COMPARATIVE STUDIES ON LIZARDS BASED ON THE CRANIAL OSTEOLOGY OF *Lacerta media* AND *Laudakia caucasia* (SQUAMATA: SAURIA)

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In spite of numerous studies done on the morphometric characters of lizards, information about the detailed characters of their skeletons remains insufficient. In this study, the skulls of two different species of lizards, cleared and double-stained, have been examined and compared: *Laudakia caucasia* Eichwald, 1831 and *Lacerta media* Lantz and Cyrén, 1920. The aim of this paper is to study the characteristics and peculiarities of the skulls of the two above-mentioned species of lizards in order to facilitate diagnosis and identification of the living species and subfossil remains and to evaluate changes in skull morphology in a phylogenetic context. For doing this, characters of the skull and mandibular elements were studied. The existence of differences between these two genera and families *Laudakia caucasia* (Agamidae) and *Lacerta media* (Lacertidae), according to the bone and skull characters, have been explained. The obvious differences that show off are: dimension of the supratemporal fossae, thickness of the individual bones, and head length/width ratio. Other obvious differences are the type of dentition, differences in form, size and special manner of joining bones like existence of differences in lower jaw and braincase architecture, and reviewing some differences in the skulls of two different phylogenetic lines.

Keywords: cranial osteology, skull, dentition, mandible, *Laudakia caucasia*, *Lacerta media*.

INTRODUCTION

The most complicated of all reptilian skeletal structures and most important in problems of classification and phylogeny is the skull. This undergone a long history of evolution and modification before reaching the reptilian stage (Romer, 1956). The familiar skull of every form from a bony fish to a mammal is a fused, unit structure, in witch braincase and endoskeletal upper jaws are welded together by a series of dermal bones; the lower is not included (Romer and Parsons, 1977).

The skull is a multi-purpose tool involved in a great variety of functions. Its designs reflect and incorporate these multiple roles, like feeding systems (Kardong, 2002). Comparative anatomy of skull between different taxa of lizards for answering to the questions such as structure of the skull and differences and origin of these differences between organisms like lizards has always been a fascinating field (Herrel et al., 1999; Bell et al., 2003; McBrayer, 2004; Stayton, 2005; Faizi and Rastegar-Pouyani, 2007). The first detailed studies on the morphology and development of the lizard skeleton date from the late 19th century (e.g., Parker, 1880, 1881; Gaupp, 1891; Cope, 1892; Siebenrock, 1892, 1893a, 1893b, 1894, 1895; Versluys, 1898).

Although literature records on the osteocranium of adult lizards are quite extensive, comprehensive and detailed descriptions are scarce (e.g., Oelrich, 1956; Jollie, 1960; Torres-Carvajal, 2003).

Some researches give us over point of diet and food habitat, and phylogenetic relationships of some species of lizards (e. g Estes et al., 1988; Etheridge and de Queiroz, 1988; Moody, 1980; Schwenk, 2000; Faizi and Rastegar-Pouyani, 2007). In addition, the skull and its associated musculature participate in sensory roles (Cooper et al., 2001) and sexual selection (Herrel et al., 1999). Nevertheless, functions of the lizard' skull are not fully known.

The two taxa studied here, *Laudakia caucasia* and *Lacerta media*, have frequently been subjects of morphological, ecological and biogeographical studies (e.g., Rastegar-Pouyani, 1999a; Rastegar-Pouyani and Nilson, 2002; Faizi and Rastegar-Pouyani, 2007).

The aim of this paper is to describe differences in the two different phylogenetic lines according to the osteology and a short look on the patterns of feeding methods, among the two above-mentioned taxa of agamiads and lacertids, based on skull elements.

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MATERIAL AND METHODS

Two specimens of *Laudakia caucasia* (mean SVL = 330 mm) (RUZM AL21.78, AL21.75) and four *Lacerta media* (mean SVL = 370 mm) (RUZM LL11.21, LL11.09, LL11.24, LL11.12) were used. The specimens were prepared and stained according to the standard methods of skull preparation (Taylor, 1967; Zug and Crombie, 1970). The prepared skulls were labeled and scanned in lateral, dorsal and ventral views using a scanner model Genius (color page hr7x). Then by use of an Olympus loop (Model: SzX12) the detailed characters of each skull were examined.

Abbreviation: RUZM, Razi University Zoology Museum.

RESULTS

Lacerta media Lantz and Cyrén, 1920

Premaxilla (pm). This element forms the anterior part of the snout and whole dorsoanterior part of the fenestra exonaria (Fig. 1**A**, **C**). It resembles a dagger that penetrates between the nasals. It bears 9 – 8 teeth anteroventrally (Fig. 1**B**).

Septomaxillae (sm). Each septomaxilla is a small bone in the anterior border of the nasal capsule (Fig. 1**C**). It contacts the premaxilla anteriorly and with the maxilla posteriorly.

Maxillae (m). The maxillae are large elements that form most of the anterolateral aspect of the skull (Fig. 1**A**, **C**). Each of them forms the ventral rim of the fenestra exonaria and has narrow contact with the premaxilla in the fenestra exonaria anteroventrally. Dorsally, it forms the posterior rim of the fenestra exonaria and contacts the nasal and prefrontal posterodorsally, and the lachrymal posteriorly. In ventral view, it forms, from anterior to posterior, the external rim of the fenestra vomero nasalis externa and fenestra exochoanalis, respectively (Fig. 1**B**). Each maxilla bears 23 pleurodont teeth (Fig. 1**B**, **C**). 5 – 6 labial foramina are present in the lateral aspect of the maxilla in two rows (Fig. 1**C**).

Nasals (n). The nasals are paired elements that contact the premaxilla (Fig. 1**A**). Each nasal forms the dorsoposterior rim of the exonalis fenestra, and contacts the anterior margin of the frontal posteriorly and the prefrontal posterolaterally.

Prefrontals (pref). The prefrontals are triangular elements that are located at the anterior angle of the orbital fossae (Fig. 1**A**, **C**). Each prefrontal contacts the maxilla anteroventrally, the frontal dorsally, and the lachrymal laterally. They form the anterior and anterodorsal rim of the orbital fossa and medial rim of the lachrymal fenestra. The prefrontal foramen is at the ventral margin between the prefrontal and frontal.

Lacrimals (l). The lacrimals are long elements located at the anteroventral angle of the orbital fossa (Fig. 1**A**, **C**). Each contacts the prefrontal dorsally and the maxilla anteroventrally. Each lachrymal forms the anteroventral rim of the orbital fossa, extending toward the suture between the maxilla and jugal. The lachrymal foramen lies in the median aspect of each lachrymal.

Frontal (f). The frontal is a long single element on the roof of the skull (Fig. 1**A**, **C**). It contacts the nasal anteriorly and the maxilla anterolaterally (an elongation of the maxilla penetrates in the gap between the prefrontal and nasal and contacts the frontal), the prefrontal laterally, and parietal posteriorly. It forms the dorsal rim of the orbital fossa, and the dorsal rim of the nasal foramen ventrally.

Parietal (pa). The parietal is a butterfly-shaped bone that contacts the posterior margin of the frontal anteriorly, and the postfrontal laterally (Fig. 1**A**, **C**). The posterior long elongation of the parietal reaches the knob (cephalic condyle) of the quadrate where it contacts the supratemporal and quadrate (Fig. 1**D**). It contacts the supraoccipital at the processus ascendens in the posterior of skull and the epipterygoid and prootic ventrally. In the center of the imprint of the interparietal scale, the pineal foramen can be seen (Fig. 1**A**). The distal posterior end of the parietal forms the medial rim of the supratemporal fossa and dorsal medial rim of posttemporal fossa.

Supratemporals (sut). Each supratemporal is a small bone that lies on supratemporal process of the parietal (Fig. 1**A**). It contacts the quadrate and paraoccipital process of the otoccipital posteriorly. The ossified quadrate cartilage is in the angle between paraoccipital process, supratemporal and long process of parietal and the supratemporal contacts it laterally (Fig. 1**D**).

Postfrontals (posf). The postfrontals are triangular bones that lie at the posterior corner of the orbital fossa (Fig. 1**A**, **C**). Each postfrontal contacts the parietal dorsally and postorbital lateroventrally. It forms the posterior rim of the orbital fossa and the anterior rim of the supratemporal fossa.

Postorbitals (porb). Each postorbital is an cultriform element that is located in the posterior region of the orbital fossa (Fig. 1**A**, **C**). It serves as a link between the jugal and postfrontal. It contacts the postfrontal dorsally and the jugal ventrally. It forms a small part of the posterior rim of the orbital fossa and the dorsal rim of the temporal fossa (Fig. 1**C**).

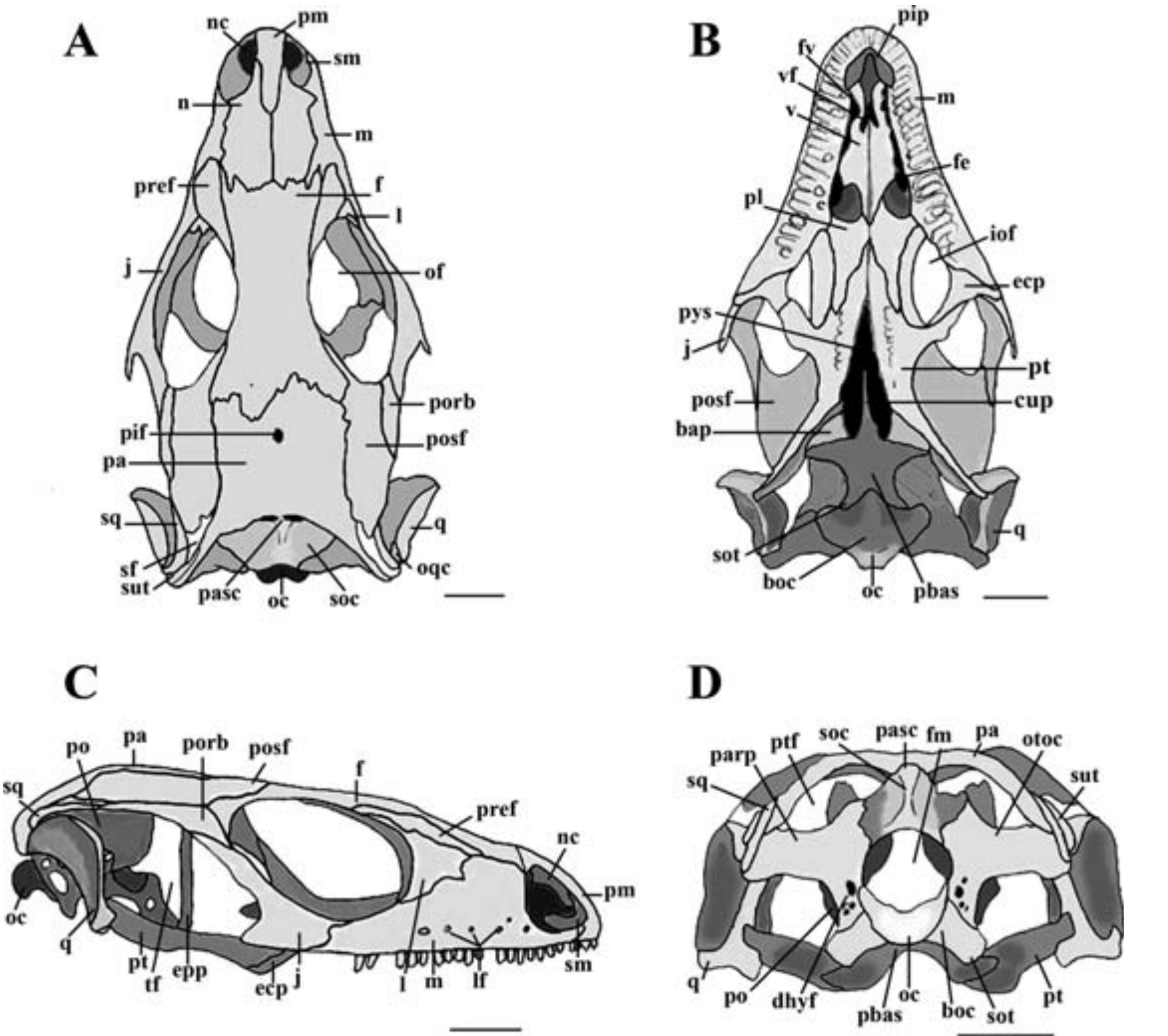

Fig. 1. *Lacerta media*. Skull of the adult in dorsal (**A**), ventral (**B**), lateral (**C**), and posterior (**D**) views: bap, basipterygoid process; boc, basioccipital; cup, cultriform process; dhyf, dorsal hypoglossal foramen; ecp, ectopterygoid; epp, epipterygoid; f, frontal; fe, fenestra exochoanalis; fm, foramen magnum; fv, fenestra vomeronasalis externa; iof, inferior orbital fenestra; j, jugal; l, lachrymal; lf, labial foramina; m, maxilla; n, nasal; nc, nasal capsules; oc, occipital condyle; of, orbital fossa; oqc, ossified quadrate cartilage; otoc, otoccipital; pa, parietal; parp, paraoccipital process; pasc, processus ascendens; pbas, parabasisphenoid; pif, pineal foramen; pip, posteromedial incisive process; pl, palatine; pm, premaxilla; po, prootic; porb, postorbital; posf, postfrontal; pref, prefrontal; pt, pterygoid; ptf, post temporal fossa; pys, pyriform space; q, quadrate; sf, supratemporal fossa; sm, septomaxilla; soc, supraoccipital; sot, sphenoccipital tubercle; sq, squamosal; sut, supratemporal; tf, temporal fossa; v, vomer; vf, vomerine foramen. Scale bars are 3 mm.

Squamosals (sq). The squamosals are long, concave and cultriform bones; each of them lies in the posterior of the postorbital and postfrontal (Fig. 1**A**, **C**). It contacts the postorbital anteriorly and postfrontal anterodorsally. Posteriorly, it contacts the supratemporal and quadrate at the cephalic condyle of the quadrate (Fig. 1**D**). It forms the dorsoposterior rim of the temporal fossa and the posterolateral rim of the supratemporal fossa.

Jugals (j). The Jugals are triradiate elements in which the anterior process contacts the maxilla anteriorly, and the lateral process of the ectopterygoid ventrally. The dorsal process contacts the postorbital. The posterior process is short and reaches the temporal fossa. This bone forms the posteroventral rim of the orbital fossa (Fig. 1**C**).

Vomers (v). The vomers can be seen in ventral view. They are the most anterior elements that contact the snout (Fig. 1**B**). They reach each other anteriorly, and contact the posteromedial incisive process. Each of the vomers contacts the anterior margin of the palatine posteriorly. Anterior to posterior, it forms the medial rim of the fenestra vomeronasalis and the fenestra exochoanalis. Between these two elements there is a gap that reaches the pyriform space posteriorly. In the posterior of the fenestra vomeronasalis, there is the vomerine foramen.

Palatines (pl). The palatines have three processes: the vomerine process that contacts the vomer anteriorly, the pterygoid process that contacts the pterygoid posteriorly, and the maxillary process that contacts the maxilla laterally (Fig. 1**B**). The vomerine and maxillary processes form the medial and posterior rims of the fenestra exochoanalis, respectively. Between the palatines, there is a gap that reaches the pyriform space. The maxillary process contacts the prefrontal dorsally and is pierced by two foramina. The vomerine process forms the ventral rim of the nasal foramen dorsally. At the entrance of the nasal foramen, the vomerine process is pierced by some small foramina. The pterygoid process forms the anteromedian rim of the inferior orbital fenestra.

Pterygoids (pt). This bone has two separated elements (Fig. 1**B**). The pyriform space is located between these elements. Anteriorly, they approach one another closely. Each element has three processes: the palatine process contacts the palatine anteriorly, the transverse process contacts the ectopterygoid process laterally, and the long, posterior quadrate process contacts the quadrate. The palatine and transverse processes form the median and posterior rims of the inferior orbital fenestra, respectively. On the pterygoid there are 10 teeth in a single straight row near the anterior pyriform space.

Ectopterygoids (ecpt). Each of these elements forms the posterolateral rim of the inferior orbital fenestra (Fig. 1**B**). It has three processes: the anterior process contacts the maxilla laterally, the posterior process contacts the jugal laterally and with the maxilla anteriorly, and the medial process contacts the ectopterygoid process of the pterygoid medially.

Epipterygoids (eppt). Each epipterygoid is a thin columnar bone with its dorsal head contacting the ventral aspect of the parietal, adjacent to the contact of the supraoccipital to the pterygoid, and its base articulates with the dorsal surface of the pterygoid adjacent to the contact of the prootic to the pterygoid (Fig. 1**C**).

Splanchnocranium

Quadrates (q). The quadrates are the most posterolateral elements in the skull. Each contacts the squamosal, the long distal supratemporal process of the parietal and supratemporal and the paraoccipital process of the otoccipital dorsally (Fig. 1**A** – **D**). The quadrate bears a crest that divides it into two concave portions: a large lateral concave depression and a small medial depression (Fig. 1**D**). The quadrate bears two condyles: the dorsal cephalic condyle and the ventral transverse condyle. The crest is between these two condyles. The ossified quadrate cartilage is located on the dorsal part of the quadrate near the supratemporal (Fig. 1**A**).

Neurocranium

Parabasisphenoid (pbas). In ventral view, the parabasisphenoid forms the anterior floor of the braincase (Fig. 1**B**, **D**). It has five processes: a cultiform process that is a long process extending to the pyriform space, two anterolateral processes that contact the quadrate process of the pterygoid, basipterygoid process, and the two posterior processes contact the basioccipital and prootic posteriorly.

Basioccipital (boc). The basioccipital forms the posterior floor of the braincase, and forms the ventral portion of the occipital condyle, and foramen magnum (Fig. 1**B**, **D**). The basioccipital articulates with the parabasisphenoid anteriorly and with the otoccipital posterolaterally. In ventral view, it bears two ventrolateral protuberances, spheno-occipital tubercles.

Supraoccipital (soc). The supraoccipital is the roof of the braincase. It is a saddle-shaped element (Fig. 1**A**, **D**). It forms the dorsal rim of the foramen magnum. It articulates with the prootic anteroventrally and with the otoccipital posterolaterally. It is separated from the parietal by a median cartilaginous, processus ascendens, that contacts the parietal. Close to this connection, it has two depressions.

Otoccipitals (otoc). The otoccipitals form the posterior portion of the braincase (Fig. 1**D**). Each otoccipital articulates with the supraoccipital dorsally, with the basioccipital ventrally, and with the prootic anteroventrally. It has a distally-compressed lateral process that reaches the condyle of the quadrate. It contacts the quadrate, squamosal and posterior process of the parietal. The otoccipital forms the lateral rim of the foramen magnum. It is pierced by the hypoglossal foramina. In lateral view, the otoccipital has two distinct foramina (Fig. 3): the vestibula fenestra or oval foramen dorsally and the recessus scalae tympani ventrally. There is a foramen that reaches the oval foramen in the lateral wall of the recessus scalae tympani, the prilymphatic foramen.

Prootics (po). Each of the prootics forms the anterolateral wall of the braincase (Fig. 1**C**, **D**). It articulates with the supraoccipital dorsally, with the parabasisphe-

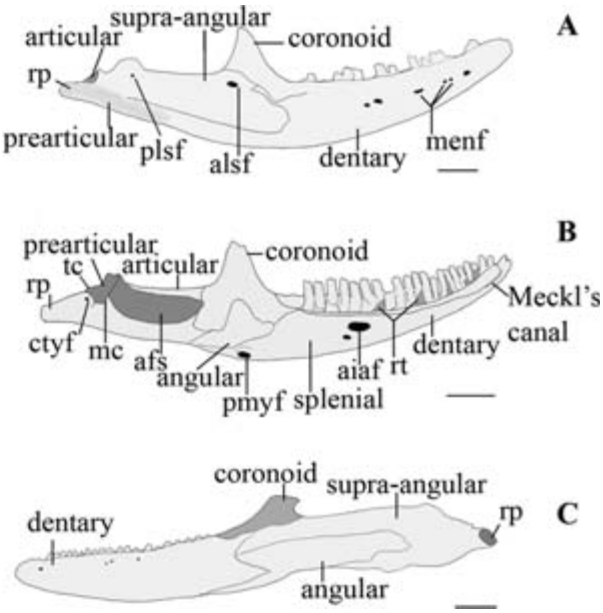

Fig. 2. *Lacerta media*. Mandible of the adult in lateral (**A**), medial (**B**), and ventral (**C**) views: afs, adductor fossa; aiaf, anterior inferior alveolar foramen; alsf, anterolateral supra-angular foramen; ctyf, chorda tympani foramen; mc, medial crest; menf, mental foramina; plsf, posterolateral supra-angular foramina; pmyf, posterior mylohyoid foramen; rp, retroarticular process; rt, replacement teeth; tc, tympanic crest. Scale bars are 3 mm.

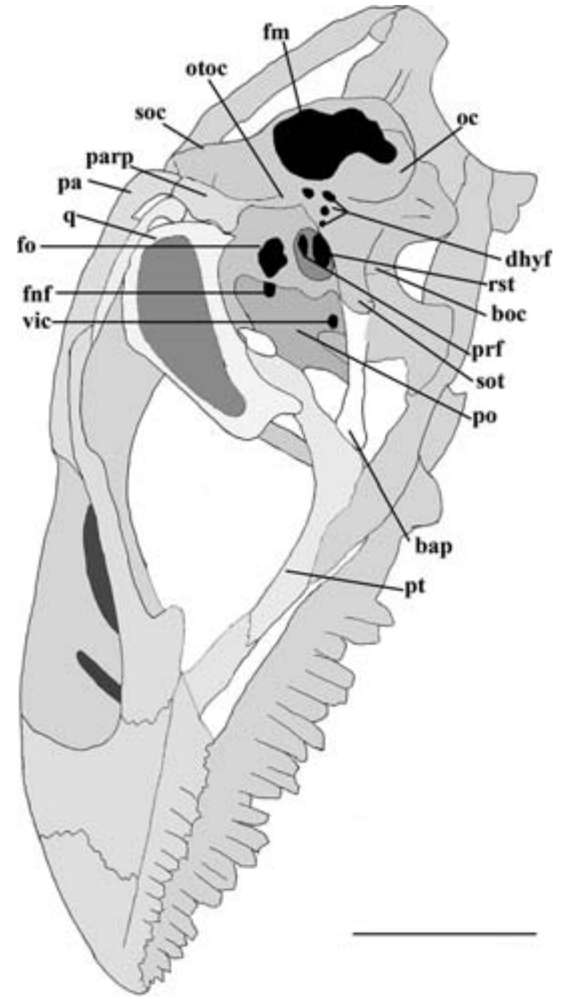

Fig. 3. *Lacerta media*. Skull of the adult in oblique view: bap, basipterygoid process; boc, basioccipital; dhyf, dorsal hypoglossal foramen; fm, foramen magnum; fnf, facial nerve foramen; fo, fenestra vestibula (fenestra ovalis); oc, occipital condyle; otoc, otoccipital; pa, parietal; parp, paraoccipital process; po, prootic; prf, prilymphatic foramen; pt, pterygoid; q, quadrate; rst, recessus scala tympani; soc, supraoccipital; sot, spheno occipital tubercle; vic, vidian canal. Scale bar is 3 mm.

noid ventrolaterally, with the basioccipital ventroposteriorly, and with the otoccipital posteriorly. The vidian canal is located at the contact between the prootic and basipterygoid process of the parabasisphenoid. The facial nerve foramen is in the fossa of the prootic (Fig. 3).

Mandibular

Dentary. The dentary is the largest bone in the mandible and the only one that bears the teeth (Fig. 2**A**, **B**). It bears 27 pleurodont teeth. The splenial penetrates into the dentary, the dentary encloses the splenial in the median view. Meckel's canal from the tip of the splenial penetrates to the dentary and reaches its tip. The dentary articulates with the coronoid posterodorsally, with the supra-angular dorsally. In lateral view, the dentary articulates with the cornoid posterodorsally, with the supra-angular and angular posteriorly. In this view, six foramina are in a straight line in the dentary. In median view, the replacement teeth can be seen clearly.

Coronoid. The coronoid is the highest element in the mandible; it is located behind the tooth row (Fig. 2**A**, **B**). It has three processes: the posterior process that articulates with the articular ventrally, in medial view the anterior process articulates with the dentary dorsally and splenial ventrally, and the ventral process that bears a protuberance enclosed by the articular. In lateral view, it contacts the supra-angular posteriorly.

Supra-angular. In lateral view, the supra-angular occupies the space between the coronoid and articular (Fig. 2**A**). It articulates with the coronoid anteriorly, with the angular ventrally and with the articular posteriorly. In this view, it has two foramina, the larger is the anterolateral supra-angular foramen, close to the coronoid and the smaller, the posterolateral supra-angular foramen, is close to the articular. In medial view, it articulates with the coronoid anteriorly and articular ventrally (Fig. 2**C**). It forms the laterodorsal wall of the adductor fossa.

Angular. This mandibular element is visible in both lateral and medial views (Fig. 2**B**, **C**). In medial view, it may be seen to articulate with the dentary anteriorly, and with the splenial and articular dorsally. In lateral view, it contacts the dentary anteriorly, with the supra-angular dorsally and the articular posteriorly. The angular and supra-angular penetrate to the dentary.

Splenial. In ventral view the splenial is the largest element visible in the mandible (Fig. 2**B**). It articulates with the dentary dorsally and ventrally, with the coronoid posterodorsally, and with the angular ventrally. It has two foramina; the larger one is the anterior mylohyoid foramina.

Articular. In lateral view, the articular is the most posterior element of the mandible (Fig. 2**A**). It articulates with the angular and supra-angular, forming the retroarticular process. In medial view, it contacts the anterior and posterior processes of the coronoid dorsally (Fig. 2**B**). The adductor fossa is in the middle of the articular. In the posterior view, the chorda tympani fenestra is close to the median crest. There is a fossa between the tympanic and median crests.

Marginal teeth. There are 27 pleurodont teeth in the dentary shell (Figs. 1 and 2). Some anterior teeth are small, becoming longer to the end. The teeth are cylindrical, with a conical apex; the replacement teeth can be seen in medial view. The premaxilla bears 9 – 8 teeth anteroventrally, each maxilla bears 23 pleurodont teeth.

Laudakia caucasia (Eichwald, 1831)

Premaxilla (pm). This small, unpaired element forms the anterior part of the snout and penetrates between the fenestra exonaria and contacts the nasals anterodorsally (Fig. 4**A**, **C**). The premaxilla contacts the maxillae ventroposteriorly. The alveolar border bearing a place for two small unicupsid pleurodont teeth anteroventrally.

Septomaxillae (sm). The septomaxillae lay anteromedially within the nasal capsules (Fig. 4**A**, **C**). Each septomaxilla forms the floor of the anteromedial portion of the nasal cavity. The septomaxilla is oriented anteroventrally and articulates with the maxilla anterolaterally and vomer ventrally.

Maxillae (m). The maxillae are triradiate elements, each of them forms most of the anterolateral aspect of the skull: the anterior process contacts the premaxilla and septomaxilla anteriorly, the dorsal process contacts the nasals dorsally, the prefrontal posterodorsally and the lachrymal posterolaterally, the posterior process contacts the jugal posteriorly and forms the anteromedian rim of the inferior orbital fenestra (Fig. 4**A**, **C**). Each maxilla bears two recurved and laterally compressed pleurodont teeth and 12 acrodont teeth on the well developed alveolar shelf. In ventral view, the maxilla forms the anterior lateral margin of each fenestra vomeronasalis and fenestra exochoanalis, respectively (Fig. 4**B**).

Nasals (n). The nasals articulate with the premaxilla process anteriorly and with the process of the frontal posteriorly, thereby they form most of the roof of the nasal capsules (Fig. 1**A**). The nasals extend to one side of the fenestra exonaria. They articulate with the maxillae anterolaterally and with the prefrontals posterolaterally. The angle between the posterolateral and posteromedial margins of the nasals is about 45°.

Prefrontals (pref). The prefrontals form the anterodorsal rim of the orbital fossa (Fig. 4**A**, **C**). Each prefrontal articulates with the maxilla anteriorly, with the nasal anterodorsally, with the frontal posterodorsally and the lachrymal laterally. The ventrolateral portion of the posterior part of each prefrontal is notched, and forms the median margin of the lachrymal foramen.

Lacrimals (l). They are small and triangular elements. Each of them completes the anterior angle of the orbital fossa (Fig. 4**C**). Each lachrymal articulates with the maxilla anteriorly and ventrally and with the prefrontal dorsally. The lachrymal foramen is in the middle of the lachrymal.

Frontal (f). The frontal is a sword-shaped element that forms most of the roof of the skull (Fig. 4**A**, **C**). The anterior process continues toward the nasals and contacts the suture between them. It contacts the parietal posteriorly, and the prefrontal anteriorly. It forms the dorsal rim of the orbital fossa.

Parietal (pa). The parietal is a butterfly-shaped element, with two short anterior and two long posterior processes (Fig. 4**A**). The anterior processes have a bend laterally. The parietal contacts the frontal anteromedially, and the postorbital laterally. It forms a small rim of the orbital fossa. The long posterior process, the supratemporal process, is a compressed descending process. It forms the dorsomedial rim of the supratemporal fossa anteriorly and the dorsal rim of the post-temporal fossa posteriorly. The distal end of each supratemporal process articulates with the paraoccipital process of the otoccipital (Fig. 4**D**). It contacts the supratemporal ventrolaterally. The parietal encloses the pineal foramen.

Supratemporals (sut). The supratemporals are small, long and compressed; each of them lies on the posterior end of the supratemporal process of the pari-

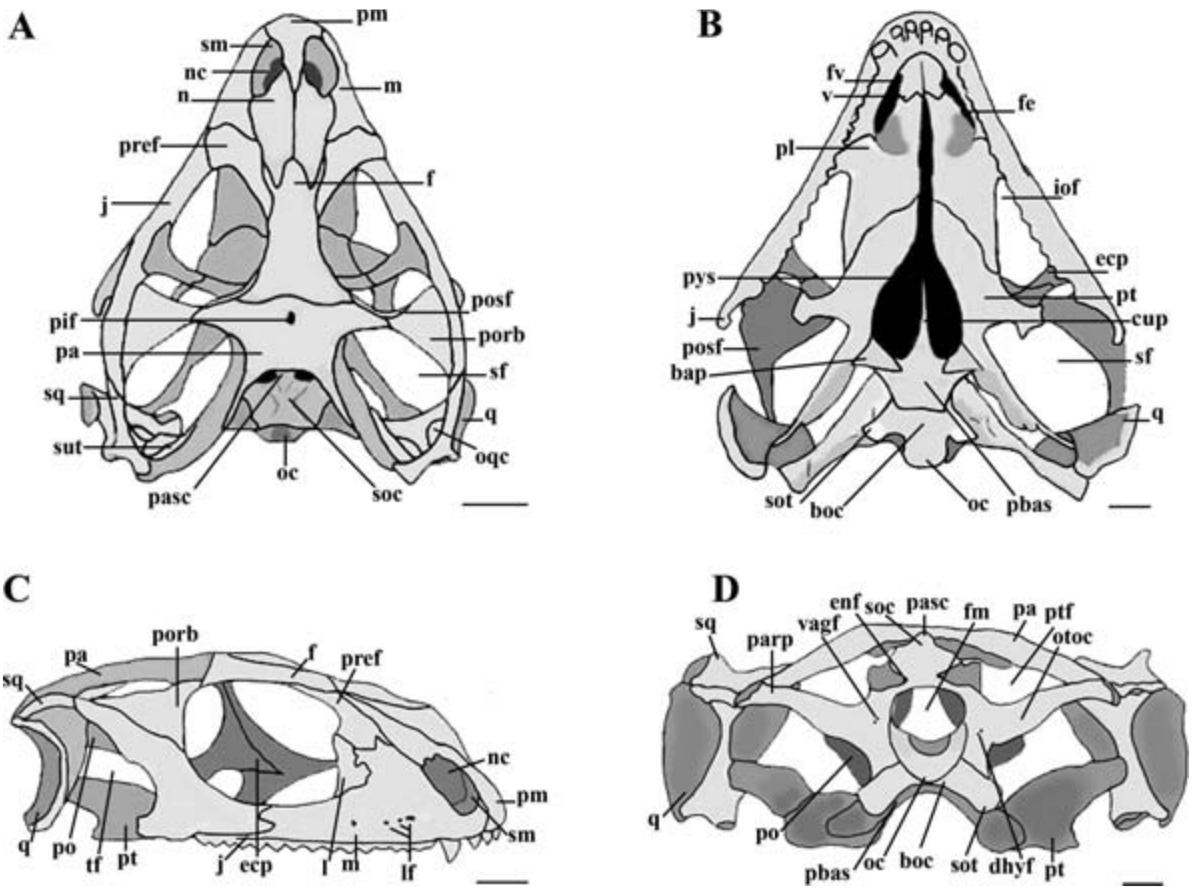

Fig. 4. *Laudakia caucasia*. Skull of the adult in dorsal (**A**), ventral (**B**), laterals (**C**), and posterior (**D**) views: bap, basipterygoid process; boc, basioccipital; cup, cultriform process; dhyf, dorsal hypoglossal foramen; ecp, ectopterygoid; enf, endolymf foramen; f, frontal; fe, fenestra exochoanalis; fm, foramen magnum; fv, fenestra vomeronasalis externa; iof, inferior orbital fenestra; j, jugal; l, lachrymal; lf, labial foramina; m, maxilla; n, nasal; nc, nasal capsules; oc, occipital condyle; of, orbital fossa; oqc, ossified quadrate cartilage; otoc, otoccipital; pa, parietal; parp, paraoccipital process; pasc, processus ascendens; pbas, parabasisphenoid; pif, pineal foramen; pl, palatine; pm, premaxilla; po, prootic; ptf, post temporal fossa; porb, postorbital; posf, postfrontal; pref, prefrontal; pt, pterygoid; ptf, post temporal foramen; pys, pyriform space; q, quadrate; sf, supratemporal fossa; sm, septomaxilla; soc, supraoccipital; sot, sphenoccipital tubercle; sq, squamosal; sut, supratemporal; tf, temporal foramen; v, vomer; vagf, vagal foramen. Scale bars are 3 mm.

etal (Fig. 4**A**). Each one continues to the half way of the supratemporal fossa, contacts the squamosal, and paraoccipital process of the otoccipital posteriorly.

Postfrontals (posf). These small elements lie in the posterodorsal rim of the orbital fossa (Fig. 4**A**). Each postfrontal contacts the frontal anteriorly, the parietal posteriorly and the postorbital laterally.

Postorbitals (porb). Each postorbital is a triangular element located between the two fossae (Fig. 4**A**, **C**). It forms the posterior rim of the orbital fossa and anterior rim of the supratemporal fossa. It contacts the jugal laterally, the short anterior process of the parietal dorsally and the postfrontal anterodorsally.

Squamosals (sq). The squamosals are L-shaped elements (Fig. 4**A**). Each one contacts the jugal anteriorly, the distal end of the long process of the parietal and posterior end of the supratemporal, and cephalic condyle of the quadrate posteriorly (Fig. 4**A**, **D**). Each squamosal forms the posterolateral rim of the supratemporal fossa and posterodorsal rim of the temporal fossa (Fig. 4**C**).

Jugals (j). The jugals are broad, triradiate elements that contact three fossae (Fig. 4**C**). Each jugal forms the half of the ventral rim of the orbital fossa and anterior rim of the temporal fossae. The anterior process contacts the maxilla, the dorsal process contacts the postorbital, it reaches the squamosal posteriorly and forms a small lateral rim of the supratemporal fossa. The posterior process reaches the temporal fossa. The jugal contacts the distal margin of the anterolateral process of the ectopterygoid ventrally (Fig. 4**B**). The jugal bears five teeth.

Vomers (v). The vomers are the most anterior elements of the palate, forming the medial border of each fenestra vomeronasalis externa anterolaterally and small rim of each fenestra exochoanalis posterolaterally (Fig. 4**B**). The vomers articulate with each other and are separated from the premaxilla by a piece of connective tissue. The lachrymal groove is located at the anterolateral margin of the vomers. The vomers reach the vomerine process of the palatines posteriorly.

Palatines (pl). The palatines are separated by the anterior pyriform space (Fig. 4**B**). Each palatine has three processes: the anterior vomerine process, the posterior pterygoid process, and the anteromedial maxillary process. The vomerine process contacts the posterior end of the vomer anteriorly. The maxillary process reaches the maxilla anteromedially and forms the posteromedial rim of the fenestra exochoanalis by the vomerine process, and the pterygoid process forms the anterior rim of the inferior orbital fenestra posteriorly. The pterygoid process contacts the palatine process of the pterygoid posteriorly and forms the medial and lateral rim of the inferior orbital fenestra.

Pterygoids (pt). The pterygoids are the longest elements of the palate (Fig. 4**B**). They are separated by the pyriform space. Each pterygoid has three processes: the anterior (palatine) process contacts the posterior process of the palatine anteriorly, the transverse (ectopterygoid) process contacts the medial process of the ectopterygoid, which forms a small portion of the posteromedial rim of the inferior orbital fenestra, and the posterior (quadrate) process which is a long process that continues to the quadrate; it is compressed lateromedially and convex laterally; at the distal end, it articulates the quadrate.

Ectopterygoids (ecp). The ectopterygoids form the posterior rim of the inferior orbital fenestra (Fig. 4**B**). Each ectopterygoid has three processes: the anterior process contacts the anterior process of the jugal and they bear five teeth, the posterior process contacts the posterior process (temporal process) of the jugal, and the medial process contacts the anterior aspect of the transverse process of the pterygoid; this process is bifurcated: the ventral branch is shorter than the dorsal branch.

Epipterygoids (epp). The epipterygoids are long and narrow columns that can be seen in the lateral view. The base of each epipterygoid rests on the columellar fossa of the pterygoid and its apex contacts the roof of the skull, anterior to the prootic.

Splanchnocranium

Quadrates (q). The quadrates are located at the posterolateral corner of the skull, articulate with the lower jaw (Fig. 4**B** – **D**). The glenoid fossa of the articular articulates with the condyle of the quadrate dorsally. There is a crest between transverse condyle to the cephalic condyle of the quadrate. This crest divides the quadrate into two parts: a wide concave lateral half and a short medial half. The medial half contacts the distal end of the pterygoid. Dorsally, the cephalic condyle contacts the squamosal, parietal, supratemporal and ossified quadrate cartilage.

Neurocranium

Parabasisphenoid (pbas). The parabasisphenoid forms the anterior floor of the braincase (Fig. 4**B**). It articulates with the basioccipital posteriorly and with the prootic lateroventrally. It has a concave depression in the middle. It has three processes: two lateral processes, the basipterygoid processes, articulate with the quadrate process of the pterygoid laterally and a single cultriform process. A long cultiform process from the anteromedian region of the parabasisphenoid continues to the pyriform space.

Basioccipital (boc). The basioccipital forms the posterior floor of the braincase and the medial portion of the occipital condyle (Fig. 4**B**, **D**). It articulates with the parabasisphenoid anteriorly. On each side, the basioccipital has a short ventrolateral protuberance that projects ventrally, the spheno-occipital tubercles.

Supraoccipital (soc). The supraoccipital is a saddle-shaped bone that forms the posterior roof of the braincase (Fig. 4**A**, **D**). It articulates with the posterior of the parietal anterodorsally, with the prootic anteroventrally, and with the otoccipital posterolaterally. It forms the dorsal portion of the foramen magnum. There is an endolymphatic foramen in the joint margin of the supraoccipital and otoccipital.

Otoccipitals (otoc). The otoccipitals form the posterolateral walls of the braincase (Fig. 4**D**). Each of them forms the lateral rim of the foramen magnum. Each otoccipital articulates with the basioccipital ventromedially, with the prootic anterolaterally, with the supraoccipital dorsally. The otoccipital has a long paraoccipital process that continues laterally toward the distal end of the parietal; in this point, the paraoccipital process contacts the parietal, squamosal, and the condyle of the quadrate dorsally. A fossa, posttemporal fossa, is made between the long process of the parietal and paraoccipital, prootic and supraoccipital. In lateral view, the otoccipital is pierced by two distinct foramina: the fenestra vestibuli (= f. ovalis) that is the dorsal one and the recessus scalae tympani is the ventral one.

Prootics (po). The prootics form the anterolateral walls of the braincase (Fig. 4**C**, **D**). Each of them contacts the supraoccipital dorsally, the paraoccipital posterodorsally, the basioccipital and the parabasisphenoid ventroposteriorly and ventroanteriorly, respectively. The vidian canal is located at the contact point between the prootic and basipterygoid process of the parabasisphenoid. The facial nerve foramen is in the cavity of the prootic (Barahona and Barbadillo, 1997; Barahona et al., 1998).

Mandibular

Dentary. The dentary is the largest anterolateral element of the mandible that bears teeth. In lateral view, it articulates with the angular ventrally and supra-angular posterodorsally (Fig. 5**A**). In this view, it is bifurcated and the supra-angular penetrates into it. In medial view, it articulates with the angular ventrally (Fig. 5**B**). The anterior inferior alveolar foramen (aiaf) starts from apex of the angle of the splanial and continues as a groove into the apex of the dentary anteriorly. The dorsal margin of the coronoid process contacts the dentary dorsally. There are two pleurodont and 17 acrodont teeth on the dentary. Laterally, the dentary has three foramina that lay in a straight line anteriorly.

Coronoid. The coronoid lays immediately behind the mandible tooth row. It has a large dorsal process (Fig. 5**A**, **B**). In medial view, it has three processes; the posterior process contacts the articular ventrally, the ventral process bears a protuberance that is enclosed by the articular, the anterior process articulates with the dentary dorsally and with the splenial anteroventrally.

Supra-angular. The supra-angular occupies the posterior half of the mandible in lateral view (Fig. 5**A** – **C**). Laterally, it penetrates into the bifurcated dentary, forms the posterior mylohyiod foramen in the angle between the supra-angular and dentary (Fig. 5**A**). The supra-angular contacts the posterior process of the coronoid anteriorly, and the prearticular posteriorly, in lateral view. The border between the supra-angular and prearticular on lateral view is unclear, and there is a posterolateral foramen under the articular and in medial view, there is the adductor fossa that has two foramina (Fig. 5**B**).

Prearticular. The prearticular forms the posterior end of each mandible especially in medial aspect. Posteriorly, it bears two processes: the retroarticular process (rp) posteriorly and the angular process (ap) medially (Fig. 5**C**). The retroarticular process has two crests dorsally: the tympanic crest (tc) laterally and the medial crest (mc) medially (Fig. 5**B**). The prearticular fused with the articular dorsally. In lateral view, the prearticular contacts the angular anteriorly, and the suprangular anterodorsally.

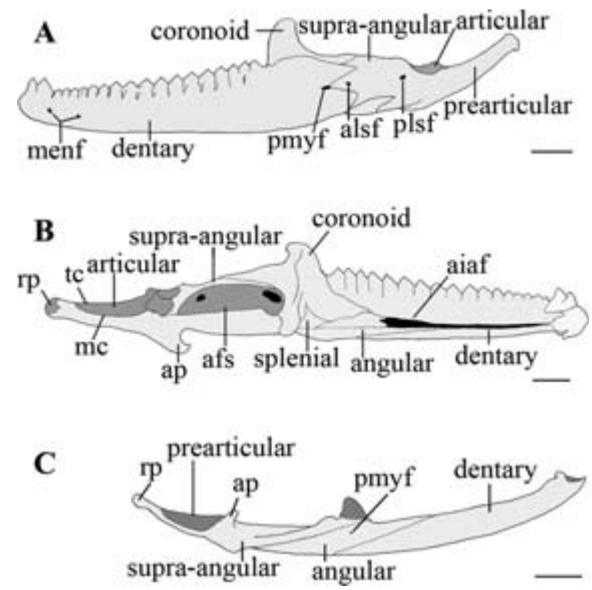

Fig. 5. *Laudakia caucasia*. Mandible of the adult in lateral (**A**), medial (**B**), and ventral (**C**) views: afs, adductor fossa; aiaf, anterior inferior alveolar foramen; alsf, anterolateral supra-angular foramen; ap, angular process; mc, medial crest; menf, mental foramina; plsf, posterolateral supra-angular foramina; pmyf, posterior mylohyoid foramen; rp, retroarticular process; tc, tympanic crest. Scale bars are 3 mm.

Angular. This element continues from the lateral view to the medial view (Fig. 5**B**, **C**). In lateral view, it articulates with the supra-angular posterodorsally, with the prearticular ventrally and the dentary anterodorsally. In medial view, it continues to the anterior inferior alveolar foramen, forming the posteroventral rim of this groove. It articulates with the splenial dorsoposteriorly and dentary ventrally.

Splenial. The splenial is a triangular element that can only be seen in medial view (Fig. 5**B**). It contacts the anterior process of the coronoid posteriorly, the dentary anteriorly and the angular ventrally. The anterior inferior alveolar foramen groove starts from its anterior angle.

Marginal teeth. The premaxilla bears two pleurodont teeth, and the maxilla 17 (two pleurodont + 15 acrodont), and the dentary 19 acrodont teeth (Figs. 4 and 5). The second tooth of the maxilla is the longest tooth. After that, there are six short teeth, then the teeth become longer towards the end. In the dentary, the first two teeth are the longest, and then there are four teeth that are short, then the teeth become longer towards the end.

DISCUSSION

Characters of the skull mostly determine the type of feeding, the amount of kinesis and evolutionary route of the taxa. The lizard world is clearly dichotomous in terms of foraging behaviors: sit-and-wait (SW) and widely foraging (WF) (Huey and Pianka, 2007). Generally, the skull of *Laudakia caucasia* (SW) and *Lacerta media* (WF) can be taken as the representatives of the iguanians and scleroglossans, respectively. A number of key distinguishing characters can be easily seen in the skull of these taxa.

The iguanians retain the ancestral traits including tongue prehension and ambush foraging, whereas scleroglossans switched from tongue prehension to the jaw prehension. This freed the tongue to evolve along new lines, ultimately leading to much keener vomerolfaction, which in turn promoted a more active lifestyle and facilitated a shift to the wide foraging (Huey and Pianka, 2007). The wide foraging (WF) lizards might have enhanced learning and memory, as well as acquiring a larger brain (Regal, 1978).

The first difference that is showed off in the two above-mentioned skulls is the differences in the head length/head width ratio: in *Laudakia caucasia* this ratio is about 1.18 whereas in *Lacerta media* it is about 1.95. The skull of *Laudakia* is relatively wide in comparison to that of other lizards. Characteristic of the *Laudakia* skull is the fusion of almost all dorsomedial bones (Ananjeva, 1977, 1980).

Other differences between these two taxa are as follows: *Lacerta media* has 23 pleurodont teeth, while in *Laudakia caucasia* only the first three teeth are pleurodont and the others are acrodont. *Lacerta media* has pterygoid teeth, but these teeth are absent in *Laudakia caucasia*; the teeth of *Lacerta media* are more cylindrical and longer than those in *Laudakia caucasia*, this is indicative of use of different food items: *Lacerta media* is exclusively insectivorous while *Laudakia caucasia* is both insectivorous and herbivorous. Another obvious difference between these two species is the presence of a big supratemporal fossa in *Laudakia caucasia*, whereas this fossa is very small in *Lacerta media*.

The frontal in *Lacerta media* continues to the anterior region of the orbital fossa but in *Laudakia caucasia* it stops at the anterior half of the orbital fossa. Here, interestingly, in *Lacerta media* the maxilla can touch the frontal but it does not touch the frontal in *Laudakia caucasia*. There is a large postorbital element in *Laudakia caucasia* but it is a small bone in *Lacerta media*, but in turn, it has a longitudinal postfrontal element behind the orbital fossa. Reduction or loss of arches along with the acquisition of intracranial joints facilitates cranial kinesis, the movement of one section of a skull independent of others (Kent and Miller, 2000).

The differences in ventral view: the maxillary process of the palatine in *Laudakia caucasia* forms the anterolateral rim of the inferior orbital fossa but this is not the case in *Lacerta media*. In *Lacerta media* the palatines are in contact, but in *Laudakia caucasia* the pyriform space continues between the palatines. The occipital condyle in *Laudakia caucasia* is more protuberant than that of *Lacerta media*. In *Laudakia caucasia* the medial process of the ectopterygoid has a more obvious protuberance than that of *Lacerta media*. The spheno-occipital tubercles in *Laudakia caucasia* are more prominent than those of *Lacerta media*. The prefrontal in *Laudakia caucasia* is wide, so it bears a clear projection in front of the orbital fossa, but this is not the case in *Lacerta media*.

The pineal foramen in *Lacerta media* can be seen clearly, but in *Laudakia caucasia* it is not clearly visible. The presence or absence and position of the pineal (parietal) foramen may indicate certain evolutionary tendencies. Size of the foramen is not always a safe index to the size and functional ability of the eye (Underwood, 1971).

Laudakia caucasia shows a relatively large braincase. This is related to the development of the semicircular canals, whose curvature necessitates a certain minimum radius for an efficient function. So, the diameter of the otic capsules is therefore relatively increased due to the necessity of achieving the required radius of curvature and hence the braincase becomes longer.

In *L. caucasia* there is no median crest on the ventral side of the parietal and the posterolateral processes of parietal are slender and the structure of the anterior margin is less complex, whereas, ascending projection on the supraoccipital is quite smaller than *L. media*, therefore does not require development of a median crest.

In *L. media* with a relatively high skull, the most dorsal unossified portion of the ascending process of the supraoccipital is attached to the posterior edge of the median crest of the partial and serves as an elastic dorsal suspension for the braincase thus supporting metakinetic movement during feeding. But in *L. caucasia* lessening of this ascending and loss of metakinetic are compensated by having large supratemporal openings.

The retroarticular process in *Laudakia caucasia* is considerably longer than that of *Lacerta media*. *Laudakia caucasia* has an obvious angular process while this element is not obvious in *Lacerta media*. In the medial view in *Laudakia caucasia* the anterior inferior alveolar foramen goes through the dentary, but in *Lacerta media* it is a small fenestra. In *Laudakia caucasia* the dentary sheath on the jugal bears the teeth, whereas in *Lacerta media* it does not. The other described feature is morphology of the mandibular crest in the lower jaw. In *L. media* the crest is located directly on the suprangular/angular suture and not clearly on the suprangular, as in many larger lacertids. The crest separates the attachment areas of the aponeuroses on which the external jaw adductor as well as the pterygoideus muscle insert. According to Rieppel (1984), it is difficult to reach an effective muscle fiber length in a small lizard skull. Thus, it is necessary to expand the jaw adductors as much as possible. When there are no reductions in the skull roof, as in *Lacerta media*, there is no possibility for the jaw muscles to extend onto the dorsal surface of the skull. Hence, the required expansion must be developed in a different way. The ventral shift of *Lacerta media* mandibular crest could develop, enabling the external jaw adductor to expand in a downward direction. Thus, the morphology of the crest would be another feature related to a small skull (Müller, 2002).

The sharp offset on the lateral side of the coronoid is the special feature of *Lacerta media*. This edge separates the prominent dorsolateral expansion of the coronoid apex from a distinct depression on the posteroventral base of the ascending coronoid process. In many other lacertids, the alignment of this offset is different, trending more obliquely into a posterodorsal direction and extending nearly up to the coronoid apex. Both areas, the dorsolateral expansion as well as the posteroventral depression, serve for the insertion of the superficial portion of the external jaw adductor. However, the muscle fibers insert only on the dorsolateral portion; the function of the depression rather is the attachment of the anterior part of the aforementioned aponeurosis.

Cope (1900) regards the acrodont and pleurodont series of parallel value and expresses the view that the Pachyglossa (Iguanidae and Agamidae) are probably ancestral to the other superfamilies. The dentition of the Agamidae is the modification of the primitive rhizodont dentition which prevailed during the Permian. It would seem from what we know of the record, that thecodonty has preceded both pleurodonty and acrodonty in the saurian line. It also appears from comparative evidence and from the embryology that thecodonty and pleurodonty has in every case preceded acrodonty (Underwood, 1971). Siebenrock (1895b) shows that the developing tooth in the *Agama* goes through a pleuro-thecodont stage. The highly acrodont teeth of the Agamidae and Chamaeleontidae may have arisen directly from a thecodont type by atrophy and shortening of the base and coincident replacement of the alveolar cups by infilling of mandibular bone. It is among the Agamidae that the most heterodont types of saurian dentition occur and this again would make it appear that the acrodont series can not be considered primitive (Underwood, 1971). Another feature which makes the hyperacrodonty of *Sphenodon* and the Agamidae and Chamaeleontidae as a highly specialized condition is the failure to develop replacement teeth in the adult. When the teeth become worn or broken away in the hyperacrodont lizards, enamel is sometimes deposited upon the edge of the mandibles which then takes on a masticatory beak-like function.

The morphology of the osteocranium of *Laudakia caucasia* and *Lacerta media* have been described in this study. Although the results presented here contribute to our knowledge of the cranial morphology in lizards, we still lack information to gain a better understanding of the patterns of morphological diversity of the cranium in these reptiles. Since general information of all the extant saurian families is unavailable; this clearly indicates that basic research on the osteology of lizards is needed. An additional purpose of this study is to identify new cranial osteological characters that could be used for phylogenetic analyses of *Lacerta* and *Laudakia*. The utility of these will only become apparent once the cranial osteology of other species of *Lacerta* and *Laudakia* has been investigated and the characters examined in a phylogenetic context.

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