

Comparative anatomy and homology of jaw adductor muscles of some South Asian colubroid snakes (Serpentes: Colubroidea)

SUNANDAN DAS * & KOUSIK PRAMANICK

Department of Life Sciences, Presidency University, Kolkata – 700073, West Bengal, India — *Corresponding author: sdassnake@gmail.com

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Abstract

We studied jaw adductor muscles in eighteen species of South Asian colubroid snakes and presented a comparative account of their anatomy. The deepest layer of external adductor appears to be a composite of adductor mandibulae externus medialis and profundus fibres and caenophidians are characterized by an attenuation of the former muscle which may be correlated with the development of a derived type of mandible. Our observations further suggest that, though highly reduced, fibres homologous to adductor mandibulae externus medialis may be present in at least some colubroids with a bodenaponeurosis. Some hitherto unreported features pertaining to levator anguli oris and pterygomandibularis of some studied elapid, colubrine colubrid and ahaetuliine colubrid genera are also described.

Key words

Jaw adductor, snakes, Colubroidea, anatomy, musculature, adductor mandibulae externus, adductor internus, adductor posterior, levator anguli oris, pterygomandibularis.

Introduction

Jaw adductor muscles of snakes have been found to be useful in taxonomy and inferring phylogenies (e.g. McDOWELL, 1967, 1969, 1972; CUNDALL *et al.*, 1993; LEE & SCANLON, 2002; SCANLON & LEE, 2004; KHARIN & CZEBLUKOV, 2009). However, homology of snake jaw muscles has long been a subject of debate amongst anatomists (HAAS, 1973; McDOWELL, 1986; ZAHER, 1994). In the last decade, several studies (e.g. DIOGO, 2008; DIOGO *et al.*, 2008; DIOGO & ABDALA, 2010) identified homologues of jaw adductor muscles across all major tetrapod lineages and in the light of homology hypotheses offered in those studies, DAZA *et al.* (2011) presented an account of jaw adductor musculature of all major, extant Lepidosaurian clades. Recently JOHNSTON (2014) further clarified the homology relationships of external jaw adductors between snakes and lizards. This study supports the hypothesis of homology put forward by McDOWELL (1986).

Unfortunately, the knowledge of jaw adductor musculature of South Asian colubroid snakes has remained meagre, so much that the anatomy of these muscles is not known for even many common genera. Furthermore, over the last few decades many species were found to be species complexes and have been revised (for instance, Asian *Naja*: WÜSTER & THORPE, 1992), making it difficult to understand exactly which species was used for older anatomical studies. We take the opportunity of a better understanding of the homology of jaw adductors to describe the anatomy of external, internal and posterior jaw adductors of eighteen species of South Asian colubroid snakes. These information can be utilized not only in systematics but also in studies of comparative anatomy, discrete phenotypic trait evolution and functional morphology. We also discuss the homology of the snake jaw adductors on the basis of our own dissections and literature survey.

Material and Methods

Snake specimens used for the current study belong to the Presidency University Zoology Museum (PUZ), Kolkata (India). Following species were examined: Colubridae – *Ahaetulla nasuta* (LACÉPÈDE, 1789), *Amphiesma stolatum* (LINNAEUS, 1758), *Argyrogena fasciolata* (SHAW, 1802), *Boiga trigonata* (SCHNEIDER in BECHSTEIN, 1802), *Chrysopelea ornata* (SHAW, 1802), *Dendrelaphis tristis* (DAUDIN, 1803), *Lycodon aulicus* (LINNAEUS, 1758), *Oligodon arnensis* (SHAW, 1802), *Ptyas mucosa* (LINNAEUS, 1758), *Xenochrophis piscator* (SCHNEIDER, 1799); Homalopsidae – *Enhydris enhydris* (SCHNEIDER, 1799); Elapidae – *Bungarus caeruleus* (SCHNEIDER, 1801), *Bungarus fasciatus* (SCHNEIDER, 1801), *Hydrophis obscurus* DAUDIN, 1803, *Hydrophis schistosus* DAUDIN, 1803, *Naja kaouthia*, Lesson, 1831, *Naja naja* (LINNAEUS, 1758); Viperidae – *Daboia russelii* (SHAW & NODDER, 1797). For sake of comparison one non-caenophidian snake – the erycine boid *Eryx johnii* (RUSSELL, 1801) and four lizards, namely the gekkonid *Hemidactylus flaviviridis* RÜPPELL, 1835, agamid *Calotes versicolor* (Daudin, 1802), scincid *Lygosoma albopunctata* (GRAY, 1846) and varanid *Varanus flavescens* (HARDWICKE & GRAY, 1827) were also dissected. Whenever possible, we dissected more than one specimen of a species. Taxonomic identities of those species which underwent taxonomic revision since the publication of WHITAKER & CAPTAIN (2004) were reconfirmed prior to dissection using diagnoses and keys provided in revisions (VOGEL & DAVID, 2006 for *Xenochrophis* and MOHAPATRA *et al.*, 2017 for *Ahaetulla*). Registration numbers of all examined specimens are given in the Appendix. Family level taxonomy follows PYRON *et al.* (2013).

Dissections and observations were carried out under GOKO MIAMB and ZEISS Stemi 2000C dissecting binocular microscopes. Lugol's iodine solution was used to determine direction of muscles fibres in small specimens. Identification and terminology of external adductors follow MCDOWELL (1986) and JOHNSTON (2014) except for the deepest layer of external adductors which we term here 'adductor mandibulae externus medialis-profundus' for reasons elaborated in the Discussion section. Identification of internal and posterior adductor follows DAZA *et al.* (2011) and MCDOWELL (1986). Homology determination, whenever required, was done on the basis of criteria given by PATTERSON (1982). Osteological terminology follows CUNDALL & IRISH (2008).

Abbreviations

AEM – adductor mandibulae externus medialis; AEMP – adductor mandibulae externus medialis-profundus; AEP – adductor mandibulae externus profundus; AES – adductor mandibulae externus superficialis; AP – adductor posterior; BAPO – bodenaponeurosis; CG – compressor glandulae; LAO – levator anguli oris; PS – pseudotemporalis; PTM – pterygomandibularis; VG – venom gland; V₂ – maxillary branch of trigeminal nerve; V₃ – mandibular branch of trigeminal nerve.

Results

Comparative account of jaw adductor muscles

Levator anguli oris: This is the most superficial layer in all snakes examined (Fig. 1, 2). LAO originates from postorbital and anterior parietal in *Ah. nasuta*, *Ar. fasciolata*, *B. trigonata*, *C. ornata* and *P. mucosa* among colubrids and the homalopsid *E. enhydris* (Fig. 1B, 1C, 1D, 2B). The origin of LAO is restricted to the postorbital in *D. tristis*, *O. arnensis*, *X. piscator* and probably also in *Am. stolatum* (condition of this specimen was bad) (Fig. 2A). In *L. aulicus*, the postorbital is lacking (as was seen in a dried skull examined by us) and in this species LAO takes origin from the parietal, including the postorbital process of that bone (Fig 1A). In most of the aforesaid species the LAO fibres are directed posteroventrally and ends on a thin aponeurosis on the slip of AES (this aponeurosis ends on the ventrolateral edge of compound bone, below AES). However, in *C. ornata*, *D. tristis* and *O. arnensis*, the LAO turns rostrad upon reaching the rictus oris and insert on the lateral side of the compound bone, only partially covering the slips of AEMP and AES. Anterior fibres of LAO turn somewhat anteroventral upon reaching rictus oris in *P. mucosa* and *Ar. fasciolata* but does not contact compound bone (Fig. 1B, 1D). The viperid *D. russelii* shows an interesting condition where the LAO origin is separated from postorbital by superficially visible levator pterygoidei and PS (Fig. 1F), a condition also reported for *D. siamensis* by KOCHVA (1962) (KOCHVA probably worked with *D. siamensis* as he reported a distinct occipital head of depressor mandibulae in his specimens whereas *D. russelii* specimens examined by us lack that feature). In this species the LAO is a narrow muscle which originates from the parietal rostral to the anterior end of supratemporal, runs posteroventrally to pass through a loop formed by the CG part of AES, turns rostrad at the corner of the mouth and inserts on compound bone, immediately anterior to CG. In elapids the LAO acts as a CG and is horizontally divided, the dorsal part being more robust. The dorsal part originates from the small postorbital and parietal (very few anterior fibres originate from the gland itself) in *B. caeruleus*. The site of origin of the LAO in *B. fasciatus* is similar to that of its congener but while in the latter a sizable portion of the AEMP head is visible in superficial view, the LAO covers a large part of the head of the AEMP in *B. fasciatus*, leaving only a little part of the latter muscle visible. Therefore, the *B. caeruleus* LAO is of *Glyphodon* type *sensu* MCDOWELL (1986) while the condition of that muscle in *B. fasciatus* is intermediate between *Glyphodon* and *Oxyuranus* types of the same author. In *B. fasciatus*, very few anterior fibres from the dorsal part of the LAO passes medial to VG but do not insert over its tunic and eventually reach the anterior side of the ventral part of LAO whereas in *B. caeruleus* dorsal and ventral parts of the LAO are completely horizontally subdivided. The fibres of the dor-

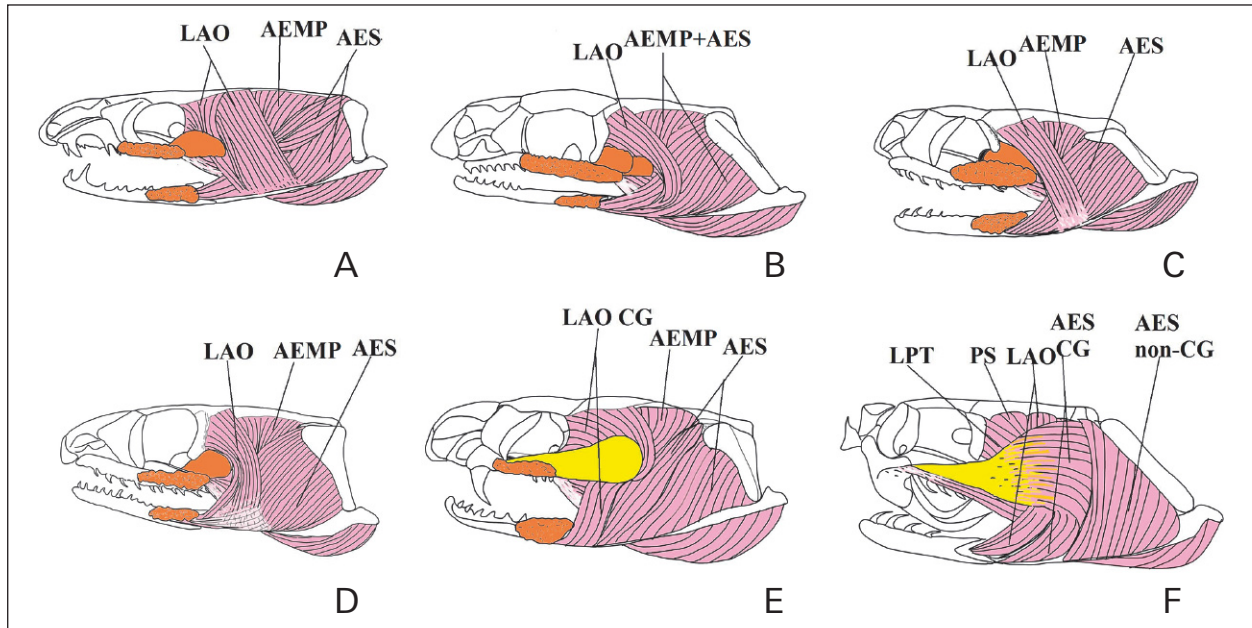


Fig. 1. Schematic diagrams of adductor mandibulae externus of **A.** *Lycodon aulicus*, **B.** *Argyrogena fasciolata*, **C.** *Boiga trigonata*, **D.** *Ptyas mucosa*, **E.** *Bungarus caeruleus*, **F.** *Daboia russelii*. Yellow – venom gland, brown – other glands, for abbreviations see Material and Methods.

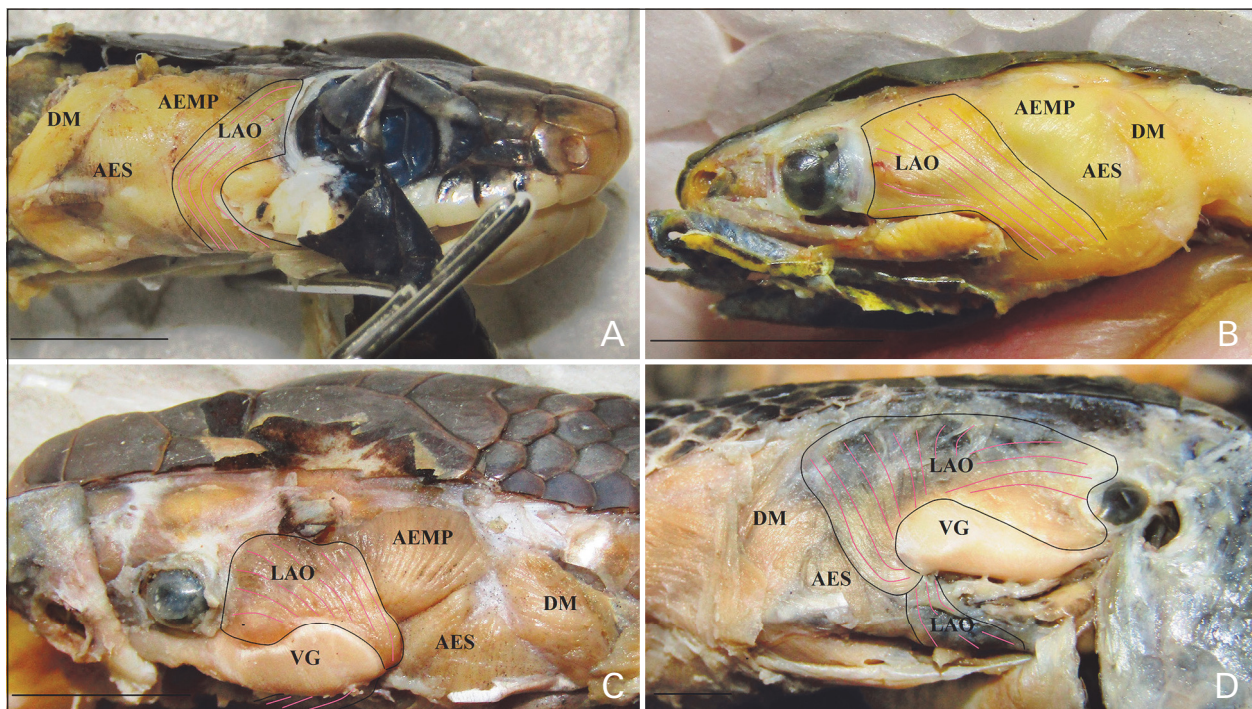


Fig. 2. Superficial layer of muscles (levator anguli oris and external adductors) on lateral side (right lateral view in A. and D. and left lateral view in B. and C.) of head after removal of skin and associated tissues, showing different types of LAO muscles (outlined with black and direction of fibres shown by the pink lines) and their position with respect to other adductors and depressor mandibulae (DM): **A.** *Dendrelaphis tristis*, origin of LAO mostly limited to postorbital; **B.** *Enhydryis enhydryis*, LAO origin includes anterior parietal besides postorbital; **C.** *Bungarus caeruleus*, LAO forms CG and horizontally divided (only the upper part is shown in the figure); LAO leaves a sizable portion of AEMP head visible; **D.** *Hydrophis obscurus*, LAO forms CG and is horizontally divided; LAO conceals AEMP and also the quadrate head of DM; Abbreviations as in Material and Methods; scale bar 5 mm.

sal part of LAO are directed posteroventrally and insert on the dorsal, dorsomedial and posteromedial surfaces of VG while the ventral part originates from the ventral and ventromedial parts of VG and inserts on the lateral side of

compound bone in *Bungarus*. The site of origin of the dorsal part of the LAO, direction of fibres and their insertion in *N. kaouthia* and *N. naja* are like those of *Bungarus*. The LAO mostly covers the head of the AEMP as in *B. fas-*

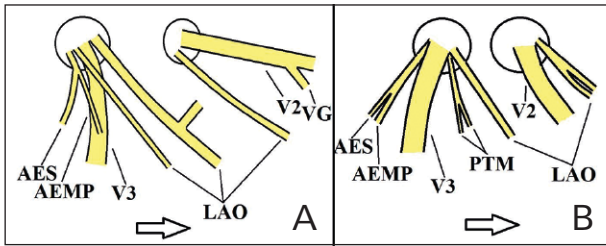


Fig. 3. Schematic diagrams of the trigeminal innervation pattern of jaw adductors (innervation to all components not shown) of A. *Bungarus caeruleus* and B. *Enhydryis enhydryis*; these two species differs from most other species in possessing a double innervation of LAO – one emerging from the anterior trigeminal foramen while the other exits through the posterior trigeminal foramen. Abbreviations as in Material and Methods; the arrowhead points toward the anterior side of head.

ciatus though no fibres are continuous between the dorsal and ventral parts. The ventral part originates from the ventromedial side of VG and inserts on the lateral side of compound bone, slightly overlapping AEMP and AES. The dorsal part of LAO originates from postorbital, parietal and supraoccipital in the two species of *Hydrophis* examined. In these species the LAO covers the head of the AEMP and the quadrate head of depressor mandibulae (depressor mandibulae has a quadrate and an occipital head in both *H. obscurus* and *H. schistosus*). The anterior fibres are directed posteroventrally while the posterior fibres are anteroventrally oriented (Fig. 2D). The insertion of those fibres to the VG is like that in *Naja* while the origin and insertion of the ventral part of LAO resemble the condition in *Bungarus*. McDOWELL (1972) illustrated (see figure 1 of that paper) the LAO of *H. obscurus* as covering neither the AEMP nor the depressor mandibulae which is clearly different to what is described here.

The LAO of *E. enhydryis* and *B. caeruleus* receives double innervations – one exiting through the anterior and another (two in *B. caeruleus*) from the posterior trigeminal foramen (Fig. 3). The posterior one is an anterior branch from V_3 while the other one is a branch from V_2 in *E. enhydryis* and either from V_2 or from V_3 in *B. caeruleus*. If the branch exiting through the anterior trigeminal foramen really represents a branch from V_3 in *B. caeruleus* then it will be the second species known to have such an innervation besides *Anomochilus weberi* (CUNDALL & ROSSMAN, 1993).

We have given a first account of the anatomy of LAO of several species here (this also applies to other muscles described below). Apart from the unusual innervation pattern observed in a homalopsid and an elapid, the presence of uninterrupted muscle fibres, which are dissociated from VG tunic, in the LAO of a terrestrial elapid, *B. fasciatus*, is noteworthy.

Adductor mandibulae externus: The AES is the superficial component of this complex. In all colubrid, homalopsid and elapid taxa studied, the AES originates from the anterior side of the quadrate and its anteroventrally directed fibres insert on the lateral side (surangular) of the compound bone (Fig. 1). The AES is distinctly pinnate in *L. aulicus* and *B. caeruleus* (Fig. 1A, 2C) whereas it is only slightly so in *B. fasciatus*. The anterior part of the pinnate muscle is less extensive than the posterior part and originates mainly from the cephalic condyle of the quadrate whereas the latter part arises from the shaft of this bone. Upon reaching lower jaw the direction of fibres

from both parts becomes more parallel to each other and the muscle inserts on the lateral side of the compound bone. AES is not very clearly separable from AEMP in *Ah. nasuta*, *Ar. fasciolata*, *B. trigonata*, *P. mucosa* and *H. schistosus*. However, there seems to exist intraspecific variation in this characteristic, for example among two *Ah. nasuta* specimens dissected AES and AEMP are less clearly separable in PUZ 179 than in PUZ uncatalogued. AES is clearly divisible into two parts in *D. russelii* – the anterior CG part originates from the dorsal and lateral side of the VG, loops around this gland and finally run anteroventrally, inserting on the lateral side of compound bone whereas the non-CG part takes origin from the quadrate and its anteroventrally running fibres insert on the lateral side of compound bone just behind the slip of CG part (Fig. 1F). In none of the studied taxa did fibres attributable to the AES insert on BAPO.

AEMP originates from the braincase immediately dorsal and rostral to the supratemporal (mainly parietal and some posterior fibres from the supraoccipital) and from the supratemporal itself in those colubrids and elapids where AEMP and AES are separable. In *E. enhydryis* AEMP originates from the supraoccipital above the supratemporal and meet its fellow on the midline of cranium. AEMP of *D. russelii* is a narrow strip of muscle that originates from the parietal just above the supratemporal. AEMP fibres descend ventrally and anteroventrally (some anterior fibres may initially run posteroventrally for some length) to insert on the dorsolateral side of mandible rostral to the adductor fossa (a few may enter the adductor fossa in *L. aulicus* where this fossa is very well developed) in all colubroids studied by us except *D. russelii* where AEMP inserts on the mouth lining at the angle of jaw just above the lower lip. A distinct BAPO is present in *L. aulicus*, *B. caeruleus*, *N. kaouthia* and *H. obscurus* (Fig. 4) and such a structure seems to be present in a specimen of *X. piscator* (the only specimen dissected was not in good condition). In all the species mentioned above BAPO is the most well developed in *L. aulicus* followed by *B. caeruleus* and *N. kaouthia* and it was least developed is *H. obscurus*. The BAPO is attached to the dorsal side of the compound bone rostral to the adductor fossa. The majority of AEMP fibres insert on the mandible medial to BAPO in *L. aulicus* and *N. kaouthia* but very few posterior fibres attach lateral to BAPO, near the dorsal edge of this aponeurosis.

Adductor internus: PS and PTM are the two components of adductor internus. PS originates from the lateral

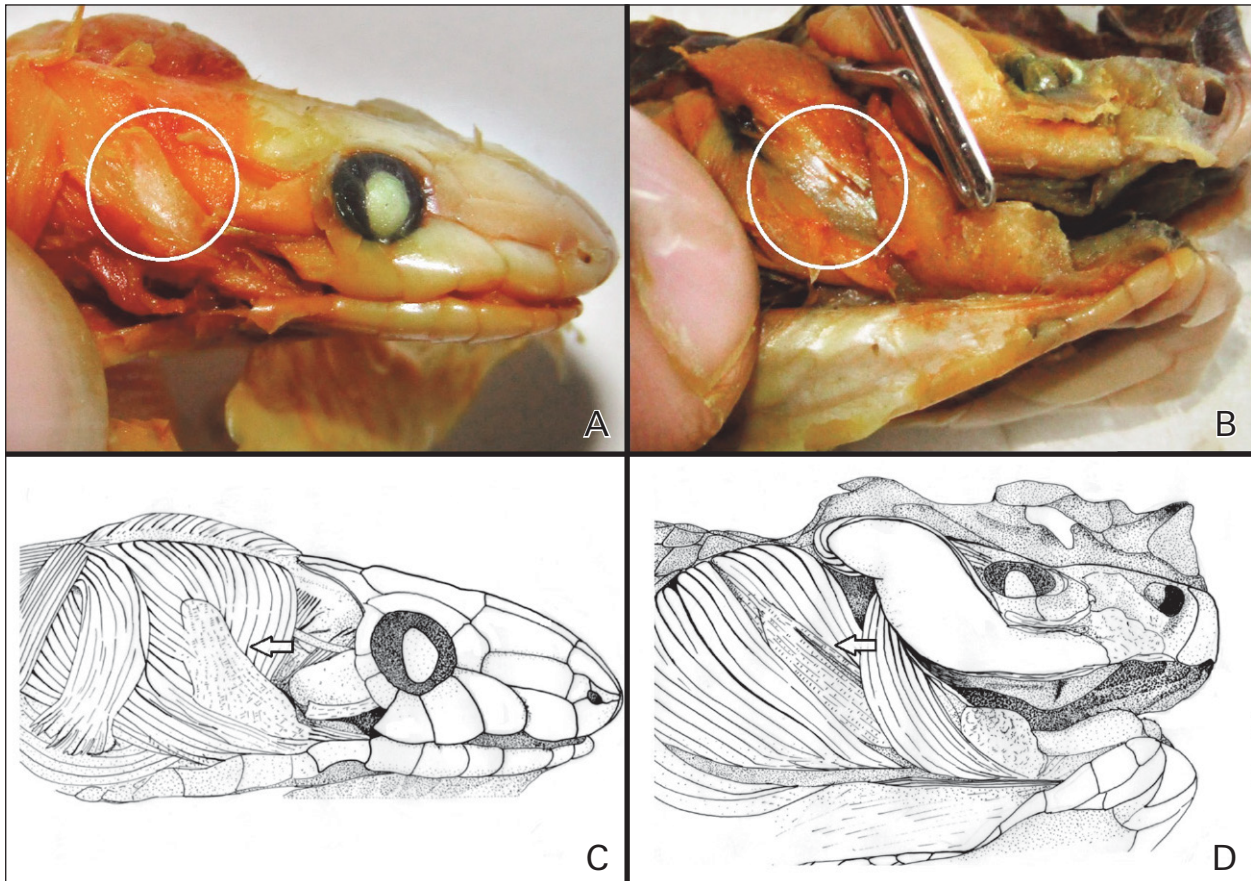


Fig. 4. Bodenaponeurosis (indicated by circle in photo and arrow in drawing) in **A.** and **C.** *Lycodon aulicus* (right lateral view; after removal of a few fibres attaching lateral to bodenaponeurosis, along the posterodorsal part of the aponeurosis); **B.** and **D.** *Bungarus caeruleus* (right lateral view).

wall of parietal caudal to the postorbital and descends in a ventral or somewhat posteroventral direction and insert on mandible beneath the slip of AEM. This muscle is a thin, narrow strip of muscle and located medial to the maxillary branch of the trigeminal nerve and the LAO in the species studied. Only in *D. russelii* this muscle's origin is visible in superficial view.

PTM, however, presents a greater amount of variation (Fig. 5). The dorsal side of pars major of PTM gives rise to several fibres inserting to the ventromedial part of the mandible immediately rostrad to the origin of accessorius fibres in *B. trigonata* and *P. mucosa* and these may represent vestigial pars minor. *Ar. fasciolata*, *L. aulicus*, *B. caeruleus* and *B. fasciatus* have a pars minor but so much intermingling of fibres occurs between this part and pars major that making clear cut distinction between these two parts is not possible (Fig. 5A, 5E). In those species, the pars minor fibres show a fleshy origin on the dorsal and dorsolateral surfaces of the ectopterygoid. *O. arnensis* and *E. enhydris* have distinct pars minor originating over ectopterygoid and inserting to the ventromedial side of the mandible in front of PTM accessorius insertion (Fig. 5D). In all the taxa studied the pars major originates tendinously from the lateral side of the anterior lateral process of ectopterygoid and inserts to the ventral side of the retroarticular process of mandible.

All colubrids, homalopsid and viperid have the origin at ectopterygoid-maxilla junction. In elapids the tendinous origin starts from the angulation of ectopterygoid and extends anteriorly up to ectopterygoid-maxilla articulation in *N. kaouthia* and *N. naja* whereas it stops behind last maxillary teeth in *B. caeruleus* and *B. fasciatus* (Fig. 5E) and stops short of ectopterygoid-maxilla joint in *H. obscurus* and *H. schistosus*. All the species possess a PTM accessorius which originates from the ventral surface of the quadrate ramus of pterygoid and inserts to the ventromedial side of mandible, below articular (Fig. 5). In genera *Ahaetulla*, *Chrysopelea* and *Dendrelaphis*, all placed in the recently erected subfamily Ahaetuliinae (FIGUEROA *et al.*, 2016), a few fibres of PTM accessorius and some fibres inserting on the dorsal side of the PTM arise from the shaft of ectopterygoid (Fig. 5B).

Adductor posterior: This muscle shows the least variation among all the species examined. It arises from the anteromedial side of quadrate, beneath AES in transverse plane and behind the mandibular ramus of the trigeminal nerve. The fibres are directed anteroventrally in all taxa except *B. trigonata* where it is somewhat posteroventral or almost straight ventrally directed (owing to more posteroventrally slanted quadrate and more posteriorly placed adductor fossa on mandible so that no part of that

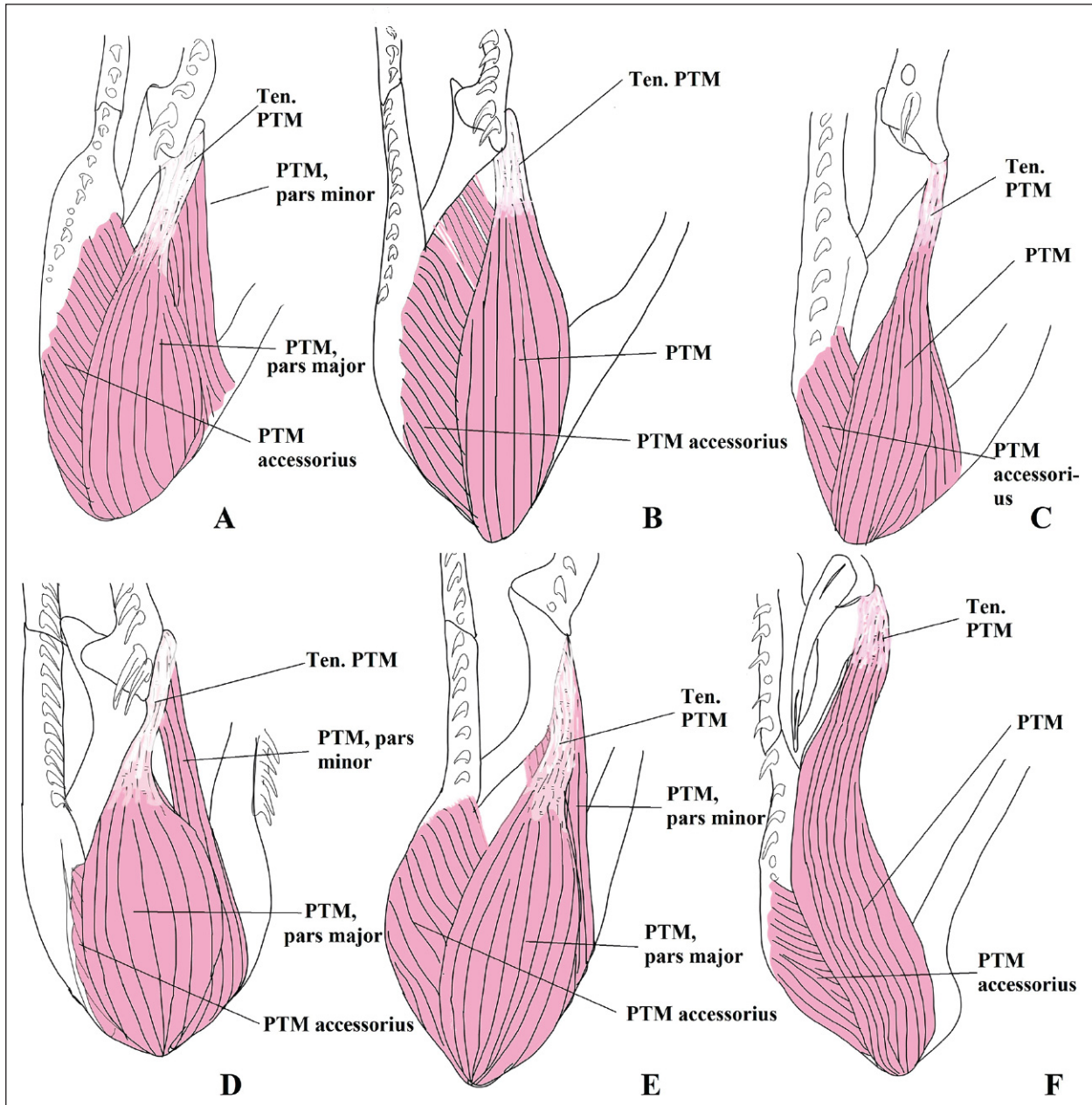


Fig. 5. Schematic diagrams of PTM and associated structures in A. *Argyrogena fasciolata*, B. *Dendrelaphis tristis*, C. *Boiga trigonata*, D. *Enhydryis enhydryis*, E. *Bungarus caeruleus*, F. *Daboia russelii*. PTM inserts tendinously (Ten. PTM) on the anterior lateral process of ectopterygoid. Abbreviations as in Material and Methods; scale bar 5 mm.

fossa lies anterior to cephalic condyle of quadrate). The fibres insert in the adductor fossa and on dorsal edge of the prearticular crest of the compound bone.

Discussion

Homology and evolution of caenophidian jaw adductors

The homology of external adductors have generated a lot more debate than any other jaw adductors of snakes.

The traditional practice was to call the anterior-most, superficial layer as AES, medial and deepest part as AEM and the posterior-most component superficial to 'AEM' as AEP (e.g. FRAZZETTA, 1966; MCDOWELL, 1967; HAAS, 1973; CUNDALL, 1987). Anatomists, however, noted problems with this system (e.g. HAAS, 1973) and many of them (RIEPEL, 1980; MCDOWELL, 1986; ZAHER, 1994; JOHNSTON, 2014) attempted to rectify it. Solutions offered by RIEPEL (1980) and ZAHER (1994) conflict with that of MCDOWELL (1986) and JOHNSTON (2014). We, however, believe that a combination of some elements from both viewpoints makes the most plausible homology hypothesis. Furthermore, even though morphologists repeatedly cautioned against using the traditional identification of

external adductors, the older scheme still occasionally appears in literature, especially in those papers not specifically dealing with musculature (e.g. JACKSON *et al.*, 2017). Hence, we think a reemphasis is necessary. As HAAS (1973) and ZAHER (1994) already summarized variations of the external adductors in various snake families, the variations will not be discussed here and instead we keep our discussion of external adductors focused on the issue of their homology.

The LAO is no longer regarded as part of the A2 group of muscles in tetrapods (DIOGO *et al.*, 2008; DAZA *et al.*, 2011) and therefore is not really a division of the external adductors. In *Sphenodon* and lizards the LAO is the most superficial layer, originating from the upper temporal arch and occasionally also the quadrate and inserting on the rictal plate (OELRICH, 1956; RIEPPEL, 1980; DAZA *et al.*, 2011; present study). The most superficial layer in snakes generally originates from postorbital and anterior parietal, runs posteroventrally and usually ends on the slip of the posterior most division of external adductors (regarded here as AES). We homologize this superficial layer with the LAO of *Sphenodon* and lizards, as did MCDOWELL (1986) and JOHNSTON (2014), for following reasons – 1. fibres from an anterior division of this muscle or the so called ‘1a’ group of fibres often insert on the rictal plate (HAAS, 1973) but fibres constituting the posterior part or ‘1b’ has also been observed to insert on the rictal plate in *Cylindrophis* and *Uropeltis* (RIEPEL, 1980). JOHNSTON (2014) listed this as a reason behind homologizing this muscle with LAO. We would like to add here that seldom even in species possessing an undivided muscle, some fibres may insert on rictal plate, as FRAZZETTA (1966) observed in *Python*; 2. coronoid, surangular and lateral side of BAPO are the insertion sites of AES in *Sphenodon* and lizards (DAZA *et al.*, 2011) but in snakes the most superficial layer most commonly inserts over the posterior most division of external adductor and only infrequently inserts on the lateral side of compound bone (mainly in Elapidae); 3. the muscle in question never shows anteroventral fibre orientation from origin to insertion typical of *Sphenodon* and lizard AES but runs posteroventrally, a point also noted by MCDOWELL (1986); 4. in *Daboia palaestinae* and *Natrix natrix*, the most superficial muscle was shown to develop somewhat earlier than other external adductors by KOCHVA (1963) and RIEPPEL (1988) respectively. This was noted by JOHNSTON (2014). In fact, it lends support to the idea that this muscle may not be a division of external adductors; 5. In *Lanthanotus*, a member of Toxicofera clade to which Serpentes belong (PYRON *et al.*, 2009), an anterior branch from V₃ innervates LAO (figure 7 of RIEPPEL, 1980). Be it basal alethinophidian or advanced caenophidian lineages, it is always a nerve branch anterior to V₃ which innervates the most superficial muscle layer (RIEPEL, 1980; ZAHER, 1994; present study).

The argument presented also makes it clear that the posterior-most layer of external adductor, which originates from the quadrate, runs anteroventrally and inserts on the surangular component of the compound bone (a

few anterior fibres may insert lateral to BAPO) and thus perfectly resembles the AES of *Sphenodon* and lizards, is indeed the AES. In caenophidians, this muscle commonly inserts on the surangular, even when divided into two parts (e.g. in *Lycodon aulicus* and *Bungarus caeruleus*). Therefore, in our opinion MCDOWELL (1986) correctly identified this muscle as the AES in caenophidians.

The deepest layer of external adductor was identified as the AEM by MCDOWELL (1986) and JOHNSTON (2014) whereas RIEPEL (1980) concluded that it is actually a composite of AEM and AEP fibres, a viewpoint supported by ZAHER (1994). HAAS (1973) wrote that most snakes lack a BAPO, an opinion subsequently echoed by MCDOWELL (1986) and JOHNSTON (2014). However, our own dissections and the observations made by ZAHER (1994) clearly demonstrates that not only members of basal alethinophidian lineages but also many ‘booids’ and several caenophidians possess a distinct BAPO. In *Sphenodon* and lizards, AEP fibres always insert medial to the BAPO (OELRICH, 1956; HAAS, 1973; RIEPEL, 1980; MORO & ABDALA, 2000; ABDALA & MORO, 2003; DAZA *et al.*, 2011) and therefore the insertion of AEP medial to the BAPO is a more or less conserved trait. We concur with RIEPEL (1980) and ZAHER (1994) that fibres medial to the BAPO in snakes, where the latter structure is present, are, in all probability, homologous to the lizard AEP. Muscle fibres which descend vertically and attach lateral to the BAPO were identified by RIEPEL (1980) and ZAHER (1994) as homologous to the AEM (‘adductor mandibulae externus medialis, pars anterior’ of ZAHER, 1994). Though the slip of the AEM remains separated from the slip of the AEP by the BAPO when it is present, the heads of the muscles cannot be separated and AEP and AEM fibres cannot be differentiated when the BAPO is absent. A well developed AEM (the ‘pars anterior’ of ZAHER) has been found in Aniliidae, Uropeltidae, Anomochilidae, Cylindrophiiidae, Xenopeltidae, Loxocephalidae, Pythonidae, Boidae and Bolyeriidae whereas it is extremely reduced (although may not be altogether absent, see the description for *Lycodon* and *Naja*; presence of very few fibres attaching lateral to BAPO in these species [especially *Lycodon*] raises the possibility that even caenophidians without BAPO may possess homologues of these fibres) in Tropidophiidae and Caenophidia (RIEPEL, 1980; ZAHER, 1994; present study). For the reasons discussed above, we call this muscle AEMP, which most probably is a composite of AEM and AEP (with a much higher contribution of AEP fibres, especially in the Caenophidia).

Why did the fibres homologous to the AEM of *Sphenodon* and lizards become so much reduced – to point of being almost absent – in Caenophidia? All alethinophidians except caenophidians and some tropidophiids possess a coronoid bone and a coronoid process (CUNDALL & IRISH, 2008), characteristics also possessed by *Sphenodon* and lizards (EVANS, 2008). Many of those snakes, especially the members of families Aniliidae, Anomochilidae, Cylindrophiiidae, some uropeltids and booids, have relatively heavy mandible and interestingly the AEM

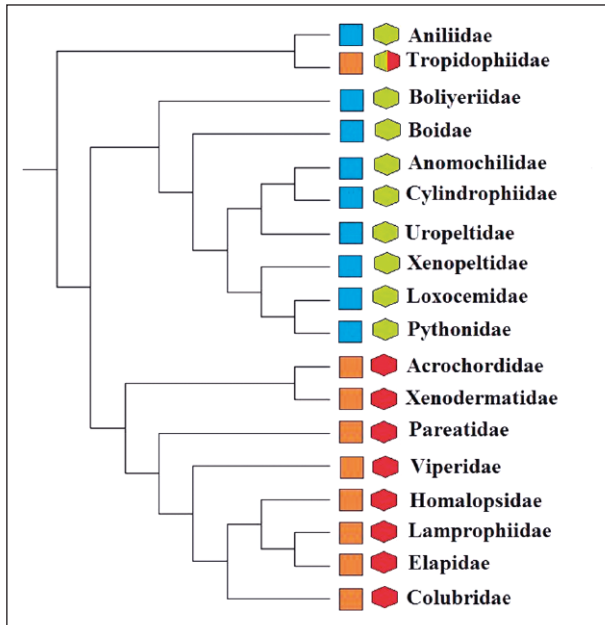


Fig. 6. Phylogenetic tree of alethinophidian snakes (simplified after PYRON *et al.*, 2013) showing the distribution of two character states, namely a well developed AEM (pars anterior of AEM of ZAHER, 1994) and different types of mandible. Blue square – well developed AEM, orange square – AEM fibres very much reduced, green hexagon – primitive type of mandible possessing a coronoid bone and often a coronoid process, red hexagon – advanced type of mandible, characterized by the lack of the aforesaid components.

part (ZAHER's pars anterior of AEM) is well developed in these snakes with a primitive, lizard-like mandible (i.e. with a prominent coronoid process and coronoid bone). It seems likely that higher amount of force required to adduct a heavier mandible resulted in retention of a well developed AEM in lizards and members of many basal alethinophidian lineages while a lighter, streamlined mandible and development of alternative efficient mechanisms of subduing prey in Caenophidia might have resulted in reduction of AEM fibres (Fig. 6). Moreover, teeth act as prey snaring organ in caenophidian snakes (and in most snakes for that matter) and a wider jaw opening is more important for macrostomatan snakes – therefore bite force is also not important (in fact, lizards, possessing a primitive mandible and distinct AEM, are capable of generating higher bite force than a colubrid snake, PENNING, 2017). Macrostomatan mode of feeding might have also been a factor in producing the modifications seen in the caenophidian jaw adductors.

Amongst internal adductors it is undoubtedly the PTM which underwent modifications during the evolution of alethinophidians. Whereas the tendinous origin of PTM does not usually reach ectopterygoid-maxilla junction in alethinophidians 'below' Caenophidia (e.g. FRAZZETTA, 1966; RIEPPEL, 1980; CUNDALL & ROSSMAN, 1993), it does so, albeit with exception, in caenophidians (e.g. MCDOWELL, 1986; UNDERWOOD & KOCHVA, 1993; CUNDALL, 1986; DEUFEL & CUNDALL, 2003; present study) and this anterior shift in attachment site appears

to be a derived state. Another important state is the presence of pars minor. Such a division, though probably incomplete, is indicated only in *Tropidophis* among basal alethinophidians lineages (see figure 8 in MCDOWELL, 1986). Pars minor, either fully separate or vestigial / incompletely separate, is present sporadically among members of Caenophidia. If *Tropidophiidae* is really a basal alethinophidian lineage, as recovered in molecular phylogenetic studies (e.g. PYRON *et al.*, 2013; FIGUEROA *et al.*, 2016; STREICHER & WIENS, 2016), then the aforementioned structure might have evolved independently in *Tropidophiidae* and Caenophidia. UNDERWOOD & KOCHVA (1993) opined that pars minor fibres are the homologues of the medial fibres of the undivided PTM but we suggest, on the basis of observations presented by MCDOWELL (1986) and our own dissections, it would be more appropriate to homologize the pars minor with dorsomedial fibres of an undivided PTM. Another interesting situation is where some PTM fibres attach on the tunic of the VG, as seen in African file snakes (currently classified in four genera – *Gonionotophis*, *Gracililima*, *Limaformosa* and *Mehelya* – by BROADLEY *et al.*, 2018) of the family Lamprophiidae, some crotaline viperids and possibly also the elapid *Dendroaspis* (BISESWAR, 1981; MCDOWELL, 1986). This, however, seems to be independently derived. The other component of adductor internus, the PS, does not show any major modifications or reorganizations. The same can be said for the adductor posterior.

Areas in need of further research

Anatomy of jaw adductors of the vast majority of snake genera remains unstudied. Aspects of cephalic musculature of elapids and viperids (especially viperine viperids), however, are relatively well studied (e.g. KOCHVA, 1958; YOUNG, 1987; GOPALAKRISHNAKONE & KOCHVA, 1990). Unfortunately snakes belonging to other more speciose clades have never been that well studied. DIOGO & ABDALA (2010) argued that characters from musculature may be more conservative than osteology and therefore useful for inferring deeper level phylogenies. However, the total evidence analyses often rely on secondary sources for data and in order to integrate myological data more into total evidence datasets we must have such data available. Furthermore, RIEPPEL (1988) stressed upon the importance of developmental information on jaw adductors of non-caenophidian taxa but unfortunately we still lack data on this issue. Aforesaid facts demonstrate the need to carry out thorough work on descriptive anatomy and developmental biology of cephalic musculature of a diverse array of snakes.

Conclusions

LAO and components of adductor mandibulae externus shows a number of modifications in different colubroid

snake families. The modification of LAO and AES is mostly associated with their role as CG in studied elapid and viperid taxa while the presence or absence of a bode-naponeurosis is the most notable variation associated with AEMP in the colubroids studied. We support the homology hypothesis of RIEPPEL (1980) and ZAHER (1994) for AEMP whereas our dissections support the conclusions reached by McDOWELL (1986) and JOHNSTON (2014) when it comes to LAO and AES. The presence of a well developed AEM may be correlated with a primitive type of mandible. In Caenophidia, AEM fibres are very much reduced in number or almost absent. PTM is the most variable component of adductor internus and we found a poorly differentiated pars minor in *Bungarus*. Such a structure has not so far been reported for members of family Elapidae. Several fibres from dorsal side of PTM and PTM accessorius attach to ectopterygoid shaft in the members of Ahaetuliinae subfamily and this may serve as an anatomical diagnostic character for this subfamily. Adductor posterior shows a stable morphology in different families.

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References

- ABDALA, V. & MORO, S. (2003). A cladistic analysis of ten lizard families (Reptilia: Squamata) based on cranial musculature. *Russian Journal of Herpetology*, **10**, 53–73.
- BISESWAR, R. (1981). The jaw musculature of *Dendroaspis angusticeps* and *Dendroaspis polylepis polylepis* (Ophidia, Proteroglypha) with some remarks on the venom apparatus. *South African Journal of Zoology*, **16**, 101–108.
- BROADLEY, D. G., TOLLY, K. A., CONRADIE, W., WISHART, S., TRAPE, J., BURGER, M., KUSAMBA, C., BOULOU, A. Z. & GREENBAUM, E. (2018). A phylogeny and genus-level revision of the African file snakes *Gonionotophis* Boulenger (Squamata: Lamprophiidae). *African Journal of Herpetology*, **67**, 43–60.
- CUNDALL, D. (1986). Variations of the cephalic muscles in the colubrid snake genera *Entechinus*, *Ophiodryis* and *Symphimus*. *Journal of Morphology*, **187**, 1–21.
- CUNDALL, D. (1987). Functional morphology, pp. 106–140 in: SEIGEL, R. A., COLLINS, J. T. & NOVAK, S. S. (eds.) *Snakes. Ecology, and evolutionary biology*. New York, McGraw-Hill Publishing Company.
- CUNDALL, D. & ROSSMAN, D. A. (1993). Cephalic anatomy of the rare Indonesian snake *Anomochilus weberi*. *Zoological Journal of the Linnean Society*, **109**, 235–273.
- CUNDALL, D., WALLACH, V. & ROSSMAN, D. A. (1993). The systematic relationships of the snake genus *Anomochilus*. *Zoological Journal of the Linnean Society*, **109**, 275–299.
- CUNDALL, D. & IRISH, F. (2008). The snake skull, pp. 349–692 in: GANS, C., GAUNT, A. S. & ADLER, K. (eds.) *Biology of the Reptilia*. Vol. 20. New York, Society for the Study of Amphibians and Reptiles.
- DAZA, J. D., DIOGO, R., JOHNSTON, P. & ABDALA, V. (2011). Jaw adductor muscles across lepidosaurs: a reappraisal. *The Anatomical Record*, **294**, 1765–1782.
- DEUFEL, A. & CUNDALL, D. (2003). Feeding in *Atractaspis* (Serpentes: Atractaspididae): a study in conflicting functional constraints. *Zoology*, **106**, 43–61.
- DIOGO, R. (2008). Comparative anatomy, homologies and evolution of mandibular, hyoid and hypobranchial muscles of bony fish and tetrapods: a new insight. *Animal Biology*, **58**, 123–172.
- DIOGO, R., ABDALA, V., LONERGAN, N. & WOOD, B. A. (2008). From fish to modern humans – comparative anatomy, homologies and evolution of the head and neck musculature. *Journal of Anatomy*, **213**, 391–424.
- DIOGO, R. & ABDALA, V. (2010). *Muscles of vertebrates. Comparative anatomy, evolution, homologies and development*. Enfield, Science Publishers.
- EVANS, S. (2008). The skull of lizards and tuatara, pp. 1–347 in: GANS, C., GAUNT, A. S. & ADLER, K. (eds.) *Biology of the Reptilia*. Vol. 20. New York, Society for the Study of Amphibians and Reptiles.
- FIGUEROA, A., MCKELVY, A. D., GRISMER, L. L., BELL, C. D. & LAILVAUX, S. P. (2016). A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PloS ONE*, **11**, e0161070.
- FRAZZETTA, T. H. (1966). Studies on the morphology and function of the skull in the Boidea (Serpentes). Part II. Morphology and function of the jaw apparatus in *Python sebae* and *Python molurus*. *Journal of Morphology*, **118**, 217–296.
- GOPALAKRISHNAKONE, P. & KOCHVA, E. (1990). Venom glands and some associated muscles in sea snakes. *Journal of Morphology*, **205**, 85–96.
- HAAS, G. (1973). Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata, pp. 285–490 in: GANS, C. & PARSONS, T. S. (eds.) *Biology of the Reptilia*. Vol. 4. New York, Academic Press.
- JACKSON, T. N. W., YOUNG, B., UNDERWOOD, G., MCCARTHY, C. J., KOCHVA, E., VIDAL, N., WEERD, L. V. D., NABUURS, R., DOBSON, J., WHITEHEAD, D., VONK, F. J., HENDRIKX, I., HAY, C. & FRY, B. G. (2017). Endless forms most beautiful: the evolution of ophidian oral glands, including the venom system, and the use of appropriate terminology for homologous structures. *Zoomorphology*, **136**, 107–130.
- JOHNSTON, P. (2014). Homology of the jaw muscles in lizards and snakes – a solution from a comparative gnathostome approach. *The Anatomical Record*, **297**, 574–585.
- KHARIN, V. E. & CZEBLUKOV, V. P. (2009). A revision of the sea snakes of subfamily Hydrophiinae. 1. tribe Disteirini nov. (Serpentes: Hydrophiidae). *Russian Journal of Herpetology*, **16**, 183–202.
- KOCHVA, E. T. (1958). The head muscles of *Vipera palaestinae* and their relation to the venom gland. *Journal of Morphology*, **102**, 23–53.
- KOCHVA, E. (1962). On the lateral jaw musculature of the Solenoglypha with remarks on some other snakes. *Journal of Morphology*, **110**, 227–271.
- KOCHVA, E. (1963). Development of the venom gland and trigeminal muscles in *Vipera palaestinae*. *Acta Anatomica*, **52**, 49–89.
- LEE, M. S. Y. & SCANLON, J. D. (2002). Snake phylogeny based on osteology, soft anatomy and ecology. *Biological Reviews*, **77**, 333–401.
- MCDOWELL, S. B. (1967). *Aspidomorphus*, a genus of New Guinea snakes of the Family Elapidae, with notes on related genera. *Journal of the Zoological Society of London*, **151**, 497–543.
- MCDOWELL, S. B. (1969). *Toxicocalamus*, a New Guinea genus of snakes of the family Elapidae. *Journal of the Zoological Society of London*, **159**, 443–511.
- MCDOWELL, S. B. (1972). The genera of sea-snakes of the *Hydrophis* group (Serpentes: Elapidae). *Transactions of the Zoological Society of London*, **32**, 189–247.
- MCDOWELL, S. B. (1986). The architecture of the corner of the mouth of colubroid snakes. *Journal of Herpetology*, **20**, 353–407.

- MOHAPATRA, P. P., DUTTA, S. K., KAR, N. B., DAS, A., MURTHY, B. H. C. K. & DEEPAK, V. (2017). *Ahaetulla nasuta anomala* (Annandale, 1906) (Squamata: Colubridae), resurrected as a valid species with marked sexual dichromatism. *Zootaxa*, **4263**, 318–332.
- MORO, S. & ABDALA, V. (2000). Cladistic analysis of the Teiidae (Squamata) based on mycological characters. *Russian Journal of Herpetology*, **7**, 87–102.
- OELRICH, T. (1956). The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Miscellaneous Publications, Museum of Zoology, University of Michigan, **94**, 1–122.
- PATTERSON, C. (1982). Morphological characters and homology, pp. 21–74 in: JOYSEY, K. A. & FRIDAY, A. E. (eds.) *Problems in phylogenetic reconstruction*. London, Academic Press.
- PENNING, D. A. (2017). The scaling of bite force and constriction pressure in kingsnakes (*Lampropeltis getula*): Proximate determinants and correlated performance. *Integrative Zoology*, **12**, 121–131.
- PYRON, R. A., BURBRINK, F. T. & WIENS, J. J. (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, **13**, 1–53.
- RIEPEL, O. (1980). The trigeminal jaw adductors of primitive snakes and their homologies with the lacertilian jaw adductors. *Journal of the Zoological Society of London*, **190**, 447–471.
- RIEPEL, O. (1988). The development of the trigeminal jaw adductor musculature in the grass snake *Natrix natrix*. *Journal of the Zoological Society of London*, **216**, 743–770.
- SCANLON, J. D. & LEE, M. S. Y. (2004). Phylogeny of Australasian venomous snakes (Colubroidea, Elapidae, Hydrophiinae) based on phenotypic and molecular evidence. *Zoologica Scripta*, **33**, 335–366.
- STREICHER, J. W., WIENS, J. J. (2016). Phylogenomic analyses reveal novel relationships among snake families. *Molecular Phylogenetics and Evolution*, **100**, 160–169.
- UNDERWOOD, G. & KOCHVA, E. (1993). On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). *Zoological Journal of the Linnean Society*, **107**, 3–64.
- VOGEL, G. & DAVID, P. (2006). On the taxonomy of the *Xenochrophis piscator* complex (Serpentes, Natricidae), pp. 241–246 in: VENCES, M., KÖHLER, J., ZIEGLER, T. & BÖHME, W. (eds.) *Herpetologia Bonnensis II*. Proceedings of the 13th Congress of the Societas Europaea Herpetologica. Bonn, Societas Europaea Herpetologica.
- WHITAKER, R. & CAPTAIN, A. (2004). *Snakes of India. The field guide*. Chennai, Draco books.
- WÜSTER, W. & THORPE, R. (1992). Asiatic cobras: population systematics of the *Naja naja* species complex (Serpentes: Elapidae) in India and central Asia. *Herpetologica*, **48**, 69–85.
- YOUNG, B. A. (1987). The comparative cephalic osteology and myology of three species of sea snakes. *Zoologische Jahrbücher, Ableitung für Anatomie und ontology der Tiere*, **116**, 421–452.
- ZAHER, H. (1994). Comments on the evolution of the jaw adductor musculature of snakes. *Zoological Journal of the Linnean Society*, **111**, 339–384.

Appendix

List of specimens examined for the present study

(Localities, where available, is mentioned within square bracket beside registration numbers)

Ahaetulla nasuta (PUZ 179 [‘Deulti, West Bengal, India’], PUZ uncatalogued); *Amphiesma stolatum* (PUZ uncatalogued); *Argyro-gena fasciolata* (PUZ 322); *Boiga trigonata* (PUZ 332 [‘West Bengal, India’]); *Bungarus caeruleus* (PUZ 327 [‘India’]); *Bungarus fasciatus* (PUZ 175); *Chrysopelea ornata* (PUZ 186); *Calotes versicolor* (PUZ uncatalogued – 2 examples); *Daboia russelii* (PUZ 186A and 186B); *Dendrelaphis tristis* (PUZ 334 [‘Jessore, Bengal’ – currently Bangladesh]); *Enhydryis enhydryis* (PUZ 144); *Eryx johnii* (PUZ 333 [‘Rajasthan, India’]); *Hemidactylus flaviviridis* (PUZ uncatalogued [‘Presidency College Campus, Kolkata, West Bengal’]); *Hydrophis obscurus* (PUZ 328 [‘River mouth, 24 parganas, Bengal’ – currently south 24 paragana district, West Bengal, India]); *Hydrophis schistosus* (PUZ 331 [‘Chandipur, Orissa, India’]); *Lycodon aulicus* (PUZ 325A and 325B, PUZ uncatalogued); *Lygosoma albopunctata* (PUZ uncatalogued); *Naja kaouthia* (PUZ 324 [‘Burdwan, West Bengal, India’]); *Naja naja* (PUZ 192 [‘Madras, India’ – currently Chennai, India]); *Oligodon arnensis* (PUZ 326A and 326B); *Ptyas mucosa* (PUZ 193, PUZ uncatalogued); *Varanus flavescens* (PUZ 199); *Xenochrophis piscator* (PUZ 195).