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The unique locomotor apparatus of whirligig beetles of the tribe Orectochilini (Gyrinidae, Coleoptera)

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Abstract

Whirligig beetles, which are known for their rapid gliding on the water surface, have evolved a unique locomotor apparatus. External and internal thoracic structures of *Orectochilus villosus* (Orectochilini) are described in detail and documented with micro-computed tomography, computer based 3D reconstructions, and scanning electronic microscopy (SEM). The results are compared with conditions found in other genera of Gyrinidae and other groups of Coleoptera. The focus is on structures linked with locomotion, especially on the unusual flight apparatus, which differs strongly from that of other beetles. As in other Orectochilini, the prothorax of *Orectochilus* displays characters typical for Gyrinidae, with triangular procoxae and fore legs transformed into elongated, sexually dimorphic grasping devices. The musculature of this segment is similar to the pattern found in other Coleoptera. Simlar to all other extant Gyrinidae, the mesothorax is characterized by an extensive and flat mesoventrite, suitable for gliding on the water surface. As in Heterogyrinae and the other Gyrininae, the pterothoracic legs are transformed into paddle-like structures, enabling the beetles to move with high speed on the surface film. The musculature of the mesothorax is reduced compared to other Coleoptera, but similar to what is found in the other Gyrininae. The metathoracic skeleton and musculature are simplified in Orectochilini compared to other Gyrininae and other groups of Coleoptera. In *O. villosus* only 10 metathoracic muscles are preserved. Thirty-six are present in an archostematan beetle, a condition probably close to the coleopteran groundplan. The metathoracic dorsal longitudinal bundles are absent in Gyrininae, muscles that play a role as indirect flight muscles in most other neopteran insects. The rest of the posteromotoric flight apparatus is distinctly modified, with a limited number of skeletomuscular elements taking over more than one function, i.e. leg movements and flight. The large muscle **M84** (IIIdvm7) M.

noto-trochanteralis, for instance, functions as dominant wing levator, but is also responsible for the powerful and rapid backstroke of the hind legs. The presence of this muscle is a synapomorphy of Heterogyrinae and Gyrininae. The narrow metafurca in the latter group is likely linked to its large size. The elytra likely contribute to the control of the flight of the beetle, whereas they shield and inhibit the flight apparatus during swimming.

Keywords: Gyrinidae – *Orectochilus* – thorax – morphology – locomotor apparatus

1. Introduction

Whirligig beetles or Gyrinidae are known for swimming rapidly in circles on the water surface, usually forming groups of several dozens or thousands of individuals (Bott 1928; Omer-Cooper 1934; Larsén 1966). According to Nachtigall (1961) their swimming apparatus is the most efficient in the entire animal kingdom. The habitat with small arthropods caught in the surface film was referred to as a "world of the dead and the dying" (Omer-Cooper 1934). The unusual life habits of whirligig beetles are linked with a series of autapomorphies, including the subdivided compound eyes and the antennae with fringes of setae on the pedicellus registering movements of the water surface (e.g. Larsén 1966). The systematic position of the family within the suborder Adephaga is not fully settled (e.g. McKenna et al. 2015). However, a sistergroup relationship with all other adephagan families appears most likely, supported by morphological characters (Beutel and Roughley 1988; Beutel, et al. 2013) and also by a recent molecular study (Baca et al. 2017).

A comprehensive morphological study on the locomotor organs of Gyrinidae was published by Larsén (1966), together with the thoracic morphology of 54 species in the suborders Adephaga and Polyphaga. However, the work of Larsén (1966) was exclusively based on dissections and focused on the species *Gyrinus marinus* Gyllenhal, 1808 (Gyrinini). At that time, the gyrinid key taxon *Spanglerogyrus albiventris* Folkerts, 1979 and the sistergroup of all the remaining genera was unknown. Besides this, no information on the thoracic morphology of the plesiomorphic suborder Archostemata was available (Baehr 1975; Friedrich et al. 2009).

In this study we focus on the tribe Orectochilini, which includes the genera *Gyretes*, *Orectogyrus*, *Orectochilus* and *Patrus* (formerly a subgenus of *Orectochilus*; Miller and Bergsten 2012). It is the subgroup with the most advanced features in this family according to phylogenetic analyses of Gyrinidae (Larsén 1966; Beutel 1989a, b, 1990; Miller and Bergsten 2012). It cannot be excluded that some flightless species occur in Orectochilini (Larsén 1954).

However, there are records indicating that members of different genera of this tribe have retained their flight capacity (Larsén 1966; Ochs 1966; Brinck 1982), including the one in the focus of this study, *Orectochilus villosus* (Müller, 1776). The thoracic morphology of this species is described in detail and documented using µ-CT data, computer based 3D reconstructions and scanning electronic microscopy (SEM). The locomotor organs are discussed from evolutionary and functional perspectives, especially the flight apparatus, which is characterized by a distinctly modified skeleto-muscular apparatus compared to beetles of other families or representatives of other groups of Neoptera (Larsén 1966; Brodsky 1994).

2. Materials and Methods

2.1. Materials

Orectochilus villosus (Müller, 1776), fixed in FAE (formaldehyde-acetic acid-ethanol) and stored in ethanol, collected in the Saale river, 8 Km south of Jena (Thuringia, Germany).

Heterogyrus milloti Legros, 1953 (Heterogyrinae; MILLER & BERGSTEN 2012), fixed and stored in 97% ethanol; collected at Fianarantsoa, small stream ~8km W Ranomofana, Ranomofana NP, Madagascar, 21º 14.992' S 47º 24.332' E, 2 November 2014, Miller, Gustafson and Bergsten.

Additional morphological data were extracted from the literature (Larsén 1954, 1966; Beutel 1989a, b, 1990; Friedrich et al. 2009).

2.2. Synchrotron radiation based micro-computed tomography (SR-µCT)

One specimen was dehydrated in an ethanol series and dried at the critical point (EmiTech K850 Critical Point Dryer). It was scanned in a small Eppendorf tube at Beamline BW2 of German Electron Synchrotron Facility (DESY, Hamburg) using a stable low photon energy beam (8 kVP) and absorption contract.

2.3. Computer based 3D-reconstruction

Based on the µCT-image stack the thoracic segments of *O. villosus* were reconstructed three-dimensionally using FEI Amira 6.0. Segmented structures were exported as stacks of tiff files into Volume Graphics VGStudiomax 2.0, which was used for volume rendering.

99

100 **2.4. Scanning electronic microscopy**

101 For the examination of external skeletal structures, a dried specimen was coated with gold
102 (EmiTech K500 sputter coater). Micrographs were taken with Philips XL 30 ESEM and
103 ResAlta Scandium software.

104

105 **2.5. Microscopic photography**

106 To document the coloration and general body shape, the specimens were photographed with
107 Keyence VH-Z20R.

108

109 **2.6. Line drawings**

110 Exposed body parts of the specimen were drawn with full lines, structures below other sclerites
111 with dotted lines. In Fig. 3 wings and legs were omitted, except basal elements. In Fig. 6 elytra
112 are omitted. The figures were drawn with a pencil based on microscopic observations (with a
113 camera lucida) or on 3D-reconstructions, scanned and finally completed with Adobe Illustrator
114 CC.

115

116 **2.7. Measurements**

117 Measurements were taken from digital photographs, SEM micrographs, line drawings and 3D-
118 reconstruction according to respective scale bars. The original scale bars can be accurate to
119 0.001 mm. Considering the calculation error, we kept the accuracy to 0.01 mm. We consistently
120 chose the longest portion in each dimension for measurement (e.g. ventrite of the mesothorax).

121

122 **2.8. Terminology**

123 The terminology for the thoracic skeleton was adopted from Friedrich et al. (2008) and Larsén
124 (1966). Muscle names of both Larsén (1954) and Friedrich and Beutel (2008) are used for easy
125 comparison with other coleopteran taxa. Both studies were also used in the context of functional
126 interpretations of thoracic structures. Basisubcostale (bsc) as a significant structure during wing
127 stroke is also adopted from Brodsky (1994).

128

129 **Abbreviations:**

130 1/2/3ax – first/second/third axillary sclerite; aest2/3 – mes-/metanepisternum; alc – alacrista;
131 anp – anterior notal process; ba3 – metabasalare; bsc – basisubcostale; cx1/2/3 – pro-/meso-

/metacoxa; dis – discrimen; el – elytron; elap – articulatory process of elytron; ep2/3 – mes/metepimeron; epl1 – proepipleuron; fem1/2/3 – pro-/meso-/metafemur; fu1/2/3 – pro-/meso-/metafurca; hw – hind wing; fup – profurcal process; mnp – median notal process; nt1 – pronotum; ph1/2 – pro-/mesophragma; pl1 – propleuron; pls2/3 – meso-/metapleural suture; pn3 – metapostnotum; pnp – posterior notal process; prsc – prealar sclerite; pwp3 – metathoracic pleural wing process; sc2/3 – meso-/metascutum; scl2/3 – meso-/metascutellum; scsh – mesoscutellar shield; se – spatulate setae; spi2 – mesothoracic spiracle; su3 – metasubalare; tar1/2/3 – pro-/meso-/metatarsus; tib1/2/3 – pro-/meso-/metatibia; tr1/2/3 – pro-/meso-/metatrochanter; v1/2/3 – pro-/meso-/metaventrite.

3. Results

Thoracic morphology of *Orectochilus villosus*

General appearance

Body length: 9.65 mm, width: 3.83 mm, height: 2.86 mm (length : width : height ratio = 3.4 : 1.3 : 1.0). The thorax appears compact, stream-lined and laterally compressed, with a flat ventral surface and a convex dorsal side. The pronoto-elytral angle is indistinct. The pronotal and elytral surfaces (Fig. 1A) bear a dense vestiture of fine setae.

3.1. Prothorax

Length: 1.87 mm (pronotum), width: 3.21 mm (pronotum), height: 2.16 mm (length : width : height ratio = 1.0 : 1.7 : 1.2). Cervical sclerites are missing. The head and prothorax are connected by a cervical membrance, which is not visible externally. A dense pubescence is present on the entire pronotal surface. The anterior and posterior margins of the convex pronotum (nt1: Figs. 1A, C; 3C; 5A) are not distinctly extended. The anterior pronotal area covers the occipital region of the head and appears almost merged with it. The anterior pronotal margin is very finely serrated. The proepipleuron (epl1: Figs. 1B; 3C; 5A) is narrow as in the other Orectochilini (Larsén 1966). The propleuron (pl1: Figs. 1B; 3C; 5A) is delimited by a suture extending obliquely from the antero-ventral margin of the epipleuron to the prothoracic pleuro-coxal joint. The internalized crytopleura are extended mesad and fused with the pronotum, only leaving a narrow tergal region for muscle attachment. This is a character shared in Orectochilini and Enhydrini (Larsén 1966; Baehr 1979). The posterior wall (Fig. 3C) of the prothorax is formed by the posterior area of pronotum, the posterolateral epipleural area and the transverse concave ventral propleural lobe. The posterior pronotum (nt1: Fig. 3C) is narrow in *O. villosus*, but even narrower in the other Orectochilini (Larsén 1966). The line separating

the epipleural and propleural elements of the posterior wall is indistinct, probably an autapomorphy of Orectochilini (Larsén 1966). A projecting process bears a tuft of spatulate setae (se: Fig. 3C), which form the proprioreceptive sense organ located ventro-laterally on the posterior segmental wall, as in other Orectochilini (Larsén 1966). The process is short and rounded in *O. villosus* and *Gyretes*, but blunt in *Orectogyrus* (Larsén 1966). The proventrite (Figs. 2A; 3C) is bulging medially as in *Orectogyrus* (Larsén 1966), gradually shortened paramedially and laterally connected with the propleura. Medially it is divided by a distinct median ridge, and another ridge is present along its posterior margin. The prosternal process is reduced, not reaching between the procoxae. The profurca (fu1: Figs. 3C; 4C) bears a long posterior arm, which is bent laterad and reaches deeply into the mesothoracic lumen as in other Orectochilini and Enhydrini (Larsén 1966; Baehr 1979; Beutel 1989b). Anteriorly it bears a vertically oriented profurcal process (fup: Fig. 3C).

The fore legs (Figs. 1B; 2A) are modified as elongate grasping devices. The procoxa (cx1: Figs. 2A; 4A; 3C; 5A) is triangular and only slightly protruding. It lacks a ventral condyle articulating with the prosternal process. The triangular protrochanter (tr1: Figs. 2A; 3C; 5A), equipped with a group of setae ventrally, connects the procoxa with the elongate profemur (fem1: Fig. 1B; 2A) (length: 1.83 mm, width: 0.46 mm; length : width ratio = 4.0 : 1.0). The anterior profemoral margin bears a row of spines. The elongate protibia (tib1: Figs. 1B; 2A; length: 1.47 mm, width: 0.26 mm; length : width = 5.7 : 1.0), basally narrow and distally widening, bears a mesal comb of spines. Apical tibial spurs are missing. The sexually dimorphic laterally compressed protarsus (tar1: Figs. 1B; 2A) is composed of five tightly connected tarsomeres. The tarsal segments in males are equipped with a brush-like dense vestiture of adhesive hairs with apical suckers. The distal tarsomere bears a pair of curved claws.

Musculature (Figs. 4; 5; see Table 1 for an overview of all muscles; abbreviations from Friedrich and Beutel (2008) in brackets)**: M1** (Idlm2) M. pronoti primum: O (= origin): antero-median area of pronotum; I (= insertion): dorso-lateral area of occipitale. **M2** (Idlm1) M. pronoti secundus, bent upwards: O: first phragma; I: dorso-lateral area of occipitale. **M3** (Idlm3) M. pronoti tertius, bent upwards: O: first phragma; I: anterior pronotal margin. **M5** (Ivlm3) M. prosterni primus: O: basal area of profurca; I: ventro-lateral area of occipitale. **M6** (Ivlm1) M. prosterni secundus: O: profurcal process; I: ventral cervical membrane. **M7** (Idvm6) M. dorsoventralis primus, broader on pronotum, narrowing towards occipitale: O: central area of pronotum; I: ventro-lateral area of occipitale. **M10** (Idvm2/3) M. dorsoventralis quartus: O: anterior margin of prosternum; I: dorso-lateral area of occipitale. **M11** (Idvm10) M. dorsoventralis quintus, triangular muscle, narrower on mesoscutum; broadening towards

profurca: O: dorsal area of profurca; I: antero-lateral area of mesoscutum. **M13** (Itpm6) M. pronoto-mesepisternalis, broader on pronotum, narrowing towards mesanepisternum: O: central area of pronotum; I: intersegmental membrane anterior to mesanepisternum. **M14** (Idvm13) M. noto-trochantinalis, broader on pronotum, narrowing towards procoxa: O: antero-lateral area of pronotum; I: lateral procoxal rim. **M15** (Idvm16/17) M. noto-coxalis, broader on pronotum, narrowing towards procoxa: O: lateral area of pronotum; I: posterior procoxal rim. **M16** (Ipcm4) M. epimero-coxalis, broader on propleuron, narrowing towards procoxa: O: antero-dorsal area of propleuron; I: antero-lateral procoxal rim. **M20** (Ipcm8) M. pleura-trochanteralis, broader on prothoracic posterior wall, narrowing towards trochanter: O: prothoracic posterior wall; I: protrochanter. **M21** M. pleura-trochanteralis medialis, wide area of origin on procoxa, converging towards protrochanter: O: procoxal mesal wall; I: protrochanter. **M22** M. coxa-trochanteralis lateralis, at least two bundles, wide area of origin on procoxa, converging towards protrochanter: O: lateral procoxal wall; I: protrochanter.

The prothoracic muscles, especially those that attach to the cervical region and legs, are similar to those of the other examined species of Gyrinidae or other groups of Coleoptera (Larsén 1966; Baehr 1975; Beutel 1989b; Friedrich and Beutel 2006; Friedrich et al. 2009). The modifications compared with the general coleopteran muscular pattern reported by Larsén (1966: table II) and Beutel and Haas (2000: appendix IV) are the following: **M4** (Idlm5) M. pronoti quartus, **M8** (Idvm8) M. dorsoventralis secundus, **M9** (Idvm5) M. dorsoventralis tertius, **M12** (Itpm3?) M. pronoto-pleuralis, **M17** (Ipcm8) M. epimero-coxalis, **M18** (Iscm1) M. sterno-coxalis and **M19** (Iscm2) M. furca-coxalis are absent. The origin of **M1** (Idlm2) M. pronoti primum is shifted anterad. The origin of **M7** (Idvm6) M. dorsoventralis primus is shifted mesad. The original area of one subcomponent of **M15** (Idvm16/17) M. noto-coxalis is transverse and shifted to the postero-lateral region of the pronotum.

3.2. Mesothorax

Length 1.62 mm (mesoventrite + mesocoxa), width 3.48 mm (mesoventrite), height 1.76 mm (from mesoscutellar shield to mesoventrite, without elytra) (length : width : height ratio = 1.0 : 2.1 : 1.1). A flat median concavity is present at the anterior margin of the mesoscutum (sc2: Fig. 3A) and both sides of the sclerite are protruding anteriorly. Paired, distally rounded processes extending postero-ventrad from the anterior concavity form the prophragma (ph1: Fig. 4C) in *O. villosus*. It is a single and apically truncated structure in *Orectogyrus* and also a single median lobe in a few species of *Gyretes*, whereas it is bilobed in the other Gyrinidae (Hatch 1926; Larsén 1966). The narrow sclerotized lateral edge of the mesoscutum lacks

recognizable notal processes. An axillary ligament connects it with the articulatory process of the elytron (elap: Fig. 3A). The area between the mesoscutum and the posterior mesoscutellum is unsclerotized, nearly membranous. The mesoscutellum (scl2: Fig. 3A) bears a sclerotized triangular mesoscutellar shield (scsh: Fig. 3A) on its middle region, and its lateral parts are very narrow. The mesopleuron is triangular. The mesanepisternum (aest2: Fig. 3D) bears a small process on its dorsal margin, arguably a reduced mesobasalare. As in other Orectochilini, the opening between the elytron and laterally expanded dorsal margin of the mesanepisternum is narrow in *O. villosus* (Larsén 1966), an autapomorphy of the tribe (Beutel 1990). The ventral mesanepisternal margin broadly connects with the dorso-lateral margin of the mesoventrite (v2: Figs. 1B; 2A, B; 3D) and meets the lateral mesocoxal edge posteriorly. This ventral margin forms an excavation for the profemora in the resting position. Postero-mesally the mesanepisternum is adjacent to the narrow triangular mesepimeron (ep2: Fig. 3D), both separated by the mesopleural suture (pls2: Fig. 3D). The mesokatepisternum is completely fused with the main part of the mesoventrite, without a transverse ridge. Anteriorly the mesoventrite forms a triangular process that bears two separate groups of setae, and postero-mesally a discrimen (dis: Fig. 4A) is present protruding dorsad into the mesothoracic lumen. The short but well-developed mesofurca (fu2: Fig. 4B) originates dorsally on the discrimen. It bears a large apical disc for muscle attachment.

The mesocoxae are approximately triangular (cx2: Figs. 1B; 3D; 4A; 5A), medially adjacent and diverging antero-laterally. The anterior edge is immovably attached to the posterior margin of the mesoventrite. This is also the case in *Orectogyrus*, whereas a certain movability is retained in *Gyretes* (Larsén 1966). The median line separating the round median mesocoxal lamellae is anteriorly continuous with the discrimen. Antero-laterally an extensive triangular apodeme is present for muscle attachment. Dorsally, the large trochanteral tendon for muscle attachment expands to the region of the mesoventrite and the mesanepisternum. Compared with generalized coleopteran walking legs, the distal parts of the middle legs are strongly modified. The mesotrochanter (tr2: Figs. 1B; 2B; 3D; 4A; 5A) connects the mesocoxa with the shortened, flattened and roughly triangular mesofemur (fem2: Figs. 1B; 2B; 5A; length: 0.77 mm, width: 0.45 mm; length : width ratio = 1.7 : 1.0). The mesofemur broadly connects with the similarly broadened and flattened mesotibia (tib2: Figs. 1B; 2B; 5A; length: 0.75 mm, width: 0.52 mm; length : width ratio = 1.4 : 1.0), which bears swimming lamellae antero-distally and a row of spines posteriorly. The mesotarsus (tar2: Figs. 1B; 2B) inserts onto the apical mesotibial margin. Its posterior margin is also equipped with swimming lamellae. The internal walls of the mesotibiae and the proximal tarsomere are connected by the cuticular columnae,

as in the other Orectochilini and Enhydrini (Larsén 1966; Beutel 1990). The five tarsomeres are flattened, together forming a fan-shaped structure. The distal margin of the tarsomere 4 is bent dorsad, thus forming a shovel-like structure with the shape of the proximal 3 tarsomeres, similar to the condition found in other Orectochilini and some Enhydrini (Larsén 1966; Beutel 1990). Tarsomere 5 is proximo-mesally connected with the tarsomere 4 and bears a pair of curved claws apically.

The elytra (el: Figs. 1A, C; 5A) are posteriorly truncated and bear a dense vestiture of short and thin setae, similar to the pronotal vestiture. The pubescent dorsal side of the body is a diagnostic character of *Spanglerogyrus*, *Heterogyrus* and Orectochilini (Folkert 1979; Larsén 1966; Miller and Bergsten 2012). Elytral striae are absent. The glossula is present, as in the other Orectochilini and Enhydrini (Larsén 1966; Beutel 1990).

Musculature (Figs. 4; 5; Table 1)**: M28** (IIdlm1) M. mesonoti primus: O: first phragma; I: second phragma. **M30** (Ivlm7) M. mesosterni secundus: O: basal area of profurca; I: mesofurcal arm. **M33** (IItpm2) M. noto-pleuralis: O: process of mesopleural ridge; I: dorso-lateral area of intersegmental membrance between pro- and mesothorax. **M38** (Ispm5) M. profurca-mesepisternalis: O: profurcal arm; I: anterior margin of mesanepisternum. **M40** (IIdvm4/5) M. noto-coxalis, slightly broader medially: O: lateral area of mesoscutum; I: postero-lateral mesocoxal rim. **M41** (IIpcm4) M. episterno-coxalis, broader on mesanepisternum, narrowing towards mesocoxa: O: central area of mesanepisternum; I: antero-lateral mesocoxal rim. **M43** (IIdvm6) M. coxa-subalaris, slightly broader medially: O: membranous area between mesoscutum and mesanepisternum; I: postero-lateral mesocoxal rim. **M46** (IIscm2) M. furca-coxalis posterior, broader on mesofurca, narrowing towards mesocoxa: O: basal area of mesofurca; I: posterior mesocoxal rim. **M47** (IIdvm7) M. noto-trochanteralis: O: mesoscutum; I: mesotrochanter. **M48** (IIpcm6) M. episterno-trochanteralis, triangular, narrower on mesanepisternum, broadening towards mesotrochanter: O: dorsal area of mesanepisternum; I: mesotrochanteral tendon. **M51** (?) M. sterno-trochanteralis: O: invaginated area of mesoventrite; I: mesotrochanteral tendon. **M52** (IIscm6) M. furca-trochanteralis, broader on mesofurca, narrowing towards mesocoxa: O: antero-ventral area of mesofurcal arm; I: mesotrochanter. **M53** M. coxa-trochanteralis medialis, several bundles, distributed over wide area of mesocoxa, converging towards mesotrochanter: O: mesocoxal anterior rim and median wall; I: mesotrochanter. **M54** M. coxa-trochanteralis lateralis, two bundles, the anterior one larger and stronger, the posterior one shorter: O: lateral mesocoxal wall; I: mesotrochanter.

The muscular apparatus of the mesothorax comprises only 12 muscles (excl. **M53** and **M54** as intrinsic mesocoxal muscles), compared to 25 in a more plesiomorphic pattern in other groups of Adephaga and in Polyphaga (Larsén 1966; Beutel and Haas 1966) and 33 in the archostematan *Tetraphalerus bruchi* Heller, 1913 (Friedrich et al. 2009). According to the coleopteran musculature by Larsén (1954), **M29** (IIdlm2) M. mesonoti secundus, **M31** (Ivlm9) M. mesosterni secundus, **M32** (IIdvm8) M. dorsoventralis, **M34** (IItpm10?) M. noto-epimeralis, **M35** (IItpm10) M. epimero-subalaris, **M36** (IItpm7 & 9) M. pleura-alaris, **M37** (IIspm2) M. furca-pleuralis, **M39** (IIdvm2) M. noto-trochantinalis, **M42** (IIpcm3) M. episterno-coxalis, **M44** (IIscm1) M. furca-coxalis anterior, **M45** (IIscm4) M. furca-coxalis lateralis, **M49** (?) M. epimero-trochanteralis and **M50** (IIpcm5) M. trochantero-basalaris are absent.

3.3. Metathorax

Length: 0.98 mm (metacoxa), width: 3.28 mm (paired metacoxae), height: 1.87 mm (from central metascutal area to level of ventral mesocoxal surface) (without hind wings) (length : width : height = 1.0 : 3.3 : 1.9. The propulsive force during flight is only created by the metathorax as in the other beetles and in Strepsiptera (posteromotorism; e.g. Friedrich et al. 2010). The dorsal metathoracic parts are large compared with the corresponding mesothoracic elements. The median portion of the metascutum (sc3: Fig. 3A, B, D) is short and lacks a membranous area, but is widened laterally, as in other Orectochilini and Enhydrini (Hatch 1926; Larsén 1966; Beutel 1990). The paired processes of the anterior metascutal margin bends postero-ventrad into the thoracic lumen thus forming the mesophragma (ph2: Fig. 4D). Antero-laterally the metascutum bears a very small sclerotized process, the metaprealar sclerite (prsc: Fig. 3D), similar to a homologous structure in *Orectogyrus* (Larsén 1966). The alacristae (alc: Fig. 3B) are short (length: 0.24 mm) but distinctly developed, with a sharp posterior edge. A dense field of microtrichia is present on a transverse posterior metascutal concavity. The metascutellum (scl3: Fig. 3B, D) attaches to the posterior metascutal margin. Postero-laterally the postnotum (pn3: Fig. 3B, D) is inflected below the mesoscutum. Its lateral part forms a triangle which is distinctly widening laterally. No metaphragma is developed. The oblique metapleural suture (pls3: Fig. 3D) divides the metapleuron into the anterior metanepisternum (aest3: Fig. 3D) and posterior metepimeron (ep3: Fig. 3D). The posterior edge of the narrow metabasalare (ba3: Fig. 3D) runs parallel to the metathoracic pleural wing process (pwp3: Fig. 3D) and comes close to the dorsal area of the metanepisternum ventrally. The metabasalare of other species in *Orectochilus* and Orectochilini is solidly attached to the metanepisternum (Larsén 1966). The metasubalare (sa3: Fig. 3D) is very small (length: 0.02 mm, height: 0.02

mm) and embedded in the membranous area above the sclerotized metapleuron. The metanepisternum is narrower than in *Orectogyrus* and *Gyretes* (Larsén 1966). The metepimeron connects with the lateral metapostnotal edge postero-dorsally, and with a semicircular disc-like element formed by the first abdominal pleuron.

The metaventrite (v3: Figs. 1B; 2B; 3D; 4A; 5A) reaches its maximum length at midline, with narrow oblique lateral wings enclosed between the posterior margin of the mesocoxae and the anterior margin of the metacoxae. The metakatepisternum is fused with the ventrite, without a trace of a transverse ridge. The discrimen is also lacking, and the metatrochantin is not visible externally. The metaventrite bears a narrow median process (width: 0.68 mm) fitting between the postero-median mesocoxal edges. A visible cleft separates the dorsal metanepisternum from the ventral metaventrite and metacoxa. The metacoxae (cx3: Figs. 1B; 2B, C; 3D; 4A; 5A) are greatly enlarged compared to most other beetles and rectangular, extending far anterolaterad as in other Orectochilini and Gyrinini (Hatch 1926; Larsén 1966). The oblique anterior margin is fused with the posterior margin of the metaventrite. An anterolateral extension reaches into the metathoracic lumen as a disc-like structure for muscle attachment. The fused median metacoxal lamellae are longer than those of the mesocoxae. The connection area of the paired metacoxae is visible as a median suture as in *Heterogyrus* and other Gyrininae (Larsén 1966). The narrow metafurca (fu3: Fig. 4B) with paired parallel arms extends antero-dorsad from the metacoxal lamella and almost reaches the mesofurca anteriorly. The hind legs as a whole are larger than the middle legs. Their distal parts are similar, also forming shortened paddle-like structures for swimming (metafemur length: 0.98 mm, width: 0.72 mm; length : width ratio = 1.4 : 1.0. metatibia length: 1.11 mm, width: 0.79 mm; length : width ratio = 1.4 : 1.0). The internal walls of the metatibiae (tib3: Figs. 1B; 2C; 5A) and the proximal tarsomere are also connected by cuticular columnae (Larsén 1966). Tarsomere 4 is similar to its mesothoracic equivalent, also forming a shovel-like structure with the proximal 3 tarsomeres. This structure is similar to the condition found in other Orectochilini and Enhydrini (Larsén 1966; Beutel 1990).

The sclerotized anterior notal process (anp: Fig. 3B) is attached to the middle region of the lateral metascutal margin. The elongate first axillary sclerite (1ax: Fig. 3B) is separated into two parts by a suture in its middle section, and its antero-proximal part is close to the basisubcostale (bsc: Fig. 3B). The narrow second axillary sclerite (2ax: Fig. 3B) is tightly adjacent to the distal portion of the mesal margin of the first axillary sclerite. The third axillary sclerite (3ax: Fig. 3B) bears three processes and a small proximal sclerite close to the posterior part of the first axillary sclerite (length: 0.80 mm, width: 0.11 mm). The median plate (mp: Fig.

3B) is weakly sclerotized and not distinctly delimited from the membranous area of the wing base. It is divided by a fold along its midline.

Musculature (Figs. 4; 5; Table 1)**: M62** (IIvlm3) M. metasterni primus: O: posterior surface of mesofurcal arm; I: anteriorly on metafurcal arm. **M67** (IIItpm2) M. pleura-praealaris: O: metapleural wing process; I: metaprealar sclerite. **M69** (IIItpm3) M. noto-basalaris, elongated triangular: O: lateral margin of metascutum; I: metabasalare. **M70** (IIItpm10) M. epimero-subalaris, triangular, broader on metapostnotum, narrowing towards metasubalare: O: postero-ventral margin of metapostnotum; I: metasubalare. **M71a** (IIItpm9) M. pleura-alaris a, triangular, broader on metapleural ridge; narrowing towards third axillary sclerite: O: median area of metapleural ridge; I: third axillary sclerite. **M71b** (IIItpm7) M. pleura-alaris b, elongated triangular, broader on metanepisternum, narrowing towards third axillary sclerite: O: antero-dorsal area of metanepisternum; I: third axillary sclerite. **M72** (IIIppm1) M. sterno-episternalis: O: antero-dorsal area of metanepisternum; I: dorsal area of metaventrite. **M76** (IIIdvm5) M. noto-coxalis posterior, broad origin on metascutum, converging on a tendon inserted on metacoxa: O: postero-lateral area of metascutum; I: postero-lateral metacoxal rim. **M84** (IIIdvm7) M. noto-trochanteralis: O: dorsal area of metascutum; I: large disc-shape apodeme of metatrochanter. **M85** (IIIscm6) M. furca-trochanteralis: O: metafurcal arm; I: metatrochanter. **M86** M. coxa-trochanteralis medialis, several bundles: O: anterior metacoxal rim and mesal wall; I: metatrochanter. **M87** M. coxa-trochanteralis lateralis, two bundles, the anterior one stronger with fibers converging medially, the posterior one shorter: O: lateral metacoxal rim; I: metatrochanter. **Mx**, elongated conical, broader on first abdominal pleuron, narrowing towards metacoxa: O: semicircular disc of first abdominal pleuron; I: postero-lateral metacoxal rim.

The metathoracic muscular apparatus metathorax comprises only 10 muscles (excl. **M86** and **M87** as intrinsic metacoxal muscles, **Mx** as abdominal muscle), compared to 27 in a more plesiomorphic pattern in other groups of Adephaga and in Polyphaga (Larsén 1966; Beutel and Haas 2000) and 36 in the archostematan *Tetraphalerus bruchi* (Friedrich et al. 2009). Compared to the coleopteran muscular pattern reported by Larsén (1966), **M60** (IIIdlm1) M. metanoti primus, **M61** (IIIdlm2) M. metanoti secundus, **M63** (IIvlm5) M. metasterni secundus, **M64** (IIIdvm1) M. dorsoventralis primus, **M65** (IIIdvm8) M. dorsoventralis secundus, **M66** (IIIdvm8) M. dorsoventralis tertius, **M68** (IIItpm6) M. noto-pleuralis, **M73** (IIIspm1) M. sterno-episternalis, **M74** (IIIdvm2) M. noto-trochantinalis, **M75** (IIIdvm4) M. noto-coxalis anterior, **M77** (IIIpcm4) M. episterno-coxalis, **M78** (IIIpcm3) M. coxa-basalaris, **M79** (IIIdvm6) M. coxa-subalaris, **M80** (IIscm7?) M. sterno-coxalis, **M81** (IIIscm1) M. furca-coxalis anterior, **M82** (IIIscm4) M. furca-coxalis lateralis and **M83** (IIIscm2) M. furca-coxalis

posterior are absent. Only two dorsoventral muscles **M76** (IIIdvm5) and **M84** (IIIdvm7) are present as indirect flight muscles. **M67** (IIItpm2), **M69** (IIItpm3), **M70** (IIItpm10) and **M71** (IIItpm7 & 9) are present as direct flight muscles. **M85** (IIIscm6) is present, but the other furcacoxal muscles are absent.

4. Discussion

4.1. Phylogenetic and evolutionary interpretations

Even though Gyrinidae are arguably the "basal" sistergroup of the remaining adephagan families and may have originated in the early Triassic or even the late Permian (Ponomarenko 1977; Beutel and Roughley 1988; Beutel et al. 2013; Baca et al. 2017), their morphology and life habits are distinctly modified compared to the hypothetical groundplan of the suborder and of Coleoptera (Beutel 1997; Beutel and Haas 2000; Friedrich et al. 2009). As is sometimes the case with so-called "basal groups" (e.g. Monotremata in mammals or Struthiones in birds; Mickoleit 2004), the autapomorphies (Beutel 1989a, b, 1990; Miller and Bergsten 2012) outweigh few preserved plesiomorphies, such as the lack of the torsion of aedeagus or the retained intrinsic movability of the larval maxilla (Beutel and Roughley 1988). This mainly reflects adaptations to surface swimming in the case of adults, and a preference for greater water depths of the larvae, which are equipped with tracheal gills (Larsén 1966; Beutel and Roughley 1988).

The forelegs of Gyrinidae are long grasping devices suitable for seizing prey objects on the water surface, apparently an autapomorphy of the family (Beutel 1989b). In contrast to most other groups of Adephaga, the ventral procoxal joint is reduced in Gyrinidae, with the exception of the "ancestral" *Spanglerogyrus* (Beutel 1989b), increasing the degrees of freedom at the leg base. This character supports the monophyletic origin of the subfamilies Heterogyrinae (*Heterogyrus*) and Gyrininae (Miller and Bergsten 2012; Beutel et al. 2017). Other features characterizing this clade are the presence of a prothoracic proprioreceptive organ with spatulate setae (se: Fig. 3C) and the laterally compressed protarsi (tar1: Fig. 1B; 2A). In contrast to the pterothoracic segments, the musculature of the prothorax is plesiomorphic, with a well-developed set of neck muscles moving the head and normally developed leg muscles, similar as in other groups of Coleoptera.

The mesothorax of Gyrinidae differs from all other Adephaga by the extensive and flat mesoventrite, which does not articulate with the prosternal process. Phylogenetically this character is ambiguous. Arguably it is a plesiomorphic trait compared with the short and grooved mesoventrite found in the other aquatic families, and also in the terrestrial

Trachypachidae and Carabidae (partim) (Beutel and Roughley 1988; Beutel 1997). However, this structure is apparently suitable for gliding on the surface film of the water and more likely a secondarily acquired feature and autapomorphy of Gyrinidae.

The most conspicuous (and unique) synapomorphy of *Heterogyrus* and Gyrininae is the transformation of the middle and hind legs into shortened and flattened paddle-like structures (Fig. 2B, C), with a fan-shaped tarsus. The swimming lamellae (Larsén 1966), which do not occur in any other aquatic group of beetles, create 52% of the propulsion force (Nachtigall 1961). These conditions are in contrast to the moderately modified middle and hind legs of Dytiscidae and *Spanglerogyrus* (Beutel 1990; Nachtigall 1960), which are more or less elongated and equipped with simple or feather-like swimming hairs, respectively. The paddle-like middle and hind legs enable whirligig beetles to swim rapidly on the water surface, with a frequency of the hind legs of about 60 strokes/sec and about 30/sec of the middle legs (Bott 1928; Nachtigall 1961). It was pointed out by Nachtigall (1961) that the paddle-like legs of Gyrininae exceed the performance of comparable technical machines and form the best-known thrust apparatus in the animal kingdom. The distal leg elements of *Gyrinus* investigated by Nachtigall (1961) are plesiomorphic compared with those of Orectochilini and most Enhydrini. The distal tarsomeres of Orectochilini and most enhydrine genera form a shovel-like structure with the basal ones (Larsén 1966; Beutel 1990), which likely improves the efficiency.

An unusual apomorphy of Orectochilini is the far-reaching reduction of the metathoracic muscular system. Compared with other groups of Neoptera, Coleoptera in general are characterized by a simplified pterothoracic muscular system, probably linked with the strong sclerotization without exposed membranes and reduced degrees of freedom, especially at the leg bases (Beutel and Haas 2000; Friedrich et al. 2009). In contrast to more than 100 pterothoracic muscles suggested for the neopteran groundplan (Friedrich and Beutel 2008), Larsén (1966) proposed 52 muscles as a plesiomorphic status of Coleoptera after a broad investigation of Adephaga and Polyphaga. More recent studies suggest that more muscles are present in the coleopteran groundplan (Beutel and Haas 2000; Friedrich et al. 2009). Sixty-nine muscles were identified in *Tetraphalerus bruchi*, a species of Ommatidae in Archostemata, which is currently recognized as an evolutionary relict (Friedrich et al. 2009). Other thoracic plesiomorphies preserved in Ommatidae (and the closely related Cupedidae) are a transverse ridge of the mesoventrite and exposed metatrochantins (Baehr 1975; Beutel and Haas 2000; Friedrich et al. 2009). Within Orectochilini, only 22 pterothoracic muscles are preserved in *O. villosus*, 17 in *Gyretes zimmermanni* Ochs, 1929 and 16 in *Orectogyrus ornaticollis* Aubé, 1838 (Table 1; Larsén 1954). Among them, 10 are preserved in the metathorax of *O. villosus* and 7

in the metathorax of the other two species examined by Larsén (1966). This is in agreement with a general trend of decreasing complexity of the thoracic musculature in Pterygota and in Coleoptera (Beutel and Haas 2000; Friedrich et al. 2009; Friedrich and Beutel 2010). The metathoracic muscular number observed in Orectochilini are the lowest among 54 beetles examined by Larsén (1966), also including flightless species if degenerated muscles are considered as present (marked as 0 in Larsén 1966), and also less than those observed species in more recent studies on the thorax of Coleoptera (Baehr 1975; Beutel 1986, 1988; Belkaceme 1991; Beutel and Komarek 2004; Friedrich and Beutel 2006). Derived skeletal features correlated with the muscular reductions exclude the interpretation that conditions observed in Orectochilini are due to slight intraspecific variation of the flight muscles. A conspicuous of feature Orectochilini (and the enhydrine genera) is the medially shortened metanotum (Hatch 1925; Larsén 1966; Beutel 1990), which provides limited space for the dorsoventral muscles and no suitable attachment areas for dorsal longitudinal muscles. The loss of the metaphragma is apparently also linked with this modification.

4.2. Functional interpretations of the locomotor apparatus (Fig. 6)

Coleoptera are characterized by reduced degrees of freedom in their thoracic skeleton, and also a distinctly reduced muscular system compared with other groups of Neoptera (Beutel and Haas 2000). The tendency to increase the efficiency and economy of the locomotor apparatus is intensified in the non-archostematan suborders, notably in Polyphaga and Myxophaga (Beutel and Haas 2000). However, a culminating point is reached in the adephagan tribe Orectochilini of Gyrinidae, for instance *O. villosus*. Whriligig beetles in general have optimized surface swimming and retained the capacity of flight with a distinctly reduced pterothoracic muscle set (Larsén 1966).

The dorsal longitudinal muscles are completely missing in Orectochilini and other groups of Gyrinidae (Larsén 1966), apparently linked with modifications of the metanotum (Beutel 1990). They are usually important elements of a flight apparatus operating with the neopteran (and ephemeropteran) indirect mechanism (Brodsky 1994). The function of the metathoracic dorsal longitudinal muscle **M60** (IIIdlm1) in Coleoptera is the longitudinal contraction of the notum, which results in the initial depression of the wings with the first axillary sclerite (Figs. 6Ai, Aii; Brodsky 1994; Haas and Beutel 2001). This muscle is not only lacking in Orectochilini but also in *Heterogyrus* and Gyrininae (pers. obs. R.G. Beutel; Larsén 1966). The intrinsic elasticity of the metanotum alone (Larsén 1966) does not provide a sufficient explanation of the mechanism without adequate muscular control. Interestingly, the dorsal longitudinal

muscles are not only reduced in Gyrinidae, but also poorly developed in two distantly related orders with posteromotorism, Orthoptera and Blattodea (Polyneoptera). In these cases, this is compensated by the metabasalar muscles according to Brodsky (1994). In most examined species of Gyrininae, the tergo-pleural muscle **M69** (IIItpm3) is present and the only muscle attached to the metabasalare (Larsén 1966; Beutel 1990). Therefore, it is likely that this muscle takes over the function of hind wing depression (Figs. 6Bi, Bii), with adduction and pronation of the hind wing through the metabasalare as additional functions (Brodsky 1994). However, **M69** (IIItpm3) is absent in most Orectochilini, and the metabasalare is solidly attached to the metanepisternum in species of this tribe (Larsén 1966; Beutel 1990). We hypothesize that the functions are taken over by the metapleural muscle **M72** (IIIppm1) which moves the sclerite, with a cleft forming a joint between the metanepisternum, the metaventrite and the metacoxa (Fig. 3D) (Larsén 1966: Orectochilini and *Dineutus*). **M72** (IIIppm1) is missing in *Gyrinus* and *Aulonogyrus* (Larsén 1954, 1966; Beutel 1990), whereas **M69** (IIItpm3) is present in the species of both genera. Under the control of the metabasalare, the basisubcostale also becomes responsible for the depression (Brodsky 1994). The control of the first axillary sclerite is shifted from the median notal process to the anterior notal process (Brodsky 1994), which is generally preserved in Gyrinidae (Hatch 1926; Larsén 1966; Beutel 1990).

The large metathoracic dorso-ventral muscle **M84** (IIIdvm7; in *O. villosus* length: 2.20 mm, width: 0.45 mm; length : width ratio = 4.9 : 1.0) of Gyrininae (Larsén 1966) must play a dominant role as a levator of the hind wing, considering the absence of most other dorso-ventral muscles (Fig. 6F; Larsén 1966). Additionally, this muscle is responsible for the backstroke of the hind leg during swimming, as synergist of the large metacoxal muscle **M87** (Fig. 6F; Larsén 1966; in *O. villosus* length: 1.80 mm, width: 1.69 mm). During this activity, the hind wings and associated elements of the flight apparatus are shielded and locked by the elytra, with the mesonotal scutellar shield and the metanotal alacristae forming a combined elytral arresting mechanism (Larsén 1966; Beutel 1990; Beutel and Haas 2000). The activity of **M84** (IIIdvm7) during flight is probably supported by another dorso-ventral muscle, **M76** (IIIdvm5). However, as this muscle is extremely slender (width 0.07 mm) compared with **M84** (IIIdvm7), its effect is probably minimal.

In the groundplan of Coleoptera and in most species examined, two muscles connect with the metasubalare, the dorsal-ventral muscle **M79** (IIIdvm6) and the tergo-pleural muscle **M70** (IIItpm10) (Fig. 6C; Larsén 1954; Haas and Beutel 2001; Friedrich et al. 2009; Friedrich and Beutel 2010). Due to the absence or reduction of **M79** (IIIdvm6) in Gyrinidae except *Dineutus* (Larsén 1966), its function has to be taken over by another muscle (Fig. 6D). It is conceivable

538 that the function of supination (Brodsky 1994) is taken over by **M70** (IIItpm10) in Orectochilini
539 and most other Gyrinidae (Larsén 1966).
540 It is noteworthy that the two bundles of the tergo-pleural muscle **M71** (IIItpm7 and 9) are
541 absent in the two orectochiline species *O. ornaticollis* and *G. zimmermanni* (Larsén 1966), as
542 in some other coleopteran species with reduced flight apparatus (Haas and Beutel 2001). As the
543 only muscle connected with the third axillary sclerite in Neoptera (Friedrich and Beutel 2008),
544 it is involved in at least three of the four stages of the wing stroke (Brodsky 1994), also initiating
545 the processes of unfolding and folding the wings (Brodsky 1994; Haas and Beutel 2001). We
546 cannot exclude the possibility that these two orectochiline species are flightless. However,
547 flight appears rather possible, as the hind wings and skeletal parts of their flight apparatus show
548 no observable traits of reduction compared with the other Gyrinidae (Larsén 1966). If indeed
549 individuals of these two species are able to fly, it is unclear how the loss of **M71** is compensated
550 for.
551 It was pointed out that elytral movement of beetles play a minor role in creating
552 propulsive forces during flight (Haas and Beutel 2001). Their obvious function is protecting the
553 hind wings at rest, also shielding and locking the flight apparatus during swimming in Gyrinidae
554 (Haas and Beutel 2001; Larsén 1966). Aside from this, they are probably also involved in flight
555 control, improving the maneuverability of beetles and directing the airflow to the hind wings
556 (Brodsky 1994). It was demonstrated for species of Orthoptera that the control of
557 posteromotoric flight is the most important function of the leathery forewings (Brodsky 1994).
558 The synchronous pronation and supination of coleopteran elytra during flight is probably not
559 only a passive movement (Haas and Beutel 2001), but also under the control of a series of
560 mesothoracic flight-related muscles associated with the articulatory processes of the elytra (elap:
561 Fig. 3A).
562 The pterothoracic segments of Orectochilini differ strongly from conditions observed in
563 other groups of Coleoptera (e.g. Larsén 1966; Belkaceme 1991; Beutel 1986, 1988; Beutel and
564 Komarek 2004, Friedrich et al. 2009), with a remarkable degree of reduction of the muscular
565 system. It is conceivable that this optimizes efficiency, especially in the context of dual
566 alternative functions of flight and swimming on the water surface. Future investigations with
567 biomechanical and physiological approaches may improve the understanding of the
568 Orectochilini locomotor system, and possibly inspire interesting applications in bionics in the
569 future.
570

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682 **Table 1: The Thoracic Musculature of Orectochilini**

683 (Muscular nomenclatures from Larsén (1954) and Friedrich and Beutel (2008) are listed
684 respectively in the first and second rows due to homology (Friedrich et al. 2009). Here we revise
685 M38 is homologous as Ispm5 instead of Ispm6, according to the origin and insertion of this
686 muscle in the same side of the insect body. Muscle present is represented with "+" in green,
687 absent with "-" in orange, unsure with "?" or "/"in yellow.)

Larsén 1954	Friedrich & Beutel 2008	*Orectochilus villosus*	*Orectogyrus ornaticollis*	*Gyetes zimmermanni*
Prothorax				
M1	ldlm2	+	+	-
M2	ldlm1	+	+	+
M3	ldlm3	+	+	+
M4	ldlm5	-	-	-
M5	lvlm3	+	+	+
M6	lvlm1	+	+	+
M7	ldvm6	+	+	+
M8	ldvm8	-	-	-
M9	ldvm5	-	-	-
M10	ldvm2/3	+	+	+
M11	ldvm10	+	+	+
M12	ltpm3?	-	-	-
M13	ltpm6	+	+	+
M14	ldvm13	+	+	+
M15	ldvm16/17	+	+	+
M16	lpcm4	+	+	+
M17	lpcm8	-	-	-
M18	lscm1	-	-	-
M19	lscm2	-	-	-
M20	lpcm8	+	+	+
M21	/	+	/	/
M22	/	+	/	/
Mesothorax				
M28	lldlm1	+	+	+
M29	lldlm2	-	-	-
M30	lvlm7	+	+	+
M31	lvlm9	-	+	+
M32	lldvm8	-	-	-
M33	lltpm2	+	+	-
M34?/35	lltpm10	-	-	-
M36a	lltpm9	-	-	-
M36b	lltpm7	-	-	-
M37	llspm2	-	-	-
M38	lspm5	+	+	+
M39	lldvm2	-	-	-
M40	lldvm4/5	+	-	-
M41	llpcm4	+	-	+
M42	llpcm3	-	-	-
M43	lldvm6	+	-	-
M44	llscm1	-	-	-
M45	llscm4	-	-	-
M46	llscm2	+	-	+
M47	lldvm7	+	+	+
M48	llpcm6	+	+	+
M49	/	-	-	-
M50	llpcm5	-	-	-
M51	?	+	+	+
M52	llscm6	+	+	+
M53	/	+	/	/
M54	/	+	/	/

Metathorax				
M60	IIIdlm1	-	-	-
M61	IIIdlm2	-	-	-
M62	IIvlm3	+	+	+
M63	IIvlm5	-	-	-
M64	IIIdvm1	-	-	-
M65	IIIdvm8	-	-	-
M66	IIIdvm8	-	-	-
M67	IIItpm2	+	+	+
M68	IIItpm6	-	-	-
M69	IIItpm3	+	-	-
M70	IIItpm10	+	+	+
M71a	IIItpm9	+	-	-
M71b	IIItpm7	+	-	-
M72	IIIppm1	+	+	+
M73	IIIspm1	-	-	-
M74	IIIdvm2	-	-	-
M75	IIIdvm4	-	-	-
M76	IIIdvm5	+	+	+
M77	IIIpcm4	-	-	-
M78	IIIpcm3	-	-	-
M79	IIIdvm6	-	-	-
M80	IIscm7?	-	-	-
M81	IIIscm1	-	-	-
M82	IIIscm4	-	-	-
M83	IIIscm2	-	-	-
M84	IIIdvm7	+	+	+
M85	IIIscm6	+	+	+
M86	/	+	/	/
M87	/	+	/	/
Mx	/	+	/	/

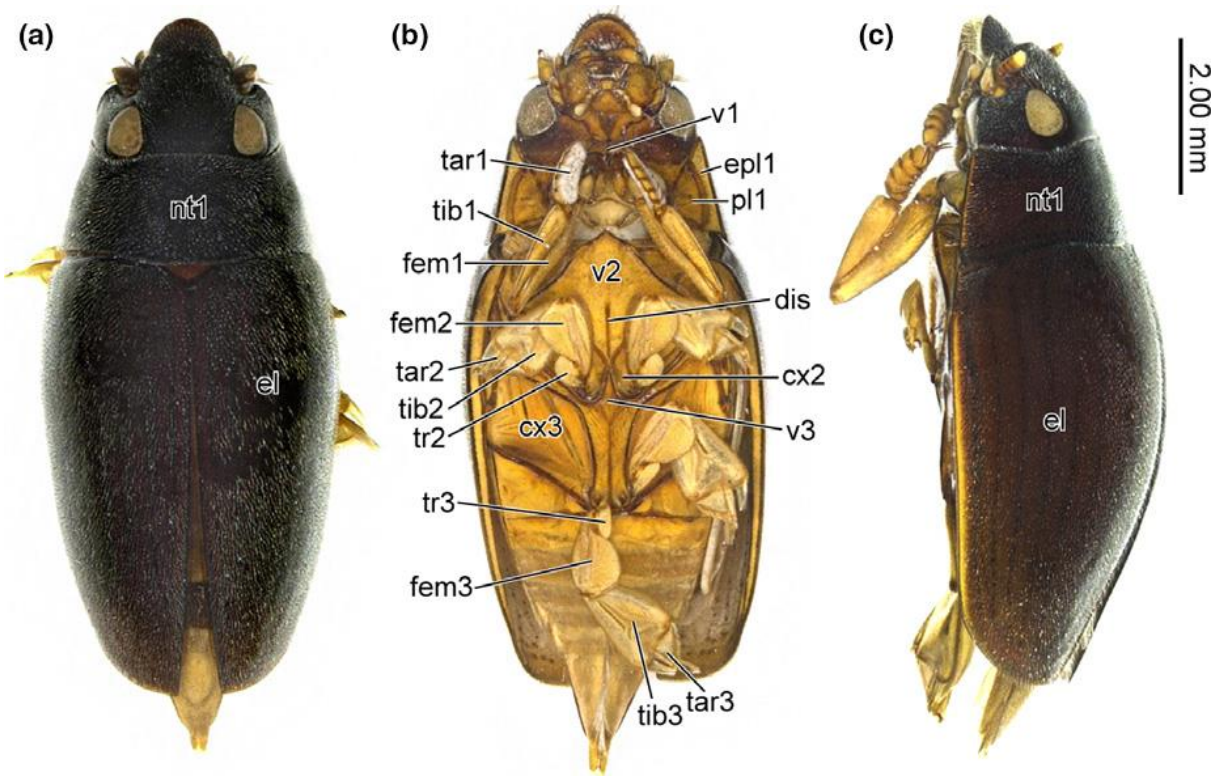


Fig. 1. *Orectochilus villosus*, digital photographs, male habitus. **A:** dorsal view; **B:** ventral view; **C:** lateral view.

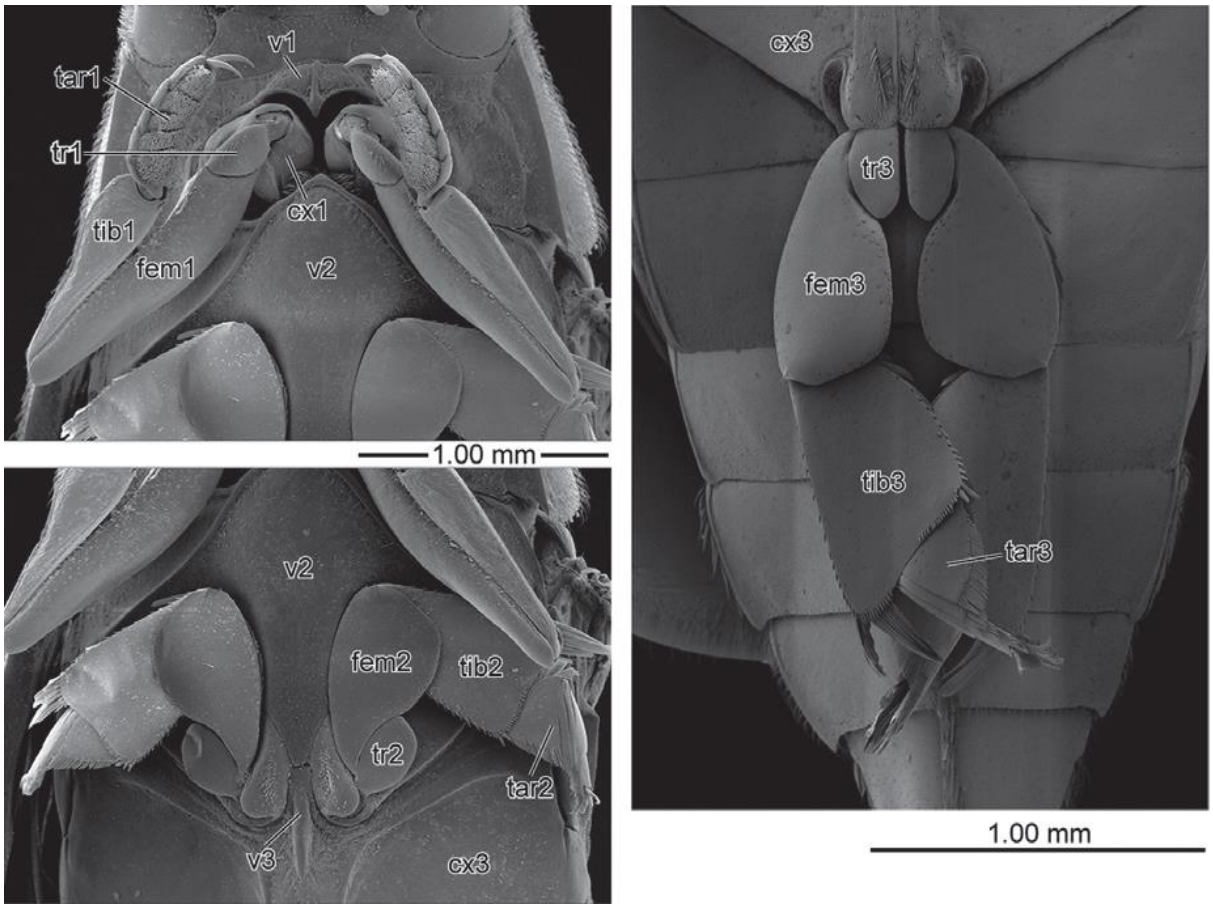


Fig. 2. *Orectochilus villosus*, SEM micrographs, male legs. **A:** fore leg; **B:** mid leg; **C:** hind leg.

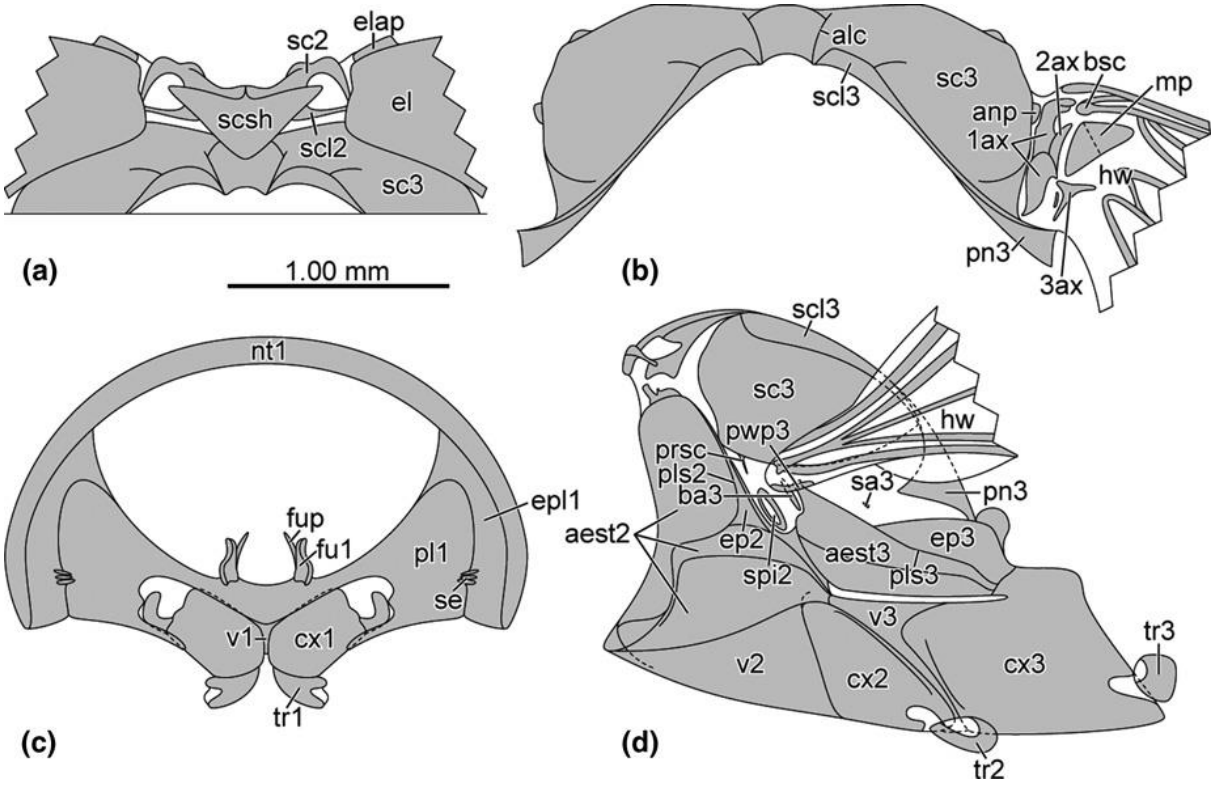


Fig. 3. *Orectochilus villosus*, line drawing, thoracic skeleton. **A:** dorsal view of mesothorax; **B:** dorsal view of metathorax; **C:** posterior view of prothorax; **D:** lateral view of pterothorax.

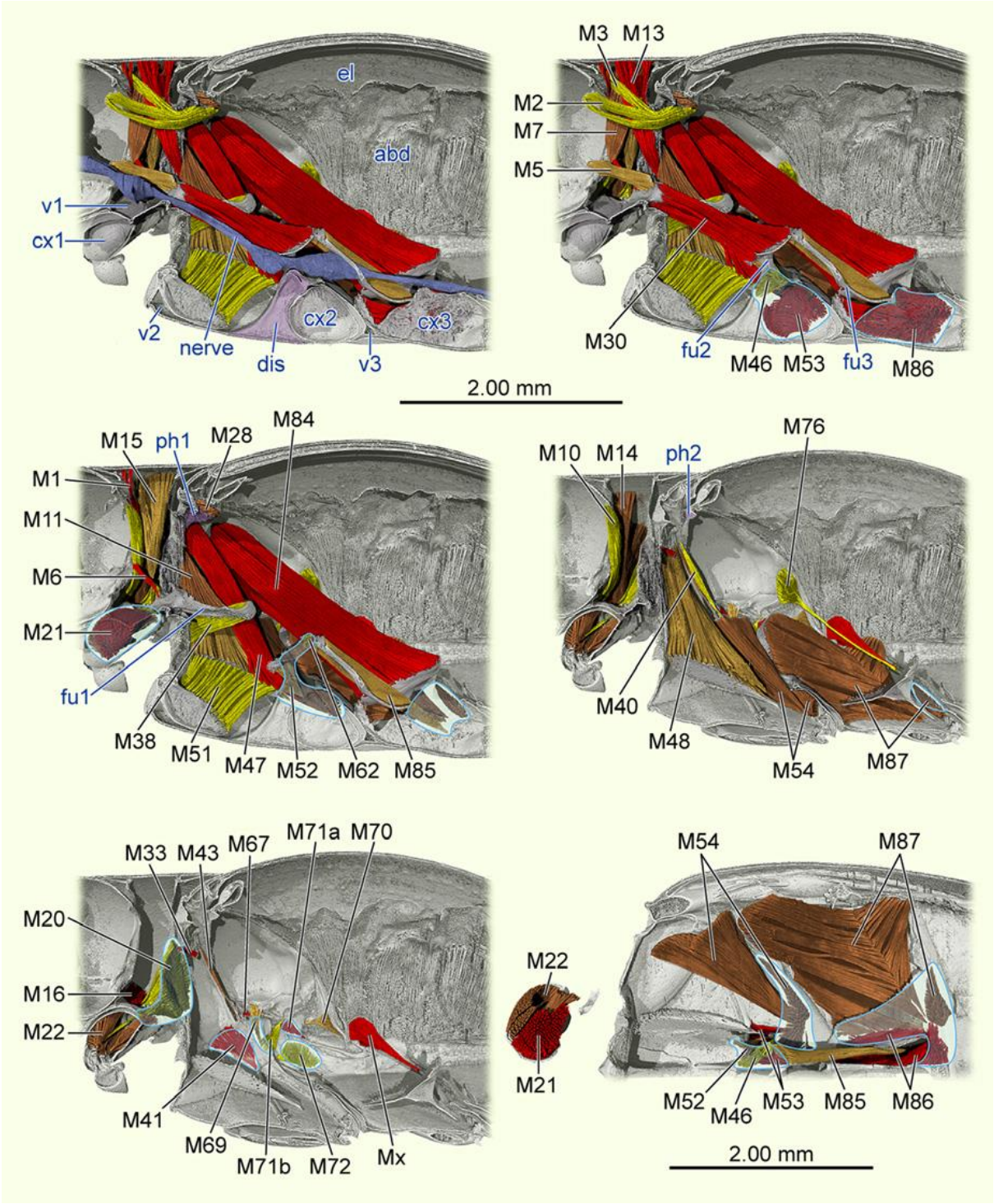


Fig. 4. *Orectochilus villosus*, 3D-reconstruction, thoracic endoskeleton and muscles. Skeletal structures in blue lines rendered transparent to show muscles behind them. Skeletal structures labeled in blue, muscles in black. **A-E:** lateral view, dis and ph1/2 in pink; **F:** dorsal view, coxal muscles. **Scale bars:** upper 2.00 mm for **A-E**, lower 2.00 mm for **F**.

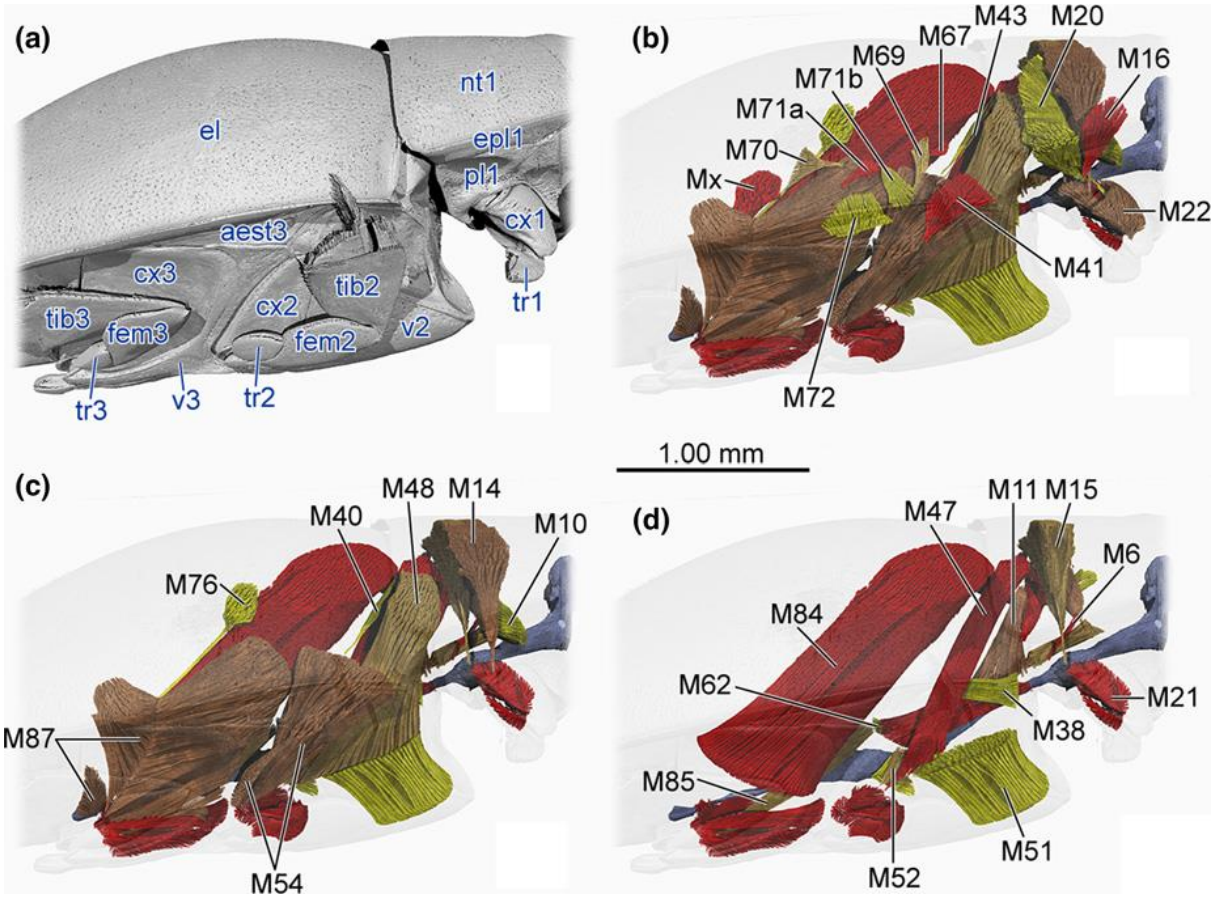
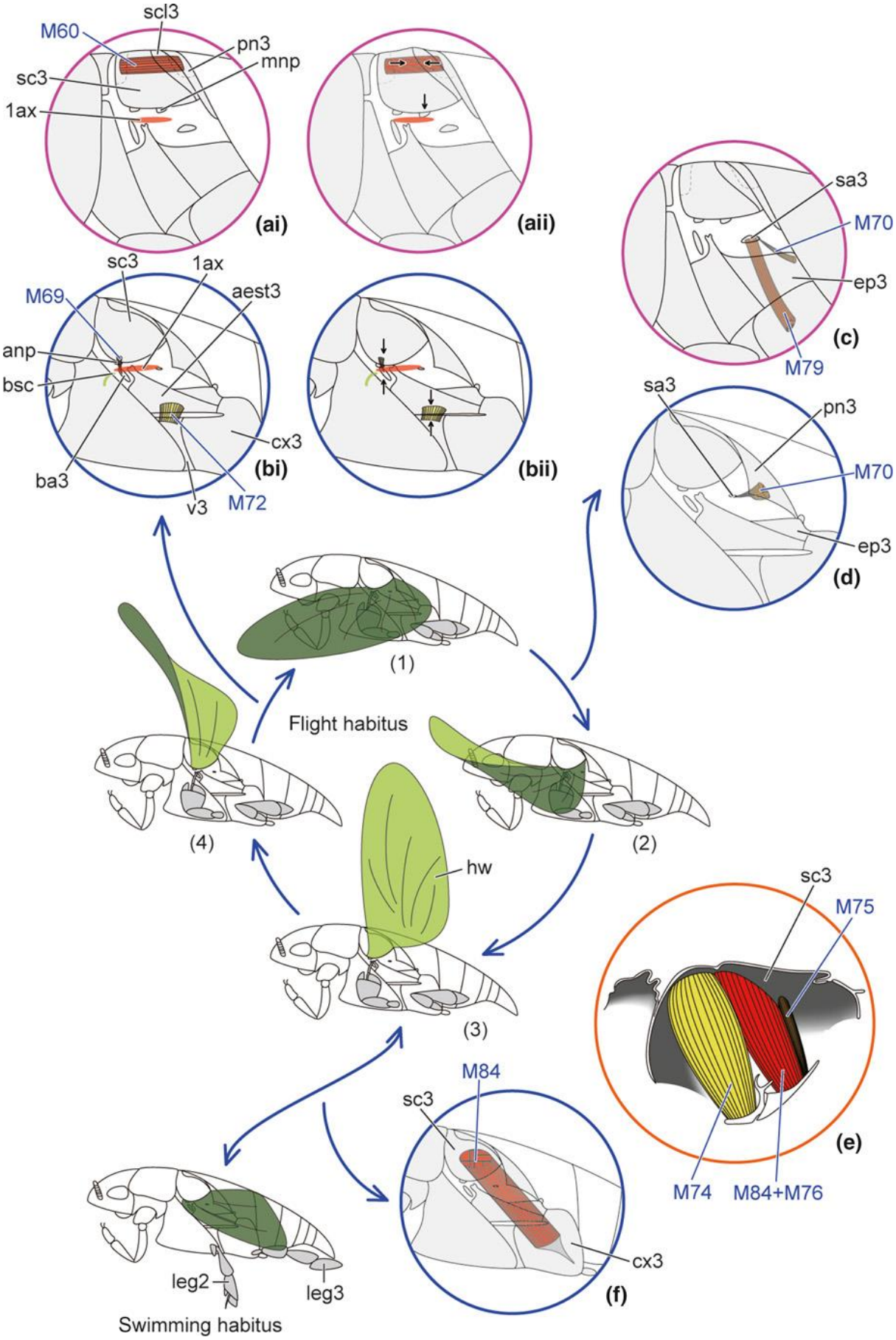


Fig. 5. *Orectochilus villosus*, 3D-reconstruction, thoracic skeleton and muscles. Skeletal structures labeled in blue, muscles in black. **A:** lateral view, exoskeleton; **B-D:** lateral view, skeleton transparent.


scl3
M60
pn3
mnp
sc3
1ax
(ai)
(aii)
sa3
M70
ep3
M79
(c)
sc3
1ax
M69
aest3
anp
bsc
cx3
ba3
v3
M72
(bi)
(bii)
sa3
pn3
M70
ep3
(d)
(1)
Flight habitus
(4)
(2)
hw
(3)
sc3
M75
(e)
M74
M84+M76
M84
sc3
cx3
(f)
leg2
leg3
Swimming habitus

747

748 **Fig. 6.** Schematic diagram for functional interpretation. The insect wing stroke can be divided
749 into 4 distinct stages (Brodsky 1994): **(1)** depression and turning forward; **(2)** turning backward
750 and beginning supination; **(3)** elevation and end of supination; **(4)** pronation. In Gyrinidae, the
751 mid- and hind legs (leg2, 3) are laid close to the body during flight (Larsén 1966), and
752 alternatively extended and flexed during swimming (Nachtigall 1961). Elytra omitted. **Ai, Aii:**
753 **M60** (IIIdlm1) initiates depression in generalized Coleoptera; **Bi, Bii:** either **M69** (IIItpm3) or
754 **M72** (IIIppm1) initiate depression in Gyrinidae; **C:** both **M70** (IIItpm10) and **M79** (IIIdvm6)
755 control supination in generalized Coleoptera; **D:** only **M70** (IIItpm10) controls supination in
756 Gyrinidae; **E:** the large metacoxal muscles nearly form a single compact unit in the cricket
757 *Gryllus bimaculatus* (redrawn from Brodsky 1994: fig. 7.13a(ii)); **F:** extremely large **M84**
758 (IIIdvm7) controls both hind wing elevation and hind leg backstroke.
759