Proc. Arthropod. Embryol. Soc. Jpn. 55, 1–7 (2025)

ISSN 1341–1527

What are the epipleuron, cryptopleuron, and pleuron in the prothorax of the adult Carabidae (Coleoptera, Insecta)?: Redefinitions based on the muscular system

Yukimasa KOBAYASHI[1], Karen TERADA[2], Akihiro HIRAYAMA[3], Yuuki OOSAWA[4], Kazuhiro NIIKURA[5] and Yasuoki TAKAMI[2]

[1] *Sayamadai 2–21–18, Sayamashi, Saitama 350–1304, Japan*
[2] *Graduate School of Human Development and Environment, Kobe University, Nada, Kobe, Hyogo 657–8501, Japan*
[3] *Hyogo Prefectural Institute of Technology, Suma, Kobe, Hyogo 654–0037, Japan*
[4] *Toyogaoka 2–1–10–302, Tama-shi, Tokyo 206–00341, Japan*
[5] *Forestry Agency, Ministry of Agriculture, Forestry and Fisheries, Kasumigaseki 1–2–1, Chiyoda-ku, Tokyo 100–8952, Japan*
E-mail: dineutus@hotmail.co.jp (YK)

https://doi.org/10.60372/paesj.55.0_1

ABSTRACT

The lateral body walls of the adult prothorax of adepahgan beetles consist of the epipleuron and the pleuron which are divided dorso-ventrally by the cryptopleural suture running antero-posteriorly. The body wall invaginated from this suture is called cryptopleuron. The epipleuron is generally interpreted as the structure of the lateral side of the tergum (notum) inflexed ventrally; thus, as a part of the tergum. However, there are different interpretations for the pleuron and cryptopleuron; that is, the katepisternum for the pleuron, and katepimeron or anepisternum for the cryptopleuron. To resolve such difference of interpretations, we analyzed the larval muscular system of the carabid beetle, *Carabus insulicola*, using an X-ray micro-CT. Chiefly based on the arrangement of landmark muscles for the paracoxal suture (PCXS) and paracoxal ridge (PCXR) which demarcate the pleuron into the basal anapleuron and the distal katapleuron in both larval and adult Carabidae, we redefine the epipleuron as the anapleuron (precoxa) (not a part of the tergum), the pleuron as the katapleuron, and the cryptopleuron as the PCXR which is the body wall invaginated from the PCXS. The cryptopleural suture thus corresponds to the PCXS. The dorsal side of the PCXR corresponds to the invaginated ventral area of the anapleuron, and the ventral side of the PCXR corresponds to the invaginated dorsal area of the katapleuron. Our redefinitions of the epipleuron, pleuron, and cryptopleuron, thus are largely different from any interpretations so far proposed, and also suggest that the hypomeron (homologue of the epipleuron) of the prothorax of the polyphagan beetles corresponds to the ventrally extended anapleuron but not to a part of the tergum.

INTRODUCTION

According to the traditional nomenclature for the thoracic sclerites, the lateral body walls of the adult prothorax of the suborder Adephaga, including the Carabidae, consist of the epipleuron and the pleuron. These two areas are separated dorso-ventrally by the cryptopleural suture which runs antero-posteriorly (Fig. 1). The body wall invaginated from this suture is called cryptopleuron (endopleuron), and the dorsal and ventral sides of the cryptopleuron form the apodeme to which muscles are attached. The epipleuron is generally interpreted as the structure of the lateral side of the tergum (notum) inflexed ventrally; thus, as a part of the tergum (e.g., Hlavac 1972; Naomi 2014, 2024). On the other hand, Matsuda (1970) interpreted the pleuron of Adephaga (based on a gyrinid beetle) as the katepisternum, and the cryptopleuron as the katepimeron (cf. Matsuda 1970, Fig. 85B), although he did not directly refer to the morphology of the Carabidae. Naomi (2014), however, interpreted only the narrow sclerite located near the dorso-posterior region of the coxa as the katapleuron, and the broad

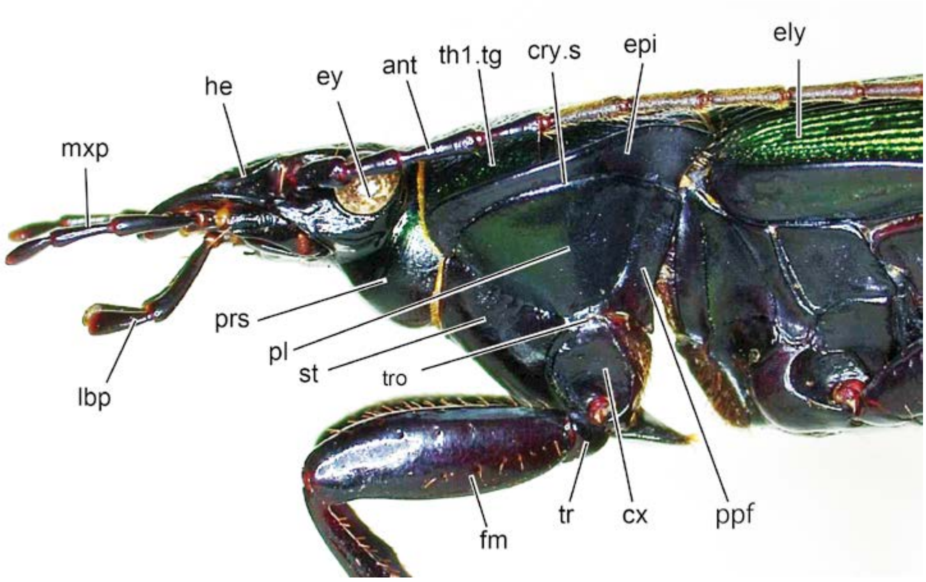

Fig. 1 Lateral view of the prothorax of *Carabus insulicola*. Names of sclerites follow the traditional nomenclature. ant: antenna, cry.s: cryptopleural suture, cx: coxa, ely: elytron, epi: epipleuron, ey: eye, fm: femur, he: head, lbp: labial palp, mxp: maxillary palp, pl: pleuron, ppf: posterior pleural flange (sensu Hlavac 1972), prs: presternum, st: sternum, th1.tg: prothoracic tergum, tr: trochanter, tro: trochantin.

area between the epipleuron and katapleuron as the anepisternum (Naomi 2014, Fig. 1A). He regarded a plate-like structure ('posterior pleural flange' sensu Hlavac 1972) extended posteriorly from his anepisternum as the epimeron, and also regarded the furrow running vertically between the anepisternum and epimeron as the pleural suture. Moreover, Naomi (2014) interpreted that the cryptopleuron is an inner structure of the body wall formed near the dorsal edge of the anepisternum and its deepest region corresponds to the dorsal edge of the anepisternum. Naomi (2024), however, corrected his interpretations for these prothoracic structures as follows. He regarded the pleuron (first interpreted as the anepisternum) as the katepisternum, and the cryptopleuron (first interpreted as a part of the anepisternum) as 'a candidate of internalized (or invaginated) anepisternum'. Naomi (2024) also corrected his 'epimeron' to the anepimeron, and newly interpreted a small projection formed below the anepimeron as the katepimeron. Matsuda (1970) and Naomi (2024) thus share a common interpretation that the pleuron corresponds to the katepisternum and the epipleuron belongs to the tergum, but they differ in the interpretations of both cryptopleuron and epimeron.

To resolve such difference in interpretations of the prothorax of adult Adephaga, it is important to analyze not only the outer structure of the body wall but also the inner structure such as a muscular system. The larval muscular system generally has lower specialization than that of the adult system (Kobayashi, unpublished data); hence, the larval system helps to validate the homologous constituents of different thoracic segments. Based on the analysis of the muscular system of the first instar larva of *Carabus insulicola* (Carabidae), Kobayashi et al (2022) proposed the idea that the area so far called larval pleuron is derived from the two basal leg segments, or podomeres, of Arthropoda; that is, the proximal precoxa (known as the anapleuron) and the distal subcoxa (known as the katapleuron). This idea is based on the mode of arrangements of muscles attached to the dorsal or ventral side of the paracoxal suture (PCXS) / paracoxal ridge (PCXR) which are formed along the boundary between the precoxa and subcoxa.

As mentioned before, although there are different interpretations for the lateral part of the adult prothorax of Adephaga, the most problematic structure is the epipleuron which is distinguished by the dorsal side of the cryptopleuron. Kobayashi et al (2022) confirmed the presence of the PCXS/PCXR in the larval prothorax as well as meso and metathoraxes (Fig. 2, PCXR; Fig. 3, PCXS). This larval prothoracic PCXS seems to be comparative to the adult cryptopleural suture that define the lower (ventral) limit of the epipleuron. In the present paper, we try to verify if this generalization is correct.

MATERIALS AND METHODS

An adult male of *Carabus insulicola* was pinned and dried, the forebody of which was photographed using a digital camera equipped in the stereo microscope S9i (Leica Microsystems, Wetzlar, Germany).

For X-ray micro-CT scanning, the first instar larvae of *C. insulicola* were fixed using alcoholic

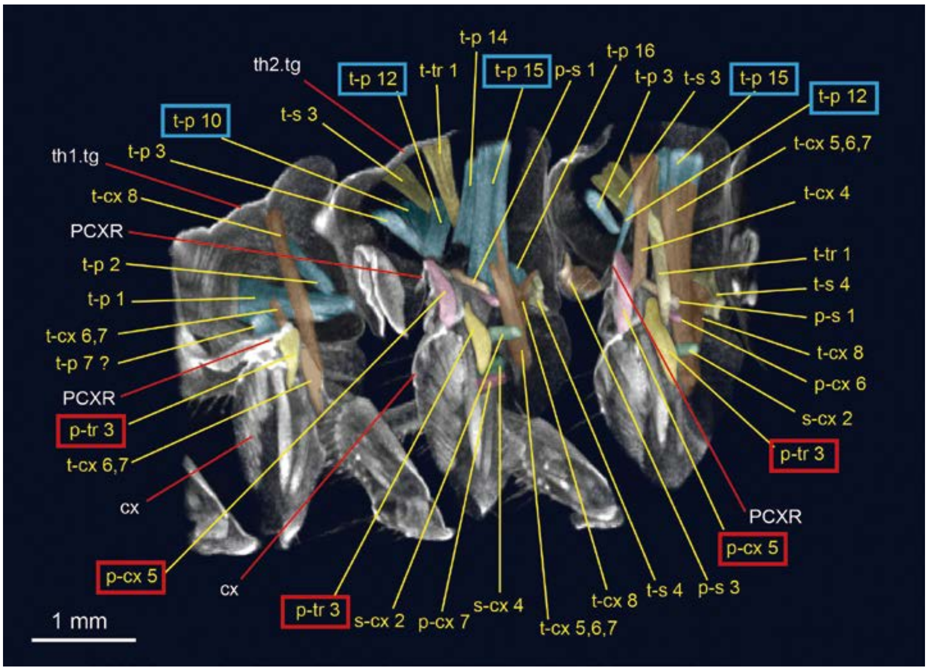

Fig. 2 Parasagittal-sectioned micro-CT image of the newly hatched larva of *Carabus insulicola*, mesal view of the right half of thoracic segments. The image of the alimentary canal was digitally removed from the original image. Abbreviations for muscles follow Matsuda's system and are highlighted in yellow letters. Red squares indicate pleuro-coxal (p-cx 5) and pleuro-trochanteral (p-tr 3) muscles attached to the ventral side of the paracoxal ridge (PCXR). Blue squares indicate tergo-pleural (t-p 10, t-p 12, and t-p 15) muscles attached to the dorsal side of the PCXR. cx: coxa, th1, 2.tg: pro- and mesothoracic tergum.

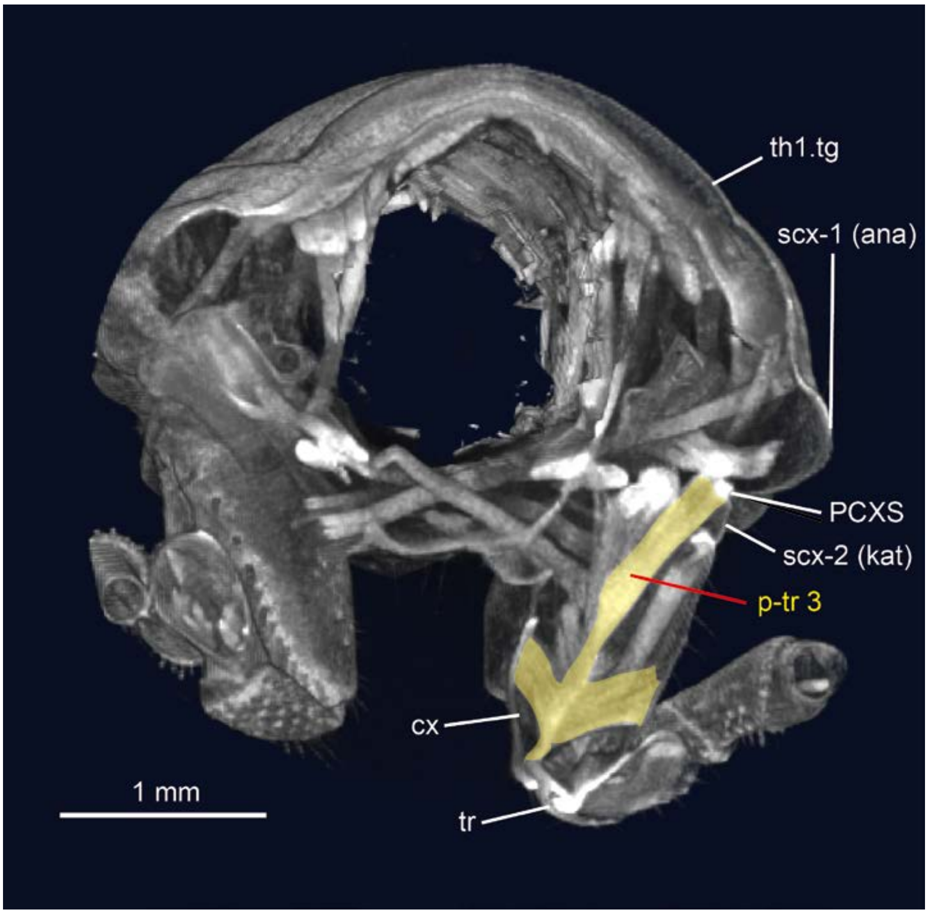

Fig. 3 Cross-sectioned micro-CT image of the middle part of the larval prothorax of *Carabus insulicola*, showing the muscle p-tr 3 (highlighted in yellow). The larva in this image is the same as in Fig. 2. The image of the alimentary canal was digitally removed from the original image. ana: anapleuron, cx: coxa, kat: katapleuron, PCXS: paracoxal suture, scx-1, 2: subcoxa-1 and 2, th1.tg: prothoracic tergum, tr: trochanter.

Bouin's fluid for several hours, and then preserved in 70% ethanol. Fixed larvae were soaked in 1% ethanol iodine for a week. Infiltrated larvae were washed with 70% ethanol and mounted individually in a plastic tube (diameter, 1 cm; height, 5 cm) just before scanning.

X-ray micro-CT scans were performed using the XRadia Micro XCT-400 system (Carl Zeiss, Oberkochen, Germany). The acquisition parameters for scans were as follows: accelerating voltage = 150 kV, source current = 65 µA, exposure time = 10 sec; samples rotated from -90° to 90°, with a rotation step of 0.01°. A total of 1,800 images were obtained per sample, resulting in a voxel size of 6.43 µm. Scans were converted to stacks of digital image slices, which were reconstructed into three-dimensional (3D) images and analyzed using Amira 6.4 (Thermo-Fisher, Waltham, MA, USA). Volume-rendered images were edited by deleting the alimentary canal and viewed from the longitudinally or latitudinally sliced plane of the larval body.

RESULTS AND DISCUSSION

Landmark muscles for the PCXS and PCXR

In all thoracic segments in the larvae of *Carabus insulicola*, the pleuro-trochanteral muscle p-tr 3 (sensu Matsuda 1970) attaches to the ventral side of the posterior PCXR (Figs. 2, 3, p-tr 3). Moreover, the pleuro-coxal muscle p-cx 5 attaches to the ventral side of the anterior PCXR of meso and metathoraxes (Fig. 2, p-cx 5). The muscle p-tr 3 extends from the PCXR to the trochanter, and p-cx 5 extends from the PCXR to the coxa. These muscles are thus the landmark muscles attaching on the ventral side of the PCXR.

On the other hand, there exist such tergo-pleural muscles as t-p 10, t-p 12, t-p 14, and t-p 15 (Fig. 2) which connect the tergum and the dorsal side of the PCXR in meso and metathoraxes. In our previous analysis (Kobayashi et al. 2022), the presence of t-p 10 was not certain. In this paper, however, we regarded this muscle as a muscle independent from t-p 12. These muscles exist in homologous positions between these body segments, and thus are landmark muscles attaching on the dorsal side of the PCXR. In the prothorax, however, the homology of these landmark muscles is slightly ambiguous, because several muscles attaching to the head capsule intervene among these tergo-pleural muscles.

Redefinitions of the epipleuron, cryptopleuron, and pleuron

In Holometabola, there is little literature tracing how the larval muscles are transferred to the adult ones. However, as in the case of larval muscles, it is possible to identify the constituents of adult body walls by focusing on the homology of muscles attaching to the PCXR. Using this method, we redefine the epipleuron, cryptopleuron, and the area previously referred to as the pleuron as follows. Our redefinitions are also schematically shown in Fig. 4.

Cryptopleuron: In the prothorax of the adult carabid species (*Carabus granulatus*, *Trechiotes perroti*, and *Sinaphaenops wangorum*), the broad fun-like muscle M 20 (sensu Larsén 1966) lies just inside the exoskeleton hitherto referred to as the pleuron (Larsén 1966, Figs. 66, 67, M 20; Luo et al. 2018, Figs. 5C, D, 10C, D, M 20). This muscle arises along the whole

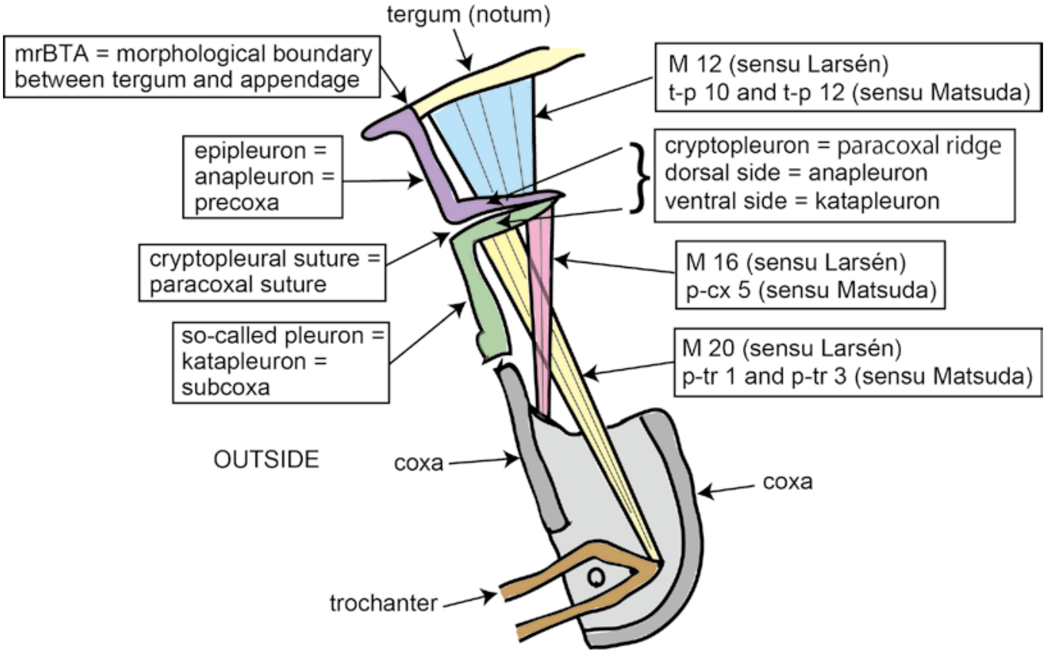

Fig. 4 The lateral body wall of the prothorax of the Carabidae. The figure is a schematic cross section of the right lateral body wall and coxa (anterior view).

ventral side of the cryptopleuron and inserts to the trochanter (Fig. 4, M 20). Judging from the origin and insertion of this muscle, M 20 is presumed to be p-tr 3 and p-tr 1 supposedly derived from the larval p-tr 3. Larsén also noted the possibility that mesothoracic pleuro-trochanteral muscles M 48 (p-tr 1) and M 49 (p-tr 3) together are serially homologous with M 20 (Larsén 1966, p. 173). Just inside M 20, there exists the thin muscle M16 arising from the anterior part of the cryptopleuron and attaching by a tendon to the anterior rim of the coxa (Larsén 1966, Figs. 66, 67, M 16; Luo et al. 2018, Figs. 5B, 10B, M 16) (Fig. 4, M 16). Although, p-cx 5 cannot be detected in the larval prothorax of *C. insulicola*, M 16 of the adult *C. granulatus* almost certainly corresponds to p-cx 5 judging from the homologous position of the mesothoracic pleuro-coxal muscle M 41 of this species (Larsén 1966, Fig. 87, M 41). In other carabid species, *T. perroti* and *S. wangorum*, their prothoracic M 16 is homologous with the mesothoracic M 41, because both muscles are regarded as muscles Ipcm4 and IIpcm4, respectively (Luo et al. 2018, Table 1). In polyphagan beetles also, M 41 is interpreted as p-cx 5 (Beutel and Hass 2000; Friedrich and Beutel 2006). Such interpretations of the muscles M 16 and M 20 naturally lead to the presumption that the ventral side of the cryptopleuron is homologous with the ventral side of the larval PCXR, and the cryptopleural suture with the PCXS.

Pleuron: The muscles p-tr 1 and p-cx 5 are regarded as the muscles originating in the katepisternum, and p-tr 3 as the muscle originating in the katepimeron (Matsuda 1970). In the prothorax of the Carabidae, however, there exists no trace of the pleural suture that divides the so-called pleuron (Fig. 1, pl) into the anterior episternum and the posterior epimeron as in the case of pterothoraxes. Therefore, the arrangements of these muscles lead to the presumption that the pleuron corresponds to the katapleuron where the katepisternum and katepimeron are fused together (Fig. 4, katapleuron; Fig. 5, kat). Since p-tr 1 (M 20), p-tr 3 (M 20), and p-cx 5 (M 16) attach to the ventral side of the cryptopleuron, this ventral side corresponds to the invaginated dorsal area of the katapleuron (Fig. 4). Our definition of the pleuron (katapleuron) thus differs from both Matsuda's (1970) and Naomi's (2024) interpretation (only katepisternum). Our definition of the ventral side of the cryptopleuron (invaginated dorsal area of katapleuron) also differs from the Matsuda's (1970) definition (katepimeron), and also differs from the Naomi's (2024) one (invaginated

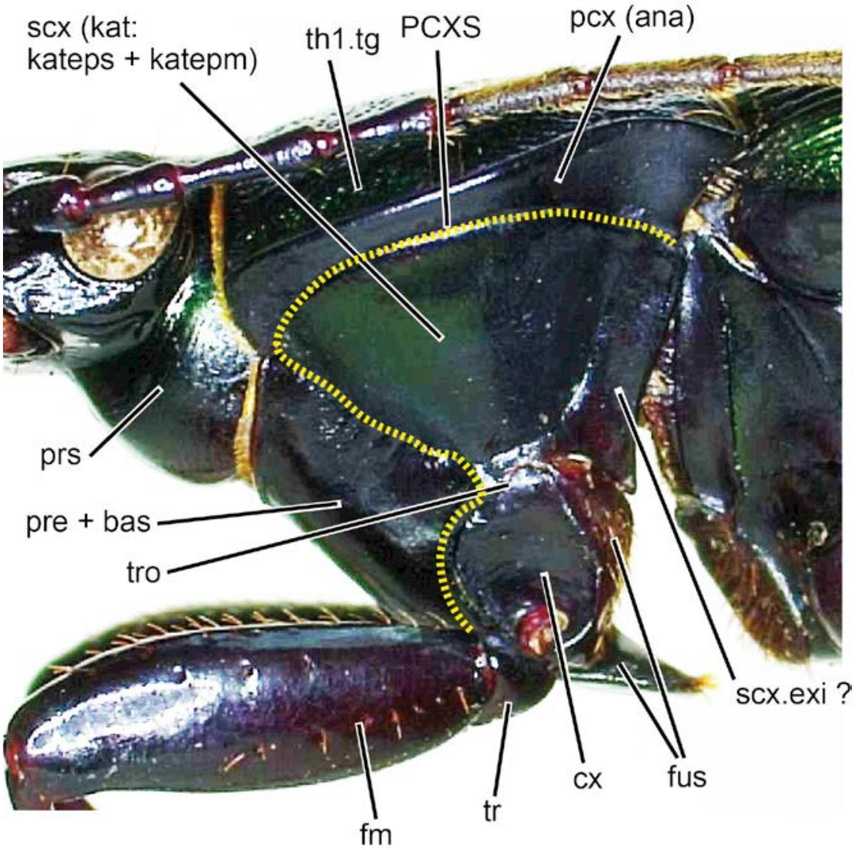

Fig. 5 Lateral view of the prothorax of *Carabus insulicola*, showing our new interpretation of the lateral body wall. ana: anapleuron, bas: basisternum, cx: coxa, fm: femur, fus: furcasternum, kat: katapleuron, katepm: katepimeron, kateps: katepisternum, pcx: precoxa, PCXS: paracoxal suture, pre: preepisternum, prs: presternum, scx: subcoxa, scx.exi ?: subcoxal exite ?, th1.tg: prothoracic tergum, tr: trochanter, tro: trochantin.

anepisternum).

Epipleuron: Inside the epipleuron of the Carabidae, there exists the antero-posteriorly wide muscle M 12 (sensu Larsén 1966) arising from the lateral edge of the tergum and attaching to the dorsal side of the cryptopleuron (Larsén 1966, Fig. 67, M 12; Luo et al. 2018, Figs. 5C, D, 10C, D, M12) (Fig. 4, M 12). This muscle is present in the prothorax of not only Adephaga but also of the suborder Archostemata (Baehr 1975, Figs. 11, 12, Muskel 11; Friedrich et al. 2009, Fig. 8C, M. 17). Baehr supposed this muscle (Muskel 11) to be homologous with t-p 12 or t-p 15 of the pterothoraxes of *Priacma* (Baehr 1975, Figs. 13, 14, 18, 19, Muskel 28 in the mesothorax, 59 in the metathorax). Friedrich et al. (2009) also interpreted these pterothoracic muscles of *Tetraphalerus* (Archostemata) as probably t-p 12, and they noted that these muscles are lacking in non-archostematan beetles. Actually, in mature adults of the Carabidae, these muscles are lacking in both meso and metathoraxes. Larsén (1966), however, noted that the tergo-pleural muscle M 68 is present only in the metathorax of newly emerged immature adults of the Carabidae, and Matsuda (1970) interpreted M 68 as t-p 12 or t-p 15. However, we presume that these tergo-pleural muscles in Archostemata and M 68 correspond to t-p 15 but not to t-p 12, because these tergo-pleural muscles originate from near the posterior notal wing process (t-p 15) but not from the tergal edge between anterior and posterior notal wing processes (t-p 12). We therefore presume that t-p 12 is absent in the pterothoraxes of all adult Coleoptera.

On the other hand, in the larva of *C. insulicola*, t-p 10 and t-p 12 are present in all thoracic segments (in Fig. 2, t-p 10 of the pro and metathoraxes is not shown, and t-p 12 of the prothorax is not shown). The muscle t-p 15 is present in meso and metathoraxes, but it is absent in the prothorax. In pterothoraxes, t-p 15 is located in the more medio-posterior position than t-p 10 and t-p 12. Based on the arrangement of these tergo-pleural muscles and the lack of t-p 15 in the prothorax in this species, we presume that M 12 corresponds to both t-p 10 and t-p 12 (Fig. 4). In the larval pterothoraxes, t-p 10 and t-p 12 originate from the lateral part of the tergum and attached to the PCXR (Fig. 2), and the exoskeleton outside these muscles corresponds to the anapleuron (= precoxa) (Kobayashi et al. 2022); thus, the adult epipleuron corresponds to the anapleuron, but not to a part of the tergum (Fig. 4). The dorsal side of the cryptopleuron to which the M 12 attaches corresponds to the invaginated ventral area of the anapleuron. The anterior edge of the epipleuron (= anapleuron) extends ventrally and forms the preepisternum and the basisternum (Fig. 5, pre + bas). The furcasternum is located in the ventroposterior end of the prothorax (Figs. 1, 5, fus), and it is probably derived from the anapleuron. The plate-like structure extending from the posterior edge of the katapleuron ('posterior pleural flange' sensu Hlavac 1972) is not the epimeron but the posterior extension of the katapleuron, because there exist no muscles inside this extension (Larsén 1966, Figs. 65, 67). This extension may correspond to a subcoxal exite (Fig. 5, scx.exi?). As noted before, the cryptopleural suture corresponds to the PCXS. The latter, moreover, potentially exists anteriorly between the katapleuron (so far referred to the pleuron) and the preepisternum plus basisternum, and posteriorly between the katapleuron and anapleuron (so far referred to the epipleuron), reaching the posterior end of the prothorax (Fig. 5, yellow dotted line). In summary, according to our definitions, the epipleuron is not the inflexed tergum, but a part of the anapleuron (precoxa).

Perspective

In the larval thoracic segments of *C. insulicola*, the PCXS and PCXR are easily observed by micro-CT, and the landmark muscles attached to the PCXR are clearly identified (Kobayashi et al. 2022). In the mesothorax of the adult *C. insulicola*, however, the PCXS is undetected externally, but p-cx 5 and p-tr 1, the landmark muscles for the PCXR, are probably present in the place corresponding to the katapleuron (katepisternum), because these muscles are present in the mesothorax of other carabid species (e.g., *C. granulatus*) (Larsén 1966, Table 2, Fig. 87, M 41, M 48). In another species also, *T. perroti*, the PCXS is not shown externally in the meso and metathoraxes, whereas p-cx 5 (M41) and p-tr 1 (M48) are present in the mesothorax but are absent in the metathorax (Luo et al. 2018, Figs. 2, 10, Table 1). To elucidate what process leads to such discrepancies between external sclerites and the muscular system, we need to further analysis of both larval and adult muscular systems in major coleopteran lineages, especially in the larval stage of Archostemata whose muscular system is entirely unknown.

Kobayashi et al. (2022) proposed the presence of both the morphological and molecular biological boundaries between the tergum and appendage (mrBTA and mlBTA); the latter being located more medial (dorsal) than the former (Kobayashi et al. 2022, Fig. 6). In the present paper, M 12 is regarded as a tergo-pleural muscle on the basis of the positional criterion of mrBTA (Fig. 4). However, if based on the criterion of mlBTA, this muscle should be interpreted as an intrinsic leg muscle of the precoxa.

Each lateral side of the prothorax in polyphagan beetles is covered with one large sclerite, called the hypomeron, and lacks the cryptopleural suture. Evans (1974) hypothesized that the hypomeron is formed in the history of Coleoptera by a downgrowth of tergal edge over the real pleuron as far as the sternal margin. Evans thus presumed that the hypomeron is homologous with the adephagan and archostematan epipleuron. On the basis of our definition shown here, however, the hypomeron as well as the epipleuron belongs to the anapleuron (precoxa).

Acknowledgements: We are grateful to Dr. Heather S. Bruce and two anonymous referees for their critical comments that helped to improve the manuscript.

REFERENCES

Baehr M (1975) Skelett und Muskulatur des Thorax von *Priacma serrata* Leconte (Coleoptera, Cupedidae). Zeitschrift für Morphologie und Ökologie der Tiere, **81**, 55–101.

Beutel RG, F Hass (2000) Phylogenetic relationships of the suborders of Coleoptera (Insecta). Cladistics, **16**, 103–141.

Evans MEG (1974) Propleural structures in Coleoptera. International Journal of Insect Morphology & Embryology, **3**, 67–72.

Friedrich F, RG Beutel (2006) The pterothoracic skeletomuscular system of Scirtoidea (Coleoptera: Polyphaga) and its implications for the high-level phylogeny of beetles. Journal of Zoological Systematics & Evolutionary Research, **44**, 290–315.

Friedrich F, BD Farrell, RG Beutel (2009) The thoracic morphology of Archostemata and the relationships of the extant suborders of Coleoptera (Hexapoda). Cladistics, **25**, 1–37.

Hlavac TF (1972) The prothorax of Coleoptera: Origin, major features of variation. Psyche, **79**, 123–149.

Kobayashi Y, HS Bruce, K Terada, A Hirayama, Y Oosawa, K Niikura, Y Takami (2022) Paranotal lobes are appendicular in origin: Elucidation by micro-CT analysis of the thoracic muscular system in the larvae of *Carabus insulicola* (Insecta, Coleoptera). Proceedings of the Arthropodan Embryological Society of Japan, **54**, 1–9.

Larsén O (1966) On the morphology and function of the locomotor organs of the Gyrinidae and other Coleoptera. Opuscula Entomologica, Supplementum, **30**, 1–242.

Luo XZ, B Wiphler, I Ribera, HB Liang, MY Tian, SQ Ge, RG Beutel (2018) The thoracic morphology of cave-dwelling and free-living ground beetles from China (Coleoptera, Carabidae, Trechinae). Arthropod Structure & Development, **47**, 662–674.

Matsuda R (1970) Morphology and evolution of the insect thorax. Memoirs of the Entomological Society of Canada, **76**, 1–431.

Naomi S (2014) A morphological study on the prothorax of Coleoptera (Arthropoda: Insecta). Japanese Journal of Systematic Entomology, **20**, 47–59.

Naomi S (2024) A new homologization of the sclerites of pleuron in the prothorax of Adephaga and Archostemata, with major correction of morphological terms used in the figures of my paper (Naomi, 2014). Japanese Journal of Systematic Entomology, **30**, 105–106.