

Entomology Group, Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, FSU Jena, Jena, Germany

## The pterothoracic skeletomuscular system of Scirtoidea (Coleoptera: Polyphaga) and its implications for the high-level phylogeny of beetles

F. FRIEDRICH and R. G. BEUTEL

### Abstract

External and internal structures of the pterothorax of six adult representatives of three families of Scirtoidea were examined. A detailed description of the skeleton and musculature is presented for the scirtid species *Elodes pseudominuta*. Phylogenetically relevant characters are discussed and a comprehensive table of thoracic muscles of adult beetles is presented. The monophyly of Scirtoidea is supported by derived features of the skeleton, the musculature and the hind wing. Thoracic characters suggest a branching pattern {Decliniidae + [Eucinetidae + (Clambidae + Scirtidae)]}. However, the interrelationships of the scirtoid families were difficult to reconstruct, as internal characters of Decliniidae are unknown and Clambidae are characterized by many autapomorphic features related to miniaturization. The largest family, Scirtidae, is well supported as a clade. The position of the superfamily remains ambiguous. A basal position within Polyphaga is only suggested by one character state, the complete absence of the bending zone of the hind wing in all other lineages of the suborder. A position of Scirtoidea within Elateriformia is tentatively supported by the elongated anepisternum 3 (polarity unclear), a triangular radial cell, and the reduction of the apical branches of the radius posterior in the hind wing. The thoracic features of Scirtoidea – like those of all polyphagan lineages – are clearly derived compared with the conditions in Adephaga, and especially Archostemata. A basal position of Archostemata and a sister group relationship between Polyphaga and Myxophaga is supported by the results of this study. Characters in support of a basal position of Polyphaga were not found.

**Key words:** Scirtoidea – morphology – thorax – Polyphaga – suborders – phylogeny

### Introduction

The Scirtoidea are one of the smallest superfamilies of Coleoptera but crucial for the understanding of the phylogeny and evolution of the extremely species rich Polyphaga (c. 330 000 spp.). Their key role in the context of one of the major controversies in beetle systematics, the interrelationships of the four suborders, was emphasized by Lawrence (1999, 2001).

Archostemata, Myxophaga, Adephaga and Polyphaga are well supported by morphological characters, and their monophyly has rarely been questioned. In contrast to this, the relationships between the suborders are still discussed controversially (see Kukalová-Peck and Lawrence 1993, 2004; Beutel and Haas 2000; Caterino et al. 2002; Hughes et al. 2006) (Fig. 1). Crowson (1960) proposed a sister group relationship between Myxophaga and Polyphaga and a basal position of Archostemata. This topology, which was also adopted by Klausnitzer (1975), was strongly supported in an extensive cladistic analysis carried out by Beutel and Haas (2000). A sister group relationship between Myxophaga and Polyphaga was also proposed by Baehr (1976) based on characters of the prothorax, but Archostemata were placed as sister group of Adephaga in that study. Lawrence and Newton (1982) and Kukalová-Peck and Lawrence (1993, 2004) considered Polyphaga as the basal suborder and Archostemata as the sister group of a clade comprising Myxophaga and Adephaga. This hypothesis is mainly based on characters of the hind wing. An analysis of 18S rDNA sequences (Caterino et al. 2002) yielded a basal position of Archostemata and a sister group relationship between Polyphaga and Adephaga, whereas the myxophagan–polyphagan sister group relationship was tentatively supported by the results of a recent analysis of an extensive molecular data set (Hughes et al. 2006).

Scirtoidea were not included in the phylogenetic analysis of Beutel and Haas (2000), and this was pointed out as a potential weakness by Kukalová-Peck and Lawrence (2004). The

superfamily, which comprises Scirtidae, Clambidae, Eucinetidae (sensu Crowson 1960) and Decliniidae (Nikitsky et al. 1994), was considered as the ‘most primitive’ polyphagans and perhaps the most ancestral lineage of beetles (Lawrence 2001; Kukalová-Peck and Lawrence 2004). Lawrence (2001) described a membranous joint between the pterothoracic ventrites of members of Scirtoidea and considered this condition as a ground plan feature of Polyphaga. This would imply that the fusion, which was considered as a synapomorphy of Myxophaga and Polyphaga in Beutel and Haas (2000), has evolved independently in these suborders. Kukalová-Peck and Lawrence (2004) have also pointed out that a full set of muscles resembling that of Archostemata may be present in scirtoid (and derodontid) beetles.

The main purpose of the present morphological investigation of scirtoid thoracic structures is to verify or falsify these assumptions. The results are also discussed with respect to the systematic placement of Scirtoidea within Polyphaga, the monophyly of the group, and the interrelationships of the four families. Additionally, a comprehensive table of thoracic muscles of Scirtoidea and many other representatives of beetles is presented.

### Materials and Methods

The easily available central European species *Elodes pseudominuta* (Klausnitzer, 1971) was chosen for detailed morphological investigations. Additionally, specimens of *Cyphon coarctatus*, *Pseudomicrocara* sp., *Ora* sp. (Scirtidae), *Calyptomerus dubius* (Clambidae) and *Eucinetus* sp. (Eucinetidae) were examined. Specimens of Decliniidae were not available for dissection. Information on their external features was taken from the literature.

The specimens were fixed and stored in formaldehyde : ethanol : acetic acid 3 : 6 : 1. For the reconstruction of the musculature, cross and longitudinal serial sections were made. The specimens were embedded in Araldid and cut at 1.5 µm with a Microm microtome (HM 360; Microm, Walldorf, Germany). The histological sections were stained with methylene blue and acid fuchsin.

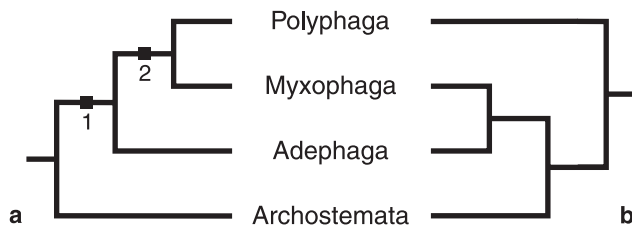


Fig. 1. Two main hypotheses of the interrelationships of the coleopteran suborders. (a) After Crowson (1960). (b) After Lawrence and Newton (1982). The autapomorphies relevant for this study are marked by a black square (after Beutel and Haas 2000). 1 – Five muscle losses in the pterothorax; loss of the mesothoracic discrimininal line; metathoracic trochantin not exposed or lost. 2 – Firm fusion of mesoventrite and metaventrite

For the examination of the endoskeleton, the pterothoracic segments were macerated in KOH and dissected. For scanning electronic microscopy, specimens were cleaned with ultrasonic sound and stored in 90% ethanol. They were air-dried and sputter coated with gold (Emitech K500 sputter coater; Ashford, Kent, UK). Single sclerites were critical point dried (Emitech K850; Ashford, Kent, UK). Pictures were taken with an FEI scanning electronic microscope (XL 30 ESEM; Philips, Wien, Austria).

Drawings of the skeleton were made with a camera lucida on a Leica MZ 125 (Leica, Wetzlar, Germany). For the documentation of serial sections, a Zeiss Axioplan microscope (Göttingen, Germany) and AnalySIS<sup>®</sup> software (Soft Imaging Systems, Münster, Germany) were used.

All pictures were evaluated and assembled with Adobe Photoshop<sup>®</sup> Elements 2 and Illustrator<sup>®</sup> CS software (San Jose, USA).

The preliminary phylogenetic interpretations are based on a mental (Hennigian) character evaluation. As a cladistic character analysis with a broader sample of taxa and characters is planned in the near future, partly based on the data presented by Beutel and Haas (2000), a character state matrix is not presented in this study.

## Results

### Morphology of the pterothorax of *Elodes pseudominuta*

#### Mesothorax

The mesothorax is distinctly smaller than the other thoracic segments. The dorsal side is weakly sclerotized. An articulatory area for the elytral base is present at the anterolateral edge of the scutum (Fig. 3). The anterior margin fits into the well-developed undivided prothorax (Fig. 2a); the lateral parts are bent forwards; an arrow-shaped median process is directed posteriorly. The lateral part of the scutum forms the large anterior notal process and a finger-shaped posterior notal process (Fig. 2a,b); both are in contact with the axillary sclerites (shape and arrangement shown in Fig. 2b). The scutoscuteellar suture is indistinct. A flexible axillary cord connects the scutellum and the mesal base of the elytron (Figs 2 and 3a). The postnotum is reduced to yoke plates (Figs 9 and 10a). The anepisternum is distinctly sclerotized and nearly rectangular; the dorsal part is slightly bent inwards; the pleural wing process of the anepisternum is hook shaped (Figs 4 and 6e). The anepisternum is distinct (Figs 4a–c and 6a,e). The almost vertical pleural suture separates the anepisternum from the epimeron; the corresponding pleural ridge is strongly developed; it bears the S-shaped pleural arm (Figs 4a,b, 5a and 18). The epimeron is narrow, clip-like, with an elongated subelytral part (Fig. 4a). A connection between the epimeron and the scutum (prealar bridge; Larsén 1966) is lacking. The ventral parts of the epimeron and anepisternum together form the pleurocoxal joint (Fig. 4a,b).

The mesoventrite is short and laterally pointed (Figs 4, 5b and 6a). The anterior part forms the posterior part of the procoxal cavities. A discrimininal line or a corresponding internal median ridge is not present. A transverse suture or ridge is also lacking. The mesocoxal cavity is bordered by the mesoventrite and metaventrite and by the mesothoracic

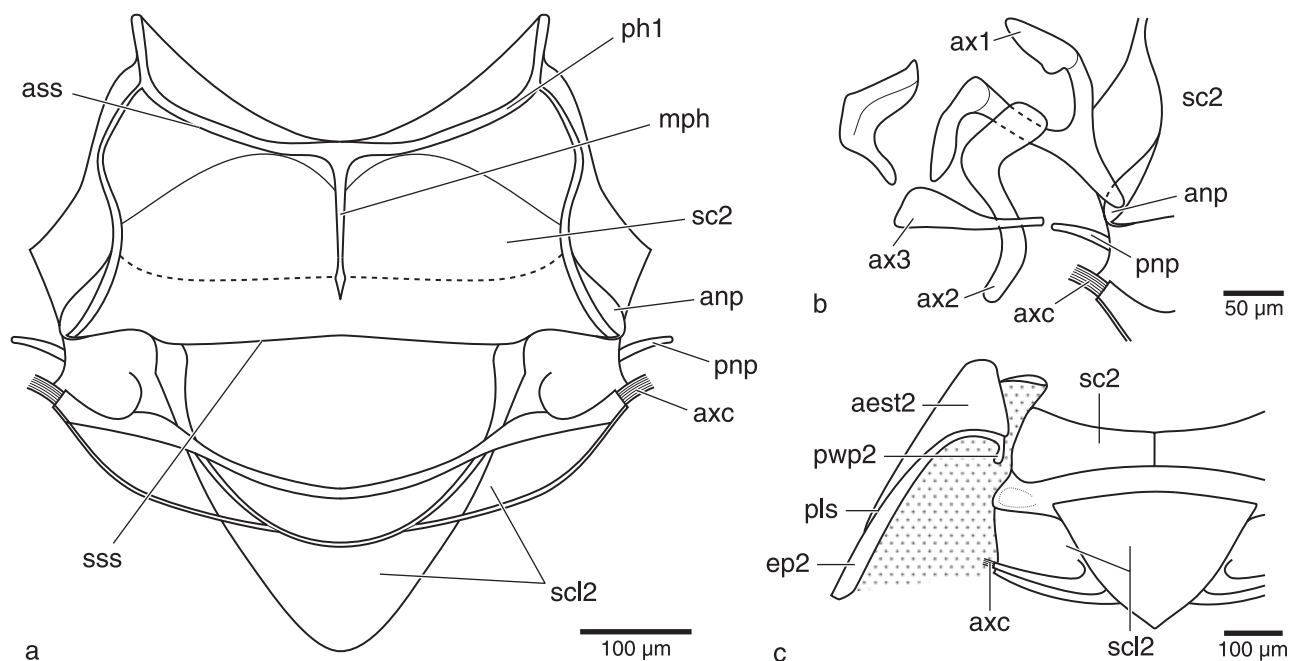


Fig. 2. Mesonotum, *Elodes pseudominuta*. (a) Inner surface. (b) Dorsal view of the wing base. (c) Dorsal view of the mesothorax (wing base removed). Abbreviations: aest2, mesanepisternum; anp, anterior notal process; ass, anterolateral scutal suture; ax1/2/3, first, second, third axillary sclerite; axc, axillary cord; ep2, mesepimeron; mph, median phragma; ph1, prothorax; pls, pleural suture; pnp, posterior notal process; pwp2, pleural wing process of mesothorax; sc2, mesoscutum; scl2, mesoscutellum; sss, scuto-scutellar suture

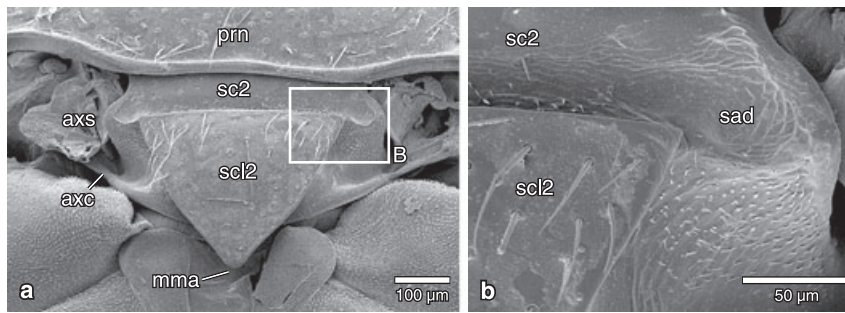


Fig. 3. SEM, dorsal view of the mesothorax, *Elodes pseudominuta*. (a) Prothorax, slightly inclined. (b) Detail of metanotum. **Abbreviations:** axc, axillary cord; axs, axillary sclerites; mma, median membranous area; prn, pronotum; sad, scutal articular depression; sc2, mesoscutum; scl2, mesoscutellum

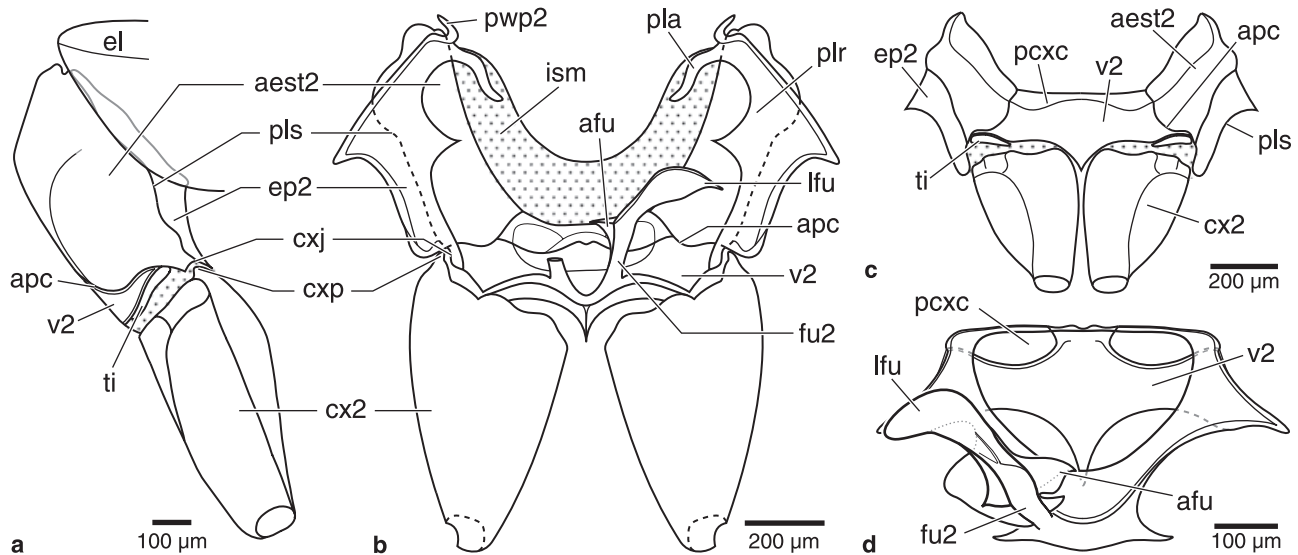


Fig. 4. Mesothorax, *Elodes pseudominuta* (membranous parts punctured). (a) Lateral view with closed elytron. (b) Posterior view, interior of mesothorax (notum removed). (c) Anterior view of ventral part. (d) Dorsal view of endoskeleton and inner surface of the mesoventrite. **Abbreviations:** aest2, mesanepisternum; afu, anterior furcal arm; apc, anapleural cleft; cx2, mesocoxa; cxj, coxal joint; cxp, coxal process; el, elytron; ep2, mesepimeron; fu2, mesofurca; ism, intersegmental membrane; lfu, lateral furcal arm; pcxc, procoxal cavity; pla, pleural arm; plr, pleural ridge; pls, pleural suture; pwp2, pleural wing process of mesothorax; ti, trochantin; v2, mesoventrite

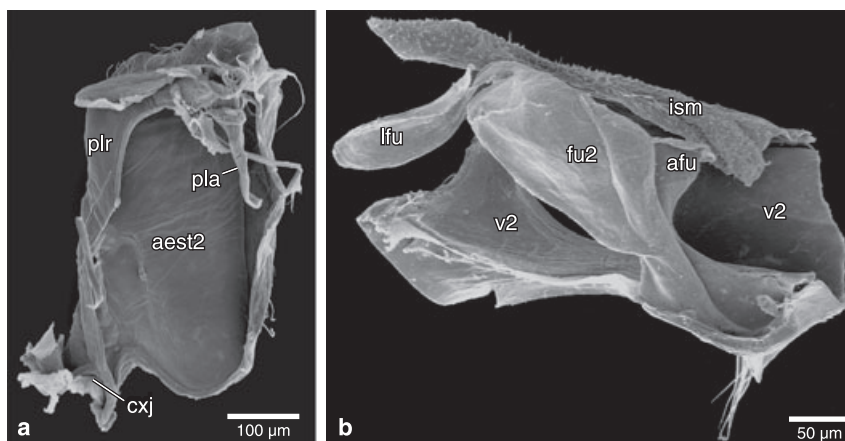


Fig. 5. SEM, mesothoracic endoskeleton, *Elodes pseudominuta*. (a) Inner surface of mesanepisternum. (b) Posterior view of left part of mesoventrite and mesofurca (lateral arm damaged). **Abbreviations:** aest2, mesanepisternum; afu, anterior furcal arm; cxj, coxal joint; fu2, mesofurca; ism, intersegmental membrane; lfu, lateral furcal arm; pla, pleural arm; plr, pleural ridge; v2, mesoventrite

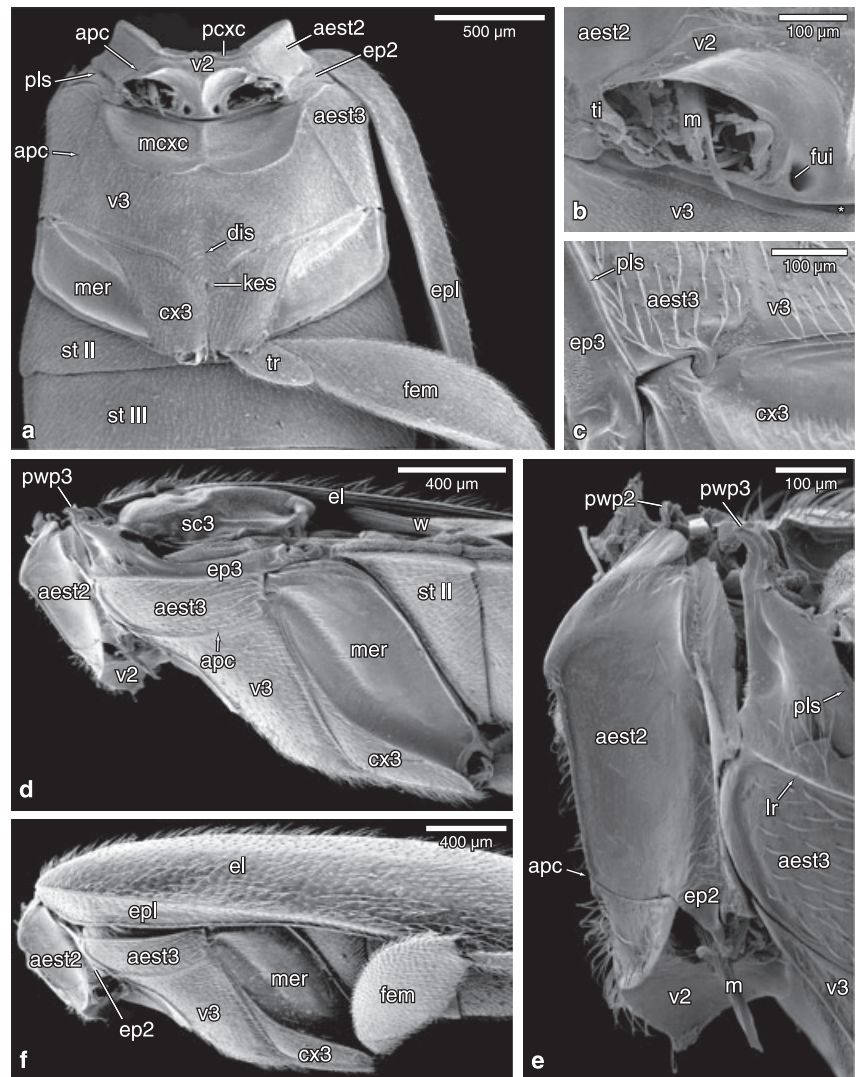
anepisternum and epimeron (Fig. 6a,b). The mesotrochantin is exposed (Figs 4a,c and 6b). The cone-shaped mesocoxae are not completely separated by the mesoventrite (Fig. 4b–d). The well-developed and sclerotized mesofurca originates with two stems, which are divided into a large lateral and a short and triangular anterior arm distally (Figs 4b,d and 5b); the origins of the stems are visible externally as invaginations on the

posterior mesoventrite (Fig. 6a,b). Within the mesocoxal cavities, the mesoventrite and metaventrite are not firmly fused but separated by an intersegmental membrane (Figs 6b and 23a).

The elongated elytra (length : width 4 : 1) cover the dorsal and dorsolateral parts of the pterothorax and abdomen (Figs 6f and 7a). The lower surface is very densely covered



Fig. 6. SEM, pterothoracic skeleton of *Elodes pseudominuta* (mesocoxae, left hind leg and elytron removed). (a) Ventral view. (b) Mesocoxal cavity, connection between mesoventrite and meta-ventrite (membranous part marked with asterisks). (c) Lateral view of coxo-pleural junction. (d) Lateral view of pterothorax and anterior abdominal segments. (e) Lateral view on the mesothorax and the metathoracic pleural wing process. (f) Lateral view on the left pterothorax and the first abdominal segments. **Abbreviations:** aest2/3, meanepistanum/metanepisternum; apc, anapleural cleft; cx3, metacoxa; dis, discrimininal line; el, elytron; ep2/3, mesepimeron/metepimeron; epl, epipleuron; fem, femur; fui, furcal invagination; kes, katapisternum; lr, longitudinal ridge of anepisternum 3; m, musculature; mcxc, mesocoxal cavity; mer, metacoxal meron; pcxc, procoxal cavity; pls, pleural suture; pwp2/3, mesothoracic/metathoracic pleural wing process; sc3, metascutum; st, abdominal sternite; ti, trochantin; tr, trochanter; v2/3, mesoventrite/metaventrite; w, wing



with microtrichia (average length  $8 \mu\text{m}$ ,  $300\,000 \text{mm}^{-2}$ ) (Fig. 7e). The proximal part of the mesal rim is adapted to the outline of the scutellar shield ('Schildchen'); it forms the elytral part of the mesoscutellar interlocking device ('Schildchen-Scutellum-Sperre'; Heberdey 1938; 'Scutellum-Sperre'; Baehr 1980); the remaining part of the mesal rim is straight (Fig. 7a). Both elytra are held together by a tongue-and-groove-mechanism in the resting position ('Nahtrand-Sperre'; Heberdey 1938). The connected mesal rims fit into a median impression of the metascutum; the metascutal interlocking device is supported by fields of scale-like microtrichia (see below) (Figs 7f and 8). The elytral base (Fig. 7b) bears a cylindrical mesal process, which corresponds with a specific area of the mesoscutum (see above). Two sockets of the lateral process of the elytral base articulate with the mesothoracic pleural wing process and the axillary sclerites, respectively. An oval field of cone-shaped microtrichia (length c.  $3.5 \mu\text{m}$ ) interacts with the mesonotum in the resting position (Fig. 7c). The lateral rim of the elytron is sharply turned downwards into the epipleuron. Its marginal ridge is very thin compared with that of the mesal rim; its proximal part is covered with triangular microtrichia (Fig. 7g), which interacts with the pterothoracic pleural sclerites and the first abdominal

segments; the remaining distal portion is smooth and rests on the abdominal pleura (Fig. 7i).

**Musculature** (Figs 17 and 18) Muscle numbers are taken from Beutel and Haas (2000), the names from Larsén (1966) (Tables 1 and 2). Statements on muscle functions were inferred from origin and insertion and from interpretations suggested by Larsén (1966).

**Dorsal muscles:** M. 39: M. mesonoti primus (Larsén 1966: M28; Matsuda 1970: t 14; Baehr 1975: 23), well developed; O (=origin): prothorax, I (=insertion): mesophragma, F (=function): fixation of elytron in resting position. M. 40: M. mesonoti secundus (Larsén 1966: M29; Matsuda 1970: t 12; Baehr 1975: 24), oblique, moderately conical; O: median prothorax, I: ventrolateral edge of mesophragma, F: releasing of elytral fixation, antagonist of M. 39.

**Ventral muscles:** M. 42: M. mesosterni primus (Larsén 1966: M30; Matsuda 1970: s 13; Baehr 1975: 25), very large; O: apical part of profurca, I: apical part of mesofurca, F: retractor of prothorax. M. 43: M. mesonoti secundus (Larsén 1966: M31; Matsuda 1970: s 12; Baehr 1975: 26), absent.

**Dorsoventral muscles:** M. 44: Mm. noto-sternales (Larsén 1966: –; Matsuda 1970: t-p 5; Baehr 1975: 27), absent. M.

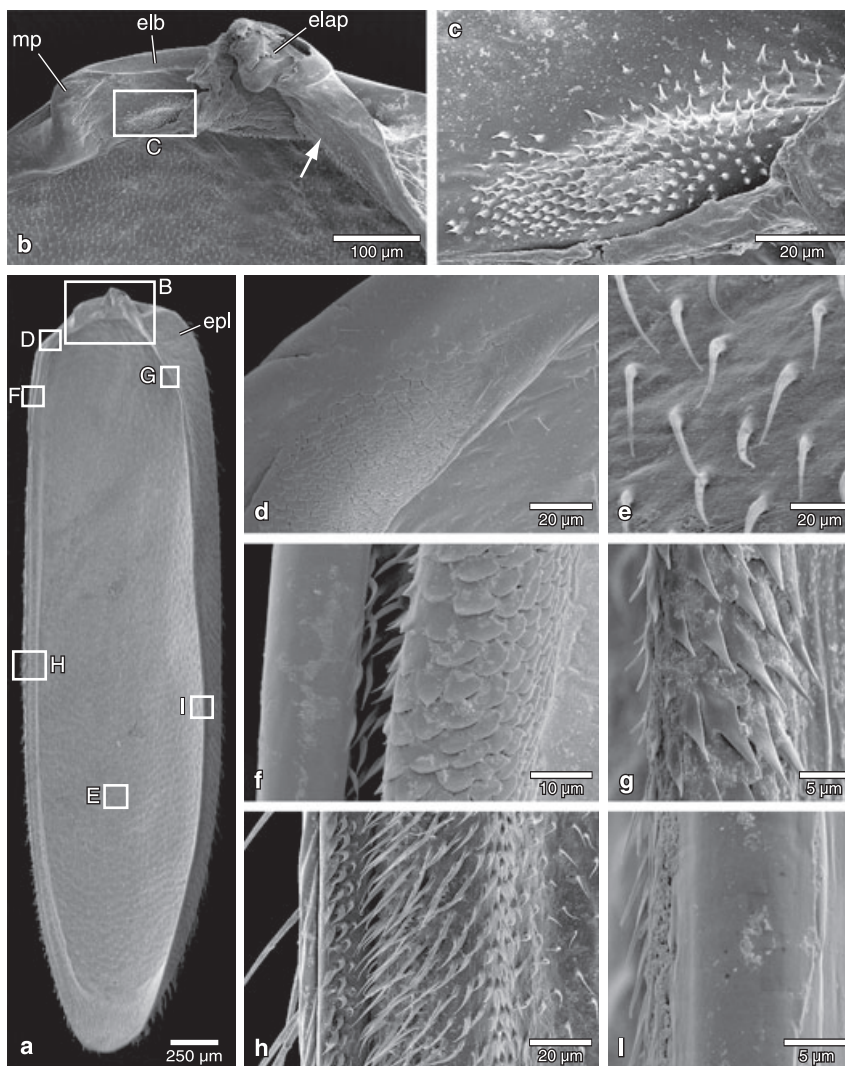


Fig. 7. SEM, left elytron, *Elodes pseudominuta*. (a) Ventral side (position of b–i marked). (b) Base of elytron. (c) Microtrichial pad of the elytral base. (d) Smooth transition between the inner rim and the elytral base. (e) Ventral elytral surface. (f) Proximal part of the inner rim. (g) Proximal part of the outer rim. (h) Inner rim. (i) Outer rim. Abbreviations: elap, lateral articulating process of elytron; elb, base of elytron; epl, epileuron; mp, mesal process of elytral base

45: *M. dorsoventralis* (Larsén 1966: M32; Matsuda 1970: t-s 1; Baehr 1975: 32), short, flattened; O: ventral process of mesophragma, I: upper side of lateral mesofurcal arm, F: depressor of mesonotum.

**Lateral muscles:** M. 46: *M. noto-pleurocostalis longus* (Larsén 1966: –; Matsuda 1970: t-p 12; Baehr 1975: 28), absent. M. 47: *M. noto-pleuralis* (Larsén 1966: M33; Matsuda 1970: t-p 3; Baehr 1975: 29), short but well developed; O: anterior side of pleural arm, I: lateral part of prothorax, F: depressor of the lateral notum, releases the elytral base. M. 50: *M. episterno-sternalis* (Larsén 1966: –; Matsuda 1970: p 3; Baehr 1975: 33), absent. M. 51: *M. episterno-spinalis* (Larsén 1966: –; Matsuda 1970: p-s 2; Baehr 1975: 35), absent. M. 52: *M. epimero-subalaris* (Larsén 1966: M35; Matsuda 1970: t-p 16; Baehr 1975: –), short and thin; O: epimeron close to pleural ridge, I: subalare, F: opens the elytron. L 34: *M. noto-epimeralis* [Larsén 1966: M34; Matsuda 1970: t-p 16 (?); Baehr 1975: –], slender; O: mesepimeron close to pleural ridge, I: lateral edge of mesonotum with a long tendon, F: stabilization of the connection between notum and epimeron and fine regulation of elytral closing movement. M. 53: *M. pleura-alaris a* (Larsén 1966: M36a; Matsuda 1970: t-p 14; Baehr 1975: 30), very large, flattened; O: ventral part of anepisternum, close to anapleural cleft, I: combined with following muscle on third axillary,

F: movement of axillary 3. M. 54: *M. pleura-alaris b* (Larsén 1966: M36b; Matsuda 1970: t-p 13; Baehr 1975: 31), very short and thin; O: posterior face of the pleural arm, I and F: see above (M. 53). M. 55: *M. furca-pleuralis* (Larsén 1966: M37; Matsuda 1970: p-s 1; Baehr 1975: 34), short; O: upper side of lateral mesofurcal arm, I: process of pleural ridge, F: stabilization of metafurca. M. 58: *M. profurca-mesepisternalis* (Larsén 1966: M38; Matsuda 1970: p-s 3; Baehr 1975: –), absent.

**Leg muscles:** M. 59: *M. noto-trochantinalis* (Larsén 1966: M39; Matsuda 1970: t-ti (cx) 2; Baehr 1975: 36), absent. M. 60: *M. noto-coxalis* (Larsén 1966: M40; Matsuda 1970: t-cx 6; Baehr 1975: 37), strongly developed; O: extensive area on posterior prothorax, I: posterior part of coxal margin with a strong, long tendon, F: open the elytron. M. 61: *M. episterno-coxalis* (Larsén 1966: M41; Matsuda 1970: p-cx 5; Baehr 1975: 38), large and flattened; O: ventral half of anepisternum and pleural ridge, I: combined with following muscle on antero-lateral coxal margin with a short but very strong tendon, F: promotion of metacoxa. M. 62: *M. coxa-basalaris* (Larsén 1966: M42; Matsuda 1970: p-ti (cx) 2; Baehr 1975: 39), long but very thin; O: basalare, I: see above (M. 61), F: supports M. 61, minor influence on motion of basalare. M. 64: *M. coxa-subalaris* (Larsén 1966: M43; Matsuda 1970: t-cx 8; Baehr

Table 1. Homologization of different nomenclatures of the mesothoracic musculature of Coleoptera

Muscle name (according to Larsén 1966)	Present study	Beutel and Haas (2000)	Larsén (1966)	Baehr (1975)	Matsuda (1970)
M. mesonoti primus	M. 39	M. 39	M28	23	t 14
M. mesonoti secundus	M. 40	M. 40	M29	24	t 12
M. mesosterni primus	M. 42	M. 42	M30	25	s 13
M. mesosterni secundus	M. 43	M. 43	M31	26	s 12
Mm. noto-sternales	M. 44	M. 44	–	27	t-p 5
M. dorsoventralis	M. 45	M. 45	M32	32	t-s 1
M. noto-pleurocostalis longus	M. 46	M. 46	–	28	t-p 12
M. noto-pleuralis	M. 47	M. 47	M33	29	t-p 3
M. episterno-sternalis	M. 50	M. 50	–	33	p 3
M. episterno-spinalis	M. 51	M. 51	–	35	p-s 2
<b>M. noto-epimeralis</b>	<b>L 34</b>	<b>M. 52</b>	<b>M34</b>	–	<b>t-p 16 ?</b>
<b>M. epimero-subalaris</b>	<b>M. 52</b>	<b>M. 52</b>	<b>M35</b>	–	<b>t-p 16</b>
M. pleura-alaris a	M. 53	M. 53	M36a	30	t-p 14
M. pleura-alaris b	M. 54	M. 54	M36b	31	t-p 13
M. furca-pleuralis	M. 55	M. 55	M37	34	p-s 1
M. profurca-mesepisternalis	M. 58	M. 58	M38	–	p-s 3
M. noto-trochantinalis	M. 59	M. 59	M39	36	t-ti (cx) 2
M. noto-coxalis	M. 60	M. 60	M40	37	t-cx 6
M. episterno-coxalis	M. 61	M. 61	M41	38	p-cx 5
M. coxa-basalaris	M. 62	M. 62	M42	39	p-ti (cx) 2
M. coxa-subalaris	M. 64	M. 64	M43	40	t-cx 8
M. furca-coxalis anterior	M. 65	M. 65	M44	41	s-cx 5
M. furca-coxalis lateralis	M. 66	M. 66	M45	42	s-cx 2
M. furca-coxalis posterior	M. 67	M. 67	M46	43	s-cx 3
M. noto-trochanteralis	M. 69	M. 69	M47	44	t-tr 1
M. episterno-trochanteralis	M. 70	M. 70	M48	45	p-tr 1
M. trochantero-basalaris	M. 71	M. 71	M50	46	p-tr 2
M. furca-trochanteralis	M. 72	M. 72	M52	47	s-tr 1
M. epimero-trochanteralis	M. 73	M. 73	M49	–	–
M. sterno-trochanteralis	M. 74	M. 74	M51	–	s-tr 1
M. coxa-trochanteralis medialis	M. 75	M. 75	M53	48	–
M. coxa-trochanteralis lateralis	M. 76	M. 76	M54	49	–

1975: 40), absent. M. 65: M. furca-coxalis anterior (Larsén 1966: M44; Matsuda 1970: s-cx 5; Baehr 1975: 41), moderately sized; O: anterior part of mesofurcal stalk and lateral arms, I: anterior mesocoxal margin, F: mainly promotion of coxa. M. 66: M. furca-coxalis lateralis (Larsén 1966: M45; Matsuda 1970: s-cx 2; Baehr 1975: 42), well developed, cone shaped; O: lateral surface of mesofurcal stalk, I: lateral coxal margin with a strong tendon, F: stabilizator of mesofurca and abductor of coxa. M. 67: M. furca-coxalis posterior (Larsén 1966: M46; Matsuda 1970: s-cx 3; Baehr 1975: 43), moderately sized; O: lower surface of lateral mesofurcal arms, I: posterior coxal margin, F: retractor of coxa. M. 69: M. noto-trochanteralis (Larsén 1966: M47; Matsuda 1970: t-tr 1; Baehr 1975: 44), absent. M. 70: M. episterno-trochanteralis (Larsén 1966: M48; Matsuda 1970: p-tr 1; Baehr 1975: 45), absent. M. 71: M. trochantero-basalaris (Larsén 1966: M50; Matsuda 1970: p-tr 2; Baehr 1975: 46), strongly developed; O: basalar, lateral M. 62, I: combined with muscles M. 72 and M. 75 on trochanteral tendon, F: adduction of trochanter and motion of basalar. M. 72: M. furca-trochanteralis (Larsén 1966: M52; Matsuda 1970: s-tr 1; Baehr 1975: 47), well developed; O: ventral side of lateral mesofurcal arm, I: trochanteral tendon, F: adductor of trochanter. M. 73: M. epimero-trochanteralis (Larsén 1966: M49; Matsuda 1970: –; Baehr 1975: –), absent. M. 74: M. sterno-trochanteralis (Larsén 1966: M51; Matsuda 1970: s-tr 1; Baehr 1975: –), absent. M. 75: M. coxa-trochanteralis medialis (Larsén 1966: M53; Matsuda 1970: –; Baehr 1975: 48), very strong; O: anterior and medial inner surface of mesocoxa, I: trochanteral tendon, F: adductor of trochanter. M. 76: M. coxa-trochanteralis lateralis (Larsén 1966: M54; Matsuda

1970: –; Baehr 1975: 49), very large; O: laterally on inner surface of mesocoxa, I: base of trochanter, F: abductor of trochanter.

#### Metathorax

The large metascutum is subdivided by several sutures (Figs 8a and 9). Internal ridges form an X-shaped apodeme (Figs 9b, 10a and 11). The mesophragma is subdivided into two arched sections. The median membranous area of the anterior metascutum contains the mesothoracic yoke plates (Figs 9 and 10a). Alacristae bordering the deep median impression of the scutum are part of the metathoracic elytral locking system (Figs 8, 9a and 11a), which is supported by fields of flat microtrichia on both corresponding structures (Figs 7f, 8b and 11). The triangular anterior notal process is separated from the remaining scutum by the anterolateral scutal suture. The medial notal process is finger-like (Figs 8a, 9, 10a,b and 12b). Both structures interact with the first axillary sclerite (see below). The posterior notal process is minute (Figs 9, 10a and 12b). The prealar sclerite is embedded in the lateral membranous area between the mesonotum and the metanotum; it extends into the lumen of the segment as an elongated apodeme (Figs 9a, 12b, 19 and 20g). The axillary muscle disc is adjacent with the medial notal process and connected with the median process of the third axillary sclerite by means of a short tendon (Figs 9a and 10c). The first axillary is composed of a blunt head, a more constricted neck and a horseshoe-shaped body. The medial margin is connected with the anterior and medial notal processes (Figs 9, 10a,b and 13). The angle  $\alpha$  between axillary 1 and scutum (sensu Hörnschemeyer 1998)

Table 2. Homologization of different nomenclatures of the metathoracic musculature of Coleoptera

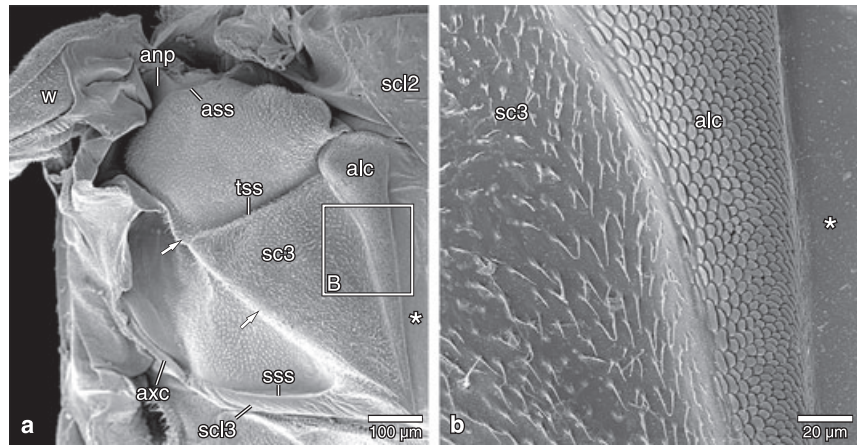
Muscle name (according to Larsén 1966)	Present study	Beutel and Haas (2000)	Larsén (1966)	Baehr (1975)	Matsuda (1970)
M. metanoti primus	M. 79	M. 79	M60	50	t 14
M. metanoti secundus	M. 80	M. 80	M61	51	t 12
M. metasterni primus	M. 82	M. 82	M62	52	s 13
M. metasterni secundus	M. 83	M. 83	M63	53	s 12
M. dorsoventralis primus	M. 84	M. 84	M64	55	t-p 5
M. dorsoventralis secundus	M. 85	M. 85	M65	62	t-s 1
M. dorsoventralis tertius	M. 86	M. 86	M66	63	t-s 1 ?
M. episterno-spinalis	M. 87	M. 87	–	67	p-s 2
M. mesofurca-basalaris	M. 88	M. 88	–	68	p-s 2
Mm. noto-episternales breves	M. 89	M. 89	–	56	t-p 3
M. pleura-praealaris	M. 90	M. 90	M67	58	t-p 4
M. noto-pleuralis	M. 91	M. 91	M68	59	t-p 12 ?
M. noto-pleuralis	M. 92	M. 92	M68	57	t-p 15 ?
M. noto-basalaris	M. 93	M. 93	M69	57	t-p 8
M. epimero-subalaris	M. 94	M. 94	M70	66	t-p 16
M. pleura-alaris a	M. 95	M. 95	M71a	60	t-p 14
M. pleura-alaris b	M. 96	M. 96	M71b	61	t-p 13
M. sterno-episternalis	M. 97	M. 97	M72	64	p 1
M. sterno-basalaris	M. 98	M. 98	M73	65	p 3
M. noto-trochantinalis	M. 100	M. 100	M74	69	t-ti(cx) 2
M. noto-coxalis anterior	M. 101	M. 101	M75	70	t-cx 6 ?
M. noto-coxalis posterior	M. 102	M. 102	M76	71	t-cx 7 ?
M. episterno-coxalis	M. 103	M. 103	M77	72	p-cx 5
M. coxa-basalaris	M. 104	M. 104	M78	73	p-cx 4
M. coxa-subalaris	M. 105	M. 105	M79	74	t-cx 7
M. sterno-coxalis	M. 106	M. 106	M80	–	s-cx 5
M. furca-coxalis anterior	M. 107	M. 107	M81	75	s-cx 5
M. furca-coxalis lateralis	M. 108	M. 108	M82	76	s-cx 2
M. furca-coxalis posterior	M. 109	M. 109	M83	77	s-cx 3
M. noto-trochanteralis	M. 111	M. 111	M84	78	t-tr 1
M. trochantero-basalaris	M. 112	M. 112	–	79	p-tr 2
M. furca-trochanteralis	M. 113	M. 113	M85	80	s-tr 1
M. coxa-trochanteralis medialis	M. 114	M. 114	M86	81	–
M. coxa-trochanteralis lateralis	M. 115	M. 115	M87	82	–

amounts c. 30° (Fig. 13a). The rounded head of axillary 2 bears a median process that articulates with the neck of the first axillary, and a long, slightly curved caudal process that contacts the medial side of axillary 3 (Figs 9, 10 and 13b). The well-developed caudal arm of the flat third axillary sclerite is connected to the posterior notal process by a membranous joint; the large caudal arm of axillary 3 is adjacent to the anal veins, whereas the small median process is in contact with the second axillary sclerite and the axillary muscle disc (Figs 9a, 10c and 13c). The scutellum is very short but broadly extended between the alacristae; it is laterally continuous with the axillary cord that connects the anal field of the wing and the metanotum (Figs 8a, 9 and 10a). The transverse metapostnotum splits laterally into two branches (Figs 9, 10a and 12). The anterior branch ends below the axillary cord; the posterior arm contacts the dome-shaped sclerite (see below). The hind margin of the postnotum is continuous with the undivided metaphragma (Figs 9b and 10a). The exposed part of the basalar is fused with the dorsal parts of the anepisternum and distally expanded into an elliptic resting knob (Figs 12b, 14 and 15); the internal part is enlarged and forms an oval muscle disc (Fig. 15). The subalare is elongated, rounded and ventrally covered by a part of the semimembranous area of the metepimeron (Figs 9a and 12). The pleural suture connects the pleural coxal joint and the pleural wing articulation and separates the episternal and epimeral parts of the pleuron (Fig. 12); the pleural ridge is strongly sclerotized (Fig. 19b). Following Larsén (1966), the epimeral part is divided into a

ventral sclerite, a dorsal sclerite and a semimembranous area. The ventral sclerite is located at the lateral end of the paracoxal suture; a long process is present anteriorly and a short process posteriorly; dorsally it contacts the dome-shaped sclerite; a discrete dorsal sclerite is not developed; it is probably merged with the extensive semimembranous area (Figs 9a and 12a). The anepisternum is slightly bent at the longitudinal ridge; the upper part bears the pleural wing process (Figs 6d–f, 12b, 14 and 15). The rounded fulcrum lies below the neck of the first axillary sclerite. The finger-shaped posterior process of the anepisternum and a depression of the anterior metacoxal margin form an interlocking device (Fig. 6c). The interior surface of the anepisternum is enclosed by duplicatures (Fig. 15); the curved anapleural cleft separates the anepisternum and metaventrite. The pentagonal metaventrite is well sclerotized; the distinct discriminial line corresponds with a low internal median ridge (Figs 6a, 14 and 17); the katepisternum, which is separated from the anterior metaventrite by a transverse suture (Figs 14 and 23a), is triangular and enclosed by the oblique anterior margins of the metacoxae (Figs 6a, 14 and 15). The metafurca is completely sclerotized; the stem is long, thin and anteriorly continuous with laminar extensions; the anterior furcal arms are inconspicuous; the lateral arms are proximally broadened and very thin in their distal parts; the unpaired ventral process is trapezoid shaped (Figs 15, 17 and 19a). The enlarged hind coxae are immobilized but not firmly fused and reach the hind margin of the second abdominal sternite posteriorly (Figs 6a,d, 12a and 14).



Fig. 8. SEM, dorsal view of metathorax, *Elodes pseudominuta* (median groove for reception of inner elytral rims marked by an asterisk). (a) Left side. (b) Details of metascutum. Abbreviations: alc, alacrista; anp, anterior notal process; ass, anterolateral scutal suture; axc, axillary cord; sc3, metascutum; scl2/3, mesoscutellum/metascutellum; sss, scuto-scutellar suture; tss, transversal scutal suture; w, wing



The metacoxal meron (as defined by Larsén 1945a) is smooth, concave and separated from the elevated mesal part of the coxa by a distinct edge (metacoxal plates). The external part of the metatrochantin is indistinguishably fused with the metaventrite; the internal part forms a strongly sclerotized trochantinal muscle disc close to the metacoxal rim (Fig. 19a).

The terminology of the wing structures and venation was adapted from Kukalová-Peck and Lawrence (1993) (Fig. 16). The corresponding terms used by other authors (e.g. Snodgrass 1909; Ponomarenko 1972) can be traced in Kukalová-Peck and Lawrence 1993 (p. 193, Table 1). The more recent work of these authors (Kukalová-Peck and Lawrence 2004) was not used, as most figures in that study do not refer to explicit species but hypothetical ground plan conditions.

The wing (Fig. 25a) is compact and the apex is evenly rounded. The entire posterior margin and a part of the anterior margin are covered with microtrichia. The dorsal and ventral surfaces of the wing are also densely covered with very short microtrichia. An incision between the anal field and the medial field is not present; the anal field is distinctly developed and separated from the remaining wing by a deep incision. The radius anterior (RA) and the subcosta posterior form the stiff radial bar. The branches  $RA_{1+2}$  and  $RA_{3+4}$  border the rounded radial cell. The shortened  $RA_{3+4}$  do not enter the apical field. Veins are absent from the apical field, as the branches of radius posterior ( $RP_{1-4}$ ) are missing. The radial cell and the indistinct RP are connected by the fourth radial cross-vein (r4). RP and the second radio-medial cross-vein (rp-mp2) form the medial hook. The third radial cross-vein (r3) disintegrates into a darkly pigmented area. A zone of weakness is present in the distal part of the medial bar (media posterior,  $MP_{1+2}$ ). The medial spur extends to the posterior margin of the wing and forms the borderline between the apical and medial fields. The anal anterior (AA) continues with its branch  $AA_{3+4}$  along the anal fold;  $AA_{1+2}$  is fused with the cubital anterior (CuA); the MP contacts the posterior margin of the wing and runs parallel to  $CuA + AA_{1+2}$ ;  $MP_3$  and  $CuA + AA_{1+2}$  are connected by a cross-vein, which perhaps corresponds to  $MP_4$ . The third branch of the anal posterior ( $AP_3$ ) runs along the wing margin and fuses distally with the apical part of  $AP_4$ .

#### Musculature (Figs 17, 19 and 20)

**Dorsal muscles:** M. 79: M. metanoti primus (Larsén 1966: M60; Matsuda 1970: t 14; Baehr 1975: 50), very strong; O: mesophragma, I: metaphragma, F: wing depressor. M. 80: M.

metanoti secundus (Larsén 1966: M61; Matsuda 1970: t 12; Baehr 1975: 51), well developed; O: paramedian area of scutum, I: metaphragma, F: wing depressor.

**Ventral muscles:** M. 82: M. metasterni primus (Larsén 1966: M62; Matsuda 1970: s 13; Baehr 1975: 52), conical, moderately sized; O: posterior face of mesofurcal stalk, I: anterior metafurcal arms with a long, thin tendon, F: stabilization of metafurca. M. 83: M. metasterni secundus (Larsén 1966: M63; Matsuda 1970: s 12; Baehr 1975: 53), absent.

**Dorsoventral muscles:** M. 84: M. dorsoventralis primus (Larsén 1966: M64; Matsuda 1970: t-p 5; Baehr 1975: 55), moderately developed muscle; O: anterior area of metanotum and upper part of mesophragma, I: metaventrite close to median ridge, F: levator of the wing. M. 85: M. dorsoventralis secundus (Larsén 1966: M65; Matsuda 1970: t-s 1; Baehr 1975: 62), well developed but strongly flattened; O: dorsal side of lateral metafurcal arms, I: posterior surface of metaphragma, F: adjustment of the metafurca and postnotum during flight, together with M. 86. M. 86: M. dorsoventralis tertius [Larsén 1966: M66; Matsuda 1970: t-s 1(?); Baehr 1975: 63]; O: apex of lateral metafurcal arm, I: ventrolateral part of metaphragma, F: see above.

**Lateral muscles:** M. 87: M. episterno-spinalis (Larsén 1966: –; Matsuda 1970: p-s 2; Baehr 1975: 67), absent. M. 88: M. mesofurca-basalaris (Larsén 1966: –; Matsuda 1970: p-s 2; Baehr 1975: 68), absent. M. 89: Mm. noto-episternales breves (Larsén 1966: –; Matsuda 1970: t-p 3; Baehr 1975: 56), absent. M. 90: M. pleura-praealaris (Larsén 1966: M67; Matsuda 1970: t-p 4; Baehr 1975: 58), very short, fan shaped; O: prealar sclerite, I: pleural ridge with a tendon, F: disengage semimembranous area from wing. M. 91: M. noto-pleuralis [Larsén 1966: M68; Matsuda 1970: t-p 12(?); Baehr 1975: 59], absent. M. 93: M. noto-basalaris (Larsén 1966: M69; Matsuda 1970: t-p 8; Baehr 1975: 57), short but very strong; O: anterolateral edge of metascutum, I: dorsal side of muscle disc of basalar, F: stabilizer of basalar muscle disc and antagonist of Mm. 98 and 104. M. 94: M. epimero-subalaris (Larsén 1966: M70; Matsuda 1970: t-p 16; Baehr 1975: 66), short, flattened; O: posterior part of epimeron, I: posterior edge of subalare, F: movements of subalare and attached second and third axillary sclerites. M. 95: M. pleura-alaris a (Larsén 1966: M71a; Matsuda 1970: t-p 14; Baehr 1975: 60), very short but well developed; O: epimeral part of pleural ridge, I: combined with



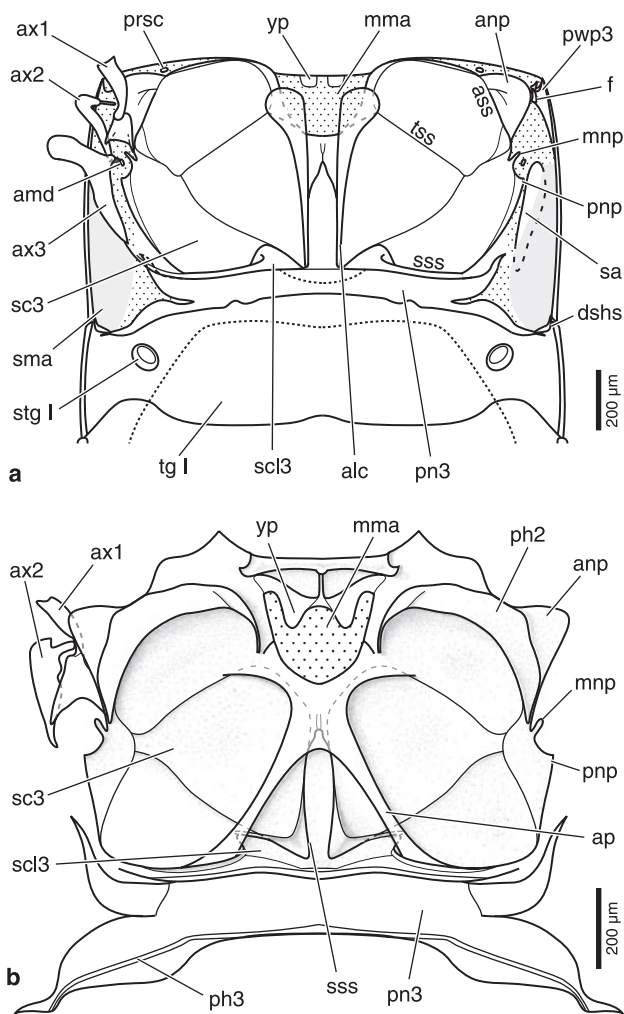


Fig. 9. Dorsal part of metathoracic skeleton, *Elodes pseudominuta* (elytra removed; semimembranous areas grey; membranous parts labelled with dot pattern). (a) Dorsal view. Axillary sclerites of the right side are removed. (b) View of the endoskeleton. Axillary sclerites of the left side removed. **Abbreviations:** alc, alacrista; amd, axillary muscle disc; anp, anterior notal process; ap, apodeme; ass, anterolateral scutal suture; ax1/2/3, first, second, third axillary sclerite; dshs, dome-shaped sclerite; f, fulcrum; mma, median membranous area; mnp, median notal process; ph2/3, mesophragma/metaphragma; pn3, metapostnotum; pnp, posterior notal process; prsc, prealar sclerite; pwp3, metathoracic pleural wing process; sa, subalare; sc3, metascutum; scl3, metascutellum; sma, semimembranous area; sss, scuto-scutellar suture; stg, first abdominal stigma; tg I, first abdominal tergite; tss, transversal scutal suture; yp, yoke plate

following muscle on muscle disc of third axillary sclerite, F: movements of axillary 3. M. 96: M. pleura-alaris b (Larsén 1966: M71b; Matsuda 1970: t-p 13; Baehr 1975: 61), strongly developed; O: anterior part of anepisternum, I and F: see above (M. 95). M. 97: M. sterno-episternalis (Larsén 1966: M72; Matsuda 1970: p 1; Baehr 1975: 64), absent. M. 98: M. sterno-basalaris (Larsén 1966: M73; Matsuda 1970: p 3; Baehr 1975: 65), long, moderately sized; O: metaventrite lateral M. 84, I: ventral surface of muscle disc of basalare, below M. 104, F: pronator and depressor of the wing.

**Leg muscles:** M. 100: M. noto-trochantinalis (Larsén 1966: M74; Matsuda 1970: t-ti(cx) 2; Baehr 1975: 69), strongly developed; O: metascutum anterior to M. 101, I: disc-like

process of trochantin, F: indirect flight muscle and levator of the wing. M. 101: M. noto-coxalis anterior (Larsén 1966: M75; Matsuda 1970: t-cx 6?; Baehr 1975: 70), very large; O: scutum, between M. 80 and M. 100, I: lateral metacoaxal rim, F: levator of the wing. M. 102: M. noto-coxalis posterior (Larsén 1966: M76; Matsuda 1970: t-cx 7?; Baehr 1975: 71), moderately sized with very long tendon; O: lateral margin of scutum, above subalare, I: posterolateral edge of metacoxa by means of a strong tendon. M. 103: M. episterno-coxalis (Larsén 1966: M77; Matsuda 1970: p-cx 5; Baehr 1975: 72), absent. M. 104: M. coxa-basalaris (Larsén 1966: M78; Matsuda 1970: p-cx 4; Baehr 1975: 73), large; O: metacoxa, posterior to M. 98, I: lower surface of basalar muscle disc, F: pronator and depressor of the wing. M. 105: M. coxa-subalaris (Larsén 1966: M79; Matsuda 1970: t-cx 7; Baehr 1975: 74), very strong complex composed of three bundles; O: lateral wall of metacoxa lateral to M. 104, I: subalare, F: supination of the wing triggered by movements of subalare and axillary 3. M. 106: M. sterno-coxalis (Larsén 1966: M80; Matsuda 1970: s-cx 5; Baehr 1975: -), absent. M. 107: M. furca-coxalis anterior (Larsén 1966: M81; Matsuda 1970: s-cx 5; Baehr 1975: 75), small and cone-like; O: lateral face of proximal metafurca, I: anterior rim of metacoxa by means of a tendon, F: stabilization of metacoxa, possibly promotor to a lesser degree. M. 108: M. furca-coxalis lateralis (Larsén 1966: M82; Matsuda 1970: s-cx 2; Baehr 1975: 76), well developed and fan shaped; O: enlarged area of distal metafurcal stalk, I: on lateral edge of metacoxa with a very long, sclerotized tendon, F: stabilization of metafurca. M. 109: M. furca-coxalis posterior (Larsén 1966: M83; Matsuda 1970: s-cx 3; Baehr 1975: 77), absent. M. 111: M. noto-trochantinalis (Larsén 1966: M84; Matsuda 1970: t-tr 1; Baehr 1975: 78), absent. M. 112: M. trochantero-basalaris (Larsén 1966: -; Matsuda 1970: p-tr 2; Baehr 1975: 79), absent. M. 113: M. furca-trochantinalis (Larsén 1966: M85; Matsuda 1970: s-tr 1; Baehr 1975: 80), strongly developed; O: base of lateral metafurcal arms, I: trochanteral tendon, F: depressor of the hind leg. M. 114: M. coxa-trochantinalis medialis (Larsén 1966: M86; Matsuda 1970: -; Baehr 1975: 81), strong, two subcomponents; O: 114a: anterior part of metacoxa, 114b: lateral metacoaxal wall, I: trochanteral tendon, F: depressor of the hind leg. M. 115: M. coxa-trochantinalis lateralis (Larsén 1966: M87; Matsuda 1970: -; Baehr 1975: 83), very large muscle composed of two subcomponents; O: 115a: medial surface of metacoxa, 115b: posterior area of metacoxa, I: trochanteral tendon, F: levator of the hind leg.

### Comparison with other scirtoid species

#### *Scirtidae*

The shape of mesonotum and metanotum is very uniform (Figs 9a and 21). The mesoventrite is always short, posterolaterally pointed and devoid of a transverse suture and discriminial line (Figs 4c, 6a, 22a-c and 23a-d). A median furrow for reception of the prosternal process ('Mesosternal-grube', Nyholm 1967) is generally present but varies in shape between species (Figs 22a-c and 23a-d). The short postero-medial process is always present. It separates the mesocoxal cavities partially in *Cyphon* and *Pseudomicrocara* (Figs 22b,c and 23b,c), but not in *Ora* (Figs 22a and 23d). The shape of the mesocoxae varies only slightly and the mesofurcae are also largely uniform. The shape of the mesotrochantin varies from roundish to elongate. It is always exposed and articulates with the anterolateral edge of the mesocoxa (Fig. 23a-d). The

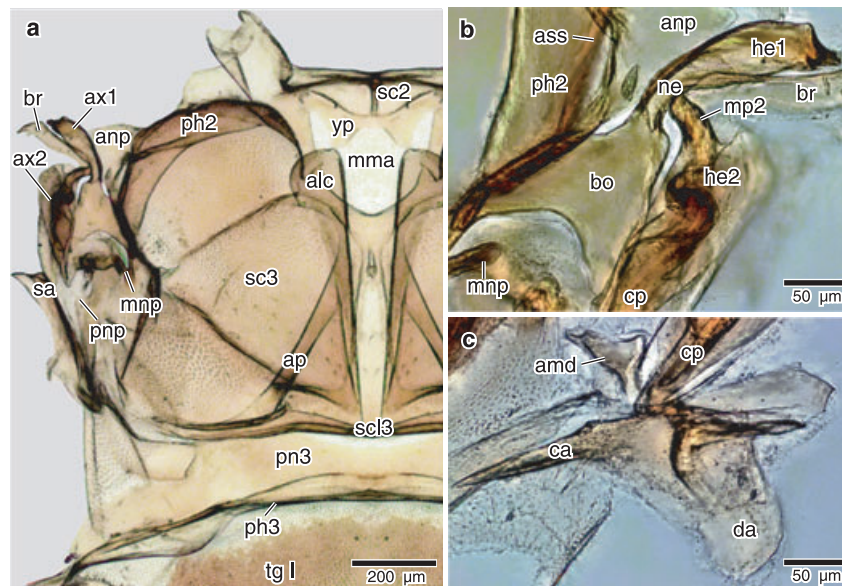


Fig. 10. Light microscopy photographs. Ventral view of metanotum and axillaria, *Elodes pseudominuta*. (a) Endoskeleton. (b) First and second axillary sclerites. (c) Second and third axillary sclerites. **Abbreviations:** alc, alacrista; amd, axillary muscle disc; anp, anterior notal process; ap, apodeme; ass, anterolateral scutal suture; ax1/2/3, first, second, third axillary sclerite; bo, body; br, basiradial; ca, caudal arm; cp, caudal process; da, distal arm; he1/2, head of first/second axillary; mma, median membranous area; mnp, median notal process; mp2, median process of second axillary; ne, neck; ph2/3, mesophragma/metaphragma; pn3, metapostnotum; pnp, posterior notal process; sa, subalare; sc2, mesoscutum/metascutum; scl3, metascutellum; tg I, first abdominal tergite; yp, yoke plate

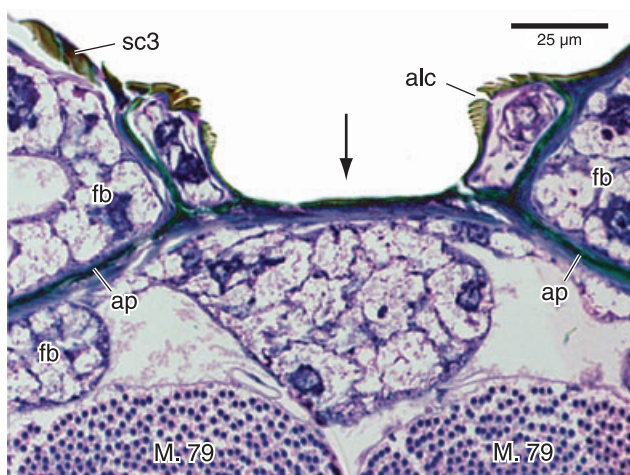


Fig. 11. Histological cross section, dorsomedian part of metascutum, *Elodes pseudominuta*. **Abbreviations:** alc, alacrista; ap, apodeme; fb, fat body; M. 79, M. metanoti primus; sc3, metascutum (median metascutal groove marked by an arrow)

connection between the mesoventrite and metaventrite within the mesocoxal cavities is membranous (Fig. 23a–d). The membranous part in *Elodes* and *Cyphon* is a short, broad stripe (Fig. 23a,b) but extended over the entire anterior half of the mesocoxal cavities in *Ora* and *Pseudomicrocara* (Fig. 23c,d).

The metaventrite of *Elodes* is conspicuously elongated compared with the other examined scirtids (Fig. 23a versus Fig. 23b–d). A metathoracic discriminial line is present in *Elodes* and also in *Ora* and *Pseudomicrocara* but absent in *Cyphon* (Fig. 23a–d). A small, triangular katapisternum is always present between the metacoxae. It is separated from the metaventrite by a distinct transverse suture and divided medially by a longitudinal suture (Fig. 23a–d). The metacoxae

are broadened and enlarged and contact the epipleura of the closed elytra. The meron (see list of phylogenetically relevant characters) is the broadest part of the hind coxae and usually forms a flat and distinctly delimited depression for reception of the hind femur. Coxal plates are usually present but small. The shape of the metacoxae in *Ora* and *Scirtes* differs from the typical condition: the meron is not distinctly separated from the medial part and coxal plates are completely absent (Fig. 22a).

The musculature is very uniform (Tables 3 and 4). Yet, the arrangement is somewhat modified in *Cyphon* as a result of the flattening of the pterothorax. The mesothoracic M. furca-coxalis anterior (M. 65) and M. noto-epimeralis (L 34) are less strongly developed than in *Elodes*. In *Ora*, M. epimero-subalaris (M. 52), M. coxa-basalaris (M. 62) and M. noto-epimeralis (L 34) are weakly developed, but M. mesosterni primus (M. 42) is very strong. The muscles of the metathorax show conspicuous modifications related to jumping behaviour: M. furca-trochanteralis (M. 113), M. coxa-trochanteralis medialis (M. 114) and M. coxa-trochanteralis (M. 115), which insert on the trochanteral tendon and move the hind legs, are strongly enlarged, and also M. furca-coxalis lateralis (M. 108), which stabilizes the metafurca.

The shape of the wing depends on its size: large wings are elongated (Fig. 25c), whereas small wings are shorter and broader (Fig. 25b). In all scirtids examined except for *Elodes*, the medial and apical fields are separated by a notch in the hind margin, and the radial cell, which may be triangular or more or less rounded sends out a short r3 proximal to r4 (Fig. 25b,c). The anal field is separated from the medial field by a very deep incision (less so in *Pseudomicrocara*). The connection between the r4 and the medial hook is indistinct in some species (e.g. *Cyphon*, Fig. 25b). In *Cyphon*, the medial bar lacks a zone of weakness; the CuA-AA<sub>1+2</sub> ends in the medial field and does not contact the fourth branch of the MP (MP<sub>4</sub>).

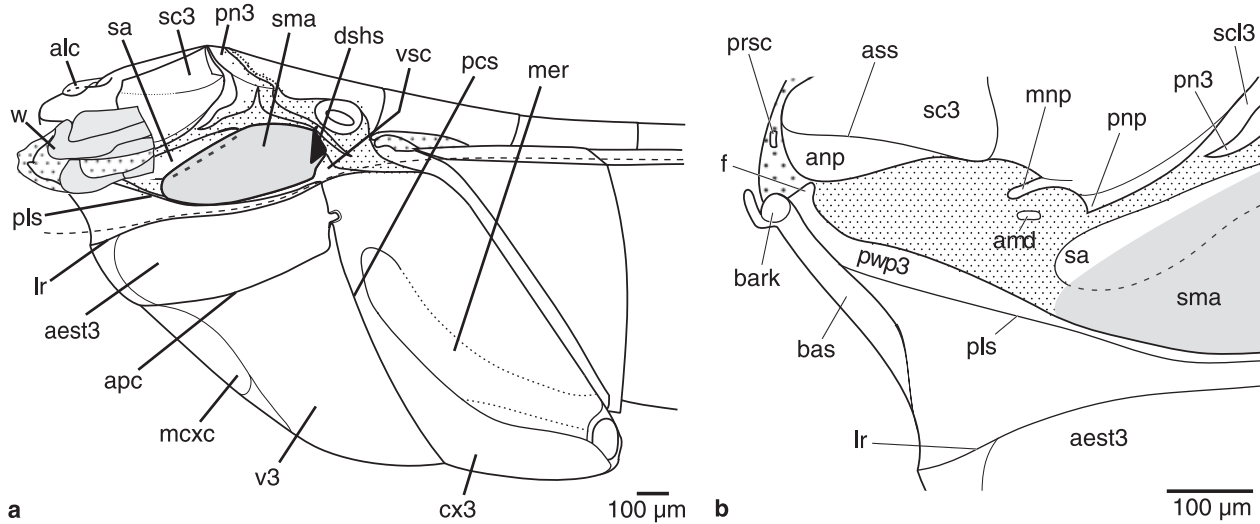


Fig. 12. Lateral metathorax and wing base, *Elodes pseudominuta* (semimembranous areas grey, membranous parts punctured). (a) Lateral view (wing removed close to wing base; lower rim of elytron marked by dotted line). (b) Left pleural and notal wing processes (wing and axillaria completely removed). **Abbreviations:** aest3, metanepisternum; alc, alacrista; amd, axillary muscle disc; anp, anterior notal process; apc, anapleural cleft; ass, anterolateral scutal suture; bas, basalare; bark, projection on the dorsal margin of basalare; cx3, metacoxa; dshs, dome-shaped sclerite; f, fulcrum; lr, longitudinal ridge of anepisternum 3; mcxc, mesocoxal cavity; mer, metacoxal meron; mnp, median notal process; pcs, paracoxal suture; pls, pleural suture; pn3, metapostnotum; pnp, posterior notal process; prsc, prealar sclerite; pwp3, metathoracic pleural wing process; sa, subalare; sc3, metascutum; scl3, metascutellum; sma, semimembranous area; v3, metaventricle; vsc, ventral sclerite; w, wing

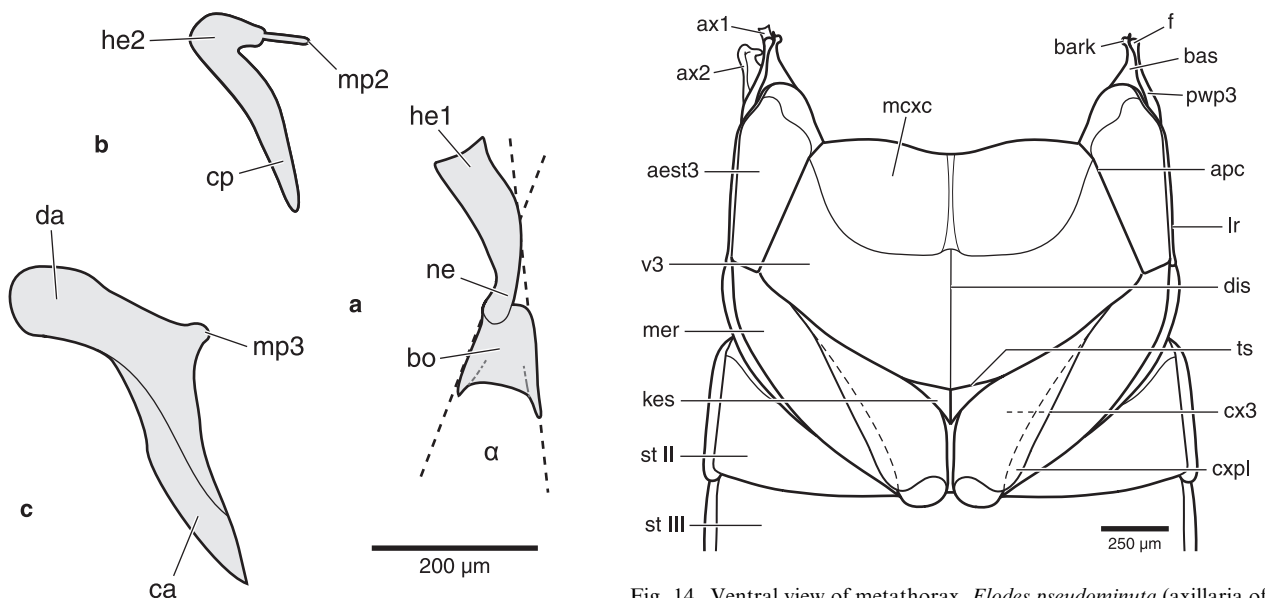


Fig. 13. Isolated axillary sclerites of left wing base, *Elodes pseudominuta*. (a) First axillary (angle  $\alpha$  marked by dotted lines). (b) Second axillary. (c) Third axillary. **Abbreviations:** bo, body; ca, caudal arm; cp, caudal process; da, distal arm; he1/2, head of first/second axillary; mp2/3, median processes of second/third axillary; ne, neck

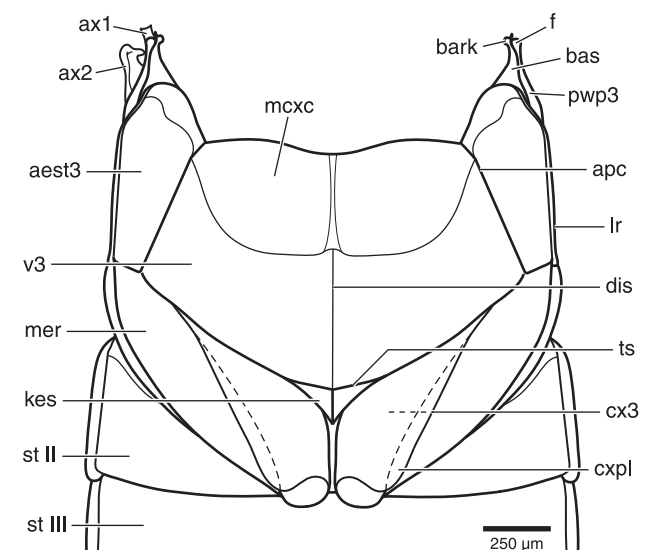


Fig. 14. Ventral view of metathorax, *Elodes pseudominuta* (axillaria of left side removed). **Abbreviations:** aest3, metanepisternum; apc, anapleural cleft; ax1/2, first, second axillary sclerite; bas, basalare; bark, projection on the dorsal margin of basalare; cx3, metacoxa; cxpl, coxal plate; dis, discriminial line; f, fulcrum; kes, katepisternum; lr, longitudinal ridge of anepisternum 3; mcxc, mesocoxal cavity; mer, metacoxal meron; pwp3, metathoracic pleural wing process; st II/III, second, third abdominal sternite; ts, transverse suture; v3, metaventricle

### *Eucinetus* (*Eucinetidae*)

The mesoventrite is posteriorly elongated and fused with the mesothoracic anepisternum. A recognizable exposed katepisternum, a transverse suture and the median furrow are absent. The enlarged mesocoxae are completely separated by the strong posteromedian process of the mesoventrite (Figs 22e and 23e). The trochantin is not exposed. The insertion areas of

the trochanters are more laterally oriented. The membranous connection between the mesoventrite and the metaventricle is very short.

The short metaventricle is characterized by large anterior impressions, which are part of the mesocoxal cavities. It lacks a discriminial line (Fig. 23e). The katepisternum is elongated in correlation with the elongation of the hind coxae (Fig. 22e).



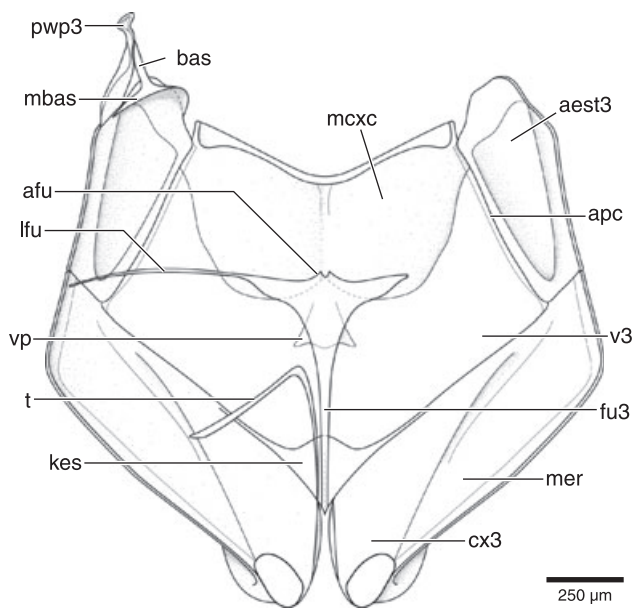


Fig. 15. Interior view of ventral metathorax, *Elodes pseudominuta* (basalare and wing base of right body side removed). Abbreviations: aest3, metanepisternum; afu, anterior furcal arm; apc, anapleural cleft; bas, basalare; cx3, metacoxa; fu3, metafurca; kes, katepisternum; lfu, lateral furcal arm; mbas, muscle disc of basalare; mcxc, mesocoxal cavity; mer, metacoxal meron; pwp3, metathoracic pleural wing process; t, tendon; v3, metaventrite; vp, ventral process of metafurca

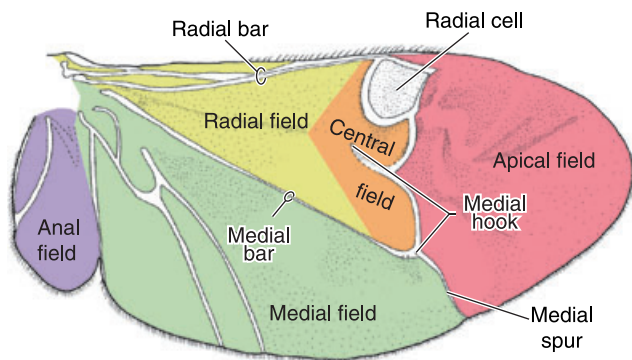


Fig. 16. Fields and major veins of the hind wing, *Elodes pseudominuta* (nomenclature adopted from Kukalová-Peck and Lawrence 1993)

The enlarged metacoxae bear moderately sized coxal plates and cover most parts of the second abdominal sternite.

The lateral mesofurcal arms are largely reduced (Fig. 24) and the associated muscles are lacking [Mm. dorsoventralis (M. 45), furca-pleuralis (M. 55) and furca-trochanteralis (M. 72)] or strongly reduced [M. mesosterni primus (M. 42)]. Mm. furca-coxalis anterior, lateralis and posterior (M. 65, M. 66, M. 67) and M. noto-epimeralis (L 34) are also absent. A hitherto undescribed muscle originates on the anterior rim of the mesocoxae and inserts on the median ridge of the mesoventrite. This muscle perhaps represents a modified M. furca-coxalis anterior (M. 65). The Mm. mesonoti secundus (M. 40) and noto-coxalis (M. 60) are slender. Due to the enlargement of the metacoxae, the leg muscles are elongated and run nearly parallel to the longitudinal body axis. M. furca-trochanteralis (M. 113) and Mm. dorsoventralis secundus (M. 85) et tertius (M. 86) are strongly enlarged, but M. furca-coxalis

lateralis (M. 108) and M. metasterni primus (M. 82) are thin. The direct wing muscles [(mainly M. pleura-praealaris (M. 90) and M. noto-basalaris (M. 93)] are very strongly developed.

The overall shape of the wing of *Eucinetus* is similar to that of *Elodes* (Fig. 25e), although they are only about half as long. Yet, they differ in several structural details. The medial and anal fields are separated by a broader incision. The radial cell is triangular with pointed angles. The cross-veins r3 and r4 are well developed. A short zone of weakness is present in the medial bar proximal to the contact with the second radio-medial cross-vein (rp-mp2). The fourth medial vein (MP<sub>4</sub>) does not fuse with the CuA vein. The CuA splits into a very short CuA<sub>1+2</sub> branch and a strong CuA<sub>3+4</sub>, which is fused with the AA vein (AA<sub>1+2</sub>). A single cross-vein without connection to any other vein is present in the medial field. The venation of the anal field is almost completely reduced. Only a short proximal part of the AP vein is present.

#### *Calyptomerus* (Clambidae)

Despite the distinct degree of miniaturization the dorsal part of the pterothorax is almost identical with what is found in other members of the superfamily. The mesoventrite, anepisternum and epimeron together form a structure, which appears as an undivided sclerite externally. However, internally the sclerites are divided by several sutures or ridges (e.g. the pleural ridge). The metaventrite lacks a medial furrow, a discrete katepisternum and the transverse suture (Figs 22d and 23f). A postero-medial process is present as in Scirtidae. The mesocoxae are more flattened than in other scirtoids and the mesotrochantin is not exposed (Fig. 22d). The mesofurca is similar to those of Scirtidae. The mesoventrite and metaventrite are connected by a short membrane (Fig. 23f).

The metaventrite lacks a discriminial line (Figs 22d and 23f). The katepisternum cannot be distinguished easily from the metaventrite and the enlarged coxal plates. The hind coxae are strongly miniaturized and are adjacent medially. The strongly enlarged coxal plates cover the entire hind leg (Fig. 22d).

The mesothoracic musculature is poorly developed. Especially, the Mm. pleura-alaris a (M. 53), episterno-coxalis (M. 61) and furca-trochanteralis (M. 72) are very slender. M. dorsoventralis (M. 45) and M. furca-pleuralis (M. 55) are absent. M. coxa-basalaris (M. 62) and M. noto-epimeralis (L 34) could not be identified and are probably completely reduced. In the metathorax, the furca-coxal region is strongly flattened. M. noto-basalaris (M. 93) is remarkably thin. M. furca-trochanteralis (M. 113) is reduced to two small bundles. M. noto-coxalis posterior is strongly enlarged.

The minute wing of *Calyptomerus* is nearly rectangular (Fig. 25d). The entire margin is fringed with microtrichia of heterogenous length. The effects of miniaturization are apparent in the venation and the proportions of the fields of the wing: The apical field is strongly enlarged (c. 50% of the wing surface); the anal field is very small and lacks veins; a part of the RA is transformed into a flexible bending zone (Fig. 25d: bz), which plays an important role in the folding of the proximal part of the wing. Consequently, the strong medial bar (MP<sub>1+2</sub>) is also divided into two parts. The radial cell is not clearly defined and only bordered by RA<sub>1+2</sub>. In the proximal part of the apical field, veins are recognizable. The first branch of the RP (RP<sub>1</sub>) emanates from the r4 cross-vein; the second branch runs parallel to RP<sub>1</sub>. The RP part of the medial hook is elongated.



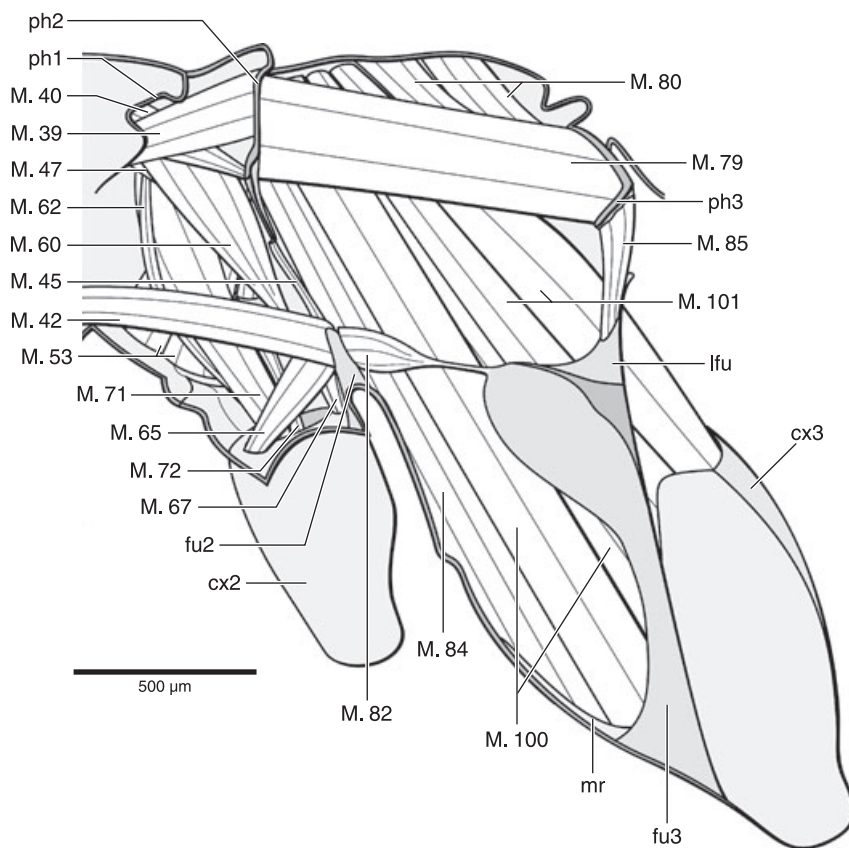


Fig. 17. Pterothorax, sagittal section, *Elodes pseudominuta* (reconstruction based on serial sections; ganglia and nerves removed; musculature white, skeletal parts grey). Abbreviations: cx2/3, mesocoxa/metacoxa; fu2/3, mesofurca/metafurca; lfu, lateral furcal arm; mr, median ridge; ph1/2/3, prophragma/mesophragma/metaphragma. For muscle terminology, see Tables 1 and 2

### Phylogenetically relevant characters

The polarity interpretations presented below should be regarded as preliminary as they are not based on a formal cladistic analysis. As the phylogenetic position of Scirtoidea within Polyphaga is not sufficiently clarified yet (see Lawrence and Newton 1995; Lawrence et al. 1995; Lawrence 1999, 2001), a broad spectrum of polyphagan taxa is included in the following considerations, especially representatives of Staphyliniformia and Elateriformia. Myxophaga, Adephaga and Archostemata are also taken into account, as a basal position of Polyphaga within Coleoptera and a basal position of Scirtoidea within Polyphaga are possible, as also one of the hypotheses to be tested in this study.

Scirtoidea is used in the sense of Nikitsky et al. (1994) and Elateriformia in the sense of Lawrence and Newton (1995) unless otherwise noted.

#### *Discriminal line of the mesoventrite: (0) present; (1) absent*

A mesothoracic discriminal line is absent in all species of Scirtoidea examined here (Fig. 23a–e) but is present in Decliniidae (Fig. 22f; *Declinia*; Lawrence et al. 1995) and few genera of Scirtidae (e.g. *Stenocyphon*, *Macrodascillus*, *Heterocyphon*; Lawrence 2001), in Eucinetidae (Leschen 2005a), and also in Buprestidae and Psephenidae (Kukulová-Peck and Lawrence 2004). As a discriminal line is also present in Cupedidae, Ommatidae (Archostemata; Baehr 1975; Beutel and Haas 2000) and Gyrininae (Adephaga; Larsén 1966; Beutel and Roughley 1988), this is perhaps a ground plan feature of Coleoptera (Lawrence 2001). The results of the cladistic analysis in Beutel and Haas (2000) suggest that the absence of a discriminal line is an autapomorphy of

Coleoptera excluding Archostemata. Considering the presence in adephagan and several polyphagan taxa, this interpretation appears unlikely. The loss of the discriminal line has apparently taken place several times independently [e.g. Micromaltidae, Myxophaga, Adephaga (*partim*), different lineages of Polyphaga].

#### *Transverse suture of mesoventrite: (0) present; (1) absent*

A katepisternum isolated from the anterior part of the mesoventrite by a transverse suture is absent in Scirtoidea (Fig. 23; *Declinia*; Lawrence et al. 1995), Myxophaga (Beutel 1999) and Adephaga (Beutel and Haas 2000) but present in Archostemata (Baehr 1975; Beutel and Haas 2000). Kukulová-Peck and Lawrence (2004) state the presence of a katepisternum in 'some basal Polyphaga (e.g. *Stenocyphon* and few other Scirtidae)', but this is not traceable in the detailed morphological description of *Stenocyphon* by Lawrence (2001) and was never explicitly described for any scirtid species so far. The absence of a distinct katepisternum was considered as an autapomorphy of Coleoptera excluding Archostemata by Beutel and Haas (2000).

#### *Intercoxal process: (0) present; (1) reduced or absent*

A broad intercoxal process separates the mesocoxal cavities in Eucinetidae (Figs 22e and 23e), Decliniidae (Fig. 22f; Lawrence et al. 1995) and members of most other elateriform families (e.g. Lampyridae; Geisthardt 1974; Dascillidae, Rhinorhipidae, Rhipiceridae; Lawrence 1988). The presence of a well-developed intercoxal process is likely a plesiomorphic character for Scirtoidea and possibly for Elateriformia. A highly reduced intercoxal process is a possible synapomorphy of Clambidae and Scirtidae.

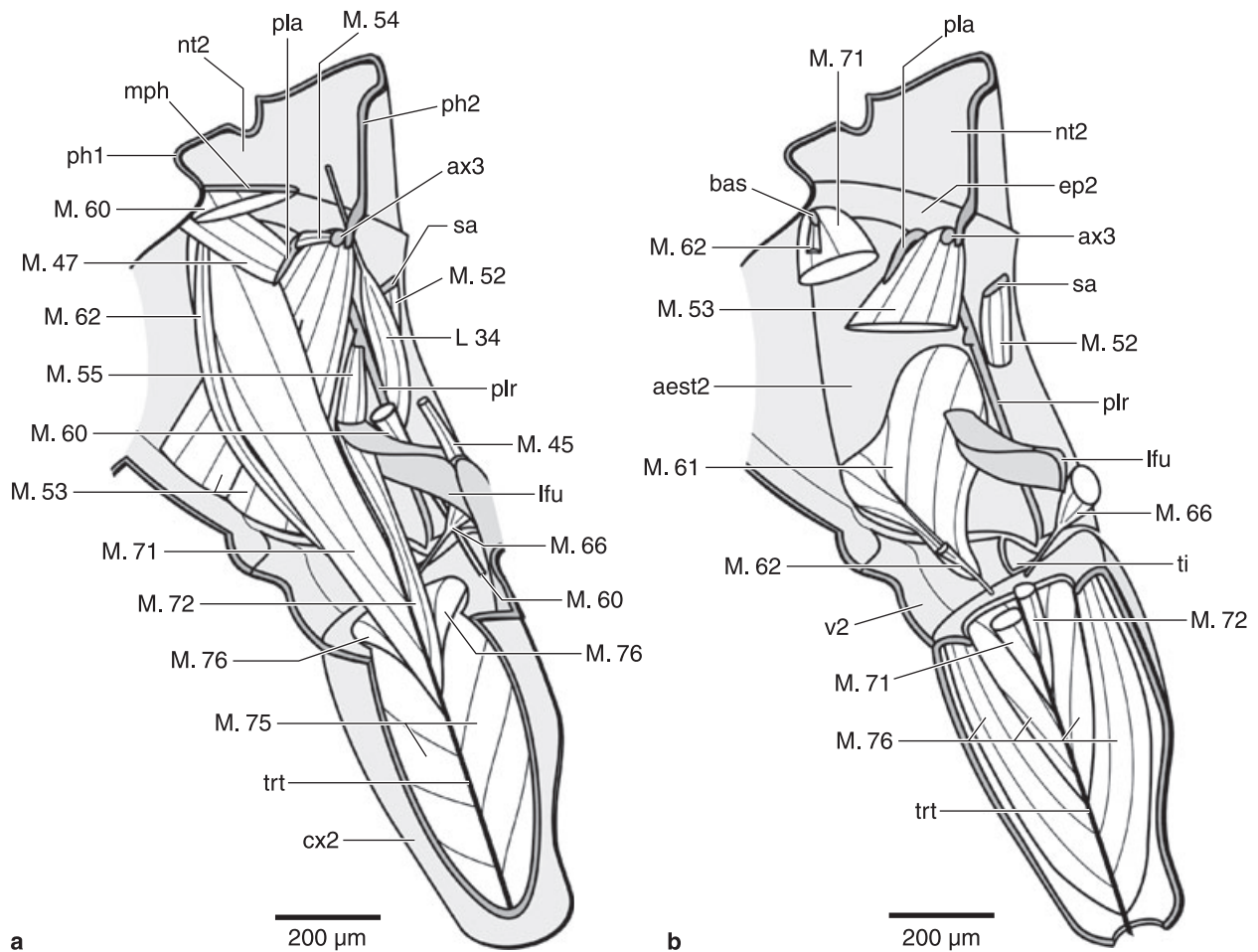


Fig. 18. Mesothorax, sagittal section, *Elodes pseudominuta* (reconstruction based on serial sections; ganglia and nerves removed; musculature white, skeletal parts grey). (a) Median layer of muscles removed. (b) Lateral muscles. Abbreviations: aest2, mesanepisternum; ax3, third axillary sclerite; bas, basalar; cx2, mesocoxa; ep2, mesepimeron; lfu, lateral furcal arm; mph, median phragma; nt2, mesonotum; ph1/2, prophragma/mesophragma; pla, pleural arm; plr, pleural ridge; sa, subalare; ti, trochantin; trt, trochanteral tendon; v2, mesoventrite. For muscle terminology, see Table 1

*Mesothoracic katepisternal joint: (0) present; (1) absent*

A katepisternal coxal joint with two separate apices is present in Archostemata (Cupedidae; Baehr 1975; Ommatidae; Beutel and Haas 2000) and adults of other endopterygote orders (e.g. Neuropterida; Ferris and Pennebaker 1939; Mecoptera; Mickoleit 1967). This type of coxal articulation is absent in all members of Scirtoidea examined (Fig. 23), in Myxophaga and in Adephaga (Beutel and Haas 2000). The intercoxal process with a deep median cleft in *Declinia* (Decliniidae; Fig. 22f; Lawrence et al. 1995) is not articulated with the mesocoxae as in Archostemata and is likely a secondary modification. In agreement with Beutel and Haas (2000), the loss of the mesothoracic katepisternal joint as a potential autapomorphy of Coleoptera excluding Archostemata is considered.

*Mesocoxae: (0) rounded; (1) moderately elongated (2) cone shaped, distinctly elongated*

The more or less globular mesocoxae of *Eucinetus* (Fig. 22e) and *Declinia* (Fig. 22f; Lawrence et al. 1995) are likely plesiomorphic within Scirtoidea, as a similar condition is found in most groups of Polyphaga, Adephaga and Myxophaga. A moderate elongation is probably a derived ground plan

feature of a clade comprising Scirtidae and Clambidae (Fig. 22a–d). The cone-shaped and distinctly elongated coxae of Scirtidae are very likely autapomorphic. Similar conditions have evolved independently in non-related taxa such as Leiodidae and Agyrtidae (Staphyliniformia; Beutel and Leschen 2005a).

*Mesothoracic meron: (0) present; (1) absent*

The mesocoxae of all examined scirtoid species (except *Calyptomerus*) show a distinct suture, which connects the trochanteral joint and the anterolateral edge of the mesocoxae (Fig. 22). As the mesal tergocoxal muscle ('innerer tergocoxaler Muskel'; Larsén 1945a) is always absent in Coleoptera (Beutel and Haas 2000) and *M. coxa-subalaris* (*M. 64*) ('coxosubalarer Muskel'; Larsén 1945a) is lacking in Scirtoidea as in all other polyphagans (Larsén 1966; Beutel and Haas 2000; Beutel and Komarek 2004), the lateral part of the mesocoxae is not considered as a true meron (Kristensen 1981). The loss or change of function of the primarily meron-associated muscles, respectively, is typical for Coleoptera (Larsén 1945b) and an autapomorphic character of this taxon (Beutel and Haas 2000).





Fig. 20. Lateral musculature of the metathorax of *Elodes pseudominuta* (associated with wing movements). (a) Lateral view (position of following cross sections marked). Histological cross sections: (b) Sector used in c–g. (c) Posterior rim of basalar muscle disc. (d) Middle of basalar muscle disc. (e) Transition between muscle disc and basalar stem. (f) Anterior end of pleura-prealar muscles. (g) Prealar sclerite. Abbreviations: amd, axillary muscle disc; mbas, muscle disc of basalare; ph2, mesophragma; plr, pleural ridge; prsc, prealar sclerite. For muscle terminology, see Table 2

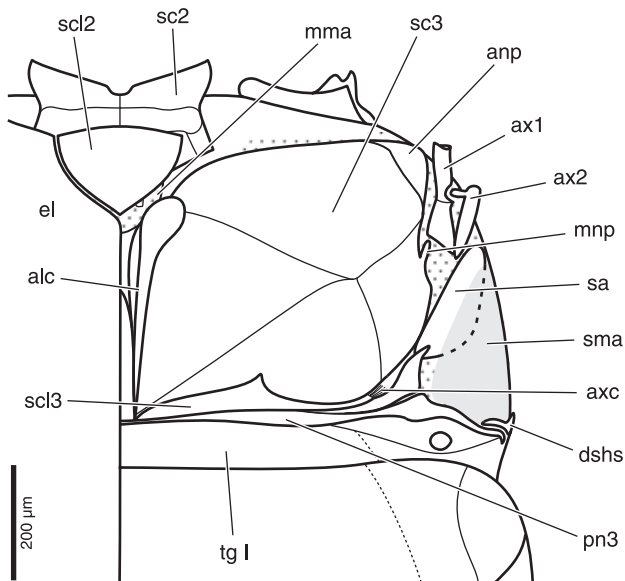
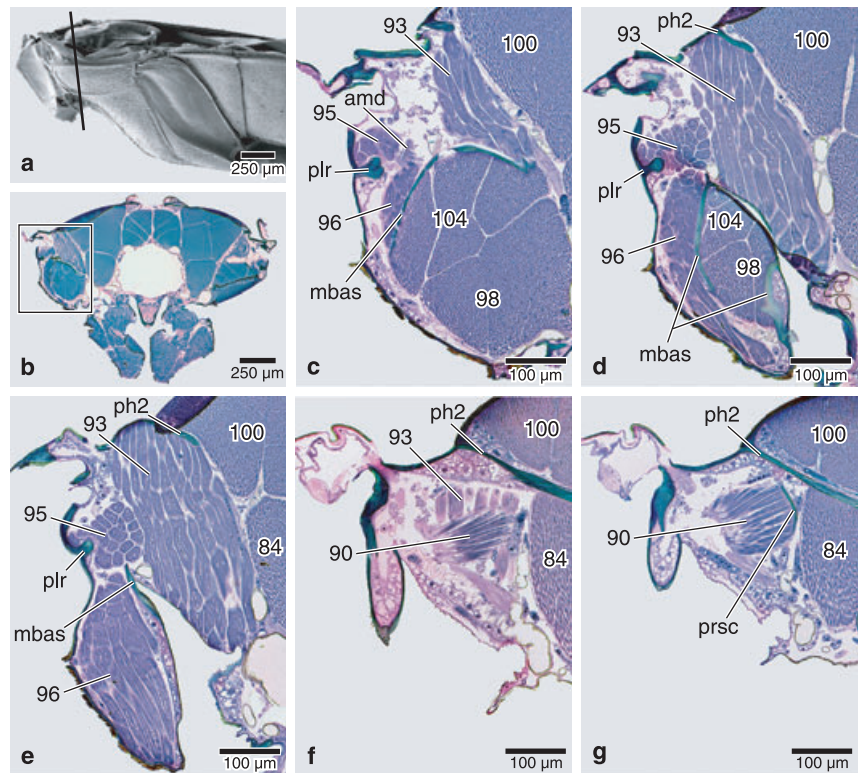


Fig. 21. Dorsal view of pterothorax, *Cyphon coarctatus* (right elytron and wing removed; semimembranous areas grey, membranous parts punctured). Abbreviations: alc, alacrista; anp, anterior notal process; ax 1/2, first, second axillary sclerite; axc, axillary cord; dshs, dome-shaped sclerite; el, elytron; mma, median membranous area; mnp, median notal process; pn3, metapostnotum; sa, subalare; sc2/3, mesoscutum/metascutum; scl2/3, mesoscutellum/metascutellum; sma, semimembranous area; tg I, first abdominal tergite

(partim); Crowson 1944; Geisthardt 1974; Lawrence 1988; Beutel and Komarek 2004] in different groups of Adephaga (e.g. Beutel 1986, 1992; Belkaceme 1991), in Lepiceridae (Myxophaga; Beutel 1999) and in Archostemata (Baehr 1975).

**Katepisternum 3 and transverse suture:** (0) present; (1) absent  
A metathoracic katepisternum with a narrow median triangular part as it is present in Scirtidae and Eucinetidae (Figs 22a–c, e and 23a–e) is a potential synapomorphy of these families. A more or less narrow lateral portion of the katepisternum is present (Fig. 22a, b) or absent (Fig. 22c, e). A broad katepisternum with a laterally obliterating transverse suture is present in Decliniidae (Lawrence et al. 1995). This may represent the plesiomorphic condition within Scirtoidea. The complete fusion of the katepisternum 3 with the metaventrite and the coxal plates in *Calyptromerus* (Figs 22d and 23f) is a potential autapomorphy of Clambidae (Leschen 2005b) and possibly correlated with miniaturization. A similar condition has evolved in Myxophaga (except Lepiceridae; Beutel 1999), which is also characterized by small body size. A distinct transverse suture is present in several groups of Elateriformia (Dascilloidea, Buprestoidea; Crowson 1944; Lawrence and Newton 1982), in most Adephaga and Archostemata (Baehr 1975; Lawrence 1982; Beutel 1988, 1997) and also in other endopterygote lineages (e.g. Sialidae; Beutel 1999).

**Metathoracic trochantin:** (0) exposed; (1) internalized or absent

A broad, exposed metathoracic trochantin is usually present in Archostemata (Cupedidae; Baehr 1975; Ommatidae; Beutel and Haas 2000) and also in Neuropterida (Ferris and Pennebaker 1939; Ferris 1940; Acker 1958; Matsuda 1970). It is internalized absent in Scirtoidea and all other groups of Polyphaga, in Myxophaga and Adephaga (Beutel 1999; Beutel and Haas 2000). The loss is likely an autapomorphy of Coleoptera excl. Archostemata (Beutel and Haas 2000).

**Metacoxal meron:** (0) present; (1) absent

A distinct meron is present in all examined scirtoid species (Fig. 22). The associated M. coxa-basalaris (M. 104;



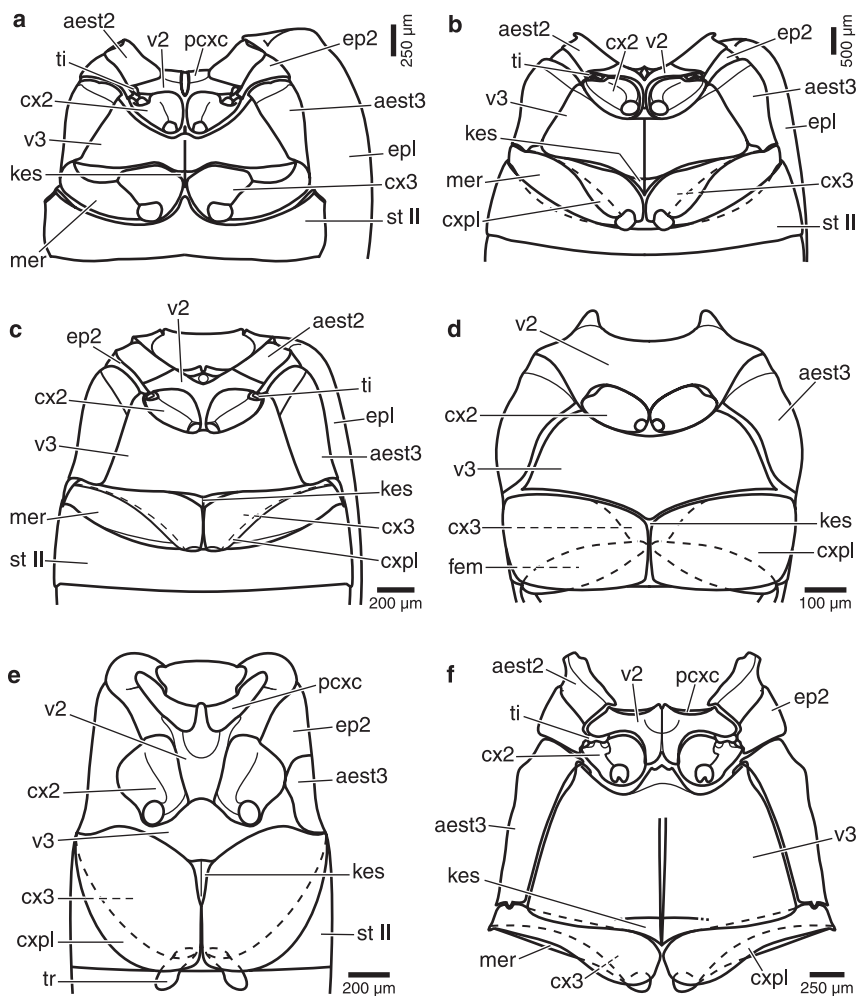


Fig. 22. Ventral view of pterothorax and anterior abdominal segments. Scirtidae: (a) *Ora* sp. (b) *Pseudomicrocara* sp. (c) *Cyphon coarctatus*. (d) *Calyptomerus dubius* (Clambidae). (e) *Eucinetus* sp. (Eucinetidae). (f) *Declinia relicta* (Decliniidae; redrawn from Lawrence et al. 1995). Abbreviations: aest2/3, mesanepisternum/metanepisternum; cx2/3, mesocoxa/metacoxa; cxpl, coxal plate; ep2, mesepimeron; epl, epipleuron; fem, femur; kes, katepisternum; mer, metacoxal meron; pcxc, procoxal cavity; st II, second abdominal sternite; ti, trochantin; tr, trochanter; v2/3, mesoventrite/meta-ventrite

'coxosubalarer Muskel' in Larsén 1945a) and *M. notocoxalis anterior* (*M.* 101; 'innerer tergocoxaler Muskel' in Larsén 1945a) are well developed. The enlargement of the meron in Scirtidae is perhaps autapomorphic for the family. The erroneously postulated absence of the metathoracic meron in Coleoptera (Beutel and Haas 2000; character 70) is revised here. A meron and associated muscles are present in most members of Polyphaga (Larsén 1966; Beutel and Komarek 2004), Myxophaga (Beutel and Haas 2000), Archostemata (Baehr 1975) and Neuropterida (Maki 1936; Czihak 1953, 1957; Mickoleit 1965; Beutel and Haas 2000).

*Metacoxal plates: (0) present; (1) absent*

The more or less strongly enlarged metacoxal plates of Scirtoidea (Fig. 22b–f; Lawrence et al. 1995; Lawrence 2001) are a ground plan feature of this taxon (Beutel and Leschen 2005a). The complete reduction of these coxal duplicatures in *Scirtes* and *Ora* (Fig. 22a) are likely correlated with the jumping capacity and are clearly apomorphic within Scirtidae. Lawrence (1988) considered this kind of locomotion and the weak sclerotization of the beetles as the main reasons for the loss of coxal plates in several elateriform taxa. Coxal plates are present in many polyphagan groups (e.g. Derodontidae, Dascillidae, Ptiliidae; Hansen 1997; Beutel and Leschen 2005a), in Myxophaga (e.g. Torridincolidae; Beutel 1999; Microsporidae; Hansen 1997) and in Adephaga (e.g.

Amphizoidae, Haliplidae, Trachypachidae, Carabidae; Belkaceme 1986; Beutel 1997). Contrary to a statement of Hansen (1997), Archostemata lack coxal plates (Baehr 1975; Beutel 1997; Beutel pers. obs.: *Tetraphalerus*). A reliable phylogenetic interpretation of this character in a broader taxonomic context has to be based on a comprehensive cladistic analysis. A multiple, independent reduction of the plates within Polyphaga is likely, and parallel re-acquisition in different groups is also possible.

*Position of the fulcrum: (0) beneath second axillary; (1) beneath first axillary*

The fulcrum lies beneath the axillary 1 in Polyphaga including Scirtoidea (Fig. 9a), in Myxophaga and in Adephaga (Hörschemeyer 1998). It is located below the axillary 2 in Archostemata, Mecoptera and Plecoptera and between the first and second axillary in Sialidae, Corydalidae and Raphidiidae (Hörschemeyer 1998).

*Angle  $\alpha$  between first axillary and notum: (0)  $> 50^\circ$ ; (1)  $\leq 50^\circ$*

An angle  $\alpha$  of c.  $40^\circ$  is present in *Elodes* (Fig. 13a). Less than  $50^\circ$  is a synapomorphic feature of Polyphaga and Myxophaga according to Hörschemeyer (1998). The angle is more or less obtuse (wider than  $50^\circ$ ) in Archostemata, Adephaga and Neuropterida (Hörschemeyer 1998).

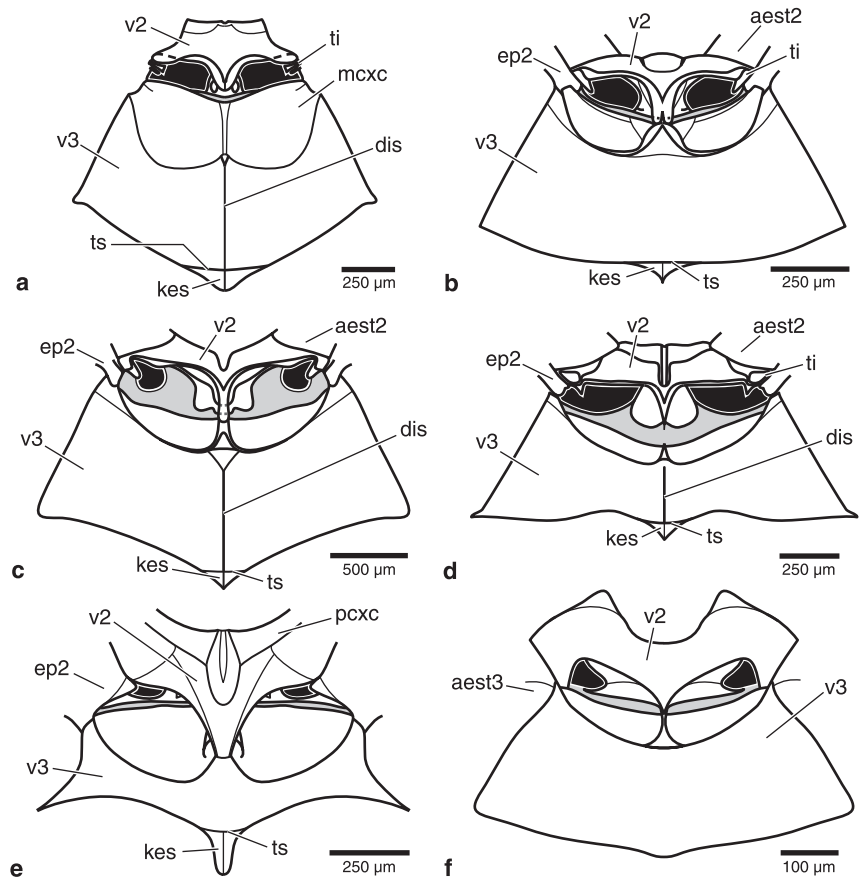


Fig. 23. Ventral view of the connection between the mesoventrite and metaventrite (mesocoxae removed from cavities; membranous areas grey). Scirtidae: (a) *Elodes pseudominuta*. (b) *Cyphon coarctatus*. (c) *Pseudomicrocara* sp. (d) *Ora* sp. (e) *Eucinetus* sp. (Eucinetidae). (f) *Calyptomerus dubius* (Clambidae). Abbreviations: aest2/3, mesanepisternum/metanepisternum; dis, discriminial line; ep2, mesepimeron; kes, katapisternum; mcxc, metacoxal cavity; ti, trochantin; ts, transverse suture; v2/3, mesoventrite/metaventrite

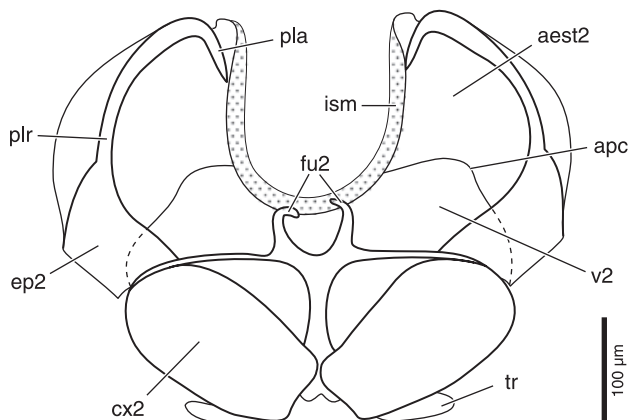


Fig. 24. Posterior view of ventral mesothorax, *Eucinetus* sp. (mesonotum removed; membranous parts punctured). Abbreviations: aest2, mesanepisternum; apc, anapleural cleft; cx2, mesocoxa; ep2, mesepimeron; fu2, mesofurca; ism, intersegmental membrane; pla, pleural arm; plr, pleural ridge; tr, trochanter; v2, mesoventrite

*Shape of the posterior notal process:* (0) long and/or apically broadened; (1) short, apically narrowed

A short posterior notal process is present in Myxophaga and most polyphagan taxa. This character state is an uncertain potential synapomorphy of these taxa according to Hörnschemeyer (1998). An apically narrowed posterior notal process as it is present in *Elodes* (Figs 9 and 12b) is a derived condition within Polyphaga (Hörnschemeyer 1998).

*Caudal arm of the third axillary:* (0) absent; (1) short; (2) moderately sized; (3) elongated

The caudal arm is elongated in *Elodes* (Figs 9a, 10c and 13c) and in most other polyphagan taxa (except for Helophoridae, Hydrophilidae, Scarabaeidae, Buprestidae, Lampyridae and others; Hörnschemeyer 1998). The elongation of the caudal arm was interpreted as an autapomorphy of Polyphaga (Hörnschemeyer 1998). This implies secondary shortening in several lineages. The caudal arm is absent in Neuropterida (except for Raphidiidae) and Myxophaga (Hörnschemeyer 1998).

*Radial cell:* (0) rounded; (1) triangular; (2) absent

The radial cell of Elateriformia is triangular (Lawrence 1988; Kukalová-Peck and Lawrence 1993) and is a possible autapomorphy of this group. It is rounded or absent in other polyphagan groups (e.g. Staphylinidae, Scarabaeoidea; Kukalová-Peck and Lawrence 1993). Within Scirtoidea, the typical triangular shape is found in Decliniidae (Fig. 25f; Lawrence et al. 1995) and Eucinetidae (Fig. 25e). The condition is less distinct in the modified wing of Clambidae (Fig. 25d; Kukalová-Peck and Lawrence 1993). The more or less rounded radial cell in Scirtidae (e.g. *Elodes*: Fig. 25a) is possibly autapomorphic.

*Apically directed branches of radius posterior:* (0) present; (1) strongly reduced or absent

The apically directed branches of RP are absent or strongly reduced in Scirtoidea (Fig. 25) and most other elateriform beetles but present in Staphylinidae, Scarabaeoidea,

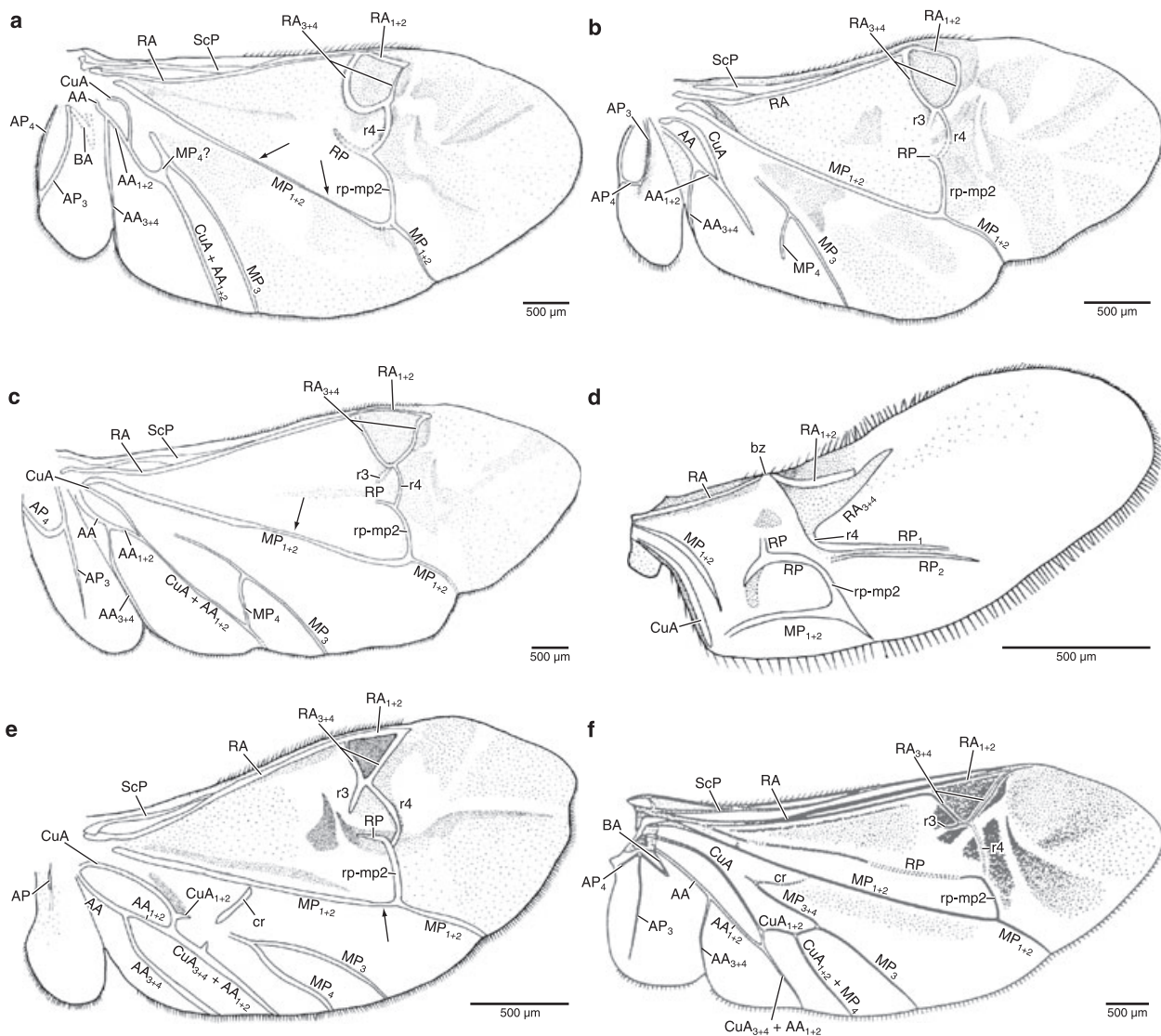


Fig. 25. Venation and pigmentation of the wing of scirtoid beetles (terminology following Kukulová-Peck and Lawrence 1993). (a–c) Scirtidae: (a) *Elodes pseudominuta*. (b) *Cyphon coarctatus*. (c) *Pseudomicrocara* sp. (d) *Calyptomerus dubius* (Clambidae). (e) *Eucinetus* sp. (Eucinetidae). (f) *Declinia relicta* (Decliniidae; modified after Lawrence et al. 1995). Abbreviations: AA, anterior anal vein; AP, posterior anal vein; BA, basiventral anal vein; bz, bending zone; cr, cross-vein; CuA, anterior cubital vein; CuA + AA<sub>1+2</sub>, fusion of CuA and AA<sub>1+2</sub>; MP, posterior medial vein; r3/4, third/fourth radial cross-vein; RA, anterior radial vein; RP, posterior radial vein; rp-mp2, second radio-medial cross-vein; ScP, posterior subcostal vein. The venal branches are indicated by subscript numbers. The arrows refer to the weakness of the medial bar (MP<sub>1+2</sub>)

Myxophaga, Adephaga and Archostemata (Kukulová-Peck and Lawrence 1993; Hansen 1997).

*Radial cross-vein 3:* (0) distinctly present; (1) obsolete or absent

In Eucinetidae (Fig. 25e), Decliniidae (Fig. 25f; Lawrence et al. 1995), Scirtidae (Fig. 25a–c) and all representatives of other elateriform groups examined by Kukulová-Peck and Lawrence (1993), a similarly shaped, distinct third radial cross-vein (r3) is present. The reduction of r3 has almost certainly taken place independently in several coleopteran lineages [e.g. Histeroidea, Scaraboidea, Adephaga (*partim*); see Kukulová-Peck and Lawrence 1993].

*Medial spur:* (0) bent anteriorly; (1) bent posteriorly

The medial spur (distal part of MP<sub>1+2</sub>) is bent anteriorly in Archostemata, Adephaga and Myxophaga (Haas 1998; Beutel

and Haas 2000). A posteriorly directed medial spur is an autapomorphic feature of Polyphaga (Fig. 25; Haas 1998; Beutel and Haas 2000).

*Bending zone of the medial bar:* (0) present; (1) absent

A bending zone in the medial bar ('Biegungszone', Schneider 1978; weakness, Kukulová-Peck and Lawrence 1993; medial hinge, Hansen 1997) is present in Scirtidae and Eucinetidae (Fig. 25a–c,e) but absent in all other polyphagans examined (e.g. Kukulová-Peck and Lawrence 1993). The interpretation of the bending zone as an autapomorphy of Polyphaga (Hansen 1997) is not conclusive. A medial hinge is also present in representatives of Adephaga and Myxophaga (Kukulová-Peck and Lawrence 1993).

Table 3. Mesothoracic muscles occurring in the examined scirtoid taxa (bold letters), representatives of other coleopteran lineages and neuropterid species (partly based on Beutel and Haas 2000 and Beutel and Komarek 2004)

Taxon	Muscle																				
	39	40	42	43	44	45	46	47	50	51	52	L 34	53	54	55	58	59	60	61	62	64
Mymeleon	x	x	x	–	x	x	x	x	x	–	x	–	x	x	–	x	x	x	x	x	x
Sialis	x	x	x	x	x	x	x	x	x	x	x	–	x	x	x	–	x	x	x	x	x
Corydalus	x	x	x	x	x	x	x	x	x	–	x	–	x	x	x	–	x	x	x	x	x
Chauliodes	x	x	x	–	x	x	x	x	x	–	x	–	x	x	x	–	x	x	x	x	x
Priacma	x	x	x	x	x	x	x	x	x	x	–	–	x	x	x	–	x	x	x	x	x
Hydroscapha	x	–	x	–	–	x	–	–	–	–	x	–	a	b	x	x	–	x	x	–	x
Microspor	x	–	x	–	–	–	–	–	?	–	–	?	?	?	x	x	–	x	x	–	x
Gyrinus	x	–	x	x	–	–	–	–	x	–	–	–	a	b	–	x	–	x	x	–	x
Haliplus	x	x	x	–	–	–	–	–	x	–	–	–	a	b	–	–	x	x	x	x	x
Noterus	x	x	x	–	–	–	–	x	–	–	–	–	a	b	–	–	x	x	x	–	x
Hygrobia	x	–	x	–	–	x	–	x	–	–	–	–	a	b	–	–	x	x	x	–	x
Dytiscus	x	–	x	x	–	x	–	x	–	–	–	–	a	b	x	–	x	x	x	–	x
Carabus	x	–	x	x	–	–	–	–	–	–	–	–	a	b	x	x	x	x	x	–	x
Elaphrus	x	x	x	x	–	–	–	x	–	–	–	–	a	b	–	x	x	x	x	–	x
Pterostichus	x	–	x	x	–	–	–	x	–	–	–	–	a	b	–	x	x	x	x	–	x
Ochthebius	x	–	x	x	–	–	–	?	x	–	–	?	–	?	?	–	–	?	x	–	–
Sphaeridium	x	x	x	–	–	–	–	x	–	–	x	–	a	b	–	–	–	x	x	x	–
Hydrophilus	x	x	x	–	–	x	–	x	–	–	x	–	a	b	–	–	–	x	x	x	–
Helophorus	x	x	x	–	–	–	–	x	–	–	–	–	a	b	x	–	–	x	x	x	–
Margarinotus	x	x	x	–	–	x	–	x	–	–	?	–	a	b	x	–	–	x	x	x	–
Nicrophorus	x	x	x	–	–	–	–	x	–	–	–	–	a	b	x	–	–	x	x	x	–
Creophilus	x	x	x	–	–	x	–	x	–	–	x	–	a	b	–	–	–	x	x	–	–
Aphodius	x	x	x	–	–	x	–	x	–	–	x	x	a	b	x	–	–	x	x	x	–
Cetonia	x	x	x	–	–	x	–	x	–	–	x	–	a	b	–	–	–	x	x	x	–
Selatosomus	x	x	x	–	–	x	–	x	–	–	x	–	a	b	x	–	–	x	x	x	–
Cantharis	x	x	x	–	–	x	–	x	–	–	x	–	a	b	–	–	–	x	x	–	–
Lytta	x	x	x	x	–	–	–	x	–	–	x	–	a	b	x	–	–	x	x	x	–
Coccinella	x	x	x	–	–	–	–	x	–	–	x	–	a	b	x	–	–	x	x	x	–
Tenebrio	x	x	x	–	–	–	–	x	–	–	x	–	a	b	x	–	–	x	x	x	–
Cassida	x	x	x	–	–	–	–	x	–	–	x	–	a	b	x	–	–	x	x	x	–
Donacia	x	x	x	–	–	–	–	x	–	–	x	–	a	b	x	–	–	x	x	x	–
<b>Eucinetus</b>	<b>x</b>	<b>x</b>	<b>?</b>	–	–	–	–	<b>x</b>	–	–	<b>x</b>	–	<b>a</b>	<b>b</b>	–	–	–	<b>x</b>	<b>x</b>	<b>x</b>	–
<b>Calyptomerus</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	–	–	<b>x</b>	–	–	<b>x</b>	<b>?</b>	<b>a</b>	<b>b</b>	–	–	–	<b>x</b>	<b>x</b>	<b>?</b>	–
<b>Elodes</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	<b>x</b>	–	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>a</b>	<b>b</b>	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>x</b>	–
<b>Cyphon</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	<b>x</b>	–	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>a</b>	<b>b</b>	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>x</b>	–
<b>Ora</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	<b>x</b>	–	<b>x</b>	–	–	<b>?</b>	<b>?</b>	<b>a</b>	<b>b</b>	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>?</b>	–

Taxon	Muscle											
	65	66	67	69	70	71	72	73	74	75	76	
Mymeleon	x	x	x	x	x	x	x	?	?	x	x	
Sialis	x	–	x	x	x	x	x	?	?	x	x	
Corydalus	x	x	x	x	x	x	x	?	?	x	x	
Chauliodes	x	x	x	x	x	x	x	?	?	x	x	
Priacma	x	x	x	x	x	x	x	–	–	x	x	
Hydroscapha	x	x	x	x	x	–	x	–	–	x	x	
Microspor	x	–	x	–	x	–	x	–	–	x	x	
Gyrinus	–	–	x	x	x	–	x	–	x	x	x	
Haliplus	x	–	x	x	x	–	x	–	–	x	x	
Noterus	x	x	x	x	x	–	x	–	–	x	x	
Hygrobia	x	x	x	x	x	–	x	–	–	x	x	
Dytiscus	x	x	x	x	x	–	x	–	–	x	x	
Carabus	x	–	x	x	x	–	x	–	–	x	x	
Elaphrus	x	–	x	x	x	–	x	–	–	x	x	
Pterostichus	x	–	x	x	x	–	x	–	–	x	x	
Ochthebius	?	–	x	–	x	–	–	–	–	x	x	
Sphaeridium	x	–	x	–	x	–	x	–	–	x	x	
Hydrophilus	x	–	x	–	–	–	x	–	–	x	x	
Helophorus	x	–?	x	–	x	–	–	–	–	x	x	
Margarinotus	x	–	x	–	?	–	x	–	–	x	x	
Nicrophorus	x	–	x	–	x	–	x	–	–	x	x	
Creophilus	x	–	x	–	x	–	–	–	–	x	x	
Aphodius	x	–	x	–	–	x	x	–	–	x	x	
Cetonia	x	–	x	–	–	–	–	x	–	x	x	
Selatosomus	x	–	x	–	x	–	x	–	–	x	x	



Table 3. (Continued)

Taxon	Muscle											
	65	66	67	69	70	71	72	73	74	75	76	
Cantharis	x	x	x	–	x	–	x	–	–	x	x	
Lytta	x	x	x	–	x	–	x	–	–	x	x	
Coccinella	–	x	x	–	x	–	x	–	–	x	x	
Tenebrio	x	–	x	–	x	–	x	–	–	x	x	
Cassida	x	–	x	–	x	–	x	–	–	x	x	
Donacia	x	–	x	–	x	–	x	–	–	x	x	
<b>Eucinetus</b>	?	–	–	–	–	x	–	–	–	x	x	
<b>Calyptomerus</b>	x	–	x	–	–	x	x	–	–	x	x	
<b>Elodes</b>	x	x	x	–	–	x	x	–	–	x	x	
<b>Cyphon</b>	x	x	x	–	–	x	x	–	–	x	x	
<b>Ora</b>	x	x	x	–	–	x	x	–	–	x	x	

a, first part of the muscle; b, second part of the muscle; x, present; –, absent; ?, state unknown.

*Anal field: (0) moderately sized; (1) enlarged; (2) largely reduced or absent*

A distinctly enlarged anal field occurs only in Scirtoidea (Fig. 25a–c,e) and is a potential autapomorphy of the superfamily. This implies secondary reduction in Clambidae, which may be a result of miniaturization (Fig. 25d; Kukulová-Peck and Lawrence 1993). The anal field is moderately sized in representatives of other polyphagan lineages (e.g. Staphyliniformia, Elateriformia; Kukulová-Peck and Lawrence 1993).

*Incision between anal field and medial field: (0) indistinct; (1) moderately deep; (2) very deep*

A very deep incision is present in Scirtidae, Eucinetidae and several species of Scarabaeoidea and Histeroidea (Fig. 25a–c,e; Kukulová-Peck and Lawrence 1993; Lawrence et al. 1995). This is a potential autapomorphy of Scirtoidea excl. Decliniidae. The incision is moderately deep in Decliniidae (Fig. 25f) and absent or obsolete in Clambidae, apparently as a result of the reduction of the anal field (see character 25; Fig. 25d). A distinct cleft or incision between the anal field and the medial field is absent in Archostemata, most groups of Adephaga, Myxophaga, Scarabaeoidea, some Staphyliniformia (e.g. Hydrophilidae) and the large majority of Elateriformia (excl. Scirtoidea).

*Mm. noto-sternales (M. 44): (0) present; (1) absent*

Mm. noto-sternales are present in Archostemata (*Priacma*; Baehr 1975) and Neuropterida (e.g. Ferris and Pennebaker 1939; Czihak 1953, 1957; Matsuda 1970). The absence of these muscles in all other examined beetles (including Scirtoidea) is a potential synapomorphy of the non-archostematan suborders (Larsén 1966; Beutel 1986; Belkaceme 1991; Beutel and Haas 2000; Beutel and Komarek 2004).

*M. noto-pleurocostalis (M. 46): (0) present; (1) absent*

M. noto-pleurocostalis is present in Neuropterida (Ferris and Pennebaker 1939; Korn 1943; Czihak 1953, 1957; Matsuda 1970) and Archostemata (*Priacma*; Baehr 1975). The muscle is absent in Adephaga, Myxophaga and Polyphaga (incl. Scirtoidea) and an apomorphy of Coleoptera excl. Archostemata (Larsén 1966; Beutel 1986; Belkaceme 1991; Beutel and Haas 2000; Beutel and Komarek 2004).

*M. episterno-sternalis (M. 50): (0) present; (1) absent*

M. episterno-sternalis occurs in Neuropterida (e.g. Ferris and Pennebaker 1939; Korn 1943) and Archostemata (*Priacma*; Baehr 1975). The absence in Scirtoidea and all other non-archostematan beetles is a potential synapomorphy of Adephaga, Myxophaga and Polyphaga (Larsén 1966; Beutel 1986; Belkaceme 1991; Beutel and Haas 2000; Beutel and Komarek 2004).

*M. noto-epimeralis (L 34): (0) present; (1) absent*

Larsén (1966) recorded M. noto-epimeralis (as M34) for *Aphodius* (Scarabaeidae) and *Trox* (Trogidae). It is absent in other polyphagans and in Myxophaga, Adephaga, Archostemata and Neuropterida (Czihak 1953, 1957; Larsén 1966; Matsuda 1970; Baehr 1975; Beutel and Haas 2000). Beutel and Haas (2000) interpreted this muscle as a second branch of M. epimero-subalaris (M. 52; M35 of Larsén 1966), which is present in most coleopterans examined (except Adephaga; Larsén 1966; Baehr 1975; Beutel and Haas 2000; Beutel and Komarek 2004). In all scirtids dissected during this study, two completely separate muscles are present (L 34, partly very thin; Fig. 18; Table 3). Therefore, homologization of M. 52 (Beutel and Haas 2000) with M35 of Larsén (1966) is proposed. Larsén's M34 is probably a derivative of M. epimero-subalaris but should be considered as a discrete muscle (present study: L 34). For a phylogenetic interpretation, the presence or absence in more taxa has to be clarified (e.g. Decliniidae, Derodontidae, Dascillidae).

*Mm. pleura-alaris a and b (M. 53, M. 54): (0) clearly separated; (1) single muscle or two branches with a common insertion*

Two muscles with separate origins and insertions are present in Neuropterida (Maki 1936; Korn 1943; Czihak 1953, 1957; Beutel and Haas 2000) and in Archostemata (*Priacma*; Baehr 1975). Only one branch is developed in all non-archostematan beetles (e.g. Beutel and Haas 2000) or both branches insert together on the third axillary (e.g. Scirtoidea; Fig. 18a).

*M. pleura-alaris a (M. 53): (0) moderately sized; (1) enlarged*

A strongly enlarged M. pleura-alaris a is present in all scirtoids examined in this study (Fig. 18). A comparatively large M. 53 is even found in the poorly developed mesothoracic

Table 4. Metathoracic muscles occurring in the examined scirtoid taxa (bold letters), representatives of other coleopteran lineages and neuropterid species (partly based on Beutel and Haas 2000 and Beutel and Komarek 2004)

Taxon	Muscle																		
	79	80	82	83	84	85	86	80	90	91	92	93	94	95	96	97	98	100	101
<i>Mymeleon</i>	x	x	–	–	x	x	x	x	x	–	x	x	x	x	x	–	x	x	x
<i>Sialis</i>	x	x	x	x	x	x	–	x	x	x	x	x	x	x	x	x	x	x	x
<i>Corydalus</i>	x	x	x	x	x	x	–	x	x	x	x	x	x	x	x	x	x	x	x
<i>Chauliodes</i>	x	x	x	–	x	x	–	x	x	x	x	x	x	x	x	x	x	x	x
<i>Priacma</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Hydroscapha</i>	x	x	–	–	x	x	x	x	x	–	–	x	–	a	b	x	x	–	x
<i>Microsporus</i>	x	x	–	–	x	x	x	x	x	–	–	x	x	a	b	x	x	–	–
<i>Gyrinus</i>	–	–	x	–	–	–	–	–	x	–	–	x	x	a	b	–	–	–	–
<i>Haliphus</i>	x	x	x	x	x	–	–	x	x	–	–	x	x	a	b	x	x	–	x
<i>Noterus</i>	x	x	x	–	x	x	–	x	x	–	–	x	–	a	b	x	x	–	x
<i>Hygrobia</i>	x	x	x	–	x	x	–	x	x	–	–	x	x	a	b	–	x	–	x
<i>Dytiscus</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	–	x
<i>Carabus</i>	–	–	x	x	–	–	–	–	x	–	–	x	x	a	b	–	–	–	–
<i>Elaphrus</i>	x	x	x	x	x	x	–	x	x	–	–	x	x	a	b	–	x	–	x
<i>Pterostichus</i>	x	x	x	x	x	x	–	x	x	–	–	x	x	a	b	–	x	–	x
<i>Ochthebius</i>	x	x	x?	–?	x	x	x	x	x	–	–	x	x?	a	b	x	x	–	x
<i>Sphaeridium</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	–	x
<i>Hydrophilus</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	–	x
<i>Helophorus</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	–	x
<i>Margarinotus</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	–	x	x	–
<i>Nicrophorus</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	x	x
<i>Creophilus</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	x	x
<i>Aphodius</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	x	x
<i>Cetonia</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	–	x	–	x
<i>Selatosomus</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	x	x
<i>Cantharis</i>	x	x	–	–	x	x	–	x	x	–	–	x	–	a	b	x	x	x	x
<i>Lytta</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	x	x
<i>Coccinella</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	x	x	x	–
<i>Tenebrio</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	–	x	x	x
<i>Cassida</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	–	x	x	–
<i>Donacia</i>	x	x	x	–	x	x	x	x	x	–	–	x	x	a	b	–	x	x	–
<b><i>Eucinetus</i></b>	<b>x</b>	<b>x</b>	<b>x</b>	–	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>a</b>	<b>b</b>	–	<b>x</b>	<b>x</b>	<b>x</b>
<b><i>Calyptomerus</i></b>	<b>x</b>	<b>x</b>	<b>x</b>	–	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>a</b>	<b>b</b>	–	<b>x</b>	<b>x</b>	<b>x</b>
<b><i>Elodes</i></b>	<b>x</b>	<b>x</b>	<b>x</b>	–	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>a</b>	<b>b</b>	–	<b>x</b>	<b>x</b>	<b>x</b>
<b><i>Cyphon</i></b>	<b>x</b>	<b>x</b>	<b>x</b>	–	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>a</b>	<b>b</b>	–	<b>x</b>	<b>x</b>	<b>x</b>
<b><i>Ora</i></b>	<b>x</b>	<b>x</b>	<b>x</b>	–	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	<b>x</b>	–	–	<b>x</b>	<b>x</b>	<b>a</b>	<b>b</b>	–	<b>x</b>	<b>x</b>	<b>x</b>

Taxon	Muscle													
	102	103	104	105	106	107	108	109	111	112	113	114	115	
<i>Mymeleon</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Sialis</i>	x	x	x	x	x	x	–	x	x	x	x	x	x	
<i>Corydalus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Chauliodes</i>	x	x	x	x	x	–	x	x	x	x	x	x	x	
<i>Priacma</i>	x	x	x	x	–	x	x	x	x	x	x	x	x	
<i>Hydroscapha</i>	–	x	x	x	–	?	–	x	–	–	x	x	x	
<i>Microsporus</i>	–	x	x	x	–	?	–	x	–	–	x	x	x	
<i>Gyrinus</i>	x	–	x	–	–	–	–	x	x	–	x	x	x	
<i>Haliphus</i>	x	–	–	x	–	x	x	x	–	–	x	x	x	
<i>Noterus</i>	x	–	–	x	–	–	–	–	–	–	x	x	x	
<i>Hygrobia</i>	x	–	–	x	–	–	x	–	–	–	x	x	x	
<i>Dytiscus</i>	x	–	x	x	–	–	x	–	–	–	x	x	x	
<i>Carabus</i>	x	–	–	–	–	x	x	x	–	–	x	x	x	
<i>Elaphrus</i>	x	–	x	x	–	x	x	x	–	–	x	x	x	
<i>Pterostichus</i>	x	–	x	x	–	x	x	x	–	–	x	x	x	
<i>Ochthebius</i>	x	x	?	x	–	x	x	x	x	–	x	x	x	
<i>Sphaeridium</i>	x	x	x	x	–	x	x	x	x	–	x	x	x	
<i>Hydrophilus</i>	x	x	–	x	–	x	x	x	–	–	x	x	x	
<i>Helophorus</i>	x	x	x	x	–	x	x	x	x	–	x	x	x	
<i>Margarinotus</i>	x	x	–	x	–	x	–?	x	–	–	x	x	x	
<i>Nicrophorus</i>	x	x	x	x	–	x	x	x	–	–	x	x	x	
<i>Creophilus</i>	x	x	–	x	–	x	x	x	–	–	x	x	x	
<i>Aphodius</i>	x	x	x	x	–	x	x	x	–	–	x	x	x	
<i>Cetonia</i>	x	x	–	x	–	x	x	x	–	–	x	x	x	
<i>Selatosomus</i>	x	x	x	x	–	x	x	x	–	–	x	x	x	

Table 4. (Continued)

Taxon	Muscle												
	102	103	104	105	106	107	108	109	111	112	113	114	115
<i>Cantharis</i>	x	x	x	x	–	x	x	x	–	–	x	x	x
<i>Lytta</i>	x	x	x	x	–	x	x	x	–	–	x	x	x
<i>Coccinella</i>	x	x	–	–	–	x	x	x	–	–	x	x	x
<i>Tenebrio</i>	x	x	x	–	–	x	x	x	–	–	x	x	x
<i>Cassida</i>	x	x	x	–	–	x	x	x	–	–	x	x	x
<i>Donacia</i>	x	x	–	x	–	x	x	x	–	–	x	x	x
<i>Eucinetus</i>	x	–	x	x	–	x	x	–	–	–	x	x	x
<i>Calyptomerus</i>	x	–	x	x	–	x	x	–	–	–	x	x	x
<i>Elodes</i>	x	–	x	x	–	x	x	–	–	–	x	x	x
<i>Cyphon</i>	x	–	x	x	–	x	x	–	–	–	x	x	x
<i>Ora</i>	x	–	x	x	–	x	x	–	–	–	x	x	x

a, first part of the muscle; b, second part of the muscle; x, present; –, absent; ?, state unknown.

musculature of *Calyptomerus*. This feature is an autapomorphy of Scirtoidea or Scirtoidea excl. Decliniidae. More information on the musculature of Decliniidae and other elateriform beetles (e.g. Dascilloidea) is required.

*M. noto-trochantinalis* (M. 59): (0) present; (1) absent

*M. noto-trochantinalis* is absent in all representatives of Polyphaga and Myxophaga examined (Larsén 1966; Beutel and Haas 2000; Beutel and Komarek 2004) but is present in Neuropterida (Maki 1936; Korn 1943; Czihak 1953, 1957; Beutel and Haas 2000), Archostemata (*Priacma*; Baehr 1975) and Adephaga (except for Gyrinidae; Larsén 1966; Belkaceme 1986, 1991; Beutel and Roughley 1988). The loss is a potential synapomorphy of Myxophaga and Polyphaga (Beutel and Haas 2000).

*M. coxa-subalaris* (M. 64): (0) present; (1) absent

*M. coxa-subalaris* is present in Neuropterida (Maki 1936; Korn 1943; Czihak 1953, 1957; Beutel and Haas 2000) and in non-polyphagan beetles (Larsén 1966; Beutel and Haas 2000; Beutel and Komarek 2004). The absence of M. 64 is an autapomorphic feature of Polyphaga including Scirtoidea.

*M. furca-coxalis lateralis* (M. 66): (0) present; (1) absent

*M. coxa-subalaris* is present in Archostemata (*Priacma*; Baehr 1975), some members of Adephaga (Larsén 1966; Beutel 1986; Belkaceme 1991; Beutel and Haas 2000), in several myxophagan representatives (*Hydroscapha*; Beutel and Haas 2000) and in few polyphagans [e.g. Scirtidae; Fig. 18; Meloidae, Cantharidae, Pyrochroidae, Coccinellidae (partim); Larsén 1966]. It is likely that the muscle was reduced several times independently within Polyphaga.

*M. episterno-trochanteralis* (M. 70): (0) present; (1) absent

*M. episterno-trochanteralis* is present in Archostemata (*Priacma*; Baehr 1975), Adephaga, Myxophaga (Beutel and Haas 2000) and most polyphagan Taxa (Larsén 1966; Beutel and Haas 2000; Beutel and Komarek 2004). The muscle was probably independently reduced in Scarabaeoidea, Pyrochroidae, Dermestidae (Larsén 1966) and Scirtoidea.

*M. trochantero-basalaris* (M. 71): (0) present; (1) absent

*M. trochantero-basalaris* is well developed in Neuropterida (Maki 1936; Korn 1943; Czihak 1953, 1957; Beutel and Haas 2000), Archostemata (*Priacma*; Baehr 1975) and members of some groups of Polyphaga [e.g. Pyrochroidae, Dermestidae,

Cerambycidae, Scarabaeidae (partim); Larsén 1966; Beutel and Haas 2000]. It is also present in the examined species of Scirtoidea (except *Eucinetus*) and is a potential autapomorphy of this group. However, the presence of absence in Decliniidae has to be clarified.

*Mm. noto-episternales breves* (M. 89): (0) present; (1) absent

*Mm. noto-episternales breves* are present in Neuropterida (Maki 1936; Korn 1943; Czihak 1953, 1957; Beutel and Haas 2000) and Archostemata (*Priacma*; Baehr 1975) and are absent in Adephaga, Myxophaga and Polyphaga, including Scirtoidea (e.g. Larsén 1966; Beutel 1986; Beutel and Haas 2000; Beutel and Komarek 2004). The absence is an autapomorphy of Coleoptera excl. Archostemata (Beutel and Haas 2000).

*M. noto-pleuralis a* (M. 91): (0) present; (1) absent

*M. noto-pleuralis a* is present in most Neuropterida (except *Myrmeleon*; Korn 1943) and Archostemata (*Priacma*; Baehr 1975) but is absent in all non-archostematan beetles (e.g. Larsén 1966; Belkaceme 1986, 1991; Beutel 1986, 1999; Beutel and Haas 2000; Beutel and Komarek 2004). The loss of this muscle is a potential autapomorphy of Coleoptera excl. Archostemata.

*M. noto-pleuralis b* (M. 92): (0) present; (1) absent

*M. noto-pleuralis a* is present in Neuropterida (Maki 1936; Korn 1943; Czihak 1953, 1957; Beutel and Haas 2000) and Archostemata (*Priacma*; Baehr 1975). *M. 92* is absent in Adephaga (Larsén 1966; Belkaceme 1986, 1991; Beutel 1986, 1999), Myxophaga (Beutel and Haas 2000) and Polyphaga including Scirtoidea (Larsén 1966; Beutel and Haas 2000; Beutel and Komarek 2004). The absence of *M. 92* is likely a synapomorphy of these three taxa.

*Mm. pleura-alaris a and b* (M. 95, M. 96): (0) clearly separated; (1) two branches with a common insertion

In Neuropterida, Megaloptera (Korn 1943; Czihak 1953, 1957; Matsuda 1970) and Archostemata (*Priacma*; Baehr 1975) *M. pleura-alaris a* and *M. pleura-alaris b* are clearly separated. Both muscles insert together on the third axillary in Adephaga (Beutel 1986, 1988; Belkaceme 1991), Myxophaga (Beutel and Haas 2000) and Polyphaga (Fig. 19b; Larsén 1966; Beutel and Haas 2000; Beutel and Komarek 2004). The common insertion is the derived condition within Coleoptera and an autapomorphy of Coleoptera excluding Archostemata.



*M. noto-trochantinalis* (*M. 100*): (0) present; (1) absent

*M. noto-trochantinalis* is present in Neuropterida (Maki 1936; Korn 1943; Czihak 1953, 1957; Beutel and Haas 2000), Archostemata (*Priacma*; Baehr 1975) and most polyphagan taxa examined (absent in Hydrophilidae and *Cetonia*). It is absent in Myxophaga and Adephaga (Beutel 1986, 1988; Belkaceme 1991; Beutel and Haas 2000). In contrast to Beutel and Haas (2000), the absence of *M. 100* is not a synapomorphy of Adephaga, Myxophaga and Polyphaga.

*M. episterno-coxalis* (*M. 103*): (0) present; (1) absent

*M. episterno-coxalis* is present in Archostemata (*Priacma*; Baehr 1975), Myxophaga (Beutel and Haas 2000) and usually also in Polyphaga. It is present in Scirtoidea and also in Elateridae (Larsén 1966). The muscle is always absent in Adephaga (Beutel 1986, 1988; Belkaceme 1991; Beutel and Haas 2000). It is likely that the muscle was reduced independently in Adephaga (autapomorphy) and different lineages of Polyphaga. More data are required for a reliable phylogenetic interpretation (e.g. Decliniidae, Derodontidae, Dascillidae).

*M. furca-coxalis posterior* (*M. 109*): (0) present; (1) absent

*M. furca-coxalis posterior* is present in all Coleoptera except for some representatives of Adephaga (Larsén 1966; Beutel 1986, 1988; Belkaceme 1991; Beutel and Haas 2000) and Scirtoidea. The absence is a potential synapomorphy of Scirtidae, Clambidae and Eucinetidae. Whether the muscle is also absent in Decliniidae is unknown at present.

*M. trochantero-basalaris* (*M. 112*): (0) present; (1) absent

*M. trochantero-basalaris* is present in Neuropterida (Maki 1936; Korn 1943; Czihak 1953, 1957; Beutel and Haas 2000) and Archostemata (*Priacma*; Baehr 1975). The muscle is absent in all non-archostematan beetles (Larsén 1966; Belkaceme 1986, 1991; Beutel 1986, 1988; Beutel and Haas 2000; Beutel and Komarek 2004) including Scirtoidea and is likely a synapomorphy of Adephaga, Myxophaga and Polyphaga (Beutel and Haas 2000).

## Discussion

### Monophyly of Scirtoidea and the relationships of the scirtoid families

The monophyly of Scirtoidea excl. Decliniidae (=Scirtoidea sensu Crowson 1960) is tentatively supported by two derived non-muscular features of the pterothorax: the main part of the katepisternum is triangular and located between the metacoxae, and the anal field of the hind wing is separated from the medial field by a deep incision. The validity of these presumptive synapomorphies of Scirtidae, Eucinetidae and Clambidae is somewhat reduced by the fact, that both characters are not applicable in the latter family as a result of miniaturization. Shared derived features of the muscular apparatus of the three families are a strongly enlarged mesothoracic *M. pleura-alaris* (*M. 53*; less distinct in *Calyptomerus*) and the loss of three muscles in the metathorax [*Mm. episterno-trochanteralis* (*M. 70*), *episterno-coxalis* (*M. 103*) and *furca-coxalis posterior* (*M. 109*)]. As the condition in Decliniidae is unknown, these character states are either autapomorphies of Scirtoidea or of Scirtoidea excluding this family. An enlarged anal field is the only verified autapomorphy of Scirtoidea sensu Nikitsky et al. (1994). The reduction of this wing area in *Calyptomerus* is very

likely a secondary feature and as a result of miniaturization. The membranous junction in the mesocoxal cavities (between the mesoventrite and metaventrite) is another potential autapomorphy of Scirtoidea sensu Nikitsky et al. (1994). However, it cannot be ruled out with certainty that this membranous connection represents a ground plan feature of Elateriformia and Polyphaga (see Lawrence 2001; Kukulová-Peck and Lawrence 2004). To clarify this controversy, a broad cladistic character evaluation including representatives of the major polyphagan lineages is required (e.g. Derodontidae, Dascillidae, Rhipiceridae). Preliminary analyses based on an extended version of the data matrix in Beutel and Haas (2000) clearly suggest that the membranous connection of the pterothoracic ventrites is a secondary feature.

The monophyly of Scirtidae is well supported by pterothoracic characters. The cone-shaped, distinctly elongated mesocoxae and an elongated metafurcal stalk are derived skeletal characters. In the hind wing, the indistinct or absent third radial cross-vein and the radial cell with more or less rounded edges are very likely autapomorphic. The separation of *M. noto-epimeralis* (*L. 34*) and *M. epimero-subalaris* (*M. 52*) is another possible autapomorphy of Scirtidae, but information about these muscles in Decliniidae and many other elateriform beetles is lacking.

The results obtained tentatively suggest that Scirtidae are the sister group of Clambidae. The moderate elongation of the mesocoxae, the reduction of the intercoxal process of the mesoventrite and the resulting adjacent position of the metacoxae are potential synapomorphies.

### Systematic position of Scirtoidea within Polyphaga

The position of Scirtoidea within Polyphaga remains ambiguous. The lack of a bending zone in the medial bar of the hind wing could be interpreted as an autapomorphy of Polyphaga excl. Scirtoidea. If the membranous connection between mesoventrite and metaventrite would indeed be a ground plan feature of Polyphaga, the firm connection would be another potential apomorphy of Polyphaga excl. Scirtoidea, with reversal in some groups (e.g. Derodontidae, few representatives of Leioididae). Yet, this scenario appears rather unlikely (see above). A sister group relationship between the Scirtoidea and the remaining Polyphaga as implicitly suggested by Lawrence (1999, 2001) is not well supported.

The monophyly of Elateriformia sensu Lawrence and Newton (1995) (i.e. including Scirtoidea) is also far from being well established (Beutel and Leschen 2005b: 'What if anything is Elateriformia'; see also Vogler 2005). A triangular radial cell and the reduction of the apically directed branches of RP are features of the hind wing shared by Scirtoidea and Elateriformia (Fig. 25; Kukulová-Peck and Lawrence 1993). The elongation of the anepisternum 3 (more than 2.5 times longer than wide) was suggested as a potential autapomorphy of Elateriformia excl. Scirtoidea by Lawrence (1988). However, this condition is also found in this superfamily (Fig. 22). The character should not be overvalued. It is a gradual modification and the length of the anepisternum depends simply on the length of the entire metathorax. A very long anepisternum 3 is also present in Cupedidae (Baehr 1975) and Ommatidae and many other beetles.

It is evident that more data (including DNA sequences) and an extensive cladistic character evaluation with a representative

taxon sampling are necessary to solve the question of the basal branching pattern within Polyphaga and the position of Scirtoidea (see also Vogler 2005; Hughes et al. 2006). The results of the comprehensive phylogenetic analysis carried out by Lawrence (1988) are somewhat affected by the very limited outgroup. The polarity interpretations (e.g. anepisternum 3) may have changed considerably, if a more inclusive outgroup would have been chosen.

### Relationships of the coleopteran suborders

The results of the study support the sister group relationship between Polyphaga and Myxophaga (e.g. Crowson 1960; Beutel and Haas 2000). The autapomorphies based on characters of the wing base proposed by Hörnschemeyer (1998) are confirmed for Scirtoidea (characters 16, 17). The most parsimonious interpretation of the membranous connection between the mesoventrite and the metaventrite is likely a secondary reduction correlated with the generally weak sclerotization of the short-lived adults.

In contrast to the assumptions in Lawrence (1999, 2001) and Kukulová-Peck and Lawrence (2004), the derived muscular features proposed by Beutel and Haas (2000) as synapomorphies of Adephaga, Myxophaga and Polyphaga are present in all representatives of Scirtoidea examined (characters 26–28, 30, 38–40, 44). The bending zone of the hind wing and the absence of an exposed metathoracic trochantin (Beutel and Haas 2000) are also confirmed as synapomorphies of these three suborders. A joint between the mesothoracic katepisternum and the mesocoxae is not present in any scirtid species examined in contrast to (Kukulová-Peck and Lawrence 2004). In agreement with Beutel and Haas (2000), the absence of this joint can be considered as a synapomorphy of the non-archostematan suborders.

In contrast to Beutel and Haas (2000), the absence of the mesothoracic discriminial line is no-apomorphy of Coleoptera excl. Archostemata. This structure is distinctly present in some Scirtoidea (e.g. *Declinia*; Lawrence et al. 1995; *Stenocyphon*, *Heterocyphon*; Lawrence 2001; Eucinetidae; Leschen 2005a) and other polyphagans (e.g. Buprestidae, Psephenidae; Kukulová-Peck and Lawrence 2004).

In conformity with Beutel and Haas (2000) and several other authors (e.g. Machatschke 1962; Klausnitzer 1975; Hörnschemeyer 1998; Hughes et al. 2006), the results of this study strongly support the hypothesis of Crowson (1960) on relationships of the coleopteran suborders (Fig. 1a). The hypothesis presented by Kukulová-Peck and Lawrence (1993, 2004) is clearly affected by the use of a limited morphological character system (of adults), which is subject to strong functional restrictions.

### Acknowledgements

The authors are grateful for the valuable specimens provided by S.A. Ślipiński (CSIRO, Australian National Insect Collection, Canberra), E. Anton (Institut für Spezielle Zoologie, University of Jena) and A.F. Newton (Field Museum of Natural History, Chicago). Valuable comments made by two anonymous reviewers are also gratefully acknowledged.

### Zusammenfassung

Das Skelettmuskelsystem des Pterothorax von sechs adulten Vertretern von drei der vier Familien der Scirtoidea (Scirtidae, Clambidae,

Eucinetidae) wurde detailliert untersucht. Phylogenetisch relevante Merkmale werden diskutiert. Eine umfangreiche Tabelle zur pterothorakalen Muskulatur der Coleoptera wird vorgestellt. Die Monophylie der Scirtoidea wird von abgeleiteten Merkmalen des Skeletts, der Muskulatur und des Hinterflügels unterstützt. Die Rekonstruktion der Verwandtschaftsverhältnisse innerhalb der Scirtoidea bleibt problematisch. Einerseits fehlen Daten zur inneren Anatomie der Decliniidae, andererseits weisen die Clambidae bedingt durch ihren hohen Grad an Miniaturisierung eine Vielzahl autapomorpher Merkmale auf. Die systematische Stellung der Scirtoidea ist weiterhin unklar. Eine basale Stellung innerhalb der Polyphaga wird nur von einem Merkmal gestützt (Fehlen einer Biegungszone im Hinterflügel bei allen Linien der Polyphaga). Mögliche Apomorphien die für eine Position innerhalb der Elateriformia sprechen sind ein verlängertes Anepisternum 3, eine dreieckige Radialzelle und die Reduktion der apikalen Äste des Radius posterior im Flügelgeäder. Die thorakalen Strukturen der Scirtoidea sind wie bei allen übrigen bisher untersuchten polyphagen Coleopteren im Vergleich mit den Adephaga und v.a. den Archostemata klar abgeleitet. Eine basale Stellung der Archostemata und ein Schwestergruppenverhältnis zwischen den Polyphaga und Myxophaga werden von den Resultaten der vorliegenden Arbeit gestützt. Merkmale, die für die alternative Hypothese, ein Schwestergruppenverhältnis zwischen den Polyphaga und den übrigen Unterordnungen sprechen, wurden nicht gefunden.

### References

- Acker TS (1958) The comparative morphology of *Stenorrhachus walkeri* (McLachlan) and of *Nemopterella* sp. (Neuroptera: Nemopteridae). *Microentomology* **23**:106–130.
- Baehr M (1975) Skelett und Muskulatur des Thorax von *Priacma serrata* Leconte (Coleoptera, Cupedidae). *Z Morphol Tiere* **81**:55–101.
- Baehr M (1976) Das Prothorakalskelett von *Atractocerus* (Lymexylonidae) und seine Bedeutung für die Phylogenie der Coleopteren, besonders der Polyphagen (Insecta: Coleoptera). *Zoomorphologie* **85**:39–58.
- Baehr M (1980) Zur Funktionsmorphologie und evolutiven Bedeutung der elytralen Sperrmechanismen der Scaritini (Coleoptera: Carabidae). *Entomol Gen* **6**:311–333.
- Belkaceme T (1986) Skelet und Muskulatur der Hinterhüfte von *Haliphys lineatocollis* Mrsh. (Haliphiidae, Coleoptera). *Stuttgarter Beitr Naturk (A)* **393**:1–12.
- Belkaceme T (1991) Skelet und Muskulatur des Kopfes und Thorax von *Noterus laevis* Sturm. Ein Beitrag zur Morphologie und Phylogenie der Noteridae (Coleoptera: Adephaga). *Stuttgarter Beitr Naturk (A)* **462**:1–94.
- Beutel RG (1986) Skelet und Muskulatur des Kopfes und Thorax von *Hygrobia tarda* (Herbst). Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Hydradephaga (Insecta: Coleoptera). *Stuttgarter Beitr Naturk (A)* **388**:1–54.
- Beutel RG (1988) Studies of the metathorax of the trout-stream beetle, *Amphizoa lecontei* Matthews (Coleoptera: Amphizoidae): contribution towards clarification of the systematic position of Amphizoidae. *Int J Insect Morphol Embryol* **17**:63–81.
- Beutel RG (1992) Phylogenetic analysis of thoracic structures of Carabidae (Coleoptera: Adephaga). *Z Zool Syst Evol Forsch* **30**:53–74.
- Beutel RG (1997) Über Phylogenese und Evolution der Coleoptera (Insecta), insbesondere der Adephaga. *Abh Natur Ver Hamburg* **31**:1–164.
- Beutel RG (1999) Phylogenetic analysis of Myxophaga (Coleoptera) with a redescription of *Lepicerus horni* (Lepiceridae). *Zool Anz* **237**:291–308.
- Beutel RG, Haas F (2000) Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics* **16**:103–141.
- Beutel RG, Komarek A (2004) Comparative study of thoracic structures of adults of Hydrophiloidae and Histeroidea with phylogenetic implications (Coleoptera, Polyphaga). *Org Divers Evol* **4**:1–34.
- Beutel RG, Leschen RAB (2005a) Phylogenetic analysis of Staphyliniformia (Coleoptera) based on characters of larvae and adults. *Syst Entomol* **30**:510–548.

- Beutel RG, Leschen RAB (2005b) 14. Elateriformia Crowson, 1960. In: Beutel RG, Leschen RAB (vol eds), Coleoptera, Beetles. Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Kristensen N-P, Beutel RG (eds), Handbook of Zoology. Vol. IV Arthropoda: Insecta Part 36. Walter de Gruyter, Berlin and New York, pp 427–429.
- Beutel RG, Roughley RE (1988) On the systematic position of the family Gyrinidae (Coleoptera: Adephaga). *Z Zool Syst Evol-Forsch* **26**:380–400.
- Caterino MS, Shull VL, Hammond PM, Vogler AP (2002) Basal relationships of Coleoptera inferred from 18S rDNA sequences. *Zool Scr* **31**:41–49.
- Crowson RA (1944) Further studies on the metendosternite in Coleoptera. *Trans R Entomol Soc Lond* **94**:273–310.
- Crowson RA (1960) The phylogeny of the Coleoptera. *Annu Rev Entomol* **5**:111–134.
- Czihak G (1953) Beiträge zur Anatomie des Thorax von *Sialis flavilatera* L. *Österr Zool Zeitschr* **4**:421–448.
- Czihak G (1957) Beiträge zur Anatomie des Thorax von *Ascalaphus macaronicus* Scop., *Myrmeleon europaeus* McLach und *Palpares libelluides* Dalm. *Zool Jahrb Anat* **75**:401–432.
- Ferris GF (1940) The morphology of *Plega signata* (Hagen) (Neuroptera: Mantispidae). *Microentomology* **5**:35–56.
- Ferris GF, Pennebaker P (1939) The morphology of *Agulla adnixa* (Hagen) (Neuroptera: Raphidiidae). *Microentomology* **4**:121–142.
- Geisthardt M (1974) Das thorakale Skelett von *Lamprohiza splendidula* (L.) unter besonderer Berücksichtigung des Geschlechtsdimorphismus (Coleoptera: Lampyridae). *Zool Jahrb Anat* **93**:299–334.
- Haas F (1998) Geometrie, Mechanik und Evolution der Flügelfaltung bei den Coleoptera (Insecta). PhD Thesis. FSU, Jena.
- Hansen M (1997) Phylogeny and classification of the staphyliniform beetle families (Coleoptera). *Biol Skrifter Dan Vid Selsk* **48**:1–339.
- Heberdey RF (1938) Beiträge zum Bau des Subelytrales und zur Atmung der Coleopteren. *Z Morphol Ökol Tiere* **33**:667–734.
- Hörschemeyer T (1998) Morphologie und Evolution des Flügelgelenks der Coleoptera und Neuropterida. *Bonn Zool Monogr* **43**:1–126.
- Hughes J, Longhorn SJ, Papadopolou A, Theodorides K, de Riva A, Mejia-Chang M, Foster PG, Vogler AP (2006) Dense taxonomic EST sampling and its applications for molecular systematics of the Coleoptera (beetles). *Mol Biol Evol* **23**:268–278.
- Klausnitzer B (1975) Probleme bei der Abgrenzung von Unterordnungen bei den Coleoptera. *Entomol Abh Staatl Mus Tierk Dresden* **40**:269–275.
- Korn W (1943) Muskulatur des Kopfes und des Thorax von *Myrmeleon europaeus* und ihre Metamorphose. *Z Morphol Tiere* **68**:273–330.
- Kristensen NP (1981) Phylogeny of the insect orders. *Ann Rev Entomol* **26**:135–157.
- Kukalová-Peck J, Lawrence JF (1993) Evolution of the hind wing of Coleoptera. *Can Entomol* **125**:181–258.
- Kukalová-Peck J, Lawrence JF (2004) Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. *Eur J Entomol* **101**:95–144.
- Larsén O (1945a) Das Meron der Insekten. *Kungl Fysiogr Sällsk Lund Förhandl* **15**:96–104.
- Larsén O (1945b) Die hintere Region der Insektenhüfte. *Kungl Fysiogr Sällsk Lund Förhandl* **15**:105–116.
- Larsén O (1966) The skeleton and muscles of the thorax in the Coleoptera. *Opusc Entomol* **10**:1–241.
- Lawrence JF (1988) Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invertebr Taxon* **2**:1–53.
- Lawrence JF (1999) The Australian Ommatidae (Coleoptera: Archostemata): new species, larva and discussion of relationships. *Invertebr Taxon* **13**:369–390.
- Lawrence JF (2001) A new genus of valdivian Scirtidae (Coleoptera) with comments on Scirtoidea and the beetle suborders. *Spec Publ Japan Coleoptera Soc Osaka* **1**:351–361.
- Lawrence JF (2005a) 15.1. Decliniidae Nikitsky et al., 1994. In: Beutel RG, Leschen RAB (vol eds), Coleoptera, Beetles. Vol. 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Kristensen N-P, Beutel RG (eds), Handbook of Zoology. Vol. IV Arthropoda: Insecta Part 36. Walter de Gruyter, Berlin and New York, pp 431–433.
- Lawrence JF (2005b) 15.4. Scirtidae Fleming, 1821. In: Beutel RG, Leschen RAB (vol eds), Coleoptera, Beetles. Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Kristensen N-P, Beutel RG (eds), Handbook of Zoology. Vol. IV Arthropoda: Insecta Part 36. Walter de Gruyter, Berlin and New York, pp 443–450.
- Lawrence JF, Newton AF Jr (1982) Evolution and classification of beetles. *Annu Rev Ecol Syst* **13**:261–290.
- Lawrence JF, Newton AF Jr (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk J, Ślipiński AS (eds), Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum I Instytut Zoologii Polska Akademia Nauk, Warszawa, pp 779–1006.
- Lawrence JF, Nikitsky NB, Kirejtshuk AG (1995) Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (sensu lato). In: Pakaluk J, Ślipiński AS (eds), Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum I Instytut Zoologii Polska Akademia Nauk, Warszawa, pp 375–410.
- Leschen RAB (2005a) 15.2. Eucinetidae Lacordaire, 1857. In: Beutel RG, Leschen RAB (vol eds), Coleoptera, Beetles. Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Kristensen N-P, Beutel RG (eds), Handbook of Zoology. Vol. IV Arthropoda: Insecta Part 36. Walter de Gruyter, Berlin and New York, pp 433–438.
- Leschen RAB (2005b) 15.3. Clambidae Fischer, 1821. In: Beutel RG, Leschen RAB (vol eds), Coleoptera, Beetles. Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Kristensen N-P, Beutel RG (eds), Handbook of Zoology. Vol. IV Arthropoda: Insecta Part 36. Walter de Gruyter, Berlin and New York, pp 438–443.
- Machatschke JW (1962) Bemerkungen zum System der Coleoptera. *Ber. 9 Wandervers.dtsch.ent.Ges.1961, Berlin* **45**:121–137.
- Maki T (1936) Studies on the skeletal structure musculature and nervous system of the Alder Fly *Chauliodes formosanus* Petersen. *Mem Fac Sci Agric Taihoku Imp Univ* **16**:117–243.
- Matsuda R (1970) Morphology and evolution of the insect thorax. *Mem Entomol Soc Can* **76**:1–431.
- Mickoleit G (1965) Über die morphologische Deutung des caudalen Sternocoxalmuskels im Pterothorax der Neuropteroiden. *Zool Jahrb Anat* **82**:521–531.
- Mickoleit G (1967) Das Thorakalskelet von *Merope tuber* Newman (Protomecoptera). *Zool Jahrb Anat* **84**:313–342.
- Nikitsky NB, Lawrence JF, Kirejtshuk AG, Gratshev WG (1994) A new beetle family, Decliniidae fam. n., from the Russian Far East and its taxonomic relationships (Coleoptera: Polyphaga). *Russ Entomol J* **2**:3–10.
- Nyholm T (1967) Zur Kenntnis der Gattung *Hydrocyphon* Redtenbacher (Coleoptera: Helodidae). *Opusc Entomol* **32**:9–48.
- Ponomarenko AG (1972) The nomenclature of wing venation in beetles (Coleoptera). *Entomol Rev* **51**:454–458.
- Schneider P (1978) Die Flug- und Faltungstypen der Käfer (Coleoptera). *Zool Jahrb Anat* **99**:174–210.
- Snodgrass RE (1909) The thorax of insects and articulation of the wing. *Proc US Nat Mus* **26**:511–595.
- Vogler AP (2005) 3. Molecular systematics of Coleoptera: what has been achieved so far? In: Beutel RG, Leschen RAB (vol eds), Coleoptera, Beetles. Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Kristensen N-P, Beutel RG (eds), Handbook of Zoology. Vol. IV Arthropoda: Insecta Part 36. Walter de Gruyter, Berlin and New York, pp 17–27.

*Authors' addresses:* Frank Friedrich (corresponding author) and Rolf G. Beutel, Institut für Spezielle Zoologie und Evolutionsbiologie, Friedrich-Schiller-Universität, Erbertstr 1. 07743 Jena, Germany. E-mail: frank.friedrich@uni-jena.de, rolf.beutel@uni-jena.de