

Comparative skull osteology of the lacertid lizards *Eremias persica* and *Mesalina watsonana* (Sauria: Lacertidae)

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The skull of two lacertid lizards of Iran including *Eremias persica* from Isfahan Province, Central Iranian Plateau and *Mesalina watsonana* from Birjand in Southern Khorasan Province, Eastern Iran, was described and compared based on seven dry skull preparations. Prominent differences included: the shape of the premaxilla and its articulation with other skull elements, the shape of the frontal (particularly the form of its processes), the number of dentary teeth, the shape of the jugal, and the position of the parietal opening. Also in *E. persica*, the nasals were in contact with each other whereas in *M. watsonana* they were separated by the nasal process of the premaxilla and anteromedial process of the frontal. Absence of pterygoid teeth in *M. watsonana* and extended pyriform recess in *E. persica* also represented further differences. Our study contributes to the baseline understanding of squamate osteology and more specifically will facilitate further studies on lacertid morphological disparity.

Key words: Lacertidae, *Mesalina*, *Eremias*, Iran, Osteology, skull, Squamata

INTRODUCTION

The lizard skull has provided plentiful data for phylogenetic and functional studies (Evans 2008). In some morphological phylogenetic studies of lizard relationships, such as Estes et al. (1988), Etheridge and de Quiroz (1988), Moody (1980) and Conrad (2008), skull characters were employed as phylogenetic signals.

The Lacertidae represent a clade of about 280 species of lizards that are widespread being distributed in the old world, with greatest diversity in the areas around the Mediterranean Sea and in the deserts of the Middle East (Müller, 2001; Arnold et al., 2007; Hipsley et al., 2009). Lacertid lizards are generally considered to exhibit a very conservative morphology (e.g. Müller, 2002). The Palearctic representatives are extremely uniform and what characters have been recorded appear subject to homoplasy (Müller, 2002). Hence, although lacertids have been studied for a long time (e.g. Bojanus, 1821; Parker, 1879), the phylogenetic relationships within the clade remain largely unresolved (e.g. Arnold, 1989 a & b; Mayer and Benyer, 1994; Harris, et al., 1998; Fu, 2000). Comparatively little is known about their fossil history (Müller, 2001; Augé and Hervet, 2009; Čerňanský, 2010) but molecular data is now also being used to evaluate their relationships (Mayer and Pavlicev, 2007; Hipsley et al., 2009). Despite the taxonomic diversity of lacertid lizards, and wide interest in their ecology, physiology, ecology and behaviour (e.g. Scheers and van Damme 2002;

Surget-Groba et al., 2006), detailed descriptions of their skulls are not exhaustive in number. Anatomical studies of adult articulated skulls include those on *Lacerta viridis* (Bojanus, 1821; Parker, 1879; Gaupp, 1906), *Takydromus wolteri* (Evans, 2008), *Acanthodactylus boskianus* (El-Toubi and Soliman, 1967), *Gallotia* sp., *Psammodromus* sp., and *Algyroides marchi* (Barhona and Barbadillo, 1997, 1998), *Lacerta agilis* and *Zootoca vivipara* (Parker, 1879; Gaupp, 1900; Goodrich, 1930). The relationship between the skull roofing bones and cephalic scales in *Lacerta* and *Podarcis* was recently explored by Costantini et al. (2010).

The lacertid genus *Eremias* Fitzinger, 1834 encompasses about 37 species of mostly sand, steppe, and desert dwelling lizards which are distributed from northern China, Mongolia, Korea, and Central and southwest Asia to southeastern Europe (Rastegar-Pouyani and Nilson, 1997; Rastegar-Pouyani and Rastegar-Pouyani, 2001). The genus is Central Asian in its relationships and affinities (Szczerbak, 1974; Anderson, 1999). About 15 species of the genus *Eremias* occur on the Iranian Plateau, mostly in northern, central, and eastern regions (Rastegar-Pouyani and Nilson, 1997; Anderson, 1999).

Szczerbak (1974) revised *Eremias* and divided it into two distinct genera based on morphological characters: *Mesalina* Gray, 1838 and *Eremias* Fitzinger, 1834, thus the genus *Mesalina* was resurrected for the characteristic groups of 14-15 small lacertid species found in desert and semidesert regions of North Africa and the Saharo-Sindian region of Southwest Asia. Arnold (1986) confirmed the holophyly of *Mesalina* based on hemipenial evidence.

Mesalina and *Eremias* belong to a clade named Eremiinae (Arnold et al., 2007), which includes all Afrotropical species and four genera that are distributed mainly in xeric areas of North Africa and non-tropical Asia (*Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops*). Morphological studies demonstrated phylogenetic structures within this unit (Arnold, 1989a, b, 1991). Subsequent molecular studies (Harris et al., 1998; Fu, 1998, 2000; Arnold et al., 2007) support this relationship.

Eremias persica and *Mesalina watsonana* are common throughout the central and eastern Iranian Plateau on open slopes and plains. They are found on a variety of surfaces including gravel alluvium, silt and gravel, sand and gravel, dry loose and compacted loess, gravel and rock, and Hamada (Anderson, 1999; Rastegar-Pouyani et al., 2007). The vegetation is almost always open steppe such as *Artemisia* and *Zygophyllum*. The lizards traverse around the base of shrubs when pursued, breaking cover when hard-pressed and running directly for the nearest large shrub. Their diet is composed of spiders, crickets, beetles, ants and other small insects (Anderson, 1999; Rastegar-Pouyani et al., 2007). They stay near the bushes and darting forward to capture insects attracted the shrubs (Anderson, 1999; Rastegar-Pouyani et al., 2007).

In this paper, we compare the skull anatomy of *Eremias persica* and *Mesalina watsonana* to further confirm the generic difference between these taxa.

MATERIAL AND METHODS

Specimens examined in this study were collected in the field during 2005–2007 in different localities (*Eremias persica* collected from Isfahan Province, Central Iranian Plateau and *Mesalina watsonana* from Birjand in Southern Khorasan Province, Eastern Iran). To compare the skull morphology, a series of seven dry skulls of adult specimens was used, i.e. four adult specimens of *E. persica* [Skull-Length (SL): 18.33 mm, Skull Height (SH): 6.50mm, Skull Width (SW): 9.61mm], and three adult specimens of *M. watsonana* [(SL): 11.18 mm, (SH): 3.50mm, (SW): 5.53mm]. The specimens were prepared according to the standards of skull preparation by Davis and Gore (1893). Following preparation, specimens were labeled and photographs of skulls in lateral, dorsal, and ventral views were taken using stereomicroscope (Olympus SZX12, Japan). The morphological characters listed in Lee (2005) were used as a guide for the morphological survey.

TABLE 1- The main differences in skull elements between *Eremias persica* and *Mesalina watsonana*.

Skull elements	<i>Eremias persica</i>	<i>Mesalina watsonana</i>
Nasals	Contacted medially	Separated
Posteromedial incisive processes (pip) of	Present	Absent
Premaxilla		
Maxillary teeth	17-20	14 - 16
Number of labial foramen (maxillary)	5-7	3
Angle of Supratemporal process with parietal body	70°	86°
Parietal foramen situation	Near the Frontoparietal suture	Entirely within parietal
Palatines	Contacted	Separated
Ptrygoid	Contacted anteriorly	Separated
Ptrygoid teeth	Present	Absent
Angle of quadrate process with transverse process (Ptrygoid)	110°	126°
Number of dentary tooth	20-22	15-17
Number of mental foramen	6-7	4-5
Angular (in lateral aspect)	Bifurcated anteriorly	Not bifurcated anteriorly
Adductor fossa (afs)	Anteriorly bordered by Coronoid	Anteriorly not bordered by Coronoid

RESULTS

THE SKULL OF *Eremias persica*

General features

The skull of *Eremias persica* is relatively small with large orbits and a small, sharply pointed rostrum (Fig. 1-a, Fig. 2-a). The upper temporal fenestrae are very narrow and obviously small (Fig. 1-c). The bones of the skull roof are very thin but those of the palate are more gracile still (Fig. 1-c). The lower jaw has a tall coronoid process and curved toward ventral margin (Fig. 3-a, 3-b).

Premaxilla (pm)

The premaxilla is a small, robust, unpaired element forming the anterior tip of the snout. It bears a narrow posterodorsally oriented nasal process whose base is narrow and dorsoventrally expanded. More posteriorly it widens before narrowing again and extending between the anteromedial corners of each nasal. The posterolateral end of the premaxilla contacts the maxilla beneath the naris. Anteroventrally, the alveolar border of the premaxilla bears 6–7 small, unicuspid teeth, arranged with three on either side of a median tooth; the median tooth is relatively larger and has a greater apicobasal dimension in relation to the remaining teeth. The premaxilla teeth are relatively curved posteriorly (Fig. 1-a). In ventral view the premaxilla bears two posteromedial incisive processes (pip). This tongue-shaped process extends ventrally and is less than half of the width and one-third the length of an average (or median) premaxillary tooth (Fig. 1-c).

Maxilla (m)

The maxilla is a paired triradiate element, with anterior, dorsal (facial), and suborbital processes, and a strong medial shelf that supports the tooth row between the naris and orbits. In lateral aspect, each maxilla extends approximately half the length of the skull (Fig.1-a). In an anterior to posterior sequence, the dorsal margin of the maxilla contacts the premaxilla, septomaxilla, nasal, prefrontal,

lacrimal, and jugal, respectively. The lateral surface of the preorbital facial process of the maxilla forms the ventral and posterodorsal rims of the fenestra exorarina. There are five to seven labial foramina (lf) on the lateral surface. The orientation of the labial foramina shifts from posterior to anterior, so that the posterior foramina are larger than the anterior ones. Most of the foramina are arranged in a semi-straight line that parallels the ventrolateral margin of each maxilla, but two foramina may be located above the level of the 2nd and 3rd anterior foramina (Fig. 2-a). The posterior part of the maxilla, bearing the last five to six teeth, contributes to the floor of the orbit and is dorsally overlapped by the palatine anteriorly, the jugal laterally, and the ectopterygoid posteriorly. This portion also constitutes the anteromedial rim of the inferior orbital fenestra (iof) and forms the floor of the maxillopalatine foramen anteriorly. The maxillopalatine foramen is less than half the size of the lacrimal foramen. Each maxilla bears 17-20 teeth on a well-developed alveolar shelf, their tips extending backwards (in microscopic view).

Nasal (n)

The nasal bones are small, ellipsoidal, paired elements which articulate anterolaterally with the frontal process of the maxilla, anteromedially with the nasal process of the premaxilla and posteriorly overlap the frontal, thereby forming most of the roof of the nasal capsules. Anteriorly, the nasal forms the posterodorsal rim of the fenestra exorarina. The dorsal surface of each nasal bears three (right) to five (left) small foramina arranged on an oblique line parallel to the posterolateral margin of the bone (Fig. 1-a).

Prefrontal (pref)

The prefrontals are paired and lie in the anterolateral portion of the skull table and form the anterodorsal rim of the orbit. Together with the frontal and palatines, they border the orbitonasal fenestra that connects the nasal and orbital cavities (Fig. 2-a). Each prefrontal articulates with the frontal and facial process of the maxilla dorsomedially, the maxilla anterodorsally and anterolaterally, and the lacrimal ventrolaterally. The anterior part of the articulation between the prefrontals and the anterolateral processes of the frontal is overlapped by the frontal process of maxilla (Fig. 2-a). The ventrolateral portion of the posterior surface of each prefrontal is notched and forms the medial margin of the lacrimal foramen. Ventral to this foramen, the ventrolateral end of each prefrontal is separated from the lacrimal by connective tissue. Ventral to the prefrontal–frontal suture, each prefrontal bears a foramen, herein termed the prefrontal foramen (pff).

Lacrimal (l)

These are paired sliver-shaped bones which completes the anterior orbit between the prefrontal and the jugal (Fig. 2-a). The lacrimal articulates with the maxilla anteriorly, the prefrontal dorsolaterally and medially and the jugal ventrolaterally and posteromedially.

Frontal (f)

The frontal is a single, hourglass shaped element which lies between the orbits and forms most of the dorsal orbital margin. Anteriorly, the frontal bears five processes: one anteromedial and four anterolateral, which are partially overlapped by the frontal processes of the maxilla and the nasals (Fig. 2-a). The anterolateral processes are thinner and longer than the anteromedial process. The external anterolateral processes extend to the anterior point of the prefrontal and articulate with the facial process of the maxilla laterally and with the prefrontal ventrolaterally. The internal anterolateral processes articulate with the dorsal process of the maxilla laterally and posterolateral margin of the nasals medially. The anteromedial (midline) process of the frontal articulates with the posteromedial margin of each nasal and meets the posterior end of the internasal suture.

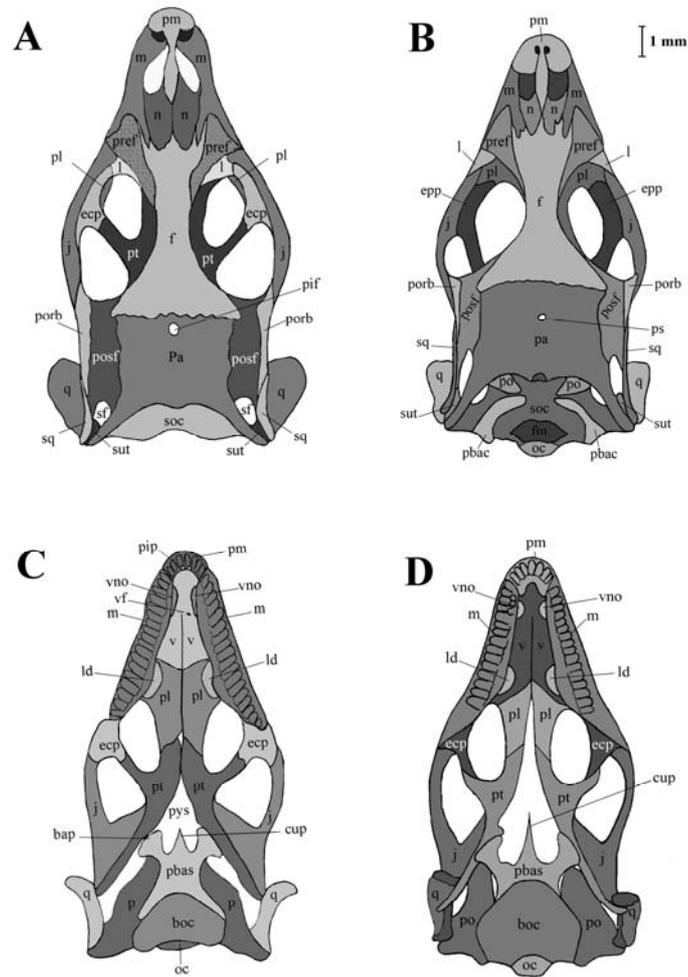


FIGURE 1. Dorsal view of the skulls of *Eremias persica* (A) and *Mesalina watsonana* (B). Palatal view (ventral view) of *Eremias persica* (C) and *Mesalina watsonana* (D). Abbreviations: ecp, ectopterygoid; f, frontal; fm, foramen magnum; oc, occipital; pbas, parabasisphenoid; po, prootic; j, jugal; l, lacrimal; m, maxilla; n, nasal; pa, parietal; pl, palatine; pref, prefrontal; q, quadrate; sq, squamosal; pt, pterygoid; pif, pineal foramen; pm, premaxilla; posf, postfrontal; porb, postorbital; q, quadrate; sf, supratemporal fossa; soc, supraoccipital; sut, supratemporal. Scale bar: 1 mm.

Posterolaterally, the frontal articulates with the anteromedial margin of the postfrontal. The transverse posterior margin of the frontal lies anterior to the posterior margin of the orbits and articulates with the anterior margin of the parietal.

Parietal (pa)

The parietal is a quadrangular and single element which occupies the central part of the skull table. Its dorsal ornamentation does not correspond to the pattern of the scales that closely adhere to its surface (the parietal and interparietal scales). Laterally, the parietal is medially concave and articulates with the posterolateral margin of the postfrontal. The parietal bears a pair of supratemporal processes, which form the lateral margin of the supratemporal fossae (sf) (Fig. 1-a). The ventrally

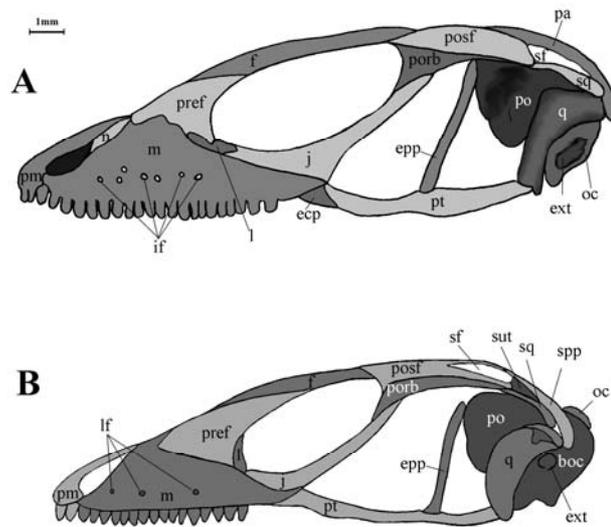


FIGURE 2. Left lateral view of the skull of *Eremias persica* (A) *Mesalina watsonana* (B). Abbreviations: epp, epipterygoid; ex, exoccipital; lf, labial foramina; oc, occipital condyle; p, prootic; pt, pterygoid. Scale bar: 1 mm.

oriented supratemporal processes are mediolaterally compressed, and relative to the midline project with an angle of approximately 70° ; the squamosals overlap these processes ventrolaterally. The distal end of each supratemporal process articulates with the paraoccipital process (parp) of the otoccipital. Medially, the posteroventral surface of the parietal bears the parietal fossa, which receives the distal end of the cartilaginous processes ascendens of the supraoccipital.

Supratemporal (sut)

This is a small and laterally compressed paired element, which lies entirely between the supratemporal fossa, squamosal, quadrate and each supratemporal process of the parietal (Fig. 1-a). The anterior end of each supratemporal forms the posterior margin of the supratemporal fossa (sf), whereas its posterior end articulates with the posterior end of the quadrate, the posterior end of the squamosal and the lateral surface of the supratemporal process of parietal.

Postfrontal (posf)

The postfrontal is a large, paired, quadrangular bone that forms part of the posterodorsal rim of the orbit. The postfrontal bears an anteromedial process that articulates with the posterior end of the lateral margin of the frontal (Fig. 1-a, Fig. 2-a). The postfrontal articulates with the postorbital anterolaterally, with the squamosal posterolaterally and with the parietal medially. The posterior ends of the postfrontal form the anterior margin of the supratemporal fossa.

Postorbital (porb)

The postorbital is a triangular bone that lies on the posterior margin of each orbit in posterolateral view (Fig. 2-a). The anterior margin of each postorbital, together with the anterior margin of each postfrontal, forms the posteroventral rim of the orbit. It articulates with the jugal anteroventrally and the postfrontal dorsally. The postorbital has a long posterior process extending backwards; it is overlapped by the postfrontal and articulates with the anterior end of the squamosal.

Squamosal (sq)

The squamosal is a long and slender bone which forms the posterolateral rim of the supratemporal fossa. The anterior portion of each squamosal articulates with the posteroventral margin of the postorbital (Fig. 3-a). Posteriorly, the squamosal is expanded and articulates dorsally with the venterolateral margin of the supratemporal and ventrally with the cephalic condyle of the quadrate.

Jugal (j)

This is a paired curved bone that forms the ventral rims of each orbit. Each jugal is composed of two elongate processes that enclose an angle of 110° with the vertex lying halfway between the anterior and posterior ends of the skull (Fig. 2-a). The anterior, or maxillary, process articulates ventrally with the posterodorsal portion of the maxilla, posteromedially with the distal margin of the anterolateral process of the ectopterygoid, and anteriorly with the lacrimal. The dorsal half of the anterior margin of the posterior or temporal process articulates with the anterior portion of the ventral margin of the postorbital. Medially, the temporal process bears the maxillary foramen, which lies immediately anterior to the anteroventral end of the postorbital. The ventral surface of the jugal articulates with the ventral portion of the palatine.

Vomer (v)

The vomers are paired, slender and relatively large bones which represent the most anterior element of the palate and forms the medial border of the vomeronasal opening (vno) anterolaterally (Fig. 1-c). The vomers are fused with each other along the anterior half of their length and are separated from the posteroventral margin of the premaxilla and premaxillary process of the maxilla by connective tissue. Each vomer bears a small groove anteriorly. The anterior half of each vomer bears a vomerine foramen (vf) posteriorly, the vomers are invested by the vomerine processes of the palatines. The posteromedial part of each vomer is dorsally concave.

Palatine (pl)

The palatine is a paired element as long as the vomer; forming the posterior region of the palate. Each palatine bears three processes: the vomerine process anteromedially, the pterygoid process posteriorly, and the maxillary process anterolaterally (Fig. 1-c). The vomerine process overlaps the corresponding vomer dorsally, thereby lying in the most dorsal aspect of the palate. Together with the anterior margin of the maxillary process, the lateral margin of the vomerine process forms the laterally concave rim of the opening of the lacrimal duct (ld). The wide pterygoid process descends posteroventrally and forms the medial margin of the inferior orbital fenestra. This process overlaps the dorsal surface of the palatine process of the pterygoid posteriorly and bears a series of small foramina on its ventral surface. The maxillary process overlaps the dorsal surface of the maxilla at the level of the anterior end of the orbit forming, the roof of the maxillopalatine foramen. This process articulates with the prefrontal, the jugal, the ectopterygoid and the maxilla at the level of the anterior part of orbit. The palatines are posteromedially separated from each other by the anterior half of the pyriform space (pys).

Ectopterygoid (ecp)

The ectopterygoid is a pillar-like paired element that enters the cheek as a bony sliver sandwiched between the maxilla and the jugal. Each ectopterygoid bears three short processes; the anterolateral process overlaps the dorsal surface of the posterior portion of the maxilla and bears the last five or six maxillary teeth. Laterally, this process articulates with the posterior portion of the ventromedial margin of the maxillary process of the jugal. The anterior portion of the posterolateral process overlaps the anteroventral end of the temporal process of the jugal dorsally and the posterior end of

the maxilla ventrally. The medial process overlaps the anterior portion of transverse process of the pterygoid (Fig. 1-c). The ectopterygoid forms the lateral rim of the inferior orbital fenestra (Fig. 2-a).

Pterygoid (pt)

This is a slender, gracile bone in comparison to the robust built of the skull roof. It is paired and the largest palate elements that are located in most posterior position rather than other elements. There are small, conical denticles (pterygoid teeth) on each pterygoid plate (Fig. 1-c). The posteromedial rim of the inferior orbital fenestra was formed by pterygoid; also, in formation of posterior, two-thirds of pyriform space posteriorly participates with the parabasisphenoid (pbas). Anteriorly, the pterygoid bears two processes: the palatine process medially and the transverse process laterally. The flat, triangular medial process is overlapped by the pterygoid process of the palatine dorsally. The oblique transverse process encloses an angle of 56° with the palatine process, extends dorsolaterally, and is anteriorly embraced by the medial process of the ectopterygoid. Posteriorly, the pterygoid bears the long, laterally compressed quadrate process, which constitutes two – thirds of the length of the bone. The quadrate process is medially convex and laterally concave, forming an angle of 110° with the transverse process. This process extends posterolaterally to articulate with the posterior portion of the medial part of the quadrate (Fig. 2-a).

General features of the braincase

Parabasisphenoid (pbas)

The parabasisphenoid forms the anterior floor of the braincase and articulates with the basioccipital posteriorly and the prootic dorsally. Except for its anteromedial cultriform process (cup), the dermal parasphenoid is indistinguishably fused to the basisphenoid, which has both cartilaginous and membranous origins (Patterson, 1977; Rieppel, 1993, Torres-Carvajal, 2003). Therefore, these bones are here described as a single parabasisphenoid (pbas).

The parabasisphenoid bears five processes. Anteriorly, there are two wand-like basiptyergoid processes which, as in the tropodurid lizard *Stenocercus guentheri* (Torres-Carvajal, 2003) articulate with the partly ossified meniscus pterygoideus lying on the pterygoid notch of the quadrate processes of the pterygoid. Dorsal to each basiptyergoid process the parabasisphenoid bears a short dorsolateral alar process. Two, long slender posterolateral processes overlap the basioccipital anterolaterally and extend to the anterodorsal aspect of its spheno-occipital tubercles. The thin, triangular cultriform process (cup) underlies the trabecula communis and extends anterodorsally to a point corresponding to the posterior limit of the maxillary arcade along the posterior half of the pyriform space (Fig. 1-c).

Basioccipital (boc)

As in the gymnophthalmid lizard *Neusticurus epleopus* (Bell et al., 2003), this is a relatively simple pentaradiate structure which lies between the two otic capsules and forms the posterior floor of the braincase and the medial portion of the occipital condyle (oc). It articulates broadly with the parabasisphenoid anteriorly and is ventrally invested by the posterolateral processes of the parabasisphenoid. The basioccipital articulates with the inferior process of the prootic anterolaterally (Fig. 1-c).

Otoccipitals (otoc)

Early in development, the exoccipital fuses with the opisthotic on each side of the braincase in most species of lizards (Gaupp, 1906; De Beer, 1937; Oelrich, 1956; Torres-Carvajal, 2003). Therefore, these elements are herein described as a single unit: otoccipital (otoc).

The otoccipital forms the posterolateral wall of the braincase. The otoccipital bears two pairs of processes. The anterior process articulates with the posterior end of the quadrate process of the

parietal anterolaterally. The posterior process is overlapped by the dorsal surface of the supraoccipital ventromedially and articulates with the basioccipital posteroventrally.

Prootic (po)

As stated by Bell et al. (2003), “the prootic forms the anterior wall of the otic capsule and part of the anterolateral wall of the braincase.” or alternatively “The prootic represents the anterior part of the otic capsule and helps form the anterolateral boundary of the braincase (Bell et al., 2003).”

Supraoccipital (soc)

The supraoccipital is a saddle-like bone that is anteroposteriorly short and wide. The bone lays posteroventral to the parietal and forms the posterior roof of the braincase (Fig. 1-a). The medial portion of its posteroventral margin forms the dorsal rim of the foramen magnum (fm). The anterior margin of the supraoccipital is separated from the parietal by a gap filled with connective tissue.

The ventral margin of the supraoccipital is overlapped by the ventral surface of the anteromedial process of the otoccipital posteriorly its dorsomedial and anterodorsal surface is overlapped with the prootic anteriorly.

Quadrate (q)

The quadrate is a semicircular, concave, small and gracile bone. The lateral concha is well defined and has a relatively weak tympanic crest. The dorsal region of the quadrate is cartilaginous in the hatchling (Romer and Parsons, 1978). The quadrates are located at the posterolateral corners of the skull, and articulate with and support the lower jaw (Fig. 2-a). Ventrally, each quadrate bears a large condyle, which articulates with the medial and lateral portions of the glenoid fossa of the prearticular. The cephalic condyle articulates with the intercalary cartilage ventromedially, the distal end of the supratemporal dorsomedially and the distal end of squamosal dorsolaterally.

Epipterygoid (epp)

The epipterygoid is a rod-shaped, slender bone of relatively constant diameter. It sits in the fossa columellae of the pterygoid and projects towards the skull roof. It is posterodorsally tilted and provide an angle of about 95° with the pterygoid (Fig. 2-a). Its dorsal half is laterally bowed and each tip is capped with partly ossified cartilage.

The lower jaw

Dentary (d)

This is the most prominent and largest of all the jaw elements and the only one that bears teeth. It is more than half the length of the lower jaw laterally and bears 20 (22 on left ramus) teeth on a well-defined alveolar shelf. The dentary invests the anterior half of Meckel's cartilage (mc); however, the anterior end of the cartilage exits the dentary anterolingually through the anterior end of the Meckel's canal, which lies ventral to the second tooth.

In lateral aspect, the dentary is posteriorly separated into an angular process and a surangular process. The angular process articulates with the anteromedial surface of the angular dorsolaterally. The surangular process articulates with the coronoid dorsally and with the surangular ventrolaterally. There are 6-7 mental foramina (menf) on the lateral surface of dentary (Fig. 3-a). In lingual aspect, the dentary is bifurcate; the ventral splenial process and anteroventral portion of the dorsal coronoid process articulate with the splenial, whereas the posterior aspect of the dorsal coronoid process overlaps the anteromedial process of the coronoid (Fig. 3-b).

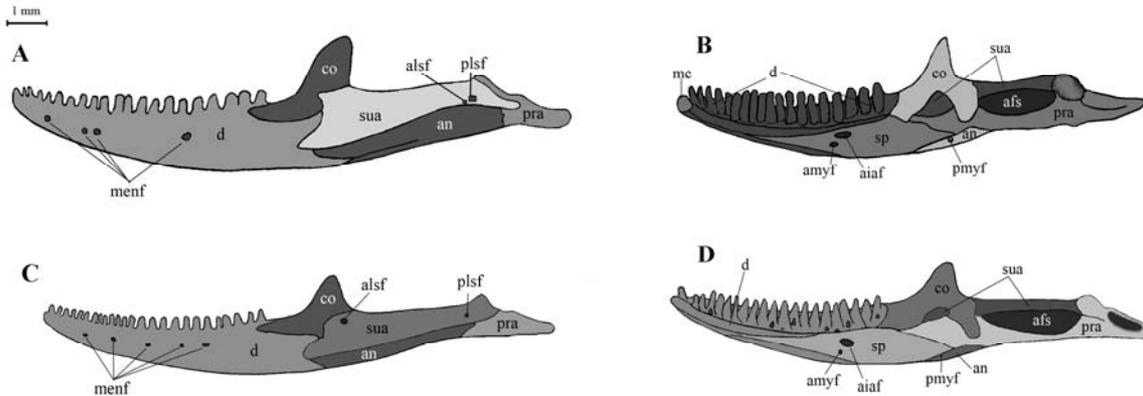


FIGURE 3. Right lower jaw ramus in lateral (A) and medial (B) views in *Eremias persica* and in *Mesalina watsonana*, lateral (C) and medial (D) views. Abbreviations: an, angular; afs, adductor fossa; aiaf, anterior inferior alveolar foramen; alsf, anterolateral surangular foramen; amyf, anterior mylohyoid foramen; co, coronoid; d, dentary; mc, Meckel's cartilage; menf, mental foramina; plsf, posterolateral surangular foramen; pmyf, posterior mylohyoid foramen; pra, prearticular; sp, splenial; sua, surangular. Scale bar: 1 mm.

Coronoid (co)

The triradiate coronoid in medial view bears three processes, dorsal, anteromedial and posteromedial processes. The dorsal process extends above the rest of the dorsal margin of the mandible; the height of the dorsal process is nearly as high as the maximum height of the dentary (Fig. 3-a).

In medial aspect, the coronoid bears two processes: the anteromedial process articulates with the dentary anteriorly, the splenial ventrally, the prearticular posteroventrally and the surangular posterodorsally. The posteromedial process overlaps the anteromedial portions of the surangular dorsally and the prearticular ventrally. The base of the lingual bifurcation of the coronoid is dorsally concave and articulates with the anterior end of the surangular.

Ventrolaterally, the coronoid bears a small labial process, which overlaps the posterolateral margin of the dentary. Posterior to the labial process, the coronoid articulates ventrolaterally with the dorsal margin of the anterolateral process of the surangular (Fig. 3-b)

Surangular (sua)

The surangular occupies the upper posterior part of the lateral surface of the mandible and forms the dorsolateral portion of the lower jaw between the coronoid and prearticular (Fig. 3-a). In lateral view, the surangular bears two foramina, the anterolateral (alsf) and posterolateral (plsf) surangular foramina, and two processes, the dorsolateral process, which articulates with the posterior portion of the coronoid and the anterolateral process, which articulates with the posterior portion of dentary. The ventrolateral border of the surangular articulates with the dorsal border of the angular and posteriorly with part of the anterodorsal border of the prearticular.

Lingually, the anterior portion of the surangular is overlapped by the coronoid; as a consequence, a small portion of the surangular is exposed between the lingual processes of the coronoid (Fig. 3-b). The ventromedial and posteromedial margins of the surangular are fused with the prearticular. The articulation between the surangular and prearticular forms the lingual wall of the adductor fossa (afs). On the posterolateral wall of the adductor fossa (afs), the surangular bears a foramen, herein termed the posteromedial surangular foramen.

Angular (an)

The angular is a slender posteroventral element, comprising less than one-third of the length of the mandible. It lies behind the splenial and dentary and below the surangular. In the lateral view, the angular bears two processes: an anterolateral and a anteroventral process. The anterolateral process articulates with the posterior end of the dentary and with the surangular dorsally. The anteroventral process is long and slender and articulates with the posterolateral margin of the dentary. In the lingual view, the angular articulates with the splenial anteriorly and the prearticular posteriorly. Ventromedially, each angular is pierced by a small, posteriorly directed posterior mylohyoid foramen (pmyf) at the level of the anterior end of the adductor fossa (Fig. 3a-b).

Prearticular (pra)

The prearticular as a major element of the inner surface of the jaw, forms the posterior end of each mandible ramus and lies mostly on the ventral and lingual aspects of the mandible (Fig. 3a-b). The large adductor fossa lies between the prearticular and surangular, as known in teiid and lacertid lizards. This feature is due to unique arrangement of prearticular component so that its dorsal border lies more medially than its ventral one (Estes et al., 1988; Bell et al., 2003). The anteromedial portion of the prearticular is overlapped with the lingual process of the coronoid. The prearticular articulates with the surangular dorsally, the splenial medially and the angular ventrolaterally. The dorsal portion of the prearticular, together with the ventromedial margin of the surangular, forms the ventral wall of the adductor fossa.

Splenial (sp)

The splenial is a large blade-like element which lies on the medial surface of the mandible, between the closed end of the Meckelian fossa and the coronoid. The anterior half of its dorsal margin articulates with the dentary anteriorly and the ventral border of the anterior lingual process of the coronoid posteriorly, whereas the posterior half articulates with the prearticular. The anterior half of the ventral margin articulates with the dentary and the posterior half of the ventral border articulates with the angular. The anterior end of the splenial forms the posterior rim of the anterior inferior alveolar foramen (aiaf). The anterior portion of the splenial bears the anterior mylohyoid foramen (amyf), which is located at the same vertical level of the ventral rim of the adductor fossa. The anterior inferior alveolar foramen (aiaf) is located posterodorsal to the amyf, and is nearly two times larger than the amyf (Fig. 3-b).

THE SKULL of *Measalina watsonana***General features**

The skull of *Measalina watsonana* is superficially very similar to *Eremias persica* in terms of general proportions and the relationship between individual bones (Fig. 1-b, Fig. 2-b). For example, there are obvious similarities in the construction of the snout and palate (Fig. 1-d, Fig. 2-c, 2-d). The ornamentation of the elements is also similar.

Premaxilla (pm)

The premaxilla is a small unpaired element, forming the anterior tip of the snout. Unlike *E. persica* in which the nasal processes of the premaxilla becomes narrow and thin in the median region, in *M. watsonana* this process retains the same thickness across its entire length (Fig. 1-b). The short posterior end of the nasal process of the premaxilla contacts the anteromedial corners of the nasal process of the frontal by a very slender connective tissue, but in *E. persica* this process is shorter and extends just to the middle of the nasal. As a result, the nasals are separated from each other in *M. watsonana*, whereas in *E. persica* they meet each other medially. Unlike *E. persica*, in *M. watsonana* the premaxilla has no pip process. As in *E. persica*, there are seven teeth on the premaxilla of *M.*

watsonana. The teeth are all of the same size, and their shape is similar to the teeth of the maxilla, i.e. they are vertical and not curved posteriorly, only their tips are directed backwards (Fig. 1-d).

Maxilla (m)

The maxilla is triradiate and large, reaching past the middle of the ventral margin of the orbit; occupying most of the anterolateral aspects of the skull between the orbits and the snout (Fig. 1-b). This species differs from *E. persica* in the number of labial foramina, which in *M. watsonana* is about 3-4 foramina on each side of the maxillary bone. The number of teeth on the maxilla is about 14 to 16. The shape of the teeth is the same as in *E. persica* (Fig. 2-b).

The nasals are paired ellipsoid bones and are in contact with the posterior process of the premaxilla anteromedially, the maxilla anterolaterally, the nasal process of the frontal posteromedially and the frontal posteriorly. The nasals are totally separated from each other due to the penetration of the nasal process of the frontal and strong posterior extension of the premaxillary process toward the nasals (Fig. 1-b).

Nasal (n)

The nasals have one to two foramina on their posterolateral margins, located near the frontal process of the maxilla. In *M. watsonana* the articulation surface of the nasals with the maxilla is reduced; compared to the increase extension of frontal processes in *E. persica*.

Prefrontal (pref)

The prefrontals are smooth and medially concave, meeting the maxilla and contributing to the anteriodorsal margin of the orbit with a slender posterodorsal orbital process that contacts and overlaps with the frontal (Figs. 1-b, 2-b).

Lacrimal (l)

The lacrimals are small and vertically compressed, each of which completes the anterior orbit between the prefrontal and the jugal (Fig. 2-b). The prefrontal and the lacrimal of *M. watsonana* are in most respects similar to those of *E. persica*, with the following differences: the lacrimal in *E. persica* overlaps the jugals but in *M. watsonana* the two bones articulate with each other, and also the prefrontal more strongly occupies the dorsal rim of the orbit in relation to *E. persica*.

Frontal (f)

The frontal lies between the orbits and forms most of the dorsal orbital margin (Fig. 1-b). In *M. watsonana*, the anterolateral processes are completely equal with each other and the anteromedial process comes close to the dorsal portion of the maxilla, only separated by a very small connective tissue, leading to the separation of the nasals. The posterior surface of the frontal is medially concave and articulates with the anterior margin of the parietal.

Parietal (pa)

The parietal is a single flattened median element and forms most of the posterior surface of the skull table (Fig. 1-b). In *M. watsonana* the parietal foramen is located nearly in the center of the parietal, whereas in *E. persica* it is located near the frontoparietal suture. The articulation surface of the frontal with the parietal is almost flat rather than having a jagged articulation surface as seen in *E. persica*. The ventrally-oriented supratemporal processes are laterally compressed forming an angle of approximately 86°.

Supratemporal (sut)

The supratemporal is a longitudinal bone, in which the width is the same throughout its length. The anterior end of each supratemporal forms the posterior margin of the supratemporal fossa (sf) (Fig. 1-b). The supratemporal fossa (sf) of *M. watsonana* is larger than in *E. persica*.

Postfrontal (posf)

The postfrontal and postorbital are separate bones but closely associated to form a functional unit. The postfrontal is large, quadriradiate, and extends beyond the orbital margin. The postorbital is a small triradiate bone, situated at the posterolateral orbital margin. The postorbital weakly overlaps the jugal in anteroventral articulation and anterodorsally is in contact with the postfrontal (as mentioned above).

Postorbital (porb)

In *M. watsonana*, the postorbital extends more posteriorly and the squamosal is shorter than in *E. persica* (Figs. 1-b, 2-b).

Squamosal (sq)

The squamosals are long and slender (Fig. 2-b). Like in *E. persica*, the anterior portion of the lateral margin of each squamosal articulates with the posteroventral margin of the postorbital. Dorsally, the posterior area articulates with the supraoccipital and the ventral area articulates with the cephalic condyle of the quadrate.

Jugal (j)

The jugal is a large and V-shaped element centered beneath the orbit. The slender bone anteriorly meets the maxilla and the ectopterygoid. The jugal processes enclose an angle of 120° which are wider than this angle in *E. persica* (Fig. 2-b). There are two or three foramina near the temporal process. The articulation of this bone is like that in *E. persica*, whereas the jugal is somewhat thinner in *M. watsonana* than in *E. persica*. The posterior margin also appears to be straighter in *M. watsonana* than in *E. persica*.

Vomer (v)

The vomers are the most anterior elements of the palate and form the medial border of each ventronasal opening (vno) anterolaterally and the medial rim of each lacrimal duct opening (ld) posterolaterally. The vomers are fused with each other along the anterior one-fourth of their length (Fig. 1-d). In *M. watsonana* the vomers are more extended than in *E. persica*, therefore the vomers are extended to the end of the maxillary tooth row whereas in *E. persica* they are only extended to the 9th and 10th maxillary teeth, and their thickness and roughness is less than that of *E. persica* (Fig. 1-d).

Palatine (pl)

The palatines are medially separated by the anterior third of the pyriform space (pys), whereas in *E. persica* the palatines are in contact, in their most medial borders, so the pyriform space (pys) is more extended anteriorly (Fig. 1-d). In *M. watsonana* the palatine articulates with the maxilla and vomer at the level of the 13th and 14th (last maxillary teeth row) tooth whereas in *E. persica*, this articulation occurs at the level of the 17th and 18th tooth (middle maxillary teeth row). This means that the palatines in *E. persica* are more extended anteriorly than in *M. watsonana*.

Ectopterygoid (ecp)

The ectopterygoid enters the cheek between the maxilla and jugal (Fig. 1-d). The ectopterygoid runs from the lateromedial pterygoid to the posterolateral maxilla; its lateral head contacts both the maxilla and the jugal.

Pterygoid (pt)

The pterygoids are the largest and most posterior elements of the palate and bear no teeth. In *E. persica*, the medial (palatine) processes of the pterygoid adjoin with each other at the medial margin, so that the pyriform space (pys) is divided into anterior and posterior regions. The anterior region lies between the anterior portion of the pterygoid and the posterior portion of the palatine (Fig. 1-d). However, in *M. watsonana* the medial (palatine) process of the pterygoid is separated and the pyriform space is not divided. The quadrate process encloses an angle of 126° with the transverse process of the pterygoid, leading to a broader space for the pyriform recess in *M. watsonana*.

General features of the braincase

The general features of the braincase of *M. watsonana* are, more or less, similar to those of *E. persica*

The Lower Jaw**Dentary (d)**

The dentary element in both *Mesalina watsonana* and in *E. persica* is the major element of the mandible, which bears the marginal teeth and lies opposite to the maxilla and the premaxilla of the upper jaw (Fig. 3, c-d). The dentary is narrow and long; it carries 15-17 teeth positions, obviously less than in *E. persica*. There are at least 4-5 mental foramina on the lateral surface, as compared to 6-7 in *E. persica*. The angular and surangular processes of the dentary in *M. watsonana* are less extended posteriorly and are more strongly overlapped by the coronoid, in relation to *E. persica* (Fig. 3-c). Both taxa, however, have a long splenial.

Coronoid (co)

The coronoid is triradiate in medial view and lies immediately behind the mandibular tooth row (Fig. 3-c). The dorsal lingual process of the coronoid is less extended dorsally in *M. watsonana*, such that a part of the contact surface of surangular and prearticular is visible medially, whereas in *E. persica* the contact surface of the surangular and prearticular is entirely overlapped by the dorsal lingual process of the coronoid. The labial process in *M. watsonana* extends anteriorly almost to the first and second dentary teeth, whereas in *E. persica*, it is short and only overlaps the posterolateral margin of the dentary. The labial process in *M. watsonana* extends more dorsally and comes close to the posterior portion of the anterolateral process of the surangular. In *E. persica* this process is oblique, so its posterior part has fewer curves toward the back than the *E. persica* (Fig. 3-d).

Surangular (sua)

The surangular extends dorsally to overlap with the posterior part of the coronoid process. This element is a flattened bone that forms most of the lateral surface of the mandible posterior to the coronoid (Fig. 3-c). It is similar to *E. persica*, but differs in the following aspects: On the lateral surface, there is an anterolateral foramen (alsf) located near the border of the surangular and coronoid but in *E. persica* the foramen is located behind the posterolateral foramen (plsf) near the angular. On the other hand, the (alsf) and (plsf) are located on the most lateral margin of the surangular toward in *E. persica* located in most medially region of surangular. The anterior process of the surangular, where it articulates with the dentary and the coronoid encloses a sharp angle in *E. persica*, but in *M. watsonana* this process has a concave shape and does not form an angle in the front

(Fig. 3-c). In *M. watsonana*, the posteromedial foramen of the surangular is more strongly visible than in *E. persica*. In that species, this foramen is located on the posterpdorsal margin of the surangular, but in *M. watsonana*, it is located more anteriorly (Fig. 3-d).

Angular (an)

The angular is a slender bone, confined to the ventral margin of the mandible. The anterolateral process of the angular is small and extends lingually. The main portion of the angular volume is located on the ventral surface of the mandible in contrast to *E. persica* in which the angular occupies more space in the lateral aspect of the mandible (Fig. 3, c-d).

Prearticular (pra)

The prearticular forms the posteromedial and terminal parts of the jaw ramus. The prearticular component of the bone is angled so that its dorsal border lies more medially than its ventral one. It is in all respects similar to *E. persica*, only the adductor fossa (afs) in *E. persica* is more extended anteriorly, reaching the posterior process of the coronoid (Fig. 3, c-d).

Splénial (sp)

The splénial is a large, triradiate element in lingual view, extending anteriorly past the middle of the teeth row, and also extending posteriorly onto the postdentary bones, past the apex of the coronoid process. The splénial contacts the dentary anteriorly and the angular posteriorly (Fig. 3, c-d). This element in *M. watsonana* is similar in all aspects such as articulation by other bones with *E. persica*.

DISCUSSION

The skull is the most complicated of all reptilian skeletal structures and generally provides the most morphological data for phylogenetic analyses (e.g. Estes 1988; Conrad 2008). *Eremias* and *Mesalina* have previously been separated according to soft tissue anatomy (Szczerbak 1974; Arnold 1986) and molecular data (e.g., Arnold et al., 2007). In the present study, we showed that these taxa also differ in some aspects of their skull anatomy (Table 1). The three major differences between the two studied taxa comprise: 1. the nasals are in contact in *Eremias persica* but in *Mesalina watsonana*; they are separated by the nasal process of the premaxilla and the anteromedial process of frontal, 2. the absence of pterygoid teeth in *M. watsonana*, 3. due to the pterygoid position in *M. watsonana*, the pyriform space is larger in this taxon. Other notable differences include: the shape of the premaxilla and its articulation with other skull elements, the shape of the frontal and the form of its processes, the number of dentary teeth, the shape of the jugal and amount of its curvature, and the position of the parietal opening,

Shared similarities may be related to parallelism, similar habitats leading to similar selective pressures and, thereby, organisms with similar general characters (Kardong, 2005). However, they are more likely related to plesiomorphic retentions. A wider survey is required to evaluate this similarity.

The form and tip shape of the dentary and maxillary teeth are similar in both taxa: the narrow curved tip of their teeth may facilitate prey capture for their insectivorous diet. The coronoid is large relative to the other lower jaw elements in both taxa. This feature maybe is related to the possession of a relatively high bite force and effective jaw leverage (Rieppel, 1984), since a long jaw may be useful for the rapid consumption of small, abundant insects. The evolution of a long jaw and inclined jaw musculature results in a fast (although relatively weak) jaw lever, which would facilitate the capture of elusive prey (Stayton, 2005; Jones, 2008).

E. persica and *M. watsonana* show little differences in such niche parameters as feeding strategy, diet, time of activity, the range of substrates occupied or escape techniques (Anderson, 1999; Rastegar-

Pouyani et al., 2007). It suggests that in their evolution they have been subjected to similar selective pressures.

However, in the last decade, molecular, craniological and external morphology studies have changed the taxonomic/systematic spectrum of some lacertid lizard species (e.g., Arnold, 1983; Arnold et al., 2007; Fu and Murphy, 1997; Fu, 1998) and shed more light on the evolutionary history of this lizards, but further detailed studies are necessary since they permit more accurate character definition in the determination of phylogenetic relationships and other biological aspects of these lizards.

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