THE FUNCTIONAL ANATOMY OF THE MESOTHORACIC LEG OF THE WATERSTRIDER, *GERRIS REMIGIS* SAY (HETEROPTERA)*

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INTRODUCTION

Gerris remigis is a heteropteran which spends most of the time on the surface of flowing streams. On the surface of the water it moves by rowing, during which the meso- and metathoracic legs, especially the former, sweep powerfully backwards pushing against the surface film of the water (Darnhofer-Demar, 1968). In order to stand, the animal needs a large area of contact with the surface. Both standing and rowing require that these legs extend laterally consequently they differ from the more or less vertically orientated legs of most other insects, including many terrestrial Heteroptera. In a recent review of the evolution of Heteroptera, Popov (1971) discussed the divergence of the coxae in the infraorder Leptopodidomorpha — of which the Gerridae are members — in order to move on the surface of the water. It thus seemed interesting to compare these legs with those of Heteroptera having a different life style. Those Heteroptera whose mesothoracic legs have already been studied in sufficient detail are *Gelastocoris oculatus* (Parsons, 1960) and *Belostoma flumineum* (Segal, 1962). Since these two insects belong to the Hydrocorisae, and since *Gerris* belongs to the Amphibicorisae, *Gelastocoris* and *Belostoma* are not closely related to *Gerris*. Nevertheless, they provide an interesting comparison, especially since *Gelastocoris* is littoral, *Belostoma* is totally aquatic and *Gerris* is surface-living.

The primary purpose of this study, therefore, was to explore the modifications of the mesothoracic leg in terms of the external anatomy, musculature and pattern of innervation and to relate

*Note added in proof: In a recently published paper, N. M. Andersen includes a brief description of the functional anatomy of the mesothoracic leg of *Gerris lacustris* which accords well with that presented here for *Gerris remigis*. [Vidensk Meddr dansk naturh Foren, 1976, 139:337–396.]

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this both to other Heteroptera and to the mode of locomotion of *Gerris remigis.*

Materials and Methods

Animals were collected from local streams in western Massachusetts. Mesothoracic anatomy was studied by conventional dissections of specimens preserved in 70% alcohol. Nerves were traced in animals which had been injected with a 1% solution of methylene blue in Insect Ringer (Becht, Hoyle and Usherwood, 1960) shortly before they were killed.

Results

Skeleton of the Leg

The mesothoracic leg consists of the usual five segments, but some have become highly modified. The coxa, the most proximal segment, is about 2.5 mm long. In comparison with the coxae of most insects (Snodgrass, 1935) the gerrid coxa has rotated so that the coxal dorso/ventral axis of most insects has become the anterior/posterior axis in the gerrid coxa (Fig. 1a, b). The proximal two thirds of the coxa lies within the coxal groove in the mesothoracic cavity (Fig. 2). The base of the coxal groove is formed by the sternum and the lateral walls consist of the supracoxal lobes of the well developed epimeron and episternum. The anterior end of the coxa is attached to the pleuron by a heavily sclerotized region, the pleurocoxal attachment, and the posterior

TABLE 1

MESOTHORACIC MUSCLE NOMENCLATURE AS USED BY LARSÉN (1945), GUTHRIE (1961) AND DARNHOFER-DEMAR (1969).

Guthrie *G. lacustris*	Darnhofer-Demar *G. lacustris*	Larsén *G. rufoscutellatus*
52	M. mesonoto trochanteralis	46 M. nototrochanteralis
52	M. mesopleurotrochanteralis	47 M. pleurotrochanteralis
53	M. mesonototrochantinalis	41 M. nototrochantinalis
54	M. mesonotomerocoxalis	40 M. notocoxalis
	M. mesocoxa - trochanteralis lateralis	50 M. coxa - trochanteralis lateralis

(distal) end leaves the thorax by a circular opening close to the metathorax. The lateral wall of this opening is formed by the supracoxal lobes. The coxal groove and small, backwardly projecting opening severely restrict coxal movement. The only possible movement is a rotation about the anterior/posterior axis between the pleurocoxal attachment and the opening. The proximal coxal rim has a medial trochantin and a lateral apodeme on to which muscles 40 and 41, respectively, insert. The distal third of the coxa is outside the body cavity and is more rounded than the proximal two thirds.

The next segment, the trochanter, is also highly modified. It is a little shorter and rather slimmer than the coxa (Fig. 3). The medial proximal rim is extended into several large apodemes on to which muscles 46 and 47 insert. Muscle 50 inserts on a smaller lateral apodeme. The trochanter articulates with the coxa by means of a dicondylic joint. This forms the axis about which muscles 50 and 46 plus 47 act antagonistically and is in the dorso/ventral plane. As the trochanter leaves the coxa, it makes a sharp, right-angled turn so that the surface which was medial in the proximal part of the segment is the posterior surface in the distal part of the segment (Fig. 1d).

The femur is fused directly to the trochanter and so has no independent movement. It consists of a smple cylinder, a little longer than 1 cm. The femoro-tibial joint has been described in great detail by Darnhofer-Demar (1973) and is a simple hinge. The tarsus is two-segmented and has two, backwardly directed, subapical claws. The exposed parts of each segment are covered with a variety of sensory hairs (Weber, 1930; Lawry, 1973), which are doubtless of importance in orientation during courtship (Wilcox, 1972) and capture of prey (Murphey, 1971).

Muscles

The mesothorax is by far the largest segment of the body, occupying about one third of the length of the body. Its musculature has already been described in detail by Larsén (1945), for *G. rufoscellutus,* and by Guthrie (1961) and Darnhofer-Demar (1969) for *G. lacustris.* For convenience it will here be described briefly for *G. remigis.* For reasons of historical precedence and to facilitate comparison of gerrids with other Heteroptera, Larsén's numbering system is used here. A comparison of nomen-

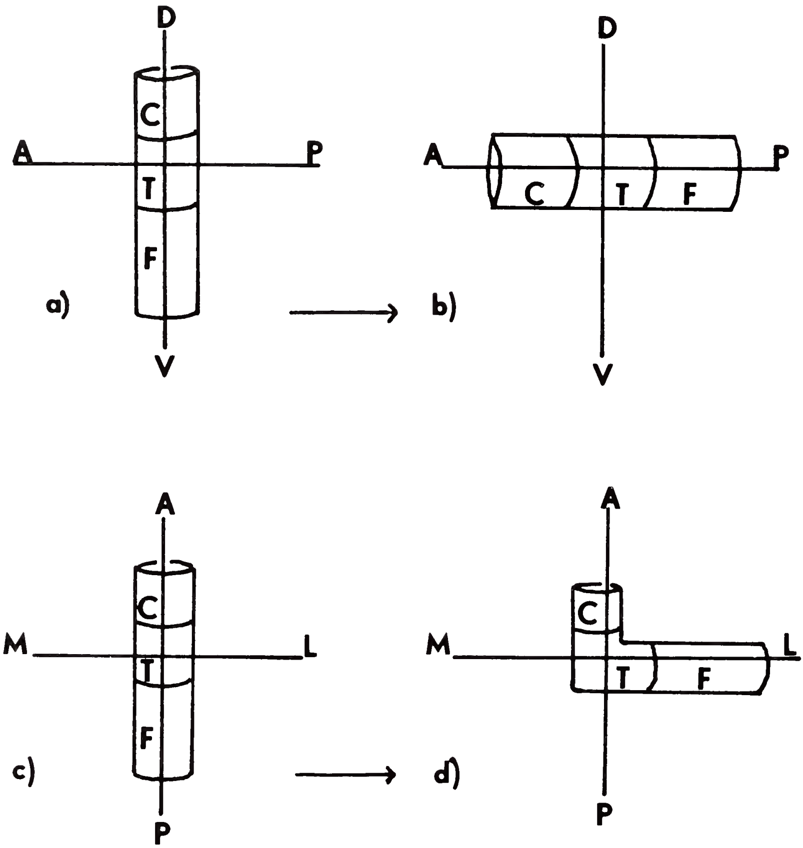

Figure 1: Diagram to illustrate the orientation of the gerrid leg with reference to the simple cylinder shown in (a). Reorientation of the coxal axis causes the dorso-ventral axis of the leg to become the anterior/posterior axis (b). The trochanteral bend causes the anterior/posterior axis of the distal part of the leg (c) to become the medio/lateral axis (d). (b) and (c) represent the same leg but viewed from a 90° shift so that the medio/lateral axis can be seen in diagram (c).

A	anterior	M	medial
C	coxa	P	posterior
D	dorsal	T	trochanter
F	femur	V	ventral
L	lateral		

The orientation symbols used in this diagram are used similarly in succeeding diagrams, unless otherwise stated.

clature used by these three workers is given in table 1.

Since in New England, adult *G. remigis* are usually wingless, only wingless animals were used in this study. Both direct and indirect flight muscles are lacking in the wingless animals and rather few muscles remain (Fig. 4), as follows:

Muscle 40 (M. nototrochantinalis) is a coxal rotator. It originates near the mid-line of the mesotergum and inserts directly on the trochantin, a precoxal sclerite which has fused with the coxal rim.

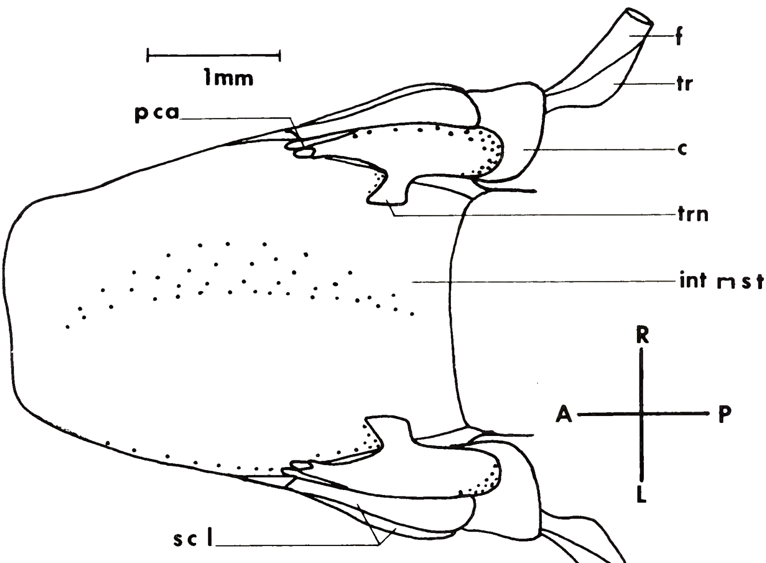

Figure 2: Internal view of the ventral exoskeleton of the mesothorax of *G. remigis* to show the relationship of the coxa to the mesothorax. The tergum and pleura have been dissected away

c	coxa
f	femur
int m s t	internal exoskeleton of the mesothorax
p c a	pleurocoxal attachment
s c l	suprocoxal lobes
tr	trochanter
trn	trochantin
L	left
R	right

Muscle 41 (M. notocoxalis) is also a coxal rotator and is antagonistic to muscle 40. It originates on the lateral wall of the mesotergum and inserts on an apodeme on the lateral coxal rim.

Muscle 44 (M. furca-coxalis) is a third coxal rotator. It is a very small muscle originating on the furca — a sternal process — and inserting on the anterior coxal wall.

Muscle 46 (M. nototrochanteralis). This is an extremely well developed muscle which originates on the anterior two thirds of the mesotergum and the dorsal region of the first phragma and inserts on several well developed apodemes from the medial edge of the trochanter. It is a major retractor of the leg.

Muscle 47 (M. pleura-trochanteralis) is also a well developed muscle. It originates on the ventral surface of the first phragma and the anterior half of the pleuron and sternum, and inserts on the same apodemes as muscle 46. It acts with muscle 46 to retract the leg.

Muscle 49 (M. coxa trochanteralis medialis). This muscle originates on the dorsal wall of the coxa and inserts on the same apodemes as muscles 46 and 47. It is a depressor of the trochanter.

Muscle 50 (M. coxa trochanteralis lateralis). This muscle originates on the ventral wall of the coxa and inserts on a flat apodeme which extends from the lateral rim of the trochanter. It is antagonistic to muscles 46 and 47 and protracts the leg.

Muscles within the leg distal to the coxa were not considered.

Nervous System

The nervous system in *Gerris* is remarkable in being highly fused (Guthrie, 1961). All the thoracic and abdominal ganglia form a single ganglionic mass, which lies mostly in the prothorax. The three pairs of main nerves to the muscles of the mesothoracic leg arise from the more posterior region of this ganglionic mass — the region which Guthrie has identified as containing the mesothoracic ganglia. Nerve 1 sends branches to muscles 46, 40, and 41. Nerve 2 has a branch to muscle 41, but the main portion goes into the distal part of the leg and probably contains a large number of sensory fibres from the sensory receptors of the leg. Nerve 3 has branches to muscles 47, 44 and the distal part of the leg.

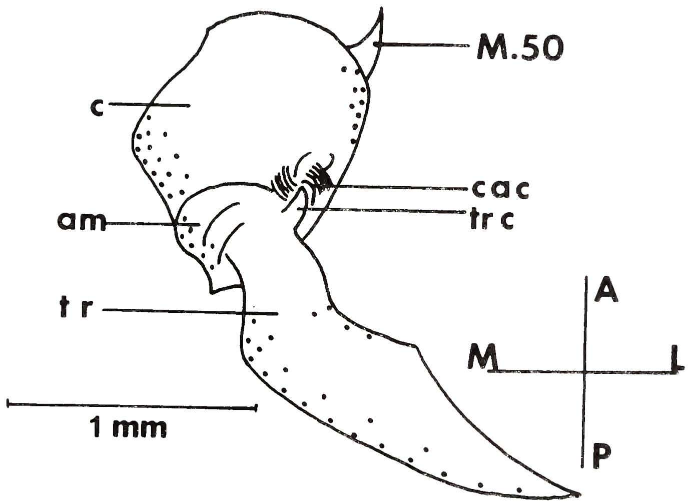

Figure 3: Right coxa and trochanter of *G. remigis* to show the articulation of the trochanter on the coxa

a m	articular membrane
c	coxa
c a c	coxal articulation for the trochanteral condyle
tr	trochanter
tr c	one trochanteral condyle, the other is directly opposite as shown in the diagram of Fig. 6.

Functions of the Muscles

The role of the coxal and trochanteral muscles can be inferred from a knowledge of their origins and insertions and of the articulations of the coxa and trochanter. These inferences have been confirmed by electrophysiological information from the muscles recorded simultaneously with monitoring of the leg movement (Bowdan, 1977).

Muscles 40 and 41 are antagonists and pivot the coxa around its anterior/posterior axis. In doing so they also lower and raise the extremities of the leg (Fig. 5). Contraction of muscle 40 rotates the coxa so that its dorsal aspect comes to lie laterally. The distal portion of the leg is lowered by this action (Fig. 5b). Contraction of muscle 41 rotates the coxa in the opposite direc-

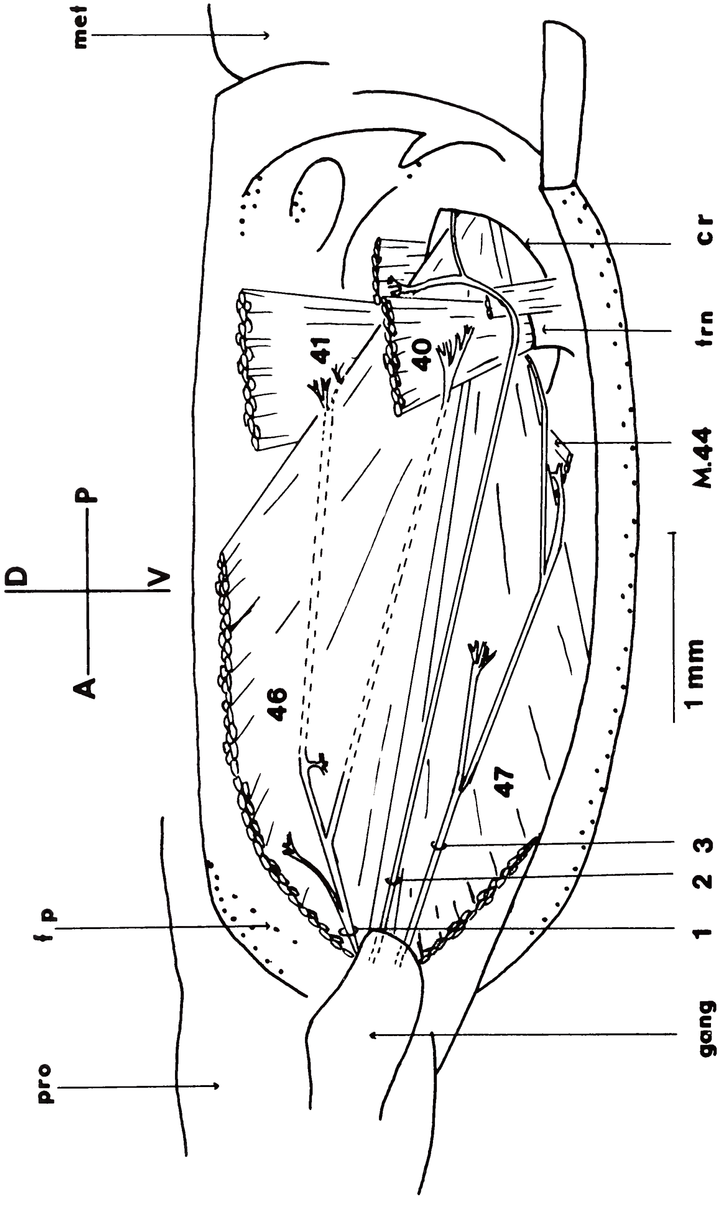

Figure 4

tion: the ventral surface of the coxa becomes lateral and the distal portion of the leg is raised (Fig. 5c). Muscles 50, and 46 plus 47 act on each side of the pivotal axis formed by the dicondylic articulation of the trochanter on the coxa (Fig. 6a). The pivotal axis is a dorso/ventral one (Fig. 6a) so the plane of movement of the leg is mediolateral (Fig. 6b). The trochanteral bend translates this into a forward and backward movement of the extremities of the leg. Contraction of muscle 50 swings the extremities forward (promotion, protraction; Fig. 6d) and contraction of muscles 46 and 47 swings them backwards (remotion, retraction; Fig. 6 c).

Thus coxal rotation can move the leg only in a dorso/ventral plane, the proximal part of the trochanter can move only in a medio/lateral plane and there are only five muscles which are important. It would seem as though the range of movement of the mesothoracic leg of *Gerris* would be very limited. In fact, however, the leg is extraordinarily versatile. It can move in a complete vertical circle, a horizontal semicircle, and any combination of the two.

Discussion

Comparison with Gelastocoris *and* Belostoma

In gerrids the mesothoracic legs and their musculature have become so highly modified for rowing that it is of interest to compare them with those of Heteroptera with a different mode

Figure 4: Hemisection of the mesothorax of *G. remigis*, to show the major muscles and their innervation.

c r	coxal rim
gang	fused ganglionic mass
f p	first phragma
met	metathorax
pro	prothorax
trn	trochantin
40	muscle 40 M. nototrochantinalis
41	muscle 41 M. notocoxalis
44	muscle 44 M. furca coxalis
46	muscle 46 M. nototrochanteralis
47	muscle 47 M. pleurotrochanteralis
1,2,3	main mesothoractic nerve branches

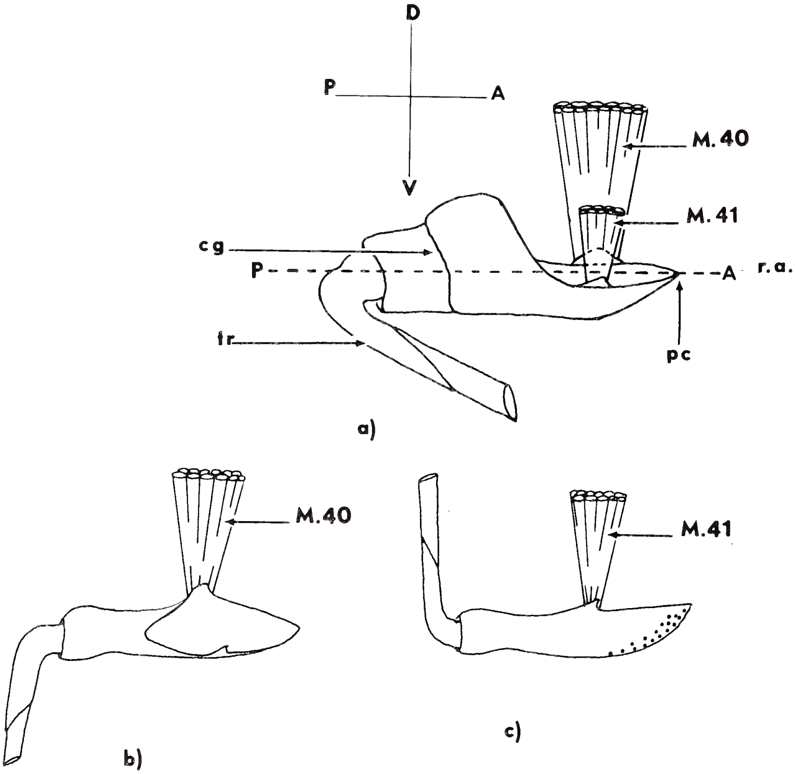

Figure 5: Lateral view of the coxa and trochanter of *G. remigis*. Diagram to illustrate the activity of muscles 40 and 41 in respectively lowering b) and raising c) the extremities of the leg.

c g point of emergence of the coxa from the coxal groove
p c position of the pleurocoxal attachment
r a axis of rotation
tr trochanter

of locomotion. Two such animals are *Gelastocoris oculatus*, the toad bug (Parsons, 1960) and *Belostoma flumineum*, the giant water bug (Segal, 1962).

The mesothoracic coxae of *Belostoma* and *Gelastocoris* are less concealed by the supracoxal lobes, which are smaller than those of *Gerris*. These coxae therefore have more freedom of movement and also possess an additional coxal rotator (muscle 42). The coxae of *Belostoma* and *Gelastocoris* have rotated some-

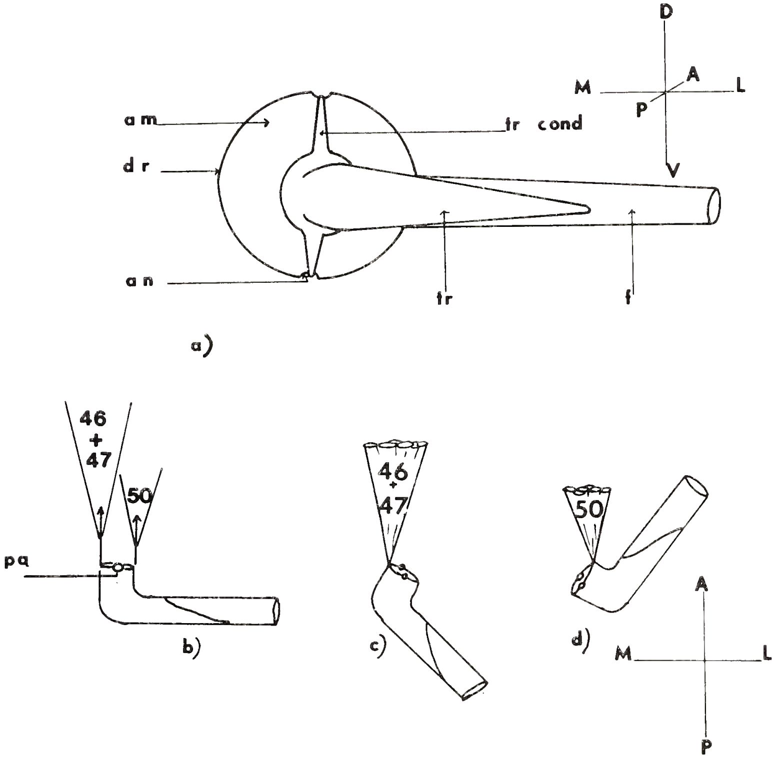

Figure 6: Diagrammatic representation of the articulation of the trochanter on the coxa, and of the actions of muscles 46, 47 and 50 on the mesothoracic leg of *G. remigis*.

a) articulation of the trochanter on the coxa

a m	articular membrane
a n	coxal articular notch
d r	distal rim of coxa
f	femur
tr	trochanter
tr cond	trochanteral condyle

b) resting position of the leg

c) contraction of muscles 46 + 47 causes the leg extremities to go backwards (retract).

d) contraction of muscle 50 causes the extremities to go forward (protract).

p a	pivotal axis
⟶	direction of the major component of the muscles' force.

Note that a) has an orientation which is different from that of b), c) and d).

what in comparison with the hypothetical plan of figure 1a, and are at an angle of about 45° from the vertical. This is in contrast with the mesothoracic coxae of *Gerris*, which have rotated so that their longitudinal axes are parallel with that of the mesothorax (Fig. 7). In addition the pleurocoxal attachments of *Gelastocoris* and *Belostoma* are medial whereas those of *Gerris* are anterior. The orientation of the coxae and the position of the pleurocoxal attachments in *Gerris* result in legs which project almost completely horizontally. In *Gelastocoris* and *Belostoma* the projection of the legs has both vertical and horizontal components. In all three insects the bend in the trochanter causes the femur to project anterolaterally.

The major change in the musculature has been the enormous development of muscles 46 and 47. In *Belostoma* these two muscles are rather small and have discrete origins, M. 46 on the lateral wall of the tergum and M. 47 on the pleural apophysis. Both insert on a single trochanteral apodeme. In *Gelastocoris* these muscles are also rather small. Muscle 46 has an origin and insertion similar to that of *Belostoma;* M. 47, however, is in two parts, one originating on the sternum, the other on the pleural apophysis. In *Gerris* these two muscles are so large as to be contiguous and it is difficult to distinguish between them; Guthrie (1961) in fact, considers them a single muscle. They originate over a wide area of the tergum, first phragma, pleuron and sternum and insert

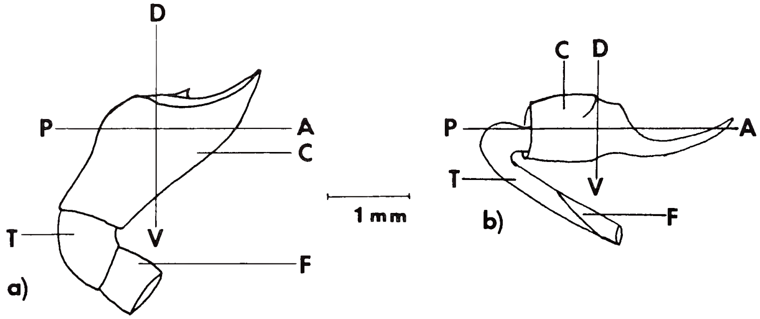

Figure 7: Coxae of the left mesothoracic legs of a) *Belostroma* b) *Gerris* to illustrate the relative positions of the coxal axes.

C coxa
F femur
T trochanter

on several long, broad, trochanteral apodemes. They effectively illustrate Hoyle's (1975) statement that powerful muscles have many points of attachment.

The reorientation of the gerrid leg about all three axes (Fig. 1), produced by the rotation of the coxa and the angle of the trochanter, has altered the functions of muscles 46/47 and 50, although they are still antagonists. The main force developed by muscles 46 and 47 in *Belostoma* and *Gelastocoris* is a vertical one, and their function is to depress the trochanter and therefore the extremities of the leg. In gerrids the main force developed is an anteriorly directed one which leads to a retraction of the leg (Fig. 6c). Muscle 50 in *Belostoma* and *Gelastocoris* raises the trochanter and the extremities of the leg. In *Gerris*, however, muscle 50 is the promotor of the leg (Fig. 6d). Muscles 40 and 41 move the leg forward and backward, respectively, in *Belostoma* and *Gelastocoris*. In *Gerris* these muscles respectively raise and lower the leg. These changes are not only the result of the rotation of the leg axis, but also of a slightly different position of the muscles themselves. In *Belostoma* the trochantin is close to the anterior margin of the coxal rim, so muscle 40 inserts anteriorly. In *Gerris* the trochantin is more posterior so that muscle 40 and 41 are in the same anterior/posterior position. Their antagonistic action is therefore across the anterior/posterior axis of the coxa. In *Belostoma* their antagonistic action is across a more mediolateral axis (Fig. 8).

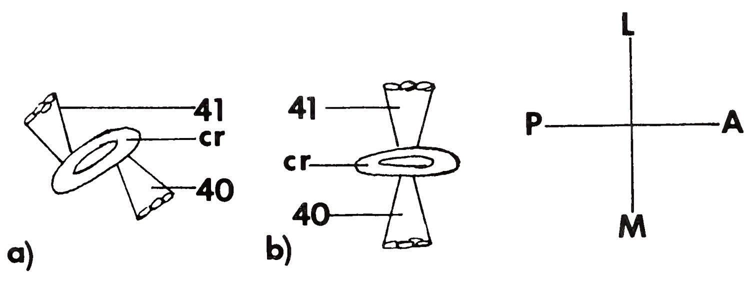

Figure 8: Diagrammatic representation of the insertions of muscles 40 and 41 in a) *Belostome* b) *Gerris*.
c r coxal rim

The mesothoracic leg of Gerris *as support and oar*

The modification of the coxal and trochanteral orientation of the gerrid mesothoracic leg has brought about a horizontal and lateral positioning of the leg which creates a wide base of support for the animal on the surface of the water. This orientation of the leg also rests the distal tip of the tibia and the whole of the tarsus on the surface of the water and puts the leg into a good position for the rowing stroke. If the leg had a more vertical orientation, only the tip of the tarsus would be on the surface of the water, providing a much smaller pushing area during the rowing stroke. During this stroke the leg sweeps powerfully backwards, pushing against the meniscus of the water surface (Darnhofer-Demar, 1968); such a stroke would be impossible if the leg were orientated vertically. Moreover, the greater the area of the leg resting on the water surface, the more efficient leg retraction will be in rowing. *Gelastocoris* walks on land and so a vertical orientation of the leg is a necessity. *Belostoma* swims underwater so that any orientation of the leg would push aside an equal volume of water. In *Gerris* the modification of the muscles' function follows directly from the change in orientation of the leg, and the increase in the size of muscles 46 and 47 leads to a very powerful rowing stroke so that, with a single stroke, the animal can cover a distance several times its own length (Darnhofer-Demar, 1968).

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Literature Cited

Becht, G., G. Hoyle and P. N. R. Usherwood
1960. Neuromuscular transmission in the coxal muscles of the cockroach. J. Insect Physiol., **4:** 191–210.

Bowdan, E.
1977. Walking and rowing in the water strider, *Gerris remigis* Say. II. Muscle activity associated with rapid and slow mesothoracic leg movement. J. comp. Physiol., in press.

Darnhofer-Demar, B.
1968. Zur Fortbewegung des Wasserläufers *Gerris lacustris* L. auf der Wasseroberfläche. Verh. dtsch. Zool. Ges., **28:** 430–439.
1969. Zur Funktionsmorphologie der Wasserläufer I Die Morphologie des Lokomotionsapparates von *Gerris lacustris* L. (Heteroptera: Gerridae). Zool. Jb. Anat., **86:** 28–66.
1973. Funktionsmorphologie eines Arthropodengelenks mit extrem grossen Aktionswinkel: Das Femoro-Tibial-Gelenk von *Gerris najas* (DeG.) (Insecta, Heteroptera). Z. Morph. Tiere, **75:** 111–124.

Guthrie, D. M.
1961. The anatomy of the nervous system in the genus Gerris (Hemiptera-Heteroptera). Phil. Trans. Roy. Soc. Lond. B., **244:** 65–102.

Hoyle, G.
1975. The neural control of skeletal muscles. In *Insect Muscle* (ed. P. N. R. Usherwood) pp 501–543. London: Academic Press.

Larsén, O.
1945. Der Thorax der Heteropteren Skelett und Muskulatur. Lunds. Univ. Arsskrift N. F. Avd. 2, **41:** 1–96.

Lawry, J. V. Jr.
1973. A scanning electron microscope study of mechanoreceptors in the walking leg of the water strider *Gerris remigis*. J. Anat., **116:** 25–30.

Murphey, R. K.
1971. Sensory aspects of the control of orientation to prey by the water-strider *Gerris remigis*. Z. vergl. Physiol., **72:** 168–185.

Parsons, M. C.
1960. Skeleton and musculature of the thorax of *Gelastocoris oculatus* (Fabricius) (Hemiptera-Heteroptera). Bull. Mus. Comp. Zool., **122:** 299–357.

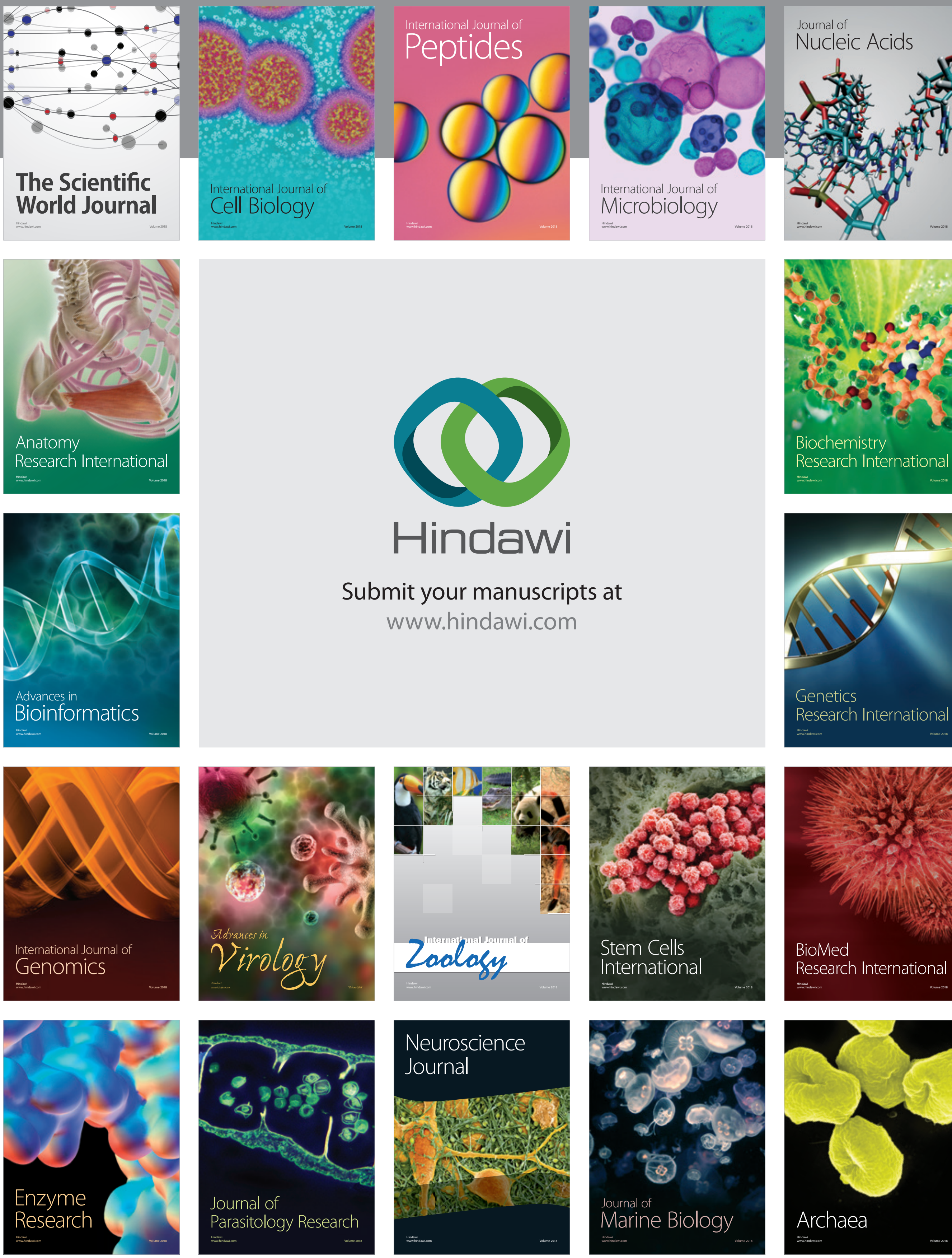
Popov, Y. A.
1971. Historical development of Hemiptera infraorder Nepomorpha (Heteroptera) (in Russian). Tr. Paleontol. Inst. Acad. Sci. USSR, **129:** 1–228.

Segal, E.
1962. A study of the morphology of the Hemipteran-Heteropteran *Belostoma flumineum* Say. M. A. Thesis. Mt. Holyoke College.

Snodgrass, R. E.
1935. Principles of Insect Morphology. pp 667 New York: McGraw Hill.

Weber, H.
1930. Biologie der Hemipteren. pp 543 Berlin: Julius Springer.

Wilcox, R. S.
1972. Communication by surface waves. Mating behavior of a water strider (Gerridae). J. comp. Physiol., **72:** 168–185.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