New cranial characters in the tribe Hydropsini (Serpentes: Dipsadidae: Xenodontinae)

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Abstract. We here describe the skull in four species of the three genera of the tribe Hydropsini (Serpentes: Dipsadidae: Xenodontinae): *Helicops infrataeniatus*, *H. leopardinus*, *Hydrops caesurus* and *Pseudoeryx plicatilis*. We compare them with several genera of Dipsadidae. We found that the unpaired foramen on the parabasisphenoid with anterior position is the only skull feature shared by all Hydropsini genera. This feature also occurs in semi-aquatic (*Erythrolamphrus semiaureus*) and fully-aquatic (*Farancia abacura*) dipsadids. All species of *Hydrops* with available skull descriptions and *Pseudoeryx plicatilis* share four features: (1) The anterior border of the angular is higher than the posterior border of the splenial, (2) the vomerine processes of the premaxilla are long, (3) the ascending process of the premaxilla overlaps the horizontal lamina of the nasals, and (4) an anterior projection of the prefrontal is present. All species of *Helicops* with available skull descriptions and *Pseudoeryx plicatilis* share three features: (1) A vertical lamina of the nasal with a notch, (2) a single foramen rotundum, and (3) the presence of a ventral projection of the transverse crista of the basioccipital. Finally, we found small, paired parietal foramina in most of the dipsadids studied here, which are filled with a Sudan-Black-positive tissue of possible nervous origin.

Keywords. Cranial osteology, Serpentes, Hydropsini

INTRODUCTION

Roze (1957 a, b) was the first to propose sister relationships of the genera *Helicops*, *Hydrops*, and *Pseudoeryx* on the basis of the presence of a single internasal scale and the dorsally-positioned external nares. Until a series of recent molecular phylogenies were published (see below), relationships among these genera were rejected (e.g., Neill, 1964; Cadle, 1984; Ferraresi, 1994). Zaher (1999) studied the hemipenes of Xenodontinae finding no useful characters to group the three genera of Hydropsini. Despite this, he considered that *Helicops*, *Hydrops*, and *Pseudoeryx* shared two features: (1) the wide origin of the muscle adductor mandibularis externus superficialis, and (2) the viviparous reproductive mode. Other studies additionally reported oviparity in Hydropsini (Scrocchi et al., 2005), including different species of the same genus (e.g., *Helicops*: see Cunha and Nascimento, 1981; Rossman, 1973, 1984). Albuquerque (2002) agrees with Zaher (1999) in placing *Helicops*, *Hydrops*, and *Pseudoeryx* in tribe Hydropsini.

In all recently published molecular phylogenies, the South American Xenodontinae form a clade that comprises several monophyletic units (tribes), one of which consists of the three genera of the tribe Hydropsini (*Helicops*, *Hydrops* and *Pseudoeryx*; Vidal et al., 2000; Lawson et al., 2004; Zaher et al., 2009; Vidal et al., 2010; Pyron et al., 2011; Grazziotin et al., 2012; Pyron et al., 2013).

Complete information on the bony skull is available for nearly a third of the Dipsadidae genera (i.e., 29 gen-

era) whereas fragmentary descriptions were published for additional 29 genera (Cundall and Irish, 2008). Information on the bony skull of Hydropsini is more complete, since descriptions are available for *Helicops carinicaudus*, *H. infrataeniatus* (Yuki and Lema, 2005), *Hydrops marti*, *H. triangularis* (Albuquerque, 2002), and *Pseudoeryx plicatilis* (Cundall and Rossman, 1984).

A comparison of the cranial osteology among the three Hydropsini genera may prove useful characters to discuss the systematic value of previously studied features and to identify new ones that could unravel relationships among species within the tribe. Thus, the main goal of this work is to describe the bony skull variation of *Helicops infrataeniatus*, *H. leopardinus*, *Hydrops caesurus*, and *Pseudoeryx plicatilis* and compare it to that of Dipsadidae species (see Appendix). This comprehensive comparison includes terrestrial, semi-fossorial, fossorial, semi-aquatic, fully-aquatic, and arboreal forms of Dipsadidae.
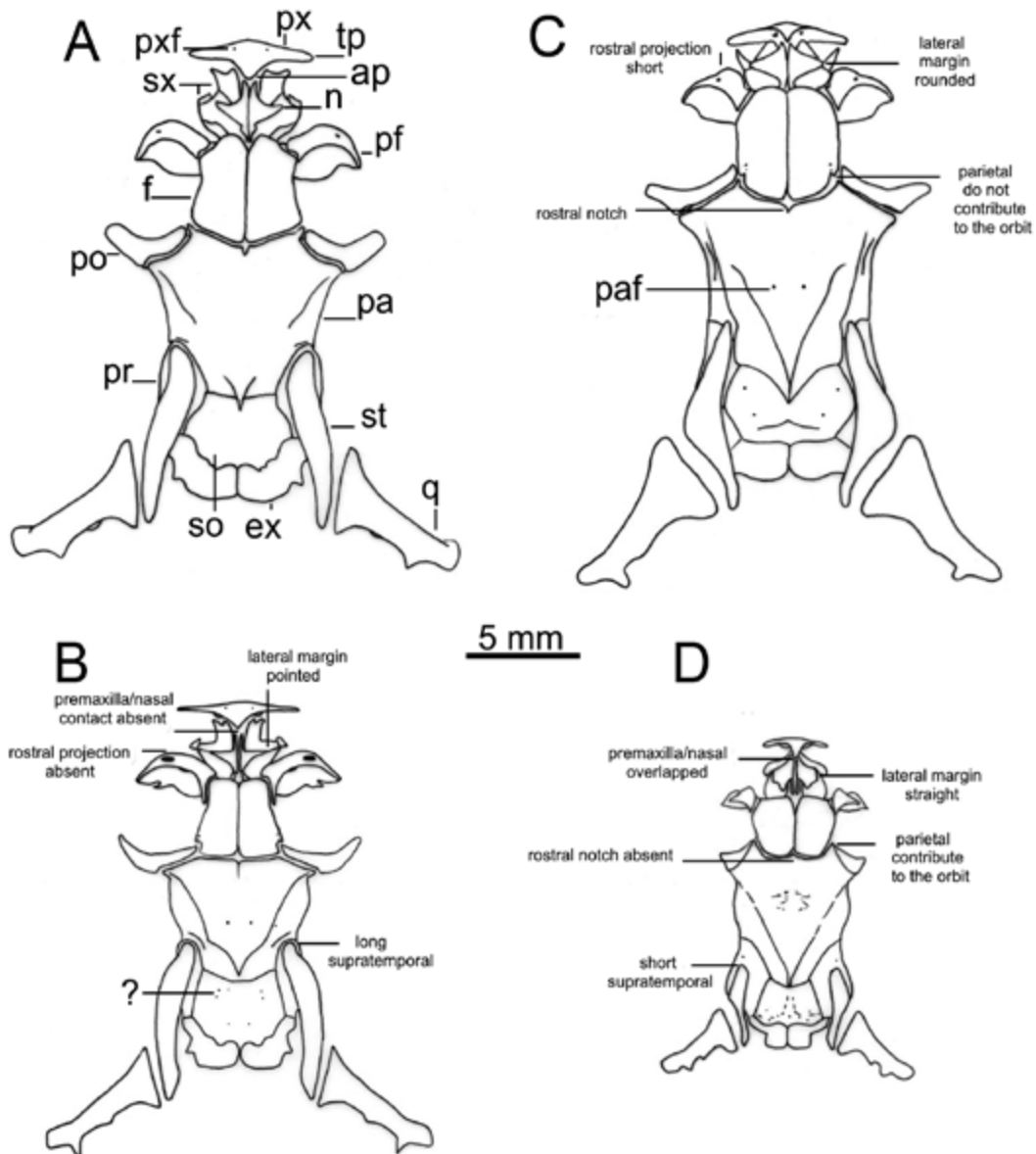
Fig. 1. Skull - dorsal views. *Helicops infrataeniatus* (A), *H. leopardinus* (B), *Pseudoeryx plicatilis* (C), and *Hydrops caesurus* (D). Abbreviations: ap, ascending process of the premaxilla; f, frontal; n, nasal; ex, exoccipital; pa, parietal; paf, parietal foramina; pf, prefrontal; po, postorbital; pr, prootic; px, premaxilla; pxf, premaxillary foramen; q, quadrate; so, supraoccipital; st, supratemporal; sx, septomaxilla; tp, transverse process of the premaxilla; ?, unnamed foramina.

MATERIAL AND METHODS

We studied double stained and cleared skulls of the following Hydropsini species (i.e., our ingroup taxa): *Helicops infrataeniatus* (n=5), *H. leopardinus* (n=5), *Hydrops caesurus* (n=2) and *Pseudoeryx plicatilis* (n=1). For skull comparisons we chose representatives of Dipsadidae (i.e., our outgroup taxa) which appear most closely related to Hydropsini in the most recent molecular phylogenies of Colubroidea (Zaher et al., 2009; Vidal et al., 2010; Pyron et al., 2011; Grazziotin et al., 2012; Pyron et al., 2013): *Hydrodynastes gigas* (n = 3), *Erythrolamprus semiaureus* (n=3), *Leptodeira annulata pulchriceps* (n=1), *Oxyrhopus rhombifer* (n= 2), *Phalotris bilineatus* (n=1), *Philodryas patagoniensis* (n=3), *Psomophis obtusus* (n=1), *Sibynomorphus turgidus* (n=1), *Thamnodynastes chaquensis* (n=1), *T. hypoconia* (n=2), and *Farancia abacura* (n=1). Specimens are from the reptilian collection of the Museo de La Plata (MLP.R. and MLP. JW.), Buenos Aires province, Argentina.

The body of each voucher specimen and the corresponding skull are deposited in its respective collection, using separate numbers. Detailed voucher information is listed in the Appendix. We prepared the skulls using the technique of Taylor and Van Dyke (1985). In addition to the double-stained and cleared skulls, we also studied selected species using dried skulls that were partially disarticulated (see Appendix). Furthermore, to identify the nervous tissue associated with particular cranial openings (e.g., parietal foramina), we dissected one specimen of *Helicops leopardinus* and one of *H. infrataeniatus* and stained them with Sudan Black following the technique of Song and Parenti (1995). The terminology used throughout this study follows Cundall and Irish (2008) for cranial bones and Grazziotin et al. (2012) for taxonomic arrangements.

RESULTS

Snout and bones of the nasal region

Premaxillae. The triangular premaxilla has three processes: the paired and laterally projecting transverse process, the paired and posteriorly-directed vomerine process, and the unpaired dorsally-projecting ascending process (Fig. 1A, 2A, 3A, B). The premaxilla is pierced by a pair of premaxillary foramina (Fig. 1A, 2C). In Hydropsini, the ascending process of the premaxilla and the anterior end of the horizontal lamina of each nasal relate to one another in two ways. In *Pseudoeryx plicatilis* and *Hydrops caesurus* the ascending process of the premaxilla overlaps the anterior end of the horizontal lamina of the nasals, whereas in *Helicops infrataeniatus* and *H. leopardinus* these bones lack contact (Fig. 3B, D). This second way, also occurs in the outgroup species *Erytrolamprus semiaureus*, *Thamnodynastes chaquensis*, and *T. hypoconia*, whereas the first way also occurs in *Hydrodynastes gigas* and *Philodryas patagoniensis*. In contrast to Hydropsini, in some of the outgroup species (*Far-*

ancia abacura, *Leptodeira annulata*, *Oxyrhopus rhombifer*, *Phalotris bilineatus*, *Psomophis obtusus*, and *Sibynomorphus turgidus*) there is contact but no overlap between the ascending process of the premaxilla and the anterior end of the horizontal nasal lamina.

The shape and length of the vomerine processes are another source of variation. The two studied *Helicops* have short processes (Fig. 2A, B), as in the outgroup species *Hydrodynastes gigas*, *Leptodeira annulata*, *Psomophis obtusus*, *Thamnodynastes chaquensis*, and *T. hypoconia*. The other Hydropsini, *Hydrops caesurus* and *Pseudoeryx plicatilis*, have a long vomerine processes of the premaxilla (Fig. 2C, D), as in the outgroup species *Eryhtrolamprus semiaureus*, *Farancia abacura*, *Oxyrhopus rhombifer*, *Phalotris bilineatus*, and *Philodryas patagoniensis*. *Sibynomorphus turgidus* is the only studied species with an azygous median process (probably by fusion of left and right separate vomerine process of the other species). The shape of each vomerine process of the premaxilla can be rounded, as in *Helicops leopardinus* and *Pseudoeryx plicatilis* (Fig. 2B, C) or more acute and pointed, as in *H. infrataeniatus* and *Hydrops caesurus* (Fig. 2A, D). Finally, the vomerine processes of the premaxilla and the anterior processes of the septomaxilla are overlapped in all studied species.

Nasals. Each nasal is formed by two bony laminae, the horizontal and the vertical lamina (Fig. 1, 3, 4). In general, the vertical lamina has not been described except in the work of Cundall and Shardo (1995). The vertical lamina of each nasal bone functions as a bony septum between the left and the right nasal capsules. Each horizontal lamina have anterior and posterior processes that extend from the anterior and posterior margins. The shape of the horizontal lamina, the extension and shape of the vertical lamina, and the length of the anterior nasal process vary in Hydropsini (Fig. 1, 3, 4). The horizontal lamina is clearly triangular (only in *Helicops infrataeniatus* and *H. leopardinus*; Fig. 1A, B; 4A, C) or almost square-shaped (*Hydrops caesurus*; Fig. 1D, 4G), with an intermediate rounded condition (in *Pseudoeryx plicatilis*; Fig. 1C, 4E). The lateral end of the horizontal lamina is rounded also in *Philodryas patagoniensis* and *Thamnodynastes chaquensis*, whereas it is square-shaped in the remaining outgroup species.

Both vertical lamina are emarginated in *Pseudoeryx plicatilis*, *Helicops infrataeniatus* and *H. leopardinus* (Fig. 3A-C; 4B, D, F), but not in *Hydrops caesurus* (Fig. 3D, 4H). The outgroup species that have such emargination are *Erythrolamprus semiaureus*, *Farancia abacura*, *Sibynomorphus turgidus*, *Thamnodynastes chaquensis*, and *T. hypoconia*.

Vomers. These complex bones and the septomaxillae are deeply integrated on each side. Each vomer has two
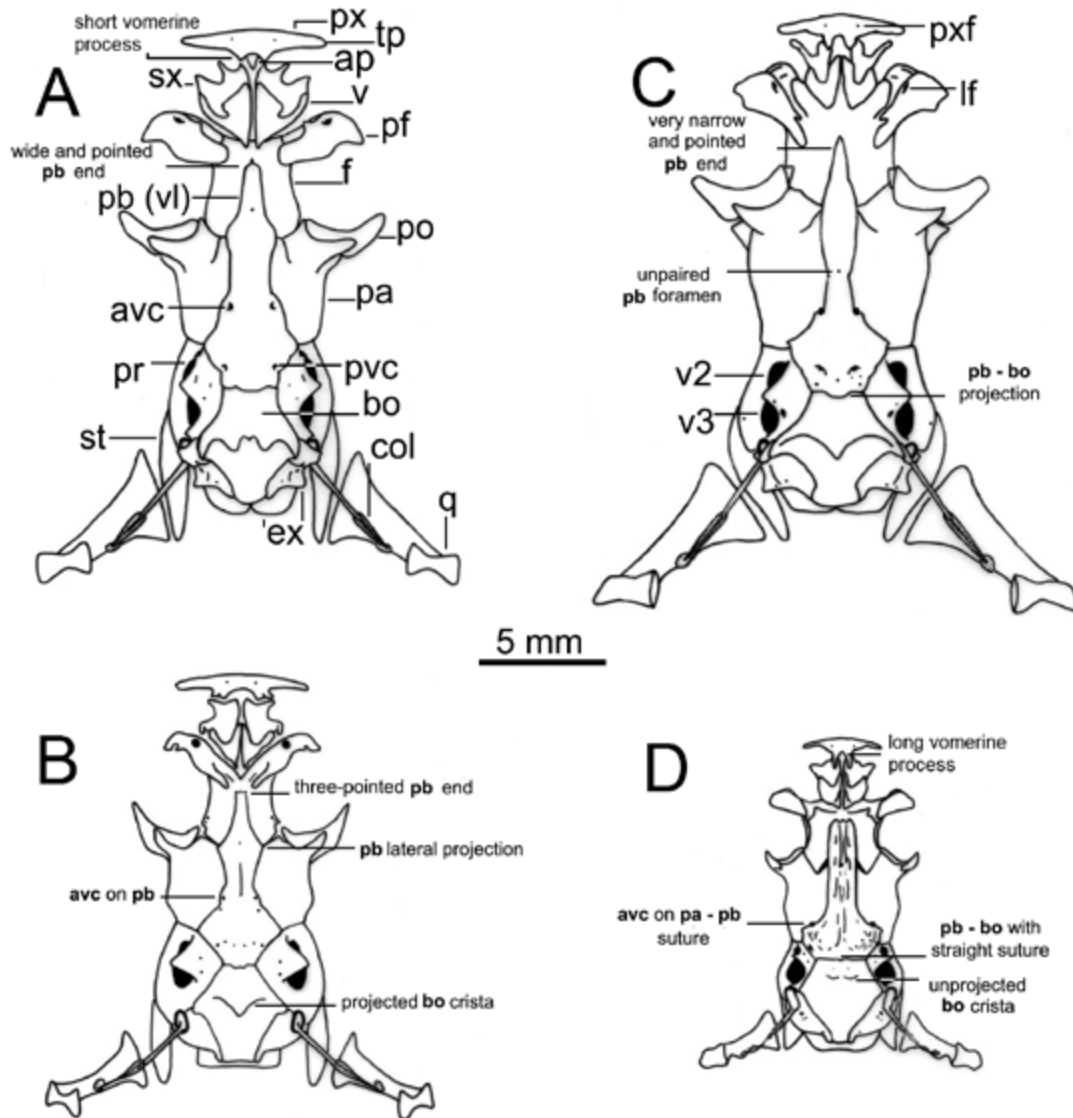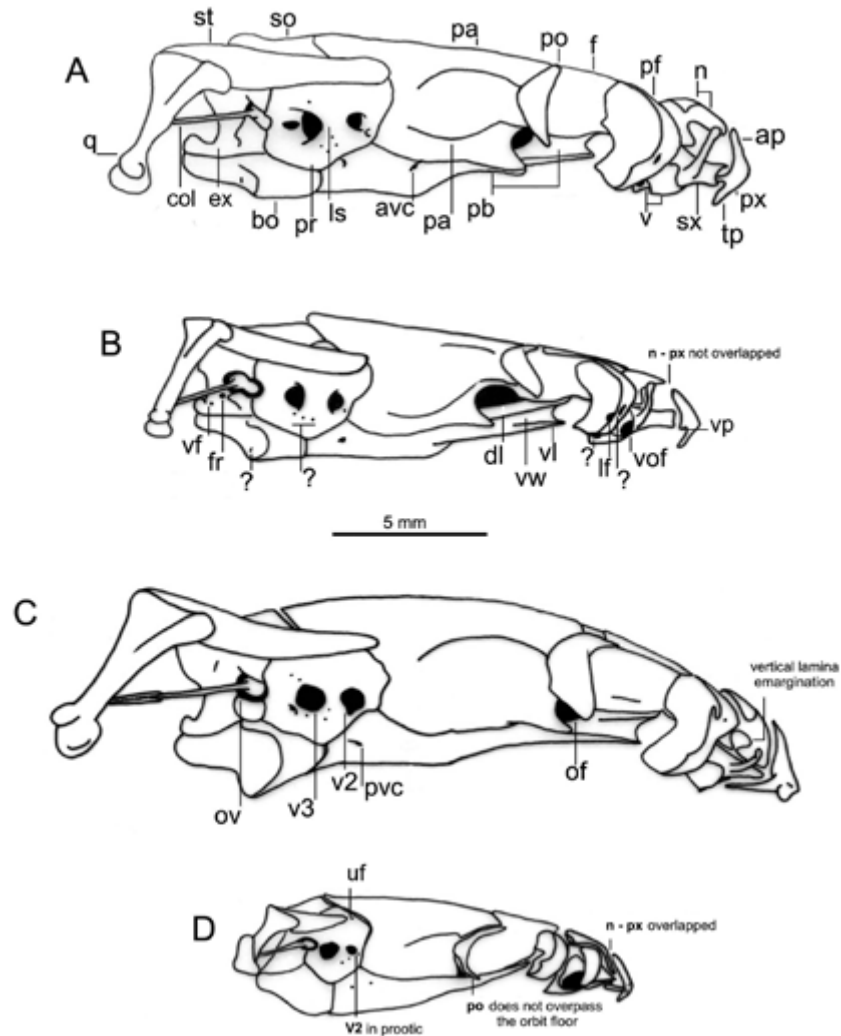
Fig. 2. Skull - ventral views. *Helicops infrataeniatus* (A), *H. leopardinus* (B), *Pseudoeryx plicatilis* (C), and *Hydrops caesurus* (D). Abbreviations: avc, anterior Vidian opening; bo, basioccipital; col, columella; lf, lacrimal foramen; pb, parabasisphenoid; pvc, posterior Vidian opening; v, vomer; (vl), ventral lamina of the parabasisphenoid; V_2 and V_3, ramus of the trigeminal nerve. Other references in Figure 1.

parts (Fig. 2, 3, 5A-D): (1) A triangular-shaped vertical plate at each side of the midline of each vomer, and (2) a cup-shaped or capsular expansion that limits the vomeronasal organ and grows laterally from the vertical plate. The vertical plate bears two foramina at its caudoventral corner (Fig. 5A, B). The smallest foramen is only present in *H. leopardinus* and the largest one occurs in all Hydropsini and outgroup species. The posterior margin of the vertical plate of the vomer is straight in all Hydropsini and most outgroup species (Fig. 5B), whereas it is emarginated in some outgroup species (*Oxyrhopus rhombifer*, *Phalotris bilineatus*, and *Sibynomorphus turgidus*). The capsular

expansion has multiple dorsal foramina with the branches of the vomeronasal nerve running through it (Fig. 5C).

Septomaxillae. The septomaxilla contacts the vertical plate of the vomer. Each septomaxilla has a rounded body enclosing anteriorly the vomeronasal organ. The body of the bone projects three processes: the anterior, the lateral, and the posterior (Fig. 2, 3, 5E-G). The anterior process varies from slightly bifid in *Helicops infrataeniatus* and *H. leopardinus* to rounded in *Hydrops caesurus* and *Pseudoeryx plicatilis*. The anterior septomaxillae process is bifid also in *Farancia abacura*, *Phalotris bilineatus*, *Psomophis obtusus*, *Sibynomorphus turgidus*, both *Thamnodynastes*
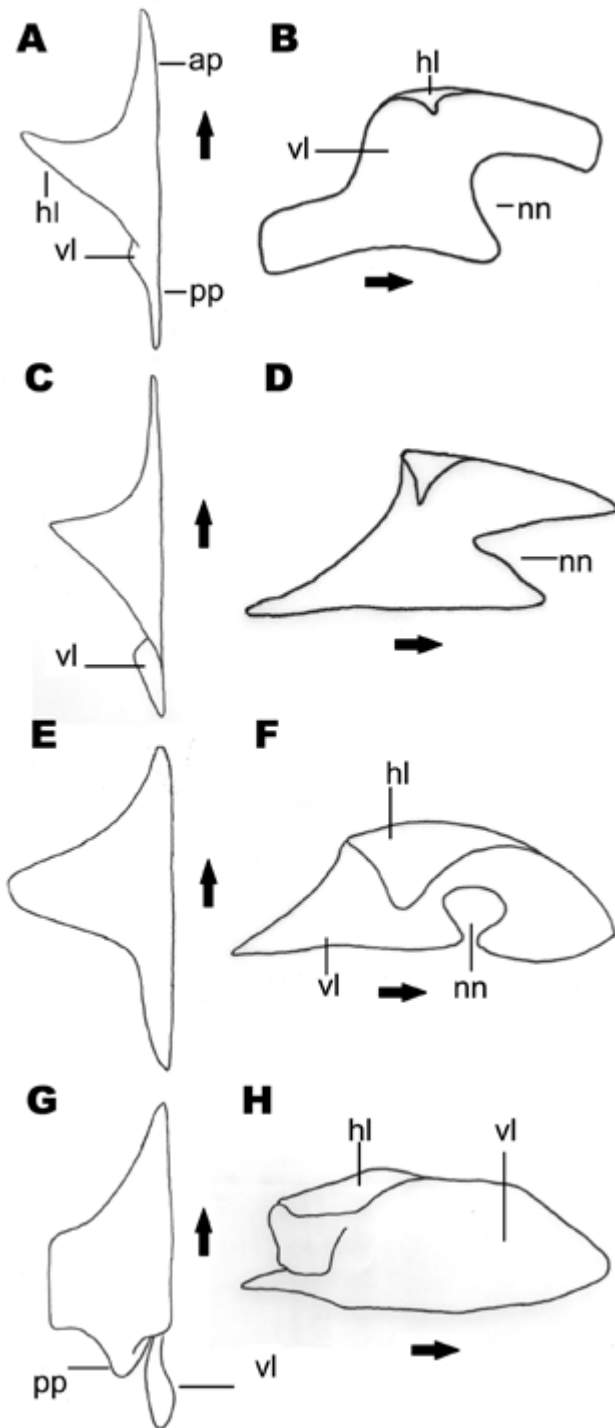
Fig. 3. Skull - lateral views. *Helicops infrataeniatus* (A), *H. leopardinus* (B), *Pseudoeryx plicatilis* (C), and *Hydrops caesurus* (D). Abbreviations: dl, dorsal lamina of the parabasisphenoid; fr, foramen rotundum; ls, laterosphenoid; of, optic foramen; ov, oval window; uf, unnamed foramen; vf, vagal foramen; vl, ventral lamina of the parabasisphenoid; vof, vomerine foramen; vp, vomerine process; vw, vertical wall of the parabasisphenoid. Other references in Figures 1 and 2.

species, and *Leptodeira annulata*, whereas it is rounded in the remaining outgroup species. The lateral process grows dorsally from the body of the septomaxilla, forming the lateral bony parts of the nasal capsule (Fig. 3). The posterior end of the posterior septomaxillary process articulates with the frontal whereas the lateral part of this process curves ventro-anteriorly. The features of the septomaxillae did not vary in any ingroup or outgroup species.

Braincase

Parabasisphenoid (sphenoid bone). The irregular, almost octagonal-shaped parabasisphenoid forms the skull floor across the otic and orbital regions and functions as part of the palate by completing the space between pterygoids and palatines (Fig. 2). Interestingly, the parabasisphenoid consists of a double-floored horizontal bone lamina (dorsal and ventral) connected through a low midline vertical lamina (Fig. 3A-C). The ventral horizontal lamina constitutes the exposed face of the bone and forms the anterior end of the parabasisphenoid (Fig. 2). The dorsal horizontal bone lamina is visible in lateral view only (Fig. 3A-C). This lamina fills the space between the two trabecula crani. The very low interorbital septum projects dorsally from the dorsal lamina of the parabasisphenoid. In *Hydrops caesurus*,

Fig. 4. Nasal - dorsal views. *Helicops infrataeniatus* (A), *H. leopardinus* (C), *Pseudoeryx plicatilis* (E), and *Hydrops caesurus* (G). Lateral views of the right nasals of *Helicops infrataeniatus* (B), *H. leopardinus* (D), *Pseudoeryx plicatilis* (F), and *Hydrops caesurus* (H). Abbreviations: ap, anterior process of the nasal; hl, horizontal lamina of the nasal; nn, nasal notch; pp, posterior process of the nasal; vl, vertical lamina of the nasal. Figure is not scaled. The arrows point toward anterior.

the vertical lamina and the short septum are completely obscured by the well-developed descending flanges of the frontals (Fig. 3D). In the other Hydropsini, the descending flanges of the frontals are less developed. Consequently, the short interorbital septum is less visible in *Hydrops caesurus* than in *Helicops* and *Pseudoeryx plicatilis* (see the description of the frontals).

The anterior projection of the parabasisphenoid varies. It can be wide with three points and double notched, as in *H. leopardinus* and *Hydrops caesurus* (Fig. 2B, D), or wide with a single point and no notches, as in *H. infrataeniatus* (Fig. 2A). In contrast, *Pseudoeryx plicatilis* has a narrow parabasisphenoid anterior projection with a single point (Fig. 2C). In the outgroups, a narrow anterior end of the parabasisphenoid with a single point occurs in *Leptodeira annulata*, *Oxyrhopus rhombifer*, *Phalotris bilineatus*, and *Sibynomorphus turgidus*, a wide anterior end with three points occurs in *Erythrolamprus semiaureus*, *Philodryas patagoniensis*, and both studied *Thamnodynastes*, and, finally, a rounded anterior end occurs in *Hydrodynastes gigas* and *Psomophis obtusus*.

All studied Hydropsini display a short axial ridge along the mid-ventral face of the parabasisphenoid. There are five paired foramina along each side of the median ridge. The identity of such foramina is uncertain and undescribed in the literature, except for the anterior-most and posterior-most largest pairs of foramina representing the anterior and the posterior Vidian openings, respectively (Fig. 2A). The anterior Vidian openings can vary in their position. They open by the suture between the parietal and parabasisphenoid in *Hydrops caesurus*, *Pseudoeryx plicatilis* (Fig. 2C, D), in one specimen of *H. infrataeniatus* (MLP.R.5624), and also in the outgroup species *Oxyrhopus rhombifer*. These openings are entirely embedded in the parabasisphenoid in *Helicops leopardinus* and the remaining specimens of *H. infrataeniatus* (Fig. 2A, B), as well as in most outgroup species.

All studied Hydropsini have an unpaired midline-placed foramen that is positioned anteriorly with respect to the anterior Vidian openings (Fig. 2A-D). Such an unpaired foramen occurs also in the outgroups *Erythrolamprus semiaureus* and *Farancia abacura*. In *Philodryas patagoniensis*, the unpaired parabasisphenoid foramen is found between the anterior and posterior Vidian openings. The remaining outgroup taxa lack this foramen.

Finally, the parabasisphenoid varies in presence/absence of lateral projections at its postorbital level. These lateral projections are present in *Helicops infrataeniatus* and *H. leopardinus* (Fig. 2A, B), but are absent in *Hydrops caesurus* and *Pseudoeryx plicatilis* (Fig. 2C, D). Among outgroup species, such lateral projections are found in

Erythrolamprus semiaureus, *Hydrodynastes gigas*, *Philodryas patagoniensis*, *Thamnodynastes chaquensis*, and *T. hypoconia*.

Prefrontals. In *Hydrops* and *Pseudoeryx* species, the dorsal margin of the prefrontal projects forming a rounded anterior process (Fig. 1C, D). This process is absent in both studied *Helicops* species (Fig. 1A, B). In the outgroup species, three conditions of the prefrontal anterior process exist: (1) it is absent in *Leptodeira annulata* and *Phalotris bilineatus*; (2) it is short (i.e., as long as or smaller than its base) in most outgroup species; and (3) it is long (i.e., clearly longer than its base) in *Oxyrhopus rhombifer*. The prefrontal-frontal articulation is strongly curved (V-shaped) in *H. leopardinus* (Fig. 1B), whereas it is almost straight in all other examined species. Finally, the anterior wall of the prefrontal is pierced by one large lacrimal foramen, two small foramina (sometimes absent), and one dorsal unnamed foramen (Fig. 1, 2, 3).

Frontals. The anterior margin of each frontal is irregular and the lateral margin is expanded, forming part of the orbit roof, between the prefrontal and the postorbital bones. The descending flange of the frontal closes the orbit medially and also forms the anterior and dorsal margin of the optic foramen (Fig. 3). These flanges reach the parabasisphenoid in *Hydrops caesurus* (Fig. 3D) where they are larger than in other Hydropsini. Large descending flanges of the frontals also occur in the outgroup species *Farancia abacura*, *Leptodeira annulata*, *Oxyrhopus rhombifer*, *Phalotris bilineatus*, *Psomophis obtusus*, and *Sibynomorphus turgidus*. Shorter descending flanges that do not reaches the level of the parabasisphenoid occur in the remaining outgroup species, and in the two *Helicops* species and *Pseudoeryx plicatilis* (Fig. 3A-C). The anterior end of each ventral flange of the frontal forms a cotyle to articulate with the condylus of the posterior process of the septomaxilla. The frontal-parietal suture is straight in *H. leopardinus* (Fig. 1B), whereas it is oblique and irregular in the other Hydropsini (Fig. 1A, C, D). The naso-frontal articulation is absent in all Hydropsini we studied. Within the present work, presence of such articulation was verified only for semi-fossorial and fossorial (*Oxyrhopus rhombifer*, and *Phalotris bilineatus* respectively) species, and also for the aquatic *Farancia abacura* as was first mentioned by Haines (1967).

Postorbitals. Each small and arched postorbital surrounds the posterodorsal end of the orbit. A full contact between postorbital and parietal is only found in *Hydrops caesurus*, but not in the other Hydropsini (Fig. 1D, 3) or the outgroup species. The postorbital extends to the cranial floor at the level of the orbit (i.e. without overpassing the floor) in Hydropsini species (Fig. 3) and most of the
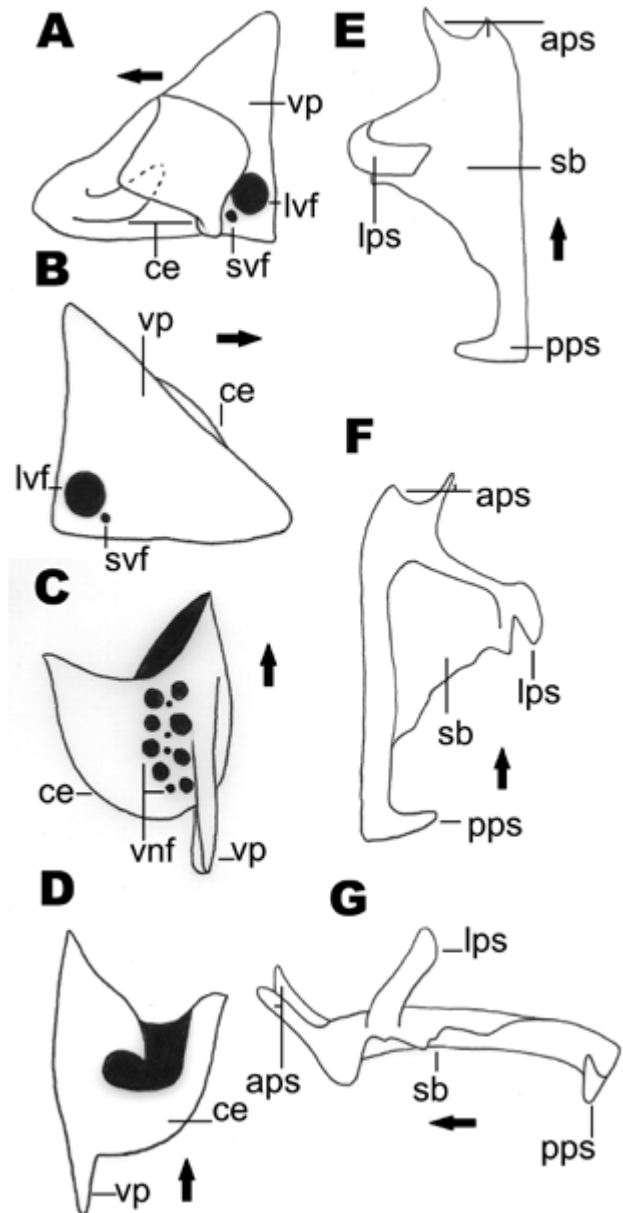
Fig. 5. Left vomer and left septomaxilla of *Helicops leopardinus*. Lateral (A), medial (B), dorsal (C), and ventral (D) views of the left vomer. Dorsal (E), ventral (F), and lateral (G) views of the left septomaxilla. The arrows point toward anterior. Abbreviations: aps, anterior process of the septomaxilla; ce, capsular expansion of the vomer; lps, lateral process of the septomaxilla; lvs, large vomer foramen; pps, posterior process of the septomaxilla; sb, septomaxillary body; svf, small vomer foramen; vp, vertical plate of the vomer; vnf, vomeronasal nerve foramina. Figure is not scaled.

outgroup species, whereas it overpasses the cranial floor in *Erythrolamprus semiaureus*, *Hydrodynastes gigas*, *Leptodeira annulata*, and *Sibynomorphus turgidus*.

Parietal. We found three variable traits in the parietal of Hydropsini: (1) a contact between the parietal and the postorbital (see above the description of the postorbitals); (2) a parietal participation in the closure of the orbital margins; and (3) presence or absence of traces of the suture between the left and the right parietals. The orbital projections of the parietal are present in all Hydropsini, but they reach the orbit only in *Helicops infrataeniatus* and *Hydrops caesurus* (Fig. 1A, D), whereas *Helicops leopardinus* and *Pseudoeryx plicatilis* lack the parietal contribution to the orbits (Fig. 1B, C). The parietal participation to the orbits occurs in all outgroup species, except *Farancia abacura*, *Oxyrhopus rhombifer*, and *Sibynomorphus turgidus*. Interestingly, some specimens of *H. leopardinus* have unknown independent ossifications instead of the orbital projections of the parietal. *Helicops infrataeniatus*, *H. leopardinus* and *Pseudoeryx plicatilis* have an incomplete fusion between the left and the right parietal, as indicated by an anterior median notch that bisects the frontals at the level of the parietal (Fig. 1A-C). In contrast, *Hydrops caesurus* has no such suture (Fig. 1D). *Phalotris bilineatus*, *Philodryas patagoniensis*, *Psomophis obtusus*, and *Thamnodynastes chaquensis* are the only outgroup species possessing the anterior notch of the parietal.

Interestingly, one pair of small foramina is sometimes found at each side of the midline of the parietal and near the posterior end of the bone in *Helicops infrataeniatus*, *H. leopardinus*, and *Pseudoeryx plicatilis* (Fig. 1B, C). Although presence of such parietal foramina varies within these species with only one foramen opening in some cases, they were completely absent in *Hydrops caesurus*. The parietal foramina represent very small areas where the cranial cavity connects to the exterior. Blood vessels are absent from this site. No nerves were found to pass through the foramina that were filled with a Sudan-Black-positive tissue. Some specimens have one or two additional foramina irregularly disposed near the parietal foramina. Parietal foramina occur in all outgroup species, except *Farancia abacura*, *Hydrodynastes gigas*, *Phalotris bilineatus*, *Psomophis obtusus*, and *Sibynomorphus turgidus*. Finally, all studied taxa have a sagittal crest of similar height that bifurcates anteriorly, forming an Y-shaped pattern (Fig. 1).

Prootics. The oval window and some additional important foramina open into the prootics. Two of them are always present and constitutes the openings for the maxillary (V_3) and mandibular (V_2) branches of the trigeminal nerve. These openings are separated by the lamellar laterosphenoid, a bone that is incorporated to the prootic (Fig. 3). The V_2 foramen opens either on the prootic (all Hydropsini and most of the outgroup species; Fig. 3) or on the prootic-parietal suture (*Leptodeira annulata*, *Oxyrhopus rhombifer*, and *Sibynomorphus turgidus*).

Other openings vary bilaterally (two to four small foramina ventral to V_2, V_3 and the oval window; Fig. 3). The dorsal face of the bone is opened by a small unnamed foramen that is consistently present in all species. This foramen is tapered by the supratemporal in most Hydropsini and outgroups species, whereas it is exposed by the short supratemporals in *Hydrops caesurus*, *Leptodeira annulata*, *Phalotris bilineatus*, and *Sibynomorphus turgidus*.

Supraoccipital. The supraoccipital bone has a low dorsal crest that is continuous with the sagittal crest of the parietal (Fig. 1). The supraoccipital is excluded from the margins of the foramen magnum by the exoccipitals (Fig. 1, 6). Many small unnamed foramina are observed on the dorsum of the supraoccipital. Two axially arranged pairs are almost always present. In addition, a medial pair and one unpaired medial foramen can occur in *Helicops leopardinus* and *Hydrops caesurus*. In the latter species the last foramen is slightly displaced towards the left.

Basioccipital. The hexagonal-shaped basioccipital forms the most posterior part of the skull floor and integrates the main body of the occipital condyle (Fig. 2, 3, 6). The suture between the parabasisphenoid and the basioccipital is straight with no projections in *Hydrops caesurus* (Fig. 2D) and the outgroup species *Farancia abacura* and *Oxyrhopus rhombifer*, whereas it bears a mid-posterior projection in the remaining Hydropsini (Fig. 2A-C) and outgroups.

The basioccipital has a characteristic transverse crista that projects ventrally from the body of the bone. This crista is present in *Helicops infrataeniatus*, *H. leopardinus* and *Pseudoeryx plicatilis* (Figs. 2A-C, 6A-C) and in some of the outgroup species (*Farancia abacura*, *Hydrodynastes gigas*, *Philodryas patagoniensis*, and *Psomophis obtusus*), whereas it is absent in *Hydrops caesurus* (Figs. 2D, 6D) and the remaining outgroup species.

Exoccipitals. These bones close the foramen magnum dorsolaterally, forming the dorsolateral parts of the occipital condyle, and close the oval window posteriorly (Fig. 2, 3, 6). The foramen rotundum opens ventrally to the oval window, whereas the hypoglossal foramina and the vagal foramen open between the rotundum and the magnum foramen (Fig. 3B, 6). The foramen rotundum can be simple or double. It is simple in *Helicops infrataeniatus*, *H. leopardinus*, and *Pseudoeryx plicatilis* and the outgroup species *Farancia abacura*, *Hydrodynastes gigas*, *Philodryas patagoniensis*, and both studied *Thamnodynastes* species. It is double in *Hydrops caesurus* and the outgroup species *Erythrolamprus semiaureus*, *Leptodeira annulata*, *Oxyrhopus rhombifer*, *Phalotris bilineatus*, *Psomophis obtusus*, and *Sibynomorphus turgidus*.
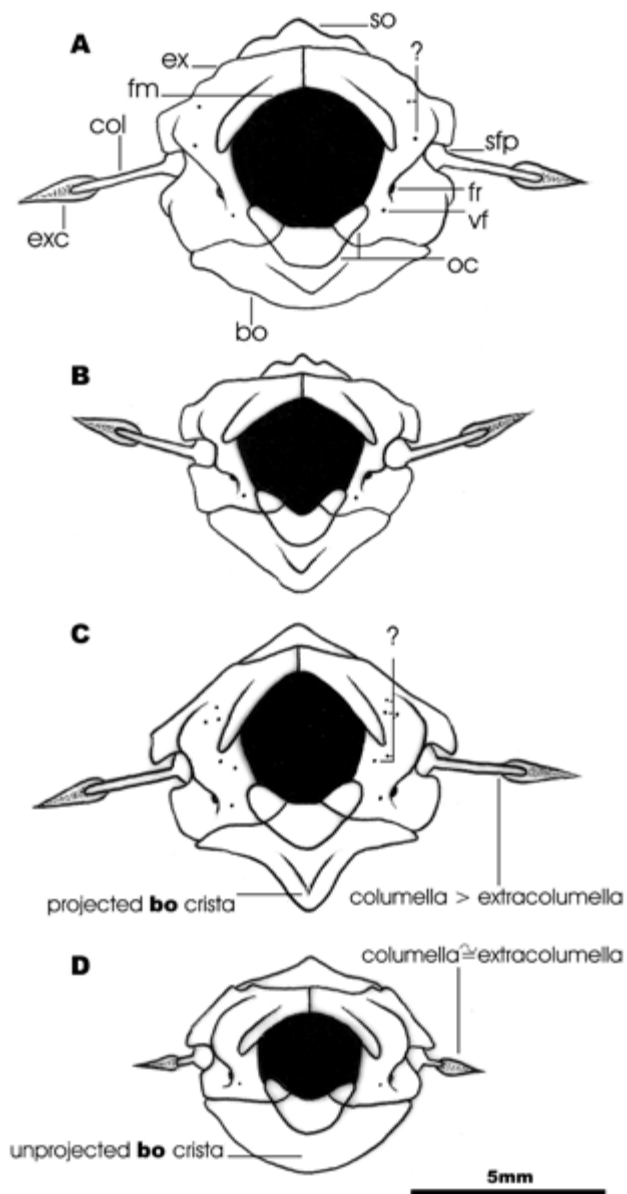
Fig. 6. Skull - posterior view. *Helicops infrataeniatus* (A), *H. leopardinus* (B), *Pseudoeryx plicatilis* (C), and *Hydrops caesurus* (D). Abbreviations: exc, extracolumella; fm, foramen magnum; oc, occipital condyle; sfp, stapedial footplate. Other references as in Figures 1-3.

Palatomaxillary arch

Maxillae. Each maxilla bears a pair of posterior processes, the medial and the lateral, at the site where the maxilla articulates with the ectopterygoid. The lateral process is always rounded, whereas the medial process is either rounded (*Pseudoeryx plicatilis* and *Hydrops caesurus*; Fig. 7F, H) or square-shaped (*Helicops infrataeniatus*

and *H. leopardinus*; Fig. 7B, D). The medial process of the outgroup taxa is either rounded (*Farancia abacura*, *Phalotris bilineatus*, *Sibynomorphus turgidus*, *Thamnodynastes hypoconia*) or squared-shaped (*Erythrolamprus semiaureus*, *Hydrodynastes gigas*, *Oxyrhopus rhombifer*, *Philodryas patagoniensis*, *Psomophis obtusus*, and *Thamnodynastes chaquensis*). *Leptodeira annulata* lacks the medial process of the maxilla. The palatine process of the maxilla is always triangular with a rounded to slightly pointed tip (Fig. 7B).

Palatines. The posterior borders of the palatines, that articulate with the pterygoids, are V-shaped (Fig. 7A, C, E, G). Within the ingroup, no important differences have been noted in relation to the square-shaped choanal processes (Fig. 7A). The maxillary process, however, varies from long and triangular-shaped (in *Hydrops caesurus, Helicops infrataeniatus and H. leopardinus*; Fig. 7A, C, G) to short and square-shaped (in *Pseudoeryx plicatilis*; Fig. 7E). The maxillary process of the palatine is square-shaped also in *Hydrodynastes gigas*, *Leptodeira annulata*, *Phalotris bilineatus*, *Psomophis obtusus*, and *Sibynomorphus turgidus*, whereas it is longer than wide in *Erythrolamprus semiaureus*, *Farancia abacura*, *Oxyrhopus rhombifer*, *Philodryas patagoniensis*, *Thamnodynastes chaquensis*, and *T. hypoconia*. In all taxa, the maxillary processes are placed slightly anterior to the choanal processes (Fig. 7).

Ectopterygoids. We found only one ectopterygoid feature that varies within the ingroup: The length of the anterior processes by which the ectopterygoid embraces the maxilla. These processes may be of subequal length (*Helicops infrataeniatus, H. leopardinus* and *Pseudoeryx plicatilis*; Fig. 7A, C, E) or the medial process may be longer than the lateral process (*Hydrops caesurus*; Fig. 7G). This latter state also occurs in most of the outgroup species: *Erythrolamprus semiaureus, Hydrodynastes gigas, Oxyrhopus rhombifer, Phalotris bilineatus, Philodryas patagoniensis, Psomophis obtusus, Thamnodynastes chaquensis*, and *T. hypoconia*. Finally, the lateral process is longer than the medial process in the outgroup species *Farancia abacura, Leptodeira annulata*, and *Sibynomorphus turgidus* (but this feature was not observed in Hydropsini).

The shape of the lateral process of the ectopterygoid is also variable. This process is square-shaped in all studied Hydropsini and in most of the outgroup species (Fig. 7A, C, E, G), and is rounded only in *Leptodeira annulata* and *Sibynomorphus turgidus*.

Pterygoids. The teeth-bearing pterygoid is the largest and most posterior element of the palatomaxillary arch (Fig. 7). We observed no variable features concerning this bone.
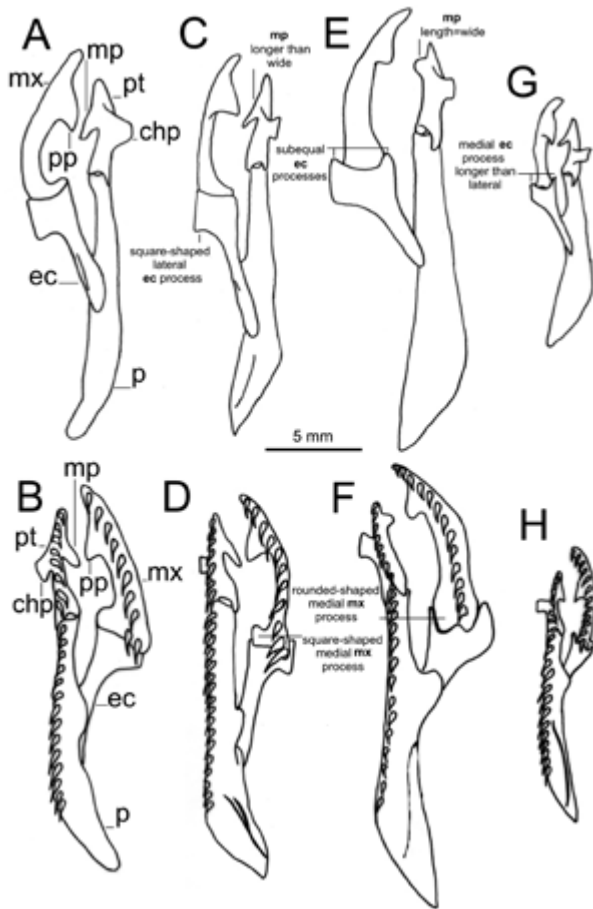
Fig. 7. Palate - left side. Dorsal (A, C, E, G) and ventral (B, D, F, H) views. *Helicops infrataeniatus* (A, B), *H. leopardinus* (C, D), *Pseudoeryx plicatilis* (E, F), and *Hydrops caesurus* (G, H). Abbreviations: chp, choanal process; ec, ectopterygoid; mp, maxillary process; mx, maxilla; p, pterygoid; pp, palatine process; pt, palatine.

Bones of the suspensorium

Supratemporals. The width and length of the supratemporal bones vary within Hydropsini. Supratemporals are of similar width along their entire length in *Helicops infrataeniatus* and *H. leopardinus*, as well as in *Erythrolamprus semiaureus*, *Hydrodynastes gigas*, *Oxyrhopus rhombifer*, and *Psomophis obtusus*. The anterior half of the supratemporals is wider than the posterior half in *Hydrops caesurus* and *Pseudoeryx plicatilis* (Fig. 1), and the remaining outgroup species. We found three conditions of the relative length of the supratemporal bone, two of which occur in Hydropsini: (1) *Helicops infrataeniatus*, *H. leopardinus*, and *Pseudoeryx plicatilis* have long supratemporals in which the anterior margin of the bone reaches or exceeds the parietal-prootic suture, and the posterior margin of the bone runs behind the pos-

terior margin of exoccipitals (Fig. 1A-C, 3A-C); and (2) *Hydrops caesurus* has short supratemporals that never extend posterior than exoccipitals and do not reach the parietal-prootic suture (Fig. 1D, 3D). The second condition also occurs in *Phalotris bilineatus* that has dorsalized supratemporals (and, therefore, the length of the supratemporals should be assessed in a dorsal view of the skull). The third condition was found in *Leptodeira annulata* and *Sibynomorphus turgidus*, which have very short supratemporals not reaching the middle of the prootic. The remaining outgroup taxa have long supratemporals.

Quadrates. Each quadrate has an ovoid-shaped bony process to receive a pair of ligaments, one projecting from the distal end of the stapes, and the other projecting from the prootic. Such bony processes are surrounded by Alcian-Blue-positive capsules (Fig. 2, 3C). The quadrate displays only very little variability in all studied ingroup and outgroup species.

Columellae. The rod-shaped, proximally-expanded, and partially ossified columella runs between the oval window and the quadrate. The columella contacts the quadrate through a ligament (Fig. 2, 3). The proximal expansion of the stapes forms the ovoid-shaped stapedial footplate that almost completely covers the oval window. The cartilaginous distal portion of the columella (extracolumella) is Alcian-Blue-positive and is feather-shaped (Fig. 2, 6). The bony part of the columella thus represents half (one specimen of *H. leopardinus* MLP.R.5627 and *Hydrops caesurus*) or two-thirds (remaining Hydropsini and outgroup taxa) of the total length of the structure (columella and extracolumella).

Mandibles

Compound bones. Three distinctive regions can be recognized: the articular region, the retroarticular process, and the adductor fossa (Fig. 8A, E, F). In all cases, the articular region represents the articular facet, is dorsally concave, runs perpendicular to the long axis of the mandible, and is shorter than the blunt retroarticular process. The studied species of Hydropsini vary in the height of the medial margin of the adductor fossa (or mandibular fossa). Although all studied species have the surangular crest taller than the prearticular crest, the grade of development of the prearticular crest may be expressed in three character conditions. The prearticular crest of the adductor fossa is clearly lower than the surangular crest in *Helicops infrataeniatus* and *H. leopardinus* (Fig. 8A, B), whereas *Hydrops caesurus* is the only species having both crests approximately of the same height (the prearticular crest is slightly lower than the surangular crest) (Fig. 8D). The prearticular crest in *Pseudoeryx*
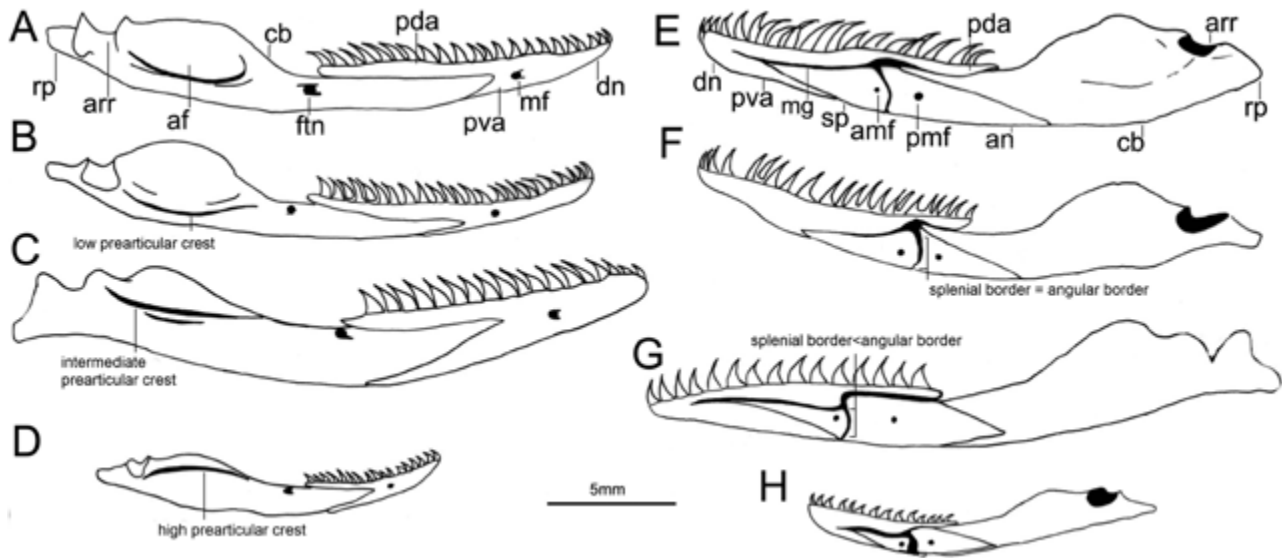
Fig. 8. Right mandible. Lateral (A-D) and medial (E-H) views. *Helicops infrataeniatus* (A, E), *H. leopardinus* (B, F), *Pseudoeryx plicatilis* (C, G), and *Hydrops caesurus* (D, H). Abbreviations: af, adductor fossa; an, angular; amf, anterior mylohyoid foramen; arr, articular region; cb, compound bone; dn, dentary; ftn, foramen trigeminal nerve; mf, mental foramen; mg, Meckel´s groove; pda, posterodorsal arm of the dentary; pmf, posterior mylohyoid foramen; pva, posteroventral arm of the dentary; rp, retroarticular process; sp, splenial.

plicatilis shows an intermediate condition (not as low as in *Helicops* spp. nor as high as in *Hydrops caesurus*) (Fig. 8C). In some dipsadids (*Erythrolamprus semiaureus*, *Hydrodynastes gigas*, *Psomophis obtusus*, *Thamnodynastes chaquensis*, and *T. hypoconia*), we found the prearticular crest lower than the surangular crest, as in *Helicops*. In the other studied dipsadids (*Farancia abacura*, *Leptodeira annulata*, *Oxyrhopus rhombifer*, *Phalotris bilineatus*, and *Sibynomorphus turgidus*), the prearticular crest shows an intermediate condition, as in *Pseudoeryx plicatilis*.

Angulars. The triangular-shaped angulars do not contact the dentaries and the Meckel's grooves are very well developed (Fig. 8E). The angular houses the posterior mylohyoid foramen that, only in *H. infrataeniatus*, is clearly bigger than the anterior mylohyoid foramen (Fig. 8E). In the remainder Hydropsini (Fig. 8F, G, H) and all outgroup species, the foramina are almost equal in size.

Splenials. The triangular-shaped splenials are slightly smaller than the angulars. They contact the dentaries and angulars and bear the anterior mylohyoid foramen (Fig. 8E). The extent of the contact area between splenial and angular can vary. Both bones may have the same height at the contact point, as in *Helicops infrataeniatus* and *H. leopardinus* (Fig. 8E, F), and also *Erythrolampreus semiaureus*, *Farancia abacura*, *Hydrodynastes gigas*, *Philodryas patagoniensis*, *Psomophis obtusus*, and *Thamnodynastes chaquensis*. In contrast, the anterior border of the angular is higher than the posterior border of splenial in *Hydrops caesurus* and *Pseudoeryx plicatilis* (Fig. 8G, H), and also

Phalotris bilineatus, *Leptodeira annulata*, *Oxyrhopus rhombifer*, *Sibynomorphus turgidus* and *Thamnodynastes hypoconia*.

Dentaries. These V-shaped bones have two processes, the posterodorsal (dentigerous) and the posteroventral one (Fig. 8). In all studied species, the mental foramen and the foramen of the mandibular branch of the trigeminal nerve are of equal size (Fig. 8A).

DISCUSSION

Although Hydropsini is monophyletic in all recently published molecular phylogenies, relationships within the tribe remain controversial, as *Hydrops* appears to form a clade with *Helicops* (Zaher et al., 2009; Pyron et al., 2010; Grazziotin et al., 2012) or with *Pseudoeryx* (Vidal et al., 2000, 2010; Pyron et al., 2013). In relation to the monophyly of Hydropsini, we found only one feature of the bony skull shared by the three genera of the tribe: the unpaired foramen on the parabasisphenoid placed anterior to the anterior Vidian openings. This feature occurs also in the semi-aquatic *Erythrolamprus semiaureus*, and the highly aquatic *Farancia abacura*. With respect to the internal relationships within the tribe, our observations support the relationship of *Hydrops* with *Pseudoeryx*.

Hydrops caesurus and other species of the genus (*Hydrops martii*, and *H. triangularis*) with published skull descriptions (Albuquerque, 2002) share four fea-

tures with *Pseudoeryx plicatilis*, and none with the *Helicops* species studied here (*Helicops infrataeniatus* and *H. leopardinus*) or for which published skull descriptions exist (*H. carinicaudus*: Yuki and Lema, 2005). However, *Helicops* species and *Pseudoeryx plicatilis* share only three features.

Helicops species are characterized by four features (putative synapomorphies): (1) a pointed lateral margin of the horizontal lamina of the nasal (unambiguous), (2) no anterior projection of the prefrontal, (3) short vomerine processes of the premaxilla, and (4) a supratemporal of similar width across its length. The lateral projections of the parabasisphenoid present in *Helicops* also occur in the two species of *Hydrops* described by Albuquerque (2002) and, therefore, they are not a synapomorphy of the species of *Helicops*. In contrast to the *Helicops* species studied here, *Helicops carinicaudus* studied by Yuki and Lema (2005) displays a contact between the ascending process of the premaxilla and the anterior end of the horizontal lamina of the nasal.

The studied species of *Hydrops* share three features: (1) short supratemporals, (2) both lateral and medial walls of the adductor fossa of same height (unambiguous), and (3) a full bone contact between the parietal and the postorbital (unambiguous). Other features (e.g., vertical lamina of the nasals not emarginated, dorsal foramen of the prootic not tapered by the supratemporal, and straight suture between parabasisphenoid and the basioccipital) are not shared by the *Hydrops* species described by Albuquerque (2002). Two characters are unique to *Pseudoeryx plicatilis*: (1) an intermediate development of the medial margin of the adductor fossa, and (2) a rounded lateral end of the horizontal lamina of the nasal. The narrow parabasisphenoid anterior projection with a single point found in *Pseudoeryx plicatilis* is also found in *Hydrops triangularis* (Albuquerque, 2002).

Hydrops species and *Pseudoeryx plicatilis* share four features: (1) an angular that is higher than the splenial at the level of the common suture of these bones, (2) long vomerine processes of the premaxilla, (3) an ascending process of the premaxilla that overlaps the anterior end of the horizontal lamina of the nasal, and (4) the presence of a anterior projection of the prefrontal. The medial articular process of the maxilla is rounded in the *Hydrops* and the *Pseudoeryx* species studied here, but not in the *Hydrops* species studied by Albuquerque (2002).

When considering the species studied here together with those for which are available skull descriptions, *Helicops* and *Hydrops* share no features uniquely. Within the sample studied by us, we found that they share a long and triangular-shaped maxillary process of the palatine, but this was not found in the species of *Helicops* and *Hydrops* studied by Yuki and Lema (2005) and Albuquerque (2002), respectively.

Helicops species and *Pseudoeryx plicatilis* share three features: (1) a transverse crista of the basioccipital projected ventrally, (2) a vertical lamina of the nasal with a notch (absent in *Hydrops caesurus* and not described in the literature for the other species of *Helicops* and *Hydrops*), and (3) a single foramen rotundum (double in *Hydrops caesurus*, and not described in the literature for *Helicops carinicaudus*, *Hydrops marti*, and *Hydrops triangularis*). Other features shared by *Helicops* and *Pseudoeryx* in our study (e.g., medial and lateral processes of the ectopterygoid of same length, anterior notch of the parietal present, and parabasisphenoid-basioccipital suture projected mid-posteriorly) are not shared by other species of these genera (Albuquerque, 2002; Yuki and Lema, 2005).

Finally, we found parietal foramina in the dipsadids *Erythrolamprus semiaureus*, *Helicops infrataeniatus*, *H. leopardinus*, *Leptodeira annulata pulchriceps*, *Philodryas patagoniensis*, *Pseudoeryx plicatilis*, *Thamnodynastes chaquensis*, *T. hypoconia*, and *Oxyrhopus rhombifer*. The unpaired parietal foramen of other tetrapods is usually filled by the sensory anterior (third eye) and the secretory posterior (pineal gland or epiphysis) organs (Quay, 1979). The parietal foramen is a midline skull roof opening that communicates with the cranial cavity independent of the presence of a pineal eye (Crumly, 1982). Crumly (1982) noted that, in contrast to previous evidence (e.g., Gaffney, 1975), a parietal foramen is present in many testudinids. Although the loss of the parietal foramen is considered one of the ophidian synapomorphies (e.g., Gauthier et al., 1988; Lee and Scanlon, 2002), we observed small paired foramina in our taxa where the parietal foramen usually opens in other lepidosaurians. Apparently, neither nerves nor blood vessels pass through these foramina, although the foramina were filled by a Sudan Black-positive tissue, probably of nervous origin. These foramina are variably present within some species (e.g., *H. infrataeniatus*), whereas in other species they are either consistently present (e.g., *H. leopardinus*) or consistently absent (e.g., *Hydrops*). These features should be evaluated with caution given the small sample sizes studied. Parietal foramina have also been reported in *Pituophis catenifer* (Bullock and Tanner, 1966), *Phalotris matogrossensis* (Lema et al., 2005), *Helicops carinicaudus* (Yuki and Lema, 2005), *Notechis scutatus*, and *Atractus erythromelas* (Cundall and Irish, 2008). These cranial-roof openings need further study in order to clarify their function and taxonomic value. Interestingly, the pineal organ of snakes is composed solely of pinealocytes, which presumably have no sensory function (Ekström and Meissl, 2003).

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APPENDIX

Studied specimens and voucher information. References: DS&C (double stained and cleared skull), D (dried skull).

Erythrolamprus semiaureus (Dipsadidae: Xenodontinae: Xenodontini: semi-aquatic) from Punta Lara (Buenos Aires province, Argentina): 1 male (TL: 642 mm, voucher MLP.JW.1549, DS&C skull MLP.R.5629); 2 females (TL: 1067mm, voucher MLP.JW.1548, DS&C skull MLP.R.5630; TL: 1150 mm, voucher MLP.JW.1831, DS&C skull MLP.R.5655); *Farancia abacura* (Dipsadidae *incertae sedis*: fully-aquatic) from Alaucha County (Florida, USA): 1 male (TL: 772 mm, voucher MLP.JW.345, DS&C skull MLP.R.5651); *Helicops infrataeniatus* (Dipsadidae: Xenodontinae: Hydropsini: fully-aquatic) from Isla del Ibicuy (Entre Ríos province, Argentina): 1 male (TL: 645 mm, voucher MLP.R.5017, DS&C skull MLP.R.5625); 2 females (TL: 543 mm, voucher MLP.R.5191, DS&C skull MLP.R.5624; TL: 487 mm, voucher MLP.R.5192, DS&C skull MLP.R.5645); *Helicops infrataeniatus* from Punta Lara (Buenos Aires province, Argentina): 1 female (TL: 335 mm, voucher MLP.JW.1528, DS&C skull MLP.R.5689); *Helicops infrataeniatus* from unknown locality: D skull (MLP.R.5957); *Helicops leopardinus* (Dipsadidae: Xenodontinae: Hydropsini: fully-aquatic) from Bella Vista (Corrientes province, Argentina): 4 females (TL: 444 mm, voucher MLP.JW.633, DS&C skull MLP.R.5626; TL: 529 mm, voucher MLP.JW.632, DS&C skull MLP.R.5627; TL: 364 mm, voucher MLP.R.5643, DS&C skull MLP.R.5644; TL: 407 mm, voucher MLP.JW.631, DS&C skull MLP.R. 5654); 1 male (TL: 680 mm, voucher MLP.JW.668, DS&C skull MLP.R.5690); *Hydrodynastes gigas* (Dipsadidae: Xenodontinae: Hydrodynastini: semi-aquatic) 2 specimens from from unknown locality: D skull (MLP.R.5638), D skull (MLP.R.5954) with no voucher specimen; *Hydrodynastes gigas* from Ituzaingó (Corrientes province, Argentina): 1 male (TL: 980 mm, voucher MLP.R.5649, DS&C skull MLP.R.5650); *Hydrops caesurus* (Dipsadidae: Xenodontinae: Hydropsini: fully-aquatic) from Yaciretá (Corrientes province, Argentina): 1 female (TL: 436 mm, voucher MLP.JW.1944, DS&C skull MLP.R.5628); *Hydrops caesurus* from Isla Yaciretá (Río Paraná, Paraguay): 1 female (TL: 610 mm, voucher MLP.JW.1693, DS&C skull MLP.R.5688); *Leptodeira annulata pulchriceps* (Dipsadidae: Dipsadinae: Imantodini: arboreal) from unknown locality: 1 male (TL: 502mm, voucher MLP.R.5642, DS&C skull MLP.R.5648); *Oxyrhopus rhombifer* (Dipsadidae: Xenodontinae: Pseudoboini: semi-fossorial) from Medanos (Buenos Aires province, Argentina): 1 female (TL: 895 mm, voucher MLP.JW.932, DS&C skull MLP.R.5631); *Oxyrhopus rhombifer* from Balcarce (Buenos Aires province, Argentina): 1 female (TL: 763 mm, voucher MLP.JW.1626, DS&C skull MLP.R.5646); *Phalotris bilineatus* (Dipsadidae: Xenodontinae: Elapomorphini: fossorial) from Sierra de la Ventana (Buenos Aires province, Argentina): 1 female (TL: 324 mm, voucher MLP.R.5640, DS&C skull MLP.R.5641); *Philodryas patagoniensis* (Dipsadidae: Xenodontinae: Philodryadini: terrestrial) from Tandil (Buenos Aires province, Argentina): two males (TL: 753 mm, voucher MLP.JW.092, DS&C skull MLP.R.5632; TL: 732 mm, voucher MLP.JW.093, DS&C skull MLP.R.5633); *Philodryas patagoniensis* from Sierra de la Ventana (Buenos Aires province, Argentina): 1 male (TL: 659 mm, voucher MLP.R.5955, DS&C skull MLP.R.5956); *Pseudoeryx plicatilis* (Dipsadidae: Xenodontinae: Hydropsini: fully-aquatic) from Paraguay: 1 female (TL: 658 mm, voucher MLP.R.5572, DS&C skull MLP.R.5634); *Psomophis obtusus* (Dipsadidae: Xenodontinae: Psomophiini: terrestrial) from Esteros del Iberá (Corrientes province, Argentina): 1 female (TL: 372 mm, voucher MLP.R.5455, DS&C skull MLP.R.5639); *Sibynomorphus turgidus* (Dipsadidae: Dipsadinae: Dipsadini: terrestrial) from Ibera (Corrientes province, Argentina): 1 female (TL: 492 mm, voucher MLP.R.5441, DS&C skull MLP.R.5647); *Thamnodynastes chaquensis* (Dipsadidae: Xenodontinae: Tachymenini: terrestrial) from Alto Paraná (Argentina): 1 female (TL: 609 mm, voucher MLP.JW.1888, DS&C skull MLP.R.5635); *Thamnodynastes hypoconia* (Dipsadidae: Xenodontinae: Tachymenini: terrestrial) from Alto Paraná (Argentina): 1 female (TL: 567 mm, voucher MLP.JW.1887, DS&C skull MLP.R.5636); *Thamnodynastes hypoconia* from Azára, Apóstoles (Misiones province, Argentina): 1 male (TL: 610mm, voucher MLP.R.5652, DS&C skull MLP.R.5653).