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Inter- and intraspecific variation in the post-natal skull of some lacertid lizards

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Abstract

Intra- and interspecific variation are analysed for the post-natal skull of the lacertid lizards *Gallotia galloti, Acanthodactylus erythrurus, Algyroides marchi, Lacerta monticola, Lacerta vivipara, Podarcis bocagei, Podarcis hispanica, Podarcis muralis, Psammodromus algirus* and *Psammodromus hispanicus*. Individual variations identified include: the presence/absence, number and morphology of some structures, mainly in the lacrimal, sclerotic ossicles and maxilla; the number and location of foramina and the degree of ossification of some processes in chondrocranial bones. No differences have been found between the sexes with respect to presence and morphology of the bones but some species show sexual dimorphism in the size and robustness of the head and this may be reflected in the individual. The most substantial variations seen are ontogenetic: the appearance of new traits; development of articulations; differences between species in the timing of the stages of development of a given structure; changes in the relative position of some cranial elements; and the degree of calcification or ossification of processes. A total of 63 characters showing interspecific variations are identified. Some have not previously been described while others used in previous studies are redefined here on the basis of new morphological information obtained.

Key words: Squamata, Lacertidae, post-natal skull development, intraspecific–interspecific variation

INTRODUCTION

Studies of inter- and intraspecific variation have gained relevance in the last two decades due to interest in heterotopy and heterochrony, and the need for information on sexual and individual variation in evolutionary and phylogenetic studies. Knowledge of intraspecific variation permits more accurate character definition and can help to interpret the evolutionary history of some groups that have been subject to evolutionary changes in development rates, timing, and spatial patterns (Irish & Alberch, 1989; Griffith, 1991; Fucik, 1992). In addition, the comparative anatomy of recent taxa is important in the identification of Plio-Pleistocene taxa.

Despite considerable work on the anatomy and development of the squamate skull, coverage has been uneven (Bellairs & Kamal, 1981). Whereas there is much information about the development of the chondrocranium, accounts of the embryonic osteocranium are relatively scarce (Haluska & Alberch, 1983; Abdeen & Zaher, 1992; Hallermann, 1992; Rieppel, 1977, 1987, 1992*b*, 1993, 1994; Good, 1995), as are those of the post-natal skull (Hikida, 1978; Mohammed, 1991; Rieppel, 1992*a*, *c*).

The present paper aims to assess similarity and differences in the anatomy and ossification of the post-natal skull within a group of closely related lizards (lacertids from the Iberian Peninsula), and to describe intraspecific variation which can be of help in the interpretation of lizard evolution.

MATERIALS AND METHODS

An ontogenetic series of cleared and stained examples of the lacertid lizard species *Gallotia galloti, Acanthodactylus erythrurus, Algyroides marchi, Lacerta monticola, Lacerta vivipara, Podarcis bocagei, Podarcis hispanica, Podarcis muralis, Psammodromus algirus* and *Psammodromus hispanicus* (hatchlings through adults of both sexes – Table 1) were prepared at constant temperature, using the methods described in Taylor (1967) and Zug & Crombie (1970). The subspecies described in the Iberian

Table 1. Measurements of the pileus length (mm) in different stages in articulated skulls (measured from tip of skull to occipital scale and determined to an accuracy of 0.5 mm). x, average; s^2, variance; min, minimum; max, maximum

	Stage 1		Stage 2		Stage 3		Stage 4	
Species	n	x, s^2 min–max	n	x, s^2 min–max	n min–max	x, s^2	n	x, s^2 min–max
G. galloti	3	10.57, 0.02 10.4–10.75	8	11.28, 0.13 10.8–11.8	4	13.03, 0.75 11.85–14	9	24.02,14.43 20.9–34.1
P. algirus	11	7.77, 0.08 7.3–8.2	6	9.08, 0.35 84–9.7	8	12.12, 0.26 11.45–13.1	15	16.01, 1.04 14.37–18.55
P. hispanicus	9	6.77, 0.07 6.27–7.3	14	7.91, 0.10 7.3–8.4	13	9.35, 0.27 8.4–10	4	10.41, 014 10–11
A. erythrurus	5	8.12, 0.22 7.2–8.5	4	9.99, 0.98 9–11.5	7	13.40, 1.37 12–15.25	14	15.97,0.24 15.55–17.35
A. marchi	5	6.8, 0.05 6.55–7.1	3	9.23, 0.01 9.1–9.4	6	10.31, 0.05 9.95–10.65	5	11.08, 0.05 10.7–11.45
P. hispanica	4	7.03, 0.07 7–7.1	8	8.37, 0.07 8.05–8.9	9	11.28, 0.65 10.1–12.9	5	14.44, 0.39 13.4–15.5
P. muralis	5	6.91, 0.01 6.8–7.05	6	7.56, 0.04 7.25–7.9	9	11.84, 1.62 9.75–13.2	10	15.58, 0.27 14.7–16.4
P. bocagei	5	6.91, 0.03 6.7–7.15	11	8.35, 0.36 7.35–9.25	14	10.51, 0.45 9.3–11.5	17	12.68, 0.53 11.95–14.8
L.. monticola	16	7.1, 0.19 6.3–8	10	10, 1.27 8.2–11.35	30	13.41, 0.96 11.35–14.75	25	16.45, 1.25 14.8–18.5
L. vivipara	4	5.98, 0.02 5.8–6.2	8	6.71, 0.02 6.4–6.9	9	8.38, 0.67 7.15–9.45	8	10.57, 0.5 9.6–11.6

Table 2. Measurements of the pileus length (mm) in disarticulated skulls (measured from tip of skull to occipital scale and determined to the accuracy of 0.5 mm). x, average; s^2, variance; min, minimum; max, maximum

Species	n	x, s^2 min–max	n	x, s^2 min–max
G. galloti	8	28.62, 13.36 24.9–24.7	6	21.35, 20.35 11.8–25.7
P. algirus	12	14.9, 10.77 8.45–18.7	12	13.43, 4.27 8.05–16.45
P. hispanicus	15	9.71, 0.66 8.3–11	19	9.28, 0.47 7.45–10.4
A. erythrurus	15	13.1, 9.79 8–17.17	12	12.4, 8.57 9–15.85
A. marchi	15	10.54, 1.12 7.9–11.75	9	9.64, 0.51 8.4–10.5
P. hispanica	15	11.04, 3.06 8.25–13.4	18	9.94, 1.62 6.95–11.5
P. muralis	18	13.13, 3.65 7.55–15.25	16	11.77, 1.92 7.5–13.7
P. bocagei	17	11.46, 4.63 8.5–15.25	8	10.68, 3.004 8.5–12.45
L. monticola	12	14.09, 4.43 11.7–17.8	13	13.05, 2.63 9.95–15.4
L. vivipara	14	9.09, 2.32 6.5–11.2	12	9.70, 0.46 7.84–10.35

Peninsula for *L. monticola* and *P. bocagei* were included. Measurements were taken with callipers before clearing and staining and the illustrations were made using a stereo microscope equipped with a camera lucida. For a more detailed understanding of the skull, the anatomy was also studied using disarticulated skull material (Table 2). The hyoid and columellar apparatus and left eye were removed in the examples to be able to see the bones covered by them. The collection is held in the Department of Biology, Universidad Autónoma de Madrid (Spain). Catalogue numbers for the specimens studied are: UAM.R.Ac1–Ac54, UAM.R.Al1–Al43, UAM.R.Gg1–Gg38, UAM.R.H1–H56, UAM.R.Lm1–Lm104, UAM.R.Lv1–Lv56, UAM.R.M1–M61, UAM.R.Pb1–Pb76, UAM.R.Ph1–Ph81, UAM.R.Ps1–Ps64. Abbreviations are as follows: UAM.R, Universidad Autónoma de Madrid Reptiles; Ac, *A. erythurus*; Al, *A. marchi*; Gg, *G. galloti*; H, *P. hispanica*; Lm, *L. monticola*; Lv, *L. vivipara*; M, *P. muralis;* Pb, *P. bocagei*; Ph, *P. hispanicus*; Ps, *P. algirus.*

We recognize 4 successive developmental stages that group specimens with similar anatomical features. The first stage represents captive bred newborn (*P. algirus, P. hispanicus, A. erythrurus* and *L. monticola*) as well as examples collected in the field with sizes similar to those described by Braña (1986), Barbadillo, Castilla and Borreguero (1987), Castanet & Báez (1991), Galán (1992) and Díaz-Uriarte (1993). The last stage describes the general morphology of the adult skull, that is, for each species, the size stage reached at which no or few further morphological modifications take place in relation to the traits under consideration. Between newborn and adult, we recognize 2 intermediate stages. The sequences of the changes are quite similar in all species, and for this reason are described in detail only for *G. galloti*. For the remaining species we note only the most important differences with reference to *G. galloti*.

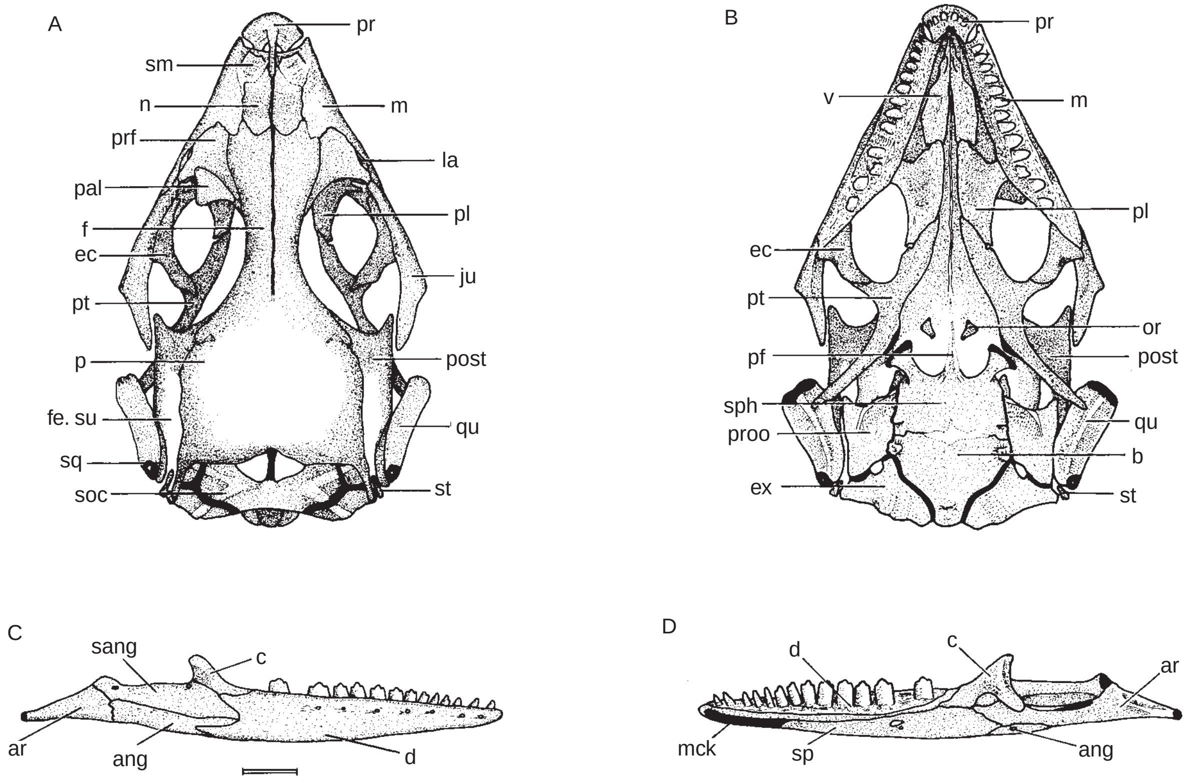

Fig. 1. Dorsal (A) and ventral (B) views of the cranium and lateral (C) and medial (D) views of the mandible of *Gallotia galloti* (UAM.R.Gg29) at Stage 1. Abbreviations: ang, angular; ar, articular; b, basioccipital; c, coronoid; d, dentary; ec, ectopterygoid; ex, exooccipital; f, frontal; fe.su, fenestra supratemporal; ju, jugal; la, lacrimal; m, maxilla; mck, Meckelian canal; n, nasal; or, orbitosphenoid; p, parietal; pal, palpebral; pf, parasphenoid ; pl, palatine; post, postorbitofrontal; pr, premaxilla; prf, prefrontal; proo, prootic; pt, pterygoid; qu, quadrate; sang, surangular; sm, septomaxilla; soc, supraoccipital; sp, splenial; sph, sphenoid; sq, squamosal; st, supratemporal; v, vomer. Scale bar = 1 mm

RESULTS

Developmental stages of the skull

Stage 1

Skull size is given in Table 1.

Figure 1. In newborn *G. galloti*, the skull is relatively shorter and broader than in the adult, is not depressed, and has large orbits and nares. All bones are present except the supraoculars, cranial and infratemporal osteoderms.

Joints between bones in the neurocranium are separated by wide growing cartilaginous areas. The distal ends of the basipterygoid processes, the orbitosphenoids and the processus ascendens of the supraoccipital also remain cartilaginous. The basicranial fenestra is open. The ventrolateral crests of the sphenoid and spheno-occipital tubercles are barely developed and do not contact. The semicircular canals and supratrigeminal processes are very conspicuous. The alar process of the prootic is scarcely developed and does not reach the epipterygoid. In the auditory fossa there are four foramina for the auditory and facial nerves. The posterior and paroccipital processes of the prootic and otooccipital are barely developed. The basipterygoid processes of the sphenoid are expanded laterally and medially, with a basal constriction at the junction with the sphenoid body.

The bones derived from the splanchnocranium also retain cartilaginous areas, notably the distal parts of the cephalic and mandibular condyles of the quadrate; the condyle and the posterior tip of the retroarticular process in the articular; and both ends of the epipterygoid. The quadrate has not developed the pterygoid lappet. At this stage the pterygoid meniscus and the intercalary cartilage are visible. The columella is completely ossified and has a relatively shorter body and a larger footplate than in adults; the extracolumella is cartilaginous. In the hyoid apparatus the first ceratobranchial is ossified, and there are 14 ossified sclerotic ossicles, as occur in other lacertid lizards (Underwood, 1984).

Some parts of the dermatocranium are either unossified (anterior and central area of the parietal and frequently posteromedial area of the frontals) or only partially ossified (dorsal process of the maxilla, anterior part of the nasal, anterolateral process of the palatine and rostrum of the parasphenoid).

The frontals are strongly constricted so that the medial edges of the pterygoid and palatine are visible in dorsal view. The anteromedial edges of both frontals touch but the posteromedial ones are divergent. The ventral process of the frontal does not reach the palatine crest and the suture between this process and the posteroventral process of the prefrontal is discontinuous, appearing as a gap between both processes. The parietal is ossified along its lateral margins and its posterior parts, so that there is no dermal bone covering of the brain (except for the olfactory tract). The lappets of the parietal are scarcely defined and the pineal foramen is not visible. The posterior processes of the parietal are short, narrow and arranged in parallel. In ventral view the parietal fossa has a broadly convex shape and the ventral crests are continuous and weakly developed.

The posterodorsal process of the premaxilla has parallel borders and barely separates the tips of the nasals. The overlap of the anterior process of the maxilla onto the premaxilla is incomplete, leaving a small gap between both structures. However, the posterior process of the nasal and the dorsal process of the maxilla overlap the frontals to some degree.

The bones of the supratemporal arch are present but the dermal covering of the upper temporal fenestra is incomplete. The posterior process of the prefrontal is short and does not reach the narrowest area of the frontal. Postfrontal and postorbital form a single postorbitofrontal bone. The quadratojugal process of the jugal is well developed. The lacrimal is tiny and very thin, with a pointed posterior end. It is located between the prefrontal, maxilla and jugal. The squamosal is slightly curved medially with a hockey stick shape. The supratemporal is also a very small bone, located between the posterior process of the parietal, squamosal, paroccipital process and quadrate.

In the palate, the anterior border of each vomer fails to reach the incisive process of the premaxilla, while the lateral margin reaches but does not overlap the medial margin of the maxilla, leaving the vomeronasal fenestra and the choana incompletely separated (paleochoanate). The septomaxilla has a rounded posterolateral margin and can be seen in a dorsal view of the cranium. The anteromedial processes of the pterygoids are convergent, enclosing a wide pyriform recess; there are no pterygoid teeth. The lateral areas of articulation between vomer–palatine and palatine–pterygoid have not established contact, and the anterior process of the ectopterygoid does not reach the palatine.

In the mandible, the anterior region of the splenial is reduced and the Meckelian canal is more open than in the adult. Meckel's cartilage extends from the articular to the symphysis of the dentary. At the posterior margin of the dentary the ventral process is larger than the dorsal one, while the dorsal process of the coronoid is directed posteriorly.

Gallotia galloti shows heterodonty. In the premaxilla, all teeth are of approximately the same size and are monocuspid, with a central cusp and a convex external surface. There is a diastema between the premaxillary and maxillary teeth. In the maxilla and dentary the morphology of the tooth crown experiences a gradual change from anterior to posterior, thus the first dental positions are occupied by small monocuspid teeth, asymmetric in lingual view with the cuspid orientated distally. In the following positions, the teeth show a groove or a small, sometimes almost imperceptible, cuspid on the anterior lingual surface, which becomes more prominent on posterior teeth. The intermediate positions are occupied by larger teeth, some bicuspid with a principal distal cusp and another much smaller mesial one, some tricuspid with a central principal cusp and smaller mesial and distal secondaries. The change from bicuspid tooth to tricuspid is similar to that described for monocuspid–bicuspid, with the difference that the groove appears in the posterior zone of the tooth. The last positions are occupied by tricuspid teeth a little larger than the more anterior ones.

At the equivalent stage, the remaining species have a similar pattern to that described for *G. galloti,* although the following differences have been found: the snout is already depressed in *A. erythrurus* and in *L. vivipara* the nares are small; in *A. erythrurus*, *A. marchi, L. monticola, Podarcis* spp.*, L. vivipara* and *P. hispanicus* the nasal lacks an anteromedial process, but this process begins to develop very early in the post-natal ontogeny; the postfrontal and postorbital remain separate in *A. erythrurus, Podarcis* spp., *L. monticola* and *A. marchi* (Fig. 5a); in *Podarcis* spp. the posterior process of the prefrontal is long and reaches the most waisted zone of the frontal; the posterior process of the maxilla has a lateral step in *L. monticola monticola* and *Podarcis* spp. (Fig. 5b); *A. erythrurus* lacks a quadratojugal process on the jugal (Fig. 5c); the quadrate has already developed a well-developed pterygoid lappet in *Podarcis* spp.; in *A. erythrurus* the septomaxilla has no posteromedial process and the posterolateral margin is angular (Fig. 5d); in *A. erythrurus* and *P. hispanicus* the lateral margin of the vomer fails to reach the medial border of the maxillary shelf; the auditory fossa of the prootic contains three instead of four foramina in *L. vivipara, A. marchi, Podarcis* spp. and *L. monticola* (Fig. 5e); in *A. erythrurus* the dentary has posterior projections of equal length, while the retroarticular process is expanded posteroventrally (Fig. 5f); in *L. vivipara* the ventrolateral crests of the sphenoid reach the sphenooccipital tubercles; *A. erythrurus* has 13 complete scleral ossicles with only the radial portion (Fig. 5g). The dentition in all of these species is formed mainly by monocuspid teeth and some bicuspid teeth.

Two intermediate stages have been defined between the hatchling and the adult. However, the changes between the stages are gradual and in some cases there is no correlation between the specimen size, the degree of ossification and development of structures.

Stage 2

Skull size is given in Table 1.

Figure 2. In this stage the skull shows the following differences with respect to those described previously: in

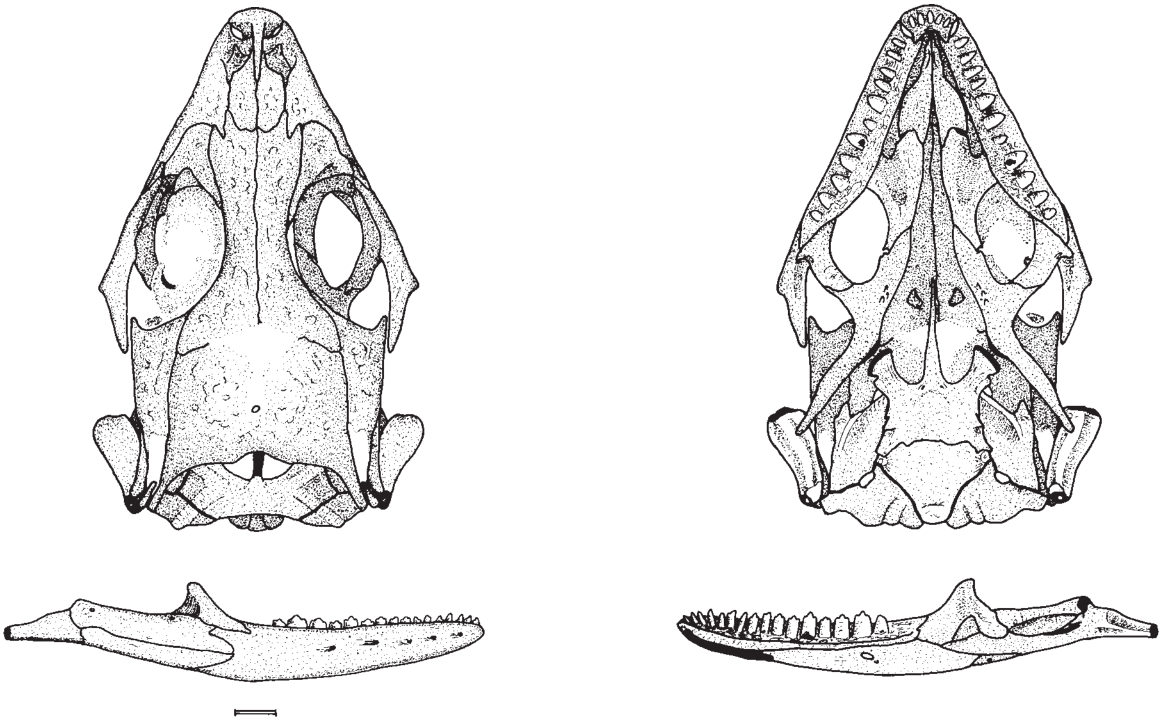

Fig. 2. Dorsal (left) and ventral (right) views of the cranium of *Gallotia galloti* (UAM.R.Gg27) at Stage 2. Scale bar = 1 mm.

the neurocranium, the joints between bones are almost calcified; the basicranial fenestra is smaller, but still open; the ventrolateral crest of the sphenoid reaches the sphenoccipital tubercles, and a lateral expansion appears at the base of each basipterygoid process.

The bones that develop from the splanchnocranium are in a similar state to that described for Stage 1, although they have experienced some degree of calcification. In the quadrate, the pterygoid lappet starts to develop.

The anterior area of the nasal is ossified and the posterior part is superimposed over the frontal. The frontal is less constricted. Both frontals increase their ossification in the medial region and the closure of the parietal progresses from lateral to medial. The area around the pineal foramen and the anterior margin of the parietal are not yet ossified, but the pineal foramen is already defined. The ventral crests of the parietal (posterolaterals and anterolaterals) touch. The posterior end of the frontal is ossified and the interdigitations become distinctive, but not very pronounced.

The posterodorsal process of the premaxilla is more developed and is introduced deeply between both nasals. The tip of the dorsal process of the maxilla is more pronounced and narrower and becomes superimposed on the anterolateral process of the frontal.

The palatal shelf of the jugal develops a medially directed process and the squamosal extends posterolaterally. The postorbitofrontal ossifies anteroposteriorly but in an unequal way, being stronger in its lateral zone.

The anterolateral process of the ectopterygoid touches the lateral process of the palatine and the first pterygoid teeth appear. The first and second supraoculars start to ossify peripherally and the third appears as a small central nodule. The parasphenoid ossifies posteroanteriorly and in its central zone. The number of teeth and the proportion of tricuspid teeth increase.

At this stage the frontals are already fused and remain waisted in *A. erythrurus* (Fig. 5h). In *L. monticola, L. vivipara, Podarsis* spp., *P. hispanicus* and *A. marchi* the projections of the dorsal process of the maxilla are ossified but do not overlap the frontal. The palatal shelf of jugal lacks a medial process in *A. erythrurus, A. marchi, Podarcis* spp., *L. monticola* and *L. vivipara* (Fig. 5i). The squamosal does not undergo posterior development in *A. erythrurus, A. marchi, Podarcis* spp. or *Lacerta* spp. (Fig. 5j), and in *L. vivipara* the anterolateral process of the ectopterygoid does not yet reach the palatine (Fig. 5k). In *P. hispanicus, A. erythrurus* and *A. marchi* the ventrolateral crests of the sphenoid are closer to the sphenooccipital tubercles but do not touch them, while in *A. erythrurus* the basipterygoid processes have retained the juvenile form with no development of the ventrolateral crest (Fig. 5l). As in *G. galloti*, the number of teeth increases in all species, but there are a majority of bicuspid teeth and only sporadically some tricuspids.

Stage 3

Skull size is given in Table 1.

Figure 3. In the neurocranium, the base of the ascending process of the supraoccipital is ossified, the sutures between the bones are visible but not cartilaginous,

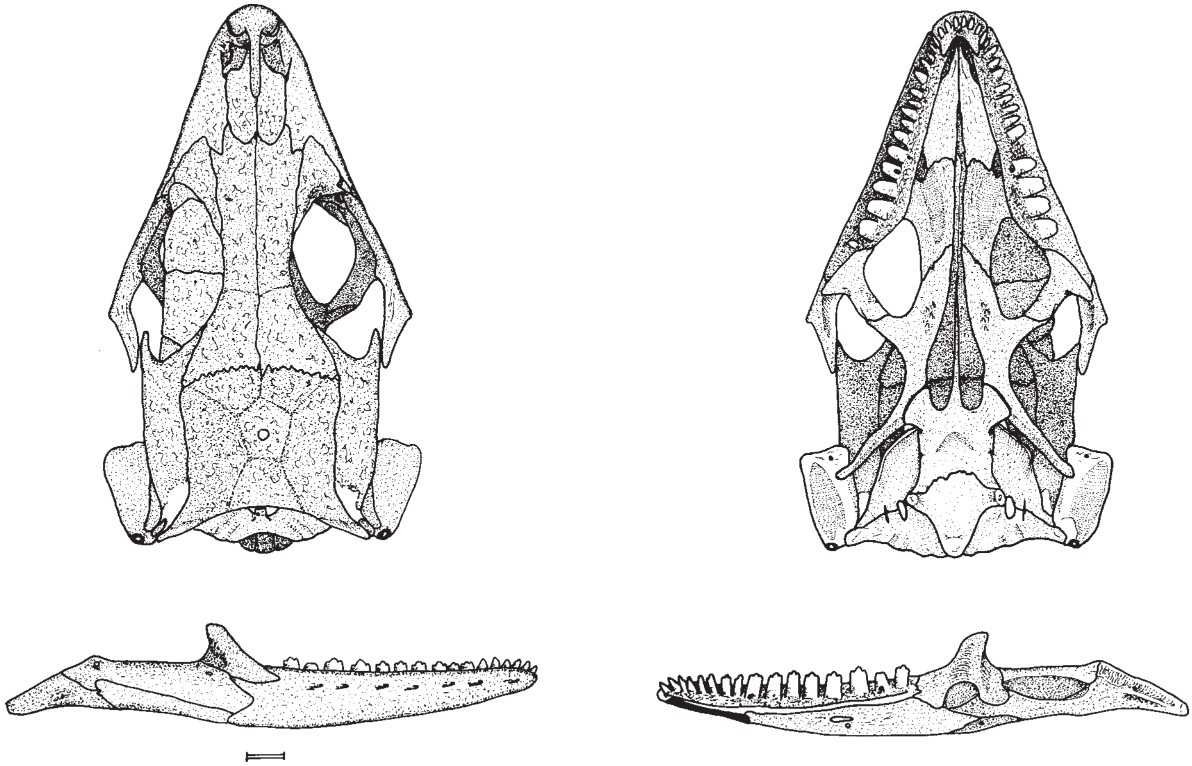

Fig. 3. Dorsal (left) and ventral (right) views of the cranium of *Gallotia galloti* (UAM.R.Gg35) at Stage 3. Scale bar = 1 mm.

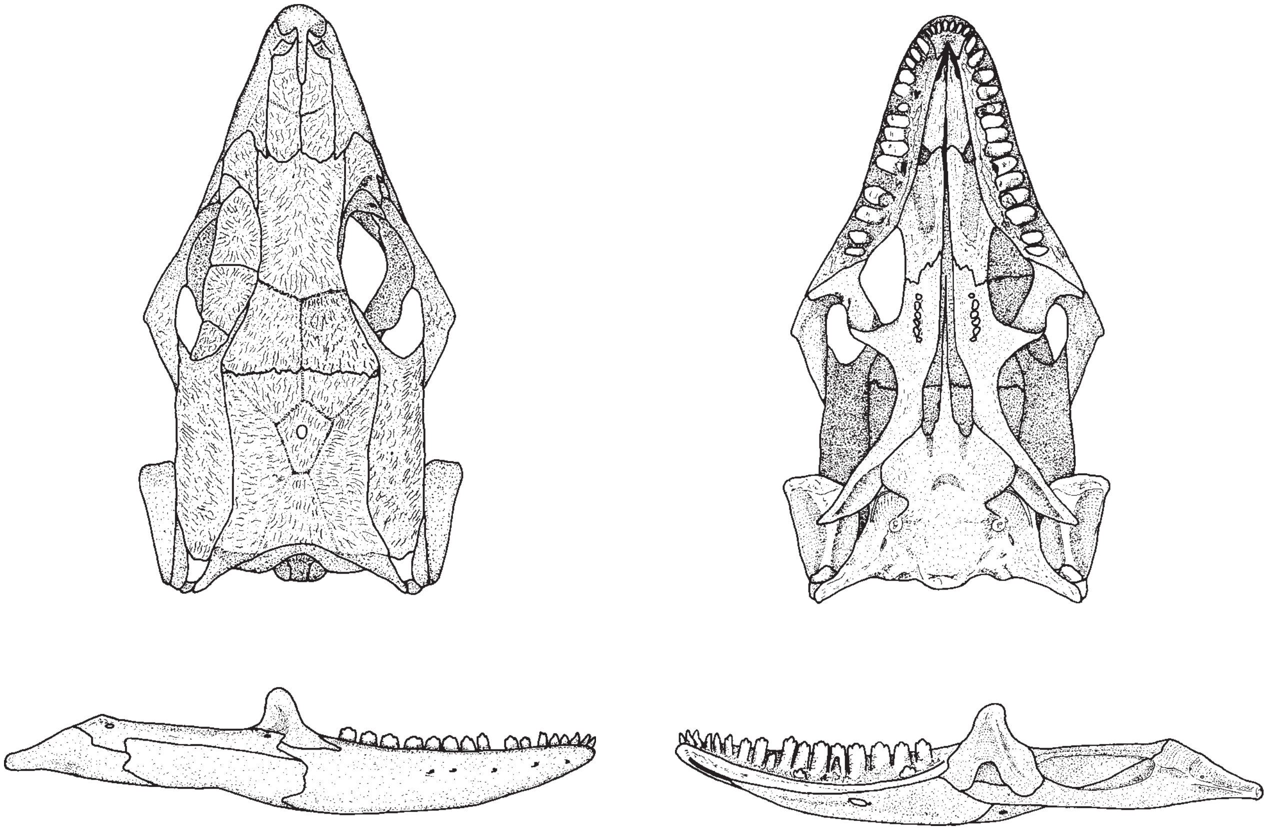

Fig. 4. Dorsal (left) and ventral (right) views of the cranium of *Gallotia galloti* (UAM.R.Gg13) at Stage 4. Scale bar = 1 mm.

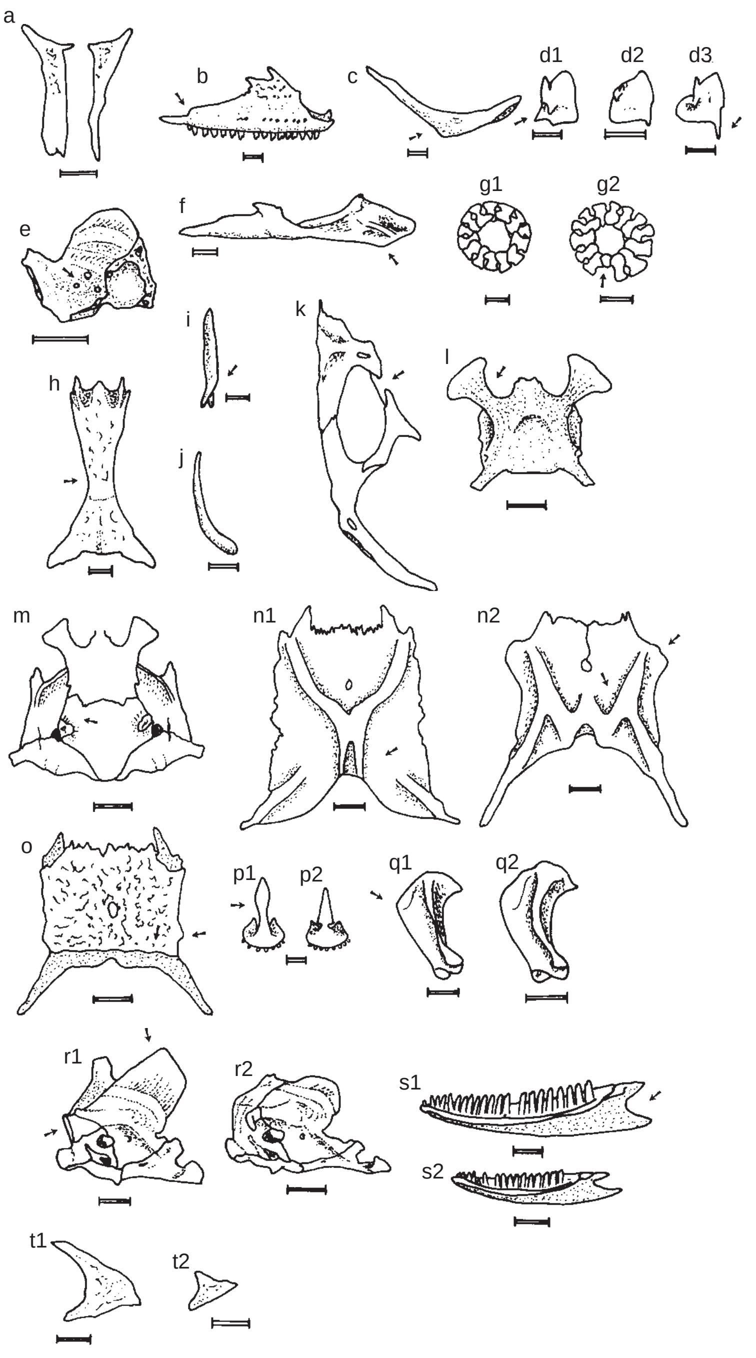

Fig. 5. a, Dorsal view of the postfrontal and postorbital of *A. marchi* (UAM.R.Al.2); b, lateral view of the maxilla of *L. m. monticola* (UAM.R.L.m.76); c, lateral view of the jugal of *A. erythrurus* (UAM.R.Ac.1); d, dorsal view of the septomaxillae, d1, *A. erythrurus* (UAM.R.Ac.1), d2, *A. marchi* (UAM.R.Al.2), d3, *P. algirus* (UAM.R.Ps.11); e, medial view of the prootic of *A. marchi* (UAM.R.Al.2); f, medial view of the articular of *A. erythrurus* (UAM.R.Ac.1); g, scleral ossicles of g1, *P. algirus* (UAM.R.Ps.54) and g2, *A. erythrurus* (UAM.R.Ac.23); h, frontals of *A. erythrurus* (UAM.R.Ac.1); i, dorsal view of the jugal of *L. monticola* (UAM.R.Lm.76), j, squamosal of *P. hispanica* (UAM.R.H.30); k, schematic illustration showing the relation between the ectopterygoid and palatine in *L. vivipara*; l, ventral view of the sphenoid of *A. erythrurus* (UAM.R.AC.11); m, ventral view of the neurocranium of *A. marchi* (UAM.R.Al.2); n, ventral surface of the parietal of n1, *P. algirus* (UAM.R.Ps.11) and n2, *A. erythrurus* (UAM.R.Ac.1); o, dorsal view of the parietal of *L. vivipara* (UAM.R.Lv.1); p, frontal view of the premaxilla in p1, *A. erythrurus* (UAM.R.Ac.1) and p2, *L. monticola* (UAM.R.Lm.76); q, medial view of the quadrate in q1, *A. erythrurus* (UAM.R.Ac.1) and q2, *L. vivipara* (UAM.R.Lv.1); r, lateral view of the neurocranium in r1, *P. algirus* (UAM.R.Ps11) and r2, *A. marchi* (UAM.R.Al.2); s, lateral view of the dentary in s1, *P. algirus* (UAM.R.Ps.9) and s2, *L. vivipara* (UAM.R.Lv.14) dentary; t, palpebral of t1, *A. erythrurus* (UAM.R.Ac.1) and t2, *P. algirus* (UAM.R.Ps.11) . Scale bars = 1 mm.

the basipterygoid processes are more robust and still have cartilage at their tips. The alar process of the prootic contacts the epipterygoid. The ventral surface of the sphenoid is depressed. The alar and basipterygoid processes touch; this feature only occurs in *Gallotia* spp. (pers. obs.). In some individuals, the quadrate already shows a developed pterygoid lappet. Both condylar areas are more ossified, but the cephalic condyle remains cartilaginous around the tympanic foramen. The anterior border of the vomer has established contact with the incisive process of the premaxilla and its posterior process now overlaps the maxillary shelf (neochoanate). The ventral process of the prefrontal touches the palatine crest. The vomer–palatine and palatine–pterygoid articulations are completely established and the supraoculars are ossified.

The parietal is ossified completely, shows interdigitations and the posterior edge of the parietal fossa is straight. The arrangement of the ventral crests of the parietal change; the posterolateral and anterolateral crests do not touch.

At this stage *P. algirus* and *A. erythrurus* already show pterygoid teeth. In *A. erythrurus* the anterior margins of the supraoccipital are in parallel. In *A. marchi* and *A. erythrurus* the alar process of the prootic fails to touch the epipterygoid and, with the exception of *A. marchi,* the ventrolateral crests of the sphenoid touch the basal tubera (Fig. 5m). *A. erythrurus* and *P. algirus* also have the ventral surface of the sphenoid depressed and with the exception of *P. algirus*, the remaining species retain the juvenile arrangement of the ventral crests of the parietal (Fig. 5n). In *A. erythrurus*, *L. m. monticola* and *L. monticola cyreni* the supraoculars are not yet completely ossified. *A. erythrurus, L. vivipara* and *P. hispanicus* retain the posterior edge of the parietal fossa concave and the parietal osteoderms do not reach the posterior edge (Fig. 5o).

Stage 4

Skull size is given in Table 1.

Figure 4. The skull in adults of *G. galloti* is relatively higher and more robust, with the snout less depressed. The nares are small and the gap between the maxilla and premaxilla disappears completely.

In the neurocranium the ascending process and the apices of the basipterygoid processes are ossified, the sphenooccipital tubercles have epiphyses and the posterior and paroccipital processes of the prootic and otooccipital are well developed. The Meckelian canal is smaller than in the anterior stages and Meckel's cartilage remains cartilaginous anteriorly. The articular condyle, retroarticular process and both ends of the epipterygoid are ossified.

The frontals are little waisted (the lateral edge of frontal reaches the level of the lateral edge of the palatine) and the dorsal process of the maxilla is superimposed extensively over the anterolateral process of the frontal. The posterior border of the parietal covers the anterior edge of the supraoccipital and reaches the level of its posterior one in larger individuals. There is no gap between the ventral processes of the frontal and prefrontal. The supratemporal fenestra is closed in larger individuals. Cephalic osteoderms are widely distributed on the skull roof and reach the posterior edge of the parietal.

The anteromedial processes of the pterygoids are arranged in parallel so that the pyriform recess is narrow throughout most of its length. The pterygoid teeth are arranged linearly. In the dentary the dorsal projection is larger than the ventral one. Adults of *G. galloti* have a majority of tricuspid teeth rather than monocuspid or bicuspid teeth. In the third or fourth tooth position, the maxillae of the largest individuals have two or three teeth larger than the rest, and these can be bicuspids or tricuspids. In general, large individuals have very worn occlusal surfaces to the teeth.

Adults of the remaining species differ from *Gallotia* in that:

a) the skull is more depressed in *P. muralis, P. hispanica* and *A. marchi,*
b) the nares are small in all species except *A. erythrurus, A. marchi,* and *L. monticola,*
c) in *P. hispanicus* and *A. erythrurus* the snout has a medial depression,
d) in *P. hispanicus, A. erythrurus, A. marchi* and *L. vivipara* the posterior margin of the parietal does not reach the anterior edge of the supraoccipital,
e) in many individuals of *A. marchi,* the anterior process of the maxilla does not completely overlap the premaxilla,
f) in *Lacerta* spp. and in *A. marchi* the dorsal process of the maxilla is not superimposed extensively on the frontal,
g) in a lateral view of the skull of *A. erythrurus,* the anterior process of the jugal is well exposed,
h) in *A. erythrurus*, the parietal lappets have got lateral expansion (Fig. 5n2),
i) the posterodorsal process of the premaxilla is leaf-shaped in *A. erythrurus* and *L. vivipara*, and arrow-shaped in *L. monticola* (Fig. 5p),
j) in *P. hispanicus* and *A. erythrurus* the superposition of the posterior process of the vomer above the palatal platform of the maxilla is less than in the other species,
k) the anterolateral process of the ectopterygoid and the palatine touch in all species except in *L. vivipara,*
l) the anteromedial processes of the pterygoids are convergent in all species except in *P. algirus* where they are almost in parallel,
m) in a medial view of the quadrate, the anterior border is angular in *A. erythrurus* and rounded in the remaining species (Fig. 5q),
n) in *P. hispanicus* the quadrate has not developed a pterygoid lappet,
o) the alar process of the prootic remains scarcely developed in *A. erythrurus* and *A. marchi* (Fig. 5r),
p) the posterior and paroccipital processes of the

prootic and otooccipital are short in *P. hispanica, P. hispanicus, L. vivipara* and *A. marchi* (Fig. 5r),

q) in the dentary, the ventral projection is longer than the dorsal one in *P. hispanicus, A. marchi, L. monticola* and *L. vivipara* while both are almost the same size in *P. algirus* (Fig. 5s),

r) the number of premaxillary teeth in *G. galloti, A. erythrurus* and *Podarcis* spp. is almost constant at seven, although *L. monticola, A. marchi* and *L. vivipara* have more than eight teeth,

s) in these species the teeth are monocuspid in the premaxilla and the first positions of the maxilla and dentary, and bicuspid in remaining positions with a few tricuspid teeth occasionally. The proportion of bicuspid teeth is highest in all these species except *L. vivipara* where the proportions of mono- and bicuspid teeth are similar,

t) dental hypertrophy in the maxilla occurs only in *G. galloti*,

u) the palpebral is relatively larger in *A. erythrurus* and has a dorsoposterolateral process and a concave posterior margin (Fig. 5t),

v) cephalic osteoderms are scarcely developed in *A. erythrurus*,

x) *P. algirus* develops infratemporal osteoderms.

Sexual dimorphism and individual variation

No differences have been found between the sexes with respect to the presence and morphology of the bones, but individual variation is relatively frequent.

The most common individual variations are: in *L. vivipara* the presence/absence of the lacrimal, of a fissure in the ventral crest of the premaxilla, and in the number of sclerotic ossicles (13–14); in *P. muralis* the different morphologies of the posterodorsal process of the premaxilla, both margins in parallel or with a leaf shape; in *P. algirus, P. hispanicus* and *G. galloti* the degree of fusion of frontals; in *A. erythrurus* the contact between posterolateral process of the premaxilla and the frontal; in *A. erythrurus, L. m. monticola* and *L. m. cantabrica* the open or closed pineal foramen; in *A. erythrurus* and *A. marchi* the presence/absence of an anterior fissure in the parietal; and in *G. galloti* and *A. erythrurus* the development of the quadrate lappet and the ossification of the cephalic condyle.

Generally, in each species, the different stages of ontogenetic ossification are reached in a range of body sizes. Thus, for a given size, some individual variation exists in the degree of ossification of the parietal, frontal, dorsal process of the maxilla, ventral process of prefrontal and the neurocranial bones. In adults of *G. galloti* and *P. algirus* the supratemporal fenestra is generally closed, but there are some exceptions in those species where the adults are small. Thus a significant proportion of adults of *A. erythrurus, A. marchi, P. bocagei bocagei, P. hispanicus, L. vivipara, L. monticola, P. muralis* and *P. hispanica* retain an open supratemporal fenestra while the posterior tip of the postorbital curves and touches the parietal in some adults of *P. bocagei, A. erythrurus* and *A. marchi.* There is also individual variation in newborns: in *G. galloti* in the degree of the contact between the anterolateral process of the ectopterygoid and palatine; in *A. erythrurus, A. marchi, Podarcis* and *L. monticola* in the presence/absence of palpebrals; and in *P. algirus* in the posterior development of the squamosal.

DISCUSSION AND CONCLUSIONS

Ontogeny, articulations and cranial kinesis

In the hatchlings of all species, all cranial bones are represented except intradermal ossifications (supraoculars, cranial and infratemporal osteoderms), although the degree of ossification varies. Thus, those bones that form the palate (vomer, palatine, pterygoid and ectopterygoid); the dermal bones of the mandible; and those that define the outline of the cranium (like the jugal, squamosal and postorbital), are completely ossified. This is probably because these bones are the first to be ossified in the dermatocranium, as in *Podarcis sicula, Lacerta agilis* and *L. vivipara* (Rieppel, 1976, 1977, 1992*b*, 1994). On the other hand, not all areas of these bones show the same level of ossification. Those areas that form the edges of the skull are more fully ossified: the palatal region of the maxilla and premaxilla, the lateral areas of the postorbitofrontal, frontal and parietal and the posterodorsal process of the prefrontal. Also, those areas that take part in the articulations, whether these are of syndesmotic or synovial nature, are scarcely defined and ossified. So, the articular areas of the bones derived from the chondrocranium and splanchnocranium show large cartilaginous areas and the bones derived from the dermatocranium have either still not established contact or the contact is incomplete.

The individual's development involves a progressive ossification of the bones and a definition of the structures that participate in the articulations. The individual sequence of ossification for each bone has not been observed but seems simultaneous for the large majority of elements. Thus, the bones of the snout region, premaxilla, maxilla and nasal finish their ossification before those of the skull roof, and the posterior region of the frontal ossifies before the anterior region of the parietal. A simultaneity exists in the full ossification of the parietal and neurocranium and this process is the last. All these processes are largely completed in Stage 3.

The changes experienced by structures involved in the joints are very important. Knowledge of these structures and their changes during post-natal ontogeny permits a general hypothesis that increase in individual size during maturity results in a loss/reduction of metakinesis and mesokinesis.

The loss of metakinesis is basically due to the progressive ossification of cartilaginous structures that facilitate the movement between the occipital and maxillary segments, of the connective tissue between the bones of the parietal, rostral and basal units, and of the cartilages of the quadrate and epipterygoid. This increased ossification is necessary for the progressive definition and robustness of the structures that participate in the articulations, and for the adhesion of osteoderms, not only on the surface of the bones, but also on their sutures. The loss of movement in the mesokinetic axis is due to the increase, in number and in grade of development, of the frontoparietal interdigitations. Nevertheless, these processes do not develop in the same way in all species. In the larger species, *P. algirus* and *G. galloti,* the interdigitations are much larger. The situation varies in species of medium size. *A. erythrurus* does not have frontoparietal interdigitations, the processus ascendens of the supraoccipital is scarcely ossified and in a large proportion of adult individuals, the cephalic condyle of the quadrate is incompletely ossified. In contrast, the condition in *L. m. monticola, L. m. cyreni, P. muralis* and *P. b. bocagei* is closer to that of the larger species, although they do not reach the grade of development. The smaller species are also variable. Both *P. hispanicus* and *L. vivipara* have a relatively more ossified skull than *A. marchi*, in which (though not matching the condition of *A. erythrurus)* the number and the development of the frontoparietal interdigitations are less than in remaining species. *P. hispanica, L. m. cantabrica* and *P. b. carbonelli* show a condition intermediate between the medium and small species.

Frazzetta (1962) described the skulls of some lacertids *(Lacerta agilis, Lacerta viridis* and *Podarcis muralis)* as amphikinetic, a condition generalized to the rest of the lacertid lizards. Like Arnold (1993), we consider that the presence of a interdigitated frontoparietal suture with adherent osteoderms effectively prevents dorsoventral movements at the mesokinetic axis. Thus, with the exception of *A. erythrurus,* we propose that all the species described here have monokinetic skulls. This loss of kinesis might be supposed to have a negative effect in the seizing and manipulation of food in the mouth. However, it has been proposed that the presence of pterygoid teeth in larger species can counter this loss (Montanouchi, 1968). Pterygoid teeth occur in the larger of the species described here and in other lacertids of large size (Arnold, 1989*b*).

New features for Lacertidae

The study of a large sample of both articulated and disarticulated skull bones has shed new light on the basic cranial anatomy of the studied lacertids. The differences between the results of this study and those obtained by other authors are due to several factors:

a) in many previous studies, results obtained from the study of a single species and/or the use of a small sample were generalized to the rest of the Lacertidae,

b) few studies have considered intraspecific variation nor included a large sample of disarticulated skull material.

Among the most outstanding anatomical features not previously described (or described for only one species), or differing from the descriptions of other authors are:

1) The presence of the supratrigeminal process. This process is more conspicuous in juveniles and in the smallest species. Estes, de Queiroz & Gauthier (1988) stated that this process is present in Iguania but absent in the rest of the Squamata.

2) Individual variation in the posterior opening of the Vidian canal. According to Estes *et al.* (1988), in lacertids, cordylids, scincids, and xantusiids, the posterior opening is on the prootic/parabasisphenoid suture. In the species studied here, the position of this opening shows individual variation in juveniles and subadults where it can appear wholly within the sphenoid or on the suture between this bone and the prootic. In adults the prootic and parabasisphenoid are fused, so the suture is not visible and the position of the foramen cannot be described with accuracy

3) According to Estes *et al.* (1988), the occipital fossa of the neurocranium is floored by the basioccipital in Scincomorpha, with a tendency for the otooccipital to exclude the basioccipital in its formation. The latter condition has been seen in some examples of *P. bocagei* and *A. erythrurus* and in all subadults of *L. viridis* (pers. obs.). In adults of all species, however, the neurocranium is fused, so this feature cannot be described with any accuracy.

4) Presence/absence of an opening in the anterior wall of the orbit between the prefrontal and frontal. According to Arnold (1983, 1989*b*) this character is variable in *Acanthodactylus, L. vivipara, P. algirus, P. hispanicus, Eremias, Mesalina* and *Ophisops*-*Cabrita* and is present in all species of *Pedioplanis.* The presence/absence of this window shows ontogenetic and individual variation in the species studied and is also present in species not described by Arnold such as *Podarcis* spp., *A. marchi, G. galloti,* and *L. monticola.*

Cranial characters and phylogeny

In addition, there are synapomorphies for Scincomorpha or some of its clades (Estes *et al.*, 1988) which have reverted to the primitive condition in some of the studied taxa:

1) The presence on the quadrate of a well-developed medial pterygoid lappet, stated by Estes *et al.* (1988) as a synapomorphy for Lacertiformes. In the studied species, this character reverts to the primitive condition in *P. hispanicus* and shows individual variation in *G. galloti.*

2) The presence of a well-developed alar process in the prootic has also been considered a synapomorphy, not only of Scincomorpha but of Scleroglossa (all squamates except iguanians) as a whole (Estes *et al.*, 1988). However, in *A. erythrurus* and *A. marchi* this character reverts to a primitive condition. A similar situation is pointed out by Lang (1991) in some genera of Cordylidae.

3) The arrangement of the anteromedial processes of

the pterygoids, which border the pyriform recess. Estes *et al* (1988) stated that the presence of a narrow pyriform recess is the primitive condition and occurs in teiids and in some lacertids, gymnophthalmids, iguanids and agamids. In the studied species, this condition is shown only in large-bodied species, *P. algirus* and *G. galloti*.

4) The participation of the ventrolateral crests of the sphenoid in the formation of the sphenooccipital tubercles is considered by Lang (1991) to be the most derived condition in Scincomorpha. Nevertheless, as in Teiidae and some genera of Cordylidae, this character reverts to the primitive condition in *A. marchi*.

5) In Scincomorpha, the nasals are usually in partial contact in the midline. However, in some individuals of *A. erythrurus*, both bones are completely separated by the posterodorsal process of the premaxilla which reaches the frontal. This same situation has been described in some teiids, gymnophthalmids, and xantusids (see MacLean, 1974; Savage, 1963).

6) The absence/presence and position of the pineal foramen is variable in Scincomorpha. In the Lacertidae, absence has been reported for genera like *Adolphus, Holaspis, Gastropholis, Bedriagaia,* "*Lacerta*" *equinata,* "*Lacerta*" *jacksoni,* and reduction in *Nucras, Poromera* and *Tropidosaura* (Estes *et al.,* 1988; Arnold, 1989*b*). In the studied group, some adults of *L. m. monticola, L. m. cantabrica* and *A. erythrurus* also lack the foramen.

The distribution of some of the characters that have been used in phylogenetic analysis also differs from that given by other authors:

1) Estes *et al.* (1988) reported the absence of a postfrontal in *Lacerta (sensu lato).* The results obtained here indicate that this condition is variable in *Lacerta* since the postfrontal and postorbital are separated in *L. monticola.* A similar situation has been observed in *Lacerta bonnali, Lacerta viridis, Lacerta schreiberi* and in juveniles and subadults of *Lacerta lepida* (pers. obs.).

2) According to Arnold (1989*b*), the squamosal contacts the posterolateral process of the parietal in *Gallotia* spp. and in the Ethiopian forms *(Nucras, Philochortus, Meroles-Aporosaura, Pseudoeremias).* In the examples studied of *G. galloti,* the bones never establish contact and the same situation is shown by *G. atlantica, G. caesaris,* and *G. stehlini* (pers. obs.).

3) The distribution of the osteoderms on the parietal in *P. hispanicus* and *L. vivipara* differs from that described by Arnold (1989*b*). Arnold described the osteoderms as reaching the posterior edge of the parietal, but our examination shows that they arrange more anteriorly.

4) According to Arnold (1989*b*), all species studied here have a squamosal with a hockey-stick shape. In fact, both *G. galloti* and *Psammodromus* spp. have the posterior area medially expanded.

Characters in need of emendation

The study of disarticulated skull bones has also helped to clarify some features that had been misunderstood because they had been described in articulated skulls:

(a) Arnold (1989*b*) described the dorsal process of the maxilla as follows: ‘dorsal process of the maxilla, broad at most only slightly embraced by processes of frontal bone, or narrower and often quite extensively embraced by narrow processes of frontal’. We consider that this character has to be redefined because the frontal does not embrace the maxilla and there is no relation between the size of the dorsal process and how much it overlaps the frontal.

Other such characters in need of emendation include:

(b) The definition of a step in ‘the lower border of outer face of jugal’ when in fact this feature is located in the maxilla, and ‘inner crest of jugal bone clearly visible behind ectopterygoid in ventral view’ when this crest is present on the palatal shelf of the jugal. Contra Arnold, who considered the latter character a synapomorphy of *Psammodromus* spp., the results obtained here show that this feature is also present in *G. galloti, G. caesaris, G. atlantica*, absent in *G. simonyi* and variable in *G. stehlini* (pers. obs.).

(c) The cephalic condyle of the quadrate presents a foramen that is visible in large specimens. Juveniles and subadults lack the foramen but, in dried bones, have in its place a recess which some authors have interpreted as a pit for the posterior tip of the squamosal (Rieppel, 1976). Observations made on stained examples show that this area remains cartilaginous in juveniles and that the foramen is in fact present. During post-natal ontogeny this area ossifies, with bone appearing around the foramen. Hikida (1978) interpreted this ossification as an independent bone, the quadratojugal.

Cranial characters and small size

Some of the characters that are shown by small-sized species have also been described in other small scincomorphs. Thus, short paraoccipital processes are described in Gymnophthalmidae, Cordylidae and burrowing scincids (Jollie, 1960; Rieppel, 1981; Lang, 1991) and Rieppel (1981, 1984) described the presence of conspicuous semicircular canals in Scincidae and Gekkonidae. The presence of a columellar apparatus with a relatively short columella and a large footplate is also true for Gymnophthalmidae (MacLean, 1974) and Feylininae (Rieppel, 1981). We consider that the decrease in cranial diameter results in a reduction in length of the paroccipital processes, a reduction of the relative length of the columella, and more conspicuous semicircular canals, so these features would be convergent in small lizards.

The most significant variations seen are ontogenetic and are related to the appearance of new traits, the evolution of articulations, changes in the relative position of some skull elements, the degree of calcification or ossification of processes, and differences between species in the timing of the stages of development of given structures (heterochrony). The absence of lacrimals in some individuals of *L. vivipara* has also been reported by Rieppel (1992*b*). Like Alberch *et al.* (1979) and Alberch (1989), who described this situation for other cranial bones, we consider that the loss of the lacrimal may be related to paedomorphosis. Also, as proposed by Rieppel (1992*b*), the lacrimal is the last bone to appear in cranial osteogenesis, and there is therefore a greater chance that it may be lost as a result of heterochronic changes.

Cranial characters: ontogeny and phylogeny

In the analysis of lacertid interrelationships (Arnold, 1989*b*), several characters were treated as plesiomorphies on the basis of outgroup comparison and their polarization is also corroborated by ontogeny. These characters are: frontal bones separate throughout life, medial depression on snout absent, postfrontal and postorbital separate, shape of squamosal bone slender, inner crest of jugal not visible behind ectopterygoid, and ossification of temporal scales not extensive. Other features also treated as plesiomorphies by Arnold but not corroborated by ontogeny are: small nasal openings, presence of interdigitations in the fronto-parietal suture and covering of cranial osteoderms extends to back of the parietal.

The results obtained emphasize the necessity of intra- and interspecific studies not only in lacertids but also in other squamates. In addition, they demonstrate the need to take the ontogenic trajectory into account in the definition of characters since there are differences between species in the timing of the stages of development of given structures. Further studies of this kind will permit a more accurate definition of those features useful in phylogenetic analysis and in the identification of fossil remains.

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