

The skull of *Vanzosaura rubricauda* (Squamata: Gymnophthalmidae)

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Abstract

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A detailed description of the cranial osteology and chondrocranium of *Vanzosaura rubricauda* is made based both on articulated and partially disarticulated material of dry skeletons and cleared and stained specimens, and is compared with other previously studied gymnophthalmids. Some features of *Vanzosaura* are interesting, such as the reduction of the supratemporal fenestrae, that may reflect a process of miniaturization, and the fusion of the occipital bones in a single oto-occipital complex with no evident sutures. Based on the anatomical evidence, the skull of *Vanzosaura* is interpreted as amphikinetic.

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Introduction

The Gymnophthalmidae comprises approximately 213 currently recognized species in 41 genera (Uetz and Hallermann 2008), but it remains one of the most poorly known of all squamate clades; many aspects of gymnophthalmid anatomy, physiology, systematics and ecology are scarcely understood (Bell *et al.* 2003). The literature on gymnophthalmid cranial osteology is, in particular, quite limited considering the size of the group (Sinitsin 1928; Dixon 1974; MacLean 1974; Presch 1976; López and Cabrera 1995; Soares 2000; Montero *et al.* 2002; Bell *et al.* 2003; Tarazona *et al.* 2008). The lack of morphological data means that the most comprehensive phylogenetic studies of this group are based mainly on molecular data (Pellegrino *et al.* 2001; Doan 2003; Castoe *et al.* 2004; Doan and Castoe 2005), and the few attempts based on morphology are very limited in scope (Presch 1980; Rodrigues 1991; Hoyos 1998; Montero *et al.* 2002).

Originally *Vanzosaura rubricauda* was described as *Gymnophthalmus rubricauda* (Boulenger 1902), but Rodrigues (1991) erected the monotypic genus *Vanzosaura*, on the basis of scutellation characters. *Vanzosaura rubricauda* is a small gymnophthalmid found in the Chaco region, from Bolivia (Dirksen and de la Riva 1999), Paraguay (Ziegler *et al.* 2002) and Brazil (Peters and Orejas Miranda 1986), to the centre of Argentina. In Argentina this species is found in Salta, Tucumán, Santiago del Estero, Catamarca, La Rioja and

Córdoba provinces (Perotti and Cruz 1990; Ávila *et al.* 2000). *Vanzosaura* is considered a rare gymnophthalmid, poorly represented in herpetological collections; it is difficult to find in nature because it is a secretive species that lives under dead leaves. Although its extremities are short, it is quick and nimble (Höfling and Renous 2004). The diet of *Vanzosaura* is essentially insectivorous (Perotti and Cruz 1990). So far, its internal anatomy has been unknown.

We provide a detailed description of the adult skull and chondrocranium of *V. rubricauda*, based on a series of dry skeletal preparations and cleared and stained specimens, and compare it with the skulls of other gymnophthalmids previously studied by several authors. Special attention is given to the cranial kinesis because this is an important feature of the skull of the Squamata.

Materials and Methods

We studied seven adult specimens of *V. rubricauda* (Boulenger 1902) from the Herpetology Collection of the Fundación Miguel Lillo, Tucumán, Argentina. We prepared five dry skulls (FML 03309-1; 03309-2; 06109-1497; 06898; 08787) and four cleared and stained skulls (FML 03309-3; 06109; 06124-1; 06124-5) following protocols by Wassersug (1976). Some dry skulls were partially disarticulated. Because of the very fragile constitution of the skulls, on the dry preparations some bones are displaced from their natural positions or even lost (as the temporal arch of Fig. 1);

therefore, for some structures we prefer to rely on the cleared preparations (as the temporal arch of Fig. 3C). The osteological terminology follows that of Montero *et al.* (2004), while the chondrocranial terminology follows that of Oelrich (1956) and Götz (2001).

Results

The skull of *V. rubricauda* (Fig. 1) is relatively elongated and dorsoventrally depressed, with large snout and orbits. The nares are wide because the nasals are short and do not completely cover the anterior part of the nasal passage; although the osteological nares are wide, the cupula nasalis anterior cartilage (terminology from Götz 2001) extends anteriorly from the nasal, shaping a much narrower functional naris. Anterolaterally, the facial lamina of the maxillae is excavated, leaving the septomaxillae well exposed through the nares (Fig. 1B). There is a secondary palate (in the sense of Presch 1976); although there is no strong sutural contact between the alar process of the vomer and the palatal process of the maxilla, the gap between them being filled by soft tissue; therefore, there is a secondary functional palate that posteriorly deflects the air flow to the palatine groove (Fig. 2B,C). The margin of the large orbital fenestra is formed by the prefrontal, frontal, postfrontal, postorbital, jugal and maxilla (Fig. 1B). The margin of the oval suborbital fenestra is formed by the palatine, maxilla, ectopterygoid and pterygoid (Fig. 1C). The supratemporal fenestra (Fig. 3C) is narrow and elongated, and the margin is formed by the postfrontal, postorbital, parietal, squamosal and supratemporal; the shape and size of this fenestra may vary because of preparation artefacts. The small post-temporal fenestra is formed between the parietal and the supraoccipital area of the oto-occipital complex and is closed by a connective membrane (Fig. 3C). The braincase components are fused to form an oto-occipital complex, with no visible sutures and with prominent semicircular canals. There is a wide nasoethmoidal fenestra that communicates between the anterior part of the braincase (olfactory lobules) and the nasal capsule. The nasoethmoidal fenestra is formed by the frontal, prefrontals and palatines. The fenestra is partially closed by the cartilaginous planum antorbitale, which forms the posterior wall of the nasal capsule.

Premaxilla

The unpaired premaxilla (Figs 1A and 2A) forms the anterior tip of the snout. The bone consists of a wide horizontal plate and a long and wide dorsal (nasal) process. The nasal process is directed dorsoposteriorly at an acute angle, shaping a sharp snout in lateral view. The process inserts between the nasals and completely separates them along the midline. Anteriorly, the nasal process forms the medial border of the nares. The base of the nasal process is narrow, but it abruptly becomes wider posteriorly, at the level where it contacts

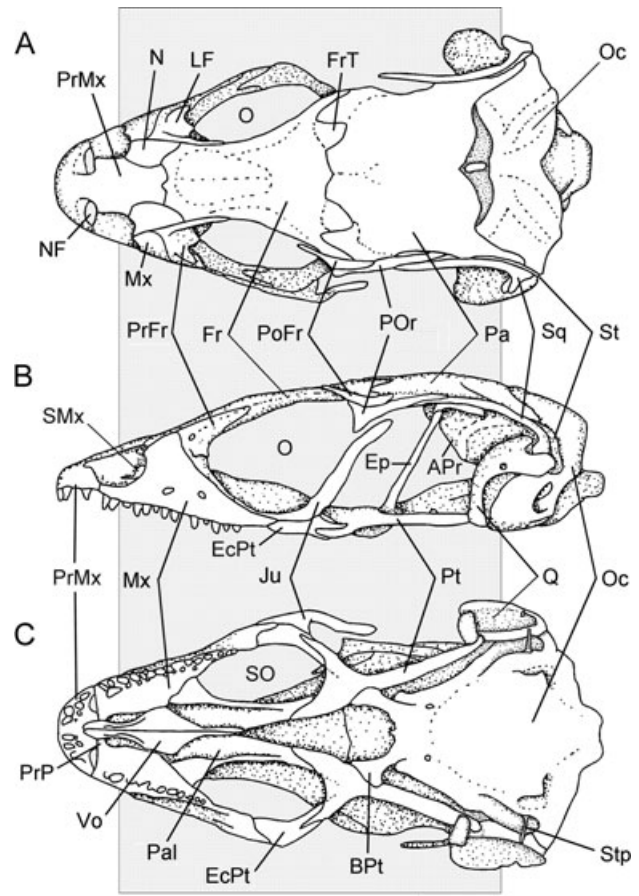


Fig. 1—The skull of *Vanzosaura rubricauda* (FML 03309-2). —**A**. Dorsal view. —**B**. Lateral view. —**C**. Ventral view. Note that, due to skull preparation, the right jugal, postfrontal and postorbital are missing, and the bones of the left temporal arch are displaced from their natural position (see Fig. 3C). Abbreviations: APr, alar process; BPt, basiptyergoid process; EcPt, ectopterygoid; Ep, epipterygoid; Fr, frontal; FrT, frontal tab; Ju, jugal; LF, lacrimal flange of the prefrontal; Mx, maxilla; N, nasal; O, orbit; Oc, oto-occipital complex; Pa, parietal; Pal, palatine; PoFr, postfrontal; POr, postorbital; PrFr, prefrontal; PrMx, premaxilla; PrP, premaxillary process of the maxilla; Pt, pterygoid; Q, quadrate; SMx, septomaxilla; SO, suborbital fenestra; Sq, squamosal; St, supratemporal; Stp, stapes; Vo, vomer. The scale corresponds to 1 mm.

ventrally the septomaxillae; from here the width and shape of the nasal process vary and it overlaps the nasals laterally. The posterior end is truncated and it forms a waved suture with the frontal. At the base of the dorsal process just anterior the nares, there are large foramina that are just anterior to the suture with the septomaxilla.

The horizontal plate is wide and high forming the most anterior tip of the snout. Ventrally, the plate bears 9 to 11 unicuspid pleurodont teeth aligned along the entire bone edge; the teeth articulate to a lower outer margin that flanges

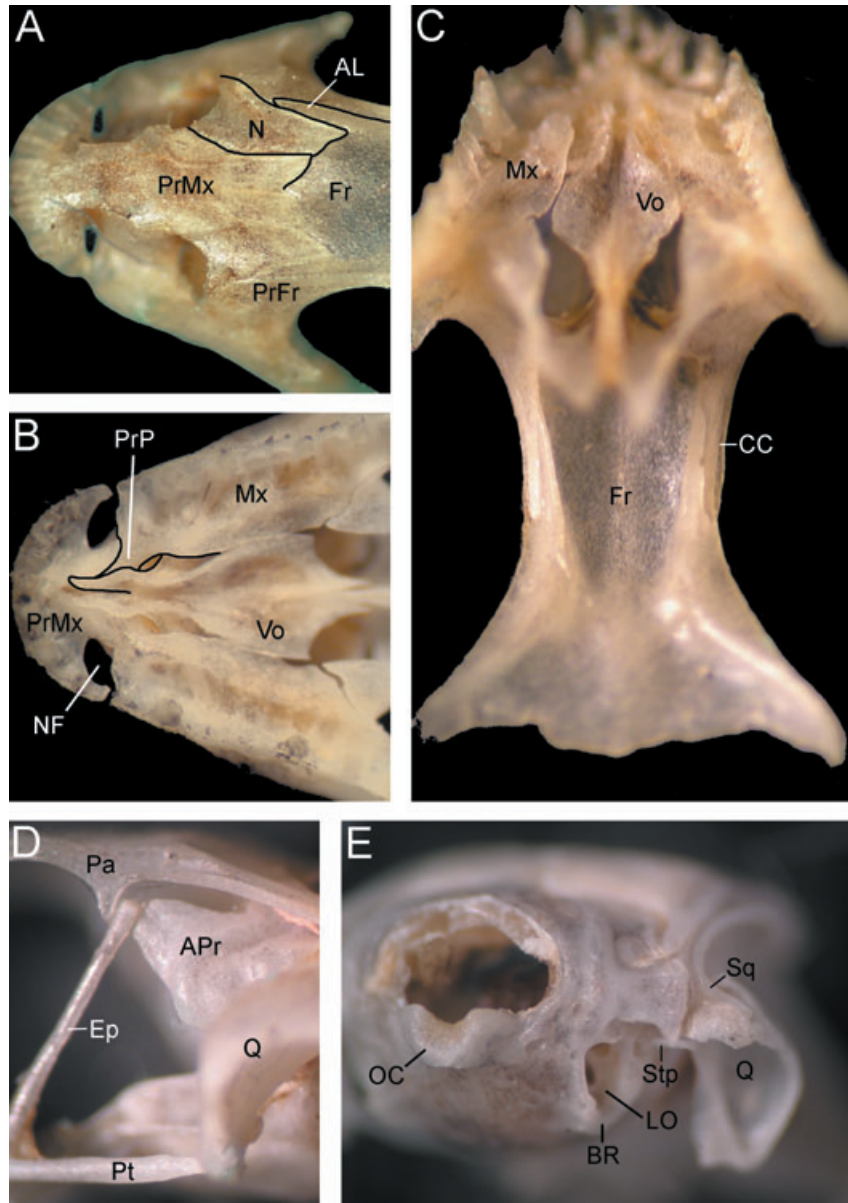


Fig. 2—Dry skulls of *Vanzosaura rubricauda*. —**A**. Dorsal view of the anterior portion of the skull (FML 03309-2). —**B**. Ventral view of the anterior portion of the skull (FML 06808). —**C**. Posterovenral view of a skull partially disarticulated to see the choanal openings; ventral and anterior sides are upward (FML 03309-2). —**D**. Lateral view of the epipterygoid contact with the parietal and the alar process (FML 06898). —**E**. Posterolateral view of the oto-occipital complex, showing the two openings of the otic capsule: the fenestra ovalis, and the rotundum foramen (FML 06898). Abbreviations: AL, anterolateral process of the frontal; APr, alar process; BR, basiooccipital ridge; CC, crista cranii of the frontal; Ep, epipterygoid; Fr, frontal; LO, lateral opening of the recessus scalae tympani; Mx, maxilla; N, nasal; NF, narial fenestra; OC, occipital condyle; Pa, parietal; PrFr, prefrontal; PrMx, premaxilla; PrP, premaxillary process of the maxilla; Pt, pterygoid; Q, quadrate; Sq, squamosal; Stp, stapes; Vo, vomer.

ventrally. Posterior to the tooth row, the horizontal plate extends, and contacts the maxillae and the vomers. The posterior border of the horizontal plate is concave, and contacts the maxillary palatal lamina at two points, leaving a semicircular fenestra between them (narial fenestra, Fig. 2B); the narial fenestra is closed by a membrane but in the dry skulls it can be seen in dorsal view through the nares (Fig. 1A). The medial portion of the horizontal plate is thicker than the rest of the plate; it forms a triangular platform, with the tip pointed anteriorly and with a broad posterior base, which is ventrally overlapped by the premaxillary (anteromedial) processes of the maxilla and, at the sagittal plane, by the anterior tips of the vomers (Fig. 2B).

Maxilla

Each maxilla consists of two wide plates at a right angle: a lateral facial lamina that shapes the lateral extent of the snout, and a ventral palatal lamina that bears the teeth and forms part of the palate anterolaterally (Figs 1A and 2B).

The facial lamina forms the lateral wall of the nasal capsule and anteriorly it forms the posterior concave border of the nares. Dorsally, the facial lamina contacts the nasals anteriorly and the prefrontal posteriorly; in some specimens, the contact with the nasals may be reduced by the extension of the anterior process of the prefrontal. The height of the facial lamina is progressively reduced posteriorly, toward the

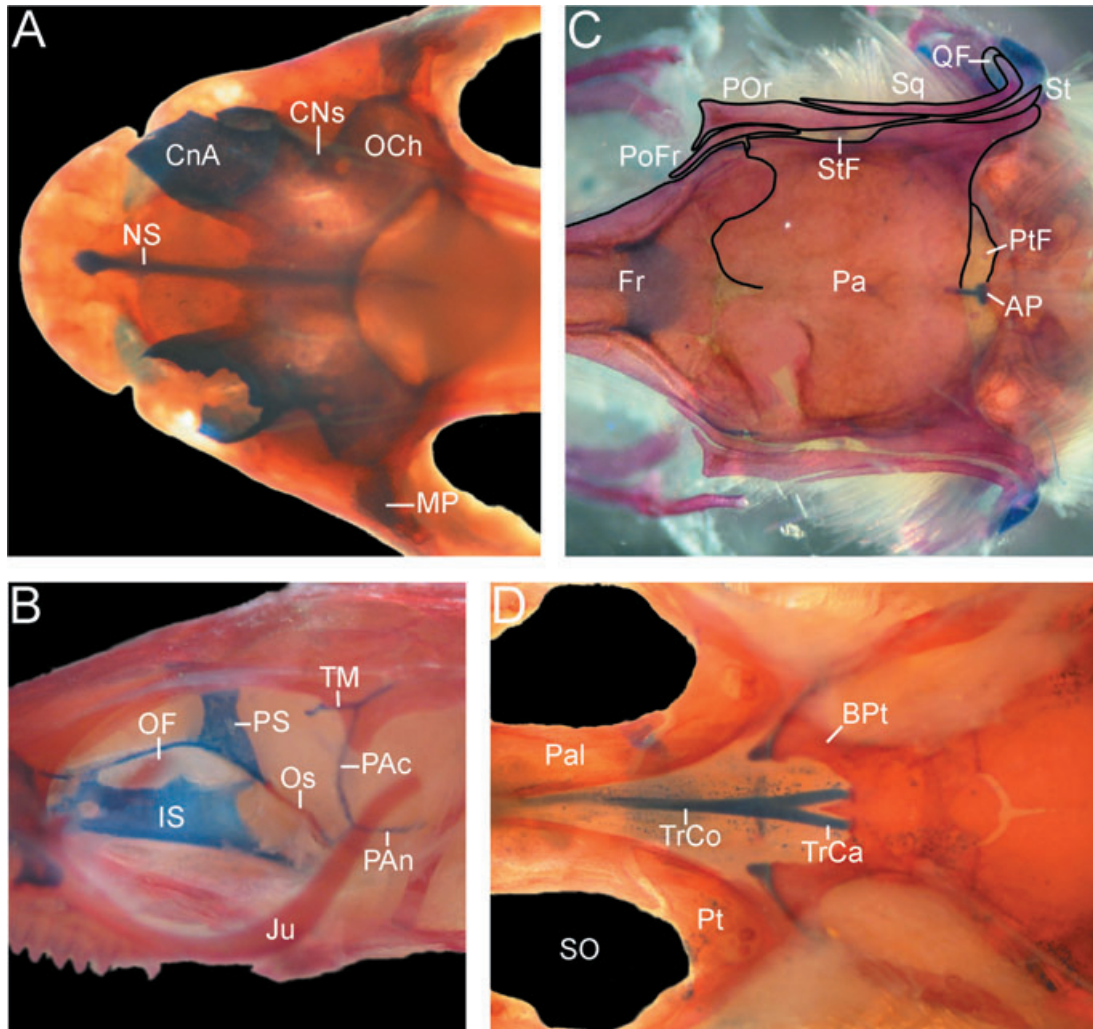


Fig. 3—Cleared and stained skulls of *Vanzosaura rubricauda* (FML 06109-4). —**A**. Dorsal view of the anterior portion of the skull showing the nasal capsule cartilages. Note that the left anterior cartilage of the cupula nasalis was broken during preparation. —**B**. Lateral view of the orbital portion of the skull showing the interorbital cartilages and the orbitosphenoid. —**C**. Dorsal view of the posterior portion of the skull; note that the sutures on the right side of the skull are enhanced. —**D**. Ventral view of the basiptyergoid processes. Abbreviations: AP, anterior process of the tecti synotici; BPt, basiptyergoid process; CnA, cupula nasalis anterior; CNs, concha nasalis; IS, interorbital septum; Ju, jugal; MP, maxillary process of the planum antorbitale; NS, nasal septum; OCh, olfactory chamber; OF, optic foramen; Os, orbitosphenoid; Pa, parietal; PAc, pila accessoria; Pal, palatine; PAn, pila antotica; PoFr, postfrontal; POOr, postorbital; PS, planum suprasetale; Pt, pterygoid; PtF, posttemporal fenestra; QF, quadrate foramen; SO, suborbital fenestra; Sq, squamosal; St, supratemporal; StF, supratemporal fenestra; TM, taenia marginalis; TrCa, trabecular cartilage; TrCo, trabecula communis.

orbital process; at this portion, the facial lamina has extensive contact with the prefrontal dorsally. The posterior end of the orbital process is overlapped dorsally by the jugal. The lateral exposure of the facial lamina is pierced by two large foramina just dorsal to the level of the palatal lamina. The ventral border of the facial lamina is a flange that hangs ventrally, supporting the maxillary teeth on its medial side.

The ventral palatal lamina is wide anteriorly, approaching medially to the vomer, closing ventrally the nasal passage and therefore forming the secondary palate. In the most posterior part, the lamina narrows toward the orbital process; the

narrowing begins approximately at the point where the maxilla contacts medially the palatine (Fig. 2B). Anteriorly, a prominent premaxillary process shapes the ventral border of the nares; posteriorly, the maxilla extends ventral to the orbit in an orbital process that contacts the jugal and ectopterygoid. The orbital process forms the ventrolateral border of the lacrimal fenestra that opens into the anterior orbital space; ventral to the lacrimal fenestra there is the posterior opening of a tunnel that pierces the maxilla anteroposteriorly and ends laterally at the posterior foramen of the facial lamina. The maxilla bears 13 to 15 unicuspid pleurodont teeth; the

tooth row runs over the lateral border of the palatal lamina, reaching almost the posterior end of the orbital process. The teeth are subequal, but the most posterior are slightly smaller, the teeth being at different stages of replacement all along the maxilla. There is no variation in crown morphology, neither along the tooth row, nor among specimens.

Nasal

The short trapezoidal nasal covers dorsally the anterior portion of the nasal passage. Anteriorly, the nasal shapes the concave posterodorsal rim of the nares. The nasal contacts the premaxilla medially, and the anteromedial tip may underlie the premaxillary nasal process; the extent of this overlapping varies among the specimens (see 'Intraspecific variation' section). The nasal contacts the frontal posteriorly, and the maxilla and the prefrontal laterally. In some specimens the frontal may have a small anterolateral process inserted between the nasal and the prefrontal (Fig. 2A). The dorsal surface of the nasal is pierced at the anterolateral corner by a foramen; the accurate position of the foramen may vary slightly among the different specimens.

Prefrontal

The prefrontal has a complicated three-dimensional structure, because it shapes the anterior border of the orbit, with a flat dorsal exposure and a posterior exposure that shapes the anterodorsal wall of the orbit; it has anterior, posterior, lateral and descending processes. There is no independent lacrimal bone, and the prefrontal forms part of the lacrimal fenestra, between its lateral and descending processes. It is not clear if the lacrimal bone is fused with the prefrontal or if it is missing; some specimens have an incomplete suture that may be the trace of the incomplete fusion between those bones.

The anterior process forms part of the dorsolateral aspect of the snout, partially separating the nasal and the maxilla. The length of the anterior process may vary among specimens; in some the process closely approaches the narial margin (although slightly out of focus, this is the case in Fig. 2A). The posterior process is slim and extends along the frontal crista crani, over the dorsal border of the orbit.

The anterolateral margin of the prefrontal has extensive contact with the maxilla, excluding it from the anterior border of the orbit; at the midpoint of the maxillary contact there is a small lateral process (lacrimal flange; Fig. 1A) that extends over the maxilla (bordering the orbit) and contacts the jugal tip. The huge lacrimal fenestra lies between the prefrontal and the maxilla; as the fenestra opens directly to the orbital space it cannot be seen in a lateral view. The lateral process of the prefrontal shapes the dorsal and part of the lateral border of the lacrimal fenestra, the maxilla shapes the lateral and ventral borders, while the descending process of the prefrontal shapes its medial border. This large lacrimal

fenestra is closed by a thin membrane that has two small openings (dorsal and ventral) that functionally restrict the bony fenestra.

The flat descending process forms the orbit anterior wall, extending medially and ventrally to contact the palatine and the maxilla. The ventrolateral tip of the descending process overlaps the palatal border of the maxilla orbital process, bending in a horizontal tip. The descending process has extensive contact with the dorsal side of the palatal trough of the palatine. The medial tip of the descending process closes partially the olfactory tracts, approaching, but not contacting, the medial tip of the contralateral bone.

Frontal

The elongated and relatively flat frontal roofs the anterior part of the braincase. Anteriorly, it contacts the premaxilla, nasals and prefrontals; posteriorly, it contacts the parietal and the postfrontal; ventrally, it projects short paired lateral cristae cranii that contact the prefrontal.

The wide anterior border of the frontal is overlapped by the premaxillary frontal process and the nasals; therefore, in articulated skulls, the shape of the anterior margin is the result of the overlapping of the other bones. In some specimens, the nasal does not cover entirely the anterolateral portion of the frontal, leaving a thin sliver (anterolateral process of the frontal) inserted between the nasal and the prefrontal (Fig. 2A).

The frontal has a broad contact with the parietal posteriorly. Laterally, very close to the lateral end of the frontoparietal suture, paired and well-developed tabs overlap the parietal; the suture between the tabs being slightly wavy and its shape varying among the specimens. At the posterior portion of its lateral margin, the frontal contacts the postfrontal (Figs 1A and 3C).

Ventrally, along the lateral margin, there are paired downgrowths of the frontal (cristae cranii), projected ventrally and slightly medially, enclosing the olfactory tracts of the brain. The anterior two-thirds of each crista are higher than the posterior one-third, which is much less developed and appears as a ridge or a bone thickening. The cristae do not follow accurately the lateral border of the frontal, but at two-thirds of their length they approach medially, enclosing the olfactory bulb; in the most posterior part of the cristae they run posterolaterally to end at the posterolateral borders of the frontal (Fig. 2C).

Parietal

The parietal body is subquadrangular, and posteriorly there are long paired posterolateral processes (postparietal processes). The body contacts anteriorly the frontal (overlapped by the frontal tabs). Laterally, the parietal contacts the postfrontal, postorbital and squamosal, forming the medial border of the supratemporal fenestrae. Each posterolateral

process dorsally overlaps the oto-occipital complex, coming into contact laterally with the supratemporal. The transversal and slightly waved posterior border of the parietal body, between the posterolateral processes, forms the anterior border of the post-temporal fenestra. At the sagittal plane, the cartilaginous anterior tip of the ascending process of the tecti synotici bridges the space of the supratemporal fenestra, running shortly into a groove on the ventral face of the parietal border (Fig. 3C). Underlying each lateral border of the main body, at the level of the supratemporal fenestra, there is a sub-triangular descending process, the tip of which has ligamentous connections with the epipterygoid and the prootic alar process. In different specimens, the relative positions of those three structures are variable (compare Figs 1B and 2D), indicating that there is a certain level of movement between those bones (as the result of cranial kinesis).

Postfrontal

The small postfrontal is an elongated, slim and medially curved sliver that borders the skull lateral roof at the level of the frontoparietal suture, separating the frontal and the parietal from the postorbital. The postfrontal bone contacts laterally with the postorbital, anteromedially with the frontal, and posteromedially with the parietal. The anterior tip extends beyond the postorbital forming part of the posterodorsal border of the orbit. The posterior tip reaches the anterior angle of the supratemporal fenestra (Fig. 3C).

Postorbital

The triangular postorbital contacts lateroventrally with the jugal, medially with the postfrontal and posteriorly it overlaps the squamosal. Anteriorly, the expanded concave base of the triangle forms the posterior angle of the orbital rim. The anterolateral border contacts the medial aspect of the posterior end of the jugal, closing the postorbital bar. The posterior part of the postorbital overlaps the anterior end of the squamosal extensively. The postorbital forms, with the squamosal, the temporal arch that limits the supratemporal fenestra (Fig. 3C).

Squamosal

The elongated and ventrally curved squamosal has the anterior end sharpened and the posterior end enlarged (posterior head). The latter articulates with the dorsal surface of the quadrate. The squamosal contacts anteriorly with the postorbital, posteromedially with the supratemporal, and posteriorly with the quadrate (into a deep notch) (Fig. 3C).

Supratemporal

The tiny elongated supratemporal is inserted between the posterolateral process of the parietal and the squamosal. The

supratemporal is sutured with the parietal, but it has a much looser syndesmotomic connection with the squamosal. The supratemporal is slightly curved ventrally, and it gradually widens from the sharpened anterior end to the posterior end. The supratemporal articulates posteriorly with the paraoccipital process of the oto-occipital complex and with the proximal quadrate articulation.

Jugal

The slim, curved jugal forms the majority of the postorbital bar, connecting the maxilla and ectopterygoid ventrally with the postorbital dorsally. The anterior portion of the jugal is dorsally concave, forming the ventral border of the orbit; this portion contacts the lacrimal flange of the prefrontal, with the posterior process of the maxilla, and with the ectopterygoid. The jugal articulates with the ectopterygoid through a small triangular process orientated medially. Behind that process, the jugal is orientated medially and posterodorsally until it approaches the postorbital (Fig. 1B).

Quadrate

The streptostylic quadrate connects the mandible with the skull; it is vertically orientated, slightly anteroventrally (at an angle of about 60° from the horizontal plane). It has a proximal (cephalic) condyle, an intermediate conch and a distal (mandibular) condyle. The proximal condyle articulates with the paraoccipital process medially, and with the supratemporal tip dorsally.

The middle portion (conch) of the quadrate is globular, with the anterior and lateral sides curved and the medial side flat (slightly out of focus in Fig. 2E). The conch surface is smooth. The lateral and medial borders are thickened, forming a semicircular tympanic (lateral) crest and a highly marked posterior (medial) crest. On the dorsal surface of the conch, there is a wide notch that holds the posterior head of the squamosal (Fig. 2E); within that notch, there is a noticeable quadrate foramen just anterior to the proximal condyle (Fig. 3C).

The wide distal condyle is transverse and saddle-shaped. The posterior process of the pterygoid wraps around it medially bending slightly at the posterior side of the condyle.

Oto-occipital complex

The posterior portion of the braincase is formed by a single bone (oto-occipital complex), with no visible sutures, that presumably is formed by the fusion of the supraoccipital, exoccipital, basioccipital, prootic, opisthotic and basisphenoid.

The roof of the oto-occipital complex (the supraoccipital area) is wide and formed mainly by a thin bone sheet that allows the examination, by transparency, of the otic capsules and the posterior semicircular canal. The anterior border of

the roof (that forms the posterior limit of the post-temporal fenestra), and the posterior one (that forms the dorsal border of the foramen magnum) are thickened. At the medial point of the anterior border, there is a small bony projection that is continued by the cartilaginous ascending process of the tecti synotici that crosses the post-temporal fenestra (Fig. 3C). The supraoccipital area extends laterally, underlying the posterolateral processes of the parietal and roofing the otic capsule. Posterolaterally, the supraoccipital area extends into the lateral paraoccipital processes.

Posteriorly, the oto-occipital complex curves smoothly at the lateral sides of the foramen magnum into the presumptive area of the exoccipital (exoccipital area). At the posterior wall of the braincase the posterior and horizontal semicircular canals protrude. The lateral paraoccipital processes are short and stout, giving support to the quadrate articulation. In most squamates, on each side of the foramen magnum, there are jugular recesses in which the posterior single end of the three canals that pierce the skull in the posterior portion opens; the vagus and the hypoglossal nerves pass through those canals together with the blood vessels (Oelrich 1956). In *Vanzosaura* there is no jugular recess and the three canals open independently. The most dorsal, presumably the vagus foramen, opens just dorsal to the sides of the occipital condyle. The two most ventral foramina are presumably hypoglossal foramina; one is located at the lateral side of the occipital condyle neck and the other one is located lateral to, but near, the former.

At the lateral side of the oto-occipital complex (otic area), the anterior semicircular canal bulges from the dorsal and anterior surface of the otic capsule. From the anterior edge of the external surface of the semicircular canal, the triangular alar process extends dorsally, and its tip almost contacts the parietal descending process and the epipterygoid dorsal tip (Fig. 2D). The anterior wall of the otic capsule is continued ventrally by the lateral border of the basisphenoid region. Behind the quadratic articulation area, the lateral side of the otic capsule has two noticeable openings: the dorsal one is the fenestra ovalis, where the stapes attaches, and the huge ventral one is the lateral opening of the recessus scalae tympani (Fig. 2E). The ventral side of the oto-occipital complex is formed by two differentiated areas: a wide posterior (basioccipital) area and a more anterior and narrower (basisphenoid) area. The globular basioccipital area forms most of the braincase floor. Posteriorly, it bears the short occipital condyle that does not have a differentiated neck; the U-shaped occipital condyle is narrower than the foramen magnum and so is restricted to its ventral border. The posterolateral limit of the basioccipital area is formed by a ridge that borders ventrally the otic capsule (basioccipital ridge; Fig. 2E). The anterolateral border of the basioccipital area narrows up to the basisphenoid area, running parallel to the pterygoid posterior process; this border is bent dorsally forming a basin that contains the base of the brain and ventrally serves as the insertion area of the protractor pterygoid muscle.

On the limit between the basioccipital and basisphenoid areas, a suture is laterally insinuated and is well marked medially, showing the partial fusion between both areas. More anteriorly, within the basisphenoid area, there are paired lateral foramina that are the posterior openings of the Vidian canal. Two well-developed basipterygoid processes are expanded distally and articulate with the pterygoids; in cleared and stained specimens, the basipterygoid articulation has cartilage lining the tip of the process. The anterior transverse border of the basisphenoid area between the basipterygoid processes has a short triangular medial tip interpreted as the parasphenoid rostrum that inserts between the trabecular cartilages. In the cleared and stained specimens, the trabecular cartilages fuse anteriorly into a long, slender bar (the trabecula communis) that runs in the anterior portion along the piriform recess up to the level of the palatines (Fig. 3D).

Vomer

Each paired vomer is formed by a longitudinal rod-like axis, and a wide lateral wing. The longitudinal axis lies ventral to the cartilaginous nasal septum and parallel to the contralateral one; anteriorly it contacts the premaxilla and posteriorly it contacts the palatine. The lateral wing forms part of the floor of the nasal passage and it laterally approaches the maxilla. Although not seen in articulated skulls, the septomaxilla covers dorsally the anterior portion of the vomer, enclosing the Jacobson's organ. The anterior end is inserted into the medial portion notch of the premaxillary horizontal plate and laterally contacts the maxilla. The lateral wing has an anterior constriction for the Jacobson's organ opening, bordered by a noticeable ridge at whose posterolateral end there is a tiny vomerine foramen. The lateral wing approaches or contacts the maxillary palatal lamina up to the choanal level, where it begins to narrow medially. The vomer-maxilla contact is variable among specimens, and may be related to cranial kinesis; in some specimens there is a gap filled with soft tissues while in others there is contact (Fig. 2B). The pointed posterior end of the vomer runs ventrally along the medial palatine border.

Septomaxilla

The septomaxilla is included in the nasal cavity and, in articulated skulls, it can only be seen partially through the nares. The septomaxilla covers Jacobson's organ dorsally and is highly domed as a characteristic of most Autarchoglossa. It is so high that it has extensive contact with the premaxillary dorsal process, covering entirely the medial cartilaginous nasal septum at the anterior part of the nasal cavity. The dorsal surface of the bone is smooth. The ventral border contacts anteriorly the horizontal plate of the premaxilla, laterally with the palatal plate of the maxilla, and posteriorly with the vomer.

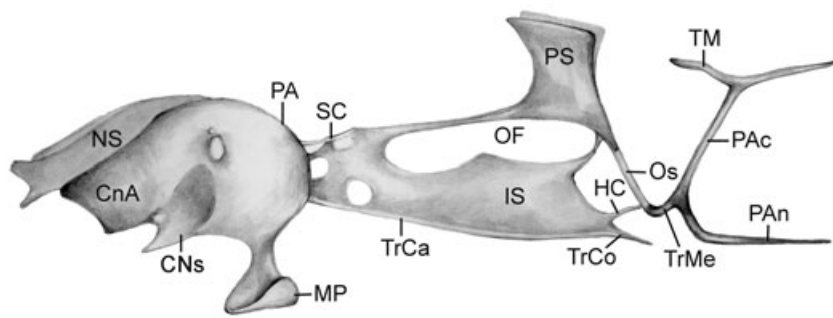


Fig. 4—Chondrocranium of *Vanzosaura rubricauda*. Abbreviations: CnA, cupula nasalis anterior; CNS, concha nasalis; HC, hypochiasmatic cartilage; IS, interorbital septum; MP, maxillary process; NS, nasal septum; OF, optic foramen; Os, orbitosphenoid; PA, planum antorbital; PAc, pila accessoria; PAn, pila antotica; PS, planum suprasettale; SC, sphenothmoidal commissure; TM, taenia marginalis; TrCa, trabecula communis; TrCo, trabecula communis; TrMe, trabecula medialis.

Palatine

Each palatine forms a trough behind the choana that gradually narrows and becomes shallower posteriorly up to the pterygoid contact; laterally, it forms the medial border of the suborbital fenestra. Anteriorly, the palatines contact each other at the sagittal plane, but in the posterior portion they are separated by the piriform recess.

The palatine anterior medial tip overlaps the vomer dorsally. The anterior area is ventrally concave to form the choanal trough; the convex dorsal surface of this area contacts the descending process of the prefrontal. Laterally, the palatine contacts the maxilla, and recurves ventrally toward the midline, defining the choana ventrally; the recurved area (the horizontal lamina of Rieppel *et al.* 2008) is triangular and its base embraces the posteromedial corner of the maxillary palatal lamina. Therefore, the palatine shows the duplicipalatinated condition of Lakjer (1927; in Rieppel *et al.* 2008), in which there is a choanal groove and a horizontal lamina. The posterior process becomes flat and pointed, overlapping dorsally the anteromedial process of the pterygoid.

Pterygoid

The Y-shaped pterygoid has two well-defined sharpened processes in the anterior portion: a medial one that contacts the palatine and a lateral one that contacts the ectopterygoid. There is a thin lamina that makes the angle between the anterior processes; the pterygoid forms the posterior border of the suborbital fenestra (Figs 1C and 3D). The posterior (quadratic) process is laterally orientated and its sharp tip has a ligamentous connection with the distal condyle of the quadrate; the process is medially concave and this area (pterygoid notch) serves as the attachment of the levator pterygoid muscle. At the meeting point of the three processes, there is a noticeable ventral ridge that runs along the base of each process, strengthening the otherwise delicate bone. The posterior ramus of this ridge serves as the articulation surface to the pterygoid process of the basisphenoid. Dorsally, slightly behind this point, the pterygoid has a pit where the epipterygoid is inserted.

Ectopterygoid

The ectopterygoid closes the suborbital fenestra in the posterolateral part, contacting the pterygoid medially and the jugal and maxilla laterally. The lateral end is bent in the anterior portion to match the maxilla orientation; this lateral tip contacts the maxilla anteriorly and the jugal posteriorly. The proximal end overlaps the pterygoid dorsally.

Epipterygoid

The epipterygoid is a vertical rod firmly inserted ventrally into the pterygoid, its dorsal end being very close, but not sutured, to the parietal descending process and to the prootic alar process. The epipterygoid is slightly tilted posteriorly (Fig. 2D). The bone is embedded in the pseudotemporalis profundus muscle.

Chondrocranium and orbitosphenoids

The chondrocranium of the adult (i.e. the remnants of the embryological chondrocranium) is restricted to the nasal capsule and the interorbital cartilages. Figure 4 shows a reconstruction of the whole adult chondrocranium based on several cleared and stained specimens. The nasal capsules are separated by a well-marked nasal septum that runs medially up to the premaxilla, with a long rostrum (Figs 3A and 4). The narina is shaped by the cartilage of the cupula nasalis anterior that connects through a long nasal tube to the anterior chamber. The elongated chamber extends posteriorly and is medially constrained laterally by the concha nasalis (that contains the lateral nasal gland; Oelrich 1956), until it opens to the posterior olfactory chamber located rather laterally, between the concha and the thin planum antorbitale that lines the anterior exposure of the prefrontal bone. The olfactory chamber opens ventral to the choana. The anterior border of the palatine bone, which forms the bony choana, is bordered by a cartilaginous cord formed by a thickened planum antorbitale. The anterior part of the palatal trough is covered ventrally by tissue and therefore the actual opening to the buccal cavity is more posterior, at the level of the

middle of the palatines, functionally expanding the bony secondary palate. The planum antorbitale extends laterally into a well-developed maxillary process that is a cartilage sheet extending over the palatal process of the maxilla until it bends dorsally, lining part of the facial lamina; this cartilaginous maxillary process lines lateroventrally the entrance of the lacrimal duct to the nasal cavity.

The nasal capsule (Figs 3A and 4) is connected posteriorly with the interorbital cartilages; ventrally the nasal septum continues posteriorly with the trabecula communis; on each posterior wall of the nasal capsule, the planum antorbitale is connected with the interorbital septum by the sphenothmoidal commissure.

The interorbital septum is located medially between the orbits (Figs 3B and 4). The trabecula communis is a ventrally thickened septum (Figs 3D and 4); dorsally, a taenia extends from the anterior point of contact of the sphenothmoidal commissures to the posterior planum suprasedptale. Between those taeniae, the thin interorbital septum is pierced by a wide optic foramen and by an anterior smaller one. Posteriorly, the planum suprasedptale is formed by two laterally orientated wings that extend dorsally until they contact the cristae cranii of the frontal. Ventrally the trabecula communis is divided into the paired short trabecular cartilages ending at the sides of the parasphenoid rostrum. Just before that division the paired hypochiasmatic cartilages branch dorsally from the trabecula communis; the hypochiasmatic cartilages end at the orbitosphenoid. From the lateroventral corners of the planum suprasedptale, the paired bony orbitosphenoids, that represent the ossification of the medial portion of the trabeculae medialis (Bellairs and Kamal 1981), are continued laterally by the cartilaginous trabeculae medialis. Each trabecula medialis is laterally bifurcated at the pila antotica and at the pila accesoria (Figs 3B and 4). The pila antotica continues posteriorly up to the level of the epipterygoid; in one specimen (FML 6109) on the left side the pila antotica is connected with the trabecula medialis, while on the right side it is represented by a loose horizontal cartilaginous rod. The pila accesoria is vertically orientated and contacts dorsally a horizontal cartilaginous rod, the taenia marginalis. The latter runs ventral to the parietal border; posteriorly, it is interrupted, but just behind the contact of the epipterygoid with the parietal, the taenia reappears and continues bordering the parietal descending process, until it reaches the otic capsule, just dorsal to the alar process.

The orbitosphenoid is a subtriangular bony sheet that is approximately horizontal and supports the brain (Figs 3B and 4). Each orbitosphenoid is connected with three chondral supports: anteriorly and medially with the planum suprasedptale, ventrally with the hypochiasmatic cartilage, and laterally with the pila accesoria (Fig. 4).

The mandible

The thin mandible has a low coronoid process (formed entirely by the coronoid bone), and a short retroarticular

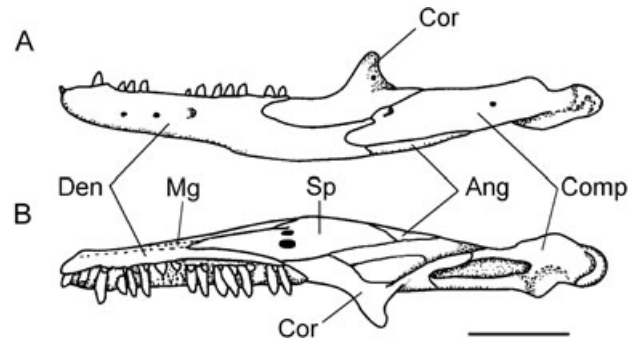


Fig. 5—The mandible of *Vanzosaura rubricauda* (FML 03309-2). —**A**. Labial view. —**B**. Lingual view. Abbreviations: Ang, angular; Comp, compound bone; Cor, coronoid; Den, dentary; Mg, Meckel's groove; Sp, splenial. The scale corresponds to 1 mm.

process posteriorly. The dorsal border of the mandible is relatively straight, while the ventral border is remarkably convex. On the cleared and stained specimens, the Meckel's cartilage runs along the mandible, through the Meckel's canal, from the adductor fossa posteriorly up to the tip of the dentary anteriorly. The anterior part of the Meckel's canal is open lingually, shown as a groove, but in its most posterior portion it is entirely enclosed by the mandibular bones (Fig. 5B).

Dentary

The dentary forms the anterior half of the jaw. By transparency, when using clove oil, the bone can be seen to be bifurcated posteriorly; the two posterior processes are covered by the coronoid, compound bone and angular. The lateral surface of the dentary is smooth and slightly convex; on the lateral side of the bone there are three labial foramina, anteriorly orientated (in one specimen FML 87 there are no labial foramina at all). The medial face is slightly concave and exhibits dental and Meckel's grooves; it contacts posteriorly the coronoid, splenial and angular. The medial face of the dentary has the narrow Meckel's groove that is open anteriorly and runs parallel to the ventral border of the dentary, until it is covered by the splenial. The wide dental groove bears 19–21 unicuspid teeth, most of which show replacement teeth, each one located at the base, clearly ventral to the oldest tooth. Tooth attachments are clearly pleurodont.

Splenial

The splenial extends on the middle of the medial face of the mandible. The narrow anterior end overlaps the posterior end of the dentary. The splenial contacts the coronoid dorsally, with the compound bone posterodorsally, and with the angular posteroventrally. The splenial has two elliptical medial foramina: the larger dorsal one is the alveolar

foramen, while the ventral smaller one is the milohyoid foramen. The pointed posterior end of the splenial runs between the compound bone and the angular.

Coronoid

The coronoid is located in the middle of the jaw, extending ventrally on both faces of the mandible, laterally and medially. The short and stout dorsal (coronoid) process has a blunt apex with a slight posterior orientation; the anterior border of the process is aligned with the main mandibular axis, but the posterior border is medially orientated. The posterior border of the dorsal process is continued on the medial side by a conspicuous crest that continues on the compound bone. Posterior to the dorsal process, the coronoid forms the anterior border of the adductor fossa, extending posteriorly along the medial border. The anterior sides of the coronoid extend over the dentary, reaching up to the level of the last tooth medially, and slightly more anteriorly on the lateral side.

Angular

The elongated angular is located on the mandible ventral border; it has a small lateral exposure, but medially it is almost completely covered by the splenial. The angular is inserted among the dentary anteriorly, the compound bone laterally, and the splenial medially. The anterior end is bifurcated and embraces the posterior ventral tip of the dentary; at this level, on the angular ventral surface, there is a noticeable foramen (not seen in lateral or medial views).

Compound bone of the mandible

The compound bone forms the posterior portion of the mandible and the mandibular joint, the retroarticular process, and the adductor fossa. It is presumably formed by the fusion of, at least, the suprangular and the articular.

The compound bone lateral exposure contacts the coronoid and the dentary anteriorly, and the angular ventrally. It has two noticeable foramina, the anterior one (suprangular foramen), near the suture with the coronoid, is larger, elongated and anteriorly orientated; the posterior one opens directly to the adductor fossa. The compound bone medial exposure contacts anteriorly the coronoid and the splenial, and ventrally with the angular. The medial ridge that originates from the coronoid is strongly continued on the compound bone, forming the medial border of the adductor fossa; posteriorly the ridge forms the bone ventral border. The wide adductor fossa opens dorsomedially, and serves for the attachment of the adductor muscles. The articular surface is saddle-shaped, convex transversally and concave longitudinally. The retroarticular process is a wide lamina orientated posteromedially, with a medial concave surface.

Intraspecific variation

We could detect some characteristics of the bones (shapes and sutures) that show some variation among specimens. It is important to define this variation to determine individual characteristics from species-specific characteristics. Moreover, knowing that variation exists for a determined characteristic in one species may help to infer that variation also exists in related species. It is noteworthy that the possibility of intraspecific variations is neglected in most anatomical studies; in this type of study it is difficult to obtain or to prepare a significant number of specimens, but regrettably most of the time it is not even attempted. Although the number of specimens studied here (nine skulls) is relatively high for most anatomical studies, it is still insufficient for statistical purposes; for this reason, we cannot identify a normal or dominant morphology. Therefore, we do not intend here to quantify but only to note the existence of variation, to advance our understanding of variation for future studies.

Most variations occur on the anterior part of the skull (snout), while the posterior (occipital) part is more stable. The number of teeth varies among specimens, ranging from 9 to 11 teeth in the premaxilla, 13 to 15 in the maxilla and 19 to 21 in the dentary. The superficial exposure of some bones in articulated skulls varies among specimens, modifying the apparent size and shape of those bones or the adjacent ones. For example, variations of the superficial exposure of the premaxillary nasal process cause changes in the shape and position of the medial border of the nasals (which underlies it). In a similar way, the variation of the posterolateral extension of the nasal may leave a small exposure of the frontal (as a small anterolateral process inserted between the nasal and the prefrontal, as in Fig. 2A), or it may cover this part of the frontal contacting extensively the prefrontal (as in Fig. 1A). The variation of the overlapping of the nasal and the facial lamina of the maxilla over the prefrontal makes the length of the anterior process of the prefrontal vary among specimens, the exposed tip of it being more or less close to the narial margin.

The relative positions of some bones may change because of artefacts during specimen preparation, particularly when preparing dry skeletons, because of loose connections between bones. For example, in most specimens we observed minor variations of the relative positions of the descending process of the parietal, the epipterygoid and the prootic alar process. Also, in the palate, the position of the lateral border of the vomer in relation to the medial border of the maxilla varies, being in apparent contact in some specimens, while in others there is a gap between them.

Discussion

The skull of *V. rubricauda* was compared with the available figures and descriptions of other gymnophthalmids from the literature: *Iphisa elegans* (Dixon 1974); *Proctoporus unicolor*,

Bachia breslaui, *Gymnophthalmus speciosus* and *Alopoglossus buckleyi* (MacLean 1974); *Cercosaura schreibersii* (López and Cabrera 1995); *Anotosaura brachilepis* and *Heterodactylus imbricatus* (Soares 2000); *Euspondylus acutirostris* (Montero *et al.* 2002); *Neusticurus epleopus* (Bell *et al.* 2003); *Bachia bicolor* (Tarazona *et al.* 2008) and *Alexandresaurus camacan* (Rodrigues *et al.* 2007).

The skull of gymnophthalmids has some common characteristics such as the fusion of the frontals, the frontal tabs that project on the parietal, and the loss of a parietal foramen (Estes *et al.* 1988; Bell *et al.* 2003).

Among gymnophthalmids there is a variety of skull patterns, somewhat reflecting the diversity of species included. The patterns range from skulls with well-developed supratemporal fenestrae, as in *Neusticurus* and *Proctoporus*, to skulls with no open fenestrae, as in *Iphisa*, *Alopoglossus* and *Anotosaura*. *Vanzosaura* has reduced supratemporal fenestrae, an intermediate state similar to that of *Bachia*, *Heterodactylus*, *Cercosaura*, *Gymnophthalmus*, *Euspondylus* and *Alexandresaurus*. The reduction of the supratemporal fenestrae may reflect a process of miniaturization (Rieppel 1984).

The reduction or closure of the post-temporal fenestra makes the posterior cranium more solid, but this fact does not seem to be related to the reduction of the supratemporal fenestrae. *Vanzosaura* has a dorsally open post-temporal fenestra, similar to that of *Gymnophthalmus*, *Cercosaura*, *Euspondylus*, *Neusticurus* and *Proctoporus*; on the other hand, in some genera the post-temporal fenestra seems to be closed in dorsal view, because of the proximity of the parietal and occipital bones, as in *Anotosaura*, *Heterodactylus*, *Bachia*, *Iphisa*, *Alopoglossus* and *Alexandresaurus*.

The snout of *Vanzosaura* is relatively slender, as in most gymnophthalmids, while in *Bachia*, *Heterodactylus*, *Iphisa* and *Alexandresaurus* it is stout.

The occipital bones of *Vanzosaura* are fused in a single oto-occipital complex with no evident sutures; a similar condition is found in other gymnophthalmids with the exception of *Cercosaura* and *Proctoporus*. The fusion may be an age-related characteristic, as can be seen in *Neusticurus* (Bell *et al.* 2003).

Cranial kinesis

We agree with Metzger (2002) that the anatomical observations may provide clues to the potential for intracranial movements, but they cannot definitively prove their presence. In *Vanzosaura* we found anatomical evidence of a posterior (metakinetic) axis of flexure, a middle (mesokinetic) axis, and evidence of movement of the quadrate and palate.

Our anatomical observations suggest that the skull has a metakinetic axis according to Frazzetta (1962) and Metzger (2002). There is a potentially movable transversal hinge at the post-temporal fenestra (between the parietal and occipital bones); moreover, the bones that form the temporal arch (postfrontal, postorbital and squamosal) are very loosely

connected with the braincase (frontal, parietal and supratemporal); this may be interpreted as an indirect evidence of kinesis. According to Metzger (2002) there are no reports of metakinesis in other scincomorph squamates.

The frontal tabs overlapping the parietal and the wavy frontoparietal suture seem to prevent mesokinetic movements, a type of cranial kinesis presumably lost in Scincomorpha (Metzger 2002). Nevertheless, some authors have argued that mesokinetic flexure may be possible even in a highly interdigitated suture (see Metzger 2002). In *Vanzosaura*, the free dorsal attachment of the elements lateral to that suture (jugal and epipterygoid) and the well-developed synovial joint of the basiptyergoid processes, two other anatomical clues of mesokinesis (Metzger 2002), suggest that the skull may have a mesokinetic axis.

There are indications of a certain degree of quadrate streptostyly in some Gymnophthalmidae (MacLean 1974), consistent with our observations in *Vanzosaura*. In *Vanzosaura* the very loose connection of the distal quadrate head with the pterygoid posterior process suggests that the quadrate has the potential capacity for some vertical and lateral movements (streptostyly). The quadrate movements may be related to the whole mandible orientation and to the movement of the palatal unit.

The palatal series (pterygoid, palatine and vomer) are highly movable because we found few differences in their relative positions among the specimens. The basiptyergoid processes are well-developed, and have a sliding articulation with the pterygoids. The vomers contact the lateral maxillae slightly but their proximity varies among specimens. Therefore, the palate seems to be a kinetic unit, having the capacity for some anteroposterior sliding, may be driven by the streptostylic quadrate. This movable palatal unit is connected dorsally with the braincase through the epipterygoid and jugal which have free moving dorsal ends; the role of the ectopterygoids during the movements of the palate remains to be investigated. Therefore, this palatal unit may move independently from the mesokinetic axis; this 'flexipalate' may have the function of accommodating the prey inside the mouth; another possible explanation is that the movement of the whole palatal unit serves for the bending of the anterior vomer that exerts a pressure on Jacobson's organ capsule to extrude its contents and suck saliva when they are released (Kritzing 1946; Pratt 1948).

The mobility of the palate relative to the maxilla suggests that neither the neochoanate nor the incomplete neochoanate conditions (Rieppel *et al.* 2008) apply to *Vanzosaura*; instead, the palate may be of the 'kinetic neochoanate' condition that Lakjer (1927; in Rieppel *et al.* 2008) applied to amphisbaenians. The ligaments that fill the gap between the vomer and maxilla allow the palate to function as a secondary palate, redirecting the airflow posteriorly; moreover, the duplicipalatin condition of the palatine also displaces the choana backwards. The ventral recurving of the anterior part of the palatine is similar to *Bachia* (Presch 1976; Tarazona *et al.*

2008) and Amphisbaenians (like *Amphisbaena alba*, Montero and Gans 1999, and *Rhineura floridana*, Rieppel *et al.* 2008).

Conclusions

The skull seems to be highly kinetic, both parietal–occipital (metakinesis) and fronto–parietal (mesokinesis) axes having movement, rendering an amphikinetic skull; the palate kinesis also suggests that it may move independently as a prey accommodation mechanism or for the functioning of the vomeronasal organ.

From the comparison with other published skulls, the skull of *Vanzosaura* seems to be morphologically closer to that of *Gymnophthalmus speciosus*. This is in agreement with its phylogenetic placement within the Gymnophthalmi tribe, given by Pellegrino *et al.* (2001) and Castoe *et al.* (2004) based on molecular characters. Therefore, considering the affinity of the monotypic *Vanzosaura* for *Gymnophthalmus*, the status of this genus should be reassessed.

The chondrocranium in reptiles was almost exclusively studied from an embryological point of view (see, for example, the classic paper of Bellairs and Kamal 1981). Although the adult chondrocranium may be a very good source of characters to compare morphology, adaptations and phylogeny, this source is almost unexploited, not only for gymnophthalmids but also for other squamates. There are several studies on the adult nasal capsule (Pratt 1948; Stebbins 1948; Parsons 1970; Gabe and Saint Girons 1976; Hallerman 1998), but the interorbital and posterior cartilages are usually ignored (a notable exception is Oelrich 1956). The intimate integration of the adult chondrocranium with the osteocranium has morphofunctional implications that are not well understood, as for example with the cranial kinesis or mastication. Here we present the first description of the whole adult chondrocranium of a gymnophthalmid and we expect that new comparative data may contribute to the phylogeny and the morphological study of this group.

The skull of gymnophthalmids reveals several potentially useful characters for phylogenetic studies. Nevertheless, the number of species that have been studied osteologically is rather low (considering the total number of the group species) to allow any acceptable morphological phylogeny. Therefore, the study of the comparative anatomy within the group should be a priority to allow a total evidence approach including molecular data.

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