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Morphology of the gas bladder in thorny catfishes (Siluriformes: Doradidae)

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ABSTRACT.—The gross morphology of the gas bladder is described, illustrated, compared and categorized among 86 of 88 nominal valid and six undescribed species representing all 31 genera of Doradidae with comments on ontogenetic and taxonomic variation when observed. The putatively basal-most doradids exhibit an unmodified cordiform gas bladder. Derived taxa exhibit an impressive suite of modifications including the addition of a secondary bladder, pronounced reduction of the posterolateral chambers, internal trabeculae, associations with bony capsule-like expansions of the anterior (Weberian) vertebrae, and accessory diverticula varying widely in size, shape, abundance, and distribution. Intra-specific differences are minor, most often reflective of ontogenetic changes especially in large-size species, whereas inter-specific and inter-generic differences are significant, in many cases diagnostic, and suggestive of phylogenetic signal excepting instances of evident convergence such as gas bladder reduction in *Rhynchodoras* and all but one species of *Leptodoras*.

Key words: diverticula, ontogenetic variation, taxonomic variation

> "It is remarkable that this important family [= Order Siluriformes] of Fishes has so little occupied the attention of morphologists, especially when we take into consideration the interesting modifications which its various members have undergone, and the fact that in this family the air-bladder and auditory ossicles are subject to greater variations, and are more highly specialized than in any other group of Ostariophyseae." Bridge and Haddon, 1893:66.

INTRODUCTION

Catfishes (Order Siluriformes) exhibit the most morphological diversity, particularly with respect to the gas bladder, among otophysan fishes (Howes, 1983:1), a monophyletic clade that also includes minnows, suckers, loaches and algae eaters (Cypriniformes), tetras and allies (Characiformes), and American knifefishes (Gymnotiformes) (Rosen and Greenwood, 1970; Nelson, 2006). Several families of catfishes exhibit modifications of the gas bladder (Bridge and Haddon, 1889, 1892, 1893; Sörensen, 1894–1895; Howes, 1983; Stewart, 1986; Lechner and Ladich, 2008), and the variety of modifications is perhaps best represented by species in the family Doradidae (Eigenmann, 1925). Furthermore, in doradids the Weberian apparatus is modified such that the parapophyses of the fourth vertebrae are flexible, with each one terminating in a discoid or conical expansion known as the Müllerian ramus (Fig. 1A) first described by Müller (1842) as the main part of the elastic spring apparatus. The dorsal anterior face of the Müllerian ramus is firmly attached to the sonic protractor or drumming muscle (Fig. 1B) which originates in a bony, posteriorly direct pocket formed by internal faces of supraoccitipal, exoccipital, Weberian supraneurals, epoccipital and anterior nuchal plate. The dorsal face of the Müllerian ramus is connected laterally by a short ligament to the first tympanal scute (Fig. 1B). Contraction of the drumming muscle pulls the elastic spring forward, extending the gas bladder; its relaxation allows elastic recoil to quickly restore the gas bladder to its normal position (Fine and Ladich, 2003). Repeated contractions of the drumming muscle causes the gas bladder and first tympanal scute to vibrate, and the rapid compression and extension of the gas bladder radiates tonal sounds with a fundamental frequency (determined by the muscle contraction rate) and harmonics (Fine and Ladich, 2003). Doradids also or alternatively produce stridulatory sounds caused during fin motion by the collisions of ridges on the dorsal process of the pectoral spine against the concave roughened floor of the pectoral-spinal fossa on the cleithrum (Fine et al., 1997;

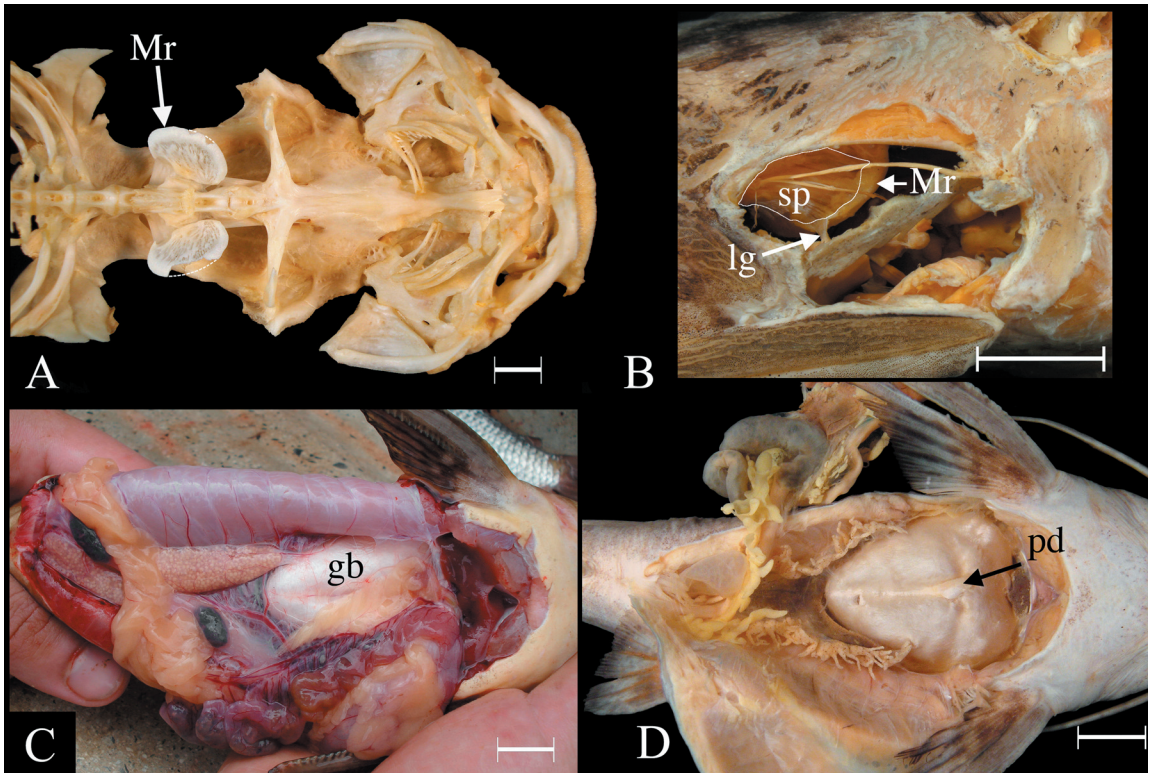


Fig. 1. A. Ventral view of head and anteriormost vertebrae in *Kalyptodoras bahiensis*, MZUSP 87841, 233 mm SL, showing Müllerian ramus (Mr, dashed lines complete circumference of damaged rami). B. Lateral view (anterior to left) of tympanal area in *Wertheimeria maculata*, MZUSP 93658, 186.9 mm SL, showing short ligament (lg) between distal rim of Müllerian ramus (Mr) and first tympanal scute. C. Body cavity in *W. maculata*, fresh specimen, MZUSP 93659, 259 mm SL, female. D. Body cavity in *W. maculata*, preserved specimen, MZUSP 93658, 167.4 mm SL, male. gb = gas bladder, pd = pneumatic duct, sp = sonic protractor (drumming) muscle (outlined in white). Scale bars equal 10 mm.

Fine and Ladich, 2003). These noisy habits have inspired the common name talking catfishes for doradids.

The siluriform gas bladder in its unmodified condition (e.g., in Ictaluridae) is a large cordiform sac with smooth walls lacking accessory diverticula, and an internal T-shaped septum that divides the lumen into a large anterior chamber (camera aerea Weberiana) and two posterolateral chambers (see Figs. 1 and 2 in Chardon, 1968:2–3; compare Figs. 1C,D and 3 herein). The walls of the gas bladder are composed of a thin internal tunica (inner bulla of Chardon et al., 2003: 78) and thick external tunica. The gas bladder is retroperitoneal, occupying the dorsal portion of the body (pleuroperitoneal) cavity outside of the parietal peritoneum that encloses most of the abdominal organs or viscera (Lawson in Wake, 1992; Figs. 1C,D herein). Dorsally the bladder is firmly attached to the vertebral column via a continuous connection between the transverse portion of the T-shaped septum and ventral superficial ossifications of the anterior compound vertebrae (Weberian complex). The anterior portion of the dorsal wall of the gas bladder contacts the tripus, that together with the other Weberian ossicles, transfers gas bladder vibrations to the inner ear (Lechner and Ladich, 2008). The bladder is connected to the esophagus via the pneumatic duct (Fig. 1D) that exits ventrally at the intersection of the transverse and longitudinal portions of the T-shaped septum. Musculature is reduced or absent in the lateral walls of the body opposite the anterior portion of the gas bladder (equivalent of lateral cutaneous area of Bridge and Haddon, 1893, and Chardon et al., 2003; also tympanum of Eigenmann, 1925), yielding fatty tissue and a thin layer of skin through which the gas bladder has close contact to the external environment.

Ichthyologists have long recognized the complexity of gas bladder morphology within the family Doradidae. In a paper on sexual differences in *Callichthys* (Callichthyidae) and gas bladders in Doradidae, Kner (1853) depicted

the disembodied gas bladders of nine species of doradids. He explicitly proposed six as new species based solely on the uniqueness of their gas bladders: *Doras polygramma* (= *Acanthodoras spinosissimus*), *D. loricatus* (= *D. fimbriatus*), *D.* (*Corydoras*) *ophthalmus* (= *Anduzedoras oxyrhynchus*), *D. asterifrons* (= *Astrodoras asterifrons*), *D.* (*Corydoras*) *punctatus* (= *Doras punctatus*), and *D.* (*Corydoras*) *brevis* (= *Trachydoras brevis*). Bridge and Haddon (1893), in their extraordinary monograph on the anatomy of the Weberian apparatus and gas bladder in catfishes, described and illustrated the gas bladder of *Doras maculatus* (= *Pterodoras granulosus*) and *Oxydoras brevis* (likely a species of *Doras sensu* Sabaj Pérez and Birindelli, 2008, based on gas bladder morphology depicted in Fig. 66, Plate 16). They included both doradids among their *Siluridae normales*, catfishes with a cordiform bladder and internal T-shaped septum vs. *Siluridae abnormales*, taxa with a very small, more or less degenerate bladder completely separated into two lateral sacs, each one usually enclosed by ossified walls (e.g., Loricariidae).

Eigenmann (1925), in his remarkable revision of doradids, assigned great importance to gas bladder morphology for diagnosing taxa. For example, Eigenmann (1925:324) diagnosed his new genus *Scorpiodoras* by having "a posterior air-bladder banjo- or scorpion-shaped". He recognized five main types of gas bladders in doradids: 1) simple subconical or subglobular as in *Centrochir*, *Franciscodoras* and *Hoplodoras* (= *Megalodoras*) *uranoscopus*, 2) gas bladder with a single posterior coecum as in *Platydoras*; 3) gas bladder with posterior coecum split longitudinally as in *Doras punctatus*, *Astrodoras asterifrons*, *Leptodoras linnelli*, and *Hypodoras forficulatus*; 4) gas bladder with three longitudinal divisions as in *Scorpiodoras heckelii*; and 5) gas bladder with many, radiating tubes or caecae as in *Pterodoras* and *Opsodoras* (= *Nemadoras*) *humeralis*. Eigenmann (1925) also noted transitional forms in the modification of the secondary bladder. More recently gas bladder morphology was used by Sabaj (2005) to help diagnose *Leptodoras*, by Birindelli et al. (2008) to distinguish a new species of *Leptodoras*, and by Birindelli et al. (2007) and Sabaj et al. (2008) to help distinguish among species of *Rhynchodoras* and *Rhinodoras*, respectively.

Gas bladder morphology also can be taxonomically misleading if not fully understood. For example, Risso and Morra (1964), unaware of ontogenetic variation, diagnosed their new genus *Parapterodoras* from *Pterodoras* based on gas bladder morphology in large specimens of *Pterodoras granulosus* compared to that of a smaller specimen illustrated in Eigenmann (1925:294, Figs. 11C,D). Higuchi (1992), in a cladistic analysis of nearly all doradid genera, emphasized that both ontogenetic and intraspecific variation in gas bladder morphology exists and its complexities required further study.

The objectives of this paper are to broadly describe, illustrate, compare and categorize gas bladder morphology among nearly all known doradids (86 nominal plus six undescribed species; *Acanthodoras depressus* and *Anadoras regani* not examined) noting inter- and intra-specific variation and ontogenetic changes where they occur. The utility of gas bladder morphology for phylogenetic analysis of doradid relationships will be addressed in a subsequent paper.

MATERIAL AND METHODS

Measurements were taken to the nearest 0.1 mm using digital calipers. Dissections were made following Bridge and Haddon (1893): body cavity opened by cutting anteriorly from anus, lateral to pelvic girdle, beneath the ribs, towards the coracoid process, then transversely along posterior limits of pectoral girdle to the opposite coracoid process, and posteriorly back to the anus without reaching it (so pelvic fins remain attached to body). The stomach, intestine, liver and associated structures were then removed, exposing the gas bladder. The bladder was removed by first disconnecting it from the complex vertebrae and the tripus, and then from the Müllerian ramus.

Terminology of shapes, conditions and morphological features of gas bladders summarized and illustrated in Fig. 2. Diverticula (= caecae of Bridge and Haddon, 1893) refer to all peripheral blind extensions of the main gas bladder and secondary one if present. Terminal diverticulum(ae) is(are) the median posterior extension(s) of one (or both) posterolateral chambers of gas bladder; secondary bladder is a modification wherein the terminal diverticulum(ae) is(are) well expanded and separated from the main bladder by a short yet distinct constriction. Müllerian window is the thin subcircular portion of the anterodorsal wall of the gas bladder to which the discoid or conical Müllerian ramus is attached.

We examined specimens of all species of Doradidae considered valid by Sabaj and Ferraris (2003; excepting *Acanthodoras depressus* and *Anadoras regani*), Ferraris (2007) and those subsequently described (Birindelli et al., 2007; Higuchi et al., 2007; Sabaj et al., 2008; Sabaj Pérez and Birindelli, 2008; Birindelli et al., 2008; Piorski et al., 2008). Six known undescribed species (herein identified as *Centrodoras* cf. *hasemani*, Doradidae sp. "Xingu", *Nemadoras* sp., *Trachydoras* sp., *Trachydoras* cf. *steindachneri*, *Oxydoras* cf. *eigenmanni*) are also included. For nearly all species multiple specimens representing different ontogenetic stages were observed (see Material Examined). Specimens are designated as alc (alcohol), sk (dry skeleton),

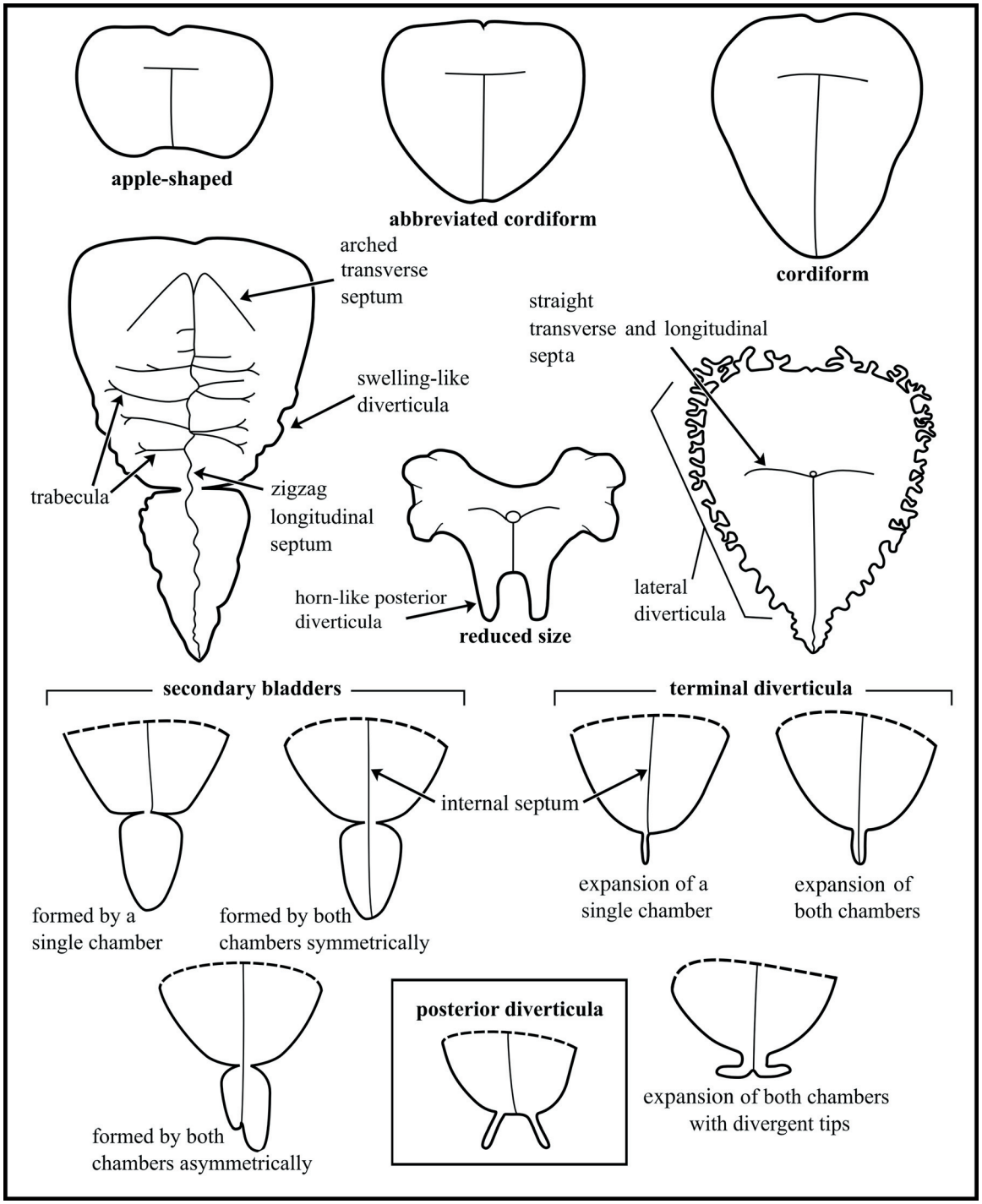


Fig. 2. Terminology of shapes, conditions and morphological features of gas bladders in Doradidae. Illustrations by L. Sousa.

and cs (cleared and double stained according to Taylor and Van Dyke (1985). Museum abbreviations follow Ferraris (2007).

RESULTS

See Appendix for summary of variation in gas bladder morphology in Doradidae described below.

Gas bladder in basal doradids and Centrochir (Figs. 1C,D, 3, 4).—Based on recent morphological studies (Higuchi et al., 1990; Higuchi, 1992; Birindelli, 2006) the basal-most doradids include: *Wertheimeria maculata*, *Kalyptodoras bahiensis*, *Franciscodoras marmoratus*, *Platydoras*, *Acanthodoras* and *Agamyxis*. *Centrochir*, a monotypic genus endemic to the Magdalena basin with uncertain relationships and an undescribed doradid from the rio Xingu are included here because their gas bladders resemble the above taxa.

In *Wertheimeria* (Figs. 1C,D, 3), *Kalyptodoras* and *Franciscodoras*, the gas bladder is unmodified, cordiform, simple (without diverticula), and with a well-developed internal T-shaped septum. In adults the anterior chamber is relatively short (transverse portion of septum displaced anteriorly) and the posterior chambers are long. There is ontogenetic variation in the relative lengths of the anterior and posterior chambers in *Wertheimeria* (Fig. 3) with the posterior chambers becoming proportionally longer as the size of the fish increases. The Müllerian windows are large, subcircular, angled dorsoposteriorly about 45 degrees from vertical. The intersection of the transverse and longitudinal portions of the T-shaped septum is located between the Müllerian windows, approximately aligned with a vertical plane through their centers.

In *Centrochir* (Figs. 4A,B) and an undescribed doradid from the rio Xingu basin (under study by LMS), the gas bladder is very similar to the foregoing, but the intersection of the T-shaped septum is displaced posteriorly, approximately aligned with a vertical plane through the posterior margins of the Müllerian windows.

In *Platydoras* (Figs. 4C,D), the gas bladder is similarly large, cordiform, with the intersection of the T-shaped septum located as in *Centrochir* or slightly posterior of the Müllerian windows. In addition, there is a large elongate secondary bladder formed by an expansion of only one terminal diverticulum (the complementary terminal diverticulum is entirely absent). The secondary bladder is thereby without an internal septum.

In *Acanthodoras* (Figs. 4E,F), the gas bladder is relatively short, apple-shaped and without diverticula. The transverse portion of the inner T-shaped septum is weakly developed and its intersection is aligned with the centers of the Müllerian windows.

In *Agamyxis* (Figs. 4G–J), the shape of the gas bladder is intermediate between the short rounded one in *Acanthodoras* and the more elongate cordiform shape in the preceding taxa. The bladder has a single well-developed terminal diverticulum, formed by an extension of only one of the two posterior chambers as in *Platydoras*. Unlike *Platydoras* the single terminal diverticulum in *Agamyxis* is relatively short, and not expanded into a secondary bladder. The intersection of the septum is located as in *Acanthodoras*. Though similar in external morphology, the two species of *Agamyxis* are readily distinguished by their gas bladders. In *Agamyxis pectinifrons* (Amazon drainage), there are about three to five small posterolateral diverticula on either side of the terminal divertiulum (Fig.

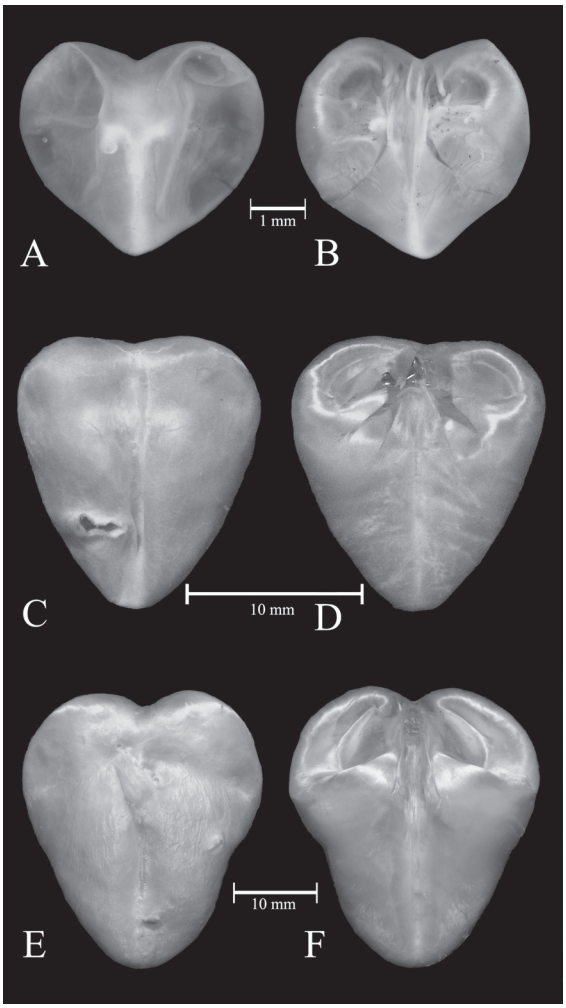


Fig. 3. Gas bladders in *Wertheimeria maculata* in ventral (A,C,E) and dorsal (B,D,F) views. A,B. MZUSP 40029, 25 mm SL. C,D. MZUSP 40229, 72.0 mm SL. E,F. MZUSP 93658, 167.4 mm SL.

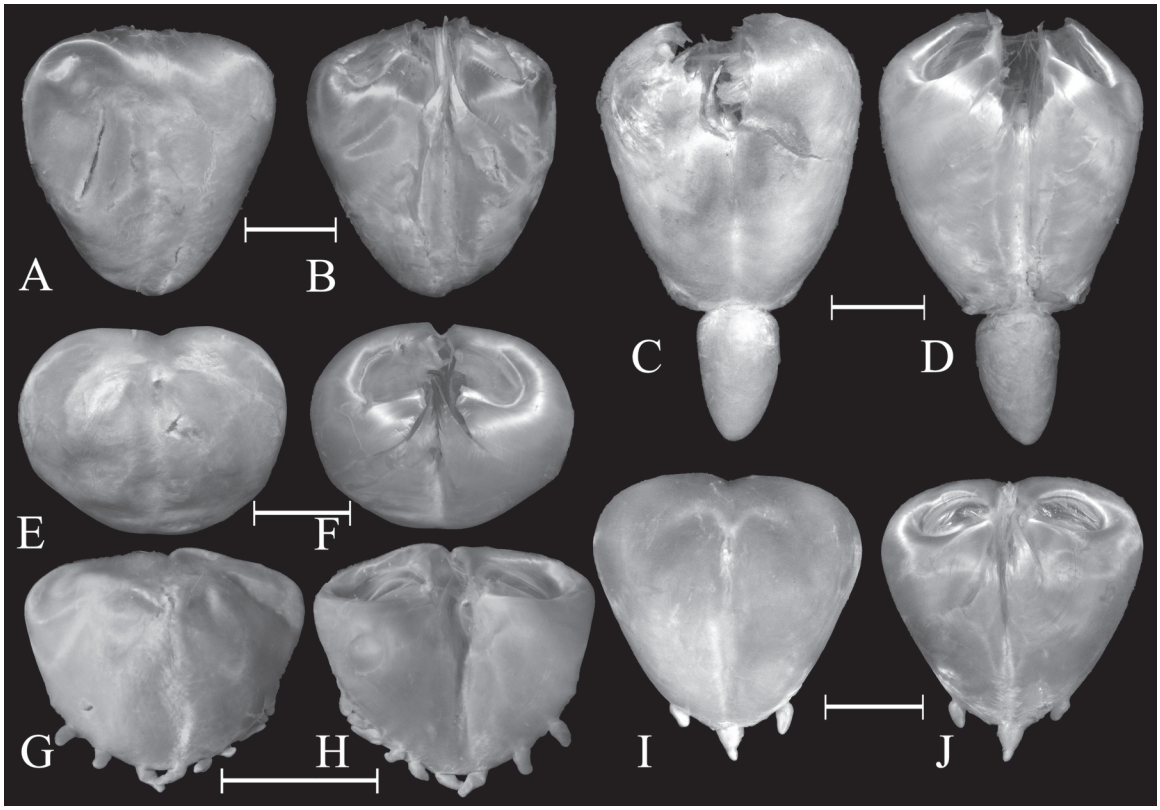


Fig. 4. Gas bladders in ventral (A,C,E,G,I) and dorsal (B,D,F,H,J) views. A,B. *Centrochir crocodili*, CU 47930, 130 mm SL. C,D. *Platydoras armatulus*, MZUSP 94088, 144 mm SL. E,F. *Acanthodoras cataphractus*, MZUSP 6831, 112 mm SL. G,H. *Agamyxis pectinifrons*, MZUSP 27806, 83.3 mm SL. I,J. *Agamyxis albomaculatus*, MZUSP 88607, 92.9 mm SL. Scale bars equal 10 mm.

4G,H), whereas in *A. albomaculatus* (Orinoco basin), there is only a single posterolateral diverticulum on either side of the terminal diverticulum (Fig. 4I,J).

Gas bladder in Astrodoradinae (Fig. 5).—In Astrodoradinae *sensu* Higuchi et al. (2007), the gas bladder is relatively short, apple shaped (except in *Anadoras*), and the intersection of the T-shaped septum is aligned with the centers of the Müllerian windows. In all species of *Amblydoras*, *Merodoras* and *Physopyxis* (Figs. 5A–G), the gas bladder has completely smooth walls and the transverse portion of the internal T-shaped septum is weakly developed. In *Merodoras* (Figs. 5C–E), the anterior chamber is partially divided medially by a thin vertical membrane (internal tunica) that is aligned with the longitudinal portion of the T-shaped septum and restricts communication between lateral halves of the chamber to a small foramen. This feature was not found in other taxa, but its presence is hard to determine because of the delicate nature of this membrane. *Merodoras* (Figs. 5C–E) is also unique in having the walls of the bladder distinctly speckled with dark pigment on the internal and external faces. *Physopyxis* (Figs. 5F–G) is unique in that the Müllerian window is barely developed as shallow longitudinally ovoid indentation complementary in outline to the more knob-like (vs. discoid or conical) terminus of the Müllerian ramus diagnostic of this genus.

In *Anadoras* (Figs. 5H–J), the gas bladder has an abbreviated cordiform shape; the walls are either completely smooth as in *A. grypus* (Figs. 5H,I), or with a minute terminal diverticulum as present in some specimens of *A. weddellii* (Fig. 5J). In *Hypodoras* (Fig. 5K), the gas bladder has two large terminal diverticula that are weakly symmetrical and proximally conjoined with divergent distal tips. In *Scorpidoras* (Figs. 5L–M), the gas bladder is more apple-shaped and has a well-developed secondary bladder formed by paired terminal diverticula (one from each posterior chamber) that are medially united via a common internal

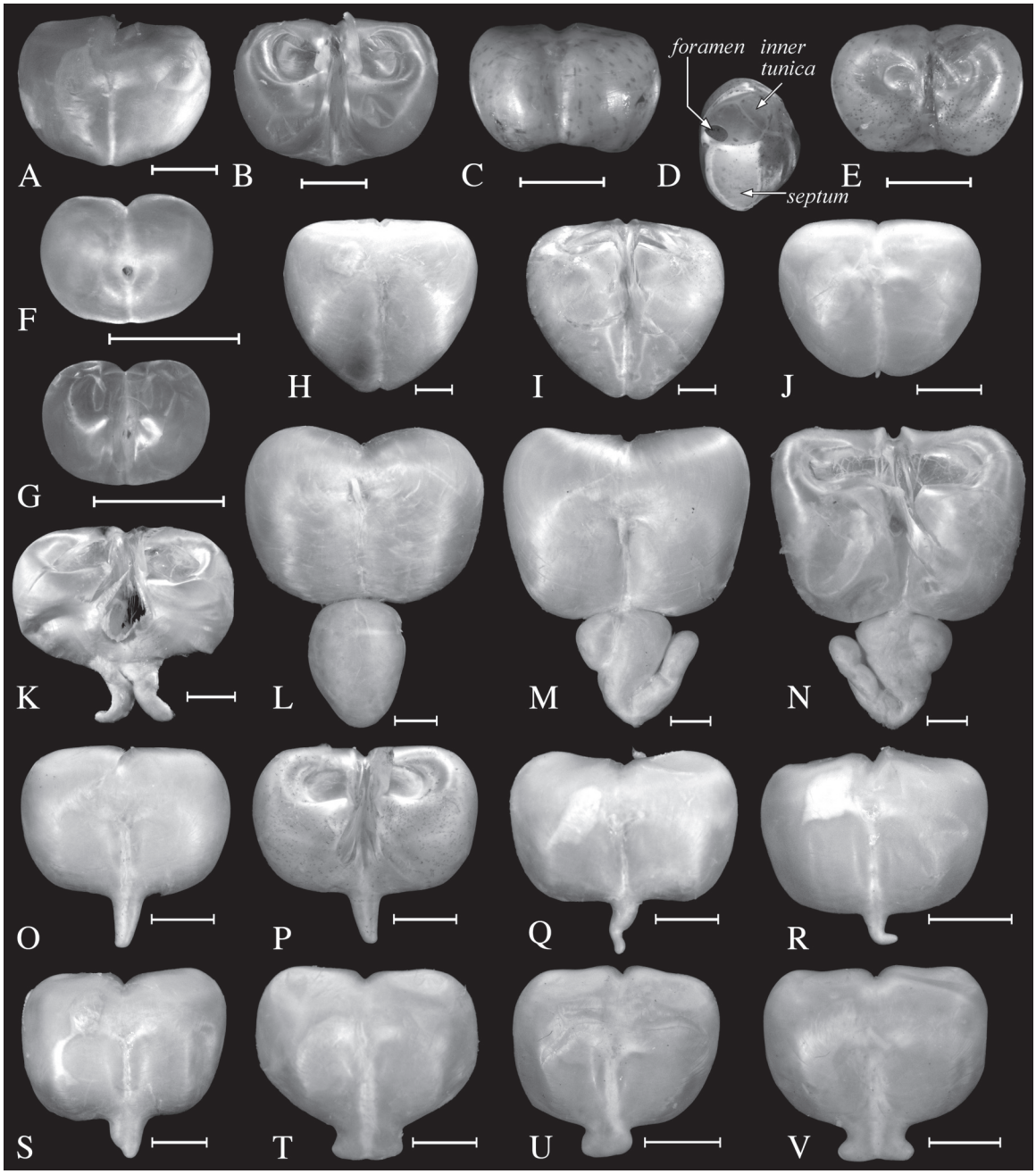


Fig. 5. Gas bladders in Astrodoradinae in ventral (A,C,F,H,J,L,M,O,Q–V), dorsal (B,E,G,I,K,N,P) and lateral view of parasagittal cut (D). A,B. *Amblydoras bolivarensis*, MZUSP 88610, 69.2 mm SL. C–E. *Merodoras nheco*, MZUSP 84414, 48.2 mm SL. F,G. *Physopyxis lyra*, MZUSP 62709, 27.2 mm SL. H,I. *Anadoras grypus*, MZUSP 74864, 140 mm SL. J. *Anadoras weddellii*, MZUSP 95023, 71.2 mm SL. K. *Hypodoras forficulatus*, ANSP 182517, 102.6 mm SL. L. *Scorpiodoras heckelii*, MZUSP 84203, 148.0 mm SL. M,N. *Scorpiodoras calderonensis* (identification tentative), MZUSP 36251, 140 mm SL. O–V. *Astrodoras asterifrons*. O,P. MZUSP 29049, 79.0 mm SL. Q. MZUSP 6784, 76.0 mm SL. R. MZUSP 29068, 62.1 mm SL. S. MZUSP 29068, 86.5 mm SL. T. MZUSP 6895, 68.1 mm SL. U. MZUSP 92780, 55.7 mm SL. V. MZUSP 92780, 58.4 mm SL. Scale bars equal 5 mm.

septum. In *S. heckelii* (Fig. 5L; compare Fig. 7 in Kner, 1853), the secondary bladder is egg-shaped with equal to weakly asymmetrical contributions from the paired terminal diverticula. In *S. calderonensis* (Figs. 5M,N; identification tentative), the contributions of the terminal diverticula are grossly asymmetrical with one side significantly longer and folded back on itself, or as Eigenmann (1925:324) noted "recurved like the whip of a scorpion" (see Fig. 12D in Eigenmann, 1925:295). In *Astrodoras* (Figs. 5O–V), the paired terminal diverticula are always present and united medially via a common septum, but vary greatly in symmetry and shape. The shape of the terminal diverticula ranges from long and slender with a somewhat cylindrical base (Figs. 5O–R) to relatively short and wide with a broader base (Figs. 5T–V; Fig. 5S represents intermediate condition). In any case the diverticula may be symmetrical (Figs. 5O,P,T,V) or asymmetrical with one side slightly to greatly reduced (Figs. 5Q,R,S,U). Furthermore, the distal tips of the diverticula may be divergent, deflected laterally (Figs. 5T,V), or conjoined and straight (Figs. 5O,P,S), or conjoined with the longer side weakly curved (Fig. 5Q) or deflected laterally (Fig. 5R).

Gas bladder in Lithodoras, Megalodoras, Centrodoras, Pterodoras *and* Doraops (Figs. 6–9).—Recent phylogenetic analyses of Doradidae based on morphology (Higuchi, 1992; Birindelli, 2006) support a clade comprised of *Centrodoras*, *Doraops zuloagai* (monotypic), *Lithodoras dorsalis* (monotypic), *Megalodoras* and *Pterodoras*. *Centrodoras* excepted, these taxa have a gas bladder with internal trabeculae radiating from the longitudinal portion of the T-shaped septum and along the walls of the posterior chambers (see Figs. 8A and 9C). The intersection of the T-shaped septum is aligned with the posterior margins of the Müllerian windows. Diverticula are present in all taxa and exhibit variation in enlargement and distribution. In all taxa, except *Doraops zuloagai* and *Pterodoras granulosus*, the paired terminal diverticula are medially united for their entire length and expanded to form a secondary bladder with smaller lateral diverticula. The secondary bladder in these taxa differs from *Platydoras* in that it has a medial longitudinal septum and is formed by a pair of terminal diverticula, each communicating with the main bladder via separate openings (one per posterior chamber, as in *Astrodoras*). In *Platydoras,* the secondary bladder is formed by only one terminal diverticulum (counterpart absent), and it communicates with the main bladder via a single opening to one of the two posterior chambers.

In *Lithodoras* (Figs. 6A–D), the secondary bladder has few lateral diverticula (simple or weakly branched) and is asymmetrical with one of the two medially united terminal diverticula more elongated than its counterpart. In larger specimens (Figs. 6C,D) the longer diverticulum may be partially subdivided distally by additional constrictions. The main bladder has a few small simple or weakly branched diverticula posterolaterally.

In *Megalodoras* (Figs. 6E–G), the secondary bladder is formed by approximately equal contributions from both terminal diverticula that may become partially subdivided distally by additional constrictions. The secondary bladder has many well-developed and often branched lateral diverticula that become particularly long and enlarged in large specimens (Fig. 6E). The main bladder also has well developed and often branched diverticula laterally and anteriorly (Figs. 6F,G).

The gas bladder in *Centrodoras* (Fig. 7) is similar to that of *Megalodoras*, particularly among small specimens. In *Centrodoras brachiatus* (Figs. 7A–E) differences include a relatively shorter secondary bladder with much more slender and intricately divided lateral diverticula in large specimens. In *Centrodoras* cf. *hasemani* (Fig. 7F), the secondary bladder is larger and the diverticula on the main and secondary bladders are much less developed by comparison.

The two species of *Pterodoras* (Figs. 8, 9A), though similar in external morphology, are readily distinguished by their gas bladders. In *P. rivasi* (Fig. 8F,G,I), the secondary bladder is formed by medially united and asymmetrically developed terminal diverticula as in *Lithodoras dorsalis*, but differs in having more numerous and slender lateral diverticula. *Pterodoras granulosus* (Figs. 8A–E,H) differs from *P. rivasi* and all related taxa in that it lacks a secondary bladder, and is unique among doradids in having posterolateral diverticula becoming grossly enlarged in specimens >200 mm SL. In smaller specimens (Figs. 8D,E) these posterolateral diverticula are similar in size and shape to the other diverticula along the lateral walls of the bladder. As specimens increase in size the posterolateral diverticula become increasingly larger, more elongate, appear segmented distally, and may extend beyond the body cavity in between layers of surrounding muscles (Fig. 9B). In both species of *Pterodoras*, the anteriormost lateral diverticulum on each side is greatly elongated, with numerous smaller branches, and curves anteromedially around the anterior face of the bladder (Fig. 8).

Doraops zuloagai (Figs. 9C–E) also has a pair of elongated, branched anterolateral diverticula that curve anteromedially; however, they are smaller and less branched than in *Pterodoras*. *Doraops* has a unique gas bladder in that the enlarged posterior diverticula are subterminal, not medially united. This condition is intermediate to the separate posterolateral diverticula in *Pterodoras granulosus* and the terminal, united diverticula forming a secondary bladder in *P. rivasi, Centrodoras, Lithodoras*, and *Megalodoras*.

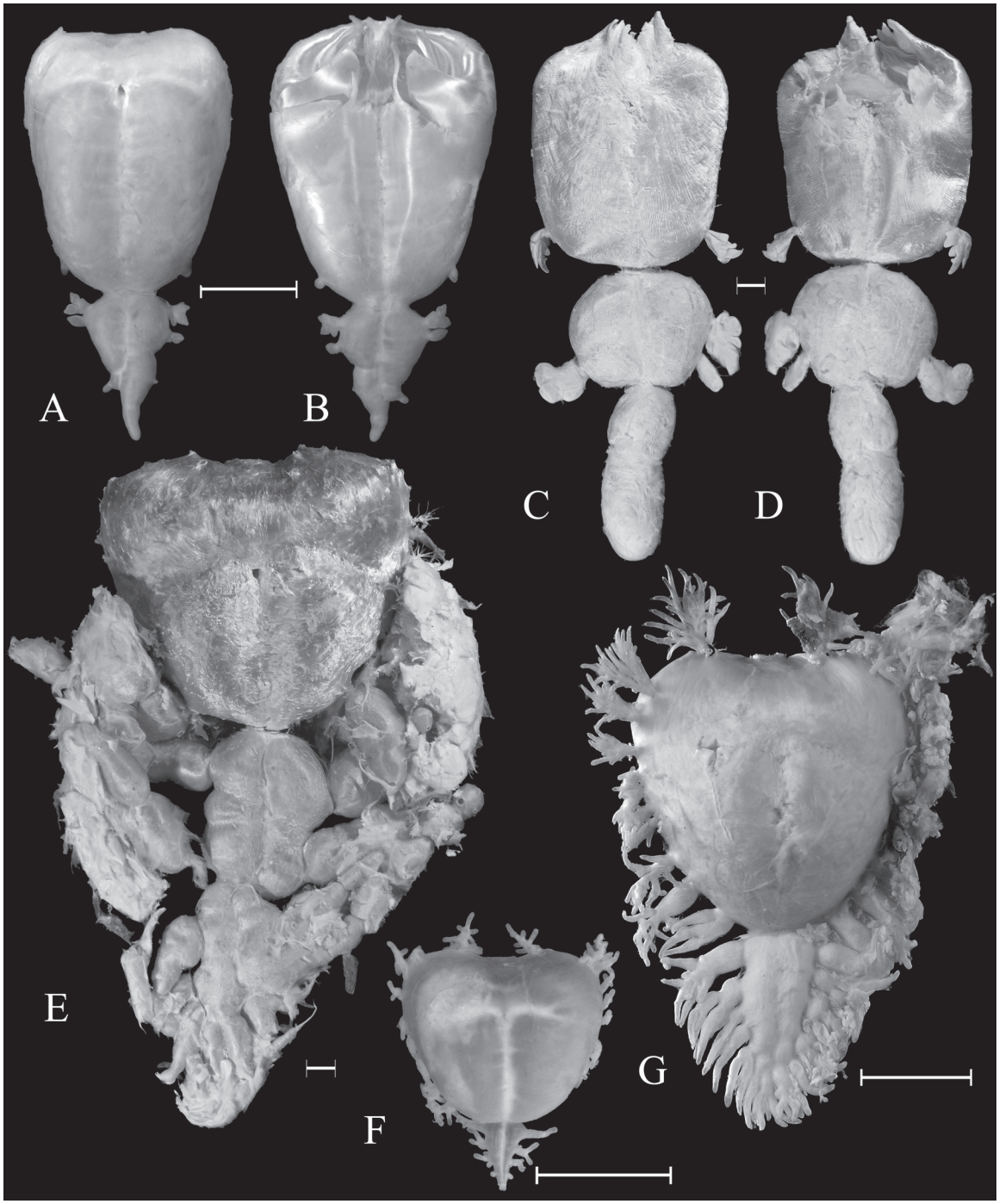


Fig. 6. Gas bladders in *Lithodoras* (A–D) and *Megalodoras* (E–G) in ventral (A,C,E–G) and dorsal (B,D) views. A,B. *Lithodoras dorsalis*, MZUSP 62584, 163 mm SL. C,D. *L. dorsalis*, MZUSP 91562, 478 mm SL. E. *Megalodoras uranoscopus*, MZUSP 5647, 570 mm SL (anterolateral diverticulae broken away). F. *M. uranoscopus*, MZUSP 55838, 73 mm SL. G. *Megalodoras guayoensis*, ANSP 177980, 143.9 mm SL (tissue surrounding diverticulae retained on left side). Scale bars equal 10 mm. Fig. 6G by T. Jones.

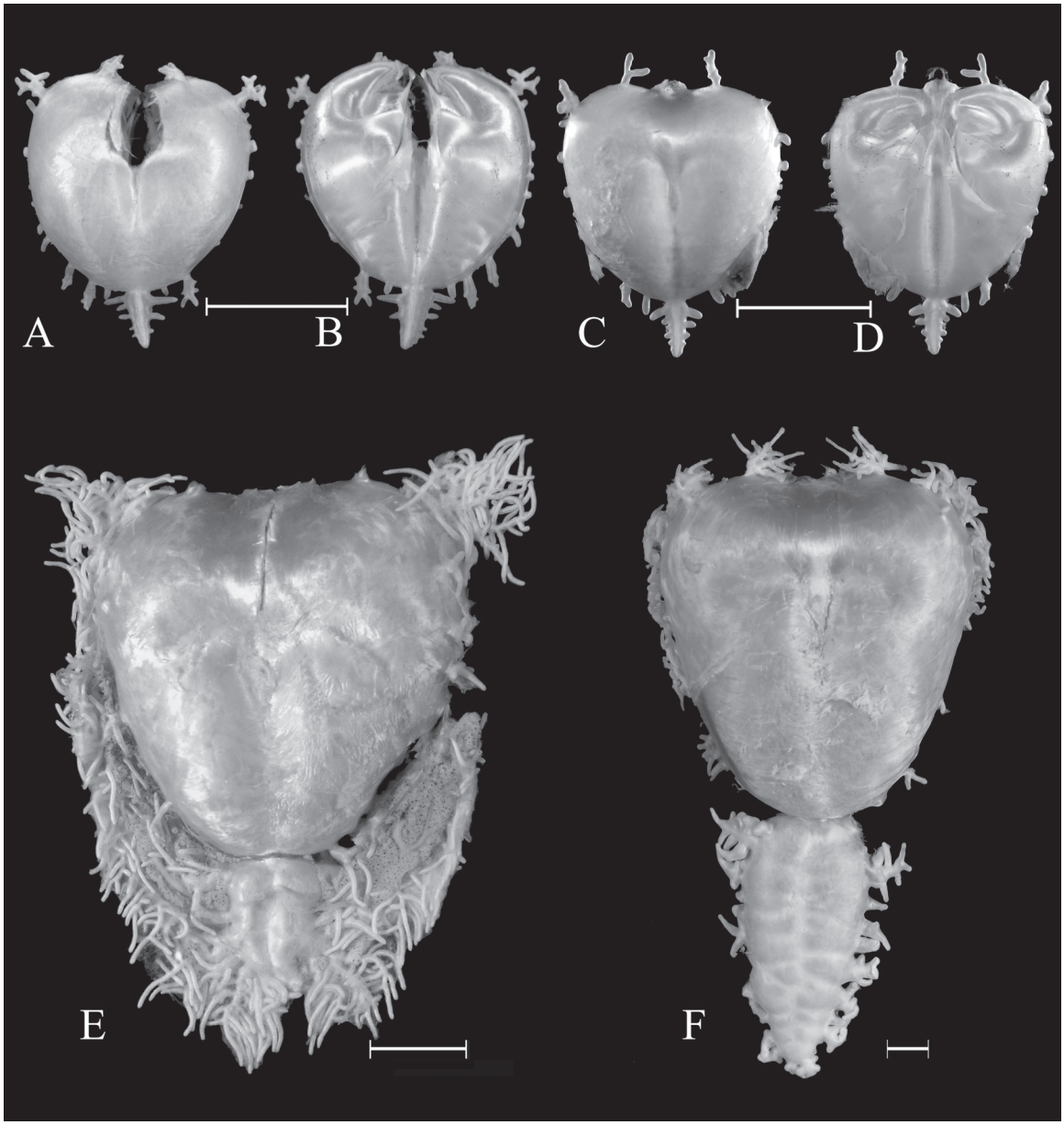
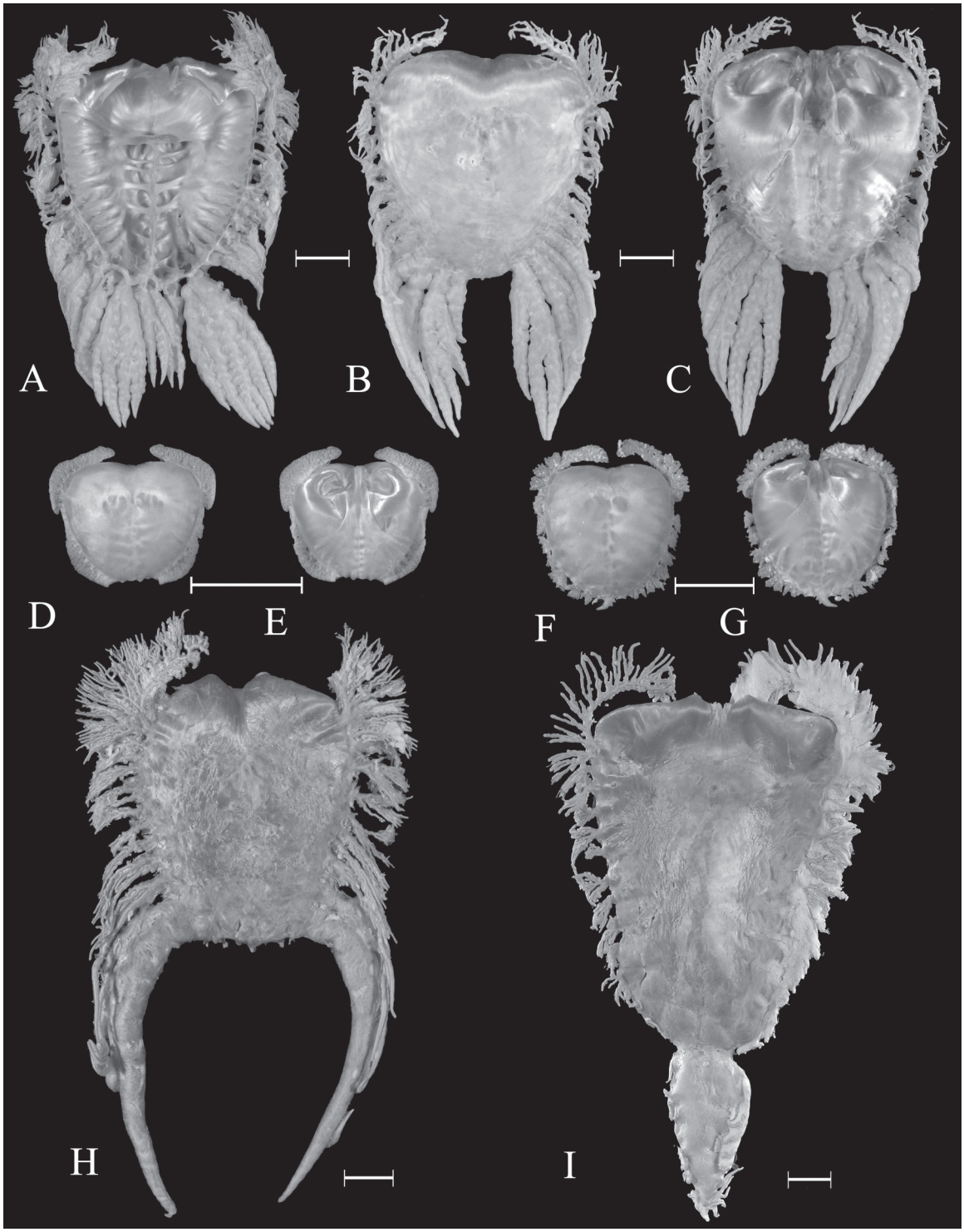


Fig. 7. Gas bladders in *Centrodoras* in ventral (A,C,E,F). A,B. *Centrodoras brachiatus*, MZUSP 55776, 74 mm SL. C,D. *C. brachiatus*, ANSP 181021, 83 mm SL. E. *C. brachiatus*, MZUSP 31306, 186 mm SL. F. *Centrodoras* cf. *hasemani*, MZUSP 91675, 202 mm SL. Scale bars equal 10 mm. Figs. 7C,D by T. Jones.

Fig. 8. (Facing Page) Gas bladders in *Pterodoras* in ventral (B,D,F,H,I) and dorsal (C,E,G) views and dorsal view of internal face of ventral wall (A). A–C. *Pterodoras granulosus*, MZUSP 38177, 143.3 mm SL (A) and 240.0 mm SL (B,C). D,E. *P. granulosus*, MZUSP 82995, 60.5 mm SL. F,G. *Pterodoras rivasi*, MZUSP 88609, 82.2 mm SL. H. *P. granulosus*, MZUSP 91441, 330 mm SL. I. *P. rivasi*, ANSP 177895, 336.1 mm SL (tissue surrounding diverticulae retained on left side). Scale bars equal 10 mm. Fig. 8I by T. Jones.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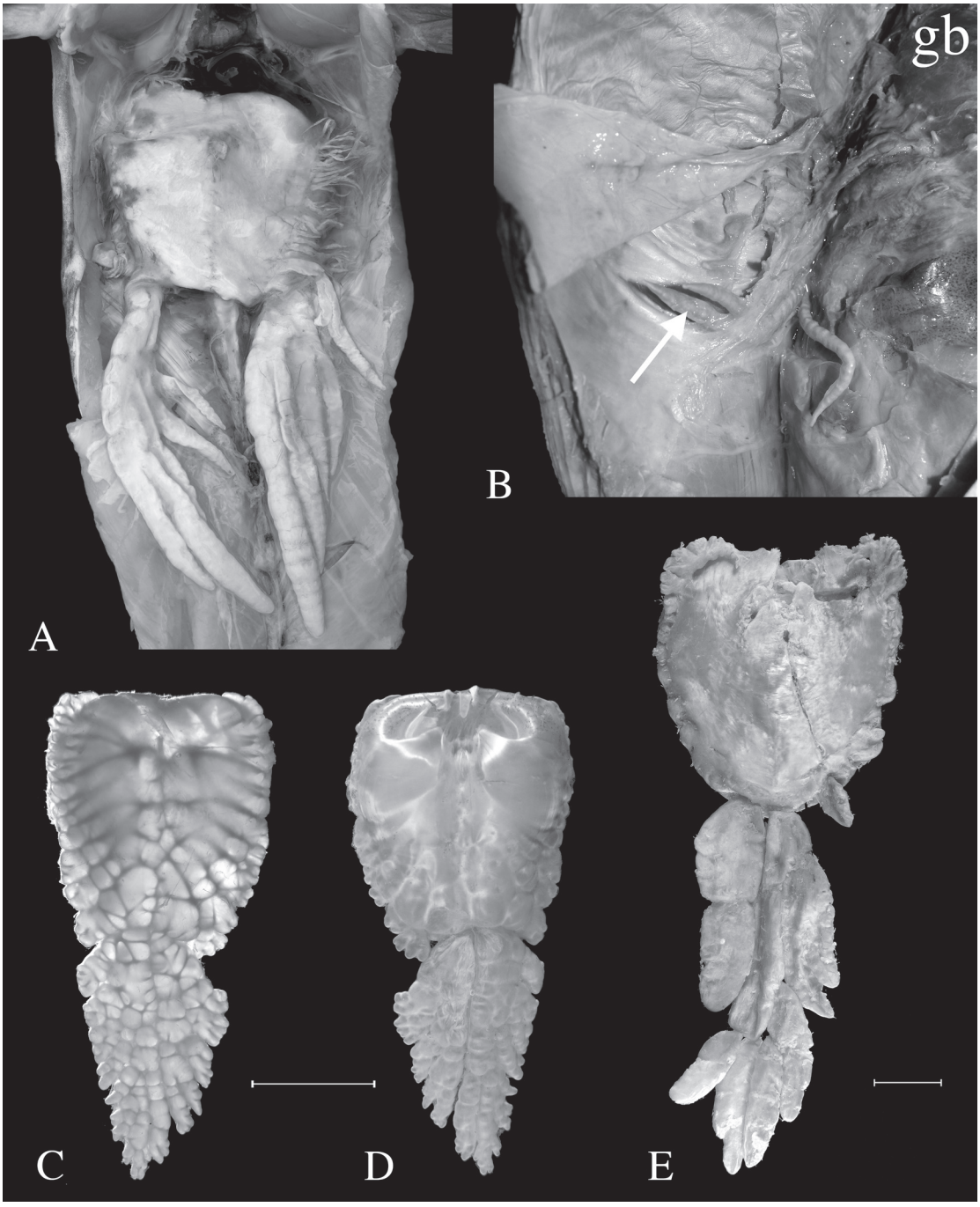


Fig. 9. Gas bladders in *Pterodoras granulosus* (A,B) and *Doraops zuloagai* (C–E) in ventral (A–C,E) and dorsal (B) views. A. Gas bladder *in situ*, ANSP 180883, 363 mm SL. B. Gas bladder diverticulae (arrow; anterior is up) between muscle layers, MZUSP 14048, 450 mm SL, gb = gas bladder. C,D. MCNG 33457, 103.8 mm SL. E. INHS 54804, 273 mm SL (market specimen). Scale bars equal 10 mm. Fig. 9E by T. Jones.

In *Doraops* the two enlarged posterior diverticula are partially subdivided by constrictions, and, as in *Lithodoras dorsalis* and *P. rivasi*, they are asymmetrical, one being longer and more branched than its counterpart.

Gas bladder in Orinocodoras *and* Rhinodoras (Fig. 10).—As hypothesized by Higuchi (1992), Birindelli (2006) and Birindelli et al. (2007), *Rhinodoras* is sister to the monotypic *Orinocodoras eigenmanni*. In *Orinocodoras* and all species of *Rhinodoras* the gas bladder is cordiform with paired terminal diverticula united and more or less equal (Fig. 10). The transverse portion of the T-shaped septum is strongly arched, and the view of the Müllerian windows is largely restricted to the anterior chamber. The internal longitudinal portion of the T-shaped septum is not straight but follows a shallow zigzag course, and is strengthened by trabeculae (Fig. 10D) similar to those found in *Doraops*, *Lithodoras*, *Megalodoras*, and *Pterodoras*. The attachment points of the internal trabeculae are visible externally giving the thin ventral wall of the bladder a honeycomb-like appearance.

In *Orinocodoras* (Figs. 10A–D), *R. dorbignyi* (Figs. 10E–H), and *R. thomersoni* (Fig. 10I), the terminal diverticula are medially united and expanded to form a secondary bladder in larger specimens. In the remaining species of *Rhinodoras* the terminal diverticula are lacking in small specimens (Fig. 10J) and weakly developed in larger specimens as short, medially united expansions of each posterior chamber (Figs. 10K–M). In *Orinocodoras* and all *Rhinodoras* except *R. thomersoni*, the posterolateral walls of the posterior chambers have a few small, blister-like swellings or short, rounded diverticula that become more developed in larger specimens.

Gas bladder in Oxydoras (Fig. 11).—*Oxydoras* contains three species all with simple barbels and a prominent conical snout. Morphological data (Eigenmann, 1925; Higuchi, 1992; Birindelli, 2006) support a sister-group relationship between *Oxydoras* and a monophyletic clade composed of all doradids with fimbriate barbels. This relationship, however, is not corroborated by available molecular data (Moyer et al., 2004; combined analysis of mitochondrial 12S and 16S rRNA and nuclear elongation factor-1 alpha genes) that group *Oxydoras* with *Doraops* + *Pterodoras*, taxa likewise with simple barbels.

The gas bladder in all three species of *Oxydoras* has a cordiform shape and an elongate posterior secondary bladder similar to *Platydoras* in that it is formed by the expansion of only one terminal diverticulum, its counterpart being absent (Figs. 11A,B,D–I). Unlike in *Platydoras*, the external walls of the main and secondary bladders are lined and presumably reinforced by trabeculae (Fig. 11H); and the lateral margins of both bladders often have low rounded tuberous swellings. The intersection of the T-shaped septum is aligned with the posterior margins of the Müllerian windows, which undergo a slight ontogenetic change in position. In juveniles (Figs. 11D,E), the windows are oblique, occupying the dorsoanterior position typical of most doradids. In larger specimens (Figs. 11A,B,F–I), the windows become more vertically aligned as they shift to a more anterior position.

Unique to *Oxydoras niger* (Amazon basin) and *O. sifontesi* (Orinoco basin) is the gradual ontogenetic enlargement of a thin bony nodule from the anterior face of the parapophysis of the sixth vertebrae in specimens greater than 200 mm SL (Fig. 11C). The paired nodules, filled with adipose tissue, expand ventrally into the anterior and posterior chambers aside the transverse portion of the internal septum, and thereby reduce the effective volume of the gas badder. The tunica externa of the gas bladder becomes thinner in the region of the expanding nodules and eventually forms a deep, rounded invagination that nearly reaches the bladder's ventral wall (Fig. 11I).

Gas bladder in fimbriate doradids except Leptodoras (Figs. 12–17).—Doradids with fimbriate barbels, including *Leptodoras oyakawai* but excluding its congeners (see next section), have a relatively large and more or less cordiform gas bladder. The greatest variation, both ontogenetic and interspecific, occurs in the development and location of diverticula (described below). The distal end of the Müllerian ramus is not flattened and disk shaped as in non-fimbriate doradids (except *Physopyxis*), but conical and invaginates the anterior chamber of the bladder (Fig. 12A). The anterior chamber is well developed and the Müllerian windows are positioned dorsoanteriorly, with their posterior margins aligned with the intersection of the T-shaped septum. In some small-sized species (e.g., *Trachydoras brevis*, Fig. 16F), there are paired patches of scattered chromatophores on the dorsal surface of the anterior chamber.

In *Doras*, the gas bladder walls are largely smooth except for a small singular terminal diverticulum in *D. carinatus*, *D. higuchii* and *D. micropoeus* (Figs. 12B–F) and paired diverticula that are separate and located posterolaterally in *D. phlyzakion* (Fig. 12G) or proximally conjoined with divergent tips and terminal in *D. zuanoni* (Fig. 12H). *Doras zuanoni* is unique among *Doras* in having an additional pair of diverticula, each one short, rounded and located on the anterolateral shoulder of the anterior chamber (Fig. 12H). In *D. carinatus*, *D. higuchii* and *D. micropoeus*, the single terminal diverculum extends from only one of the two posterior chambers and may be small (Fig. 12B) to rudimentary (Figs. 12C,E), or more

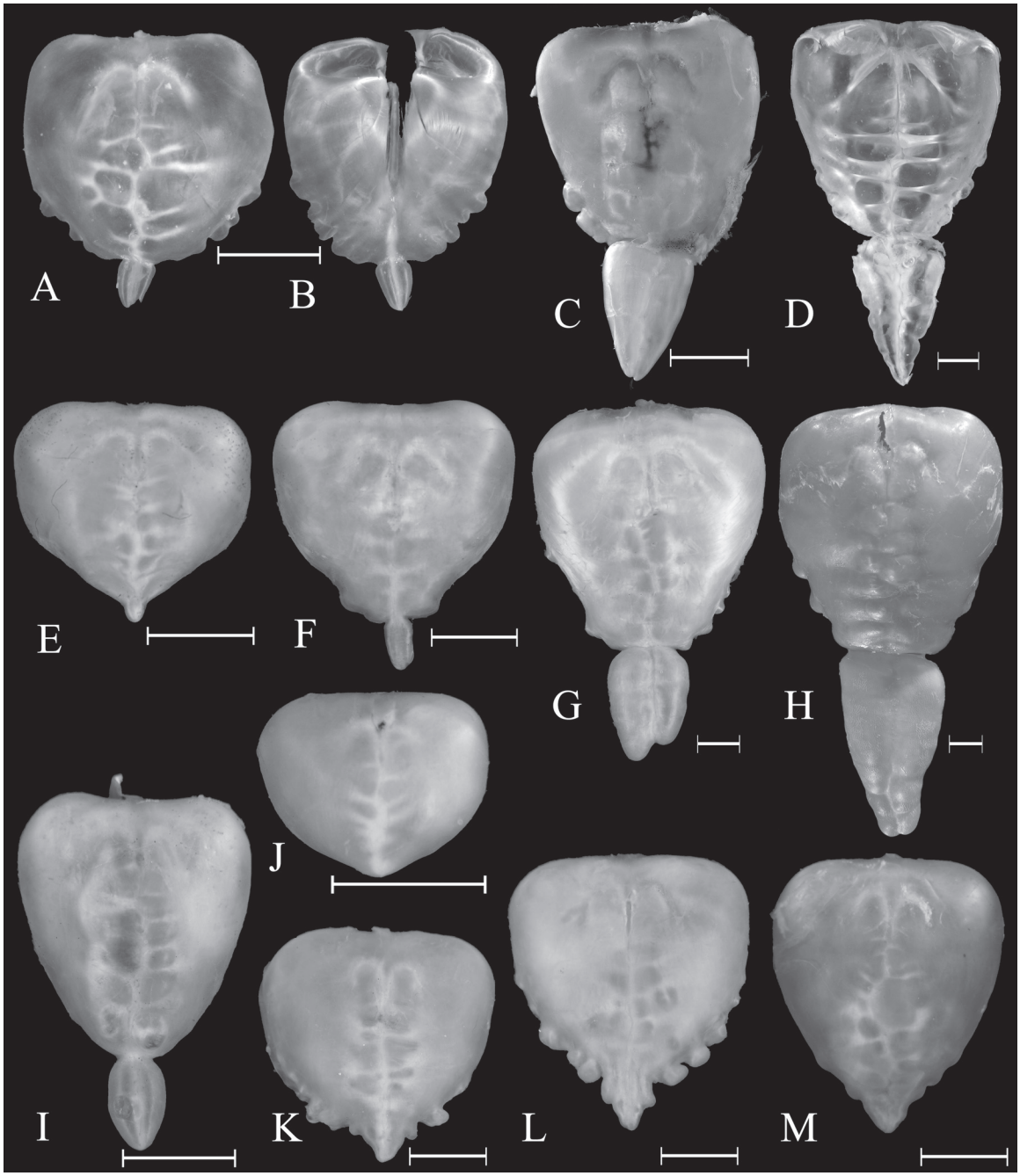


Fig. 10. Gas bladders in *Orinocodoras* and *Rhinodoras* in ventral view, except B (dorsal) and D (dorsal view of internal face of ventral wall). A,B. *Orinocodoras eigenmanni*, INHS 40330, 57.8 mm SL. C. *O. eigenmanni*, ANSP 180891, 135 mm SL. D. *O. eigenmanni*, AUM 5318, 119.6 mm SL. E. *Rhinodoras dorbignyi*, MZUSP 61456, 70.4 mm SL. F. *R. dorbignyi*, MZUSP 62683, 89.9 mm SL. G. *R. dorbignyi*, MZUSP 78461, 168 mm SL. H. *R. dorbignyi*, ANSP 179535, 194 mm SL. I. *Rhinodoras thomersoni*, MHNLS 0109, 45.5 mm SL. J. *Rhinodoras boehlkei*, MZUSP 86814, 41 mm SL. K. *R. boehlkei*, MZUSP 86812, 95 mm SL. L. *Rhinodoras gallagheri*, 86806, 93.2 mm SL. M. *Rhinodoras* sp. (Tocantins), INPA 22056, 82.7 mm SL. Scale bar equals 5 mm. Fig. 10C by T. Jones.

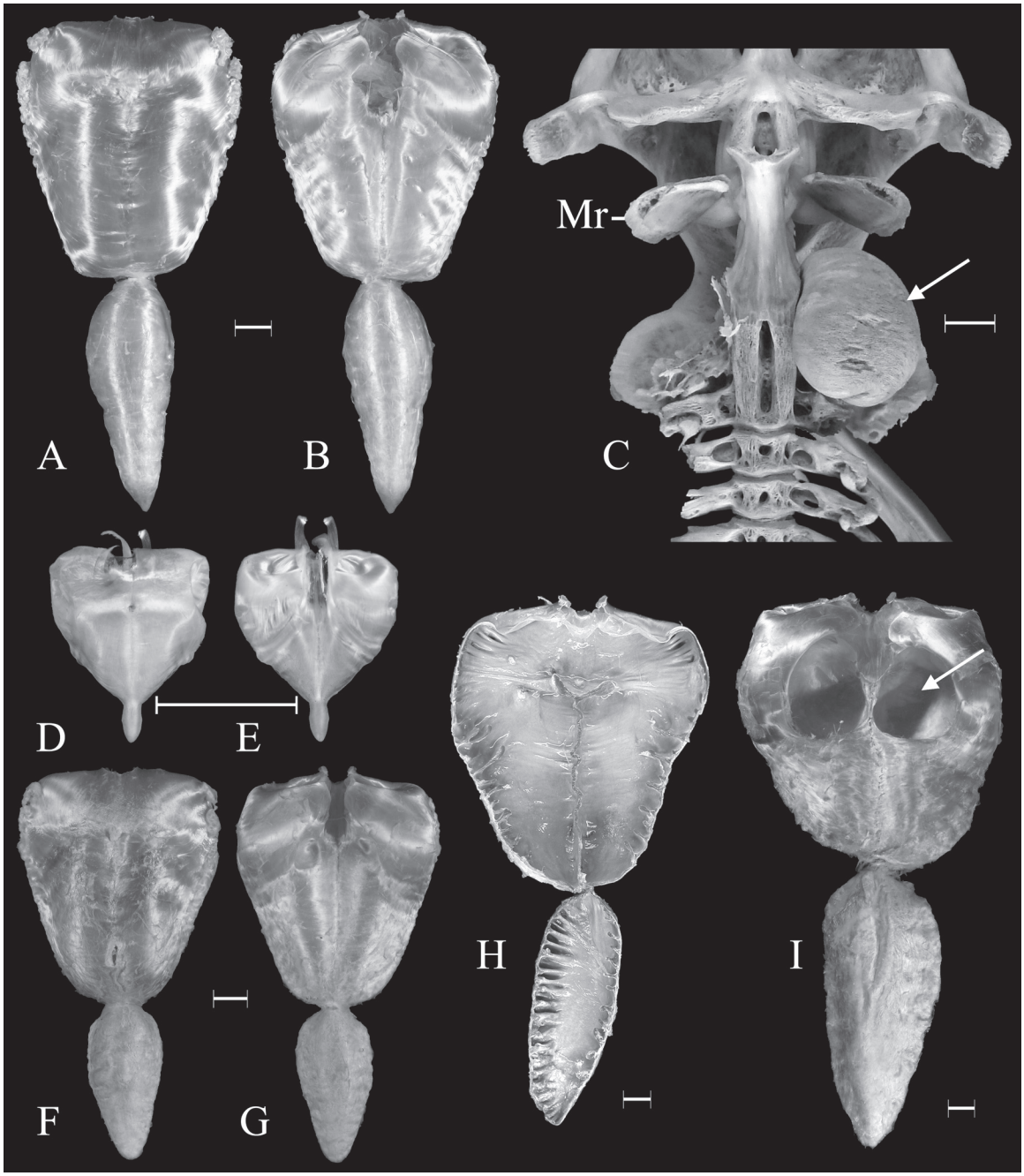


Fig. 11. Gas bladders and anteriormost vertebrae in *Oxydoras* in ventral (A,C,D,F) and dorsal (B,E,G,I) views and dorsal view of internal face of ventral walls of primary and secondary bladders (H). A,B. *Oxydoras kneri*, MZUSP 14847, 393 mm SL. C. Anteriormost vertebrae in *Oxydoras niger*, MZUSP 91654, 550 mm SL, in ventral view showing left bony capsule (arrow; right capsule broken away). D,E. *O. niger*, MZUSP 57320, 70 mm SL. F,G. *O. niger*, MZUSP 13366, 315 mm SL. H. *O. niger*, MZUSP 91654, 550 mm SL. I. *O. niger*, MZUSP 9079, 550 mm SL, showing rounded invaginations for receiving bony capsules (arrow on right invagination). Mr = Müllerian ramus. Scale bar equals 10 mm.

elongated and constricted basally to form a small, slender secondary bladder without internal septum (Figs. 12D,F).

In the monotypic *Anduzedoras oxyrhynchus*, the posterior chambers are somewhat reduced in juveniles (Figs. 13A,B) and become more fully expanded in adults (Fig. 13C,D). There is also ontogenetic variation in the development of diverticula. In small specimens (e.g., 34 mm SL; Fig. 13A), two short, rounded diverticula occur on each side of the anterior chamber, one on the anterolateral shoulder, the other posterolaterally near the transition to the posterior chamber. In larger specimens, these diverticula become gradually more elongated and branched and additional diverticula arise along the intervening lateral margin of the anterior chamber and the lateral and posterior margins of the posterior chambers (Figs. 13B–D). In *Anduzedoras*, the anteromedial wall of the anterior chamber is covered by paired capsule-like bony expansions of the anteriormost vertebrae, a condition found also in *Leptodoras* (see Fig. 6 in Birindelli et al., 2008:470).

In *Hassar* (Figs. 13E–L), there is significant interspecific variation in the development of diverticula. In *H. orestis* (Figs. 13E,F) and *H. wilderi* (Figs. 13G,H), bundles of diverticula are present along the anterior, lateral and posterior margins of the entire bladder and these diverticula become thinner and more branched in larger specimens. Also, there is a tendency for the bundles of diverticula to be more finely subdivided in *H. orestis* compared to *H. wilderi*. In both species, each posterior chamber extends posteriorly into a short terminal diverticulum that is medially united with its pair and may have smaller lateral diverticula. In *H. affinis*, the walls of the gas bladder are entirely smooth in small specimens (e.g., 54.4 mm SL; Fig. 13I), and in larger specimens have only two short rounded diverticula on each side of the anterior chamber (Figs. 13J–L) as described for juvenile *Anduzedoras*.

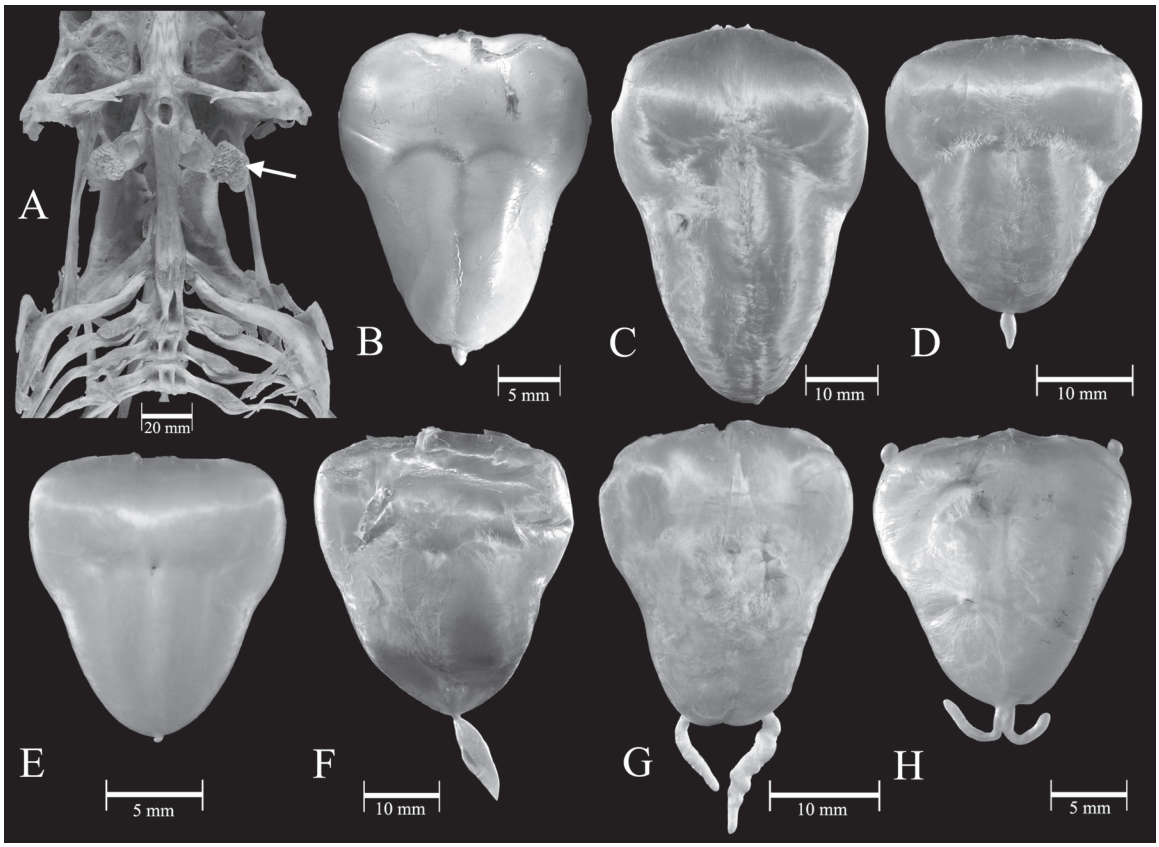


Fig. 12. A. Anteriormost vertebrae in *Doras carinatus*, AMNH 91330SD, ca. 550 mm SL, showing modified, conical Müllerian ramus (arrow). B–H. Gas bladders in *Doras* in ventral view. B. *D. carinatus*, ANSP 177276, 124.5 mm SL. C. *D. carinatus*, AMNH 96798, 302 mm SL. D. *D. higuchii*, ANSP 181057, 160 mm SL. E. *D. higuchii*, INPA 5568, 83.8 mm SL. F. *D. micropoeus*, ANSP 178703, 222 mm SL. G. *D. phlyzakion*, ANSP 181055, 148 mm SL. H. *D. zuanoni*, MZUSP 96328, 96 mm SL.

In *Hemidoras* and *Opsodoras* (Fig. 14), the anterior, lateral and posterior margins of the gas bladder have diverticula that become thinner and more branched in larger specimens as in *Hassar orestis* and *H. wilderi*. In *Hemidoras stenopeltis* (Figs. 14A–D) and *Opsodoras stuebelii* (Figs. 14I,J), each posterior chamber extends posteriorly into a short terminal diverticulum that is medially united with its pair and may have smaller lateral diverticula, again as in *Hassar orestis* and *H. wilderi*. In *Hemidoras morrisi* (Figs. 14E–H) and *Opsodoras morei* (Figs. 14K,L), these terminal diverticula are generally more elongate.

In *Nemadoras* (Fig. 15), the development of diverticula shows the greatest degree of variation. The diverticula are least developed in *N. leporhinus* from the Amazon basin (Fig. 15G), and largely restricted to the anterolateral shoulder and posterolateral portion of the anterior chamber. In *N. leporhinus* from the Orinoco basin (Figs. 15H,L), *N. ternetzi* (Fig. 15E) and *Nemadoras* sp. (Fig. 15F), the

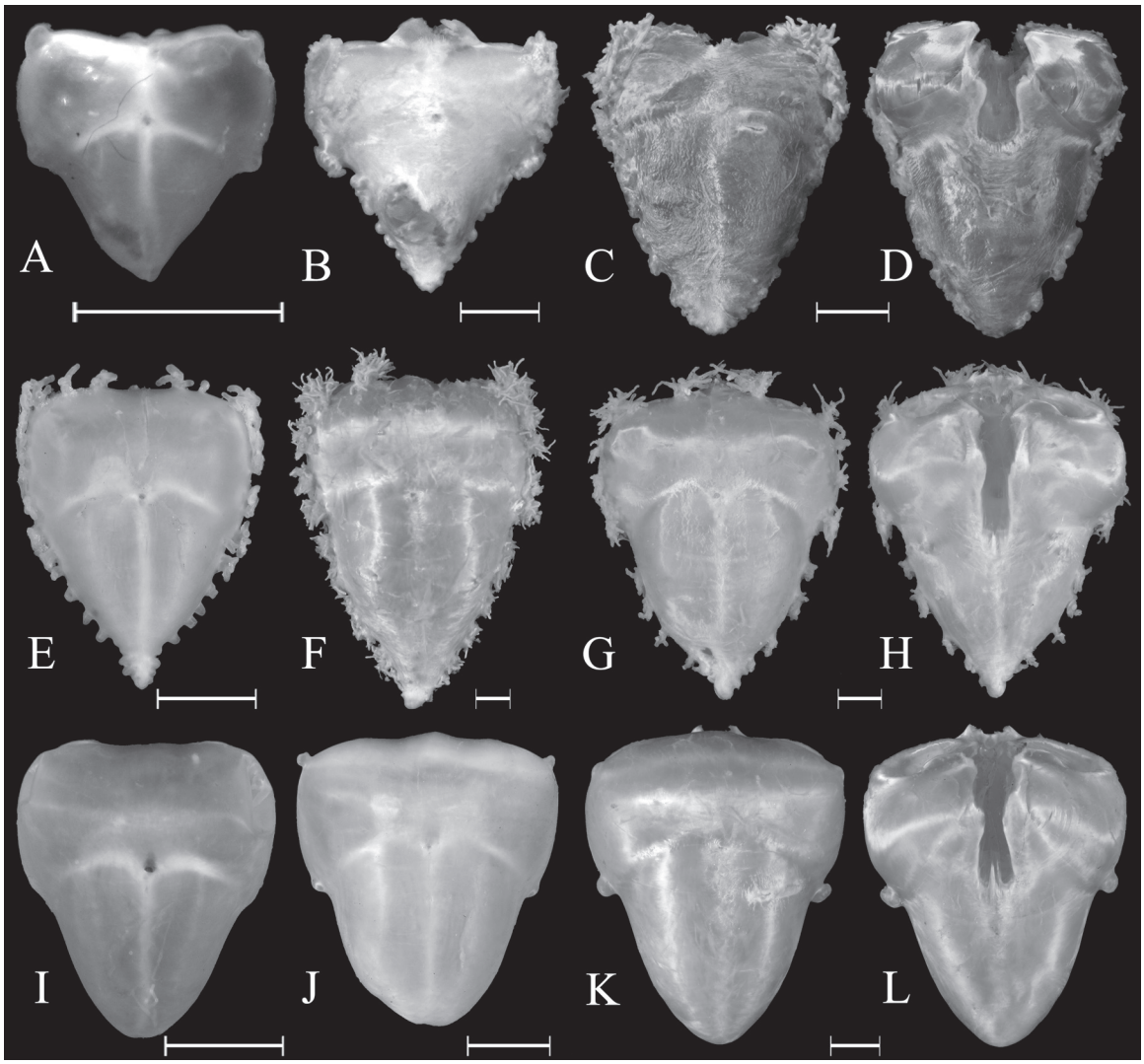


Fig. 13. Gas bladders in *Anduzedoras* (A–D) and *Hassar* (E–L) in ventral (A–C,E–G,I–K) and dorsal (D,H,L) views. A. *Anduzedoras oxyrhynchus*, MZUSP 29028, 34 mm SL. B. *A. oxyrhynchus*, MZUSP 29021, 116 mm SL. C,D. *A. oxyrhynchus*, MZUSP 91454, 228 mm SL. E. *Hassar orestis*, MZUSP 6991, 71 mm SL. F. *H. orestis*, MZUSP 32542, 220 mm SL. G,H. *Hassar wilderi*, MZUSP 63148, 148.8 mm SL. I. *Hassar affinis*, MZUSP 90583, 54.4 mm SL. J. *H. affinis*, MZUSP 74890, 85.9 mm SL. K,L. *H. affinis*, MZUSP 43604, 228 mm SL. Scale bars equal 5 mm.

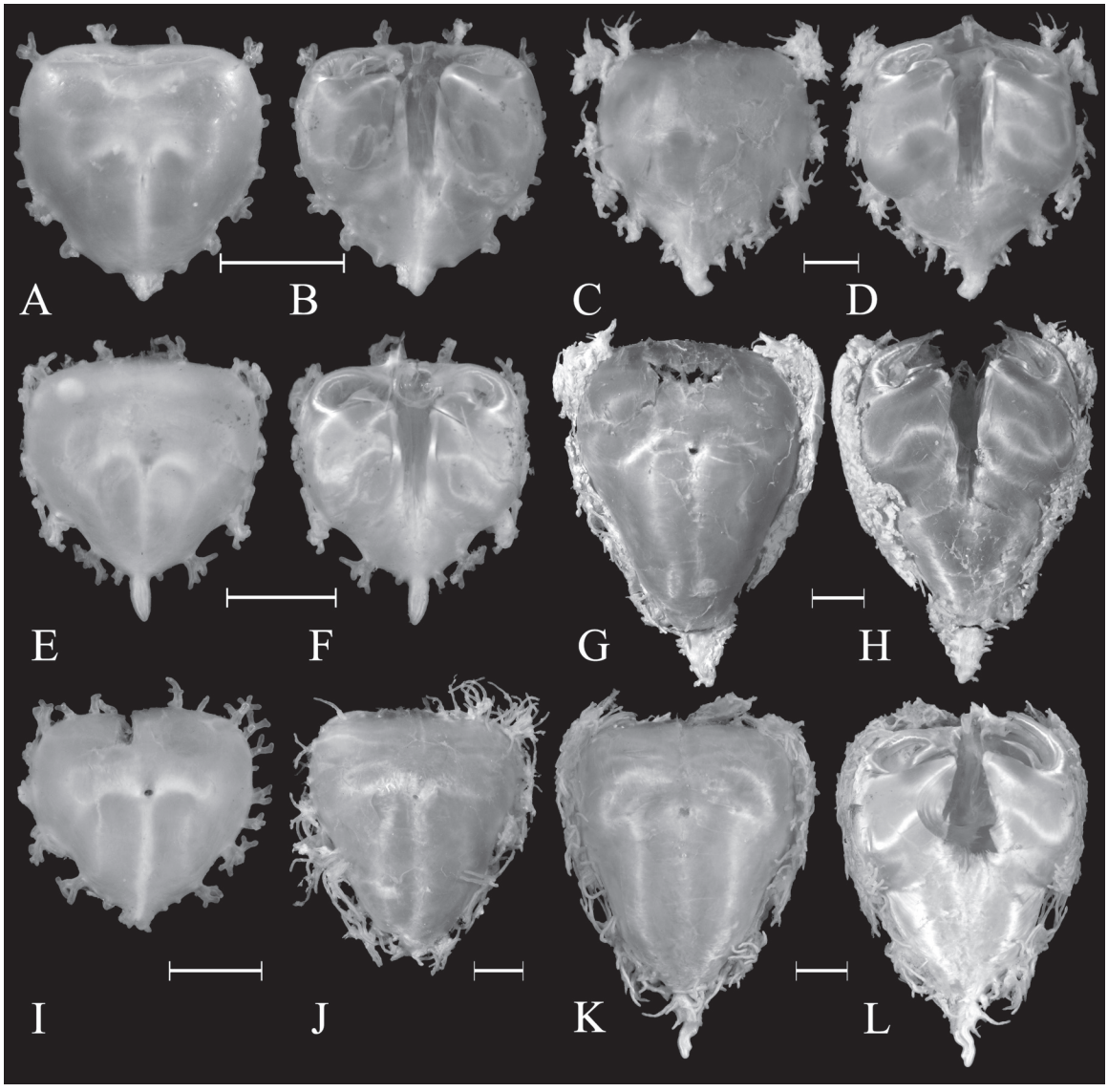
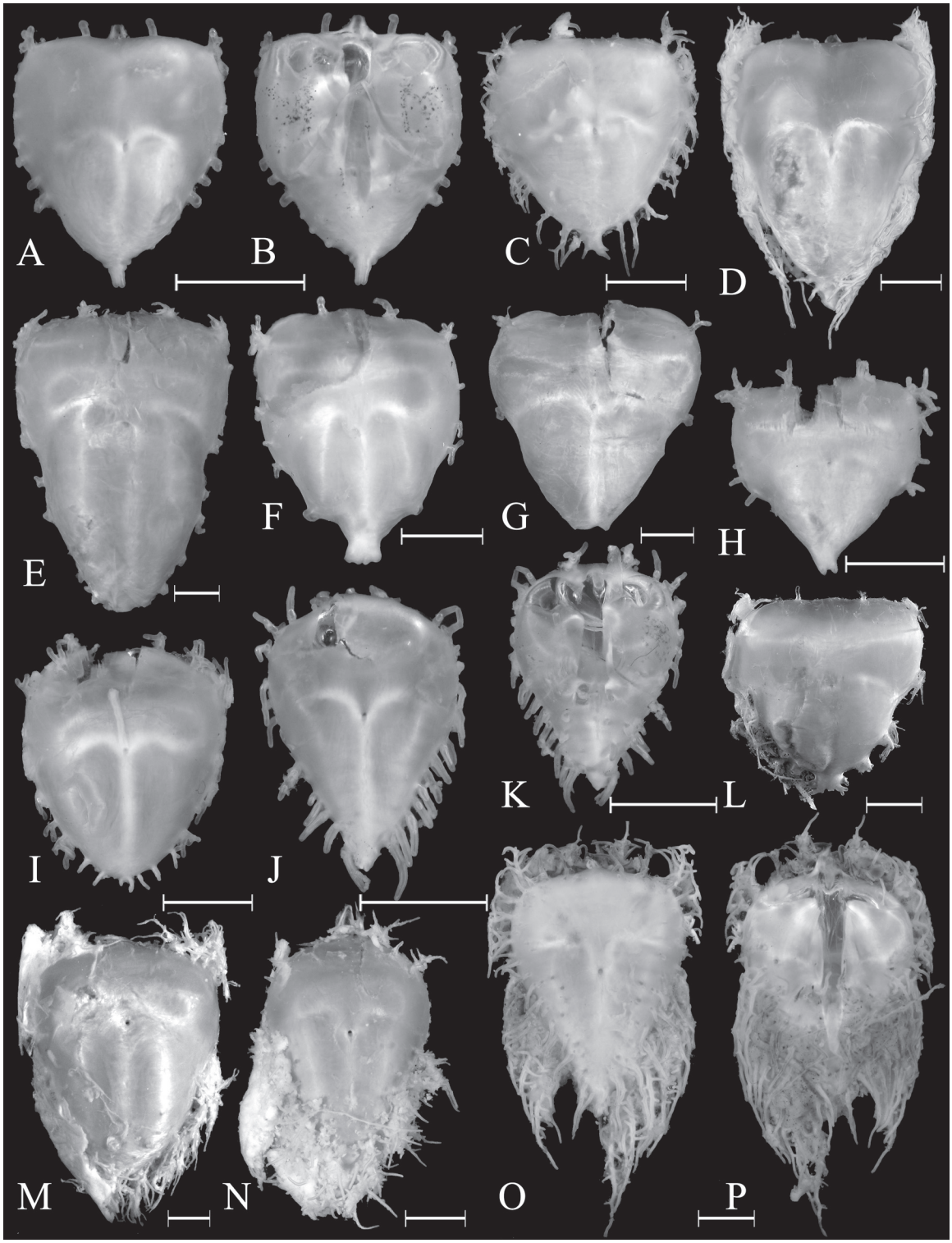


Fig. 14. Gas bladders in *Hemidoras* (A–H) and *Opsodoras* (I–L) in ventral (A,C,E,G,I–K) and dorsal (B,D,F,H,L) views. A,B. *Hemidoras stenopeltis*, MZUSP 7612, 55.3 mm SL. C,D. *H. stenopeltis*, MZUSP 42772, 108.7 mm SL. E,F. *Hemidoras morrisi*, MZUSP 56044, 58.2 mm SL. G,H. *H. morrisi*, MZUSP 28378, 157 mm SL. I. *Opsodoras stubelii*, MZUSP 56879, 64.5 mm SL. J. *O. stubelii*, MZUSP 26316, 102.3 mm SL. K,L. *Opsodoras morei*, MZUSP 31526, 137 mm SL. Scale bars equal 5 mm.

Fig. 15. (Facing Page) Gas bladders in *Nemadoras* in ventral (A,C–J,L–O) and dorsal (B,K,P) views. A,B. *N. trimaculatus*, MZUSP 56706, 46.9 mm SL. C. *N. trimaculatus*, MZUSP 53834, 75.6 mm SL. D. *N. trimaculatus*, MZUSP 92206, 93.9 mm SL. E. *N. ternetzi*, MZUSP 57682, 110.9 mm SL. F. *Nemadoras* sp., MZUSP 56004, 68.2 mm SL. G. *N. leporhinus*, MZUSP 95617, 138.1 mm SL. H. *N. leporhinus*, MZUSP 95617, 89 mm SL. I. *N. humeralis*, MZUSP 55996, 60.1 mm SL. J,K. *N. elongatus*, MZUSP 56021, 46.1 mm SL. L. *N. leporhinus*, ANSP 179204, 113.4 mm SL. M. *N. humeralis*, MZUSP 56014, 103.8 mm SL. N. *N. elongatus*, MZUSP 56013, 99.2 mm SL. O,P. *N. hemipeltis*, MZUSP 56688, 81.8 mm SL. Scale bars equal 5 mm.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diverticula are relatively short and spaced around the anterior, lateral and posterior margins of the bladder. In *N. trimaculatus* (Figs. 15A-D), the diverticula are moderately elongate and more continuously distributed. The continuity, length and branching of diverticula gradually increases in *N. humeralis* (Figs. 15I,M), *N. elongatus* (Figs. 15J,N) and *N. hemipeltis* (Figs. 15O,P), respectively. Furthermore in *N. elongatus* and *N. hemipeltis*, and to a lesser degree large specimens of *N. humeralis*, there are additional smaller diverticula on the dorsal surface of the posterior chambers; and in *N. hemipeltis* and to a lesser degree *N. elongatus*, additional small diverticula are present towards the lateral margins of the ventral surface of the posterior chambers. The latter two species also are distinguished by having the transverse portion of internal T-shaped septum forming a deep, medial, V-shaped notch pointed towards the pneumatic duct (Figs. 15J,N,O). In all species of *Nemadoras*, each posterior chamber usually extends posteriorly into a short terminal diverticulum that is medially united with its pair and may bear smaller lateral diverticula. The distal tips of the terminal diverticula are either weakly separated or completely conjoined.

In *Trachydoras* (Fig. 16), the greatest variation is in the development of the paired terminal diverticula. In *Trachydoras* sp. (Fig. 16A), the terminal diverticula are extremely asymmetrical with one side more elongate and its counterpart reduced and completely united. In *T. microstomus* (Fig. 16B), the terminal diverticula are more or less symmetrical and united with conjoined distal tips. In *T. brevis* and *T. nattereri*, the terminal diverticula are symmetrical to weakly asymmetrical, united proximally, and with distal tips weakly divergent in juveniles (Figs. 16E,F) and strongly divergent, recurved anteriorly in adults (Figs. 16G,H). In *T. paraguayensis*, the terminal diverticula are variable: entirely absent (Figs. 16I,J) or weakly developed as separate rounded swellings (Fig. 16K) to distinct, proximally united with distal tips diverging laterally in opposite directions (Fig. 16L). In *T. steindachneri*, the terminal diverticula are moderately developed and more or less symmetrical with distal tips weakly separated (Fig. 16M) to completely conjoined and bearing slender lateral diverticula in larger specimens (Fig. 16N). In *T.* cf. *steindachneri* (Figs. 16C,D,O,P), the terminal diverticula are well developed, proximally united with distal tips diverging laterally. In all species except *Trachydoras* sp., there is a diverticulum on each anterolateral shoulder of the anterior chamber that may simple or branched and relatively short (*T. microstomus*, *T. brevis*, *T. nattereri*, *T. paraguayensis*, *T.* cf. *steindachneri*) or elongate (*T. steindachneri*). *Trachydoras microstomus* (Fig. 16B) and small *T.* cf. *steindachneri* (e.g., 43.6 mm SL; Figs. 16C,D) also have a rounded swelling or short diverticulum on each posterolateral portion of the anterior chamber. *Trachydoras steindachneri* (Figs. 16M,N) and large *T.* cf. *steindachneri* (e.g., 65.2–76.6 mm SL; Figs. 16O,P) have many diverticula along the lateral margins of the anterior and posterior chambers that become more elongate and branched in larger specimens.

Three related nominal species with fimbriate barbels are currently *incertae sedis* in Doradidae (Sabaj and Ferraris, 2003): *Doras punctatus*, *Doras fimbriatus* and *Oxydoras eigenmanni*. In *Doras punctatus* (Figs. 17A–D) the walls of the gas bladder are completely smooth except for a distinct pair of terminal diverticula that may be symmetrical or asymmetrical. The terminal diverticula are united proximally with distal tips becoming more divergent and sometimes recurved anteriorly in larger specimens. In *D. fimbriatus* (Figs. 17E-H), the gas bladder has short, slender, simple or weakly branched diverticula spaced along the anterior, lateral and posterior margins, and the paired terminal diverticula are weakly developed. The gas bladder in *Oxydoras* cf. *eigenmanni* (Amazon basin; Figs. 17I–L) is similar to that of *D. fimbriatus* except the terminal diverticula are lacking or indistinguishable from the other diverticula. The gas bladder in *O. eigenmanni* (Paraná-Paraguay basin; Figs. 19M–P) differs from the aforementioned species in that the walls are entirely smooth except for a pair of slender diverticula, one on each anterolateral shoulder of the anterior chamber, that may become weakly branched in larger specimens, and the occasional occurrence of a second pair of diverticula on the anterior wall.

Reduced gas bladders in Leptodoras *and* Rhynchodoras.—In species of *Rhynchodoras* and *Leptodoras*, except *L. oyakawai*, the gas bladder has thicker walls and is significantly reduced, occupying a relatively small space in the body cavity. In *R. xingui* (Figs. 18A,B) and *R. castilloi* (Figs. 18C,D), the gas bladder is extremely short (wider than long) and without posterior diverticula. The gas bladder in *R. woodsi* (Figs. 18E–H) differs in having a pair of large, separate, horn-like posterior diverticula, one extended from each posterior chamber, that become longer in larger specimens. The gas bladder in all species of *Leptodoras* except *L. oyakawai* (Figs. 18M-O) similarly have posteriorly directed horn-like diverticula, but differ in having two additional pairs of diverticula on the anterior chamber, one on the anterolateral shoulder and the other posterolaterally. Furthermore, in all species of *Leptodoras* except *L. oyakawai*, the anteromedial wall of the gas bladder is covered by paired, deeply concave, capsule-like bony expansions of the anteriormost vertebrae (Fig. 18M-O).

The gas bladder in *Leptodoras oyakawai* (Figs. 18I–L) is unique among its congeners as it lacks diverticula and the anteromedial wall is covered by paired, shallow

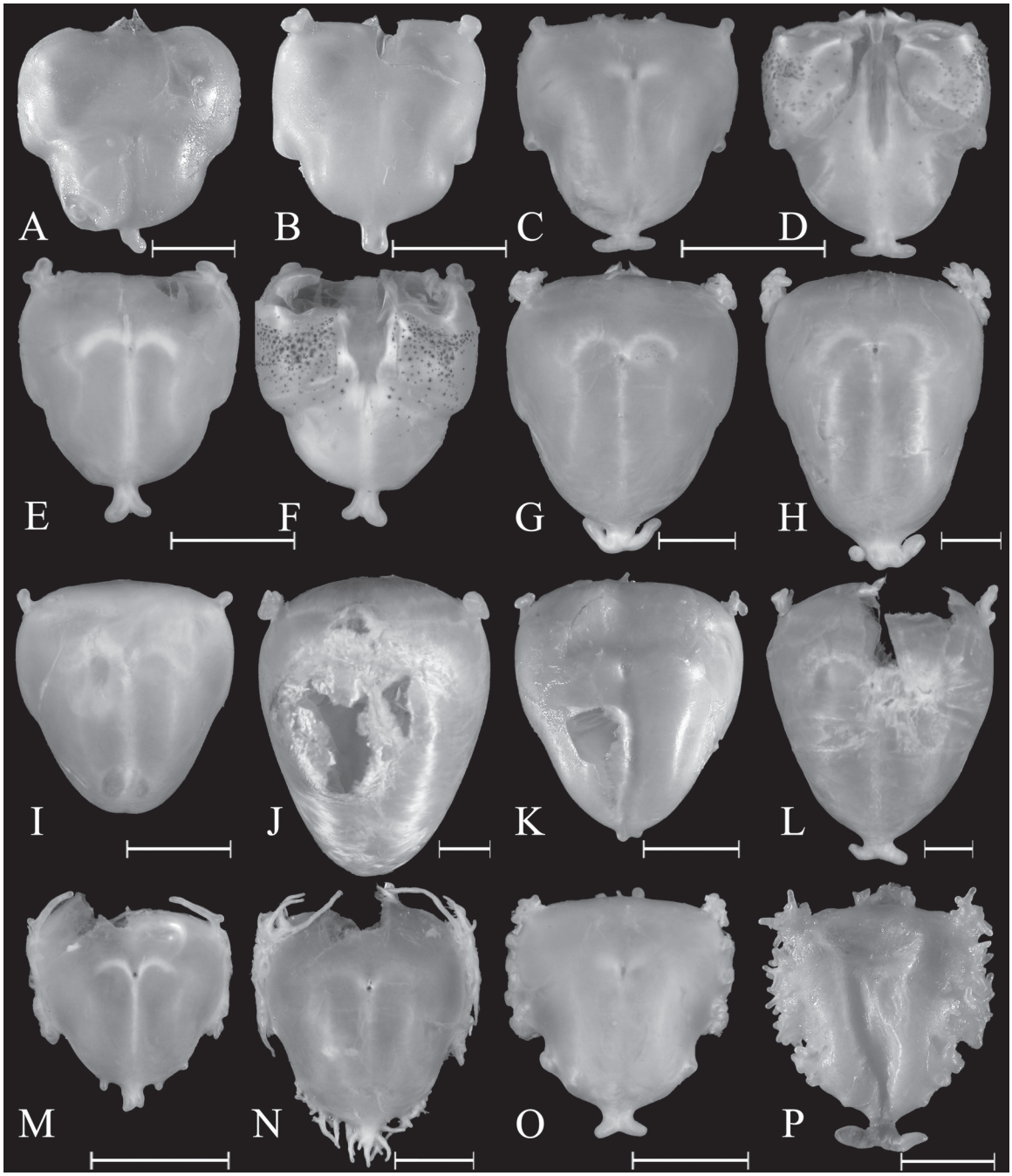

Fig. 16. Gas bladders in *Trachydoras* in ventral (A–C,E,G–P) and dorsal (D,F) views. A. *Trachydoras* sp., ANSP 161518, 71.2 mm SL. B. *T. microstomus*, ANSP 180184, 50.8 mm SL. C,D. *T.* cf. *steindachneri*, MZUSP 57703, 43.6 mm SL. E,F. *T. brevis*, MZUSP 93374, 46.5 mm SL. G. *T. brevis*, MZUSP 56713, 66.1 mm SL. H. *T. nattereri*, MZUSP 31703, 99.3 mm SL. I. *T. paraguayensis*, MZUSP 48315, 54.3 mm SL. J. *T. paraguayensis*, MZUSP 40081, 101 mm SL. K. *T. paraguayensis*, ANSP 178699, 79.2 mm SL. L. *T. paraguayensis*, MZUSP 29047, 114.2 mm SL. M. *T. steindachneri*, MZUSP 62696, 38.7 mm SL. N. *T. steindachneri*, MZUSP 62696, 72 mm SL. O. *T.* cf. *steindachneri*, MZUSP 57703, 76.6 mm SL. P. *T.* cf. *steindachneri*, ANSP 180175, 65.2 mm SL. Scale bars equal 5 mm.

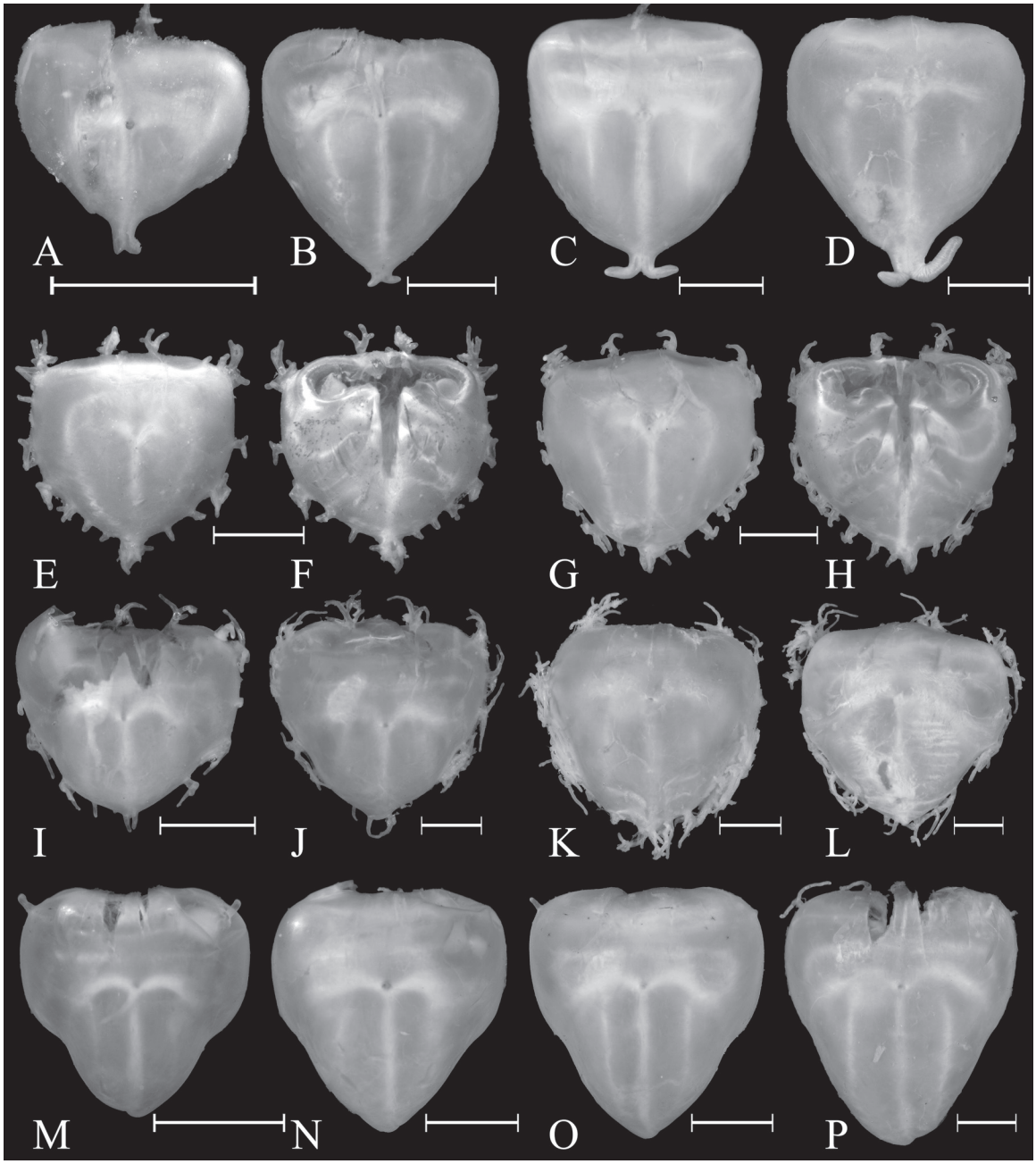

Fig. 17. Gas bladders in Doradidae *incertae sedis* in ventral (A–E,G,I–P) and dorsal (F,H) views. A. *Doras punctatus*, MZUSP 26265, 34.1 mm SL. B. *D. punctatus*, NUP 3542, 65.4 mm SL. C. *D. punctatus*, MZUSP 95000, 65.8 mm SL. D. *D. punctatus*, MZUSP 7839, 72.6 mm SL. E,F. *Doras fimbriatus*, MZUSP 55833, 42.6 mm SL. G–H. *D. fimbriatus*, MZUSP 55833, 62 mm SL. I. *Oxydoras* cf. *eigenmanni*, MZUSP 7543, 51.2 mm SL. J. *O.* cf. *eigenmanni*, MZUSP 7543, 73 mm SL. K. *O.* cf. *eigenmanni*, MZUSP 56699, 84.7 mm SL. L. *O.* cf. *eigenmanni*, MZUSP 84665, 85.7 mm SL. M. *O. eigenmanni*, MZUSP 95024, 38.3 mm SL. N. *O. eigenmanni*, MZUSP 44423, 62 mm SL. O. *O. eigenmanni*, MZUSP 95024, 65.3 mm SL. P. *O. eigenmanni*, MZUSP 38176, 85.5 mm SL. Scale bars equal 5 mm.

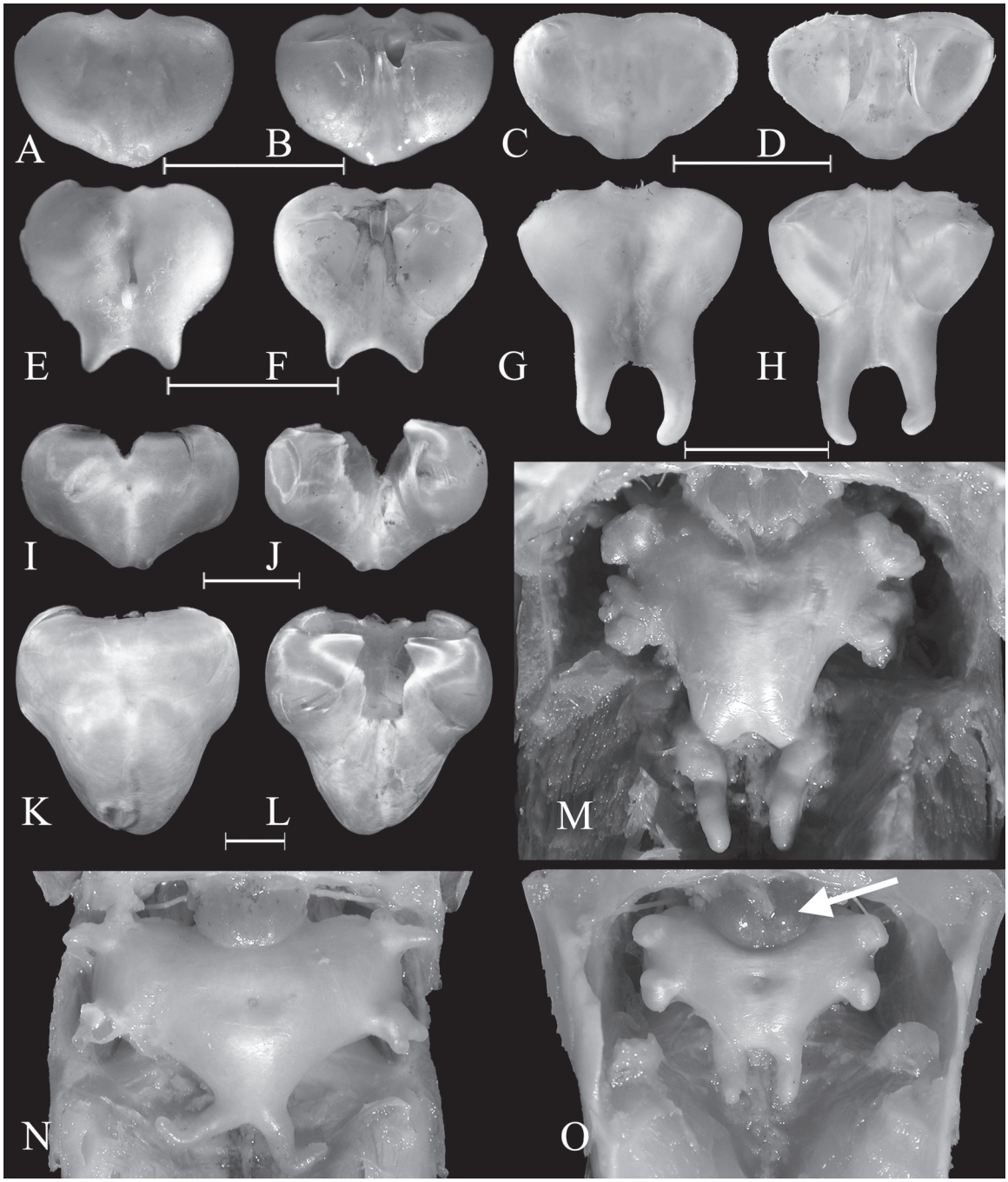

Fig. 18. Gas bladders in *Rhynchodoras* (A–H) and *Leptodoras* (I–O) in ventral (A,C,E,G,I,K,M–O) and dorsal (B,D,F,H,J,L) views. A,B. *Rhynchodoras xingui*, SMF 5282, 44.5 mm SL. C,D. *Rhynchodoras castilloi*, ANSP, 181181, 58.3 mm SL. E,F. *Rhynchodoras woodsi*, ROM 62601, 44.2 mm SL. G,H. *R. woodsi*, ANSP 181042, 72.5 mm SL. I,J. *Leptodoras oyakawai*, MZUSP 87028, 54 mm SL. K,L. *L. oyakawai*, MZUSP 97395, 121.9 mm SL. M. *Leptodoras praelongus*, ANSP 162463, 142 mm SL; N. *Leptodoras juruensis*, INHS 39465, 117.4 mm SL; O. *Leptodoras cataniai*, INHS 39814, 111.1 mm SL, showing the capsule-like bony expansion of the anteriormost vertebrae (arrow). Scale bars equal 5 mm.

cup-like (vs. deep capsule like) bony expansions of the anteriormost vertebrae (see Birindelli et al., 2008, for more complete description). In small specimens (Figs. 18I,J) the gas bladder is much wider than long, and its shape resembles that of *Rhynchodoras xingui* and *R. castilloi*. In larger specimens (Figs. 18K,L) the posterior chambers become more elongated and the overall shape of the gas bladder more closely resembles that of fimbriate doradids with normal-sized bladders.

DISCUSSION

Doradidae exhibit a tremendous amount of variation in the gross morphology of the gas bladder that may be unparalleled among catfishes. At one end of the spectrum are taxa (e.g., *Centrochir*, *Franciscodoras*, *Kalyptodoras*, *Wertheimeria*) with an unmodified and presumably primitive gas bladder characterized by its relatively large size, cordiform shape, and smooth walls. In other taxa the large, cordiform main bladder is retained, but modified by the addition of a secondary terminal bladder formed by the posterior expansion of one (e.g., *Oxydoras*, *Platydoras*, *Doras micropoeus*) or both posterior chambers (*Orinocodoras*, *Rhinodoras dorbignyi*, *R. thomersoni*), the latter accompanied by an internal longitudinal septum and the addition of blister-like swellings or short rounded diverticula along the posterolateral margins of the posterior chambers. Other taxa with a septate secondary bladder have further modifications involving the addition of diverticula to the main and secondary bladders (e.g., *Centrodoras*, *Lithodoras*, *Megalodoras*, *Pterodoras rivasi*). In fimbriate doradids the secondary bladder is absent (except in some specimens of *Doras micropoeus*) and often replaced by paired diverticulum-like expansions of the posterior chambers that may be completely separate (*Doras phlyzakion*), completely conjoined (e.g., *Hemidoras*, *Opsodoras*) or proximally conjoined with divergent distal tips (e.g., *Doras zuanoni*, *Doras punctatus*, most species of *Trachydoras*). Except for these paired posterior diverticula, the walls of the gas bladder in fimbriate doradids ranges from completely smooth (most species of *Doras* and unrelated *incertae sedis* species *Doras punctatus*) to profusely ornamented with numerous elongate and branched diverticula (e.g., *Nemadoras elongatus*, *N. hemipeltis*). Finally two doradid lineages (i.e., *Leptodoras*, *Rhynchodoras*) have converged upon a similar morphology wherein the gas bladder has thick walls and is significantly reduced in size. Furthermore, within these lineages certain species have further converged upon having a pair of large, separate, horn-like posterior diverticula, one extended from each posterior chamber. Similar morphologies are found in some species of *Ageneiosus* (Auchenipteridae, the sister family of Doradidae), wherein the gas bladder is reduced and with a pair of posteriorly directed horn-like diverticula.

Ontogenetic variation in gas bladder morphology also exists for many taxa. Such variation generally involves a gradual increase in the size, branching, and abundance of diverticula in larger specimens. In most taxa (e.g., *Wertheimeria*, *Anduzedoras*, *Leptodoras oyakawai*) ontogenetic change also involves a significant increase in the relative size of the posterior chambers in larger specimens. Finally, in taxa with a secondary bladder this structure also becomes relatively larger with body size.

In contrast, we observed few significant examples of intraspecific variation and no clear cases of sexual dimorphism. Intraspecific variation was limited to specific features of the diverticula, such as the symmetry of the lateral diverticula (e.g., Fig. 4G,H for *Agamyxis pectinifrons*), or of the terminal diverticula (e.g., Figs. 17C,D for *Doras punctatus*, Fig. 5H-O for *Astrodoras asterifrons*) or their contributions to the secondary bladder (e.g., Figs. 10G,H for *Rhinodoras dorbignyi*).

The combination of profound interspecific variation and limited intraspecific variation suggests that gas bladder morphology provides what traditional taxonomists rely upon as good characters for separating species. Among doradids there are several examples of allopatric species pairs (*Agamyxis albomaculatus* and *A. pectinifrons*, *Pterodoras granulosus* and *P. rivasi*) that are difficult if not impossible to distinguish via external morphology, but readily identified by consistent differences in gas bladder morphology.

Remarkable diversity in gas bladder morphology is similarly found and has been used for intrafamilial classification, in some cases to the species level, in Holocentridae (squirrelfishes; Nelson, 1955) and particularly Sciaenidae (croakers and drums; Trewavas 1977; Chao 1978, 1986). Furthermore, sciaenids exhibit ontogenetic, sexual and seasonal variation in the development of sonic (drumming) muscles that, in some species, are restricted to mature males (Tower, 1908; Fish, 1954; Hill et al., 1987) and become enlarged during the breeding season (Merriner, 1976; Connaughton and Taylor, 1994; Vance et al., 2002). Taxonomic and phylogenetic relevance aside, gas bladder design also has implications for the production, reception and behavioral use of sound in holocentrids (Coombs and Popper, 1979; Hawkins, 1993), sciaenids (Ramcharitar et al., 2006), and other fishes (e.g., *Opsanus tau*, Batrachoididae; Barimo and Fine, 1998). Among sound-producing fish, the sciaenids are probably the most active, and their vocalizations exhibit an impressive array of acoustic properties (Table 3 in Ramcharitar et al., 2006:1416–1417) putatively associated with spawning, feeding, and/or aggressive behaviors (Chao, 1978; Ramcharitar et al., 2006). In Sciaenidae, as in Doradidae, the functional significance

of various gas bladder modifications with respect to buoyancy, hearing and sound production, and their behavioral and ecological correlates, remains to be sorted.

MATERIAL EXAMINED

Acathodoras cataphractus: MZUSP 6831 (1 alc, 119 mm SL, 1 cs, 112.0 mm SL), rio Negro, Brazil. MZUSP 84667 (2 cs, 57.0-58.0 mm SL), Aquarium purchase. ***Acanthodoras spinosissimus***: ANSP 177260 (1 alc, 102.3 mm SL), Essequibo River, Guyana. ***Agamyxis albomaculatus***: ANSP 180889 (1 alc, 68.4 mm SL), MZUSP 88607 (2 alc, 79.2-92.9 mm SL), all Orinoco basin, Venezuela. ***Agamyxis pectinifrons***: INHS 43281 (1 alc, 91.7 mm SL), río Itaya, Peru. MZUSP 5177 (1 alc, 82.3 mm SL), MZUSP 27806 (1 alc, 83.3 mm SL), MZUSP 57766 (1 alc, 49.4 mm SL), all Amazonas basin, Brazil. ***Amblydoras affinis***: MZUSP 93080 (1 alc, 87.1 mm SL), Negro basin, Brazil. MZUSP 31699 (1 alc, 106 mm SL), Trombetas basin, Brazil. MZUSP 84398 (1 alc, 87.2 mm SL), Amazonas basin, Brazil. MZUSP 84200 (1 alc, 77.8 mm SL), Amazonas basin, Brazil. ***Amblydoras bolivariensis***: MZUSP 88610 (1 alc, 69.2 mm SL), Orinoco basin, Venezuela. ***Amblydoras gonzalezi***: INHS 61516 (1 alc, 60.8 mm SL), Cinaruco basin, Venezuela. ***Amblydoras monitor***: INHS 52478 (1 alc, 55.9 mm SL), Nanay basin, Peru. ***Amblydoras nauticus***: ANSP 167626 (1 alc, 55 mm SL), río Nanay, Peru. ***Anadoras grypus***: ANSP 166262 (1 alc, 114.3 mm SL), Marañon basin, Peru. MZUSP 74864 (1 alc, 140 mm SL), MZUSP 6896 (1 alc, 112.9 mm SL), MZUSP 50148 (1 alc, 92.5 mm SL), MZUSP 5934 (1 alc, 150 mm SL), MZUSP 50136 (1 alc, 115.7 mm SL), all Amazonas basin, Brazil. ***Anadoras weddellii***: MZUSP 92774 (1 alc, 105 mm SL), Amazonas basin, Brazil. MZUSP 50830 (2 alc, 98.4-101.3 mm SL), Paraguay basin, Brazil. MZUSP 95023 (2 alc, 71.2-77.8 mm SL), Paraguay basin, Brazil. MZUSP 89108 (1 alc, 67.9 mm SL), Araguaia basin, Brazil. MZUSP 29035 (2 alc, 114.9-126.8 mm SL), Trombetas basin, Brazil. ***Anduzedoras oxyrhynchus***: ANSP 160628 (1 alc, 108.2 mm SL), río Sipapo, Venezuela. MZUSP 29028 (2 alc, 34.5-56.8 mm SL), MZUSP 29021 (2 alc, 92.1-115.7 mm SL), MZUSP 91454 (1 alc, 228.0 mm SL), all Negro basin, Brazil. ***Astrodoras asterifrons***: MZUSP 57719 (1 alc, 50.0 mm SL), Amazonas basin. MZUSP 50834 (2 alc, 82.2-90.5 mm SL), Amazonas basin. MZUSP 6589 (2 alc, 61.0-71.4 mm SL), Amazonas basin. MZUSP 29049 (1 alc, 79.0 mm SL), Trombetas basin. MZUSP 6484 (1 alc, 64.7 mm SL), Amazonas basin. MZUSP 92780 (2 alc, 55.7-58.4 mm SL), Amazonas basin. MZUSP 6588 (1 alc, 68.4 mm SL), Amazonas basin. MZUSP 56033 (1 alc, 50.5 mm SL), Amazonas basin. MZUSP 8265 (1 alc, 77.6 mm SL), Trombetas basin. MZUSP 8534 (2 alc, 57.8-76.7 mm SL), Tapajós basin. MZUSP 57680 (3 alc, 50.6-58.9 mm SL), Tapajós basin. MZUSP 29048 (5 alc, 72.2-77.1 mm SL), Tapajós basin. MZUSP 29068 (6 alc, 61.0-85.7 mm SL), Negro basin. MZUSP 6784 (1 alc, 76.0 mm SL), Negro. MZUSP 62326 (1 alc, 72.2 mm SL), Negro basin. MZUSP 6077 (1 alc, 74.8 mm SL), Negro basin. MZUSP 77503 (1 alc, 64.5 mm SL), Negro basin. MZUSP 6722 (1 alc, 77.7 mm SL), Negro basin; all Brazil. ***Centrochir crocodili*:** CU 47930 (1 cs, 130.0 mm SL), río Magdalena, Colombia. ***Centrodoras brachiatus*:** ANSP 181021 (1 alc, 81.5 mm SL), Amazonas basin. MZUSP 31306 (1 alc, 186.0 mm SL), no data. MZUSP 42335 (1 cs, 270.0 mm SL), Amazonas basin. MZUSP 55776 (1 cs, 74.0 mm SL), Amazonas. MZUSP 51039 (1 alc, 230.0 mm SL), Amazonas basin. MZUSP 83313 (1 sk, 159.0 mm SL), Madeira basin; all Brazil. ***Centrodoras hasemani***: ANSP 177907 (1 alc, 209 mm SL), río Negro, Brazil. ***Centrodoras* cf. *hasemani*:** ANSP 181031 (1 alc, 69 mm SL). INPA 11338 (1 alc, 147.2 mm SL), MZUSP 56037 (1 cs, 74.0 mm SL), MZUSP 91675 (1 alc, 202.0 mm SL), all río Negro, Brazil. **Doradidae sp. (Xingu):** MPEG 6713 (1 cs, 107.0 mm SL), rio Xingu, Brazil. ***Doraops zuloagai*:** MCNG 33457 (1 alc, 103.8 mm SL), INHS 54804 (1 alc, 273 mm SL), all Maracaibo basin, Venezuela. ***Doras carinatus*:** ANSP 177276 (1 alc, 124.5 mm SL), Essequibo basin, Guyana. AMNH 96798 (1 alc, 302 mm SL), Orinoco basin, Venezuela. ***Doras fimbriatus*:** MZUSP 55833 (4 cs, 45.0-62.2 mm SL), MZUSP 56703 (1 cs, 59.0 mm SL), all Amazonas basin, Brazil. ***Doras higuchii*:** ANSP 181056 (1 cs, 60.0 mm SL), ANSP 181057 (1 alc, 160.0 mm SL), all Xingu basin, Brazil. INPA 5568 (1 alc, 83.8 mm SL), rio Trombetas, Brazil. ***Doras micropoeus:*** ANSP 187110 (1 alc, 174 mm SL), Maroni basin, Suriname. ANSP 178703 (1 alc, 222 mm SL), Essequibo basin, Guyana. ***Doras phlyzakion*:** ANSP 181055 (1 alc, 148.0 mm SL), Amazonas basin, Brazil. MZUSP 82294 (2 alc, 175.0-180.0 mm SL), Amazonas basin, Brazil. MZUSP 50836 (1 cs, 67.5 mm SL), Negro basin, Brazil. ***Doras punctatus*:** MZUSP 7839 (1 alc, 72.6 mm SL, 1 cs, 61.6 mm SL), Amazonas basin. MZUSP 7540 (1 cs, 61.7 mm SL), Amazonas basin. MZUSP 26265 (1 alc, 34.2 mm SL), Amazonas basin. MZUSP 95000 (1 alc, 65.8 mm SL), Madeira basin. MZUSP 41096 (1 alc, 59.3 mm SL), Paraguay basin. NUP 3542 (1 alc, 65.4 mm SL), Paraguay basin; all Brazil. ***Doras zuanoni:*** MZUSP 96328 (1 alc, 96.0 mm SL), Araguaia basin, Brazil. ***Franciscodoras marmoratus*:** MZUSP 84224 (1 cs, 103.8 mm SL), MZUSP 9380 (1 cs, 183.0 mm SL), all rio São Francisco, Brazil. ***Hassar affinis*:** MZUSP 74890 (1 cs, 85.9 mm SL), Parnaíba basin. MZUSP 43604 (1 alc, 152.0 mm SL), Pindaré-Mearim basin. MZUSP 90583 (1 alc, 54.4 mm

SL), Parnaíba basin; all Brazil. ***Hassar orestis*:** MZUSP 6991 (1 cs, 71.0 mm SL), Madeira basin. MZUSP 32542 (2 sk, 205.0-220.0 mm SL), Xingu basin. MZUSP 15512 (1 alc, 132.0 mm SL), Trombetas basin; all Brazil. ***Hassar wilderi*:** MZUSP 4857 (1 cs, 103.6 mm SL), MZUSP 63148 (1, 148.8 mm SL), all rio Araguaia basin, Brazil. ***Hemidoras morrisi*:** MZUSP 56683 (1 cs, 93.2 mm SL), MZUSP 56044 (2 alc, 58.2 mm SL), MZUSP 28378 (2 alc, 157.0-164.0 mm SL), all Amazonas basin, Brazil. ***Hemidoras stenopeltis*:** MZUSP 7612 (2 alc, 55.3-96.0 mm SL, 1 cs, 74.8 mm SL), Amazonas basin. MZUSP 29052 (2 cs, 67.9-69.4 mm SL), Madeira basin. MZUSP 7541 (1 alc, 114.1 mm SL), Amazonas basin. MZUSP 42772 (1 alc, 108.7 mm SL), Madeira basin; all Brazil. ***Hypodoras forficulatus:*** ANSP 182517 (1 alc, 102.6 mm SL), río Nanay, Peru. ***Kalyptodoras bahiensis*:** MZUSP 87842 (1 sk, 152.0 mm SL, 8 alc, 129.0-196.0 mm SL), MZUSP 87841 (1 sk, 233.0 mm SL), all rio Paraguaçu, Brazil. ***Leptodoras acipenserinus*:** ANSP 178467 (1 alc, 106.7 mm SL), río Nanay, Peru. ***Leptodoras cataniai***: ANSP 180920 (1 cs, 104.8 mm SL), rio Negro, Brazil. INHS 39814 (1 alc, 111.1 mm SL), río Nanay, Peru. ***Leptodoras copei*:** ANSP 162461 (1 alc, 96.5 mm SL), río Orinoco, Venezuela. ***Leptodoras hasemani***: ANSP 175888 (1 cs, 81.8 mm SL), Essequibo River, Guyana. ***Leptodoras juruensis***: INHS 39465, (1 alc, 117.4 mm SL), río Amazonas, Peru. ***Leptodoras linnelli*:** ANSP 179177 (1 alc, 94.6 mm SL), Takutu River, Guyana, ANSP 182791 (1 alc, 94 mm SL), río Manapiare, Venezuela. ***Leptodoras myersi***: ANSP 112319 (1 alc, 72.7 mm SL), río Amazonas, Peru. ***Leptodoras nelsoni***: MBUCV-V 23693 (1 alc, 115 mm SL), río Orinoco basin, Venezuela. ***Leptodoras oyakawai***: MZUSP 87028 (1 alc, 54 mm SL), MZUSP 97395 (1 alc, 121.9 mm SL), all rio Xingu basin, Brazil. ***Leptodoras praelongus*:** ANSP 162463 (1 alc, 142 mm SL), río Pamoni, Venezuela. ***Leptodoras rogersae***: ANSP 161534 (1 alc, 57.5 mm SL), río Orinoco, Venezuela. ***Lithodoras dorsalis*:** MZUSP 9379 (1 cs, 134.0 mm SL), Amazonas basin. MZUSP 62584 (1 alc, 163.0 mm SL), Amazonas basin. MZUSP 62585 (2 alc, 115.0-118.0 mm SL), Amazonas basin. MZUSP 58326 (1 alc, 170.0 mm SL), Amazonas basin. MZUSP 13955 (1 alc, 740.0 mm SL), Madeira basin. MZUSP 91562 (1 sk, 478.0 mm SL), Amazonas basin; all Brazil. ***Megalodoras guayoensis:*** ANSP 177980 (143.9 mm SL), río Orinoco, Venezuela. ***Megalodoras uranoscopus*:** MZUSP 14026 (1 alc, 410.0 mm SL), Madeira basin. MZUSP 55838 (1 cs, 73.0 mm SL), Amazonas basin. MZUSP 46007 (1 alc, 16.02 mm SL), Tocantins basin. MZUSP 25308 (1 alc, 315.0 mm SL), Tapajós basin. MZUSP 5647 (1 alc, 570.0 mm SL), Trombetas basin; all Brazil. ***Merodoras nheco:*** MZUSP 84414 (2 alc, 49.0-54.4 mm SL), MZUSP 47180 (1 alc, 27.4 mm SL), MZUSP 60053 (1 alc, 44.9 mm SL), all Paraguay basin, Brazil. ***Nemadoras elongatus*:** MZUSP 56021 (1 alc, 46.1 mm SL), MZUSP 56013 (1 cs, 92.0 mm SL, 1 alc, 99.2 mm SL), all Negro basin, Brazil. ***Nemadoras hemipeltis*:** MZUSP 56688 (1 cs, 81.8 mm SL), Amazonas basin, Brazil. ***Nemadoras humeralis*:** MZUSP 55996 (1 cs, 58.0 mm SL, 1 alc, 60.1 mm SL), Amazonas basin. MZUSP 56606 (1 cs, 86.4 mm SL), Amazonas basin. MZUSP 56014 (1 alc, 103.8 mm SL), Amazonas basin. MZUSP 6990 (1 alc, 75.6 mm SL), Madeira basin; all Brazil. ***Nemadoras leporhinus*:** MZUSP 95596 (3 alc, 42.0-43.0 mm SL), Tapajós basin, Brazil. MZUSP 95617 (2 alc, 89.0-138.1 mm SL), Tapajós basin, Brazil. MZUSP 88612 (1 alc, 75.3 mm SL, 1 cs, 73.8 mm SL), Orinoco basin, Venezuela. ***Nemadoras ternetzi:*** MZUSP 56694 (1 sk, 76.5 mm SL), Trombetas basin. MZUSP 57273 (1 alc, 67.8 mm SL, 2 cs, 51.6-56.7 mm SL), Jari basin. MZUSP 76422 (1 cs, 111.2 mm SL, 2 alc, 98.4-117.2 mm SL), Tapajós basin. MZUSP 57682 (1 alc, 110.9 mm SL), Tapajós basin; all Brazil. ***Nemadoras trimaculatus*:** MZUSP 57272 (1 cs, 70.1 mm SL), Amazonas basin. MZUSP 52314 (1 alc, 83.8-84.4 mm SL), Araguaia basin. MZUSP 92206 (1 alc, 93.9 mm SL), Negro basin. MZUSP 56706 (1 alc, 46.9 mm SL), Amazonas basin. MZUSP 53834 (1 alc, 75.6 mm SL), Araguaia basin. MZUSP 62656 (1 alc, 72.8 mm SL), Amazonas basin; all Brazil. ***Nemadoras* sp.:** MZUSP 58008 (1 cs, 68.3 mm SL, 1, 58.8 mm SL), MZUSP 56004 (1 alc, 68.2 mm SL), MZUSP 57012 (1 alc, 67.2 mm SL), all Amazonas basin, Brazil. ***Opsodoras boulengeri*:** MZUSP 62641 (1 alc, 147.3 m SL), Amazonas basin, Brazil. ***Opsodoras morei*:** MZUSP 27844 (1 cs, 90.6 mm SL), Madeira basin. MZUSP 32526 (2 sk, 137.7-153.2 mm SL, 3 alc, 135.0-138.0 mm SL), Amazonas basin. MZUSP 82288 (1 alc, 154.1 mm SL), Amazonas basin. MZUSP 31104 (1 alc, 167.7 mm SL), Negro basin. MZUSP 26316 (1 alc, 102.3-115.2 mm SL), Amazonas basin; all Brazil. ***Opsodoras stubelii*:** MZUSP 26316 (2 alc, 102.3-114.9 mm SL), Amazonas basin. MZUSP 56879 (1 cs, 64.5 mm SL), Amazonas basin. MZUSP 57620 (1 alc, 59.6 mm SL), Negro basin; all Brazil. ***Orinocodoras eigenmanni*:** INHS 40330 (1 cs, 57.8 mm SL), AUM 5318 (1 alc, 119.6 mm SL), all río Orinoco basin, Venezuela. ***Oxydoras eigenmanni* (Paraguay basin):** MZUSP 38176 (2 alc, 85.5-86.2 mm SL), MZUSP 95024 (2 alc, 38.3-65.3 mm SL), MZUSP 44423 (1 alc, 62.0 mm SL), all Brazil. ***Oxydoras* cf. *eigenmanni* (Amazonas basin):** MZUSP 7543 (2 alc, 50.2-73.5 mm SL, 1 cs, 77.3 mm SL), Amazonas basin. MZUSP 7838 (1 sk, 65.3 mm SL), Amazonas. MZUSP 5646 (1 alc, 95.4 mm SL), Amazonas basin. MZUSP 56699 (1 alc, 85.7 mm SL), Trombetas basin. MZUSP 84665 (1 alc, 85.7 mm SL), Guaporé basin; all Brazil. ***Oxydoras***

kneri*:** MZUSP 14847 (1 alc, 393.0 mm SL), Paraguay basin, Brazil. ***Oxydoras niger*:** MZUSP 9079 (1 alc, 550.0 mm SL), Amazonas basin. MZUSP 43466 (1 alc, 109.5 mm SL), Amazonas basin. MZUSP 56162 (1 alc, 138 mm SL), Amazonas basin. MZUSP 57320 (1 cs, 70.0 mm SL), Amazonas basin. MZUSP 14019 (1 alc, 420.0 mm SL), Madeira basin. MZUSP 91654 (1 sk, 550.0 mm SL), Tocantins basin. MZUSP 13366 (1 alc, 315.0 mm SL), Tapajós basin; all Brazil. ***Oxydoras sifontesi: INHS 33986 (1 alc, 187 mm SL), río Orinoco, Venezuela. ***Physopyxis ananas:*** MZUSP 6644 (1 alc, 17.7 mm SL), MZUSP 84307 (1 alc, 15.5 mm SL), all Amazonas basin, Brazil. ***Physopyxis cristata:*** INPA 25062 (2 cs), Branco basin, Brazil. ***Physopyxis lyra:*** MZUSP 62709 (1 alc, 27.2 mm SL), Amazonas basin. MZUSP 2766 (1 alc, 33.8 mm SL), no data. MZUSP 31693 (1 alc, 24.7 mm SL), Amazonas basin; all Brazil. ***Platydoras armatulus*:** ANSP 149463 (1 alc, 119.9 mm SL), río Orinoco, Venezuela. ANSP 163478 (1 alc, 111.7 mm SL), río Portuguesa, Venezuela. MZUSP 5645 (1 alc, 200.0 mm SL), Amazonas basin, Brazil. MZUSP 40577 (1 cs, 87.0 mm SL), Xingu basin, Brazil. MZUSP 94088 (1 alc, 144.0 mm SL), Xingu basin, Brazil. MZUSP 86217 (1 cs, 52.5 mm SL), trib Araguaia, Brazil. ***Platydoras brachylecis*:** MZUSP 5122 (1 cs, 119.0 mm SL), Parnaíba basin, Brazil. ***Platydoras costatus***: ANSP 187102 (1 sk, 185 mm SL), Maroni basin, Suriname. ***Platydoras hancockii***: ANSP 182845 (1 alc, 126.5 mm SL), río Ventuari, Venezuela. ***Pterodoras granulosus*:** MZUSP 91441 (1 alc, 330.0 mm SL), Madeira basin. MZUSP 83317 (1 alc, 143.3 mm SL), Amazonas basin. MZUSP 82995 (1 alc, 60.5 mm SL), Amazonas basin; all Brazil. MZUSP 82343 (1 alc, 435.0 mm SL), no data. MZUSP 31877 (1 alc, 220.0 mm SL), no data. ***Pterodoras rivasi*:** MZUSP 88609 (1 alc, 82.2 mm SL), ANSP 177895 (1 alc, 336.1 mm SL), Orinoco basin, Venezuela. ***Rhinodoras armbrusteri*:** ANSP 179095 (1 alc, 81.2 mm SL), Ireng River, Guyana. ***Rhinodoras boehlkei*:** MZUSP 86812 (1 alc, 95.0 mm SL), Amazonas. MZUSP 86814 (1 alc, 41.0 mm SL), Amazonas. ***Rhinodoras dorbignyi*:** ANSP 179535 (1 alc, 194 mm SL), rio Uruguai, Brazil. MZUSP 61456 (2 cs, 70.4-121.9 mm SL), Upper Paraná, Brazil. MZUSP 62683 (1 alc, 185.6 mm SL, 3 cs, 45.3-89.9 mm SL), Upper Paraná, Brazil. MZUSP 27724 (1 alc, 207.7 mm SL), Paraguay basin, Brazil. MZUSP 78461 (1 alc, 168.0 mm SL), Uruguay basin, Brazil. MZUSP 56750 (1 alc, 200.0 mm SL, 1 cs, 115.4 mm SL), Paraguay basin, Brazil. MZUSP 9381 (1 cs, 94.0 mm SL), Upper Paraná, Brazil. MZUSP 40109 (1 sk, 196.0 mm SL), Uruguay basin, Brazil. ***Rhinodoras gallagheri*:** FMNH 116466 (1 alc, 90.2 mm SL), MZUSP 86806 (1, 93.2 mm SL), all río Orinoco basin, Venezuela. ***Rhinodoras thomersoni*:** MHNLS 0109 (1 cs, 60.9 mm SL), Maracaibo basin, Venezuela. ***Rhinodoras* sp. (Tocantins basin):** MZUSP 51330 (1 alc, 102.7 mm SL). INPA 22056 (1 alc, 82.7 mm SL). INPA 508 (1 cs, 67.9 mm SL), all Brazil. ***Rhynchodoras castilloi*:** ANSP 181181 (1 alc, 58.3 mm SL), MZUSP 88604 (1 cs, 45.5 mm SL), all Apure-Orinoco basin, Venezuela. ***Rhynchodoras woodsi*:** ANSP 181042 (1 alc, 72.5 mm SL, 1 cs, 88.4 mm SL), río Amazonas, Peru. MZUSP 57992 (2 alc, 35.0-45.0 mm SL), MZUSP 56872 (1 cs, 23.1 mm SL, 3 alc, 22.5-37.3 mm SL), MZUSP 56859 (1 cs, 26.0 mm SL), all rio Amazonas, Brazil. ROM 62601 (1 alc, 44.2 mm SL), Essequibo River, Guyana. ***Rhynchodoras xingu*:** SMF 5282 (1 alc, 44.5 mm SL), rio Xingu, Brazil. ***Scorpiodoras heckelii:*** MZUSP 84743 (2 alc, 138.0-145.0 mm SL), Negro basin. MZUSP 7941 (1 alc, 108.9 mm SL), Amazonas basin. MZUSP 84203 (1 alc, 148.0 mm SL), Amazonas basin. MZUSP 8493 (1 sk, 114.4 mm SL), Amazonas basin, Brazil. ***Scorpiodoras* cf. *calderonensis:*** MZUSP 36249 (2 alc, 111.0-157.0 mm SL), MZUSP 36058 (1 alc, 133.0 mm SL), MZUSP 36251 (1 alc, 140 mm SL), all Amazonas basin, Brazil. ***Trachydoras* sp.**, ANSP 161518 (1 alc, 71.2 mm SL), río Orinoco, Venezuela. ***Trachydoras brevis*:** MZUSP 56713 (1 alc, 66.1 mm SL), Amazonas basin. MZUSP 93374 (1 alc, 46.5 mm SL), Negro basin. MZUSP 93094 (1 alc, 93.7 mm SL), Negro basin; all Brazil. ***Trachydoras microstomus***: ANSP 180184 (50.8 mm SL), Orinoco basin, Venezuela. ROM 62609 (1 alc, 27.8 mm SL), Essequibo River, Guyana. ***Trachydoras nattereri*:** 55854 (1 alc, 48.7 mm SL), Negro basin. MZUSP 31703 (1 alc, 99.3 mm SL), Amazonas basin; all Brazil. ***Trachydoras paraguayensis*:** ANSP 178699 (1 alc, 79.2 mm SL), rio Paraguai. MZUSP 48315 (1 alc, 54.3 mm SL), Paraguay basin. MZUSP 21109 (1 alc, 80.2 mm SL), Paraná basin. MZUSP 40081 (1 alc, 101.0 mm SL), Paraguay basin. MZUSP 29047 (1 alc, 114.2 mm SL), Madeira basin. MZUSP 27801 (1 alc, 84 mm SL), Madeira basin; all Brazil. ***Trachydoras steindachneri*:** MZUSP 62696 (3 alc, 38.7-77.0 mm SL), MZUSP 74867 (1 alc, 75.7 mm SL), MZUSP 7611 (1 cs, 75.8 mm SL), all Amazonas basin, Brazil. ***Trachydoras* cf. *steindachneri***: ANSP 180175 (1 alc, 65.2 mm SL), río Nanay, Peru. MZUSP 57703 (3 alc, 43.6-76.6 mm SL), Negro basin, Brazil. ***Wertheimeria maculata*:** MZUSP 40229 (3 cs, 25.0-112.0 mm SL), MZUSP 88614 (1 sk, 124.0 mm SL), MZUSP 93659 (2 sk, 217.0 mm SL), MZUSP 93658 (1 sk, 192.0 mm SL, 1 alc, 168.0 mm SL), all rio Jequitinhonha, Brazil.

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Appendix 1. Summary of variation in gas bladder morphology in Doradidae. Number of species examined (nominal and known undescribed) in parentheses following taxon name. Descriptions generally pertain to adults unless otherwise specified. 1 = *sensu* Higuchi et al., 1990; Higuchi, 1992; Birindelli, 2006 (excludes *Centrochir* and Doradidae sp. (Xingu)). 2 = *sensu* Higuchi et al., 2007. 3 = *sensu* Higuchi, 1992; Birindelli, 2006. 4 = *sensu* Birindelli, 2006; Birindelli et al., 2007. 5 = *sensu* Higuchi, 1992; Moyer et al., 2004; Birindelli, 2006.

		Overall				T-shaped septum	
	Taxa	Shape	Size	Müllerian ramus	Intersection of T-shaped septum	longitudinal portion	transverse portion
"Basal"[1]	*Wertheimeria maculata*	cordiform	normal	disc-like	aligned with centers of Müllerian windows	straight	straight
	Kalyptodoras bahiensis						
	Franciscodoras marmoratus						
	Centrochir crocodili				aligned with posterior margins of Müllerian windows		
	Doradidae sp. (Xingu)						
	Platydoras spp. (4)						
	Acanthodoras spp. (2)	apple-shaped			aligned with centers of Müllerian windows		
	Agamyxis pectinifrons	abbreviated cordiform					
	Agamyxis albomaculatus						
Astrodoradinae[2]	*Amblydoras* spp. (5)	apple-shaped			alligned with posterior margins of Müllerian windows		
	Merodoras nheco						
	Physopyxis spp. (3)			knob-like			
	Anadoras spp. (2)	abbreviated cordiform		disc-like			
	Hypodoras forficulatus	apple-shaped					
	Scorpiodoras heckelii						
	Scorpiodoras cf. *calderonensis*						
	Astrodoras asterifrons						

Appendix 1. cont.

	Internal trabeculae	Ventral wall	Terminal diverticulum(a)		Differentiated posterior diverticula	Additional diverticula (per side)
			Without proximal constriction	Constricted proximally, forming secondary bladder		
"Basal"[1]	absent	normal	absent	absent	absent	absent
				present, formed by expansion of only one posterior chamber (bladder aseptate)		
			present, small, formed by only one posterior chamber	absent		three to five short, simple diverticula posterolaterally
						one short, simple diverticulum posterolaterally
Astrodoradinae[2]			absent			absent
			absent, except in some specimens of *A. weddellii* present, minute, formed by only one posterior chamber			
			present, paired, nearly symmetrical; elongate; proximally conjoined, tips divergent			
			absent	present, formed by nearly symmetrical expansions of both posterior chambers (bladder septate)		
				present, formed by asymmetrical expansions of both posterior chambers with longer side folded back on itself (bladder septate)		
			present, paired, symmetrical or asymmetrical; short; tips conjoined or divergent	absent		

Appendix 1. cont.

	Taxa	Overall		Müllerian ramus	Intersection of T-shaped septum	T-shaped septum	
		Shape	Size			longitudinal portion	transverse portion
Clade[3]	*Lithodoras dorsalis*	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
Clade[3]	*Megalodoras* spp. (2)	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
Clade[3]	*Centrodoras* spp. (3)	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
Clade[3]	*Pterodoras rivasi*	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
Clade[3]	*Pterodoras granulosus*	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
Clade[3]	*Doraops zuloagai*	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
Clade[4]	*Orinocodoras eigenmanni*	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	shallow zigzag	strongly arched
Clade[4]	*Rhinodoras dorbignyi/thomersoni*	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	shallow zigzag	strongly arched
Clade[4]	*Rhinodoras armbrusteri/boehlkei/gallagheri*	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	shallow zigzag	strongly arched
Clade[4]	*Rhynchodoras castilloi/xingui*	cordiform	reduced	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
Clade[4]	*Rhynchodoras woodsi*	cordiform	reduced	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
	Oxydoras spp. (3)	cordiform	normal	disc-like	alligned with posterior margins of Müllerian windows	straight	straight
Clade[5] (fimbriate-barbel taxa)	*Doras carinatus*	cordiform	normal	conical	alligned with posterior margins of Müllerian windows	straight	straight
Clade[5] (fimbriate-barbel taxa)	*Doras higuchii/micropoeus*	cordiform	normal	conical	alligned with posterior margins of Müllerian windows	straight	straight
Clade[5] (fimbriate-barbel taxa)	*Doras phlyzakion*	cordiform	normal	conical	alligned with posterior margins of Müllerian windows	straight	straight
Clade[5] (fimbriate-barbel taxa)	*Doras zuanoni*	cordiform	normal	conical	alligned with posterior margins of Müllerian windows	straight	straight
Clade[5] (fimbriate-barbel taxa)	*Anduzedoras oxyrhynchus*	cordiform	normal	conical	alligned with posterior margins of Müllerian windows	straight	straight
Clade[5] (fimbriate-barbel taxa)	*Hassar orestis/wilderi*	cordiform	normal	conical	alligned with posterior margins of Müllerian windows	straight	straight
Clade[5] (fimbriate-barbel taxa)	*Hassar affinis*	cordiform	normal	conical	alligned with posterior margins of Müllerian windows	straight	straight

Appendix 1. cont.

	Internal trabeculae	Ventral wall	Terminal diverticulum(a)		Differentiated posterior diverticula	Additional diverticula (per side)
			Without proximal constriction	Constricted proximally, forming secondary bladder		
Clade[3]	present	normal	absent	present, formed by asymmetrical expansions of both posterior chambers (bladder septate); longer side partially subdivided by constrictions	absent	few short, simple or branched diverticula posterolaterally and on secondary bladder
				present, formed by nearly symmetrical expansions of both posterior chambers (bladder septate); partially subdivided by constrictions		many long, branched diverticula along anterior, lateral, and posterior margins, and on secondary bladder when present; diverticulum on anterolateral shoulder enlarged and curved anteromedially in *Doraops* and *Pterodoras*
	absent			present, formed by nearly symmetrical expansions of both posterior chambers (bladder septate)		
	present			absent	present, extremely long and often branched (adults only in *P. granulosus*)	
Clade[4]		honeycomb-like appearance		present, formed by nearly symmetrical expansions of both posterior chambers (bladder septate)	absent	absent (*R. thomersoni*) OR weakly-developed as blister-like swellings posterolaterally
			present, paired, nearly symmetrical; short; completely conjoined	absent		
	absent	normal	absent		present, paired horn-like expansions	absent
	present			present, formed by expansion of only one posterior chamber (bladder aseptate)	absent	weakly-developed as tuberous swellings laterally
Clade[5] (fimbriate-barbel taxa)	absent		present, small, formed by only one posterior chamber	absent		absent
				sometimes present, small, formed by expansion of only one posterior chamber (bladder aseptate)		
			absent	absent	present, paired, elongate, slender	
			present, paired, nearly symmetrical; elongate; proximally conjoined, tips divergent		absent	single, short diverticulum on anterolateral shoulder
			present, paired, nearly symmetrical; very short; completely conjoined			many short to elongate, simple or branched diverticula along anterior, lateral, and posterior margins, and on terminal diverticula
			absent			two small diverticula on anterior chamber (anterolateral shoulder and posterolateral portion)

Appendix 1. cont.

	Taxa	Overall		Müllerian ramus	Intersection of T-shaped septum	T-shaped septum	
		Shape	Size			longitudinal portion	transverse portion
Clade[5] (fimbriate-barbel taxa)	*Hemidoras* spp. (2)	cordiform	normal	conical	alligned with posterior margins of Müllerian windows	straight	straight
	Opsodoras spp. (3)						
	Nemadoras spp. (5, *N. elongatus* & *N. hemipeltis* excluded)						
	Nemadoras elongatus/hemipeltis						forming deep V-shaped notch pointing towards pneumatic duct
	Trachydoras sp.						straight
	Trachydoras brevis/microstomus/nattereri						
	Trachydoras paraguayensis						
	Trachydoras cf. *steindachneri*						
	Trachydoras steindachneri						
	Doras punctatus						
	Doras fimbriatus						
	Oxydoras cf. *eigenmanni*						
	Oxydoras eigenmanni						
	Leptodoras oyakawai		reduced in juveniles, normal in adults				
	Leptodoras spp. (10, *L. oyakawai* excluded)		reduced				

Appendix 1. cont.

	Internal trabeculae	Ventral wall	Terminal diverticulum(a)		Differentiated posterior diverticula	Additional diverticula (per side)
			Without proximal constriction	Constricted proximally, forming secondary bladder		
Clade[5] (fimbriate-barbel taxa)	absent	normal	present, paired, nearly symmetrical; short or elongate; usually completely conjoined	absent	absent	many short to extremely elongate, simple or branched diverticula along anterior, lateral, and posterior margins, and on terminal diverticula (except restricted to anterior chamber in some *N. leporhinus*)
			present, paired, asymmetrical; short; completely conjoined			absent
			present, paired, nearly symmetrical; short or elongate; completely conjoined or tips divergent			single, short, simple or weakly branched diverticulum on anterolateral shoulder; *T. microstomus* also with rounded swelling or short diverticulum on posterolateral portion of anterior chamber
			absent OR present, paired, nearly symmetrical; short; proximally conjoined, tips divergent			
			present, paired, nearly symmetrical; elongate; proximally conjoined, tips divergent			short to elongate, simple or weakly branched diverticulum on anterolateral shoulder; many additional diverticula along lateral margins
			present, paired, nearly symmetrical; short; completely conjoined or tips weakly separated			
			present, paired, symmetrical or asymmetrical; short or elongate; proximally conjoined, tips divergent			absent
			present, paired, nearly symmetrical; short; completely conjoined			many short to elongate diverticula along anterior, lateral, and posterior margins
			indistinguishable from lateral diverticula			
			absent			single, short to elongate diverticulum on anterolateral shoulder
						absent
					present, paired horn-like expansions	two large bulbous diverticula on anterior chamber (anterolateral shoulder and posterolateral portion)

Platydoras sp. rio Curuá, Iriri-Xingu drainage, near town of Castelo dos Sonhos, Pará State, Brazil, 23 Oct 2007, collected by J.L. Birindelli, L.M. Sousa, A.N. Ferreira, N.K. Lujan & M.H. Sabaj Pérez, PIPE Expedition.