CHAPTER V

Structure and disposition of the jaw muscles and its operative efficiency

A. Structure and disposition

Cranial kinesis during feeding is brought by functioning of the jaw-muscles. Snakes show diverse feeding habits. Since the feeding behaviour differs, the muscles involved in movements of the jaw apparatus are variously disposed. A number of workers have studied the disposition of the jaw muscles to correlate the structure with the operation for specific feeding habits in snakes. Kochva (1962) provided an account of variation of cephalic muscles in viperid genera. Bisewar (1981) described the jaw musculature of Dendroaspis angusticeps and Dendroaspis polylepis. David (1986) reported variations of cephalic muscles in colubrid snake genera; Entechinus, Opheodrys and Symphimus. Saji (1992) has given a detailed study of the jaw-muscles of Natrix piscator, Ptyas mucosus and Naja naja.

The structure and disposition of the jaw-muscles of E. conicus conicus, D. nasutus and D. tristis have studied in detail to understand the functional efficiency during feeding. The hyoid and tongue muscles are also mentioned.
Jaw-muscles

The jaw-muscles of the feeding apparatus are grouped according to their functions in cranial kinesis. They are:

I. Adductors of the lower jaw
   1. M. adductor mandibulae externus superficialis.
   2. M. adductor mandibulae externus medialis.
   3. M. adductor mandibulae externus profunds
   4. M. adductor mandibulae posterior
   5. M. pseudotemporalis.

II. Abductors of the lower jaw
   1. M. depressor mandibulae anterior.
   2. M. depressor mandibulae posterior.

III. Protractors of the upper jaw
   1. M. protractor pterygoidei
   2. M. levator pterygoidei
   3. M. protractor quadrati.

IV. Protractors of the lower jaw and retractors of the upper jaw
   1. M. pterygoideus.
   2. M. pterygoideus accessories

V. Retractors of the upper jaw
   1. M. retractor pterygoidei
2. M. retractor vomeris

3. M. cervico-mandibularis


The nomenclature of the jaw-muscles followed in this study is that of Kardong (1980).

The following is an account of structure and disposition of the jaw-muscles of *E. conicus*, *D. nasutus* and *D. tristis*.

I. Adductors of the lower jaw

1. M. adductor mandibulae externus superficialis. (Fig. 5.1, 5.2, & 5.3)

The M. adductor mandibulae externus superficialis is a parallel-fibred muscle with fleshy origin from the posterior side of the postfrontal and the anterior part of the parietal bone. Its anterior fibres pass in a long curve around the angle of the mouth. The posterior fibres terminate in a broad aponeurosis lying over the M. adductor mandibulae externus profundus. This aponeurosis is loosely associated with the epimysium of the latter muscles and attaches to the ventro-lateral surface of the compound bone.

In *E. conicus* this muscle is more massive than *D. nasutus* and *D. tristis*. The disposition is more or less similar in the three snakes.

The M. adductor mandibulae externus superficialis is innervated by the trigeminal nerve. The function of this muscle is the adduction of the mandible.
2. M. adductor mandibulae externus medialis. (Fig. 5.1, 5.2 & 5.3)

M. adductor mandibulae externus medialis originates from the dorso-lateral side of the parietal bone just posterior to the origin of the M. adductor mandibulae externus superficialis. It is a parallel-fibred muscle which takes a fleshy origin from the parieto-supratiempral region of the cranium. In *E. conicus* it extends downwards and fleshy inserts on the inner side of dorso-lateral surface of the mandible, anterior to the Meckelian vacuity. During its course, covers the M. pterygoideus. In *D. nasutus* and *D. tristis*, it extends backwards and fleshy inserts on the compound bone just anterior to the Meckelian cavity.

The M. adductor mandibulae externus medialis is innervated by the trigeminal nerve. This muscle works for the adduction of lower jaw towards the supratiempral.

3. M. adductor mandibulae externus profundus. (Fig. 5.1, 5.2 & 5.3)

M. adductor mandibulae externus profundus is a triangular block of parallel-fibred muscle originating from the outer lateral side of the entire length of the quadrate by a fleshy origin. This muscle moves downwards and gains a fleshy insertion into the low depression of the postero-lateral surface of the compound bone. In *E. conicus* this muscle is vertically placed. In *D. nasutus* and *D. tristis* this muscle runs backwards due to the posterior displacement of quadrate.

The M. adductor mandibulae externus profundus is
Figure 5.1
Figure - 5.1

Jaw muscles of Eryx conicus

5.1 (a) Lateral view.

5.1 (b) Ventral view.

Abbreviations:

Mamies - M. adductor mandibulae externus superficialis;
Mamem - M. adductor mandibulae externus medialis;
Mamep - M. adductor mandibulae externus profundus;
Mamp - M. adductor mandibulae posterior;
Mp - M. pseudotemporalis;
Mdma - M. depressor mandibulae anterior;
Mdmp - M. depressor mandibulae posterior;
Mpp - M. protractor pterygoidei;
Mlp - M. levator pterygoidei;
Mpq - M. protractor quadrati;
Mp - M. pterygoideus;
Mpa - M. pterygoideus accessories;
Mrp - M. retractor pterygoidei;
Mrv. - M. retractor vomeris;
Mcm - M. cervico-mandibularis;
Mnm - M. neuro-mandibularis.
innervated by the trigeminal nerve. This muscle functions in drawing the mandible towards the quadrate.

4. M. adductor mandibulae posterior (Fig. 5.1, 5.2 & 5.3)

M. adductor mandibulae posterior is a small muscle, lying beneath the M. adductor mandibulae externus profundus. It is a parallel-fibred muscle which originates fleshy from the base of the proximal end of the quadrate and then extends along its entire anterior, lateral edge to a point above the lateral condyle. It inserts along the dorsal edge of the surangular crest.

The muscle is divided into two slips, an inner and an outer by the prearticular crest of the mandible. The outerslip is inserted into the Meckelian canal, and the innerslip is inserted into the lateral side of the prearticular crest. The disposition of this muscle is more or less same in the three snakes.

The M. adductor mandibulae posterior is innervated by the trigeminal nerve. The function of this muscle is to draw the mandible towards the quadrate.

5. M. pseudotemporalis (Fig. 5.1, 5.2 & 5.3)

The M. pseudotemporalis is a parallel-fibred muscle arising by a small tendon from the lateral surface of the parietal, deep to the M. adductor externus superficialis. It passes ventrally to gain a fleshy insertion on the dorsal surface of the compound bone at the anterior end of the prearticular crest, slightly anterior to the front of the deep division of the M. adductor mandibulae externus medialis.
The M. pseudotemporalis lies lateral to the M. levator pterygoidei and M. pterygoideus. The disposition is more or less same in the three snakes.

The M. pseudotemporalis serves to adduct the mandible. It is innervated by the trigeminal nerve.

II. Abductors of the lower jaw

1. M. depressor mandibulae anterior. (Fig. 5.1, 5.2 & 5.3)

M. depressor mandibulae anterior has a fleshy origin from the whole length of the posterior projection on the upper region of the quadrate. It is a parallel-fibred muscle which lies just behind the M. adductor mandibulae externus profundus. In E. conicus this muscle extends downwards and backwards on the outer surface of the quadrate and inserts directly into the dorsal surface of the retroarticular process of the mandible. In D. nasutus and D. tristis this is posteriorly placed along with the quadrate.

The M. depressor mandibulae anterior is innervated by the facial nerve. The function of this muscle is to open the mouth by pulling the retroarticular process upward.

2. M. depressor mandibulae posterior (Fig. 5.1, 5.2 & 5.3)

The M. depressor mandibulae posterior is a parallel-fibred muscle which arises by a narrow tendon from the skull roof just anterior to the origin of the M. depressor mandibulae anterior. The M. depressor mandibulae anterior and M. depressor mandibulae posterior
Figure 5.2

Jaw muscles of *Dryophis nasutus*

5.2 (a) Lateral view

5.2 (b) Ventral view

Abbreviations:

Mamus - M. adductor mandibulae externus superficialis;
Mamem - M. adductor mandibulae externus medialis;
Mamet - M. adductor mandibulae externus profundus;
Mamp - M. adductor mandibulae posterior;
Mp - M. pseudotemporalis;
Mdma - M. depressor mandibulae anterior;
Mbmp - M. depressor mandibulae posterior;
Mpp - M. protractor pterygoidei;
Mlp - M. levator pterygoidei;
Mpq - M. protractor quadrati;
Mp - M. pterygoideus;
Mpa - M. pterygoideus accessories;
Mrp - M. retractor pterygoidei;
Mrv - M. retractor vomeris;
Mcm - M. cervico-mandibularis;
Mnm - M. neuro-mandibularis.
are separated by the M. cervico–quadratus, which passes between the two. The M. depressor mandibulae posterior is relatively smaller than the anterior muscle. This muscle extends backwards and downwards on the anterior muscle. It is inserted by a short tendon of the retroarticular process of the mandible. The disposition is more or less same in the three snakes.

The M. depressor mandibulae posterior is innervated by the facial nerve. This muscle serves to open the mouth by pulling the retroarticular process upward.

III. Protractors of the upper jaw

1. M. protractor pterygoidei (Fig. 5.1, 5.2 & 5.3)

M. protractor pterygoidei takes origin from the ventral surface of the sphenoid complex. It passes posteriorly and inserts across the posterio–dorsal end of the pterygoid with firm attachment to the caudal tip of the bone.

The M. protractor pterygoidei is innervated by the trigeminal nerve. It serves to protract the palato–pterygoid unit.

2. M. levator pterygoidei (Fig. 5.1, 5.2 & 5.3)

A low depression in the posterior, ventral face of the postorbital process of the parietal serves as the surface for the origin of this muscle. It passes ventrally widening along anterio–posterior axis to form a long insertion on the pterygoid. This insertion begins posteriorly on the dorsolateral side of the pterygoid, runs forward to the ectopterygoid–pterygoid articulation, across the base of the
ectopterygoid and ends on the adjacent outer side of the pterygoid. The disposition is more or less same in the three groups.

The M. levator pterygoidei is innervated by the trigeminal nerve. The function of this muscle is to protract the palato-pterygoid bar during feeding.

3. M. protractor quadrati. (Fig. 5.1, 5.2 & 5.3)

M. protractor quadrati arises from a tendon that originates from the mid-ventral of basioccipital. It is a flat muscle passing horizontally in a postero-lateral direction over the dorsal surface of the protractor pterygoidei. The muscle inserts on the quadrate and the retroarticular process of the mandibule. The disposition is more or less same in the three species.

The M. protractor quadrati is innervated by the trigeminal nerve. This muscle serves to protract the quadrato-mandibular articulation, which results in the protraction of all the bones related to it.

IV. Protractors of the lower jaw and retractors of the upper jaw
1. M. pterygoideus. (Fig. 5.1, 5.2 & 5.3)

M. pterygoideus takes origin from the lateral maxillary process of the ectopterygoid. The tendon remains superficial and passed ventrally reaching the middle of the muscle. The parallel fibres of this muscle sweep backward forming a swollen belly that projects below the compound bone. The fibres curve upward to insert on the ventral surface of the mandibular retroarticular process. In E. conicus.
Figure 5.3

Jaw muscles of Dendrelaphis tristis

5.3 (a) Lateral view

5.3 (b) Ventral view

Abbreviations:

Mames - M. adductor mandibulae externus superficialis;
Mamem - M. adductor mandibulae externus medialis;
Mamep - M. adductor mandibulae externus profundus;
Mamp - M. adductor mandibulae posterior;
Mp - M. pseudotemporalis;
Mdma - M. depressor mandibulae anterior;
Mdmp - M. depressor mandibulae posterior;
Mpp - M protractor pterygoidei;
Mlp - M. levator pterygoidei;
Mpq - M. protractor quadrati;
Mp - M. pterygoideus;
Mpa - M pterygoideus accessories;
Mrp - M. retractor pterygoidei;
Mrv - M. retractor vomeris;
Mcm - M. cervico-mandibularis;
Mnm - M. neuro-mandibularis.
Figure 5.3
the belly of the muscle is placed in the ventral groove of the pterygoid bone. In *D. nasutus* and *D. tristis* they run forward along with the pterygoid bone.

The M. pterygoideus is innervated by the trigeminal nerve. This muscle serves to protract the mandible, and to retract the palato-maxillary arch during feeding.

2. M. pterygoideus accessories (Fig. 5.1, 5.2 & 5.3)

M. pterygoideus accessories arises from the ventral surface of the pterygoid and base of the ectopterygoid. It is a parallel-fibred muscle with a fleshy origin. This muscle passes backwards parallel to the M. pterygoideus and fleshy inserts on the inner side of the retroarticular process along its medial curvature. The disposition is more or less same in the three snakes.

The M. pterygoideus accessories is innervated by the trigeminal nerve. This muscle functions to protract the mandible and retract the palato-ptyerygoid bar.

V. Retractors of the upper jaw

1. M. retractor pterygoidei (Fig. 5.1, 5.2 & 5.3)

M. retractor pterygoidei which is a parallel-fibred muscle arises directly from the anterior side of the transverse ridge on the basisphenoid, adjacent to the origin of the protractor pterygoidei. It extends obliquely forwards to a fleshy insert on the lateral surface of the palatine, anterior to the insertion of M. levator pterygoidei. The arrangement of this muscle is more or less same in the three snakes.
The M. retractor pterygoidei is innervated by trigeminal nerve. This muscle serves to retract palato-pterygoid bar.

2. M. retractor vomeris (Fig. 5.1, 5.2 & 5.3)

M. retractor vomeris is a small, parallel-fibred muscle arising from the sphenoid, lateral to the anterior end of the origin of M. protractor pterygoidei. It passes forward as a spindle-like muscle bounded laterally by M. retractor pterygoidei. Anteriorly its fibres converge into a slender cord-like tendon that accounts for half of the total muscle length. This tendon inserts on postero-dorsal corner of the vomer. The disposition is more or less same in the three snakes.

The M. retractor vomeris is innervated by the trigeminal nerve. This muscle serves to retract the snout complex.

3. M. cervico-mandibularis (Fig. 5.1, 5.2 & 5.3)

M. cervico-mandibularis is a thin muscular sheath with a fleshy origin in the midline of the cervical region, running along the epimysium of spinalis-semispinalis complex. It runs antero-ventral direction, passing over M-cervico-quadratus and narrowing so as to insert into the lateral side of the quadrato-mandibular articulation adjacent to the origin of the quadrato-maxillary ligament.

The M. cervico-mandibularis is innervated by the facial nerve. This muscle functions to draw the quadrato-mandibular articulation backward, which causes the retraction of all the bones related to it.
4. M. neuro-mandibularis (Fig. 5.1, 5.2 & 5.3)

Beginning in the neck, M. neuro-mandibularis sweeps downwards and forward around the side of the body passing under the cervico-quadratus and over the axial musculature. This muscle runs anteriorly and inserts into the latero-ventral surface of the mandible by an aponeurosis, near the dentary.

The M. neuro-mandibularis is innervated by the XIIth cranial nerve, the hypoglossal. This muscle serves to draw back the quadrato-mandibular articulation via the mandible which causes retraction of all the bones related to it.

**Hyoid and Tongue-muscles**

The nomenclature followed here is that of Bhati and Dutta (1977)

a. Hyoid-muscles.

M. neuro-costo mandibularis pars hyoideus.

This is a parallel-fibred muscle originating from the compound bone immediately after the insertion of the M. neuro-mandibularis. It extends posteriorwards and fleshly inserts on to the anterior region of the hyoid.

M. geniohyoideus.

M. geniohyoideus is a broad, parallel-fibred muscle, originating from the ventral border of the compound bone, just posterior to the origin of the M. intermandibularis. This muscle fleshly
inserts into the lateral border of the processus entoglossus and the basihyoid.

M. omnohyoideus.

M. omnohyoideus is a small, parallel fibred muscle lying below the M.neuro-costo-mandibularis. It arises from the skin in the neck region and is inserted on the anterior ventro-lateral part of the basihyoid.

M. sternohyoideus.

M. sternohyoideus is a parallel-fibred muscle, which originates fleshly from the skin of the neck region just posterior to the origin of the M. omnohyoideus. It extends along with the M. omnohyoideus and inserts into the ventro-lateral border of the basihyoid just posterior to the insertion of the M.omnohyoideus.

b. Tongue-muscles

The tongue consists of the following muscles:

M. hyoglossus.

The M. hyoglossus shares the major part of tongue musculature. This muscle originates from the posterior end of the ceratobranchial cartilage and extends forwards parallel to each other. It is enclosed in the tongue-sheath. The contraction of the perpendicular bundles causes protraction of the tongue, and contraction of logitudinal bundles causes retraction of the tongue.
M. genioglossus.

The M. genioglossus is a paired, parallel-fibred and long muscle. This muscle originates from the heads anteriorly, from the tip of the lower jaw. One head arises from the anterior tip of the mandible and the other arises just behind the former. The two heads unite, become stout, and run posteriorwards parallel to the tongue-sheath. It inserts on the fascia of the hyoglossus muscle.

The structure of the hyoid-muscles and tongue-muscles show variations in the three snakes studied. However, the structural variations are not described in detail because they do not serve in food procurement.

B.

Operative efficiency of the feeding apparatus

The operative efficiency of the feeding apparatus has been worked out with reference to:

1. lever systems of the feeding apparatus and
2. Quantitative myology.

Lever systems of the feeding apparatus

The jaw movements consist of abduction, adduction, protraction and retraction.

A. Abduction.

Abduction involves a first-class lever system. The articulation of the mandible with the quadrate forms the pivot (P) on which the
lever works. The adductor muscles are inserted into the retroarticular process, which is situated posterior to the pivot. The distance between the insertion of the muscle into the retroarticular process and the pivot forms the force arm \((d_2)\). The distance from the pivot to the symphysis of the mandible constitutes the work arm \((L)\). The contraction of the abductor muscles bring about the opening of the jaw by lowering the work arm on its pivot.

B. Adduction

The adduction involves the operation of a third-class lever system. In this the quadrato-mandibular articulation forms the pivot \((P)\). The adductor muscles insert into the lower jaw between the pivot and the point of symphysis. The distance from the insertion of the muscle into the mandible to pivot constitutes the force arm \((d)\). The distance from the pivot \((P)\) to the symphysis of the mandible forms the work arm \((L)\). Owing to the contraction of the adductor muscles the lower jaw is pulled upwards on its pivot.

C. Protraction

The protraction of the upper jaw involves a complex first class lever system in the case of M. protractor pterygoidei and M. levator pterygoidei. In this fronto-nasal hinge forms the pivot \((P_2)\). The protractor muscles are inserted into the palato-pterygoid bar. The longitudinal axis of this bar is in exact direction of the force acting on the power arm. The perpendicular distance between the fronto-nasal hinge and the palato-pterygoid bar constitutes the force arm \((R)\). The distance from the pivot \((P_2)\) to the tip of the snout.
forms the work arm (L2). The contraction of the protractor muscles pull the palato–pterygoid bar forward results in the protraction of the upper jaw.

In the case of M. protractor quadrati, the lever system involved is a simple second class. This muscle is inserted into the tip of the force arm (L3), the quadrate. The quadrato–supratemporal articulation forms the pivot (P3). Here work arm (R3) is equal to the force arm, ie, the force arm and work arm are the length of the quadrate. The contraction of the M. protractor quadrati results in the movement of the quadrato–mandibular articulation forward, which protracts all the bones of the upper jaw due to the contraction of the pterygoid with the quadrato–mandibular articulation.

The protraction of the lower jaw involves simple second class lever system. The quadrato–supratemporal articulation forms the pivot (P3). The muscles are inserted into the tip of the force arm (L3) which is the distance between the pivot (P3) and the quadrato–mandibular articulation. The contraction of this muscle results in the protraction of the lower jaw.

D. Retraction.

The retraction of the upper jaw involves first class lever system except in the case of M. cervico–mandibularis. The fronto–nasal hinge form the pivot (P2) for the muscles, M. retractor vomeris and M. retractor pterygoidei. The palato–pterygoid has given the base for the insertion of the muscles. The longitudinal axis of this bar is in
direction of the force acting on the power arm. The perpendicular distance from the fronto-nasal hinge (P2) to the palato-pterygoid bar constitutes the force arm (R). The work arm (L2) forms the distance between the fronto-nasal hinge and the tip of the snout. The contraction of the above mentioned muscles draw the palato-pterygoid bar backwards which results in the movement of all the upper jaw elements in backward direction.

In the case of M. neuro mandibularis, the quadrato-supratemporal articulation forms the pivot (P3). The muscle is inserted into the mandible in the longitudinal axis of the same as in exact direction of the force acting on the power arm. The perpendicular distance between the pivot (P3) and the mandible is considered as the force arm (R2). The distance between the pivot (P3) and the quadrato-mandibular articulation forms the work arm (L3). Owing to the contraction of the muscles, the force is transmitted to the quadrato-mandibular articulation through the mandible, which results in the backward movement of the same. The quadrato-mandibular articulation is connected with the pterygoid and the maxilla with ligaments. So the movement is transmitted to the pterygoid and maxilla which results in the retraction of upper-jaw elements.

A second-class lever system is involved in the case of the M. cervico-mandibularis. Here the pivot (P3) is the quadrato-supratemporal articulation. The distance between the pivot (P3) and the quadrato-mandibular articulation to which the muscle is attached
forms the force arm (R3). The same is considered as the work arm (L3). The contraction of the M. cervico mandibularis pulls the quadrato-mandibular articulation backwards, resulting in the retraction of the upper jaw.

Quantitative myology

The effective forces and their indices calculated during the present investigation are summarised in the following tables (5.1-24)

**TABLE 5.1: EFFECTIVE FORCE OF ADDUCTION BY THE M. ADDUCTOR MANDBULAE EXTERNUS SUPERFICIALIS**

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F'</th>
<th>Sin θFd</th>
<th>Length of the force arm 'd' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. concius</td>
<td>0.096</td>
<td>0.8071</td>
<td>9.65</td>
<td>0.7477</td>
<td>24.25</td>
<td>0.03083</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.112</td>
<td>0.9249</td>
<td>15.12</td>
<td>1.5662</td>
<td>42.82</td>
<td>0.03658</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.064</td>
<td>0.8566</td>
<td>7.34</td>
<td>0.4024</td>
<td>20.75</td>
<td>0.01939</td>
</tr>
</tbody>
</table>

**TABLE 5.2: EFFECTIVE FORCE OF ADDUCTION BY THE M. ADDUCTOR MANDBULAE EXTERNUS MEDIALIS**

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F'</th>
<th>Sin θFd</th>
<th>Length of the force arm 'd' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. concius</td>
<td>0.105</td>
<td>0.8767</td>
<td>11.95</td>
<td>1.1000</td>
<td>24.25</td>
<td>0.04536</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.124</td>
<td>0.9374</td>
<td>20.10</td>
<td>2.3361</td>
<td>42.82</td>
<td>0.05456</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.058</td>
<td>0.8929</td>
<td>11.22</td>
<td>0.5811</td>
<td>20.75</td>
<td>0.02800</td>
</tr>
</tbody>
</table>
TABLE 5.3: EFFECTIVE FORCE OF ADDUCTION BY THE M. ADDUCTOR
MANDIBULAE EXTERNUS PROFUNDUS

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F'</th>
<th>Sin Fd</th>
<th>Length of the force arm 'd'</th>
<th>Moment of torque 'T'</th>
<th>Length of the work arm 'L'</th>
<th>Index to the effective force 't'</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average weight of muscle in gm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. conicus</td>
<td>0.120</td>
<td>0.8996</td>
<td>11.12</td>
<td>1.2004</td>
<td>24.25</td>
<td>0.04950</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.1360</td>
<td>0.9435</td>
<td>22.50</td>
<td>2.8871</td>
<td>42.82</td>
<td>0.06742</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.0601</td>
<td>0.9229</td>
<td>10.82</td>
<td>0.5991</td>
<td>20.75</td>
<td>0.02887</td>
</tr>
</tbody>
</table>

TABLE 5.4: EFFECTIVE FORCE OF ADDUCTION BY THE M. ADDUCTOR
MANDIBULAE POSTERIOR

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F'</th>
<th>Sin Fd</th>
<th>Length of the force arm 'd'</th>
<th>Moment of torque 'T'</th>
<th>Length of the work arm 'L'</th>
<th>Index to the effective force 't'</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average weight of muscle in gm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. conicus</td>
<td>0.116</td>
<td>0.9055</td>
<td>6.65</td>
<td>0.6985</td>
<td>24.25</td>
<td>0.02880</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.1280</td>
<td>0.9450</td>
<td>12.50</td>
<td>1.5120</td>
<td>42.82</td>
<td>0.03531</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.0520</td>
<td>0.9205</td>
<td>4.71</td>
<td>0.2254</td>
<td>20.75</td>
<td>0.01087</td>
</tr>
</tbody>
</table>

TABLE 5.5: EFFECTIVE FORCE OF ADDUCTION BY THE M. PSEUDOTEMPORALIS

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F'</th>
<th>Sin Fd</th>
<th>Length of the force arm 'd'</th>
<th>Moment of torque 'T'</th>
<th>Length of the work arm 'L'</th>
<th>Index to the effective force 't'</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average weight of muscle in gm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eryx conicus</td>
<td>0.052</td>
<td>0.9396</td>
<td>11.12</td>
<td>0.5433</td>
<td>24.25</td>
<td>0.02240</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.064</td>
<td>0.9888</td>
<td>18.35</td>
<td>1.1603</td>
<td>42.82</td>
<td>0.02709</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.028</td>
<td>0.9659</td>
<td>7.22</td>
<td>0.19531</td>
<td>20.75</td>
<td>0.00941</td>
</tr>
</tbody>
</table>
### Table 5.6: Effective Force of Abduction by the M. Depressor Mandibulae Anterior

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Sin $\angle D_f$</th>
<th>Length of the force arm 'd' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.068</td>
<td>0.8072</td>
<td>2.65</td>
<td>0.1454</td>
<td>24.25</td>
<td>0.005996</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.052</td>
<td>0.9206</td>
<td>5.50</td>
<td>0.2650</td>
<td>42.82</td>
<td>0.00619</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.032</td>
<td>0.8749</td>
<td>2.16</td>
<td>0.0604</td>
<td>20.75</td>
<td>0.002911</td>
</tr>
</tbody>
</table>

### Table 5.7: Effective Force of Abduction by the M. Depressor Mandibulae Posterior

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Sin $\angle D_{f2}$</th>
<th>Length of the force arm 'd₂' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.056</td>
<td>0.7804</td>
<td>2.67</td>
<td>0.1168</td>
<td>24.25</td>
<td>0.004811</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.043</td>
<td>0.9105</td>
<td>5.52</td>
<td>0.2161</td>
<td>42.82</td>
<td>0.005047</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.026</td>
<td>0.8671</td>
<td>2.15</td>
<td>0.0485</td>
<td>20.75</td>
<td>0.002335</td>
</tr>
</tbody>
</table>

### Table 5.8: Effective Force of Protraction (Upper Jaw) by the M.Protaractor Pterygoidei

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Cos $\angle a$</th>
<th>Length of the force arm 'R' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L₂' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.148</td>
<td>0.9455</td>
<td>6.12</td>
<td>0.8564</td>
<td>8.73</td>
<td>0.09809</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.116</td>
<td>0.8480</td>
<td>7.62</td>
<td>0.7496</td>
<td>11.52</td>
<td>0.06506</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.067</td>
<td>0.8036</td>
<td>4.57</td>
<td>0.2644</td>
<td>5.73</td>
<td>0.04610</td>
</tr>
</tbody>
</table>
### Table 5.9: Effective Force of Protraction (Upper Jaw) by the M. Levator Pterygoidei

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>$\cos \angle a$</th>
<th>Length of the force arm 'R' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L2' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.096</td>
<td>0.9200</td>
<td>6.12</td>
<td>0.5440</td>
<td>8.73</td>
<td>0.06231</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.058</td>
<td>0.8150</td>
<td>7.62</td>
<td>0.4223</td>
<td>11.52</td>
<td>0.03665</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.040</td>
<td>0.8315</td>
<td>4.57</td>
<td>0.1619</td>
<td>5.73</td>
<td>0.02652</td>
</tr>
</tbody>
</table>

### Table 5.10: Effective Force of Protraction (Upper Jaw) by the M. Protractor Quadrati

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>$\sin \angle FR_3$</th>
<th>Length of the force arm 'R_3' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L_3' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.076</td>
<td>0.8515</td>
<td>6.42</td>
<td>0.4155</td>
<td>6.42</td>
<td>0.0647</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.041</td>
<td>0.7480</td>
<td>15.35</td>
<td>0.4707</td>
<td>15.35</td>
<td>0.0386</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.028</td>
<td>0.7646</td>
<td>5.50</td>
<td>0.1177</td>
<td>5.50</td>
<td>0.0214</td>
</tr>
</tbody>
</table>

### Table 5.11: Effective Force of Protraction (Lower Jaw) by the M. Pterygoideus

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>$\sin \angle FR_3$</th>
<th>Length of the force arm 'R_3' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L_3' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.221</td>
<td>0.9063</td>
<td>6.42</td>
<td>1.2859</td>
<td>6.42</td>
<td>0.2003</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.185</td>
<td>0.8290</td>
<td>15.35</td>
<td>2.3542</td>
<td>15.35</td>
<td>0.1534</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.092</td>
<td>0.8480</td>
<td>5.50</td>
<td>0.4291</td>
<td>5.50</td>
<td>0.07802</td>
</tr>
</tbody>
</table>
### TABLE 5.12: EFFECTIVE FORCE OF PROTRACTION (LOWER JAW) BY THE M.PTERYGOIDEUS ACCESSORIES

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Sin 2 FR₃</th>
<th>Length of the force arm 'R₃' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L₃' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.101</td>
<td>0.8746</td>
<td>6.42</td>
<td>0.5670</td>
<td>6.42</td>
<td>0.0883</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.072</td>
<td>0.7971</td>
<td>15.35</td>
<td>0.8810</td>
<td>15.35</td>
<td>0.0574</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.040</td>
<td>0.8191</td>
<td>5.50</td>
<td>0.1802</td>
<td>5.50</td>
<td>0.0328</td>
</tr>
</tbody>
</table>

### TABLE 5.13: EFFECTIVE FORCE OF RETRACTION (UPPER JAW) BY THE M.PTERYGOIDEUS

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Cos ₄ m</th>
<th>Length of the force arm 'R' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L₂' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.221</td>
<td>0.9256</td>
<td>6.12</td>
<td>1.2519</td>
<td>8.73</td>
<td>0.1434</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.185</td>
<td>0.9674</td>
<td>7.62</td>
<td>1.3672</td>
<td>11.52</td>
<td>0.1184</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.092</td>
<td>0.9460</td>
<td>4.57</td>
<td>0.3977</td>
<td>5.73</td>
<td>0.0694</td>
</tr>
</tbody>
</table>

### TABLE 5.14: EFFECTIVE FORCE OF RETRACTION (UPPER JAW) BY THE M.PTERYGOIDEUS ACCESSORIES

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Cos ₄ m</th>
<th>Length of the force arm 'R' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L₂' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.101</td>
<td>0.9068</td>
<td>6.12</td>
<td>0.5605</td>
<td>8.73</td>
<td>0.0642</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.072</td>
<td>0.9505</td>
<td>7.62</td>
<td>0.5221</td>
<td>11.52</td>
<td>0.0453</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.040</td>
<td>0.9465</td>
<td>4.57</td>
<td>0.1730</td>
<td>5.73</td>
<td>0.0302</td>
</tr>
<tr>
<td>Snake</td>
<td>Force 'F' Average weight of muscle in gm</td>
<td>Cos $\Delta m$</td>
<td>Length of the force arm 'R' mm</td>
<td>Moment of torque 'T' gm mm</td>
<td>Length of the work arm 'Lz' mm</td>
<td>Index to the effective force 't' gm</td>
</tr>
<tr>
<td>---------</td>
<td>-----------------------------------------</td>
<td>----------------</td>
<td>-------------------------------</td>
<td>----------------------------</td>
<td>-------------------------------</td>
<td>----------------------------------</td>
</tr>
<tr>
<td>E. conicus</td>
<td>0.069</td>
<td>0.9496</td>
<td>6.12</td>
<td>0.4009</td>
<td>8.73</td>
<td>0.0459</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.043</td>
<td>0.8667</td>
<td>7.62</td>
<td>0.2840</td>
<td>11.52</td>
<td>0.0247</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.029</td>
<td>0.8968</td>
<td>4.57</td>
<td>0.1191</td>
<td>5.73</td>
<td>0.0208</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Cos $\Delta m$</th>
<th>Length of the force arm 'R' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'Lz' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.034</td>
<td>0.9993</td>
<td>6.12</td>
<td>0.2079</td>
<td>8.73</td>
<td>0.0238</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.027</td>
<td>0.9962</td>
<td>7.62</td>
<td>0.2050</td>
<td>11.52</td>
<td>0.0178</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.012</td>
<td>0.9986</td>
<td>4.57</td>
<td>0.0548</td>
<td>5.73</td>
<td>0.0096</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Sin $\angle FR_3$</th>
<th>Length of the force arm 'R_3' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L_3' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.146</td>
<td>0.9760</td>
<td>6.42</td>
<td>0.9148</td>
<td>6.42</td>
<td>0.1425</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.109</td>
<td>0.9645</td>
<td>15.35</td>
<td>1.6472</td>
<td>15.35</td>
<td>0.1073</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.068</td>
<td>0.9966</td>
<td>5.50</td>
<td>0.3727</td>
<td>5.50</td>
<td>0.0678</td>
</tr>
</tbody>
</table>
# TABLE 5.18: EFFECTIVE FORCE OF RETRACTION (UPPER JAW) BY THE M. NEURO - MANDIBULARIS

<table>
<thead>
<tr>
<th>Snake</th>
<th>Force 'F' Average weight of muscle in gm</th>
<th>Cos θa</th>
<th>Length of the force arm 'R2' mm</th>
<th>Moment of torque 'T' gm mm</th>
<th>Length of the work arm 'L3' mm</th>
<th>Index to the effective force 't' gm</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.161</td>
<td>0.9826</td>
<td>7.21</td>
<td>1.1406</td>
<td>6.42</td>
<td>0.1776</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.128</td>
<td>0.9580</td>
<td>11.46</td>
<td>1.4053</td>
<td>15.35</td>
<td>0.0916</td>
</tr>
<tr>
<td>D. trisris</td>
<td>0.079</td>
<td>0.9740</td>
<td>3.92</td>
<td>0.3016</td>
<td>5.50</td>
<td>0.0548</td>
</tr>
</tbody>
</table>

# TABLE 5.19: EFFECTIVE FORCE OF ABDUCTION PER GRAM WEIGHT OF MUSCLE

<table>
<thead>
<tr>
<th>Muscle</th>
<th>E. conicus</th>
<th>D. nasutus</th>
<th>D. tristis</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. depressor mandibulae anterior</td>
<td>0.005996</td>
<td>0.00619</td>
<td>0.002911</td>
</tr>
<tr>
<td>M. depressor mandibulace posterior</td>
<td>0.004811</td>
<td>0.005047</td>
<td>0.002335</td>
</tr>
<tr>
<td>Total effective force of abduction in grams</td>
<td>0.01081</td>
<td>0.01124</td>
<td>0.005246</td>
</tr>
<tr>
<td>Total weight of muscles involved in abduction in grams</td>
<td>0.124</td>
<td>0.096</td>
<td>0.058</td>
</tr>
<tr>
<td>Effective force of abduction in grams per gram weight of muscle</td>
<td>0.0872</td>
<td>0.1183</td>
<td>0.0903</td>
</tr>
</tbody>
</table>
### TABLE 5.20: EFFECTIVE FORCE OF ADDUCTION PER GRAM WEIGHT OF MUSCLE

<table>
<thead>
<tr>
<th>Muscle</th>
<th>E. conicus</th>
<th>D. nasutus</th>
<th>D. tristis</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. adductor mandibulae externus superficialis</td>
<td>0.3083</td>
<td>0.3065</td>
<td>0.0193</td>
</tr>
<tr>
<td>M. adductor mandibulae externus medialis</td>
<td>0.0453</td>
<td>0.0545</td>
<td>0.0280</td>
</tr>
<tr>
<td>M. adductor mandibulae externus profundus</td>
<td>0.0495</td>
<td>0.0674</td>
<td>0.0288</td>
</tr>
<tr>
<td>M. adductor mandibulae posterior</td>
<td>0.0288</td>
<td>0.0353</td>
<td>0.0108</td>
</tr>
<tr>
<td>M. pseudotemporalis</td>
<td>0.0224</td>
<td>0.0270</td>
<td>0.0094</td>
</tr>
<tr>
<td>Total effective force of adduction in grams</td>
<td>0.1769</td>
<td>0.2209</td>
<td>0.0965</td>
</tr>
<tr>
<td>Total weight of muscles involved in adduction in grams</td>
<td>0.489</td>
<td>0.564</td>
<td>0.262</td>
</tr>
<tr>
<td>Effective force of adduction in grams per gram weight of muscle</td>
<td>0.3617</td>
<td>0.3917</td>
<td>0.3683</td>
</tr>
</tbody>
</table>

### TABLE 5.21: EFFECTIVE FORCE OF PROTRACTION (UPPER JAW) PER GRAM WEIGHT OF MUSCLE

<table>
<thead>
<tr>
<th>Muscle</th>
<th>E. conicus</th>
<th>D. nasutus</th>
<th>D. tristis</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. protractor pterygoidei</td>
<td>0.0981</td>
<td>0.0651</td>
<td>0.0461</td>
</tr>
<tr>
<td>M. levator pterygoidei</td>
<td>0.0623</td>
<td>0.0367</td>
<td>0.0265</td>
</tr>
<tr>
<td>M. protractor quadrati</td>
<td>0.0647</td>
<td>0.0306</td>
<td>0.0214</td>
</tr>
<tr>
<td>Total effective force of protraction in grams</td>
<td>0.2251</td>
<td>0.1324</td>
<td>0.094</td>
</tr>
<tr>
<td>Total weight of muscles involved in protraction in grams</td>
<td>0.320</td>
<td>0.215</td>
<td>0.135</td>
</tr>
<tr>
<td>Effective force of protraction in grams per gram weight of muscle</td>
<td>0.7034</td>
<td>0.6158</td>
<td>0.6963</td>
</tr>
</tbody>
</table>
### Table 5.22: Effective Force of Protraction (Lower Jaw) per Gram Weight of Muscle

<table>
<thead>
<tr>
<th>Muscle</th>
<th>E. conicus</th>
<th>D. nasutus</th>
<th>D. tristis</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. pterygoideus</td>
<td>0.2003</td>
<td>0.1534</td>
<td>0.0780</td>
</tr>
<tr>
<td>M. pterygoideus accessories</td>
<td>0.0883</td>
<td>0.0574</td>
<td>0.0328</td>
</tr>
<tr>
<td>Total effective force of protraction in grams</td>
<td>0.2886</td>
<td>0.2108</td>
<td>0.1108</td>
</tr>
<tr>
<td>Total weight of muscles involved in protraction in grams</td>
<td>0.322</td>
<td>0.257</td>
<td>0.132</td>
</tr>
<tr>
<td>Effective force of protraction in grams per gram weight of muscle</td>
<td>0.8963</td>
<td>0.8202</td>
<td>0.8394</td>
</tr>
</tbody>
</table>

### Table 5.23: Effective Force of Retraction (Upper Jaw) per Gram Weight of Muscle

<table>
<thead>
<tr>
<th>Muscle</th>
<th>E. conicus</th>
<th>D. nasutus</th>
<th>D. tristis</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. pterygoideus</td>
<td>0.1434</td>
<td>0.1184</td>
<td>0.0694</td>
</tr>
<tr>
<td>M. pterygoideus accessories</td>
<td>0.0642</td>
<td>0.0453</td>
<td>0.0302</td>
</tr>
<tr>
<td>M. retractor pterygoidei</td>
<td>0.0459</td>
<td>0.0247</td>
<td>0.0208</td>
</tr>
<tr>
<td>M. retractor vomeris</td>
<td>0.0238</td>
<td>0.0178</td>
<td>0.0096</td>
</tr>
<tr>
<td>M. cervico-mandibularis</td>
<td>0.1425</td>
<td>0.1073</td>
<td>0.0678</td>
</tr>
<tr>
<td>M. neuro-mandibularis</td>
<td>0.1776</td>
<td>0.0916</td>
<td>0.0548</td>
</tr>
<tr>
<td>Total effective force of retraction in grams</td>
<td>0.5974</td>
<td>0.4051</td>
<td>0.2526</td>
</tr>
<tr>
<td>Total weight of muscles involved in retraction in grams</td>
<td>0.732</td>
<td>0.564</td>
<td>0.320</td>
</tr>
<tr>
<td>Total force of retraction in grams per gram weight of muscle</td>
<td>0.8161</td>
<td>0.7183</td>
<td>0.7894</td>
</tr>
</tbody>
</table>

### Table 5.24: Indices to the Effective Forces of the Functional Groups of Muscles per Gram Weight of Muscle

<table>
<thead>
<tr>
<th>Snake</th>
<th>Abduction</th>
<th>Adduction</th>
<th>Protraction (upper Jaw)</th>
<th>Protraction (lower jaw)</th>
<th>Retraction (upper jaw)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. conicus</td>
<td>0.0872</td>
<td>0.3617</td>
<td>0.7034</td>
<td>0.8963</td>
<td>0.8161</td>
</tr>
<tr>
<td>D. nasutus</td>
<td>0.1183</td>
<td>0.3917</td>
<td>0.6158</td>
<td>0.8202</td>
<td>0.7183</td>
</tr>
<tr>
<td>D. tristis</td>
<td>0.0903</td>
<td>0.3683</td>
<td>0.6963</td>
<td>0.8394</td>
<td>0.7894</td>
</tr>
</tbody>
</table>
The jaw-muscles related to abduction are equipped with minimum effective force per gram weight of muscle in the snakes studied (Table 5.19 & 24). In the three snakes, *D. nasutus* contains maximum effective force of abduction. M. depressor mandibulae anterior and M. depressor mandibulae posterior of *D. nasutus* exerts 0.00619 and 0.005047 effective force per gram weight of muscle. The total effective force of abduction is least in *E. conicus* and it is 0.0872 per gram weight of muscle. In *D. tristis*, the force of abduction is 0.0903 per gram weight of muscle.

The effective force of adduction is greater than the force of abduction in the three snakes (Table 5.20 & 24). Among these, *D. nasutus* produces maximum force of adduction. The total effective force of adduction per gram weight of muscle is 0.3917 in *D. nasutus*. In *E. conicus* and *D. tristis* it is 0.3617 and 0.3683 respectively.

The effective force of protraction (upper jaw) is ranged from a minimum of 0.6158 in *D. nasutus* to a maximum of 0.7034 in *E. conicus*. It is 0.6963 in *D. tristis* (Table 5.21 & 24). The effective force of protraction (lower jaw) per gram weight of muscle (Table 5.22 & 24) is greater than the effective force of protraction (upper jaw) in the three snakes.

The maximum effective force of retraction per gram weight of muscle is observed in the retractor muscles of *E. conicus*. The total effective force of retraction (Table 5.23 & 24) in *E. conicus*, *D. nasutus* and *D. tristis* is 0.8161, 0.7183 and 0.7894 per gram weight of muscle respectively.
CHAPTER VI

STRUCTURE AND DISPOSITION OF THE LOCOMOTORY MUSCLES

Of the four classes of land vertebrates, Amphibians and Reptiles have limbless representatives. In snakes the lack of appendages presents certain basic myological changes which involve the development of increased complexity in musculature and allowing greater variety of movements.

The main groups of body muscles important in locomotion are muscles between vertebrae, between vertebrae and ribs, between ribs and the ribs or vertebrae to the integument. The musculature of the snake body is formed by the repetition of muscles throughout its length. Mosauer (1935) attempted to construct a phylogeny of snakes based on the interspecific variation of body muscles. Gasc (1967) described the axial musculature of lizards and snakes. Ruben (1977) briefly dealt with the correlations between locomotion and axial musculature in Lichanura and Masticophis. Bhati and Dutta (1977) described the trunk musculature of Ptyas mucosus.

Despite of all these studies, much remains to be learned
regarding the functional anatomy and locomotor ability in snakes. This study is important to understand the structural and functional demands placed on efficient locomotory system of Eryx conicus, Dryophis nasutus and Dendrelaphis tristis.

The nomenclature of the locomotory muscles followed in this is that of Bhati and Dutta (1977)

The following is an account of the structure and disposition of the locomotory muscles of the snakes in the present study. The relative length of muscles and snout vent length (SVL) are summarised in Table 6.1

**M. spinalis (Fig. 6.1, 6.2 & 6.3)**

M. spinalis is a parallel-fibred muscle which orginates tendinously from the lateral side of the neural spine. The muscle extends forwards by the lateral sides of the neural spines. It fuses together anteriorly with M. semispinalis preceding the third vertebrae and extends forwards as a single muscle. In D. nasutus and D. tristis, this muscle runs over thirty four vertebrae where it gets inserted tendinously on the dorso-lateral surface of the anterior part of the neural spine. The belly of the muscle covers four vertebrae. In E. conicus, it arises by a flat, very short tendon and runs over thirteen vertebrae and attaches tendinously on the fourteenth vertebra.
The relative length of M.spinalis and snout vent length shows marked variation between the three snakes. This is 20.55% in D. tristis. In E. corlicus and D. nasutus, it is 7.10% and 16.94% respectively.

**M.semispinalis (Fig. 6.1, 6.2 & 6.3)**

M.semispinalis is a parallel fibred muscle which originates from the lateral side of neural spine of each vertebra except atlas and axis. In D. nasutus and D. tristis, this muscle fuse together with M.spinalis in the region of the preceding third vertebra, from its origin and extends forwards as a single muscle. The common tendon gradually tapers and inserts on the dorso-lateral surface of the anterior part of the neural spine of the preceding thirty fourth vertebra. In E. conicus there is no marked separation between these muscles. They fuse together and function as a single muscle.

The relative length of M. spinalis and snout vent length ranges from a maximum of 22.83% in D. tristis to a minimum of 7.14% in E. conicus. It is 18.39% in D. nasutus.

**M.longissimus dorsi (Fig. 6.1, 6.2 & 6.3)**

M. longissimus dorsi is an elongated flat, parallel fibred muscle with tendinous origin from the cranio-lateral portion of the prezygapophysis. In E. conicus, it extends forwards and is tendinously
inserted on the preceding sixth vertebra. In *D. nasutus* and *D. tristis*, it extends forwards along with the M.Interarticularis inferior. At the level of the ninth vertebra, it divides into dorsal and ventral part. The dorsal part extends upwards and forwards, and tendinously inserts at the base of the neural spine. The tendon of the ventral part extends forwards and downwards, and is inserted on the tenth vertebra on the posterior face by a thin tendon.

The relative length of M. longissimus dorsi and snout vent length is 6.33% in *D. tristis*, 3.5% in *E. conicus* and 5.69% in *D. nasutus*.

**M.multifidus (Fig. 6.1, 6.2 & 6.3)**

The M. multifidus originates from the neural arches, a little behind the origin of the M.spinalis, by a flat tendon. It extends along the inner surface of the M.spinalis up to the fourth segment, where the fibres get inserted on the posterior border of the neural spine of the preceding vertebra, just above the postzygapophysis. The muscles originating from the anteriormost four vertebrae are inserted by a common flat tendon on the posterior surface of the basisphenoid bone. In *E. conicus*, this muscle spans over three vertebrae and in *D. nasutus* and *D. tristis* it spreads over four vertebrae.

The relative length of M.multifidus and snout vent length is
**Figure 6.1**

**Locomotory muscles of Eryx conicus**

6.1 (a) Lateral view of the musculature of the middle thoracic region (semi-diagrammatic)

6.1 (b) Ventral view of the musculature of the ventral body wall (semi-diagrammatic)

**Abbreviations:**

- Ms – M. spinalis; Msp – semispinalis;
- Mld – M. longissimus dorsi; Mm – multifidus;
- Mis – M. interarticularis superior;
- Mii – M. interarticularis inferior; Mi – M. intervertebralis;
- Mrc – M. retractor costae biceps;
- Mlc – M. levator costae; Mt – M. tuberculocostalis;
- Mtd – M. transversus dorsalis;
- Mcis – M. costalis internus superior;
- Mcii – M. costalis internus inferior;
- Mcv – M. costovertebrocostalis;
- Mip – M. intercostalis proprius;
- Mra – M. rectus abdominis;
- Mta – M. transversus abdominis;
- Msd – M. supracostalis dorsalis;
- Mcs – M. costocutaneous superior;
- Mci – M. costocutaneous inferior.
2.26% in *E. conicus*. This is 2.16% in *D. nasutus* and 2.48% in *D. tristis*.

**M.interarticularis superior (Fig. 6.1, 6.2 & 6.3)**

*M.interarticularis superior* is a short, parallel-fibred muscle, which originates tendinously from the dorsal surface of the postzygapophysis and extends forwards on the lateral surface of the *M.spinalis*. It is inserted tendinously on the posterior edge of the postzygapophysis of the preceding vertebra. It further runs forwards as a thin muscular slip which is inserted on the prezygapophysis of the same vertebra. The disposition of this muscle is more or less same in the three snakes.

The relative length of *M.interarticularis superior* and snout vent length in *E. conicus*, *D. nasutus* and *D. tristis* is 1.46%, 0.84% and 1.21% respectively.

**M.interarticularis inferior (Fig. 6.1, 6.2 & 6.3)**

The *M.interarticularis inferior* is a parallel-fibred muscle. It has tendinous origin from the prezygapophysis. During its course, it lies concealed by the *M.longissimus dorsi*. In *E. conicus*, it is originated from the prezygapophysis and is inserted by short tendon on the prezygapophysis of the preceding fourth vertebra. In *D. nasutus* and *D. tristis*, it is inserted by a tendon on the fifth vertebra.
The relative length of M.interarticularis inferior and snout vent length is 3.09% in E. conicus and 2.21% in D. nasutus. It is 2.88% in D. tristis.

**M.intervertebralis (Fig. 6.1, 6.2 & 6.3)**

M.intervertebralis is a short, parallel fibred muscle which connects the succeeding vertebra to each other. It has fleshy origin from the lateral part of the neural arch and is fleshly inserted on the postero-lateral side of the neural arch of the preceding vertebra. The arrangement is same in the three snakes. The relative length of M.interarticularis in E. conicus, D. nasutus and D. tristis is 0.64%, 0.49% and 0.57% respectively.

**M.retractor costae biceps (Fig. 6.1, 6.2 & 6.3)**

M.retractor costae biceps consists of two fleshy bellies, in each segment which are joined by an aponeurosis. The median belly arises by continuation of the M.longissimus dorsi. The lateral belly is like the median one. but originates from an intermediate aponeurosis. In E. conicus, it is originated by a short tendon, extends forewards and is tendinously inserted on the inner side of the nineth rib. In D. nasutus, it is inserted on the fourteenth rib. In D. tristis, it spans over fifteen ribs and is inserted on the innerside of the sixteenth rib. In D. nasutus and D. tristis anterior tendon of this muscle is long. This muscle shows marked variation among the three species.
Figure 6.2

Locomotory muscles of Dryophis nasutus

6.2 (a) Lateral view of the musculature of the middle thoracic region (semi-diagrammatic)
6.2 (b) Ventral view of the musculature of the ventral body wall (semi-diagrammatic)

Abbreviations:

Ms – M. spinalis; Msp – M. semispinalis;
Mld – M. longissimus dorsi; Mn – M. multifidus;
Mis – M. interarticularis superior;
Mii – M. interarticularis inferior; Mi – M. intervertebralis;
Mrc – M. retractor costae biceps;
Mlc – M. levator costae;
Mt – M. tuberculocostalis;
Mtd – M. transversus dorsalis;
Mcis – M. costalis internus superior;
Mcii – M. costalis internus inferior;
Mcv – M. costovertebrocostalis;
Mip – M. intercostalis proprius;
Mra – M. rectus abdominis;
Mta – M. transversus abdominis;
Msd – M. supracostalis dorsalis;
Mcs – M. costocutaneous superior;
Mci – M. costocutaneous inferior.
Figure 6.2 MCII
The relative length of M.retractor costae biceps and snout vent length is 7.07% in D. nasutus and 6.01% in E. conicus. It is 9.58% in D. tristis.

**M.levator costae (Fig. 6.1, 6.2 & 6.3)**

M.levator costae is a parallel-fibred, short muscle which tendinously arises from the posterior ventral surface of the prezygapophysis. It extends posteriorwards and downwards, which is tendinously inserted on the dorsal side of the rib of the succeeding vertebra. During its course, it covers M.tuberculocostalis, M.costovertebrocostalis and M.intercostalis proprius. In E. conicus, it is broad and massive than the other two snakes. The disposition is similar in the three snakes.

The relative length of M.levator costae and snout vent length in E. conicus, D. nasutus and D. tristis is 1.57%, 1.08% and 1.32% respectively.

**M.tuberculocostalis (Fig. 6.1, 6.2 & 6.3)**

M.tuberculocostalis is a short, parallel-fibred muscle. It orginates from the posterior surface of the capitulum of the rib by a short tendon and extends backwards between the M.costovertebrocosalis and M.levator costae. After spanning one segment, it gets fleshy insertion below the capitulum on the
antero-dorsal surface of the rib of the succeeding vertebra. This muscle has the same arrangement in the three snakes.

The relative length of M.tuberculocostalis and snout vent length varies from 1.09% in E. conicus to 1.22% in D. nasutus. In D. tristis it is 1.16%.

M.transversus dorsalis (Fig. 6.1, 6.2 & 6.3)

M.transversus dorsalis is a deep seated slender muscle lying between the proximal end of the succeeding rib. It arises fleshly from the ventral median crest of the vertebral column, and forms a muscular sheath. The muscle extends forwards and downwards, and is inserted fleshly on the second preceding rib on its medial side. The structure and disposition is same in the three snakes.

The relative length of M.transversus dorsalis and snout vent length in E. conicus, D. nasutus and D. tristis is 1.66%, 0.79% and 1.07% respectively.

M.costalis internus superior (Fig. 6.1, 6.2 & 6.3)

M.costalis internus superior has the same origin as that of M.transversus dorsalis. This muscle together form the muscular lining of the body. In D. nasutus and D. tristis, this muscle spans obliquely forwards and is fleshly inserted on the posterio-lateral surface of the preceding third rib. It is covered ventrally by M.transversus dorsalis,
Figure 6.3
Figure 6.3

Locomotory muscles of Dendrelaphis tristis

6.3 (a) Lateral view of the musculature of the middle thoracic region (semi-diagrammatic)

6.3 (b) Ventral view of the musculature of the ventral body wall (semi-diagrammatic)

Abbreviations:

Ms. M. spinalis; Msp – M. semispinalis;
Mld – M. longissimus dorsi; Mm – M. multifidus;
Mis – M. interarticularis superior;
Mii – M. interarticularis inferior;
Mi – M. intervertebralis;
Mrc – M. retractor costae biceps;
Mlc – M. levator costae; Mt – M. tuberculocostalis;
Mtd – M. transversus dorsalis;
Mcis – M. costalis internus superior;
Mcii – M. costalis internus inferior;
Mcv – M. costovertebrocostalis;
Mip – M. intercostalis proprius;
Mra – M. rectus abdominis;
Mta – M. transversus abdominis;
Msd – M. supracostalis dorsalis;
Mcs – M. costocutaneous superior;
Mci – M. costocutaneous inferior.
Figure 6.3

5 mm
and dorsally by M. costovertebrocostalis and M. costalis internus inferior. In *E. conicus*, it is inserted on the postero-lateral surface of the preceding seventh rib.

The relative length of M. costalis internus superior and snout vent length is greatest in *E. conicus*. It is ranges from a minimum of 1.37% in *D. nasutus* to a maximum of 4.12% in *E. conicus*. It is 1.79% in *D. tristis*.

**M. costalis internus inferior (Fig. 6.1, 6.2 & 6.3)**

M. costalis internus inferior is tendinously originated from the ventral side of the centrum, close to the origin of M. costalis internus superior. It extends backwards, below the M. costalis internus superior and skips over two segments. It is fleshly inserted on the distal end of the third rib. The arrangement of muscle fibres is of similar pattern in the three snakes.

The relative length of M. costocutaneous inferior and snout vent length in *D. nasutus* is 1.08%, 1.33% in *D. tristis* and 1.64% in *E. conicus*.

**M. costovertebrocostalis (Fig. 6.1, 6.2 & 6.3)**

M. costovertebrocostalis is a small, broad muscle which covers the ventro-lateral surface of the vertebra and extends backwards. It is fleshly inserted on the proximal part of the succeeding rib. During its
course it is covered ventrally by M. costalis internus superior and
dorsally by M. levator costae and M. tuberculocostalis. The disposition of
this muscle is more or less same in the three snakes.

In *E. conicus*, the relative length of M. costovertebrocostalis
and snout vent length is 1.28%. In *D. nasutus* and *D. tristis* it is
0.71% and 0.87% respectively.

**M. intercostalis proprius** (*Fig. 6.1, 6.2 & 6.3*)

M. intercostalis proprius is a thin muscular sheath which
occupies the space between the successive ribs. It fleshly originates
from the posterior surface of the rib and extends backwards. This
muscle is inserted fleshly on the anterior surface of the following rib.
It is covered dorsally by M. levator costae, M. supracostalis dorsalis and
M. costocutaneous superior. The disposition of M. intercostalis proprius
is same in the three snakes.

There is no marked variation in the relative length of
M. intercostalis proprius and snout vent length in the three snakes.

**M. rectus abdominis** (*Fig. 6.1, 6.2 & 6.3*)

M. rectus abdominis is lying between the bony extremities of
the successive ribs. It is fleshly orginated from the posterior surface
of the rib and is inserted fleshly on the anterior surface of the
following rib. The disposition of this muscle is more or less same in the three snakes.

The relative length of M.rectus abdominis and snout vent length is 0.72% in *D. nasutus*. It is 0.72% in *E. conicus* and 0.68% in *D. tristis*.

**M.transversus abdominis (Fig. 6.1, 6.2 & 6.3)**

M.transversus abdominis forms the innermost layer of the body wall. It fleshly arises from the ribs, extends slightly downwards and backwards. This muscle fleshly insert to the integument in the mid ventral line. The slips join to form a thin muscular sheath. The disposition is similar in the three snakes.

The relative length of M.transversus abdominis and snout vent length in *E. conicus* is 2.4%, 1.23% in *D. nasutus* and 1.24% in *D. tristis*.

**M.supracostalis dorsalis (Fig. 6.1, 6.2 & 6.3)**

M.supracostalis dorsalis is an elongated flat muscle which originates by a short tendon from the inner surface of the proximal part of the rib, close to the insertion of the M.retractor costae biceps. In *E. conicus*, this muscle extends backwards and downwards, gradually becomes broader, and is inserted after spanning seven segments on the anterior surface at the distal end of the eighth rib.