

The adductor mandibulae in *Elaphe* and related genera (Serpentes: Colubridae)

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Abstract. In this paper I describe the jaw adductor musculature in colubrid snakes that formerly belonged to the genus *Elaphe* Fitzinger. The group studied shows a high level of homoplasy, and particular lineages exhibit a mixture of advanced and primitive characters. The presence of the levator anguli oris in this group is questioned.

Introduction

The head anatomy of snakes has been a subject of numerous studies and the trigeminal musculature has attracted significant attention (e.g. Haas, 1973; Rieppel, 1980; Zaher, 1994). However, most of these studies have been purely descriptive and the comparisons were on a family rather than generic level. There are only a few studies dedicated to comparisons of closely related species, of *Thamnophis* (Cowan and Hick, 1951; Varkey, 1979), *Heterodon* (Weaver, 1965), *Entechinus*, *Opheodrys* and *Symphimus* (Cundall, 1986).

In this paper I present preliminary results of my studies of the jaw adductor musculature of *Elaphe* and its allies. I describe the jaw adductors and present their evolution based on a recently published reconstruction of their phylogeny. Also I discuss the 'levator anguli oris' problem.

Materials and methods

I studied the following species: *Coronella austriaca* (IZK 400-403), *Elaphe dione* (ZMB 31427), *E. quatuorlineata* (ZMB 63769), *E. quadrivirgata* (ZMB 66114), *E. schrenckii* (IZK 362-363), *Gonyosoma oxycephala* (IZK 331-333, MNHUWr unnumbered specimen), *Lampropeltis getula* (BB 008, IZK 385-386), *L. mexicana* (IZK 394) *L. triangulum* (IZK 358, MNHUWr unnumbered specimen), *Oreocryptophis porphyraceus* (ZMB 48053), *Orthriophis taeniurus friesi* (BB 042-043, IZK 365-366), *Pantherophis guttatus* (BB 015-016, 044), *Zamenis longissimus* (IZK 338, 364), *Z. situla* (IZK 384, MNHUWr 2 unnumbered specimens). The institution abbreviations are as follows: ZMB – Museum für Naturkunde, Humboldt-Universität, Berlin, IZK – Laboratory of Vertebrate Zoology Collection, University of

Wrocław, MNHUWr – Natural History Museum, University of Wrocław, BB – author's collection.

The homologies of muscles were established on the basis of their aponeuroses and topography. I follow the terminology proposed by Zaher (1994). The phylogeny I used in this studies is based on the recent papers by Rodriguez-Roblez and De Jesus-Escobar (1999), Helfenberger (2001), Lenk et al. (2001) Utiger et al. (2002, 2005) (Fig. 1). Character states were analyzed using McClade 4.03 software (Maddison and Maddison, 2001).

Results

The studied taxa show a typical colubrid pattern of the adductor mandibulae (fig. 2 a, b), as described by Albright and Nelson (1959). The main differences are the sites of origins, insertions and the aponeurotic pattern. The only two muscles that do not show variation in the studied group are the superficialis and profundus parts of the adductor posterior.

The main variation of the musculus adductor mandibulae externus superficialis proper involves its aponeurotic pattern and insertion sites (fig. 2 c). This muscle passes in postero-ventral direction and curves around the mouth corner behind the Harderian gland. In this area this muscle is tightly covered by tissue in the mouth corner, although there are no fibers inserting there. The externus adductor superficialis inserts either via its aponeurosis only, or via aponeurosis and directly to the compound bone. I haven't found any divisions of this muscle in the studied specimens. Musculus adductor mandibulae externus medialis shows variation in the pattern of its subdivision by the quadrate aponeurosis. In some cases this muscle is undivided, divided in two, or in three slips by the quadrate aponeurosis. These slips are clearly distinguished near the muscle origin, but in the ventral part they become indistinguishable. Musculus adductor mandibulae externus profundus shows interspecific variation in the origin. The

bodenaponeurosis is reduced, but present. Musculus pseudotemporalis shows variation in the pattern of origin, which can be on the parietal, parietal and occipital or parietal and postorbital.

The externus adductor medialis evolved from undivided or divided (2 subdivisions) conditions, and both scenarios are equivocal. All North American forms I studied have this muscle subdivided in two parts, and some of the Euro-Asiatic species, too. Taking into account the early divergence of Euro-Asiatic and North American lineages (e.g. Utiger et al. 2002), I suggest the primitive character state for this group is the subdivision of this muscle in two parts. The Nearctic species retain the primitive condition, and some Palearctic species have evolved independently the undivided condition or subdivided on three parts several times. The broad aponeurotic insertion of superficial externus adductor is the primitive condition. The North American forms, except *L. triangulum*, show a tendency towards a narrower insertion on the compound bone only (type II and III). Such reduction is also seen in not closely related *C. radiatus*, *E. dione*, *E. schrenckii*

and *Z. longissimus*. The hypothesis of the primitive condition of the insertion of superficial externus adductor only via its aponeurosis or the insertion of superficial externus adductor via aponeurosis and directly to the compound bone requires the same number of steps, but the first condition is more common among the studied taxa.

I cannot say which lineages of the studied group are more morphologically conservative. All studied species show a mixture of primitive and advanced characters, both myological and osteological (Borczyk, unpublished data). To resolve this problem more species have to be studied and more characters used.

Discussion

The adductor mandibulae of the studied colubrid genera is highly variable, which may reflect the adaptive plasticity of this group. However, most of the variations involve changes in relative position and shape of origins and insertions of this muscles, but it does not produce any major changes in muscle arrangement. It is possible that the observed

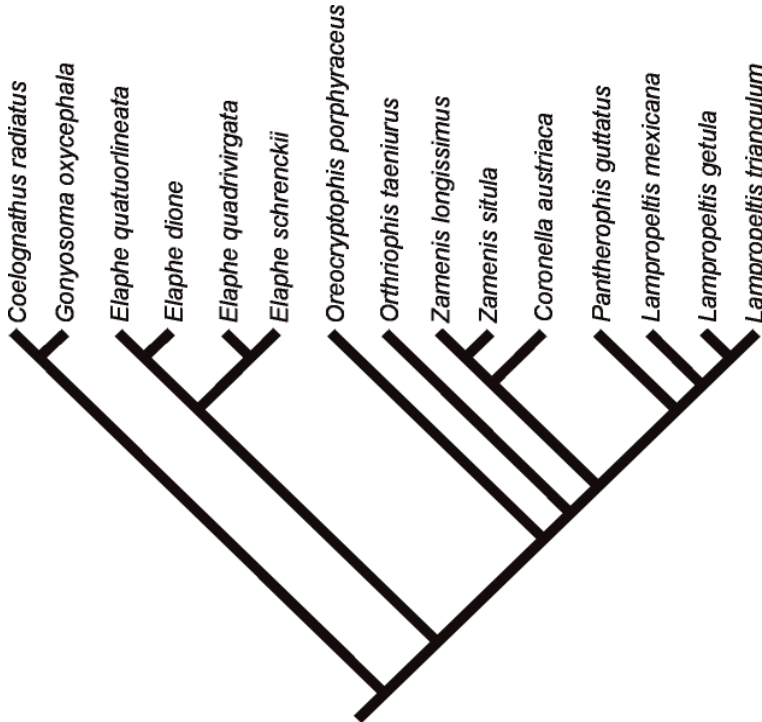
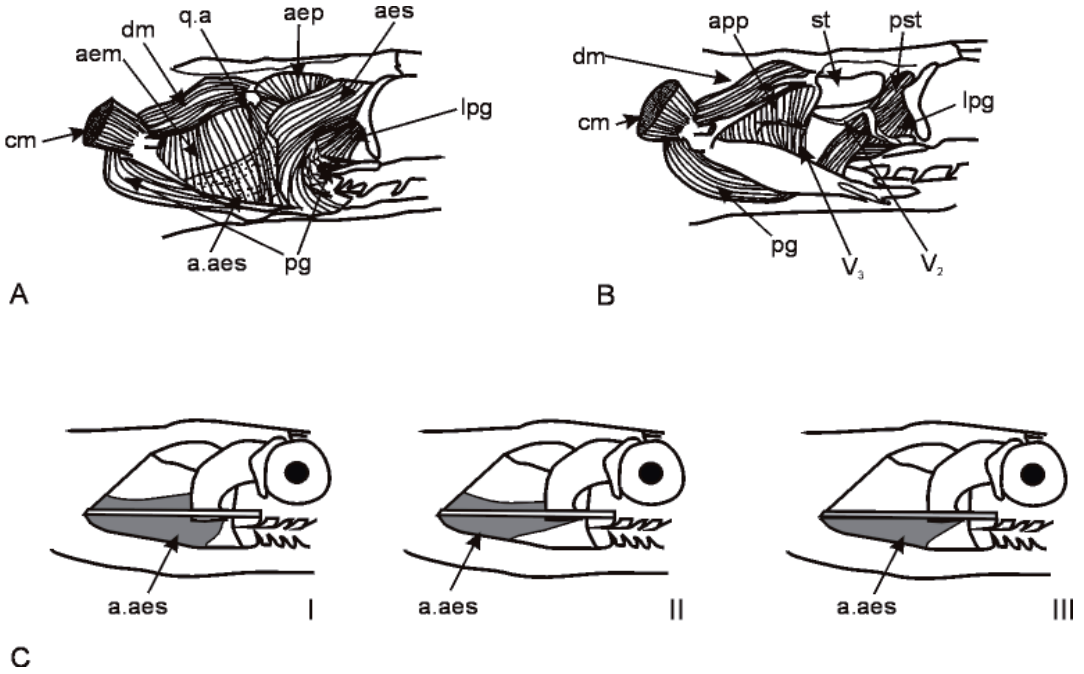


Figure 1. The phylogenetic relationships of studied species. The phylogeny used here is based on the recent papers by Rodriguez-Roblez and De Jesus-Escobar (1999), Helfenberger (2001), Lenk et al. (2001) and Utiger et al. (2002, 2005).

Figure 2. The jaw adductors of *Elaphe schrenckii* (IZK 362). A) The skin, Harderian and labial glands and quadrato-maxillary ligament removed. B) External adductors and adductor mandibulae posterior superficialis removed. C) Schematic representation of the three basic types of aponeurotic insertions of the adductor externus superficialis. Abbreviations: a.aes – aponeurosis of superficial external adductor; aes – m. adductor mandibulae externus superficialis proper; aem – m. adductor mandibulae externus medialis; aep – m. adductor mandibulae externus profundus; app – m. adductor mandibulae posterior profundus; cm – m. cervicomandibularis; lpg – m. levator pterygoidei; pg – m. pterygoideus; pst – musculus pseudotemporalis; q.a – quadrate aponeurosis; V₂ – maxillary branch of the trigeminal nerve; V₃ – mandibular branch of the trigeminal nerve.



differences in the origins, insertions and aponeurotic pattern are of little functional significance, and thus are easily accumulated during evolution. The direction of the fibers is similar in all studied species, and factors favouring the parallel fibers arrangements can limit greater variability (Cundall, 1986). The posterior adductors are constant in their arrangement. I suggest that the reason is space constraint. They originate on the antero-ventral part of the quadrate, and insert in the mandibular fossa (the superficial posterior adductor) and the profundus posterior adductor inserts on the medial part of the compound bone. Anteriorly, these muscles are constrained by the mandibular branch of the trigeminal nerve and profundus external adductor. The space constraints are believed to limit the arrangement of muscles near the mandibular articulation (e.g. Elzanowski, 1993). The levator anguli oris (LAO) is a problematic muscle in terms of its homology with the lacertilian

LAO as well as its homology among snake taxa (Zaher, 1994). The lacertilian LAO originates on the edge of the lateral temporal fenestra and inserts on to the rictal plate. The snake LAO originates on the parietal/postorbital and inserts to the rictal plate (Rieppel, 1980 McDowell, 1986). Underwood (1967) reported the superficialis inserting on the lower jaw and lower lip or rictal plate in *Coronella austriaca*, *E. quatuorlineata*, *Z. longissimus* but I have not found any insertions on the rictal plate and only in the smooth snake (*Coronella austriaca*) I found the insertion on the lower jaw. Also in *E. quatuorlineata* studied, there was no insertion of superficialis on the compound bone. This suggests a polymorphism in the attachment of this muscle. I have not found any fibers inserting on the rictal plate in the studied species, as the muscle inserts via its aponeurosis. In some cases the adductor superficialis inserts directly on the compound bone and via its aponeurosis. In addition, this muscle

does not form any slip distinct from the rest of the muscle. The distribution of character states of insertion of the superficial external adductor shows either the multiple origins of this condition or a loss in closely related species.

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