

Nasal cartilages, hyobranchial apparatus, larynx, and glottal tubes in four species of Hydropsini (Serpentes: Dipsadidae: Xenodontinae)

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Abstract

Tribe Hydropsini (Serpentes: Dipsadidae: Xenodontinae) consists of three genera of aquatic snakes, *Helicops*, *Hydrops*, and *Pseudoeryx*, in which cartilaginous cranial features have been poorly studied. We here describe the nasal cartilages, hyobranchial apparatus, larynx, and glottal tubes in four representative Hydropsini species, compare them with species from other Dipsadidae tribes, and discuss our results in the context of the adaptation to the aquatic and fossorial habit. The studied species possess two nasal features that deviate from the pattern of nasal cartilages known in other alethinophidian and caenophidian snakes: (1) a cartilaginous connection between the lamina transversalis anterior and the concha of the Jacobson's organ, and (2) a small rostral projection of the planum anteorbitale, which probably represents a reduced anterior maxillary process. Two putative synapomorphic features may be supporting the monophyly of Hydropsini: (1) a short inferior median eminence of the cricoid cartilage, and (2) a large processus entoglossus of the hyobranchial apparatus. The second feature also occurs in other snakes, such as the aquatic *Farancia abacura* (Dipsadidae: *incertae sedis*), the semi-fossorial *Oxyrhopus rhombifer* (Xenodontinae: Pseudoboini), and the fossorial *Phalotris bilineatus* (Xenodontinae: Elapomorphi). This feature may represent a convergent cranial adaptation between aquatic and fossorial snakes. Similarly, the short inferior median eminence of the cricoid cartilage, which also occurs in *Farancia abacura*, may represent a convergent adaptation to the fully aquatic habit in these species.

Key words

Adult chondrocranium, hyolaryngeal cartilages, Serpentes, Hydropsini.

Introduction

All recently published molecular phylogenies support the monophyly of the South American Xenodontinae (Dipsadidae) that comprises several monophyletic tribes. One of these is tribe Hydropsini consisting of three genera of aquatic snakes, *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). The presence of a sin-

gle internasal scale, the dorsally-positioned external nares (see ROZE, 1957a, b), a wide origin of the muscle adductor mandibularis externus superficialis, and a viviparous reproductive mode (ZAHER, 1999; ZAHER *et al.*, 2009) have been proposed as putative synapomorphies of Hydropsini. The ornamentation of the hemipenes (ZAHER, 1999) does not support the monophyly of the tribe. The viviparous reproductive mode is debatable, since ovi-

parity was reported for *Hydrops* and some species of *Helicops* (CUNHA & NASCIMENTO, 1981; SCROCCHI *et al.*, 2005).

The poor literature on the cartilaginous skull of snakes (PARKER, 1878; BROCK, 1929; PRINGLE, 1954; KAMAL & HAMMOUDA, 1965a, b; LANGERBARTEL, 1968; EL-TOUBI *et al.*, 1970, 1973a, b; BELLAIRS & KAMAL, 1981; RIEPPEL, 1981; YOUNG, 2000), and the requirement of double stained and cleared specimens may have hampered the study of this part of the skull to find phylogenetically useful characters (LEE & SCANLON, 2002; CONRAD, 2008; FENWICK *et al.*, 2009). While the cranial osteology of the Hydropsini is well documented (CUNDALL & ROSSMAN, 1984; ALBUQUERQUE, 2002; YUKY & LEMA, 2005), the chondrocranium is practically unknown, since only the histological description of the nasal cartilages of *Helicops infrataeniatus* (DOS SANTOS COSTA & HOFSTADLER-DEIQUES, 2002) is available in the literature.

A comparative analysis of the adult chondrocranium of the three Hydropsini genera may prove useful to find characters that support the monophyly of the tribe. Thus, the main objective of the present work is to describe in detail the nasal cartilages, larynx, glottal tubes, and hyobranchial apparatus in four species: *Helicops infrataeniatus*, *H. leopardinus*, *Hydrops caesurus*, and *Pseudoeryx plicatilis*. In addition to provide a description of the chondrocranial features of the Hydropsini, we highlight differences and similarities with other Dipsadidae (see Appendix).

Materials and methods

We studied double stained and cleared skulls of two *Hydrops caesurus*, two *Pseudoeryx plicatilis*, four *Helicops infrataeniatus*, and five *H. leopardinus* specimens. For our comparative analyses, we selected representative species of Dipsadidae (see Appendix), which appear closely related to Hydropsini according to 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). The studied specimens of these species are deposited in the reptilian collection of the Museo de La Plata (MLP.R. and MLP.JW.), Buenos Aires, Argentina, and the herpetological collection of the Fundación Miguel Lillo (FML), Tucumán, Argentina.

We prepared the skulls using the technique by TAYLOR & VAN DYKE (1985), in which bones stain red, cartilages stain blue, and soft tissues become cleared. Photos of

an advanced Stage 37 embryo of *Helicops leopardinus* were included to illustrate the deep integration of cartilages and some bones of the nasal region (see Fig. 1). Although, descriptions should be better understood following the camera lucida drawings of the cartilaginous structures (Figs. 2–3).

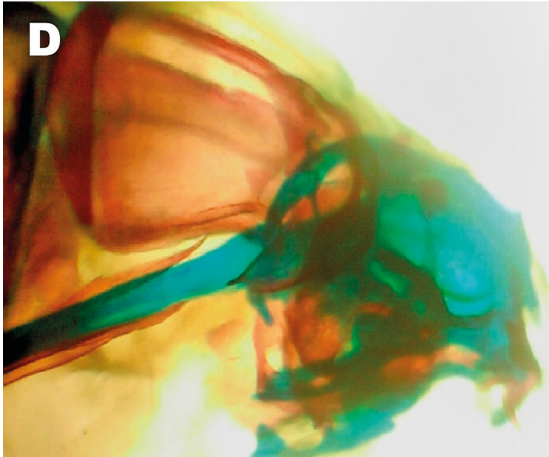
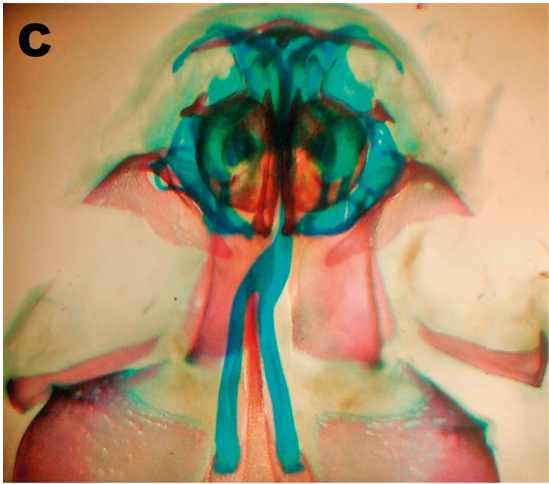
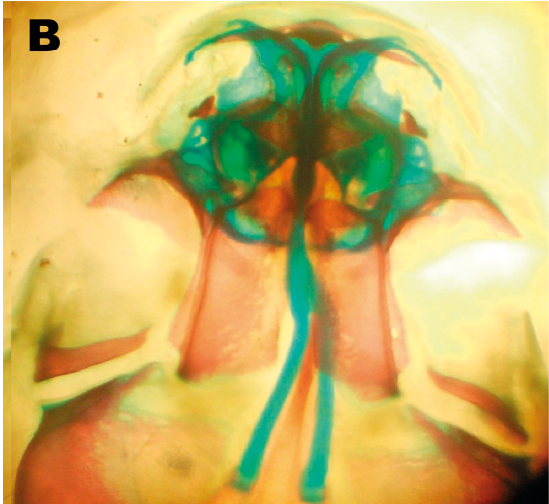
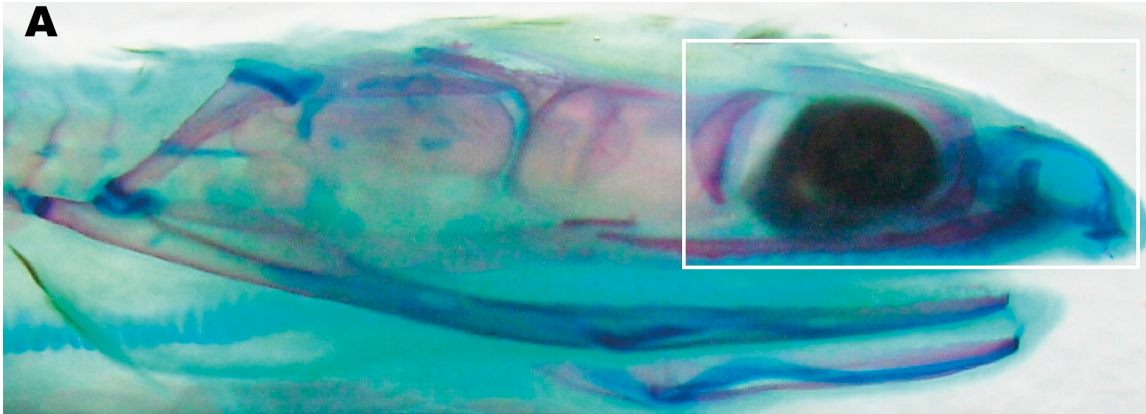
The terminology used follows YOUNG (2000) for the larynx and glottal tubes, BELLAIRS & KAMAL (1981) for nasal cartilages and the hyobranchial apparatus, CUNDALL & IRISH (2008) for cranial bones, GRAZZIOTIN *et al.* (2012) for taxonomic arrangements, and the topology of VIDAL *et al.* (2010) was employed to map some characters (Fig. 4). For character mapping we selected the topology of VIDAL *et al.* (2010) instead of GRAZZIOTIN *et al.* (2012) because the last has many poorly supported *incertae sedis* taxa.

Results

Nasal cartilages and trabecula communis

The nasal cartilages and the trabecula communis are chondrified and very well stained with Alcian Blue in the examined Hydropsini and all non-Hydropsini species (the nasal cartilages were damaged in our *Pseudoeryx plicatilis* specimens). The nasal capsule is a complex continuum of cartilages that are highly integrated in most rostral bones (prefrontals, nasals, septomaxillae, premaxilla, and vomers; Figs. 1A–D, 2A–C). The capsulae are wide open laterally and ventrally and the remaining capsula is closed anterodorsally by the nasal cupola, dorsally by the parietotectal cartilage, and posterodorsally by the planum anteorbitale (Fig. 2A). The nasal cupola leans against the interior wall of the premaxilla, whereas the most medial part of the parietotectal cartilage is dorsally covered by the nasals. The prefrontal obscures the planum anteorbitale caudally. The planum anteorbitale projects a short spicule that may represent a reduced anterior maxillary process (Fig. 2B). Two well-marked processes extend ventrolaterally from the nasal cupola and parietotectal cartilage: the inferior and the superior alary processes, respectively (Fig. 2A). The fenestra narina is limited by both of these processes. The fenestra lateralis opens between the processus alaris superior and the lateral margin of the parietotectal cartilage (Fig. 2A). The processus alaris inferior is larger in two of the examined dipsadids (*Thamnodynastes chaquensis* and *Sibynomorphus turgidus*) than in the other species. The lateral process of the

→ **Fig. 1.** Lateral view of a skull of an advanced Stage 37 embryo of *Helicops leopardinus* (A). Note the deep integration of some bones and nasal cartilages in dorsal (B), ventral (C), and lateral (D) views. Note the position of the larynx, glottal tube and hyobranchial apparatus in a ventral view between both hemimandibles (E). Detail of the larynx (F). The images are not scaled.



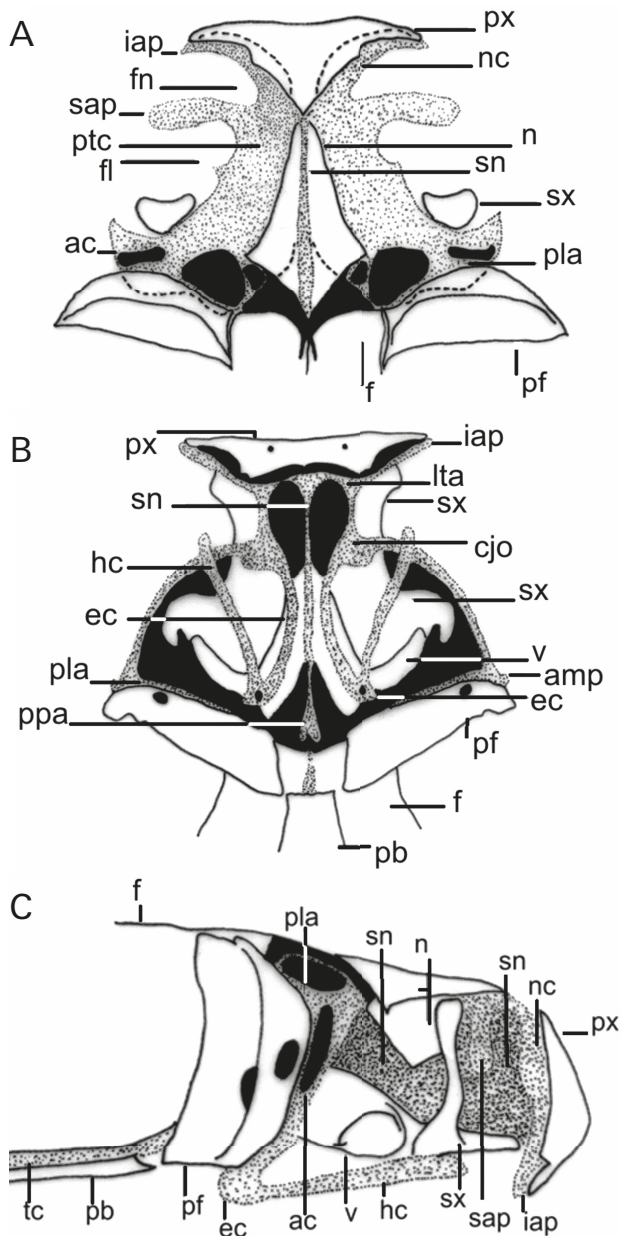


Fig. 2. Adult nasal cartilages of *Helicops leopardinus* in dorsal (A), ventral (B) and lateral (C) views. Pointed areas represent cartilage, and dark areas represent cranial fenestrations. **Abbreviations:** ac, aditus conchae; amp, anterior maxillary process; cjo, concha of Jacobson's organ; ec, ectochoanal cartilage; f, frontal; fl, fenestra lateralis; fn, fenestra narina; hc, hypochoanal cartilage; iap, inferior alary process; lta, lamina transversalis anterior; n, nasal; nc, nasal cupola; pb, parabasisphenoid; pla, planum anteorbitale; pf, prefrontal; px, premaxilla; ppa, palatine process articulation; ptc, parietotectal cartilage; sap, superior alary process; sn, septum nasi; sx, septomaxilla; tc, trabecula cranii; v, vomer. The images are not scaled.

septomaxilla occupies the space opened by the fenestra lateralis. The distal end of the superior alary process is free and rounded, whereas the distal end of the inferior alary process is connected to the lamina transversalis anterior (Fig. 2B–C). *Helicops infrataeniatus* and *H. leop-*

ardinus have several large openings between the nasal capsule roof and the prefrontal bone. The most lateral of these openings represents the aditus conchae (Fig. 2A). In *H. leopardinus*, the aditus conchae is visible also in dorsal and lateral views (Fig. 2C), since it is larger than in the other Hydropsini species (in which it is visible only dorsally). In *Hydrops caesurus*, the entire area of the capsule between the nasal and the prefrontal bones is not chondrified, impeding us to appreciate the aditus conchae. The aditus conchae is absent in one species (*Erythrolamprus semiaureus*) and has different lengths in the other species, ranging from small (*Phalotris bilineatus*), medium-sized (*Farancia abacura*, *Leptodeira annulata*, *Oxyrophus rhombifer*, *Psomophis obtusus*, and *Sibynomorphus turgidus*), to very large (*Helicops infrataeniatus*, *H. leopardinus*, *Hydrodynastes gigas*, *Thamnodynastes hypoconia*, *T. chaquensis*, and *Philodryas patagoniensis*). In all studied species, the foramen epiphaniale remains unidentified, but it presumably opens into the aditus conchae. The foramen apicale also remains unidentified. *Thamnodynastes chaquensis* is the only species in the comparative analysis to possess small supernumerary foramina on the caudal part of the parietotectal cartilage.

In ventral view, the expanded rostral end of the septum nasi connects to the lamina transversalis anterior on both sides (Fig. 2B). The lamina extends caudomedially, forming an ectochoanal cartilage that runs along both sides of the septum nasi. The ectochoanal process is pierced by a rounded small foramen and curves forward to form the hypochoanal cartilage (Fig. 2B–C). This cartilage ends free at the level of the concha of Jacobson's organ. The ventral capsular cartilages are connected to the capsular part of the vomer bone and form the border of the choana (Fig. 2B–C). At its caudal end, the septum nasi forms bifid cartilaginous processes that articulate with the medial process of the palatine bone (Fig. 2B). The trabecula communis projects into the orbital region and becomes bifid forming the trabecula cranii (Fig. 2C).

Larynx and glottal tubes

The larynx and the glottal tubes are similar among the studied Hydropsini species (Figs. 1E–F, 3A–J). The cricoid ring is either cartilaginous (*Helicops leopardinus*, *Hydrops caesurus*) or calcified (*Helicops infrataeniatus*, *Pseudoeryx plicatilis*). The inferior median eminence of the cricoid is extremely short and with calcium deposits, but not forming bone (as indicated by the manner the Alizarine Red stains) and, besides Hydropsini, this feature occurs only in *Farancia abacura*. The eminence never exceeds the rostral end of the arytenoids (Fig. 3A–D). The superior median eminence of the cricoid is poorly developed in all Hydropsini and most non-Hydropsini species studied (Fig. 3A–E). The azarous calcium deposits on the arytenoids varies within species. The arytenoids connect to the cricoids via a cartilaginous

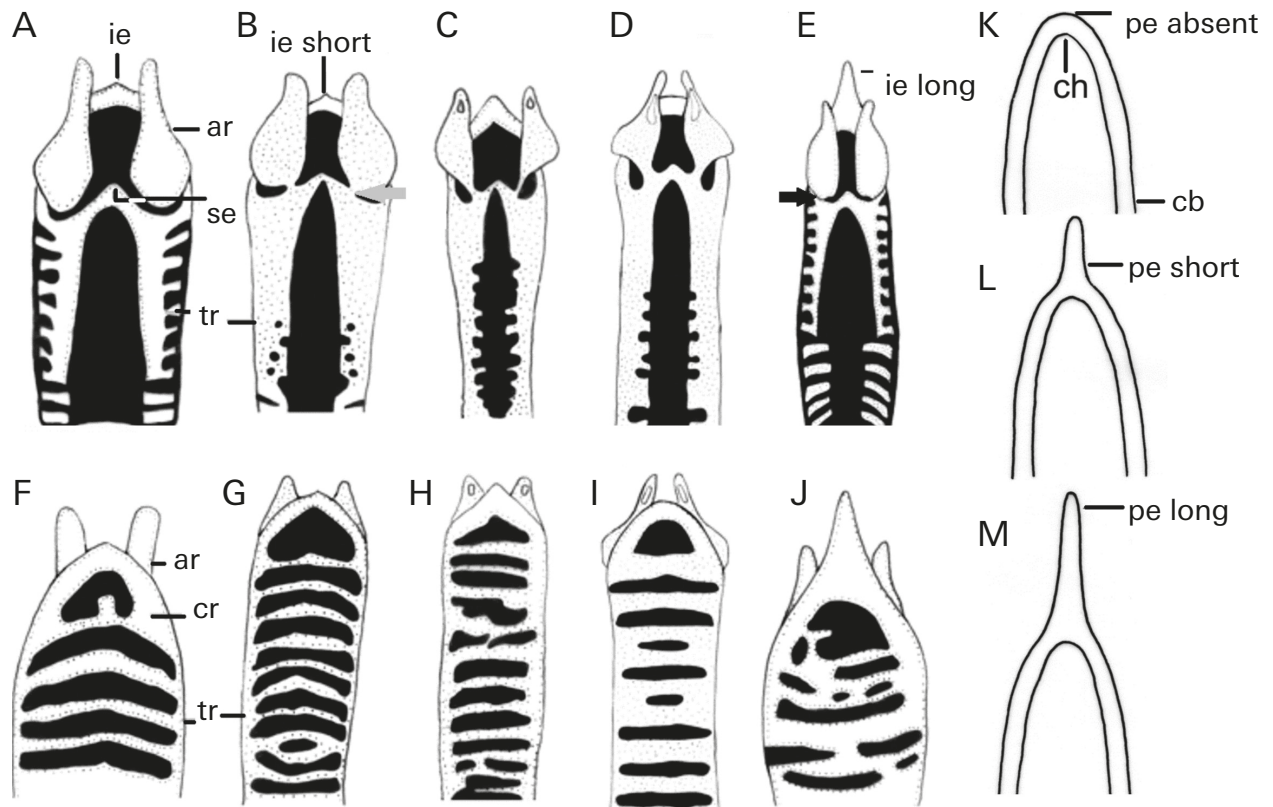


Fig. 3. Dorsal (A-E) and ventral (F-J) views of the larynx and glottal tube in (A,F) *Helicops leopardinus*, (B, G) *H. infrataeniatus*, (C, H) *Hydrops caesurus*, (D, I) *Pseudoeryx plicatilis*, and (E, J) *Thamnodynastes chaquensis*; and schematic ventral views of the three morphological types of hyobranchial apparatus (K-M) found in the studied species. In (A-J) pointed areas represent cartilage, and dark areas represent fenestrations. Grey arrows indicate cartilaginous tissue (B) and black arrows indicate soft tissue (E) connections between the arytenoids and the cricoid cartilages. **Abbreviations:** ar, arytenoids; cb, ceratobranchial; ch, corpus hyoidis; cr, cricoids; ie, inferior median eminence; pe, processus entoglossus; se, superior median eminence; tr, trachea. The images are not scaled.

bridge in *Helicops infrataeniatus*, *Hydrops caesurus*, and *Pseudoeryx plicatilis* (Fig. 3B–D). *Helicops leopardinus* (Fig. 3A) and the non-Hydropsini *Psomophis obtusus* and *Thamnodynastes chaquensis* (Fig. 3E) lack such cartilaginous connection in all studied specimens, while *Philodryas patagoniensis* includes both specimens with and specimens without the connection. The cricoid is connected to most rostral tracheal rings. The tracheal rings are incomplete dorsally (Fig. 3A–E), and the most anterior ones are disposed irregularly. They are deeply calcified and cartilaginous in all Hydropsini species, except *H. infrataeniatus*.

Hyobranchial apparatus

In the studied Hydropsini, the hyobranchial apparatus lies superficially, under the skin of the gular region. The apparatus is arch-shaped and formed by the corpus hyoidis and a pair of ceratobranchials that project caudally on each side (Figs. 1E, 3K–M). The processus entoglossus projects rostrally from the mid-rostral face of the corpus hyoidis. This process is larger in *Hydrops caesurus* than in

Helicops infrataeniatus, *H. leopardinus*, and *Pseudoeryx plicatilis*. We recognized three conditions for the processus entoglossus in Hydropsini and other species:

- Absent in *Hydrodynastes gigas* and *Sibynomorphus turgidus* (Fig. 3K);
- Short and entering completely between the two ceratobranchial arms in *Erythrolamprus semiaureus*, *Leptodeira annulata*, *Philodryas patagoniensis*, *Psomophis obtusus*, *Thamnodynastes chaquensis*, and *T. hypocoenia* (Fig. 3L);
- Large and exceeding the space between these arms, in all studied Hydropsini, *Farancia abacura*, *Phalotris bilineatus*, and *Oxyrhopus rhombifer* (Fig. 3M).

Discussion

The embryonic development of nasal cartilages was studied in a small sample of species from five caenophidian and one alethinophidian families: *Crotaphopeltis hotamboeia* (BROCK, 1929), *Dasypeltis scabra* (PRINGLE, 1954) (Colubridae); *Malpolon monspessulanus* (EL-TOUBI *et al.*,

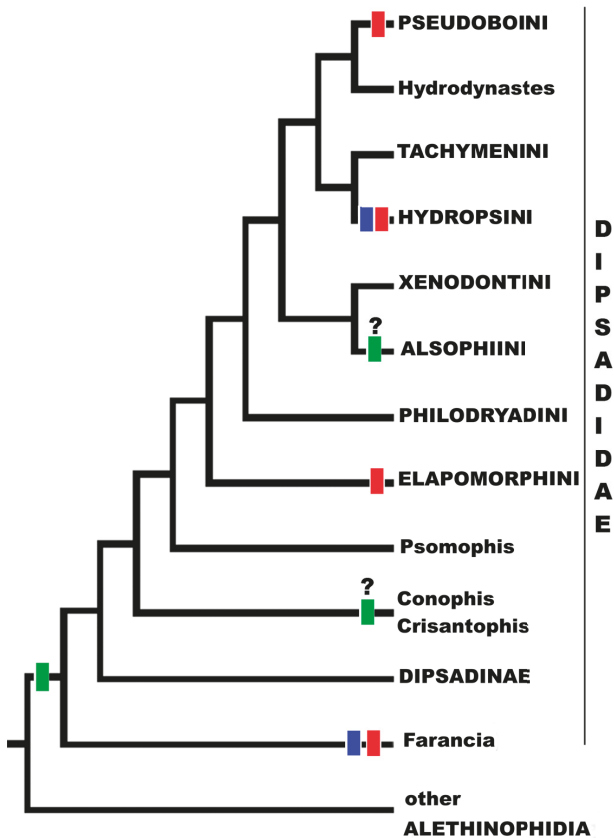


Fig. 4. Simplified phylogenetic relationships of Dipsadidae modified from VIDAL *et al.* (2010) showing some putative synapomorphies for Dipsadidae (green) and Hydropsini (blue and red). Green rectangles represent (1) lamina transversalis anterior and the concha of the Jacobson's organ connected by cartilage, and (2) very reduced anterior maxillary process. Blue rectangles represents a short inferior median eminence of the cricoid cartilage. Red rectangles represent a large processus entoglossus of the hyobranchial apparatus.

1973a, b), *Psammophis sibilans* (KAMAL & HAMMOUDA, 1965a, b) (Psammophiidae); *Natrix natrix* (PARKER, 1878; DE BEER, 1937) (Natricidae); *Lamprophis inornatus* (PRINGLE, 1954) (Lamprophiidae); *Naja haje* (EL-TOUBI *et al.*, 1970), *Hemachatus haemachatus* (PRINGLE, 1954) (Elapidae); *Cerastes vipera* (KAMAL & HAMMOUDA, 1965c), *Causus rhombeatus* (PRINGLE, 1954) (Viperidae); and *Eryx jaculus* (KAMAL & HAMMOUDA, 1965d) (Boidae). Based on the main features described in these species, BELLAIRS & KAMAL (1981) identified a general pattern in the anatomy of nasal cartilages in caenophidian and alethinopidian snakes. The more recent description of the embryonic chondrocranium of *Sibynomorphus turgidus* by SCROCCHI *et al.* (1998) lacks details on the nasal capsules. In our comparative analyses, two nasal features deviate from BELLAIRS & KAMAL (1981)'s pattern: (1) the cartilaginous connection between the lamina transversalis anterior and the concha of the Jacobson's organ, and (2) the small rostral projection of the planum anteorbitale, possibly representing a reduced anterior maxillary process. Such deviations may be explained by the fact,

that we studied the chondrocranium in adult specimens, whereas other authors generally studied embryonic developmental stages. Alternatively, these deviations may represent synapomorphies of Dipsadidae (Fig. 4). This is actually the first study to describe nasal cartilages in this group.

Considering the morphology of the larynx of the studied dipsadids, the short median eminence of the cricoid, never exceeding the rostral margin of the arytenoids, is the only feature shared by all Hydropsini studied. This feature was also found in the North American *Farancia abacura*, suggesting a possible relation between this trait and the aquatic habits of these species. A similar trend in the reduction of the inferior median eminence is observed in aquatic non-dipsadid species (see YOUNG, 2000). The inferior median eminences of these aquatic species vary from short, either not reaching the rostral arytenoid ends (*Acrochordus*) or slightly passing them (*Eunectes*, *Natrix*), to completely absent (*Lapemis*, *Pelamis*). In addition, KARDONG (1972) described a large inferior median eminence of the cricoid for *Charina bottae* (Boidae), as expected, since this is a non-aquatic snake. The author also described the insertion of the muscle sphincter laryngis on both sides of the inferior median eminence, a muscle that probably should be reduced or displaced in species with a short inferior median eminence. Finally, with respect to the connection between the cricoid and arytenoid cartilages, LANGEBARTEL (1968) considers the absence of cartilaginous continuity (articulated condition) between these cartilages as a shared feature between Boidae and Pythonidae. Our findings in *Philodryas patagoniensis* (see above) suggest that this character can vary within a species.

The hyoids studied here correspond to the "parallel" hyoid type described by LANGEBARTEL (1968). This is one of four types described by LANGEBARTEL and always consists of a pair of very long parallel cornua that are joined anteriorly by a corpus hyoidis from which the processus entoglossus may or may not project, depending on the species. The parallel hyoid type is found in the clade formed by Bolyeriidae, Tropidophiidae, and Caenophidia (Acrochordidae, Xenodermatidae and most families of Colubrifformes: Atractaspididae, Colubridae, Dipsadidae, Elapidae, Homalopsidae, Lamprophiidae, Natricidae, Pareatidae, Psamophiidae, and Viperidae; see phylogenies of LEE & SCANLON, 2002; GRAZZIOTIN *et al.*, 2012). The hyoids of Calamaridae and Pseudoxenodontidae remain unknown. We confirmed the presence of the parallel hyoid type in several Dipsadinae and Xenodontinae species not considered by LANGEBARTEL (1968). Although we found that all studied aquatic and fossorial species of Dipsadidae have a large processus entoglossus, this was not found by LANGEBARTEL (1968) in many of the aquatic and fossorial caenophidian species, including *Acrochordus javanicus*, *A. granulatus*, *Nerodia cyclopion*, *N. erythrogaster*, *N. sipedon*, *Natrix natrix*, *Regina septemvittata* (all aquatic species without such process); *Regina grahamii* and *Natrix piscator* (two aquatic species with a short process); *Carphophis amoenus* and

Oxyrhabdium leporinum (two fossorial species without the process); and *Rhinocheilus lecontei* (a fossorial species with a short process). These findings and the fact that both arboreal and terrestrial species can have a large processus entoglossus suggest no clear relationship between a large processus and the aquatic or fossorial habits of the species. However, within Dipsadidae, the aquatic or fossorial habits of the species do appear to correlate with the presence of a large processus entoglossus. A similar correlation may be suggested for some other snakes with a large process, which were studied by LANGEBARTEL (1968), such as the aquatic species of Homalopsidae (*Cerberus rhynchops*, *Homalopsis buccata*) and the fossorial Boodontinae colubrids (*Mehelya nyassae*).

In conclusion, we found two chondrocranial putative synapomorphies that may support the monophyly of Hydropsini (see Fig. 4), as was proposed by the recent molecular phylogenies mentioned above: (1) a short inferior median eminence of the cricoid cartilage (shared with the aquatic Dipsadidae *incertae sedis*, *Farancia abacura*); and (2) a large processus entoglossus (shared with other semi-fossorial, fossorial and aquatic species of Dipsadidae, the Xenodontinae *Oxyrhopus rhombifer* and *Phalotris bilineatus*, and the *incertae sedis* *Farancia abacura*, respectively).

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Appendix

List of studied species and their respective voucher specimens

Erythrolamprus semiaureus (Dipsadidae: Xenodontinae: Xenodontini: semi-aquatic) from Punta Lara (Buenos Aires province, Argentina): 1 male (TL: 642 mm, voucher MLP.JW.1549, skull MLP.R.5629); 1 female (TL: 1067mm, voucher MLP.JW.1548, skull MLP.R.5630). *Farancia abacura* (Dipsadidae: *incertae sedis*: fully-aquatic) from Alauca County (Florida, USA): 1 male (TL: 772mm, voucher MLP.JW.345, 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, skull MLP.R.5625); 2 females (TL: 543 mm, voucher MLP.R.5191, skull MLP.R.5624; TL: 487 mm, voucher MLP.R.5192, skull MLP.R.5645). *Helicops infrataeniatus* from Punta Lara (Buenos Aires province, Ar-

gentina): 1 female (TL: 335 mm, voucher MLP.JW.1528, skull MLP.R.5689). *Helicops leopardinus* (Dipsadidae: Xenodontinae: Hydropsini: fully-aquatic) from Bella Vista (Corrientes province, Argentina): 3 females (TL: 444 mm, voucher MLP.JW.633, skull MLP.R.5626; TL: 529 mm, voucher MLP.JW.632, skull MLP.R.5627; TL: 364 mm, voucher MLP.R.5643, skull MLP.R.5644); 1 male (TL: 680 mm, voucher MLP.JW.668, skull MLP.R.5690). *Helicops leopardinus* from Margarita Belén (Chaco province, Argentina): advanced Stage 37 embryo (complete double stained and cleared skeleton MLP.R.6028). *Hydrodynastes gigas* (Dipsadidae: Xenodontinae: Hydrodynastini: semi-aquatic) from Ituzaingó (Corrientes province, Argentina): 1 male (TL: 980 mm, voucher MLP.R.5649, skull MLP.R.5650). *Hydrops caesu-*

rus (Dipsadidae: Xenodontinae: Hydropsini: fully-aquatic) from Yaciretá (Corrientes province, Argentina): 1 female (TL: 436 mm, voucher MLP.JW.1944, skull MLP.R.5628). *Hydrops caesurus* from Isla Yaciretá (Río Paraná, Paraguay): 1 female (TL: 610 mm, voucher MLP.JW.1693, skull MLP.R.5688). *Leptodeira annulata pulchriceps* (Dipsadidae: Dipsadinae: Imantodini: arboreal) from unknown locality: 1 male (TL: 502 mm, voucher MLP.R.5642, 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, skull MLP.R.5631). *Oxyrhopus rhombifer* from Balcarce (Buenos Aires province, Argentina): 1 female (TL: 763 mm, voucher MLP.JW.1626, 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, 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, skull MLP.R.5632; TL: 732 mm, voucher MLP.JW.093, skull MLP.R.5633). *Pseudoeryx pli-*

catilis (Dipsadidae: Xenodontinae: Hydropsini: fully-aquatic) from Paraguay: 1 female (TL: 658 mm, voucher MLP.R.5572, skull MLP.R.5634). *Pseudoeryx plicatilis* from Paraguay, Depto. Ñeembucú, Yataity, 5 Km E: 1 male (TL: 750 mm, voucher FML 6499, larynx and glottal tube FML 6499). *Psomophis obtusus* (Dipsadidae: Xenodontinae: Psomophiini: terrestrial) from Esteros del Iberá (Corrientes province, Argentina): 1 female (TL: 372 mm, voucher MLP.R.5455, skull MLP.R.5639). *Sibynomorphus turgidus* (Dipsadidae: Dipsadinae: Dipsadini: terrestrial) from Ibera (Corrientes province, Argentina): 1 female (TL: 492 mm, voucher MLP.R.5441, skull MLP.R.5647). *Thamnodynastes chaquensis* (Dipsadidae: Xenodontinae: Tachymenini: terrestrial) from Alto Paraná (Argentina): 1 female (TL: 609 mm, voucher MLP.JW.1888, skull MLP.R.5635). *Thamnodynastes hypoco-*
nia (Dipsadidae: Xenodontinae: Tachymenini: terrestrial) from Alto Paraná (Argentina): 1 female (TL: 567 mm, voucher MLP.JW.1887, skull MLP.R.5636). *Thamnodynastes hypoconia* from Azára, Apóstoles (Misiones province, Argentina): 1 male (TL: 610mm, voucher MLP.R.5652, skull MLP.R.5653).