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The Submandibular Musculature of Phyllomedusinae (Anura: Hylidae): A Reappraisal

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ABSTRACT The submandibular musculature of 37 species of the five currently recognized genera of the subfamily Phyllomedusinae (Anura: Hylidae) is described; observations are made on the variation and ontogeny of these muscles. Supplementary apical elements of the m. intermandibularis occur in all phyllomedusines studied, in addition to the supplementary posterolateral elements previously reported. Our observations are discussed in the context of 1) the proposed homology between supplementary apical and posterolateral elements; 2) the homology with the apical elements reported for Pelodryadinae (sister taxon of Phyllomedusinae); and 3) the implications for our understanding of the relationships between Phyllomedusinae and Pelodryadinae. Anatomical differences between the apical and posterolateral elements and their co-occurrence in phyllomedusines indicate that these supplementary elements are not homologous. Despite differences between phyllomedusines and pelodryadines in the adhesion of supplementary fibers to the principal element of the m. intermandibularis and the occurrence of a broad aponeurosis or a medial raphe, the extensive morphological and developmental resemblances of the apical elements indicate that these structures are homologous, and that the presence of apical elements is a synapomorphy of Phyllomedusinae + Pelodryadinae. J. Morphol. 272:354–362, 2011. © 2011 Wiley-Liss, Inc.

KEY WORDS: Phyllomedusinae; Pelodryadinae; submandibular musculature; anatomy; systematics; supplementary elements

INTRODUCTION

The presence of supplementary elements of the intermandibularis muscle in hylid frogs was first noted by Trewavas (1933) in two species of Australopapuan hylids. In a major review, Tyler (1971) described morphological variation of submandibular musculature in hylid frogs and studied its taxonomic distribution. His observations in great part shaped ideas on higher level relationships of hylids for the next 35 years. The two most historically important results of that article are as follows. First, all Australopapuan hylids (then in the genera *Hyla* and *Nyctimystes*) have supplementary apical elements of the m. intermandibularis; these arise from the lingual surface of the mandible on each side of the m. submentalis and extend posteromedially to attach to the median raphe of the principal element of the m. intermandibularis. Second, phyllomedusines have supplementary posterolateral elements of the m. intermandibularis; these arise from the ventral surface of the mandible, near the pars articularis, and extend anteromedially to attach on the ventral surface of the principal element of the m. intermandibularis. Tyler (1971) also noted that all Australopapuan hylids possess an m. intermandibularis with a median raphe, whereas phyllomedusines have a broad median aponeurosis.

On the basis of the presence of supplementary apical elements of the m. intermandibularis, Tyler (1971) resurrected the genus *Litoria* to accommodate all Australopapuan species previously placed in *Hyla*. On the basis of the same evidence, Savage (1973) suggested that the Australopapuan hylids

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were unrelated to Hylidae and recognized them as Pelodryadidae, a group that Duellman (1977) considered to be a hylid subfamily. *Cyclorana*, a fossorial group of anurans with supplementary apical elements (Tyler, 1971, 1972), was included in Pelodryadinae by Tyler (1978). The differences in the supplementary elements in Phyllomedusinae and Pelodryadinae were one of the lines of evidence used by Tyler and Davies (1978) to justify the monophyly of Pelodryadinae with respect to Phyllomedusinae. Subsequently, the presence and nature of the supplementary elements of the m. intermandibularis in these two subfamilies were reported in the context of taxonomic descriptions (Cannatella, 1980) and revisions (Cruz, 1990), briefly discussed in reviews (Faivovich et al., 2005; Frost et al., 2006; Burton and Tyler, 2007), and included in phylogenetic analyses (da Silva, 1998; Mendelson et al., 2000; Duellman, 2001; Haas, 2003; Wiens et al., 2005; Frost et al., 2006). Herein, the submandibular musculature of species included in the five recognized genera of Phyllomedusinae (Faivovich et al., 2010; Fig. 1) is surveyed and our findings discussed in the context of previous studies.

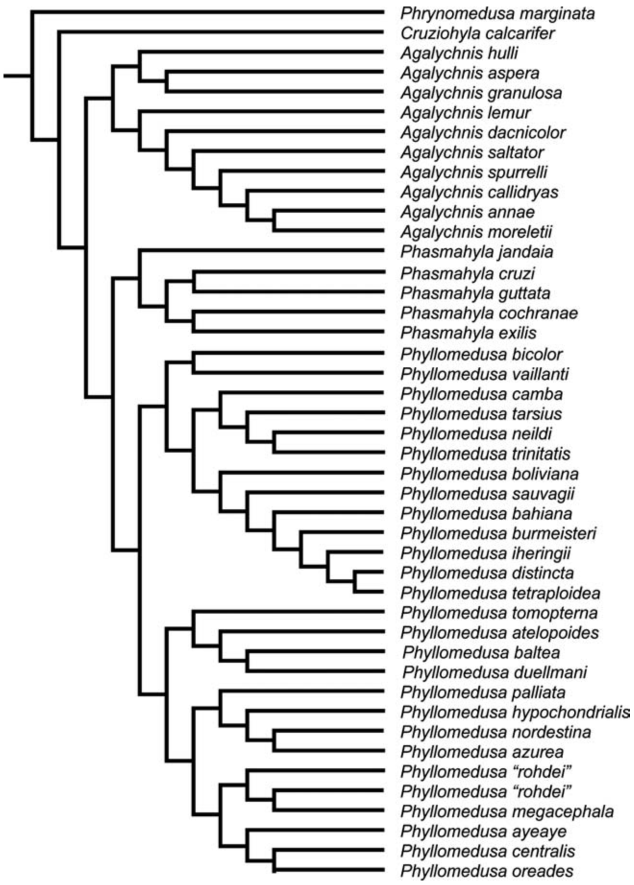

Fig. 1. Phylogenetic relationships among Phyllomedusinae. Redrawn from Faivovich et al. (2010: Fig. 6).

MATERIALS AND METHODS

We examined 95 adults representing 37 species of all five genera of Phyllomedusinae. For Pelodryadinae, we relied on Tyler's (1971, 1972) observations. We also studied metamorphic series of *Phyllomedusa azurea* and *P. boliviana* to understand details of the origin of the supplementary elements of the m. intermandibularis. We staged larvae according to Gosner's (1960) developmental table. We performed dissections with the use of a stereomicroscope and visualized muscles by applying an iodum/potassium iodide solution topically (Bock and Shear, 1972). We follow the submandibular muscle terminology of Tyler (1971) and the mandibular muscle terminology of Haas (2001). We stained larvae following the protocol of Wassersug (1976). To visualize the musculature, we applied an iodine/potassium iodide solution to specimens to improve the contrast between orange muscles and blue cartilages. Institutional codes follow Leviton et al. (1985) with the exception of CFBH: Coleção Célio F. B. Haddad, Departamento de Zoologia, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil. All material examined is listed as Supporting Information.

RESULTS

All Phyllomedusinae species examined have similarly organized submandibular musculature (Figs. 2 and 3). The m. submentalis (SM) is small and araphic and completely visible in ventral aspect; it lacks any muscular attachment to the m. intermandibularis (IM). The principal element of the m. intermandibularis is a thin sheath of muscle with a broad, median aponeurosis (AP) through which, by transparency, the mm. geniohyoidei are visible. The m. intermandibularis is differentiated to produce two pairs of supplementary elements—one apical (AE) and one posterolateral (PLE). Each apical element arises from the lingual surface of the maxilla; the fibers are oriented posteromedially and insert widely on the fibers of the principal element and along the margin of the large aponeurosis. The posterolateral elements originate from ligaments that arise from fasciae at the level of the mm. levatores mandibulae (LMEP, LMES, and LML; Fig. 4). The fibers are oriented anteromedially and insert on the surface of the principal element and on the margin of the aponeurosis (described below). The vocal sac seems to lie above the posterior part of the principal element of the m. intermandibularis, and the m. interhyoideus, which is a thin muscle possessing a raphe and lacking folds.

Observed Variation

Contact between the m. submentalis and the apical elements of the m. intermandibularis. There is a clear gap between the apical elements and the posterior margin of the m. submentalis through which the mm. geniohioydei are visible in *Agalychnis aspera*, *A. callidryas*, *A. granulosa*, *A. lemur* (Fig. 2D), *Phasmahyla cochranae*, *P. cruzi*, *P. exilis*, *P. guttata*, *P. jandaia*, *P. spectabilis*, *P. timbo* (Fig. 2F), *Phyllomedusa ayeaye*, *P. camba*, and *P. vaillanti*. The gap is present but is noticeably

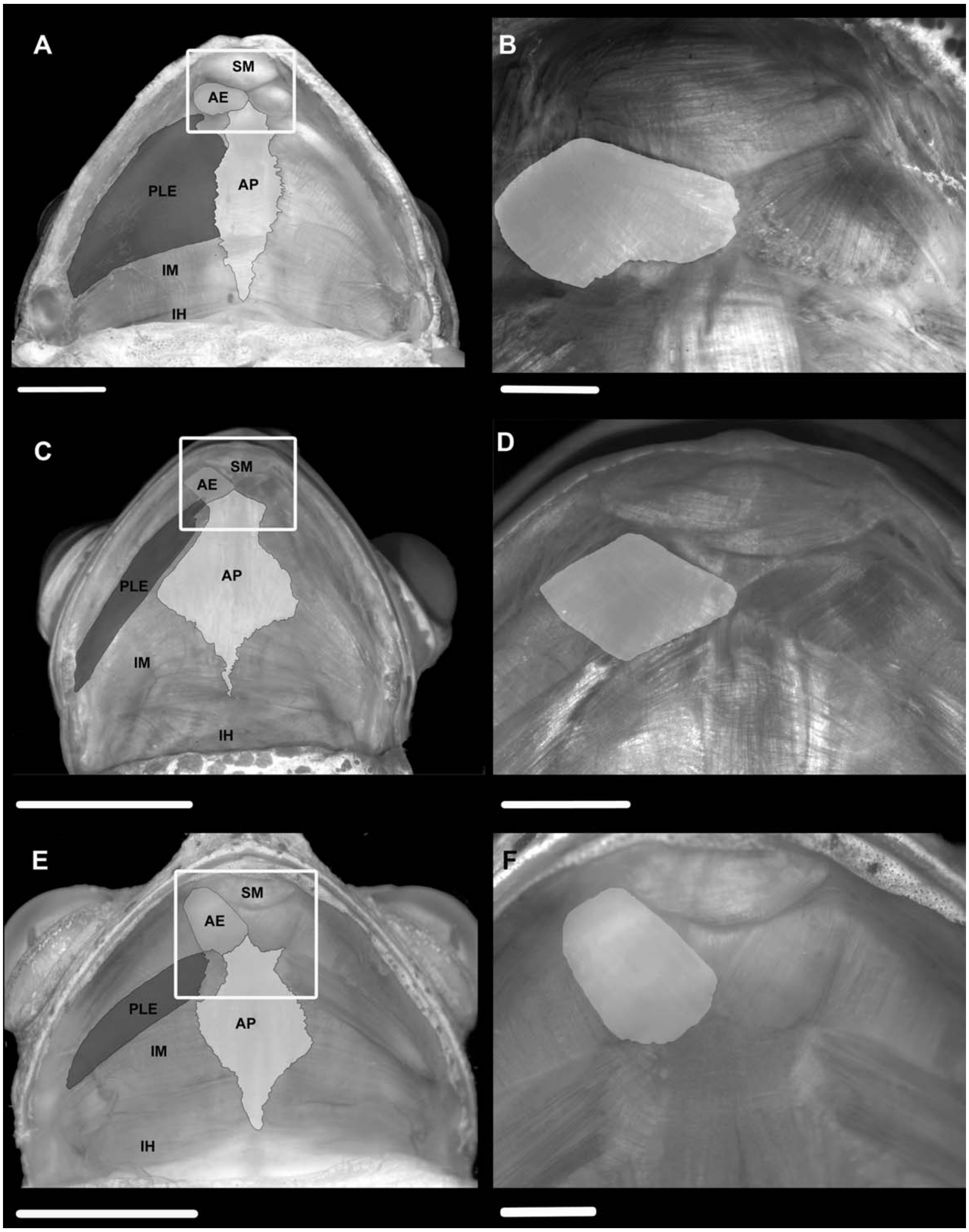

Fig. 2. Submandibular musculature in phyllomedusines. The white frames in figures on the left indicate the area detailed in the figures on the right. (**A**) *Cruziohyla calcarifer* (AMNH 107248), submandibular area, with detail (**B**) of the supplementary apical elements of the m. intermandibularis. Notice the thin gap between the m. submentalis and the apical elements of the m. intermandibularis, and the thick, prominent, supplementary apical elements. The fibers of the supplementary posterolateral element fan out, inserting on the margins of the aponeurosis, and anteriorly on the surface of the principal element of the m. intermandibularis. The configuration of the aponeurosis is intermediate between diamond and U shaped. (**C**) *Agalychnis lemur* (AMNH 124161), submandibular area, with detail (**D**) of the apical elements. Notice the distinct gap between the m. submentalis and the apical elements of the m. intermandibularis, and the thin, sheet-like supplementary apical elements. The chiefly rectangular posterolateral elements insert on the surface of the principal element of the m. intermandibularis. The most distal part of the right posterolateral element (left on this view) lies directly above the apical elements and in this view is covered by them. The aponeurosis is diamond shaped. (**E**) *Phasmahyla timbo* (MNRJ 52065), submandibular area, with detail (**F**) of the apical elements. Notice the distinct gap between the m. submentalis and the apical elements of the m. intermandibularis. The chiefly rectangular posterolateral elements insert on the surface of the principal element of the muscle and the aponeurosis is diamond shaped. AE, supplementary apical element of the m. intermandibularis; AP, aponeurosis of the m. intermandibularis; IH, m. interhyoideus; IM, principal element of the m. intermandibularis; PLE, supplementary posterolateral element of the m. intermandibularis; SM, m. submentalis. Left-hand scales = 5 mm. Right-hand scales = 1 mm.

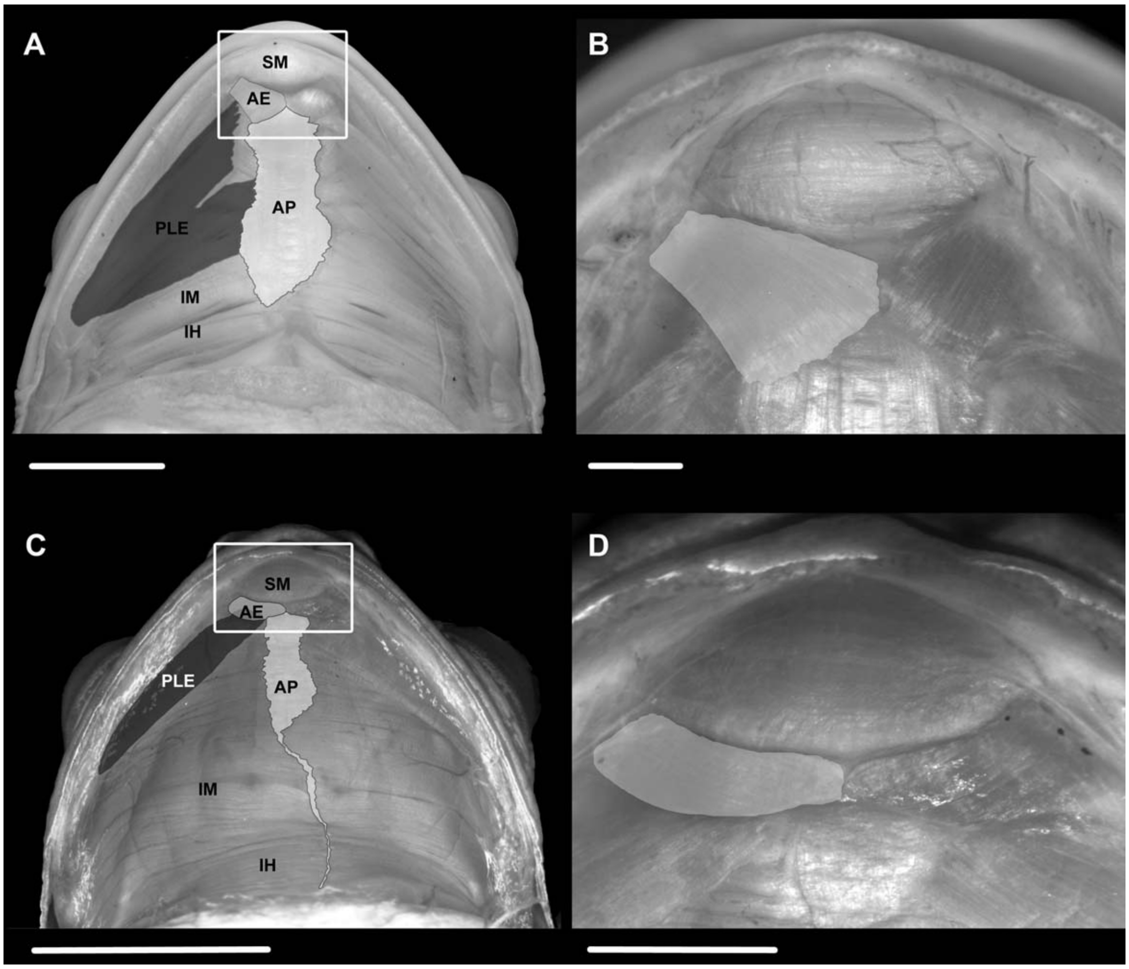

Fig. 3. Submandibular musculature in phyllomedusines. The white frames in figures on the left indicate the area detailed in the figures on the right. (**A**) *Phyllomedusa boliviana* (MACN 9831), submandibular area, with detail (**B**) of the apical elements. Notice the gap between the m. submentalis and the apical elements of the m. intermandibularis. The fibers of the supplementary posterolateral elements fan out and insert on the margins of the aponeurosis, and anteriorly, on the surface of the principal element of the m. intermandibularis. The shape of the aponeurosis is intermediate between diamond and U shaped. (**C**) *Phyllomedusa azurea* (MACN 40062), submandibular area, with detail (**D**) of the apical elements. Notice that the margins of supplementary apical elements lie adjacent to the posterior margin of the m. submentalis. The most distal parts of the chiefly rectangular posterolateral elements lie deep to the apical elements, which cover them in this view. The aponeurosis is reduced and U shaped and continues posteriorly as a raphe. Abbreviations and scales as in Figure 2.

narrower in *Cruziohyla calcarifer* (Fig. 2B) and *Phyllomedusa boliviana* (Fig. 3B).

The posterior margin of the m. submentalis and the anterior margins of the apical elements are juxtaposed in *Agalychnis dacnicolor*, *Phrynomedusa appendiculata*, *P. marginata*, *Phyllomedusa azurea* (Fig. 3D), *P. bahiana*, *P. bicolor*, *P. burmeisteri*, *P. distincta*, *P. iheringii*, *P. nordestina*, *P. tarsius*, *P. tomopterna*, *P. trinitatis*, and *P. vaillanti*.

The relationships between the m. submentalis and the apical elements of the m. intermandibularis vary in different populations of *P. rohdei*. In CFBH 9036 and 17280, the separation of the medial segments of the apical elements from the m. submentalis creates a small triangular gap in which the mm. geniohyoidei are visible. In CFBH 11954, the margins of the apical elements follow that of the m. submentalis; thus, there is no gap.

Number of fibers of each supplementary apical element involved in medial contact with fibers of the contralateral element of the m. intermandibularis. The apical elements insert widely on the fibers of the principal element and on the margin of the aponeurosis. The most anterior fibers of apical elements on each side insert adjacently to one another with little intermingling. The number of fibers involved in this contact is variable. For example, in *C. calcarifer*, about half of the fibers of each apical element lie medially adjacent to one another (Fig. 2B), whereas in most other species, only the most anterior fibers are medially adjacent (Fig. 2D,F).

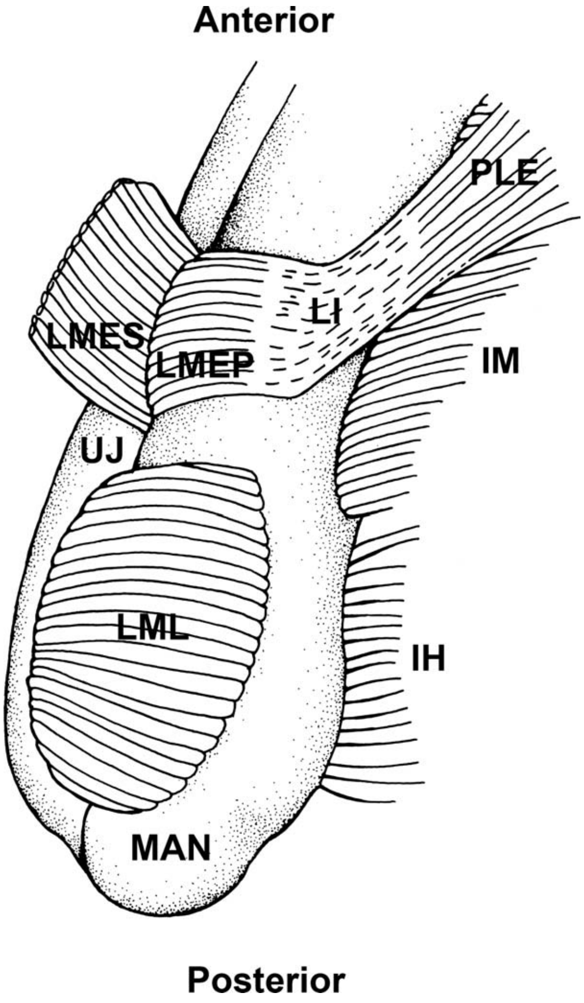

Fig. 4. Ventrolateral view of the right half of the mandible and associated submandibular musculature showing the origin of the right supplementary posterolateral element of the m. intermandibularis from a ligament that arises at the level of the mm. levatores mandibulae in *Phyllomedusa rohdei* (SAMA 4858). Usually, a sheath of connective tissue of variable thickness and transparency lies between the posterolateral element and the mandible. Redrawn from Tyler (1974). Abbreviations as in Figure 2 plus: LI, ligament; LMES, m. levator mandibulae externus superficialis; LMEP, m. levator mandibulae externus profundus; LML, m. levator mandibulae lateralis; MAN, mandible; UJ, upper jaw.

Thickness of the supplementary apical elements of the m. intermandibularis. Although always differentiated from the overlying principal element of the intermandibularis, the fibers of the supplementary apical element vary in thickness. *Agalychnis lemur* (Fig. 2D) and *C. calcarifer* (Fig. 2B) represent two extremes of a continuum between sheet-like apical elements to better-developed, more bundle-like elements.

Relationship between the apical and the posterolateral elements of the m. intermandibularis. The fibers of the supplementary posterolateral element insert on the surface of the principal element of the m. intermandibularis, sometimes reaching the margin of the aponeurosis (described below) and closely approximating the posterior margin of the apical elements anteriorly (Figs. 2A,B,E,F and 3A,B). The proximity of this contact varies intraspecifically and even bilaterally in individuals. Thus, in *A. lemur* (Fig. 2C,D), *P. azurea* (Fig. 3C,D), *P. distincta*, and *P. tarsius*, the most distal part(s) of one or both of the posterolateral element(s) lies ventrally superficial to the apical element(s).

Morphology and insertion of the supplementary posterolateral elements of the m. intermandibularis. The posterolateral elements are rectangular and insert directly on the surface of the principal element of the m. intermandibularis and sometimes on the anterolateral margins of the aponeurosis in *Agalychnis aspera*, *A. callidryas*, *A. dacnicolor*, *A. lemur* (Fig. 2C), *Phasmahyla exilis*, *P. guttata*, *P. jandaia*, *P. spectabilis*, *P. timbo* (Fig. 2E), *Phyllomedusa ayeaye*, *P. azurea* (Fig. 3C), *P. nordestina*, *P. rohdei*, and *P. tomopterna*. Alternatively, the posterolateral elements fan out medially with the medial ends of the fibers inserting along part or the entire lateral margins of the aponeurosis in *Agalychnis annae*, *A. granulosa*, *C. calcarifer* (Fig. 2A), *Phrynomedusa appendiculata*, *P. marginata*, *Phyllomedusa bahiana*, *P. bicolor*, *P. boliviana* (Fig. 3A), *P. burmeisteri*, *P. camba*, *P. distincta*, *P. iheringii*, *P. tetraploidea*, and *P. trinitatis*.

Shape of the aponeurosis of the principal element of the m. intermandibularis. All phyllomedusines examined possess a median aponeurosis in the principal element of the m. intermandibularis. The shape of the aponeurosis varies from diamond shaped in *Agalychnis annae*, *A. lemur* (Fig. 2C), *Phyllomedusa bahiana*, *P. distincta*, *P. iheringi*, *P. trinitatis* to U shaped in *Agalychnis aspera*, *A. callidryas*, *A. dacnicolor*, *A. granulosa*, both studied species of *Phrynomedusa* examined, *P. ayeaye*, *P. azurea* (Fig. 3C), *P. bicolor*, *P. burmeisteri*, *P. hypochondrialis*, *P. nordestina*, and *P. tetraploidea*. Other taxa have an intermediate morphology: *C. calcarifer* (Fig. 2A), *Phyllomedusa boliviana* (Fig. 3A), *P. camba*, *P. tomopterna*, *P. vaillanti*, and all species of *Phasmahyla* examined (Fig. 2E).

In a few species, the aponeurosis narrows to a raphe before reaching the m. interhyoideus (*Agalychnis dacnicolor*, *A. granulosa*, *Phasmahyla exilis*, *P. jandaia*, *P. timbo*, *Phrynomedusa appendiculata*, *Phyllomedusa iheringii*, and *P. tomopterna*). In some species of the *P. hypochondrialis* group (*P. ayeaye*, *P. azurea*, *P. hypochondrialis*, and *P. nordestina*), the U-shaped aponeurosis has an abbreviated anteroposterior length; posteriorly, it is represented by a raphe that terminates at the m. interhyoideus (Fig. 3D). In *P. rohdei*, the aponeurosis can have a similar morphology (e.g., MNRJ 46023) or be more elongate (MNRJ 40870).

Ontogenetic Observations

The metamorphosis of the ventral cranial musculature is described primarily on the basis of a developmental series of *Phyllomedusa azurea* (FML 452; *n* = 9; Gosner Stages 42, >42, 43, 44, >44, 45, >45, <46, and 46, staged according to the position of the angle of the jaw relative to the eye). Four muscles compose the ventral cranial musculature of larval *P. azurea* (Fig. 5).

M. mandibulolabialis. This muscle extends between the ventromedial surface of Meckel's cartilage and the lower lip as well as part of the upper lip of the oral disc. The division of the muscle into two slips is less evident than in other genera of hylids. The m. mandibulolabialis is absent in Stage 42.

M. submentalis. This compact muscle is composed of short, parallel fibers that extend between

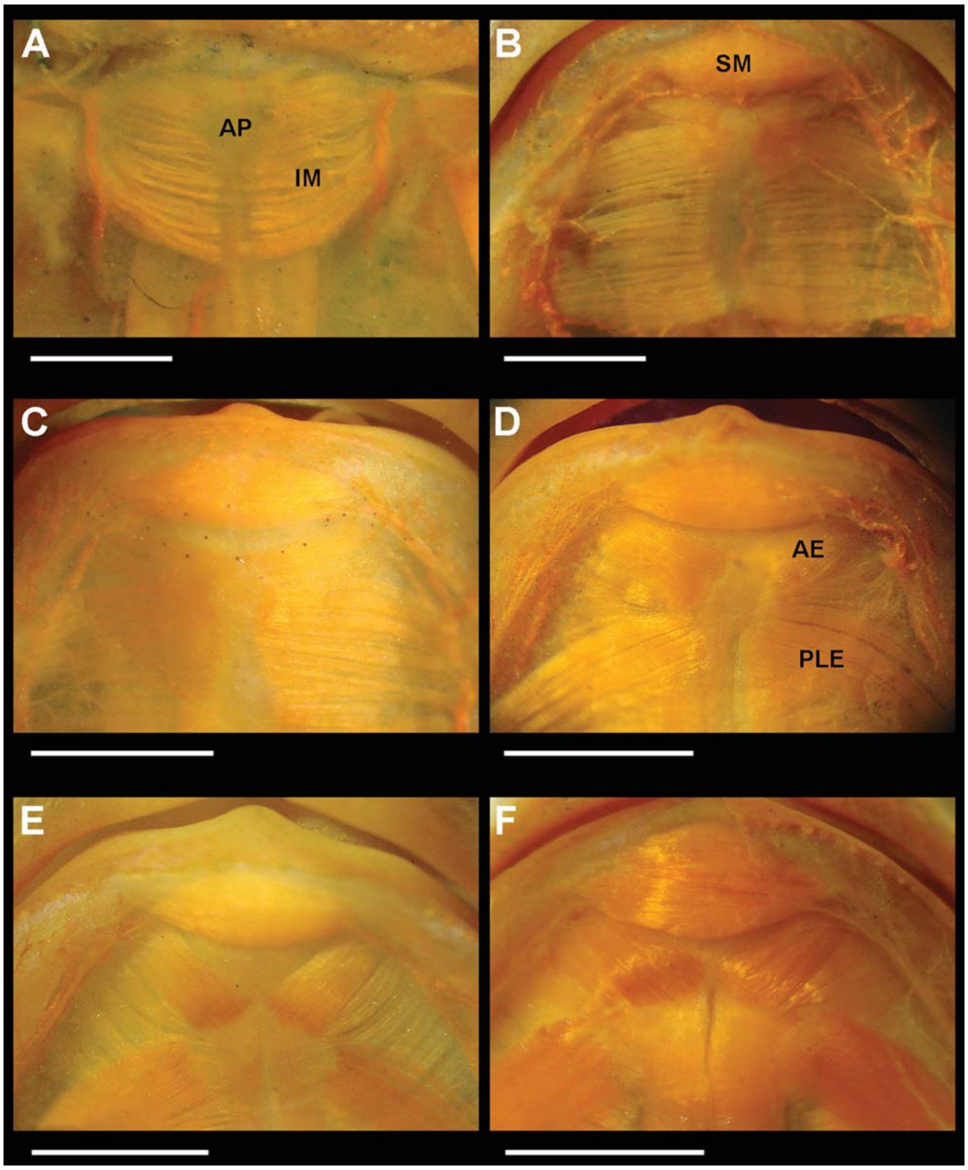

Fig. 5. The m. intermandibularis of *Phyllomedusa azurea* in ventral view at metamorphosis. (**A**) Stage 42. The most anterior fibers of the muscle are obliquely oriented and will form the supplementary apical elements of the m. intermandibularis. (**B**) Stage 44 and (**C**) Stage > 44. The apical elements are better developed and the posterolateral elements are distinguished as slips of fibers diverging posteriorly. The fibers of the principal muscle are transversely arranged, and the m. submentalis is present. (**D**) Stage 45 and (**E**) Stage > 45. The apical elements are thick muscles composed of fibers with the same orientation; the fibers are not independent from the principal element of the muscle. (**F**) Stage 46. The apical and posterolateral elements achieve their adult configuration. The most anterior fibers of the apical elements are in close contact and insert on a short median raphe. The m. submentalis has increased in width and its posterior margin is in contact with the anterior margins of the apical elements. Abbreviations as in Figure 2. Scale bars = 1 mm.

the ventromedial regions of the infrarostral cartilages. It is first evident in Stage 42 and remains separated from the m. intermandibularis until Stage 45 (Fig. 5D), at which time, the m. submentalis slightly overlaps the most apical region of this muscle.

M. intermandibularis. Originating on the medial portion of Meckel's cartilage, this muscle inserts on a median aponeurosis along with the fibers of its contralateral component; fibers are configured to form a U-shaped structure. The development of the m. intermandibularis accompanies the elongation and the rotation of the mandible, and consequently, the general configuration of the muscle changes. The fibers (especially the most caudal ones) that are disposed in a U-like pattern in tadpoles acquire a transverse arrangement at Stage 44 (Fig. 5B). The differentiation of the posterolateral elements begins at Stage 43. These elements consist of parallel fibers that lie ventrally to the principal element, from the ventral surface of the mandible to the broad, median aponeurosis. As the mandibles extend posteriorly, the fibers become more obliquely oriented, diverging posterolaterally from the cranial longitudinal axis of the cranium (Fig. 5B–F). The most anterior slips of the m. intermandibularis maintain an oblique orientation during larval development before metamorphosis; beginning at Stage 45, they become more numerous and better developed (Fig. 5D). After Stage 45, one can distinguish superficial fibers that are slightly longer than, and have similar orientation to, the underlying fibers; these superficial fibers also insert on the broad, median aponeurosis. The fibers are not independent of the principal, but their features allow them to be distinguished as a differentiated apical element.

M. interhyoideus. In tadpoles, this muscle extends between the ventral surface of the edge of the ceratohyal and a thin median aponeurosis. It is formed by parallel, transverse fibers that are broadly separated from the m. intermandibularis. As the m. intermandibularis develops, both muscles approach one another; the fusion of the principal element of this muscle with the anterior border of the m. interhyoideus begins at Stage 45, progresses in a mediolateral direction from the median aponeurosis, and continues postmetamorphically.

Three specimens of *Phyllomedusa boliviana* (FML 04949; *n* = 2; Gosner Stages 42 and 45; FML 23621; *n* = 1; Gosner Stage <46) have a similar muscle configuration. Development seems to be slower, because Stage 45 and 46 metamorphs do not yet have a thick, distinct muscle as *P. azurea* does at this stage of development.

DISCUSSION

Although Trewavas (1933) included *A. dacnicolor* (then in the genus *Phyllomedusa*) as the only phyllomedusine in her survey, she stressed that the m. intermandibularis was in too poor a condition to be studied. The first reliable observations of submandibular musculature in Phyllomedusinae were reported by Tyler (1971), who concluded that only supplementary posterolateral elements were present in Phyllomedusinae. This was corroborated by Tyler and Davies (1978), Cannatella (1980), Cruz (1990), Tyler and Duellman (1995), Mendelson et al. (2000), and Burton and Tyler (2007). Tyler (1971) and Tyler and Davies (1978) reported the same list of species. Cruz (1990) and Tyler and Duellman (1995) did not provide a list of the species that they studied. Other reports on the myology of phyllomedusines made no reference to supplementary elements (Manzano, 1995, 1997; Manzano and Lavilla, 1995). The single exception is Figure 1A of Manzano (1997), which seems to indicate the presence of both the supplementary posterolateral elements (already known at that time) and the apical elements described in this article in a schematic illustration depicting pectoral muscles in *Phyllomedusa sauvagii*.

We examined specimens of all phyllomedusine species reported by previous authors (Tyler, 1971; Cannatella, 1980; Mendelson et al., 2000) except *Agalychnis buckleyi*, *A. medinae*, *A. psilopygion*, and *A. saltator*. The apical elements of the m. intermandibularis are present in all specimens examined, despite earlier reports of their absence. In most cases, the apical elements are conspicuous and differ in form from the apical elements present in pelodryadines.

The presence of supplementary apical elements in all phyllomedusines examined (including exemplars of all five recognized genera) has phylogenetic implications and affects statements of homology. The question arises as to whether the apical elements present in pelodryadines and those in phyllomedusines are actually homologous, and more generally, whether supplementary apical and posterolateral elements are homologous, as postulated recently by some authors (Mendelson et al., 2000; Haas, 2003; Faivovich et al., 2005; Wiens et al., 2005; Frost et al., 2006; Grant et al., 2006).

The supplementary apical elements of Phyllomedusinae have a broad insertion on the fibers of the principal element of the m. intermandibularis, such that they cannot be separated from it. Therefore, apical elements are evident as a thickening of the muscle in the apical region and have fibers that usually run at a different angle from the fibers of the principal element of the muscle. In contrast, the apical elements of pelodryadines insert along a median raphe and their fibers are separate from those of the principal element of the m. intermandibularis. One peculiarity of the condition of the m. intermandibularis in phyllomedusines is the co-occurrence of apical elements and a broad aponeurosis; we have been unable to find this combination in any published account of anuran submandibular musculature (e.g., Trewavas, 1933; Burton, 1986). Perhaps, the presence or absence of the aponeurosis is correlated with the differences that we see among the elements of phyllomedusines and pelodryadines. It is worth noting that species in which the anterior portions of both apical elements are in close contact (e.g., *C. calcarifer* and *Phyllomedusa azurea*; Figs. 2B and 3D), the most anterior portion resembles a raphe, not unlike the one that occurs in pelodryadines. It is also relevant that Tyler (1971) described apical elements that meet in the median raphe in *Acris*. However, unlike pelodryadines, the apical elements of *Acris* adhere to the principal element of the m. intermandibularis similar to the condition observed in phyllomedusines.

We interpret the co-occurrence of adherent apical elements and a median raphe as clear evidence of independence of both character states. On the basis of their topography and similarity, we conclude that the supplementary apical elements found in all phyllomedusines examined are homologous with those of pelodryadines. Developmental data also support this conclusion. Differentiation of m. intermandibularis in *Phyllomedusa azurea* takes place during metamorphic climax, at stages comparable to those described by Tyler (1971) for *Litoria thesaurensis*, and which he states are representative of *L. aurea*, *L. ewingi*, and *L. wisselensis* as well. Formation of the apical element in *P. azurea* occurs through proliferation of muscular fibers at the most anterior part of the principal element, and fibers appear in an orientation similar to that of the underlying fibers. Conversely, at Stage 45 in *L. thesaurensis*, the apical element is depicted as a new sheet of fibers oriented obliquely to the principal element. In addition to the presence of the aponeurosis described above, this variation in the developmental pattern might account for the independent/fused nature of the supplementary element with respect to the principal element of the m. intermandibularis in phyllomedusines and pelodryadines.

Tyler (1971) regarded the apical and posterolateral elements as nonhomologous, because he thought that their morphological differences evidenced their independent origins. In a similar vein, but without any discussion, da Silva (1998; as published by Duellman, 2001) scored the presence and absence of each element as two different characters. In contrast, in their phylogenetic analyses, Mendelson et al. (2000), Haas (2003), Faivovich et al. (2005), Wiens et al. (2005), and Frost et al. (2006) assumed the homology of the supplementary apical and posterolateral elements. Most of these authors assumed the homology of these elements implicitly, without discussion, by including the supplementary apical and posterolateral elements as states of the same character, but an explicit justification was provided by Faivovich et al. (2005; see also Frost et al., 2006). Because our conclusions contradict the hypothesis of Faivovich et al. (2005), we consider their arguments below.

Faivovich et al. (2005) presented a phylogenetic analysis of hylids using DNA sequences from nuclear and mitochondrial genes and a dataset of foot-muscle characters extracted from Burton's (2004) observations. Although their emphasis was on Hylinae and Phyllomedusinae, Faivovich et al. (2005) included a few exemplars of Pelodryadinae. Their results strongly supported the monophyly of both Pelodryadinae and Phyllomedusinae and a sister-group relationship between the two taxa. Therefore, Faivovich et al. (2005) reasoned that it is more parsimonious to interpret the presence of supplementary elements as a putative synapomorphy of Pelodryadinae + Phyllomedusinae, rather than assuming two independent origins. In this context, there would be an ambiguity as to which of the positions of the supplementary elements (apical or posterolateral) is the plesiomorphic state. Faivovich et al. (2005) noted that this ambiguous optimization is a potential challenge to the only known morphological synapomorphy of Pelodryadinae. These arguments were cited by Frost et al. (2006).

The situation described here for phyllomedusines, in which both the apical and the posterolateral elements are present is taken to indicate that the apical and the posterolateral elements are not homologous, contra the hypotheses of Mendelson et al. (2000), Haas (2003), Faivovich et al. (2005), and Wiens et al. (2005). This reasoning might be viewed as an application of the nonconjunction rule for establishing homologies of Patterson (1982; also de Pinna, 1991). We caution that the evidence presented here has no direct bearing on the hypothesized homology of the apical and anterolateral elements, as discussed by Grant et al. (2006).

Our observations also bear on the hypothesis that the presence of apical elements is a synapomorphy of pelodryadine frogs. The possession of apical elements by phyllomedusines indicates that the presence of these structures is a synapomorphy of Pelodryadinae + Phyllomedusinae, and therefore, this character state is symplesiomorphic among pelodryadines. The adherence (phyllomedusines) or freedom (pelodryadines) of the apical elements, along with the presence of a broad aponeurosis (phyllomedusines) or a medial raphe (pelodryadines), are additional characters that may serve to delimit these groups, but the polarities of these two transformation series are unclear.

This study was aimed primarily at discerning the condition of the supplementary elements of the m. intermandibularis; nevertheless, our observations indicate the informative variation in submandibular musculature within phyllomedusines. An example of this is the morphology of the aponeurosis in the *P. hypochondrialis* group. Faivovich et al. (2010) corroborated the monophyly of this group on the basis of molecular evidence (Fig. 1). Only one putative morphological synapomorphy, with some degree of homoplasy, has been advanced in support of the group—the absence of vomerine teeth. The reduced, U-shaped aponeurosis of the m. intermandibularis, reported here, might be another synapomorphy for the group. The shape of the aponeurosis, however, is variable in *P. rohdei* (Results). The taxonomy of this species is still confusing (Faivovich et al., 2010), and it is unclear if the observed variation is intraspecific or interspecific; one specimen is a topotype from Rio de Janeiro (MNRJ 42023), whereas the other is from a population of Espírito Santo (MNRJ 40870). Moreover, this character is unknown in *P. atelopoides* and the *P. perinesos* groups, which, together with *P. tomopterna*, compose the sister taxon of the *P. hypochondrialis* group (Faivovich et al., 2010).

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MATERIAL EXAMINED. Species followed by an asterisk (*) were also studied by Tyler (1971) and Tyler and Davies (1978). The one followed by two asterisks (**) was studied by Mendelson et al. (2000). _Phrynomedusa fimbriata_ and _P. vanzolinii_ could only be studied to confirm the presence of the supplementary apical elements through previously existing dissections that did not allow to observe further details.

Agalychnis annae**: MNRJ 14633; _A. aspera_: MNRJ 35371, 42550; _A. callidryas_ *: CENAI 7796, MNRJ 49218; _A. dacnicolor_*: MNRJ 50066; _A. granulosa:_ MNRJ 50123; _Agalychnis lemur_*: AMNH 124161; _Agalychnis moreletti_: CENAI 7822, MNRJ 49228; _Cruziohyla calcarifer_: AMNH 107248; _Phasmahyla cochranae_: 61342, 64631; _P. cruzi_*: CFBH 5705, 5756; _P. exilis_: MNRJ 24633; _P. guttata_: MNRJ 4690, 41689; _P. jandaia_: MNRJ 49460, MNRJ 49690; _P. spectabilis:_ MNRJ 43077 (paratype) MNRJ 44981_; P. timbo:_ MNRJ 52065 (paratype); _Phrynomedusa appendiculata_*: MNRJ 35191; _Phrynomedusa fimbriata_*: MZUSP 619 (holotype); _Phrynomedusa marginata_: CFBH 7716, MNRJ 32861; _Phrynomedusa vanzolinii_ MZUSP 3998 (paratype); _Phyllomedusa ayeaye_: MNRJ 57656, CFBH 18420; _P. azurea_: CFBH 4429, 14181, 21380, FML 452 (ontogenetic series), MACN 40062, 40065, 40068, 40070, MNRJ 13650, 13661, 13663, 17870; _P. bahiana_*: CFBH 1447, MNRJ 50212; _P. boliviana_: FML 04949, 23621 (ontogenetic series), MACN 9831, 9839, MNRJ 44204; _P. bicolor_*: MNRJ 52970; _P. burmeisteri_*: CFBH 4024, 11080, MNRJ 27494; _P. camba_: CFBH 21724, MNRJ 44204; _P. distincta_: CFBH 11067, 13558, MNRJ 19314, 54652; _P. hypochondrialis_: CFBH 8150, 21439, 21449, MNRJ 40404; _P. iheringi_*: CFBH 21911, MNRJ 18782; _P. nordestina:_ CFBH 7329, 7330, 16327, 18762, MNRJ 9889, 13618, 44940; _P. rohdei_*: CFBH 9036, 11954, 17280, MNRJ 8011, 10375, 10377, 10378, 56167, SAMA 4858; _P. sauvagii_: CFBH 2572, MACN 38148, MNRJ 19386; _P._

*tarsius**: CFBH 2453, 2454, 2457; *P. tetraploidea*: CFBH 1795, 2599, MACN 35058, 37796, MNRJ 18704, 19409; *P. tomopterna*: CFBH 1880, 4455; *P. trinitatis*: MNRJ 32965; *P. vaillanti:* CFBH 21717, MNRJ 42728.