

The mechanism of the extrinsic coxal muscles of spiders

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The muscles assumed by earlier authors to depress the coxae (“Depressor anterior & posterior”) have no leverage acting on the coxa/cephalothorax joints. The author suggests that the contraction of the “depressors” (muscles c_7 and c_8) pulls their origin on the endosternum outwards, resulting in a piston-like action of the more dorsal muscles c_5 and c_6 against the upper part of the coxa. Another possible mechanism is a hydraulic action.

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1. Introduction

The coxae (and the basal part of the chelicera) of the spiders are assumed to have a basic complement of 4 pairs of extrinsic muscles. The names used by earlier authors for these muscles (cf. Brown 1939; Whitehead & Rempel 1959) suggest certain functions: Rotator anterior & posterior, Levator anterior & posterior, Promotor, Remotor, Depressor anterior & posterior. In an earlier paper (Palmgren 1978) I expressed some doubt concerning the validity of the functional interpretation and proposed a set of new names denoting origin and insertion: Mm tergocoxales c_1 (“rotator anterior”), c_{2-3} (“levators”), c_4 (“rotator posterior”, missing in most labidognathous spiders, present chiefly in spiders of the Amaurobiidae group sensu Lehtinen and even in them generally only present in connection with legs I–II), Mm endosterno-coxales c_5 (“promotor”), c_6 (“remotor”), c_{7-8} (“depressors”) (cf. Figs. 2–3, complete names in the list of abbreviations).

The present study aims at a more exact scrutiny of the functional anatomy of the coxa using *Dolomedes fimbriatus* (Clerck) as the study object. The technique was the same as that employed by me in 1978.

2. Anatomy of the coxal joint

The coxae of the walking legs are generally hinged on the margin of the sternum by means of

strongly sclerotized, though not markedly bulging, prominences. The anterior prominence (aj) lies at the inner end of the coxal apodeme, and the posterior one (hj) is situated almost level with it and a little ahead of the posterior coxal wall, at the lower hind angle of the aperture between the coxa and cephalothorax (Fig. 2). The rim of the sternum is correspondingly strengthened especially at the hind joint, which is marked by a triangular prominence (Fig. 4), but no sockets are formed. The attachment of the coxa to the pleura along the anterior and posterior rims of the aperture slopes strongly outwards. The soft connecting membrane widens upwards to join the dorsal margin of the coxa to the inwardly bent “doubleure” of the tergal margin as a fairly broad, folded sheet. Levation and depression of the coxa are thus possible.

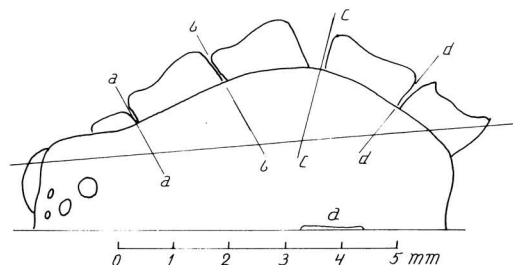


Fig. 1. Dorsal half-view. The long straight line shows the section depicted in Figs. 5–6. The plane of the cut inclines ventro-medially at an angle of 30°. The short straight lines indicate the sections of Fig. 2. All figures depict *Dolomedes fimbriatus*.

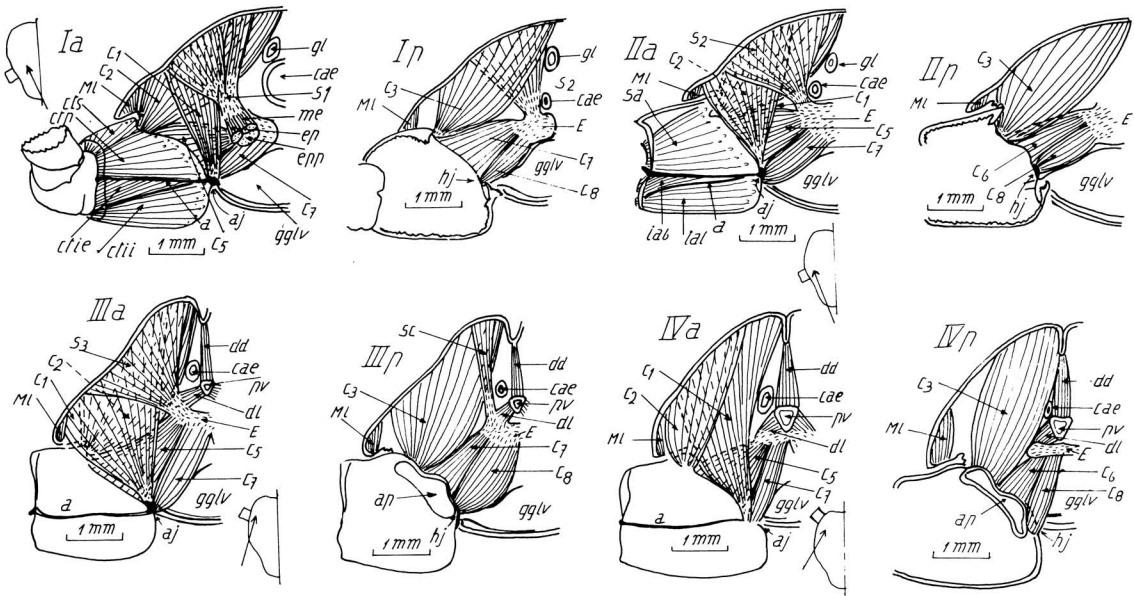


Fig. 2. Extrinsic muscles of coxae I—IV. a = anterior group, p = posterior group (exposed by removal of the muscles of the anterior group). Sections along lines a-a, b-b, c-c and d-d of Fig. 1. The small inserted figures show the direction of view.

3. Function of muscles

The primary function of muscles c_{2-3} ("levators") is not questioned. With the aid of Dr. Tom Reuter of this laboratory I carried out some experiments using electrical stimulation and found these muscles to act in accordance with their previous name and with a sensitivity comparable to frog muscles.

At the posterior attachment point (*hj*) of the coxa to the sternum no gliding movement of the coxa is possible in any direction. The anterior attachment point (*aj*), however, allows a certain amount of gliding upwards and downwards. The coxa can thus perform a rotation of about 5° with the posterior joint as fulcrum, and the muscle c_1 ("anterior rotator") works as its previous name suggests. This can be proved by pulling the muscle during the course of dissection. The returning movement is apparently due to the elasticity of the coxal-pleural membrane. The rigidity of the posterior attachment explains the more or less complete reduction of the c_4 ("posterior rotator"). The rotation of the coxa is of course manifested as a stepping movement of the tip of the strongly bent leg.

The most enigmatic issue is the depression of the coxa and the function of the strong muscles

c_{5-6} and c_{7-8} , which arise on the margin of the horseshoe-shaped endosternum.

The action of muscles c_5 and c_6 as promotor and remotor, respectively, seems very questionable. Their leverage is very inefficient and a rigid contact at the "joints" (*hj*) and (*aj*) is incompatible with coxal turning in the horizontal plane. However, if the hydrostatic pressure is normal, a kind of elastic cushion is intercalated between the hard margin of the sternum and the coxal joint prominences. Manipulating freshly killed spiders one finds that this enables a promotion/remotion of perhaps 5° .

The same kind of manipulation as well as direct observation of living spiders reveals an elevation/depression angle of at most 10° .

The supposed "depressors" c_{7-8} insert as close to the joints *aj* and *hj* as possible and thus have no leverage at all and cannot in any event bring about a depression.

It is hard to believe that muscles c_{2-3} and c_{5-6} could actively extend themselves, thus pushing the coxae into depression. Nothing of the kind is known in muscle physiology. The following hypotheses remain:

1) the depression is a purely elastic counteraction when the "levators" relax.

2) The depression of the coxa is caused by

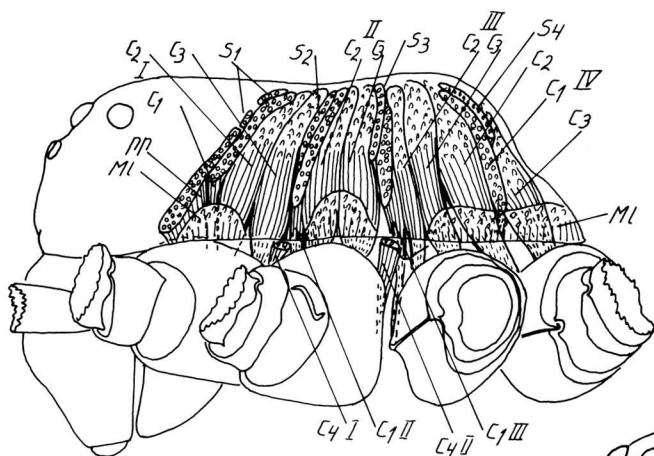


Fig. 3. Superficial layer of muscles.

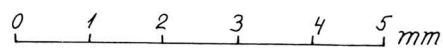


Fig. 4. Organisation of the innermost layer of muscles. As Figs. 5–6 show, the endosterno-coxal muscles are not as clearly separated as this somewhat schematic drawing suggests.

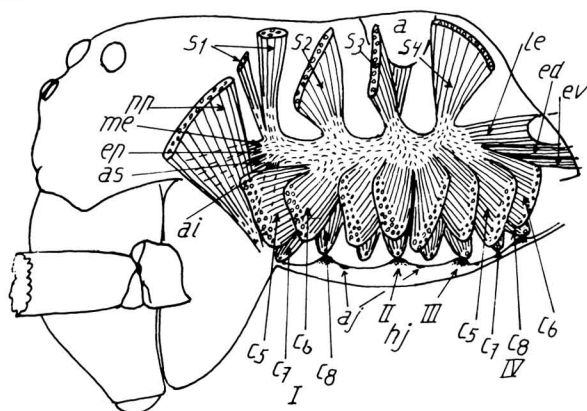


Fig. 5. Longitudinal section (see Fig. 1), view towards the median plane.

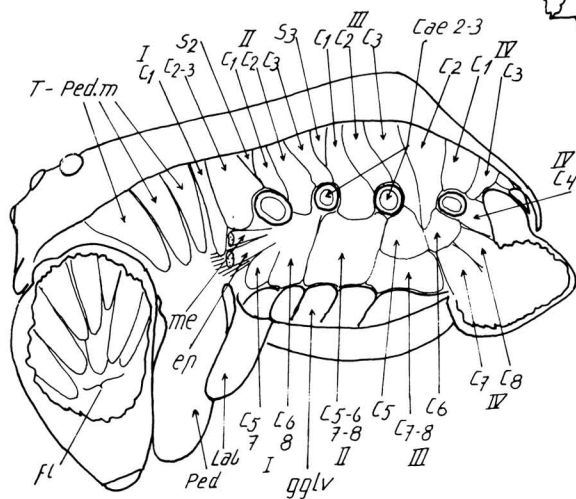
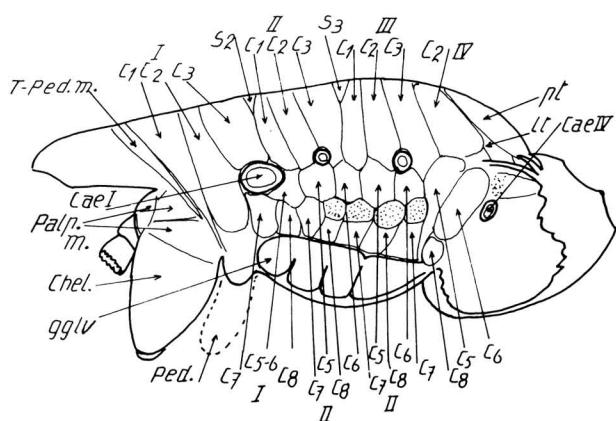


Fig. 6. Longitudinal section, view towards the legs.



raised hydrostatic pressure, corresponding to the extension of the outer segments of the legs, where no extensor muscles are present (cf., e.g., Parry & Brown 1959). Because the cephalothorax is not divided into compartments, individual depressions of the coxae must then be connected with individual relaxation of their levators.

3) The only movement which can be caused by the contraction of the powerful muscles c_{7-8} is outward pulling of their origin on the endosternum (Fig. 4, 7). This must also result in outward pulling of the closely adjacent origin of c_{5-6} . However, the whole extrinsic coxal musculature is very densely packed, as shown in Figs. 5—6. If the volume of muscles remains unchanged, not only the origin but also the insertion of c_{5-6} must be moved outwards, and this pushing must cause a depression of the coxa (cf. Fig. 7). Is it perhaps possible that the piston-like action is rendered more effective through a stiffening of the muscle?

A synergistic contraction of the adjacent suspensor muscle (*s*) seems very probable.

Even this hypothesis must apparently include a regulating co-operation of the levator muscles (c_{2-3}) as a prerequisite for individually working coxa depressions, because contraction of the c_{7-8} muscles of one leg probably to some extent involves an outward pulling also of neighbouring parts of the endosternum.

The generation of the hydrostatic pressure pulses which are responsible for the extension of the peripheral leg joints has generally been attributed to the lateral muscle (*MI*). It seems, however, very probable that the joint contraction

of the muscles c_{7-8} and the adjacent suspensors (*s*) might be a powerful agent even in this respect, perhaps more than the lateralis muscle.

On the whole, the very powerful extrinsic coxal musculature seems a little inconsistent against the background of the very limited range of motility of the coxae, as compared with the coxo-trochanteric and trochantero-femoral joints.

Unfortunately, it proved impossible to stimulate muscles c_{5-6} and c_{7-8} individually with inserted electrodes. They are closely hidden behind the coxae and it will hardly prove possible to avoid simultaneous stimulation of the adjacent lateral ganglia (*gglv*) with their motoric centra.

Abbreviations

<i>a</i>	apodeme
<i>ai</i>	M. endosterno-pedipalpalis antero-inferior
<i>aj</i>	anterior joint
<i>as</i>	M. endosterno-pedipalpalis antero-superior
<i>c₁</i>	M. tergo-coxalis anterior profundus ("Rotator anterior")
<i>c₂</i>	M. tergo-coxalis medius anterior ("Levator anterior")
<i>c₃</i>	M. tergo-coxalis medius posterior ("Levator posterior")
<i>c₄</i>	M. tergo-coxalis posterior profundus ("Rotator posterior")
<i>c₅</i>	M. endosterno-coxalis antero-superior ("Promotor")
<i>c₆</i>	M. endosterno-coxalis postero-superior ("Remotor")
<i>c₇</i>	M. endosterno-coxalis antero-inferior ("Depressor anterior")
<i>c₈</i>	M. endosterno-coxalis postero-inferior ("Depressor posterior")
<i>cae</i>	intestinal caecum
<i>Ch</i>	chelicera
<i>ctie</i>	M. coxo-trochantericus inferior externus
<i>ctii</i>	M. coxo-trochantericus inferior internus
<i>ctp</i>	M. coxo-trochantericus posterior
<i>cts</i>	M. coxo-trochantericus superior
<i>dd</i>	M. dilator proventriculi dorsalis
<i>dl</i>	M. dilator proventriculi lateralis
<i>E</i>	endosternum
<i>ed</i>	M. plagulo-endosternalis dorsalis
<i>ep</i>	M. protractor endosterni
<i>epp</i>	endosterno-pedipalpal muscles
<i>ev</i>	M. plagulo-endosternalis ventralis
<i>fl</i>	flexor muscles in the chelicera
<i>gglv</i>	ventral ganglia
<i>gl</i>	poison gland
<i>hj</i>	hind joint
<i>iab</i>	M. infra-apodemicus brevis
<i>ial</i>	M. infra-apodemicus longus
<i>lab</i>	labium
<i>le</i>	M. loro-endosternalis
<i>me</i>	M. postero-medialis endosterni
<i>MI</i>	M. lateralis
<i>Ped</i>	pedipalp
<i>Palp.m.</i>	palpal muscles

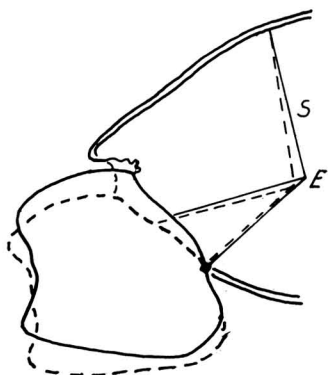


Fig. 7. Supposed coxa-depressing mechanism of muscles c_{7-8} and c_{5-6} : contraction of the lower muscles pulls the endosternum outwards and the upper muscles, acting as pistons, push the upper part of the coxa downwards.

<i>pp</i>	M. tergo-pedipalpalis posterior
<i>pt</i>	M. plagulo-tergalis
<i>pv</i>	proventriculus
<i>s₁₋₄</i>	suspensors 1—4
<i>sa</i>	M. supra-apodemicus
<i>sc</i>	suspensor centralis
<i>T-ped.m.</i>	tergo-pedipalpal muscles

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