 104-105). Since postcranial skeletons of *Latonia* and *Discoglossus* are nearly identical and precise data on the material from Spain is not available, one can only speculate about occurrence of the discoglossids other than *Latonia* in the Tertiary Spanish localities.

It follows from this account that between the Late (probably Middle, as suggested by de Bonis *et al.* 1973 : 110) Oligocene and Late Pliocene, the period for which *Latonia* is documented, other discoglossids were extremely scarce. Only in Öhningen, Opole, Séte, and with much doubt in Escobosa de Calatanazor, *Latonia* was accompanied by another discoglossid. In Bechlejovice, despite of several hundreds of anuran skeletons belonging mostly to the Palaeobatrachidae and in lesser extent to Pelobatidae, only one specimen of the Discoglossidae was found (*Opisthocolellus hessi*), but no *Latonia*. Also in Rott *Latonia* was absent and discoglossids were rare, in contrast to abundant Palaeobatrachidae. Same holds for Waze I and Rebielice Królewskie I where the discoglossid determined as *Bombina* was present but no *Latonia*. In the great majority of sites where anurans were recovered, *Latonia* was the only representative of discoglossids. This may suggest that small discoglossids could not compete with *Latonia*. *Latonia* probably did not survive climatic changes during the Early Pleistocene though it was still widely distributed at the end of the Pliocene (Fig. 20). On the other hand, discoglossids (identified as *Discoglossus*) from the Middle Pleistocene and younger deposits were much more abundant (see Lanza *et al.* 1986 : 17 for review). This seems to speak in favour of the hypothesis that *Latonia* was replaced in the early Pleistocene by *Discoglossus* and that *Latonia-Discoglossus* transition, possibly caused and accelerated by paedomorphosis (see below), was probably due to deterioration of climate expressed in cyclical seasonal changes. Thus, abbreviation of development could be an adaptive response to shortening of time available for both praemetamorphic and postmetamorphic developmental processes. Seasonality was periodically accompanied by temporary expansion of the polar glacier up to central Europe resulting in withdrawal of discoglossids (as well as of other European anurans) southwards. Whereas *Bombina* (another paedomorphic discoglossid ; see Smirnov 1989) expanded later again far northwards up to Scandinavia, the distribution of *Discoglossus* remains restricted to the Mediterranean, and *Alytes* to Atlantic climatic areas (Lanza *et al.* 1986).

EVOLUTION OF THE GENUS *LATONIA*

Early European discoglossids may be anatomically exemplified by *Eodiscoglossus santonjae* (see also Hecht 1970 ; Vergnaud-Grazzini & Wenz 1975) which is represented by nearly complete articulated skeletons. These anurans were small to medium-size, with paired and smooth frontoparietal. Their maxilla and praemaxilla were dentate, the praearticular with no distinguishable processus coronoideus. Vertebrae were with imbricate neural arches and with free ribs on V2-V4. Sacral transverse processes were dilated both anteriorly and posteriorly in the holotype, but seem to be only moderately dilated in other specimens (Vergnaud-Grazzini & Wenz 1975 : 10, figs 2, 3). This set of available characters represents the evolutionary level of early discoglossids, and

can serve for ascertainment of polarity of evolutionary trends in *Latonia*.

First undoubted *Latonia* (besides the finding from the Middle Oligocene briefly mentioned by de Bonis *et al.* 1973 : 110 and the Geiseltal anurans discussed above) is recorded from the Upper Oligocene (*L. vertaizoni*). It was of medium size and with smooth maxilla. It cannot be distinguished, on the basis of characters available, from disarticulated bones from Coderet and localities included under the name St-Gérand-le-Puy (MP30 - MN2). It is obvious that this comparatively small and "smooth" *Latonia* lived from the Late Oligocene to Early Miocene and probably continued as a lineage of *L. ragei*, characterized with a trend towards the "gigantism". This lineage probably did not survive until Middle Miocene. It should be noted that Sanchíz (1977 : 104) distinguished two forms of *Latonia* in his review of Spanish fossil anurans ; one of them (*Latonia* sp. II of the same age as *L. ragei* ; see Table 1) could be an unsculptured *Latonia*, but pertinent data are not available.

However, already in the Lower Miocene (Dolnice ; MN4) another *Latonia* appeared, the average size of which was similar to that of *L. vertaizoni*, but with sculpture on the posterior and suborbital sections of the maxilla. It may be considered as the earliest record of *L. gigantea* which rapidly spread all over the Europe and, perhaps, to north Africa (Russia, MN5 ; Morocco, MN7 ; see, however, remarks on p. 29 concerning the latter). Also this lineage was generally characterized by increasing body size but the trend did not reach the same degree in all localities (compare largest individuals from Sansan, MN6 with Ivanovce, MN15). It was already noted that sculpture was a secondary bone deposition, this being evidenced both in structure of the bone and its development. It is not excluded that this lineage includes also material from Öhningen (in such a case, because of nomenclatoric priority, the name *gigantea* should be replaced by *seyfriedi* ; see also p. 27).

It is obvious that the principal evolutionary changes which characterize the origin of *Latonia* is fusion of the both frontoparietals, appearance of two coronoid processes on the praearticular, and probably (but not for sure) slendering of sacral transverse processes. Changes that occured in the course of existence of *Latonia* are limited only to size and sculpture.

Similarity of the postcranial skeleton of *Latonia* with that of *Discoglossus* (disregarding size) and similarity of the skeleton of young *Latonia* and adult *Discoglossus* may lead to some speculative explanations concerning the origin of the latter. First, *Discoglossus* could develop from *Latonia* by cutting off final stages of development. Such developmental abbreviation, if the hypothesis would be correct, affected exclusively the cranial skeleton. It is known that neoteny, and in lesser extent also paedomorphosis, are manifested in structure of the skull. Hence, paedomorphosis would be a possible explanation for similarities of cranial structure in young *Latonia* and adult *Discoglossus*, and possible evolutionary mechanism of the origin of the latter. In such a case *Discoglossus* would not be very old ; this seems to be confirmed by recent discoveries made by Lanza *et al.* (1986) that suggest continuing rich evolutionary diversification within this genus. Second hypothesis is that *Discoglossus* can be a derivate of some ancestral discoglossid which was shared also with *Latonia*. It is not excluded that this *Latonia-Discoglossus* ancestor could come from Asia, which might be suggested by close morphological affinities of Cretaceous discoglossids from central Asia with *Discoglossus* (Roček & Nessov 1993). For a decision which of these two hypotheses is more probable a revision of European Tertiary discoglossids other than *Latonia* is urgently needed.

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Abbreviations used in figure captions :

DP FNSP - Department of Paleontology, Charles University, Albertov 6, 128 43 Prague, Czech Republic.
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