The jaw musculature of *Dendroaspis angusticeps* and *Dendroaspis polylepis polylepis* (Ophidia, Proteroglypha) with some remarks on the venom apparatus

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The venom apparatus in both species of *Dendroaspis* shows great similarity to that described in other proteroglyphs. There is a posterior bulbous portion or main gland and an anterior narrower portion, the accessory gland, that surrounds the secretory duct. The gland is enclosed in a very tough connective tissue capsule. Fibres from the m. adductor externus superficialis insert on the connective tissue capsule on the dorsal aspect of the venom gland. They serve to compress the gland and expel the venom when the snake strikes. Ventrally, fibres of the m. pterygoideus are also inserted on the investing sheath. This muscle supports the gland ventrally and also appears to play some role in venom ejection. The arrangement of the jaw musculature is similar in both species of *Dendroaspis*. Since the m. adductor externus superficialis is closely associated with the venom gland it has become highly specialized and exhibits great variation among snakes. This muscle in *Dendroaspis* differs from that in other proteroglyphs in the extension of its origin in a ventral direction over the postorbital bone to the maxilla. As in other elapids, the m. levator anguli oris is absent in both species of *Dendroaspis*.

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Die gifapparaat in beide ondersoekte spesies van *Dendroaspis* toon groot ooreenkoms met apparate soos by ander Proteroglypha beskryf. Daar is 'n agterste bolvormige deel of hoofklier en 'n voorste smaller gedeelte, die bykomstige klier, wat die afskeidingsbuis omring. Die klier is voorsien van 'n taai bindweefselomhulsel. Vesels van die m. adductor externus superficialis heg aan die bindweefselomhulsel dorsaal van die gifklier en dien om die klier saam te druk sodat die gif uitspuit wanneer die slang byt. Ventraal heg daar ook vesels van die m. pterygoideus aan die bindweefselomhulsel. Hierdie spier stut die klier aan die onderkant en dit wil voorkom asof dit ook 'n rol by gifejeksie speel. Die rangskikking van die kaakspiere is baie eenders by die twee ondersoekte spesies. Omdat die m. adductor externus superficialis baie nou met die gifklier geassosieerd is, het dit hoogs gespesialiseerd geraak en toon dit ook baie groot variasie by slange. Die spier by *Dendroaspis* verskil van dié by ander Proteroglypha deurdat die dorsale oorsprong verder ventraal uitgebrei het, nl. oor die postorbitaalbeen tot op die maksilla. Die m. levator anguli oris is soos by alle ondersoekte Elapidae ook afwesig by *Dendroaspis*.

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Many significant contributions have been made on aspects of the ophidian feeding mechanism, the ejection of venom and the capture and ingestion of relatively large prey. It is evident from the literature on the cranial muscles of snakes that more attention has been given to the Solenoglypha and comparatively little has been done on the Proteroglypha. It was primarily for this reason that a comparative study of the morphological and functional aspects of the jaw muscles and the venom apparatus of two species of *Dendroaspis* was undertaken.

The study of ophidian jaw musculature is difficult and confusing because of several different terminologies that exist in the literature. In the present descriptions of the jaw muscles of *Dendroaspis*, Kochva's (1962) version of muscle nomenclature has been adopted. The muscles have been described in the sequence in which they appear during dissection rather than on the basis of nervous innervation.

The origins and insertions of the muscles were determined mainly from transverse serial sections although the heads of some adult specimens were also dissected.

Material and Technique

A batch of newly laid eggs of *D. polylepis polylepis* was obtained from the Fitzsimons Snake Park, Durban. These were kept in damp soil at room temperature. The embryos (ranging from 10 to 50 days) were fixed in Allen's fluid and after washing with 70% alcohol were preserved in 70% alcohol. After embedding in paraffin wax, the heads of the embryos were sectioned at 10 μm. The serial transverse sections of the earlier embryos, ranging from 10 to 30 days, were stained with haematoxylin and acid fuchsin with fairly good results. The older embryos were stained in Mallory's triple stain. This staining technique produced very good results and gave exceedingly clear differentiation of the structures and tissues. A complete set of slides of the head of a late embryo of *D. angusticeps*, stained in Bismarck brown and eosin, was lent to me by Professor A.L. Smit of the Department of Zoology, University of Durban-Westville. This series of sections and 50-day-old embryos of *D. polylepis polylepis* formed the basis for the comparative study of the venom apparatus and jaw musculature.

Drawings were made with the aid of a micro-projector. A few adult heads of both species were dissected for the observation of the jaw muscles and the nerves innervating them.

Description of the venom apparatus and jaw muscles

Venom apparatus

In *Dendroaspis*, a pair of deeply grooved poison fangs are situated at the anterior end of the maxillary bone. In a few adult specimens of *D. polylepis polylepis* examined, two pairs of poison fangs, instead of the normal one pair, were visible on the maxilla. In late stages of both *D. polylepis polylepis* and *D. angusticeps*, the prefrontal appears to be hinged rather than fused to the frontal. The maxilla is also not firmly attached to the prefrontal. There is also a loose connection between the maxilla and ectopterygoid. The anterior portion of the m. adductor externus superficialis is attached by means of a strong ligament to the postero-dorsal projection of the maxilla. Muscular attachments are also present on the ectopterygoid and pterygoid bones. All these facts suggest that the maxilla in *Dendroaspis* is capable of a certain amount of movement.

The shape and location of the venom gland in both species of *Dendroaspis* is similar. It is a prominent structure lying along the border of the upper lip and extending behind the orbit. In both species, it is formed from a posterior bulbous portion or main gland and an anterior narrower portion, the accessory gland, that surrounds the secretory duct (Figure 1). At the level of the postorbital bone, the gland narrows considerably and a slender portion continues anteriad below the orbit. The gland terminates in a very short duct at the base of the fang. The main venom gland has a dorsal enlargement and is enclosed in a very tough connective tissue capsule. Medially, strong ligaments connect the gland to the postorbital and parietal bones and laterally, it is attached at several points by means of connective tissue to the dermis of the skin. Fibres from the m. adductor externus superficialis portion insert on the dorsal surface of the venom gland (Figure 1) and serve to compress the gland and expel the venom when the snake strikes. Ventrally, fibres of the m. pterygoideus are also inserted on the investing sheath (Figure 2). This muscle supports the gland ventrally and also appears to play some role in venom ejection.

The ligamentum quadrato-maxillare is a very tough ligament that arises from the quadrato-mandibular articulation and continues forward as a narrow ribbon over the m. adductor externus profundus (Figure 1). It then spreads over the lateral surface of the venom gland and some of its ligamentous fibres are connected to the capsule of the gland. This shiny and transparent ligament is also connected to the external surface of the m. adductor externus superficialis and to the postorbital bone.

Jaw musculature

Musculus adductor externus superficialis In *Dendroaspis*, this is a rather complex muscle and is visible in the anterior part of the head immediately after the removal of the skin as a wide strap-like muscle. The m. adductor externus superficialis lies lateral to the maxillary branch of V. The upper part of this muscle arises from the postorbital and parietal and is typically cleft into two for attachment to the dorsal and medial surfaces of the venom gland capsule (Figure 1). The fibres of the anterior bundle arise from the postero-dorsal projection of the maxilla by means of a very strong ligament which McDowell (1968) refers to as the 'postorbital maxillary ligament'. These fibres continue posteriorly in close association with the dorsal surface of the capsule of the venom gland and act as a compressor of the gland (Figure 2). The fibres that arise from the postorbital and parietal bones run downwards and insert on the dorso-medial surface of the posterior part of the venom gland (Figure 1). These descending fibres then merge with those fibres of the m. adductor externus superficialis that originate from the postorbital-maxillary ligament. A major part of this muscle in both species of *Dendroaspis* is associated with the venom gland and only a small portion of the fibres proceed downwards, medial to the venom gland, and insert on the ventro-lateral aspect of the anterior part of the mandible (Figures 1 & 3). It is thus not a typical adductor as in primitive snakes.

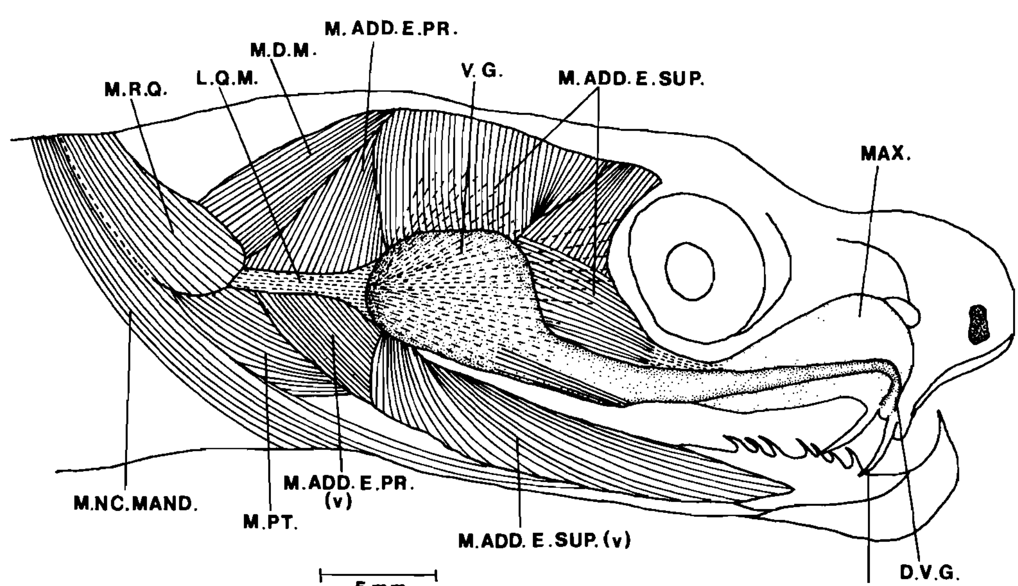

Fig. 1 Lateral view of the head muscles of *D. polylepis polylepis*. (Key to lettering — see Table 1).

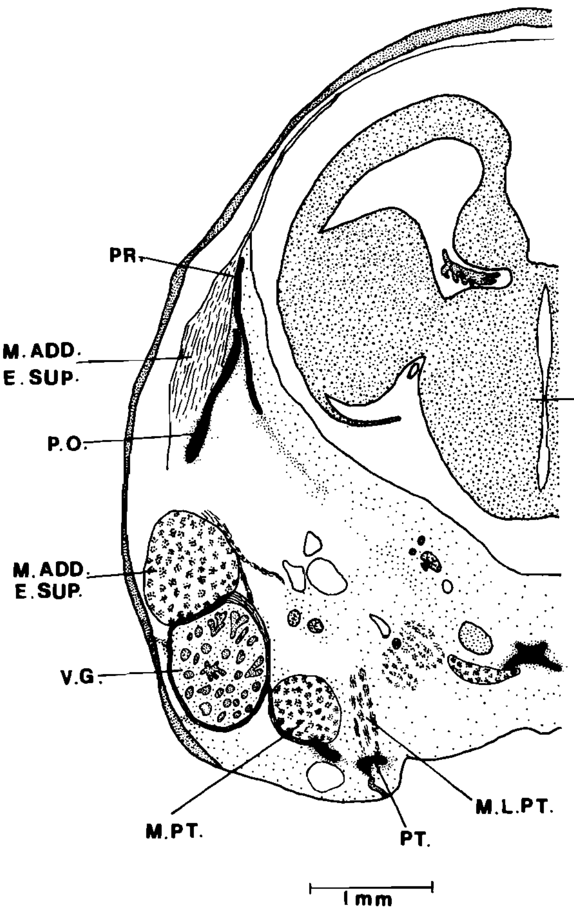

Fig. 2 Transverse section through the head of a late embryo of *D. angusticeps* showing the insertions of the m. adductor externus superficialis and the m. pterygoideus on the venom gland capsule. (Key to lettering — see Table 1).

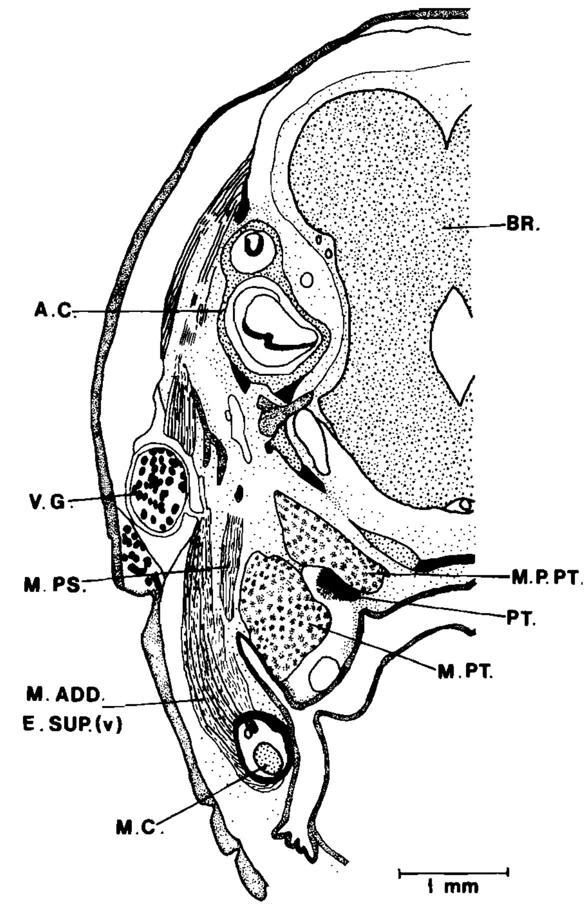

Fig. 3 Transverse section through the posterior termination of the venom gland of *D. angusticeps* showing the fibres of the m. adductor externus superficialis proceeding ventrad, median to the gland. (Key to lettering — see Table 1).

Musculus adductor externus profundus The profundus muscle lies behind the m. adductor externus superficialis and is linked with it by means of connective tissue (Figure 1). The anterior fibres of the profundus arise dorsally on the supratemporal while the posterior fibres arise from the head of the quadrate. The deeper fibres of the profundus muscle are separated from the m. adductor posterior by the mandibular branch of the trigeminal nerve. An interesting feature regarding this muscle in *Dendroaspis* is that its fibres are not attached to the venom gland, unlike the condition in almost all species of the Viperidae and Crotalidae. Ventrally, the fibres of the profundus insert on the lateral aspect of the mandible behind the insertion of the m. adductor externus superficialis portion (Figure 1).

Musculus adductor externus medialis This muscle arises from the head of the quadrate and continues downwards medial to the m. adductor externus profundus (Figure 4). It is difficult to separate the medialis from the deeper fibres of the m. adductor externus profundus. Proceeding downwards, the medialis inserts in the mandibular fossa, medial to the insertion of the m. adductor externus profundus.

Musculus adductor posterior The m. adductor posterior (Figure 4) lies beneath the profundus and is separated from it by the mandibular branch of the trigeminal nerve.

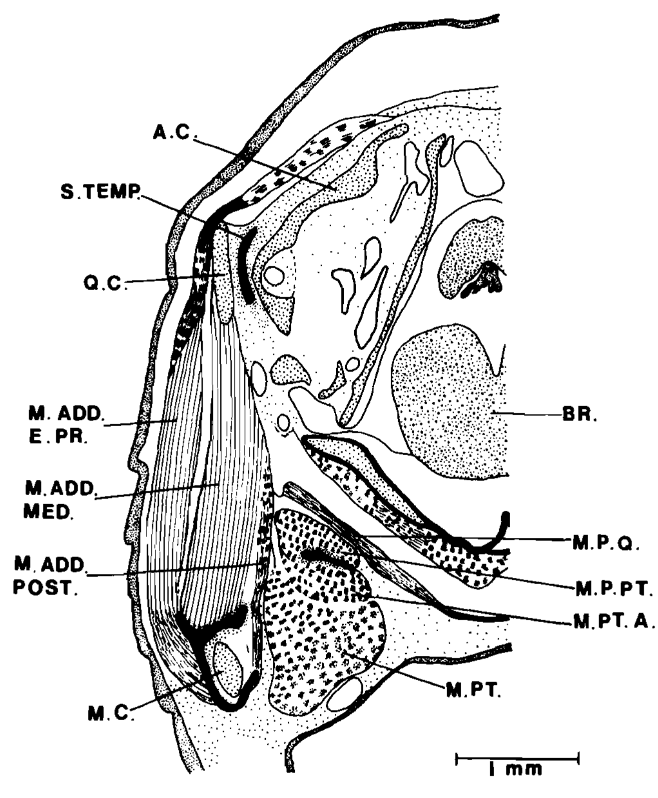

Fig. 4 Transverse section through the head of *D. angusticeps* showing the position and relationship of the m. adductor medialis to the adductor externus profundus and adductor posterior. (Key to lettering — see Table 1).

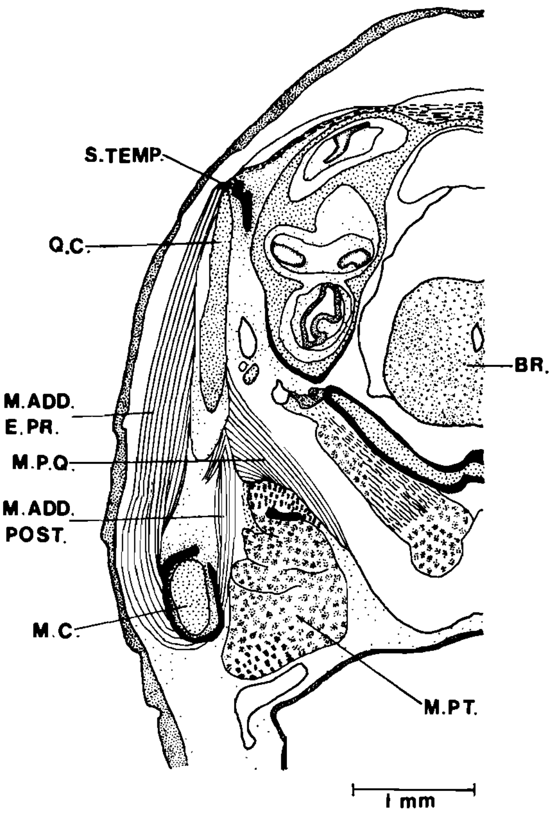

Fig. 5 Transverse section through the quadrato-supratemporal articulation of an embryo of *D. angusticeps* showing the m. adductor posterior and the m. protractor quadrati. (Key to lettering — see Table 1).

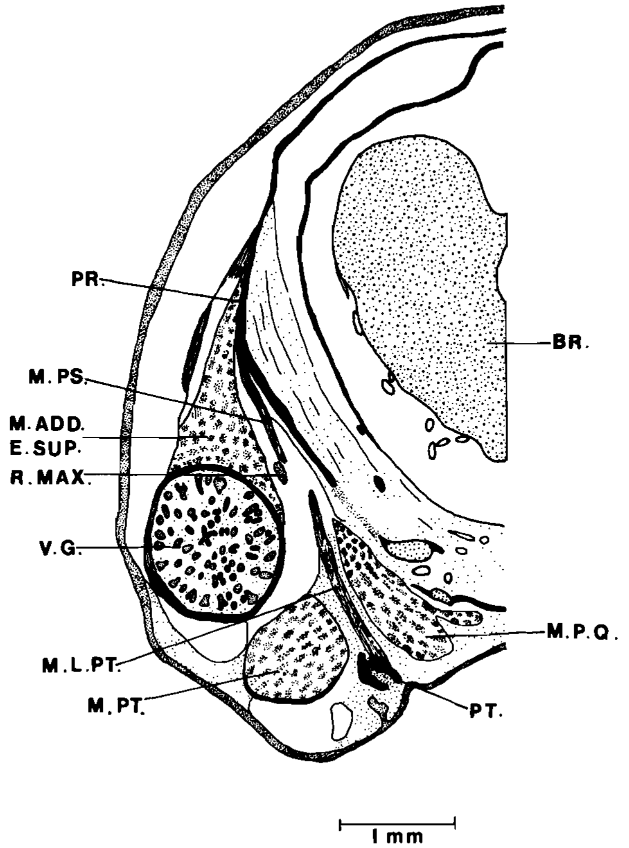

Fig. 6 Transverse section through the head of a late embryo of *D. angusticeps* illustrating the m. adductor externus superficialis, m. pseudotemporalis, m. levator pterygoidei and m. protractor pterygoidei. (Key to lettering — see Table 1).

This muscle originates on the head of the quadrate and the fibres proceed downwards anterior to the body of the quadrate and insert in the mandibular fossa. The deeper fibres of the m. adductor posterior originate on the medial face of the quadrate and insert on the medial aspect of the articular (Figure 5).

Musculus pseudotemporalis The m. pseudotemporalis originates dorsally from the parietal bone. It is a thin, ribbon-like muscle and the parallel fibres descend postero-ventrally, medial to the maxillary branch of the trigeminal nerve (Figure 6). It lies lateral to the m. levator pterygoidei and m. pterygoideus. Ventrally, some of its fibres insert at the oral angle by means of thin strands of connective tissue. The m. pseudotemporalis inserts on the inner face of the mandible, median to the insertion of the m. adductor externus medialis and anterior to the m. adductor externus profundus.

Musculus pterygoideus The m. pterygoideus is considered to be the third and deepest layer of musculature despite the fact that it can be seen ventral to the quadrato-mandibular articulation after the removal of the skin (Figure 1). This is an elaborate muscle originating on the ventral surface of the retroarticular process.

Closely associated with the m. pterygoideus is the m. pterygoideus accessorius. The latter arises from the medial aspect of the retroarticular process and lies dorsal to the m. pterygoideus (Figure 4). It inserts along the ventral posterior surface of the pterygoid bone.

The pterygoideus is an elongate muscle that continues anteriorly and lies medial to the mandible in the region where the latter articulates with the quadrate. This muscle is attached to the skin at several points by means of connective tissue. The muscle then continues ventromedial to the venom gland and some of its fibres are linked to the capsule of the gland (Figure 2). Anteriorly, the m. pterygoideus inserts on the ectopterygoid and also on the maxilla.

Musculus levator pterygoidei The m. levator pterygoidei originates from the ventral surface of the parietal bone (Figure 6). It is a rather broad sheet of muscle composed of parallel fibres that run downwards to insert on the pterygoid. This muscle passes medial to the venom gland and continues between the m. protractor quadrati and the m. pterygoideus. There are no fibres of the m. levator pterygoidei inserting on the ectopterygoid.

Musculus retractor pterygoidei The m. retractor pterygoidei is a thin sheet of muscle that originates on the parasphenoid. Its fibres proceed downwards and insert on the dorsal surface of the anterior part of the pterygoid and also on the palatine. Some of its fibres are also attached to the ectopterygoid.

Musculus protractor pterygoidei This muscle originates anteriorly on the parasphenoid and basisphenoid bones. From its origin, the muscle passes backwards along the floor of the braincase and widens to form a thick strap-like muscle (Figure 3). Posteriorly, this muscle narrows somewhat before inserting on the dorsal surface of the pterygoid (Figure 4).

Musculus protractor quadrati The m. protractor quadrati (Figure 5) originates on the basisphenoid by means of a strong tendon. This muscle extends slightly upwards and backwards and inserts on the medial aspect of the quadrate and extends to a point where the latter articulates with the mandible.

Musculus depressor mandibulae The m. depressor mandibulae lies behind the m. adductor externus profundus and partly overlaps the latter (Figure 1). The anterior fibres arise from the whole length of the posterior projection of the quadrate while the posterior fibres arise from the skull roof. Ventrally, the fibres of the m. depressor mandibulae insert on the retroarticular process and also on the quadrato-mandibular articulation.

Musculus retractor quadrati Near its origin, the m. retractor quadrati cannot be distinguished from the more posterior m. neuro-costo-mandibularis (Figure 1). Both these muscles arise from the dorsal mid-line in the cervical region and run in an antero-ventral direction. Anteriorly, the m. retractor quadrati separates from its companion and inserts on the lateral aspect of the quadrato-mandibular articulation, near the origin of the ligamentum quadrato-maxillare.

The m. neuro-costo-mandibularis continues downwards on the outer surface of the m. pterygoideus and terminates in the throat region.

Innervation of the trigeminal musculature

In both species of *Dendroaspis*, the main branches of the trigeminal nerve emerge from the cranium through two separate foramina. The ramus maxillaris (V_2) arises from the anterior foramen while the ramus mandibularis (V_3) arises from the posterior foramen (Figure 7).

The ramus maxillaris is a thick nerve that runs anteriorly below the orbit. A dorsal branch arising anteriorly from the base of the ramus maxillaris supplies the dorsal part of the m. adductor externus superficialis, while a branch issuing posteriorly gives off smaller branches to the venom gland.

The ramus mandibularis, after emerging from the posterior foramen, courses downwards and enters the foramen mandibulare. Branches arising anteriorly from the ramus mandibularis supply the ventral portion of the m. adductor externus superficialis, pseudotemporalis and m. pterygoideus (Figure 7). Branches arising posteriorly, innervate the m. adductor externus profundus and the m. adductor posterior.

Action of the muscles

Most of the lateral jaw musculature can be divided into two major groups: the adductor series and the constrictor 1 dorsalis. The muscles comprising the adductor complex group are very strong and well developed. The adductor complex comprises the following muscles: adductor externus superficialis, adductor externus profundus, adductor externus medialis, adductor posterior and the pseudotemporalis. The constrictor 1 dorsalis includes the levator pterygoidei, retractor pterygoidei, protractor pterygoidei and the protractor quadrati. Contraction of the adductor complex muscles raises the lower jaw. Besides this, the muscles have other important functions as well.

It is doubtful whether the m. adductor externus superficialis in *Dendroaspis* plays an important role in raising the mandible. This muscle has become closely associated with the venom gland and consequently has become highly specialised for the ejection of venom. A major part of this muscle has become associated with the capsule of the venom gland and only a small portion of the fibres pass downwards, on the postero-medial aspect of the venom gland to insert on the mandible. The contraction of these fibres will raise the lower jaw.

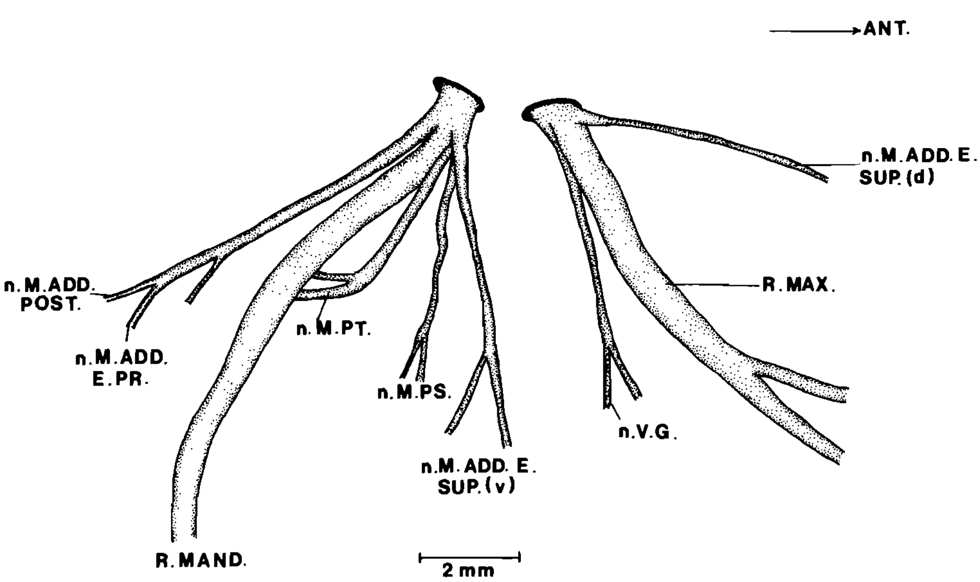

Fig. 7 Dissection of the main branches of the N. trigeminus of *D. polylepis polylepis* as seen in lateral view. (Key to lettering — see Table 1).

The function of that portion of the m. adductor externus superficialis that originates from the postero-dorsal flange of the maxilla is, however, not very clear. It is very likely that contraction of this portion will cause a slight upward tilting of the maxilla.

The m. adductor externus profundus, by virtue of its large size, appears to play an important role in the raising of the lower jaw. In the region of the quadrato-supratemporal articulation, the anterior fibres of the profundus, pass over the upper end of the quadrate and serve to hold the quadrate in position.

The m. adductor posterior and the m. adductor medialis also help to raise the lower jaw. The m. pseudotemporalis, being a rather weak muscle, plays a minor role in adducting the mandible.

The main part of the m. pterygoideus, as it continues anteriad, makes contact with the ventro-medial surface of the venom gland. This portion serves to pull the gland inward and downward. Further anteriorly, the fibres insert on the ectopterygoid and also on the maxilla. Dullemeijer (1956) was unable to assign any specific function to that portion of the m. pterygoideus that inserted on the ectopterygoid in *Vipera berus*. Boltt & Ewer (1964) hold the view that this portion participates in the retraction of the pterygoid. The function of this muscle in *Dendroaspis* appears to be to draw the maxilla back and to sheath the fang.

Table 1 Key to anatomical drawings

A.C.	auditory capsule
BR.	brain
D.V.G.	duct of venom gland
F.	fang
L.Q.M.	ligamentum quadrato-maxillare
M. ADD. E. PR.	musc. adductor externus profundus
M. ADD. E. PR. (V)	musc. adductor externus profundus (ventral portion)
M. ADD. E. SUP.	musc. adductor externus superficialis
M. ADD. E. SUP. (V)	musc. adductor externus superficialis (ventral portion)
M. ADD. MED.	musc. adductor medialis
M. ADD. POST.	musc. adductor posterior
MAX.	maxilla
M.C.	Meckel's cartilage
M.D.M.	musc. depressor mandibulae
M.L. PT.	musc. levator pterygoidei
M. NC. MAND.	musc. neuro-costo-mandibularis
M.P. PT.	musc. protractor pterygoidei
M.P.Q.	musc. protractor quadrati
M. PS.	musc. pseudotemporalis
M. PT.	musc. pterygoideus
M. PT. A.	musc. pterygoideus accessorius
M. R. Q.	musc. retractor quadrati
n. M. ADD. E. PR.	nerve of musc. adductor externus profundus
n. M. ADD. E. SUP. (d)	nerve of musc. adductor externus superficialis (dorsal portion)
n. M. ADD. E. SUP. (V)	nerve of musc. adductor externus superficialis (ventral portion)
n. M. ADD. POST.	nerve of musc. adductor posterior
n. M. PS.	nerve of musc. pseudotemporalis
n. M. PT.	nerve of musc. pterygoideus
n. V. G.	nerve of venom gland
PO.	postorbital bone
PR.	parietal
PT.	pterygoid bone
Q.C.	quadrate cartilage
R. MAND.	ramus mandibularis
R. MAX.	ramus maxillaris
S. TEMP.	supratemporal bone
V.G.	venom gland

Opening of the mouth is characterized by the elevation of the upper jaw and depression of the lower jaw. This results in an enlargement of the mouth cavity in order to accommodate relatively large prey. During the opening of the mouth, there is forward movement of the tooth-bearing bones. The elevation of the upper jaw is brought about by the contraction of the protractor and levator pterygoidei. The contraction of the protractor pterygoidei results in a forward displacement of the pterygoid. This forward movement of the pterygoid is concomitant with the elevation-abduction action brought about by the contraction of the m. levator pterygoidei. Since both these muscles work simultaneously, the net effect of their action will be a direct elevation as well as forward movement of the pterygoid. This movement of the pterygoid is imparted to the ectopterygoid which is tightly bound to the pterygoid by means of ligaments. Anteriorly, the ectopterygoid articulates with the maxilla so that the forward movement of the ectopterygoid causes the maxilla to move slightly upwards upon its articulation with the prefrontal. This results in the freeing of the fangs from the surface of the prey. The lowering of the jaw depends to a large extent on the contraction of the m. depressor mandibulae. When the depressor mandibulae contracts, it pulls the retroarticular process dorsally towards the quadrate and this results in the lowering of the mandible.

The function of the m. neuro-costo-mandibularis is not very certain. According to Albright & Nelson (1959) the lowering of the mandible is initially brought about by the depressor mandibulae and the m. neuro-costo-mandibularis comes into operation only when the mandible is at right angles to the cranium. Boltt & Ewer (1964) suggest that this muscle could be involved both in the closing and in the opening of the jaws. The function of this muscle in *Dendroaspis* appears to be to control the lateral movement of the quadrato-mandibular articulation during the swallowing of bulky prey.

Closing of the mouth is characterized by a backward movement of the tooth-bearing bones, thus bringing the teeth into position for a renewed grip on one side of the head while the opposite side is free to be carried forward over the surface of the prey. By alternating this forward movement of the jaws, first on one side and then on the other, the snake is able to draw the prey further into its mouth. The freeing of the mandibular tips is correlated with this alternate and complex swallowing mechanism in snakes.

The movement of the pterygoid in a caudal direction is brought about by the simultaneous contraction of several muscles. The two most important muscles are the m. retractor quadrati and the m. retractor pterygoidei. Contraction of the former muscle pulls the distal end of the quadrate in a posterior direction while contraction of the m. retractor pterygoidei drags the pterygoid bone backwards. Both these muscles act simultaneously and the net effect of their action will be a displacement of the pterygopalatine articulation postero-dorsally, thus engaging the teeth in the prey.

The fibres of the m. protractor quadrati insert on the medial face of the quadrate and hence the contraction of this muscle will pull the quadrate mesially. The angle of insertion is such that contraction of these fibres will not cause a forward roration of the quadrate. According to

Kochva (1958) the m. protractor quadrati together with the m. levator and m. protractor pterygoidei produce erection of the fang by protraction of the pterygoid. This imparts movement to the ectopterygoid which in turn pushes the maxilla forward. The pterygoid is not firmly articulated with the quadrate but is loosely attached to it by muscles and ligaments. This loose union allows them considerable independence of movement. It is, therefore, very unlikely that the forward rotation of the quadrate will impart any movement to the pterygoid.

Discussion

Many significant contributions have been made by various authors on the jaw muscles of snakes eg. Radovanovic 1928; Haas 1929, 1930a, b, 1931a, b, 1952; Kochva 1958, 1962; Frazetta 1959; Albright & Nelson 1959a, b; Boltt & Ewer 1964. The papers by Dullemeijer (1956, 1959) are important for their functional and comparative anatomical aspects of viperid jaw function. Bogert (1943) has made a detailed study of the dentitional phenomena in cobras and other elapids and has also considered taxonomic and phylogenetic implications. There is a profusion of synonymous terms in the literature concerning the ophidian trigeminal musculature. This very often results in confusion when anatomical accounts by various authors are compared. There is an urgent need for a revision of the muscle nomenclature in order to standardize the terminology. This will be of tremendous benefit to future workers engaged in comparative anatomical studies. The paper by Kochva (1962) is important for its simplified version of the muscle nomenclature.

The venom apparatus in both species of *Dendroaspis* is similar to that described in other proteroglyphs. The shiny ligamentum quadrato-maxillare covers the gland laterally and extends as far forward as the postorbital bone. In some species, the ligamentum quadrato-maxillare continues further forward and attaches to the maxilla (Kochva 1962). According to Kochva (1962) the ligamentum quadrato-maxillare ends at the angle of the mouth in the elapids, *Naja naja* and *Ophiophagus hannah*. Posteriorly, this ligament fastens the gland to the quadrato-mandibular articulation.

The musculus adductor externus superficialis shows much variation in snakes. It may be broken into several portions with the result that identification of its constituent parts is sometimes difficult. This muscle is similar in both species of *Dendroaspis* but differs from those described in other proteroglyphs in that its dorsal origin has extended further forwards past the postorbital and parietal to the maxilla (Figure 1). In both species of *Dendroaspis* this muscle is vertically divided into two as in *Naja naja* (Kochva 1962) and *Bungarus candidus* (Haas 1930b).

In primitive proteroglyphs, the fibres of the m. adductor externus superficialis run from the postorbital-parietal to the mandible (Kochva 1962). In *Dendroaspis*, this muscle is closely associated with the venom gland and consequently has become very highly specialized for the function of venom ejection. In most solenoglyphs, a double adductor externus superficialis is present (Kochva 1962). The deep part inserts at the corner of the mouth and forms a separate muscle the levator anguli oris. According to Rieppel (1980) the musculus levator anguli oris is directly homologous in lizards and snakes. He regards the presence of this muscle in snakes to be a primitive feature. As in other elapids, this muscle is absent in both species of *Dendroaspis*. Because of this important difference in the structure of the m. adductor externus superficialis, Haas (1952) does not see the possibility of a genetic relation between the Proteroglypha and the Solenoglypha.

According to Kochva (1962) the compressor of the venom gland in the Solenoglypha is generally very uniform and is derived from the anterior part of the m. adductor externus profundus. Unlike the condition in the Proteroglypha, the m. adductor externus superficialis does not play any part in venom ejection. The forward and backward rotation of the maxilla in viperine and crotaline snakes (solenoglyphs) causing respectively, erection and retraction of the fangs is, however, a highly specialized and complex mechanism involving a series of bones and muscles. For this reason, the maxilla in the Solenoglypha is considered to be more highly evolved when compared with the condition in the proteroglyphs. Regarding the maxilla in the solenoglyphs, Bogert (1943, p. 318) states: 'The condition in the solenoglyphs may be interpreted as an advancement from that of the proteroglyphs, and the changes that have accompanied the evolution and perfection of the tilting mechanism seem to be among the factors that enable rattlesnakes and most other solenoglyphs to possess relatively larger fangs situated farther forward in the skull'.

The fangs in *Dendroaspis* are relatively shorter than those present in the average cobra. Muscular attachments to the ectopterygoid and to the postero-dorsal extension of the maxilla indicate that limited rotation and movement of the maxilla are possible.

It has been suggested by investigators that any mechanism that causes displacement or compression of the venom gland results in the ejection of venom. Rosenberg (1967) has given a comprehensive account on the functions of the venom gland muscles and the mechanism of venom ejection in the elapid, *Bungarus caeruleus*, using electrical stimulation techniques. He holds the view that the abrupt drawing of the gland against the lateral surface of the underlying structures compresses the venom gland and increases intraglandular pressure.

In *Dendroaspis* contraction of the fibres of the m. adductor externus superficialis, that arise from the postorbital and parietal bones and insert on the dorsal surface of the venom gland, causes a dorsal displacement of the venom gland. Contraction of the posterior as well as the ventral fibres of the m. adductor externus superficialis, which attach to the medial surface of the venom gland capsule, pull the posterior part of the gland mediad. Contraction of that portion of the musculus adductor externus superficialis that originates from the postero-dorsal extension of the maxilla will result in an upward tilting of the fangs.

The fibres of the m. adductor externus profundus do not insert on the capsule of the venom gland and hence do not participate in the ejection of venom.

The m. pterygoideus attaches to the venom gland ventromedially. The exact function of this muscle, as far as venom ejection is concerned, is not clearly understood, but it probably serves to pull the gland inward and downward as well as to draw back the maxilla and sheath the fangs.

Simultaneous contraction of various components of the m. adductor externus superficialis will therefore cause an upward tilting of the fangs as well as a dorso-medial displacement of the venom gland. This sudden displacement of the gland presumably causes compression of the gland and the ejection of venom. According to Rosenberg (1967), sudden contraction of the m. adductor externus superficialis in *Bungarus caeruleus* increases the pressure within the venom gland and forces the venom through the duct. He holds the view that the pressure is always greater in the caudal end of the gland and decreases in the region where the gland is linked to the duct, thus creating a pressure gradient that propels the venom anteriorly. Furthermore, he states that the increase in pressure at the posterior end of the gland causes emptying of the accessory venom gland first which results in a mixing of accessory gland and main gland secretions.

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